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COMMUNITY-WIDE SEASONAL TRENDS IN THE NICHES OF FOREST CARABID BEETLES

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(1) Community-wide seasonal trends in some niche components, and factors that determine them were searched for in a forest carabid community. Data were collected on four niche components: diet, annual activity cycle, daily activity rhythm, and vertical distribution of activity. Quantitative data on prey availability were obtained both directly by pitfall trapping, and indirectly through the diet of the dominant carabid species.

(2) Surface activity and size of – and consequently, size of the prey consumed by – large carabid species increased during the spring and summer. A trend is also suggested towards increasing night activity.

(3) An explanation of the trends found is attempted, involving prey availability, litter morphology, predation risk and climatic factors as important variables.

The most important type of environmental changes that carabid beetles experience in the temperate zones is the annual cycle of seasons. By their cyclic nature, these changes differ from other – random or directed – changes in the environment in that they present a relatively regular, predictable pattern, on which communities of univoltine insects can structure themselves. The life history of carabid beetles is moulded to conform to that pattern, most species having evolved towards a definite annual life cycle, which represents a specific synchronization with the annual cycle of seasons. Phenology and the physical factors that control it have been studied extensively in carabids (see e.g. Thiele 1977), and the period of adult activity proved to be one of the main variables generating niche differentiation in forest carabid communities (Loreau 1986).

Though itself an important niche component, annual period of activity is in turn likely to influence all the rest of the adult's niche, in particular the other main niche component, diet. Seasonal changes in the diet of individual carabid species have been shown repeatedly (see e.g. references in Loreau 1983a, 1983b), and have generally been attributed to changes in the available prey spectrum. Thus there might also be seasonal effects on the trophic niches occupied by successive species through the year at the level of the community. This paper is concerned with the latter aspect, i.e. investigating whether there are regular seasonal trends in some niche components of forest carabids at the community level, as well as attempting to get an insight into the factors that determine these trends.

The community considered here has been studied in great detail. It is a stable community living in a beechwood close to the climax stage in Lembeek (Belgium) (Loreau 1984b). Data have been collected for the main species on four components of the adult's niche: diet (Loreau 1983a, 1983b, 1984a), annual activity cycle (Loreau 1985), daily activity rhythm (Loreau 1984c), and vertical distribution of activity (Loreau 1987). This paper presents the general results and conclusions of an analysis based on those data, complemented by quantitative data on seasonal changes in the available prey spectrum. More detailed results and discussion are given in Loreau (in press).

MATERIAL AND METHODS

The methods used to investigate the various niche components of carabids were described in the above-mentioned papers. Diet was studied by examination of the gut content (Loreau 1983a) and by experiments on food preferences under semi-natural conditions (Loreau 1984a); annual activity cycle, using pitfall traps consisting of two pots at the ends of a plastic plate (Loreau 1985); daily activity rhythm, using live traps emptied at sunrise and sunset (Loreau 1984c); and vertical distribution of activity, using special traps having windows open at various depths (Loreau 1987).

Because pitfall trapping provides a reasonable picture of the arthropod prey spectrum available to carabids (Loreau in press), seasonal changes in prey availability were studied using the permanent traps already used for the annual activity cycle of carabids. All animals larger than 0.4 mm caught in the traps were sorted both into taxonomic groups (up to the order or the family) and into 5-mm size classes. This sorting was performed for 3 to 4 randomly chosen traps from March 1978 to March 1979 (fortnightly from spring to autumn, and twice in winter). Because of the low abundance of large individuals, only the following 3 size classes were kept: 0.4–5 mm (class I), 5–10 mm (class II), and >10 mm (class III).

Indirect information on the approximate seasonal changes in the availability of annelids and molluscs, which constitute a significant part of the diet of large carabids, were obtained from the diet of the most dominant carabid species, Abax ater (Vill.). Because this has a long period of activity and an especially generalist and opportunistic feeding behaviour, the changes in the proportion of each prey group in its diet may be used to estimate the changes in the availability of that group (Loreau in press).

