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Vertical distribution of activity of carabid beetles in a beech forest floor

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With 5 figures

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1. Introduction

It is generally accepted that carabid beetles are active at the surface of the ground. This behaviour is so conspicuous that it led to the German name "Laufkäfer" (running beetles) and to the English name "ground beetles". Most forest soils, however, are complex; the upper litter layer is not compact and can be easily penetrated by invertebrates active at the surface. Presumably the classical portrait of carabids, together with methodological difficulties, has prevented a more thorough investigation of the actual vertical distribution of their activity in the superficial layers of forest soils. Yet some facts suggest that this may be a niche component allowing some differentiation between species. Loreau (1984d), for instance, hypothesized different foraging strategies accounting for the different activity/biomass ratios of the vernal *Pterostichus oblongopunctatus* and the autumnal *Carabus problematicus* and *Cychrus attenuatus:* the former species might concentrate on abundant small, not very mobile prey, while the latter two might concentrate on scarcer large, mobile prey. The most straightforward way to produce such a difference would be through foraging in different places, i.e. either within the litter or at the surface of the litter.

To investigate this, a field study of the vertical distribution of activity of carabid beetles in a beech forest floor was attempted, using a modified type of pitfall trap designed for that purpose.

2. Material and methods

The study site was a beech forest close to the climax stage in Lembeek (Belgium). It has already been described in Loreau (1984a). The acid soil has a mull-moder humus form, the structure of which is depicted in Fig. 1. The fresh litter layer (L_n horizon) is 1.5—3 cm deep in winter but gradually decreases during the course of the year until the leaf fall. The modified litter layer (L_v horizon) is 2—3.5 cm deep, and the decay layer (F horizon) 2—6 cm deep. Below begins the mineral humus layer (A_h horizon). The composition, structure and niche organization of the carabid community have been described in detail in Loreau (1984a, 1984b, 1984c)

The type of trap used to study vertical distribution of activity is represented in Fig. 1. A plastic pot (250 ml, 7 cm diameter) is situated within a plastic cylinder which has four windows 1.5 cm high at a given depth d. The top of the cylinder is closed by a chipboard plate and placed at the level of the surface of the litter (0 depth) — except for traps that record surface activity (d = 0), the tops of which are 1.5 cm above the surface. Animals enter the cylinder through the windows and fall into the pot which is filled with a 4% formalin solution as preservative. The pot is positioned by means of a wire, and thus emptying the trap does not disturb the cylinder.

Thirty such traps were distributed in the beechwood in groups of 6. In each group, the 6 traps recorded activity at different depths: window depth d was respectively 0, 2, 4, 6, 8 and 10 cm. Given the soil profile and its spatial and seasonal variations, these depths indicate in terms of soil layers: for d = 0, windows open at the surface of the litter; for d = 2 cm, windows open in the litter layer; for d = 6 cm, windows generally open in the F layer; for d = 10 cm, windows generally open in the Ah layer; for d = 4 cm and d = 8 cm, windows open in variable layers.

Traps were inspected monthly over a 2-year period, from March 1984 to December 1985. Small mammals regularly disturbed some traps by lifting the chipboard plate or filling the pot with earth; catches from those traps were excluded from the results.

