

Evaluation of the seasonality of predation and the degree of food specialization in grassland-inhabiting carabid beetles (Col., Carabidae)

by M. POLLET, K. DESENDER & M. ALDERWEIRELDT

Summary

During 1984, detailed sampling campaigns were carried out in a heavily grazed pasture ecosystem at Melle (Eastern Flanders, Belgium). Data on population dynamical aspects of predator as well as prey populations were gathered by means of several sampling techniques. Quadrat sampling yielded density estimates, pitfall trapping resulted in information on the seasonal activity patterns, whereas a time-sorting pitfall trap provided us with data on the diel activity cycles of predator and prey species. During 1985, the vertical stratification of most invertebrate groups was investigated by means of a modified quadrat sampling method.

The feeding ecology of the most abundant carabid beetles and larvae was studied by means of digestive tract analysis. A total of 2711 beetles and 73 larvae were examined. Predation rates per fortnight period were compared within and between the beetle species. In this way, the importance of food specialization and seasonal periodicity of prey accessibility were evaluated.

Key-words: Carabidae, predation, seasonality, food specialization

Samenvatting

Tijdens 1984 werd een bemonsteringscampagne uitgevoerd in een sterk begraasd weide-ecosysteem te Melle (Oost-Vlaanderen, België). Gegevens in verband met populatiedynamische aspecten van de predatoren en de prooien werden bekomen door middel van verscheidene bemonsteringstechnieken. Densiteiten werden bepaald aan de hand van kwadraatstaalnames, bodemvallen leverden informatie op betreffende de seizoensale activiteit van predatoren en prooien, terwijl we met een draaiende bodemval een idee kregen over de circadiane activiteitscycli van beide groepen. In de loop van 1985 werd daarnaast de verticale distributie van de meeste invertebratengroepen onderzocht met behulp van een gemodificeerde kwadraatstaalname-techniek.

De voedselkeuze van de meest abundant adulte en larvale loopkevers werd bestudeerd aan de hand van de darmanalyse-techniek. In totaal werden op deze manier 2711 adulten en 73 larven onderzocht. De predatie gedurende 14-daagse periodes werd vergeleken binnen en tussen de verschillende soorten door middel van een cluster- en een faktoranalyse. Op deze manier werd de invloed van de graad van voedselspecialisatie en de seizoensale periodiciteit van het prooi-aanbod geëvalueerd.

Slutelwoorden: Carabidae, predatie, seizoenaliteit, voedselspecialisatie

Introduction

Food uptake in carabid beetles is affected by several factors (e.g. CHIVERTON, 1984; CORNIC, 1973; LOREAU, 1983a,b; POLLET & DESENDER, 1986, 1987a,b, 1988; SUNDERLAND, 1975; SUNDERLAND & VICKERMAN, 1980). In general, it seems to be very difficult to deduce the separate effect of these factors from a data set, as the

observed predation can be considered as the overall result of simultaneously acting influences. When focusing on a particular part of the data set, interspecific as well as intraspecific discrepancies in predation can be rather easily investigated. However, another approach seems to be necessary to explain the differences between and within the species during their complete activity cycle. This paper is an attempt to such an approach.

Material and methods

The investigations were carried out in a heavily grazed pasture ecosystem at Melle (Eastern Flanders, Belgium). For more information about the investigated site, see DESENDER *et al.* (1985). During 1984 and 1985, the following techniques were applied to determine some of the most important features of the dynamics of prey and predator populations: quadrat sampling, pitfall trapping and a time-sorting pitfall trap. For more detailed information, we refer to POLLET & DESENDER (1987b). The integration of the information, gathered by means of these techniques, gave us an idea of (i) the abundance and activity of the predators and (ii) the real availability of a large number of potential prey groups. The feeding ecology of the most abundant carabid species was examined by means of the analysis of the digestive tract. All beetles were collected with pitfall traps. Except for *Agonum dorsale* and *Loricera pili-cornis* (adults and larvae), only samples of the following species, taken during 1984, were examined: *Pterostichus melanarius*, *Clivina fossor*, *Bembidion properans*, *B. lampros*, *Pterostichus strenuus*, *P. vernalis*, *Nebria brevicollis*, *Amara aenea*, *Agonum muelleri* and *Bembidion lunulatum*. For each species, samples (at least 20 beetles) collected during a fortnightly period were considered separately. The majority of these sets were based on 20 to 30 individuals. Nevertheless, in order to eliminate the possible effect of the varying number of beetles, predation on a particular prey item is expressed as the percentage of beetles, which proved to feed on it (predation index $II \times 100$, cf. POLLET & DESENDER, 1988). This resulted in a data matrix of 77 columns ("variables"), each of which representing the prey