RESULTS

Seasonal trends in niche components

Diet is itself a complex niche component which involves at least two dependent variables: prey type and prey size. Because prey type cannot be reduced to a continuous, quantifiable variable, it will not be included in this analysis of community-wide trends. On the other hand, the midpoint of the prey-size range on a logarithmic scale, which may be taken as an approximation of the "niche centre" along the prey-size axis, was found to be strongly correlated with the carabid's size (Loreau in press). Consequently, the carabid's size will be used as a substitute for niche position along the prey-size axis.

The niche plane defined by the two axes, size and time of activity through the year is represented in Fig. 1. When successive niche centres are joined, a distinct pattern emerges among large species: size tends to increase until August, and to decrease later. This double trend can be tested by taking a point of time just before mid-August as a pivotal value. The rank correlation between size and the distance of the time-niche centre from that pivotal point is then perfect (Spearman coefficient $r_s = 1$, $P = 0.0004$). There is also a trend towards a continuous increase in the size of small species. However, the biological significance of the latter trend is more questionable because Trichotichnus laevicollis (Duft.) is mainly phytophagous while the diet of Badister bipustulatus (F.) is unknown, so that there might be a wide gap between spring and autumn predatory species.

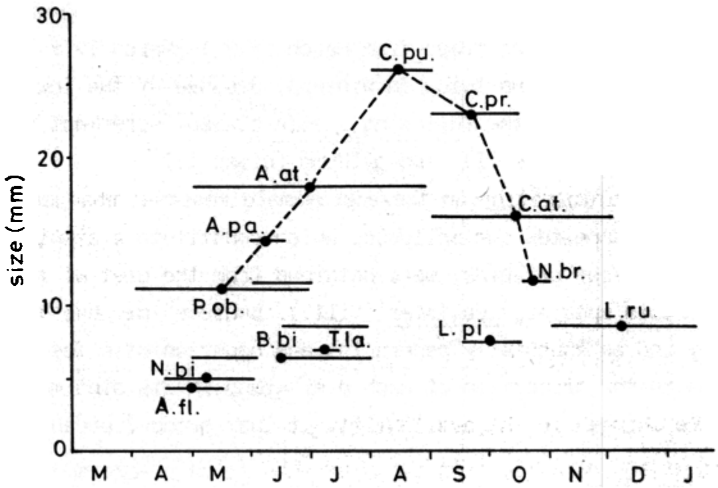

Fig. 1. Size as a function of period of activity in the 13 main species in the beechwood. For each species, the horizontal line shows the period of high activity (defined as the period over which the 4-year (1978–81) mean activity is higher than 50% of the maximum value), and the dot represents the niche centre along the time axis (defined as the midpoint of the period of high activity). The dashed line joins the successive niche centres. Note that for Cychrus attenuatus, in which the activity of males and females is out of step, the line is the addition of the periods of high activity of the two sexes considered separately, and that for species that have two periods of high activity separated by a summer dormancy, the niche centre is taken as the midpoint of the breeding period. Species are mentioned by their abbreviations: P. ob. = Pterostichus oblongopunctatus; A. pa. = Abax parallelus; A. at. = Abax ater; C. pu. = Carabus purpurascens; C. pr. = Carabus problematicus; C. at. = Cychrus attenuatus; N. br. = Nebria brevicollis; A. fl. = Asaphidion flavipes; N. bi. = Notiophilus biguttatus; B. bi. = Badister bipustulatus; T. la. = Trichotichnus laevicollis; L. pi. = Loricera pilicornis; L. ru. = Leistus rufomarginatus

A second distinct seasonal trend appears in the vertical distribution of activity of large species (Fig. 2). The proportion of activity that occurs at the surface of the litter (as opposed to within the litter) increases in successive species from spring to autumn ($r_s = 1$, $P = 0.017$). On the other hand, such a trend is unlikely among small species, for small spring carabids like Asaphidion and Notiophilus are species that hunt visually and that are, consequently, active on the soil surface.

