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The annual activity cycle of carabid beetles in the southern Finnish taiga

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Carabid beetles were collected with 300 pitfall traps throughout the growing season of 1985 in a coniferous forest in southern Finland (Musturi State Forest Reserve). The traps were emptied every five days from mid-May to late August, and at longer intervals in September–November.

The total sample was 2405 individuals of 22 species. The five-day samples (all species pooled) increased from May to July, decreased slightly in August and even more in September–November. Species richness and diversity in the samples were lowest in the spring. Especially early in the season (May–July) the samples closely followed the temperature fluctuations.

Five species dominated the total sample, and their activity patterns were studied in detail: the activity of *Pterostichus oblongopunctatus* peaked in the spring, whereas *Calathus micropterus*, *Cychrus caraboides* and *Leistus terminatus* showed a peak of activity in the middle of the summer. There was no clear peak in the activity of *Notiophilus biguttatus*. A comparison, in this study, showed that the activity patterns of the dominant species in southern Finland did correspond with those reported from central Europe, but *Calathus micropterus* and *Cychrus caraboides* tended to be active earlier in our study.

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1. Introduction

Annual activity patterns are an important part of insect life cycles, and they differ among species in most taxa, including carabid beetles. Thus, it is important that studies on the ecology of carabid beetles include information on their annual activity patterns. Detailed knowledge on the annual activity patterns of different species is also a necessary element in studies examining the structure of local carabid assemblages (e.g. Müller 1985, den Boer 1985, Loreau 1986, Müller & Kaschuba 1986). On the basis of their annual activity the species have been classified into two main reproduction and hibernation groups, namely, spring breeders and autumn breeders (Larsson 1939, Lindroth 1945). Later several authors have noticed that the time of reproduction may vary with geographical location and altitude. Accordingly, the designation of carabids into adult-overwinterers (hibernate as adults) and larval-overwinterers (hibernate mainly as larvae) may be more appropriate (Paarmann 1979, Sharova 1981, Andersen 1984, Loreau 1985, Wallin 1985, Butterfield 1986, Refseth 1988).

Though C. H. Lindroth was a pioneer in studying the annual activity patterns of carabids in Fennoscandia, the majority of the *quantitative* studies on the annual cycles of activity have been made in the temperate region (Thiele 1977, Brandmayer & Brandmayer 1986). However, many of the species studied in temperate forests are scarce in the boreal zone, and little quantitative information is available on the annual activity cycles of species abundant in Fennoscandia. The climate is different, and the patterns detected in central Europe may change towards north (van der Drift 1959, Butterfield 1986, Andersen 1988).

In this paper we describe the annual activity cycle of carabid beetles in a study plot in the southern Finnish taiga and compare the patterns of activity observed with those found in other parts of Europe.

Table 1. Total samples of the five abundant species in the 26 sampling periods between 11 May and 23 November, 1985. Dates of sample collection and the symbol of the sampling period (alphabet) are given. The other species and their samples are listed in alphabetical order (sampling period followed by the sample size).

Species	May				June						July						August						Sept.		Oct.	Nov.	
	16	21	26	31	5	10	15	20	25	30	5	10	15	20	25	30	4	9	14	19	24	29	8	23	23	23	
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	Total
Abundant																											
P. obl.	47	47	13	134	62	37	45	64	61	38	32	44	56	15	14	5	2	2	6	2	1	3	6	27	74	16	853
C. micr.	0	3	2	20	26	22	23	7	29	51	25	65	53	32	32	23	25	28	15	6	3	7	8	10	33	5	553
L. term.	0	0	0	0	0	0	0	0	1	3	5	20	63	27	26	36	11	26	15	22	19	6	5	1	1	0	287
N. big.	1	1	0	36	2	4	7	7	20	14	7	11	10	4	12	6	5	11	8	11	14	9	34	45	6	0	285
C. car.	0	0	2	5	10	14	10	13	15	21	22	24	30	23	13	8	13	13	9	4	1	2	3	1	0	0	256
Other	1	1	1	5	3	2	5	12	13	14	7	11	19	16	4	13	2	3	6	9	0	1	4	6	11	2	171
Total																											
Ind.	49	52	18	200	103	79	90	103	139	141	98	175	231	117	101	91	58	83	59	54	38	28	60	90	125	23	2405
Spec.	3	4	4	7	7	6	7	8	12	10	11	11	11	9	7	8	6	6	9	9	5	6	7	7	9	4	22

Abundant species: *Pterostichus oblongopunctatus* (F.), *Calathus micropterus* (Dft.), *Leistus terminatus* (Hellw. in Pz.), *Notiophilus biguttatus* (F.), *Cychrus caraboides* (L.).