spectrum of a predator species during a fortnight. The number of rows is 84, being the number of different prey items (on family level).

Upon this matrix, two types of multivariate analyses were applied. The first is a cluster analysis (Average Linkage Clustering) on the basis of the Renkonen similarity index (RENKONEN, 1938). By means of this technique, we investigated how similar or dissimilar the diet composition of the predator species was. When clustering the predators, all data were considered. Dendrograms of the prey groups, however, are only based on the prey items, which were found in 10 or more of the predator sets.

The same data set was also examined by means of a factor analysis (PCA)(KIM & MULLER, 1978a,b) based on the correlation matrix between variables (prey spectrum of a predator species during a fortnight period). With this approach, our aim was to find out which are the most important factors for the determination of the composition of the prey spectra of the studied predator populations. An orthogonal rotation

was applied to the factor solution in order to simplify the interpretation of the principal components. In this way variables are maximally correlated with one axis only and minimally with the other axes.

Results

When clustering the prey groups, two distinct groups and 6 single prey items are separated at a similarity level of ± 0.255 . Nevertheless, we simply consider four groups, as indicated in Fig. 1. We do take into account that the similarity between the preys of the last two groups is rather low. The first group consists mainly of large preys, whereas the remaining three clusters comprise exclusively prey types with rather small sizes. Although no clear distinction can be made between the latter groups, it is remarkable that many insect larvae and pupae belong to groups III and IV. Furthermore, we noticed that the different stages of several holometabolic prey groups are often clustered together.