No marked seasonal trend was found in daily activity rhythm. Although a trend is suggested towards increasing night activity through the year, it is not significant when the 13 main species (except Carabus viola-

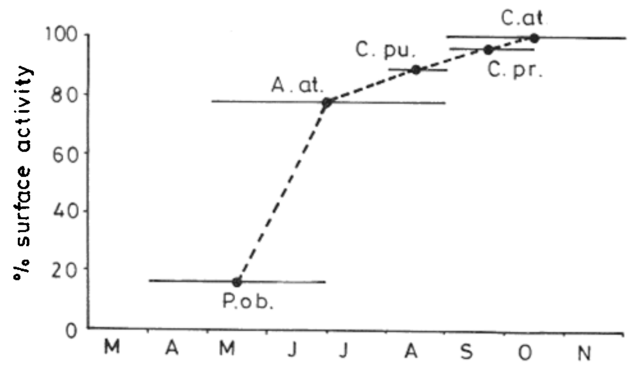

Fig. 2. Proportion of surface activity as a function of period of activity in some large species in the beechwood. Legend as in Fig. 1

ceus ssp. purpurascens F., for which data are lacking) are considered (r_s = 0.556, df = 10, 0.1 > P > 0.05). Even if it turned out to be significant if more species were considered (indeed several other, rare small spring species were found during daytime), size seems to have a stronger effect on daily activity rhythm than season. Only four main species were predominantly diurnal (>50% day activity), and they were among the five smallest ones (< 8 mm). This effect was significant: an exact test based on the hypergeometric distribution showed the proportions of diurnal and nocturnal species (< and >50% night activity, respectively) in the two size groups (< and > 8 mm) to be different (two-tailed test, P = 0.014).

Seasonal changes in prey availability

Data on the seasonal changes in prey size were collected to investigate whether they could explain the pattern observed in the size structure of the carabid community. Since the availability of the prey was approximated by their activity, and since there is no panacea for combining activities of very different groups and sizes into a single measure of availability, changes in prey size were simply described by the succession of the size classes for the main prey groups (Fig. 3).

All groups (except mites) displayed successions of classes of increasing size through the year, even though these were not identical. In insect larvae, the picture was slightly more complex, since there were seemingly two successions, one in winter and spring, the other (interrupted) from late spring to early autumn. Note that in adult insects (Fig. 3c), the peak of class III in spring is not relevant because it was very short (its apparent width in the figure is due to the use of running means) and had no impact on the actual diet of carabids.

Indirect information on the largest prey, i.e. annelids and molluscs, from their proportions in the diet of A. ater, is shown in Fig. 4. While no systematic seasonal variations appeared in annelid availability, a marked seasonal trend did appear in mollusc availability, which steadily increased from May-June to September.

Thus, on the whole, there was some evidence of seasonal trends towards increasing size of the prey available to carabids from spring to September (increasing size of arthropods, increasing availability of molluscs, which are among the largest prey), which could explain a similar trend in carabids themselves. After September–October, the availability of some large prey groups was declining (insect larvae and non-insect arthropods at least), while medium-sized (class II) adult insects were still abundant and small insect larvae were again increasing (Fig. 3). This could explain the trend towards decreasing size in autumn among large species.

DISCUSSION

The seasonal trends observed in this forest community show that niches are organized neither randomly nor uniformly in the potential niche space, but according to a well-defined seasonal pattern. That this pattern is not entirely specific to the forest studied is demonstrated by a comparison with Southwood (1978), who summarized data from all biotopes at Silwood Park in England. His Fig. 2.5 shows the same trends in size and in daily activity rhythm as were found in Lembeek.

The seasonal pattern in the size of large carabids seems correlated with that of the prey available. This correlation stands out in more relief when qualitative changes in prey types available are also taken into consideration (Loreau in press). This prompts the hypothesis that food resources are a crucial factor determining the niche structure of the community. On the other hand, such a correlation does not seem to exist among small species, as appears in the fact that they are mainly spring and autumn or winter species, while the periods of maximum activity of small collembolans