Other species: *Agonum mannerheimii* (Dej.): D 2, E 1, G 3, T 2; *Amara brunnea* (Gyll.): B 1, D 2, F 1, G 1, H 1, I 1, J 2, K 1, L 5, M 4, N 9, O 3, P 8, Q 2, R 3, S 2, T 2; *Bradycellus caucasicus* (Chaud.): Y 5, Z 1; *Calathus melanocephalus* (L.): M 1; *Carabus glabratus* Payk.: E 1, G 1, H 7, I 5, J 6, K 2, L 1, M 2, N 4, S 2; *C. hortensis* L.: H 1, I 2, J 2, K 1, L 2, M 5, P 3, S 1, W 1, X 2, Y 2; *Dromius agilis* (F.): E 1, I 2, J 1, L 1, N 2, Z 1; *Harpalus quadripunctatus* Dej.: I 1; *Leistus ferrugineus* (L.): I 1, L 1, P 2, S 1, T 2, V 1; *Loricera pilicornis* (F.): C 1, D 1, T 3; *Notiophilus reitteri* Spaeth: H 3, L 1, M 6, N 1, W 3, X 4, Y 2; *Patrobus assimilis* Chaud.: K 1; *P. atrorufus* (Ström): F 1, O 1, Y 1; *Pterostichus adstrictus* Eschtz.: I 1, K 1; *P. nigrita* (Payk.): A 1; *P. niger* (Schall.): J 3, K 1, M 1; *Trechus secalis* (Payk.): Y 1.

2. Study area and sampling design

Our study plot lay in the Musturi State Forest Reserve in southern Finland (located 8 km SW of the Hyytiälä Forestry Field Station, about 62°N, 24°E). The area of the Reserve is about 19 hectares. The dominating tree species is spruce (*Picea abies*) and the forest belongs to the *Myrtillus*-type in the Cajanderian forest-type classification. The forest has not been burnt or cut for over a century.

We selected within the forest a sampling site that was as homogeneous as possible. Trees are mostly over 140 years old, tall (mean height 24 m, basal area 37 m^2/ha), with a canopy cover of 90%. Plant species abundant in the field layer are *Vaccinium myrtillus* (cover 28%), *Deschampsia flexuosa* (4%), *V. vitis-idaea* (3%), *Maianthemum bifolium* (2%) and *Linnea borealis* (2%). The ground is mostly covered by mosses, mainly *Dicranum* spp. and *Pleurozium schreberi*. A detailed description of the vegetation in the sampling site will be published elsewhere (Niemelä et al. in prep.).

We used pitfall traps (Niemelä et al. 1986) to collect the carabids. The traps (plastic cups, diameter 65 mm, volume 170 ml) were partially filled with water and detergent. They were placed in a grid of 12 × 25 traps covering an area of about 1.3 hectares. The distance between neighbouring traps was 4–5 m. To keep rain out of the traps we placed tin plates above them. The traps were in operation from 11 May through 23 November 1985, or for 196 trap-days. The period covers the whole growing season, which at Tampere (60 km SW of the sampling site) started in 1985 on 6 May and ended on 26 October (Finnish Meteorological Institute 1985). We collected the catches every five days between 11 May and 29 August, and later in the autumn on 8 and 23 September, 23 October and 23 November. We made use of temperature data from the meteorological station at the Hyytiälä Forestry Station.

3. Activity cycles

The total sample from Musturi comprised 2405 individuals of 22 species (Table 1). The sample sizes increased from May (mean 80 individuals/period) to July (136). In August the sample sizes were lower (53) and they decreased slowly to almost nil towards the end of the study period (Fig. 1). The sample sizes of the five-day periods follow the mean temperature. The correlation was especially clear from May till mid July, whereafter the carabid samples decreased, while the temperature remained quite stable until the end of August (Fig. 1).

To examine trends in the whole carabid assemblage we divided the season into five periods of about one month each. Variation in species richness estimated by rarefaction (Simberloff 1978) was lower in

Table 2. The reproduction period (Rep; Sp=spring, Su=summer, Au=autumn) and hibernation type (Hib; A=adult, L=larva) according to Lindroth 1945, 1949, 1985, 1986, and the sample sizes of the five abundant species in May (20 trap-days), June (30 trap-days), July (30 trap-days), August (30 trap-days) and September-November (86 trap-days). The sample sizes are standardized to 20 trap-days. The number of species (rarefaction estimate, $E(S)$ with $\pm SD$) and the value of Δ_1 in a sample of 298 individuals (observed sample size in Sept.–Nov.) are given.

	Rep./Hib.	May	June	July	August	Sept–Nov
Pterostichus oblongopunctatus	Sp/A	241	205	111	11	29
Calathus micropterus	Su/A	25	105	153	56	13
Leistus terminatus	Au/L	0	3	118	66	2
Notiophilus biguttatus	Sp/A	38	36	33	39	20
Cychrus caraboides	Au/L	7	55	80	28	1
Other species		8	33	47	14	5
Total sample size		319	437	542	214	70
$E(S)_{298}$		7.9±0.3	13.2±1.2	12.5±1.3	10.9±0.3	11 (obs.)
Value of Δ_1		0.41	0.70	0.80	0.78	0.71

May than in the other periods (Table 2). We studied the species diversity by calculating the diversity index Δ_1 introduced by Hurlbert (1971):

$$\Delta_1 = \frac{N}{N-1}\left(1 - \sum_{i=1}^{S} \pi_i^2\right)$$

where $N = \sum_i N_i$ = total number of individuals in the sample, N_i = number of individuals of the ith species in the sample, $\pi_i = N_i/N$, and S = number of species in the sample.