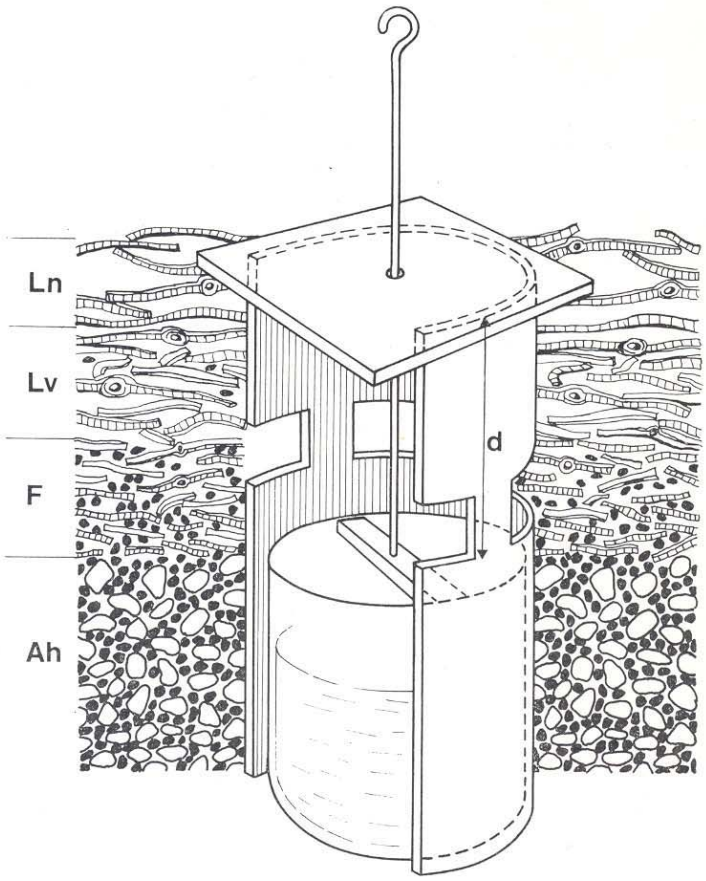

Fig. 1. Superficial soil profile of the beech forest floor, and trap used to study vertical distribution of activity. The cylinder is shown in section to display the inside of the trap. Representation and nomenclature of soil horizons after Babel (1971) and Delecour (1980).

3. Results

3.1. Adults

The dominant species *Abax ater* has a vertical distribution of activity pattern which is roughly an average pattern for the community. Its activity is predominant at the surface of the litter but gradually decreases with increasing depth in the soil (Fig. 2).

This pattern, however, is not constant. Surface activity increases during the course of the year (Fig. 3); there is a very highly significant increase in the proportion of surface activity between the April—July period and the August—November period: $\chi^2 = 29.97$ with 1 d.f., $P < 0.001$. The difference is due to a perceptible decrease in the proportion of activity in the litter layer ($d = 2$ cm) between the 2 periods: $\chi^2 = 16.96$, $P < 0.001$.

There is also a characteristic change in the sex ratio with depth (Fig. 4): while the sex ratio is more or less balanced at the surface and in the litter layer ($d = 0$—2 cm), it gradually shifts in favour of females in the lower layers ($d = 4$—10 cm; $\chi^2 = 4.80$, $P < 0.05$), leading to a significant difference between the 2 levels ($d = 0$—2 cm vs. $d = 4$—10; $\chi^2 = 5.38$, $P < 0.05$).

Pterostichus oblongopunctatus shows a quite different vertical distribution of activity (Fig. 2): activity is roughly equal at all depths. But the sex ratio in the lower layers ($d = 4$—10 cm) is even more unequal than in *Abax ater* ($\chi^2 = 7.5$, $P < 0.01$), since only females were caught there (Fig. 4).

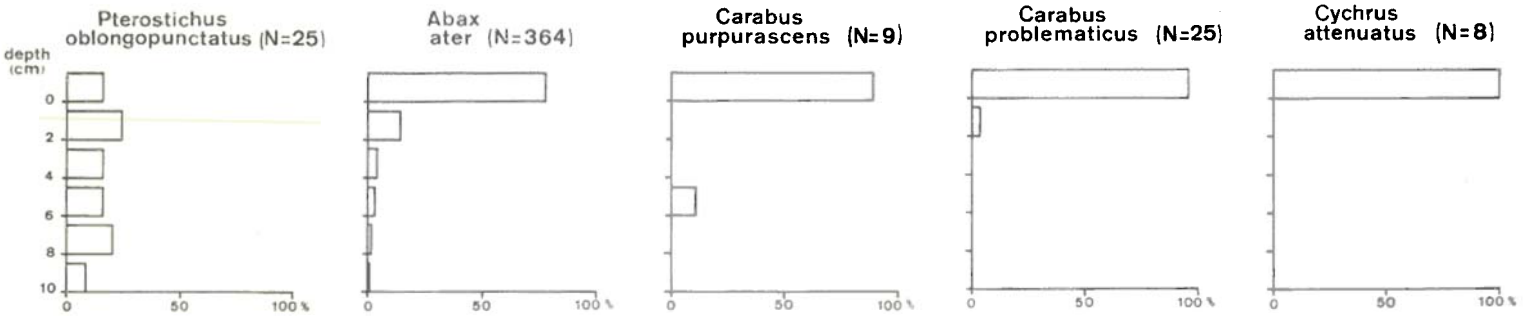

Fig. 2. Vertical distributions of activity of the different species. Total results over 2 years; N: number of individuals caught; activity is expressed in percentages of the total catch.