In Fig. 2, predator sets are divided into 6 groups (on a

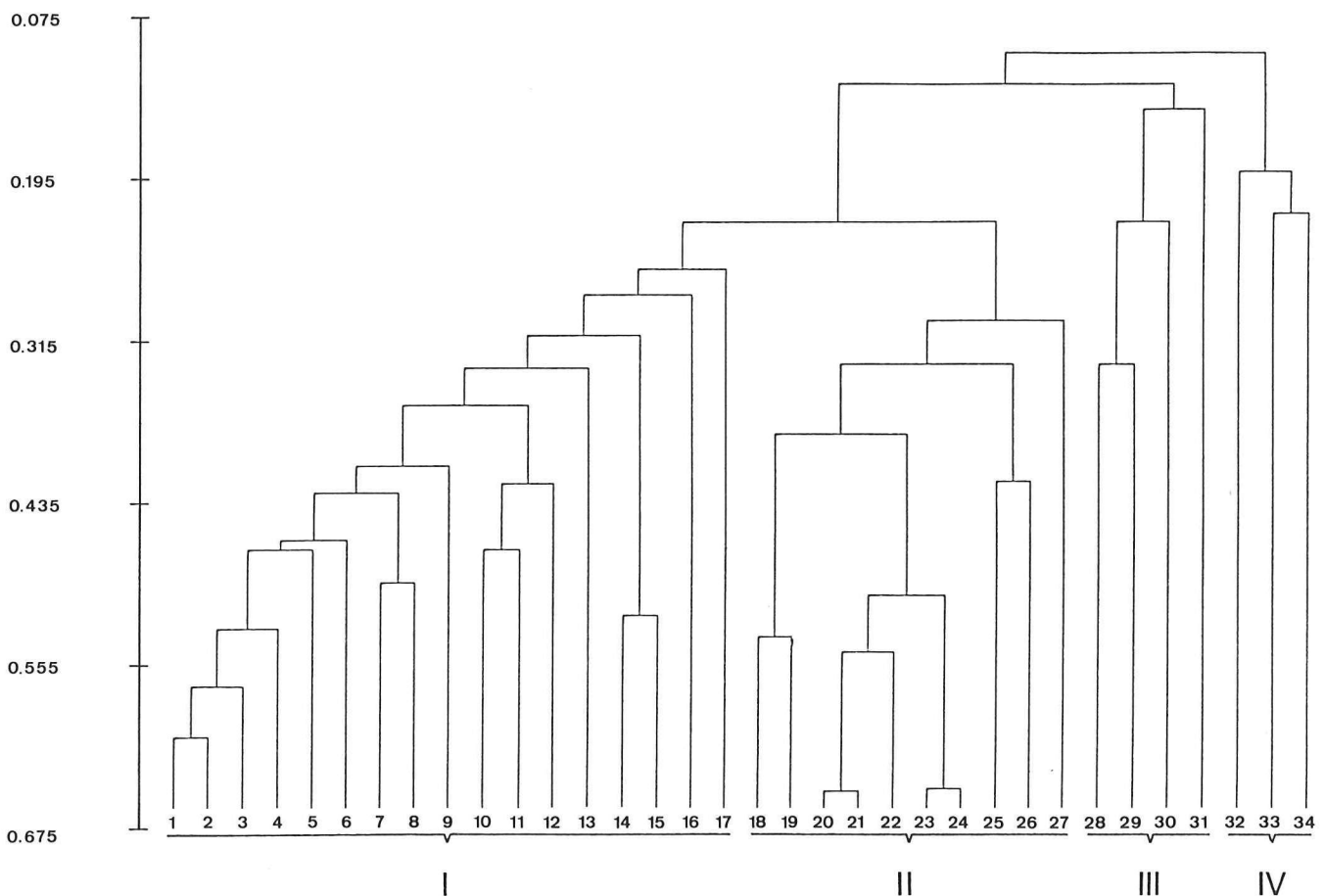


Figure 1. Dendrogram of the prey groups (pooled to family level) on the basis of the Renkonen similarity index with an indication of the prey items and the clusters, mentioned in the Text. Prey items: (1) Lumbricidae, (2) Staphylinidae, (3) Linyphiidae, (4) Staphylinidae larvae, (5) Delphacidae, (6) Chloropidae, (7) Drosophilidae, (8) Scathophagidae larvae, (9) caterpillars, (10) Scathophagidae, (11) Tipulidae larvae, (12) Carabidae larvae, (13) Sphaeroceridae, (14) Lonchopteridae larvae, (15) Musciformia larvae, (16) Anisopodidae larvae, (17) Braconidae, (18) Enchytraeidae, (19) Nematoda, (20) Acari, (21) Aphididae, (22) Sciaridae, (23) Isotomidae, (24) Sminthuridae, (25) Psychodidae pupae, (26) Psychodidae, (27) Cecidomyiidae, (28) Hypogastruridae, (29) Sciaridae larvae, (30) Sciaridae pupae, (31) Cecidomyiidae larvae, (32) Entomobryidae, (33) Chironomidae, (34) Chironomidae larvae.

similarity level of ± 0.350). The separation of three single sets is due to the discovery of only a very small number of prey items (*A. muelleri* and *C. fossor*) and a striking preference for sciarid midges (*B. properans*). Predator group I consists almost exclusively of sets of *P. melanarius*. Moreover, all sets of this predator species are present in this group. It differs from all other species investigated by its distinct polyphagous feeding behaviour. Also, *P. melanarius* feeds frequently on the large preys (prey group I). *C. fossor* makes up group V, together with larvae of *Nebria brevicollis*. Predator group II comprises mainly small to medium-sized carabid beetles, which mostly feed on prey items of prey group II. The division in subgroups within group II is due to subtle differences in diet composition. Carabids of subgroup IIa feed almost exclusively on preys of group II, of which isotomid springtails are most important. In 50 % of these beetles, remnants of chironomid larvae were remarkably frequently discovered. Subgroup IIb has a more extended prey spectrum, of which mites, aphids, isotomids and enchytraeids form the major food resources. The prey spectrum of predators of subgroup IIc is very similar to that of the

previous one, but predation on aphids and isotomids is more emphasized. Most sets in this group originate from *L. pilicornis*, *B. lampros* and *B. properans*. The following subgroup (IId) contains on average larger beetle species such as *N. brevicollis*, *P. strenuus*, *A. dorsale* and *A. aenea*. Large preys make up a greater part of the diet composition of these predators, although predation on prey group II remains most important. Finally, aphids are the main food for predators of subgroup IIe: 7 of the eight sets belong to *B. properans*.