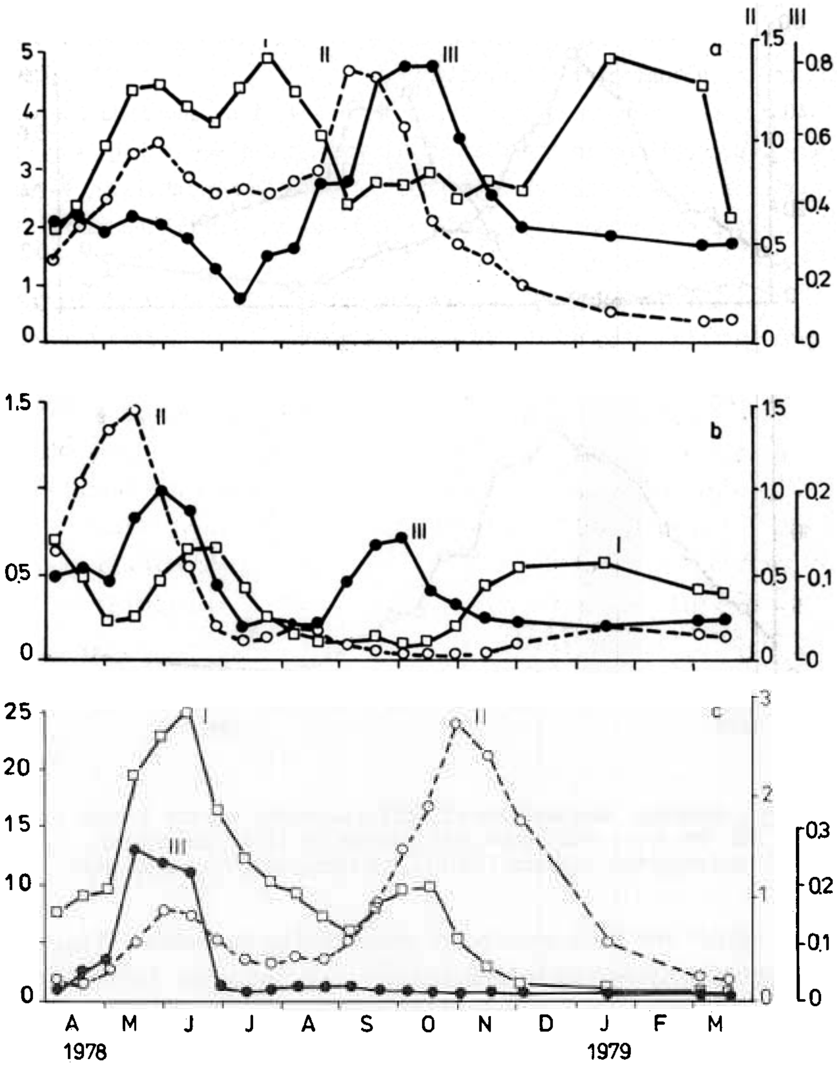

Fig. 3, a–c. Seasonal successions of activity peaks of the 3 size classes for the main arthropod prey groups in 1978 (3 point running means).
Ordinates: activity, expressed in numbers of individuals per trap per day.
The different axes refer to the 3 size classes.
a: non-insect arthropods (isopods, myriapods and arachnids, except acarines);
b: larvae of holometabolous insects (including carabid larvae);
c: adult insects (pterygotans, except staphylinids)