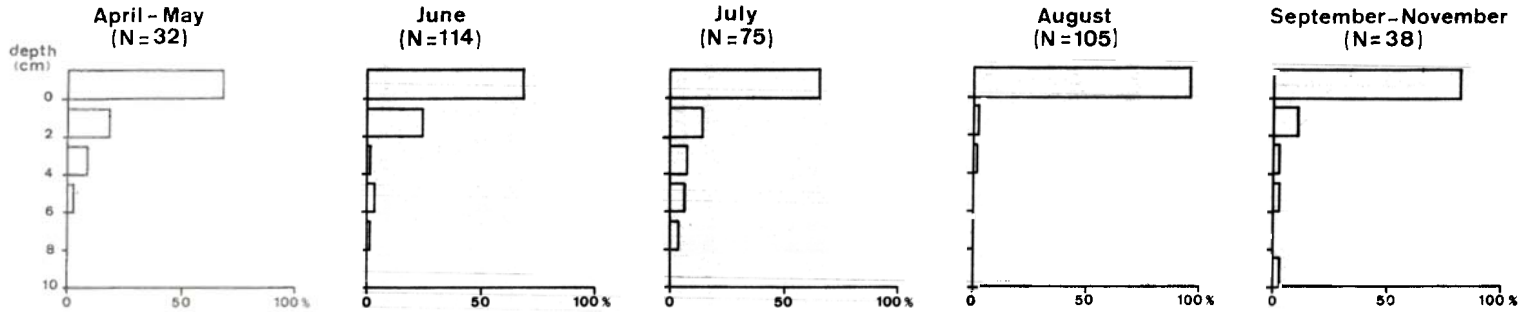

Fig. 3. Seasonal change in the vertical distribution of activity of *Abax ater*. Legend as Fig. 2.

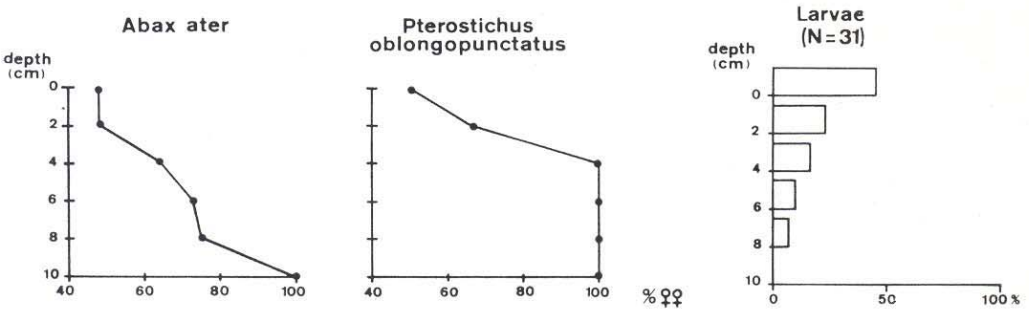

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Fig. 4. Variation of the sex ratio (proportion of female activity) according to depth in *Abax ater* and *Pterostichus oblongopunctatus*.

Fig. 5. Vertical distribution of activity of carabid larvae (all species pooled). Legend as in Fig. 2.

Table 1. Interspecific comparisons of proportions of surface activity: observed χ^2 values

	1	2	3
1. *Pterostichus oblongopunctatus*	—	45.41[3])	43.65[3])
2. *Abax ater*		—	7.24[2])
3. *Carabus* + *Cychrus* species			—

[2]) $P < 0.01$
[3]) $P < 0.001$

At the other extreme. *Carabus purpurascens*, *Carabus problematicus* and *Cychrus attenuatus* are almost exclusively active at the surface (Fig. 2).

Table 1 shows that the differences between the distributions of *Pterostichus oblongopunctatus*, *Abax ater* and the group of *Carabus* and *Cychrus* species cannot be ascribed to chance, since they are significant when χ^2 tests are performed on the proportions of surface activity.

Very few other species were caught in the traps. Let us simply mention the presence of *Notiophilus biguttatus*, *Nebria salina* and *Bembidion lampros* at the surface, and of *Leistus rufomarginatus* in the litter (d = 2 cm).

3.2. Larvae

Few larvae were caught in the traps. The overall vertical distribution of their activity differs from that of adults in that the proportion of their activity is higher in the soil (d = 2—10 cm: $\chi^2 = 13.83$, $P < 0.001$), but activity is also maximum at the surface and gradually decreases with increasing depth (Fig. 5). The species caught were: *Abax ater*, *Carabus purpurascens* and *Carabus problematicus*, which are the most abundant larvae and whose pattern of distribution is roughly that of Fig. 5; *Pterostichus oblongopunctatus* and *Nebria brevicollis*, which were caught in the soil; *Leistus rufomarginatus* and *Cychrus attenuatus*, which were caught at the surface.

4. Discussion

The results obtained in the field with special traps seem to challenge the view that ground beetles are only active at the surface, even though surface activity is predominant in most species. They tally with the expectations which were drawn in Loreau (1984d) from indirect considerations, and which were recalled in the introduction: the vernal *Ptero-*

stichus oblongopunctatus was indeed found to be active within the superficial soil layers, while the autumnal *Carabus* and *Cychrus* species were found to be typical surface-running species.