In general, we can conclude that both *P. melanarius* by its pronounced polyphagy and *C. fossor* by its special feeding behaviour are clearly different from the other predator species. The latter appear to show a more similar prey spectrum. Moreover, since sets of a particular predator species are often not clustered together, it can be assumed that feeding preference in those carabid beetles is not specific. Which factors most importantly influence the predatory behaviour in the whole carabid community considered is examined by means of a factor analysis.

In this factor analysis, only the first three factors are

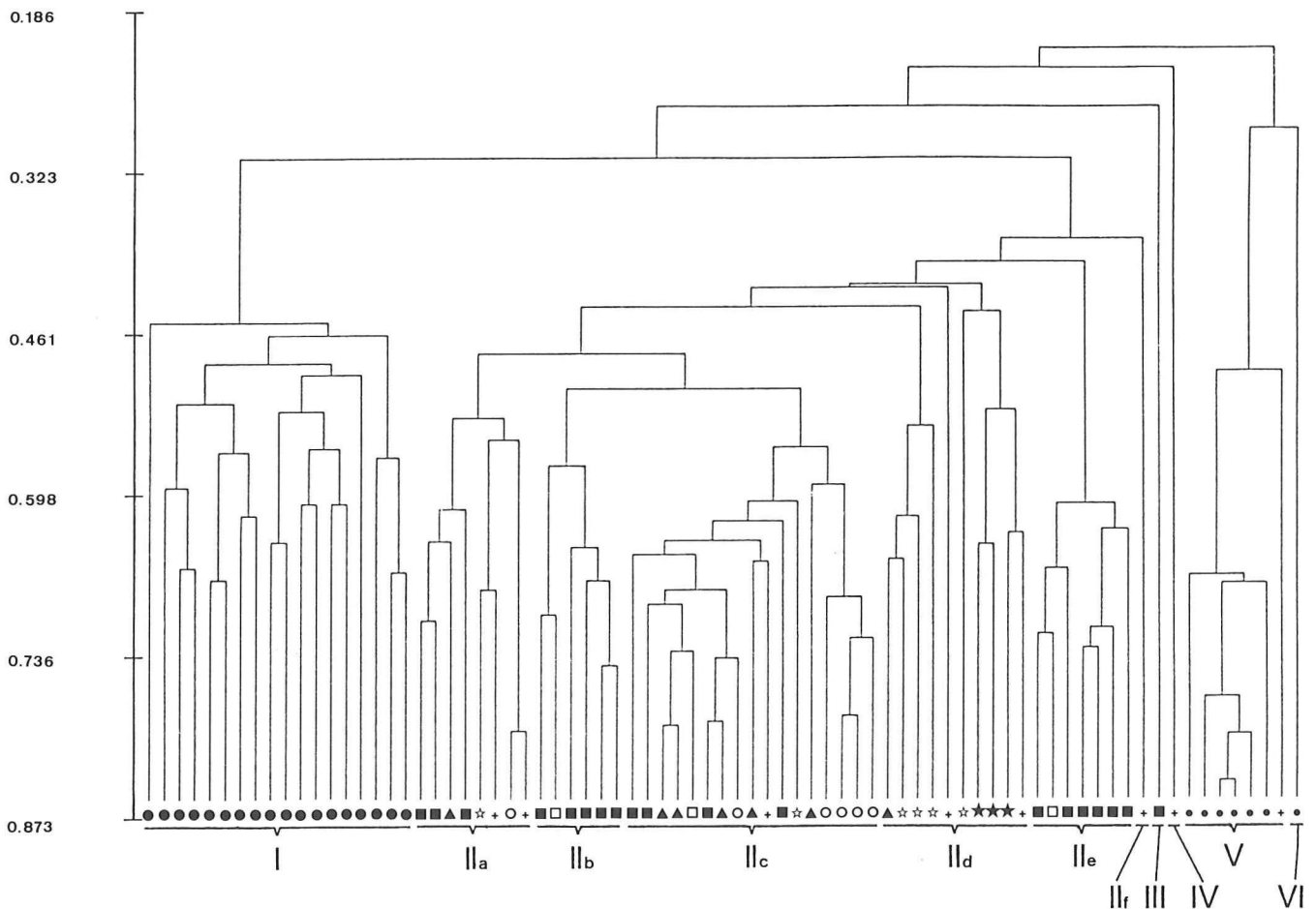


Figure 2. Dendrogram of the predator species on the basis of the Renkonen similarity index with an indication of the predator species and the clusters, mentioned in the Text.

Key: ●: *Pterostichus melanarius*; ●: *Clivina fossor*; ■: *Bembidion properans*; ▲: *Bembidion lampros*; ✱: *Pterostichus strenuus*; □: *Pterostichus vernalis*; ★: *Nebria brevicollis*; ○: *Loricera pilicornis*; +: remaining carabid species.

taken into account since these are the only ones which are responsible for more than 5 % of the observed variation among the variables (Table 1). Figures 3 and 4 represent the distribution of the sets after orthogonal rotation of the axes of factors I and II. The variables of *P. melanarius* are more or less concentrated around axis II. These of *C. fossor* are situated near the crossing of both axes, which implies that none of the factors affects its diet composition to a great extent. The remaining species are pooled together into a large group extending between the ends of both axes. Since most of these sets are situated at the end of axis I it can be assumed that this factor has the largest impact on these species.