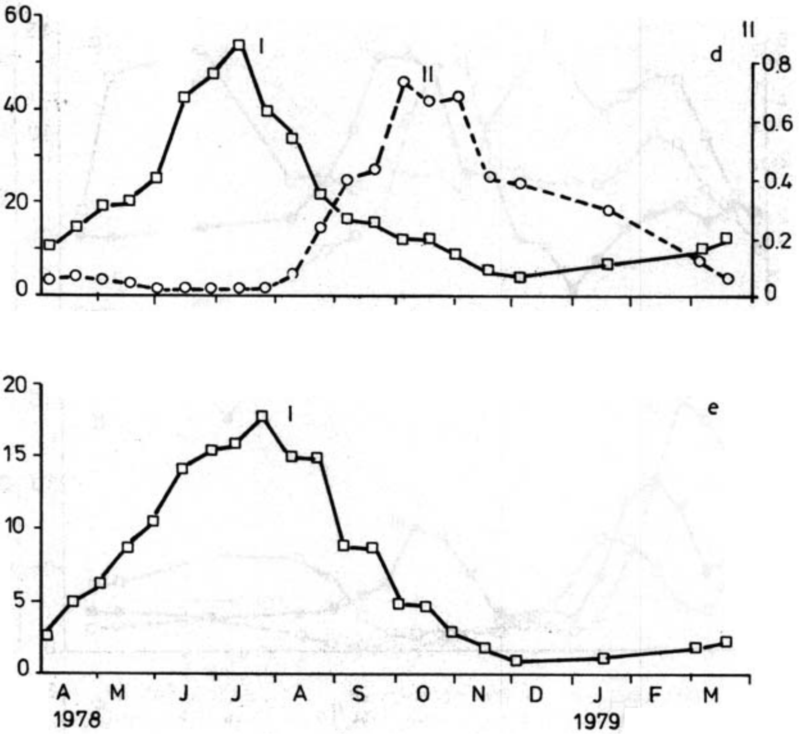

Fig. 3, d–e. Seasonal successions of activity peaks of the 3 size classes for the main arthropod prey groups in 1978 (continued). d: apterygotan insects (mainly collembolans); e: acarines

and mites (which are their main prey) occur during the summer (Fig. 3, d–e).

Some relatively simple explanations based on known facts or hypotheses can account for the trends in daily and vertical distributions of activity. The correlations between spring breeding and diurnalism on one hand, and between autumn breeding and nocturnalism on the other, have long been recognized in carabids (Thiele and Weber 1968; Thiele 1969). They are generally considered to be caused by the different microclimatic requirements of the two groups, the first tolerating dryness, the second demanding a high humidity. This hypothesis would be consistent with the faint trend towards increasing night activity through the year. However, the strong effect of size on daily activity rhythm suggests alternative hypotheses based on

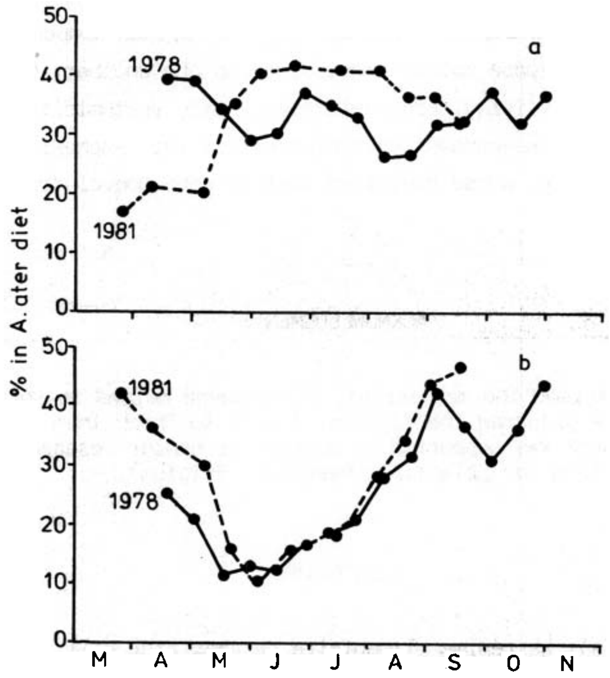

Fig. 4. Seasonal changes in the proportion of annelids (a) and molluscs (b) in the diet of Abax ater in 1978 and 1981 (3-point running means)

predator-prey relations: nocturnalism in large, common species may be the result either of predator avoidance (because they would be too exposed to predators during daytime on open surfaces such as the forest litter: Southwood 1978; Loreau 1984c; Ottesen 1985), or of most large prey being mainly nocturnal (Loreau 1984c). Actually, climatic and biotic factors are likely to act concurrently to produce the observed pattern, and thus the seasonal trends in size and in daily activity rhythm may be partly interdependent.

The trend towards increasing surface activity through the year among large species can be accounted for by a simple physical factor: the upper litter layer is progressively modified and compacted from spring till the leaf fall in autumn, thereby reducing the opportunities for movement within it (Loreau 1987). However, since the same trend does not seem to exist among small species, there might also be an intermediate size optimal for foraging within the litter, and the trend in vertical distribution of activity could be, in part, an indirect effect of the trend in size.

This short discussion indicates how the various components of a species' niche can impose mutual constraints on one another. Obviously, seasonal timing of activity, prey selection, daily rhythmicity, and place of foraging are not independent characteristics. This emphasizes the niche as a complex totality, whose evolution implies some coevolution between components.

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