Nevertheless, the grounds for such different behaviours remain an open question. Two possibilities are suggested by the present results. The first is that which was put forward originally, i.e. different foraging strategies. Several facts support this hypothesis, in particular the seasonal trend in the vertical distribution of activity. Species are ordered in Fig. 2 according to the time of their activity during the course of the year, *Pterostichus oblongopunctatus* being mainly active in April—June, *Abax ater* in May—September, *Carabus purpurascens* in August, *Carabus problematicus* in September—October and *Cychrus attenuatus* in September—November (LOREAU 1985). There thus appears a gradual concentration of activity towards the surface from spring to autumn. The same trend was shown within a particular species, *Abax ater* (Fig. 3). This trend can be explained by changes in the available resources: on the one hand, qualitative observations from pitfall trapping in the beech forest suggest a change from smaller prey, which can move within the litter, in spring to larger prey, which can move faster at the surface of the litter (notably insects descending or failling from trees) in autumn; on the other hand, the upper litter layer is progressively modified and compacted during the same period, thereby reducing the opportunities for movement within it. Quantitative analysis of these changes would without doubt be useful. In addition, there might be an optimal size for foraging within the litter, since both the largest species (*Carabus* spp.) and the smallest, visually hunting species (*Notiophilus*, *Asaphidion*, *Bembidion* spp.: see e.g. BAUER 1979) in the beech forest are typical surface species, while the medium-sized *Pterostichus oblongopunctatus* is active within the litter as well (and personal observations suggest that this would also be the case for *Leistus rufomarginatus*). The hypothesis of a different foraging strategy in *Pterostichus oblongopunctatus* is further supported by the strong correlation between the abundance of this species and the thickness of the litter layer (DEN BOER 1963, 1965).

The second hypothesis to account for the observed activity within the soil rests on the increasing proportion of females with depth, both in *Abax ater* and *Pterostichus oblongopunctatus*. A straightforward explanation for this feature is that females enter deeper into the soil to lay eggs. In that case, activity within the soil should not necessarily be related to foraging. This factor alone, however, would not explain the observed interspecific differences. Note that the 2 hypotheses are not mutually exclusive. LOREAU (1983) showed significant differences between the diets of the 2 sexes in *Abax ater*, and thus the egg-laying behaviour of females might lead to a different foraging behaviour as well.

Lastly, the low catches of the soil-dwelling larvae show that these do not have a high horizontal locomotor activity in the soil. Also it must be observed that all adult catches may not result from a locomotor activity in the soil layers themselves. Holes of small mammals were not uncommon beside traps; they might constitute a passage in the soil for carabids.

5. Résumé

[Répartition verticale de l'activité des carabides (Coleoptera) dans le sol d'une hêtraie]

La répartition verticale de l'activité des carabides dans les couches superficielles du sol d'une hêtraie fut étudiée à l'aide d'une version modifiée du piège d'activité.

Il existe une succession de différentes répartitions au cours de l'année: l'espèce printanière *Pterostichus oblongopunctatus* est active aussi bien dans le sol qu'en surface; l'activité de l'espèce dominante *Abax ater* se déroule principalement en surface, mais décroît graduellement en profondeur; les espèces automnales de *Carabus* et de *Cychrus* sont presque exclusivement actives en surface. Ces répartitions varient en outre au sein d'une même espèce selon la saison et selon le sexe, les femelles étant plus actives en profondeur.

Ces résultats suggèrent l'existence de différentes stratégies de recherche de nourriture en fonction des ressources disponibles et/ou de différents comportements des deux sexes pendant la période de reproduction.

6. Acknowledgements

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Synopsis: *Original scientific paper*

LOREAU, M., 1987. Vertical distribution of the activity of carabid beetles in a beech forest floor. Pedobiologia **30**, 173—178.

The vertical distribution of the activity of carabid beetles in the superficial layers of a beech forest floor was studied using a modified type of pitfall trap.

There is a succession of different distributions during the course of the year: the spring species *Pterostichus oblongopunctatus* is active both in the soil and at the surface; the activity of the dominant species *Abax ater* is highest at the surface but gradually decreases with increasing soil depth; the autumnal *Carabus* and *Cychrus* species are almost exclusively active at the surface. These distributions also vary within some species according to the season and to the sex, females being more active deep in the soil.

These results suggest different specific foraging strategies depending on available resources and/or different behaviours between the sexes during the breeding period.

Key words: carabid beetles, activity, soil, forest.