Table 1. Eigenvalue and percentage explained variance by factors I, II and III in factor analysis, applied on the matrix mentioned in the Text.

Factor	Eigenvalue	% of explained variance
I	37.326	48.5
II	11.478	14.9
III	7.206	9.4

To find out which influences are represented by the factors, the correlation values of the variables for factors I and II were compared with the following features of the variables: (i) predator species, (ii) predator size, (iii) sampling period, (iv) prey spectrum (total number of prey items) and (v) proportion of the most important prey item in the diet (percentage of beetles feeding on it). By convention, variables with the

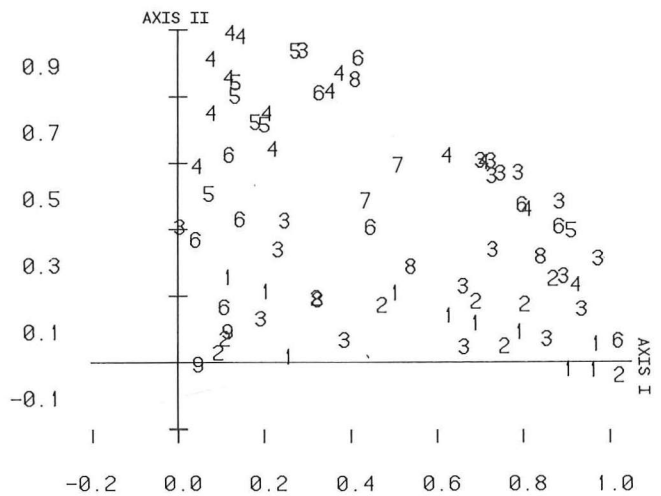


Figure 4. Location of the different seasonal sampling periods as a characteristic feature of the variables in the factor space of factors I (axis I) and II (axis II) based on the data from the matrix, mentioned in the Text.

Key: (1) 17.IV-15.V.1984 (periods 1 + 2); (2) 15.V-12.VI.1984 (periods 3 + 4); (3) 12.VI-10.VII.1984 (periods 5 + 6); (4) 10.VII-7.VIII.1984 (periods 7 + 8); (5) 7.VIII-4.IX.1984 (periods 9 + 10); (6) 4.IX-2.X.1984 (periods 11 + 12); (7) 2-30.X.1984 (periods 13 + 14); (8) 30.X-29.XI.1984 (periods 15 + 16); (9) 29.XI-26.XII.1984 (periods 17 + 18).

highest correlation values for factor I are referred to as group A. In an analogous way, variables showing the highest correlation with factor II are called group B. In order to compare the previously mentioned features, variables within group A and B were pooled together into subsequent subgroups of 5 to 6 sets and a mean value (\pm standard error) was calculated per subgroup. This was only done for the features, which proved to be suitable for a quantitative approach (excluding the feature "predator species"). This enabled us to investigate which features showed the same pattern as the corresponding correlation values. Table 2 gives a summary of this approach.

Factor I appears to be significantly negatively correlated with the prey spectrum and highly positively correlated with the proportion of the prey item "spring-tails" in the diet (Table 2). The species sets with the highest correlation values for this factor showed on average the smallest number of prey items. Moreover, in these sets springtails are relatively more important as compared to the other sets of group A (and B) (Table 2). As a result, factor I can be considered as "an increasing degree of food specialization" in particular on spring-tails. Thus catholic feeders and food specialists among the investigated carabid species are situated to the left and to the right on Fig. 3 respectively.

Contrary to group A, species sets corresponding to factor II show a strongly varying prey spectrum. However, they seem to originate mostly from the same sampling period and correspond to the proportion of

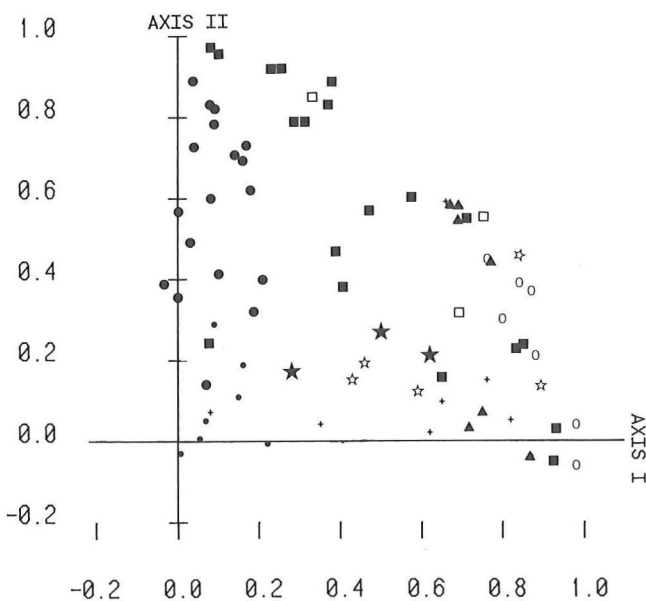


Figure 3. Location of the different predator species as a characteristic feature of the variables in the factor space of factors I (axis I) and II (axis II) based on the data from the matrix, mentioned in the Text (for the key, see legend Fig. 2).

Table 2. Comparison of various features (mean \pm standard error) of predators between and within group A and B. Subgroups are ranged to decreasing correlation values of the variables (n: number of variables).

Group	n	Prey size	Sampling period	Prey spectrum	Isotomidae	Predation on Aphididae
Group A						
Subgroup 1	6	1.24 \pm 0.13	5.33 \pm 1.63	8.33 \pm 0.61	60.83 \pm 14.65	-
Subgroup 2	6	1.19 \pm 0.15	6.00 \pm 1.71	13.00 \pm 1.00	52.67 \pm 13.92	-
Subgroup 3	6	1.19 \pm 0.15	7.50 \pm 2.05	11.17 \pm 1.62	51.00 \pm 7.22	-
Subgroup 4	6	1.00 \pm 0.09	5.17 \pm 0.48	15.00 \pm 0.97	32.67 \pm 1.80	-
Subgroup 5	6	1.44 \pm 0.24	4.83 \pm 0.95	15.17 \pm 1.47	28.67 \pm 6.65	-
Total	30	1.21 \pm 0.07	5.77 \pm 0.64	12.53 \pm 0.69	45.27 \pm 4.81	19.23 \pm 3.07
Group B						
Subgroup 1	5	0.91 \pm 0	7.80 \pm 0.96	12.40 \pm 1.12	-	72.20 \pm 7.32
Subgroup 2	5	2.51 \pm 0.58	9.60 \pm 1.36	21.40 \pm 3.83	-	66.20 \pm 9.45
Subgroup 3	5	2.44 \pm 0.62	8.80 \pm 0.86	19.80 \pm 2.08	-	61.80 \pm 9.81
Subgroup 4	6	2.60 \pm 0.53	9.50 \pm 0.96	22.00 \pm 2.59	-	56.33 \pm 9.60
Total	21	2.14 \pm 0.28	9.00 \pm 0.50	19.05 \pm 1.47	10.05 \pm 1.79	60.43 \pm 4.63

aphids fluctuating according to the correlation values (Table 2). As aphids are most abundant during a very short period and apparently act then as an important food resource, factor II most probably represents "seasonality". The variables of group B thus vary between spring + autumn (low values) and summer (high values). Indeed, the mean sample period of the subgroups of A is considerably lower as compared to those of group B.

In summary, the following conclusions can be drawn from Figs 3-4: (1) *P. melanarius* differs from all other predator species by its pronounced polyphagy. This species takes up a wide diversity of prey types. This polyphagous characteristic appears to be permanent, although, the composition of the prey spectrum strongly fluctuates according to the season;

(2) *L. pilicornis* is an example of the opposite extreme: this carabid beetle is highly specialized in its feeding ecology. Springtails are its main food, although its prey spectrum shows moderate temporal variations;

(3) *B. properans* shows a high variation in its prey spectrum. However, it must be mentioned that the data set of this species was much larger as compared to the other species. Apparently, *B. properans* is able to adapt its predatory behaviour to the varying food supply in the field rather quickly: in spring this predator feeds on a small number of prey groups, whereas in summer it becomes rather polyphagous. Analogue to this change, it switches from springtails to aphids as most important preys. After summer, its prey spectrum seems to be narrower again;

(4) Although the diet of *B. lampros* shows a small change in the course of its activity cycle, at first sight this species seems to be more specialized than its congener. By comparing data sets from the same

sample period between *B. properans* and *B. lampros*, however, no significant differences could be detected; (5) Predation by *C. fossor* is not strongly loaded on factors I and II, as mentioned before. As opposed to all other species studied, sets of *C. fossor* have high loadings on factor III only (Fig. 5). Although thus far this factor could not be characterized more specifically, it is undoubtedly related to the special feeding behaviour of this carabid species. Indeed, soil inhabiting invertebrates such as enchytraeids and nematods are the main components of its diet, which is never the case in the other species.

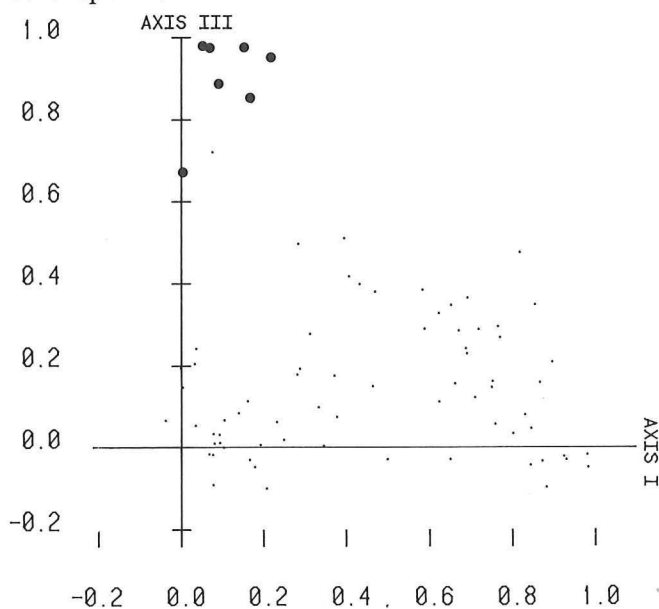


Figure 5. Location of the data sets of *Clivina fossor* within the factor space of factors I (axis I) and III (axis III) based on the data from the matrix, mentioned in the Text.

Key: ●: *Clivina fossor*; .: remaining carabid species.

Discussion

Investigations concerning the general influence of diverse factors on the diet composition in arthropods are rather scarce in the literature. Only the papers of DENNISON & HODKINSON (1984), HENGEVELD (1980, 1981, 1985), LOREAU (1984) and MULLER (1985) are dealing with it. DENNISON & HODKINSON (1984) investigated the niche overlap in woodland inhabiting carabid and staphylinid beetles. Therefore, both seasonal and diel activity cycles and aspects of the feeding ecology were considered. For the comparison of these parameters, they used a cluster analysis. This technique was also applied to compare the most abundant beetle species on the basis of a combination of the three parameters. In the first approach, distinct similarities were often apparent between species, however, these disappeared in the analysis of the combined data. Consequently, DENNISON & HODKINSON (1984) concluded that in general only small niche overlaps occur in the field and that interspecific competition can not be considered as very important. In this respect, also DAWSON (1965) and LOREAU (1984) found in marshland carabids and in woodland carabids respectively that niches of potentially competing species were generally strongly differentiated, which might allow a coexistence situation. DENNISON & HODKINSON (1984) pointed out some limitations of their approach: they did not take into account (i) the larval stages, in which cannibalism often seems to occur (HEESSEN & BRUNSTING, 1981; MURDOCH, 1966; SMIT, 1957) and (ii) other features such as spatial distribution. HENGEVELD (1980, 1981) compared the predation data of 24 carabid species. Therefore, this author used sets of complete year cycles, which differed from 12 to 2589 dissected specimens according to the species. Data were also analysed by means of PCA. Instead of defining the two factors, HENGEVELD (1980, 1981) used the angles formed between the vectors of the different individual species and that of a fixed species to investigate the significance of the factor axes. In this way, two more or less separated groups were obtained. After a further comparison of both groups with predator sizes and prey spectra, he found that one group consisted of feeding specialists and the other mainly of generalist feeders. HENGEVELD's results are concordant with the findings of SCHOENER (1969), who claimed that the prey spectrum of a predator depends in the first place on its size: "... the smaller the predator, the more limited will be its prey range ...". In our study, the larger *P. melanarius* indeed shows a more diverse diet as compared to the smaller beetle species (cf. Figs 3, 4). This is mainly due to predation on larger preys. However, this does not hold true for the other beetles, in which apparently other factors play a more important

role. When comparing for example *B. properans* to *L. pilicornis* or *P. strenuus*, the hypothesis of SCHOENER (1969) is no longer confirmed!

Since HENGEVELD (1980, 1981) compared complete year cycles, it is evident that this author was not able to show the effect of seasonality on the dietary composition. He does mention the fact that a difference must be made between true feeding specialists and oligophagous predators. The first group is characterized by the presence of conspicuous morphological, anatomical and/or ethological adaptations to capture and/or ingest their preys (e.g. *L. pilicornis*). Species of the second group, on the contrary, are restricted to smaller preys or a smaller number of prey groups due to their small body sizes.

In a later study, HENGEVELD (1985) applied a combination of a PCA and a discriminant analysis to investigate which were the most important factors in determining the prey spectra of three carabid species. The data sets consisted of 6 sample periods per species, collected during 6 consecutive years and for three separate species. In the analyses all prey items were considered, even those which were encountered in the gut of only few beetles (cf. our study). The different sets were based on a highly varying number of dissected beetles. Therefore, it is not surprising that the first factor revealed to be the number of investigated beetles. Like our investigations, the second factor represented both seasonal and between-years variation. Consequently, HENGEVELD (1985) concluded that in most cases no indirect evidence for the importance of interspecific competition was found in carabid beetle communities. This is in agreement with the results of DENNISON & HODKINSON (1984) and our own findings (POLLET & DESENDER, in prep.).

Other studies also reveal that the degree of feeding specialization and the seasonal variation in the prey supply explain the larger part of the observed differences between and within predator species. The special case of *C. fossor* seems to make an exception to this (Fig. 5). Undoubtedly, its pronounced subterranean way of life is responsible for this phenomenon.

Acknowledgments

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MARC POLLET,
 KONJEV DESENDER,
 MARK ALDERWEIRELDT
 Laboratory for Animal Ecology,
 Zoogeography and Nature Conservation,
 State University Ghent,
 K.L. Ledeganckstraat 35
 B-9000 Ghent (Belgium)