Diversity was lowest in May, increased until July, and decreased again toward late autumn (Table 2). The low diversity in May is due to the extremely high proportion (76%) of *Pterostichus oblongopunctatus* in the sample.

Five species, viz. *Pterostichus oblongopunctatus*, *Calathus micropterus*, *Leistus terminatus*, *Notiophilus biguttatus* and *Cychrus caraboides* comprise as much as 93% of the total sample, and these had different activity patterns (Fig. 1). The reproduction periods (Lindroth 1945, 1949, 1985, 1986), which are often simultaneous with a peak in the activity of the adult beetles, tended to coincide with the activity peaks of the species in our data (Table 2). Below we describe the occurrence of the five species through the season. Our data are presented in Tables 1 and 2, and in Figs. 1 and 2.

P. oblongopunctatus had its activity peak in the spring and early summer (Fig. 1). The pattern agrees with information in the literature where the species is characterized as a spring-active species reproducing in the early summer (e.g. Lindroth 1945, van der Drift 1951, Heessen 1980, Loreau 1985, Müller & Kaschuba 1986, Refseth 1988) (Fig. 2).

Many authors have noticed a very low abundance of *P. oblongopunctatus* in the late summer. A smaller peak occurs in the autumn when the newly hatched adults emerge, or when according to Penney (1967) some of the old the adults may re-emerge after summer aestivation (Fig. 2).

C. micropterus, *C. caraboides* and *L. terminatus* exhibited an activity peak in the middle of the summer. *C. micropterus* reproduces in central Europe in summer and autumn, but in Scandinavia occasional spring reproduction also occurs (Lindroth 1986). The peak of activity coincided in southern Finland and southern Sweden, but occurred slightly later in the Netherlands (Fig. 2, see also van der Drift 1951). *Cychrus caraboides* peaked in mid-July, which agrees with information from southern Sweden. In central Europe, the activity peak occurred later (Fig. 2). The activity period of *Leistus terminatus* was short in our study area, agreeing with data from southern Sweden (Fig. 2).

Notiophilus biguttatus was active throughout the season. We obtained the largest catches in late May and in late June, corresponding with temperature peaks (Fig. 1). In other parts of Europe, the species was active in the spring and early summer (Fig. 2). Larsson (1939) assumed that there were two generations occurring simultaneously; the old adults, and the

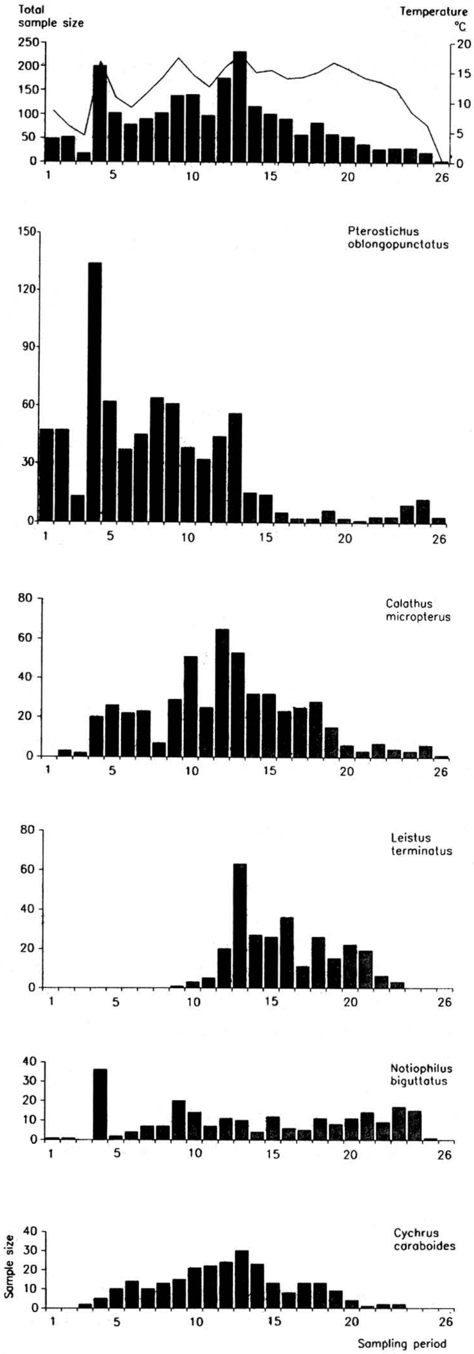

Fig. 1. The carabid samples (bars) and the mean temperature (line) in the sampling periods (upper diagram), and the sample size of the five most abundant species in each sampling period. The September–November samples (periods 23–26) are standardized to five trap-days.

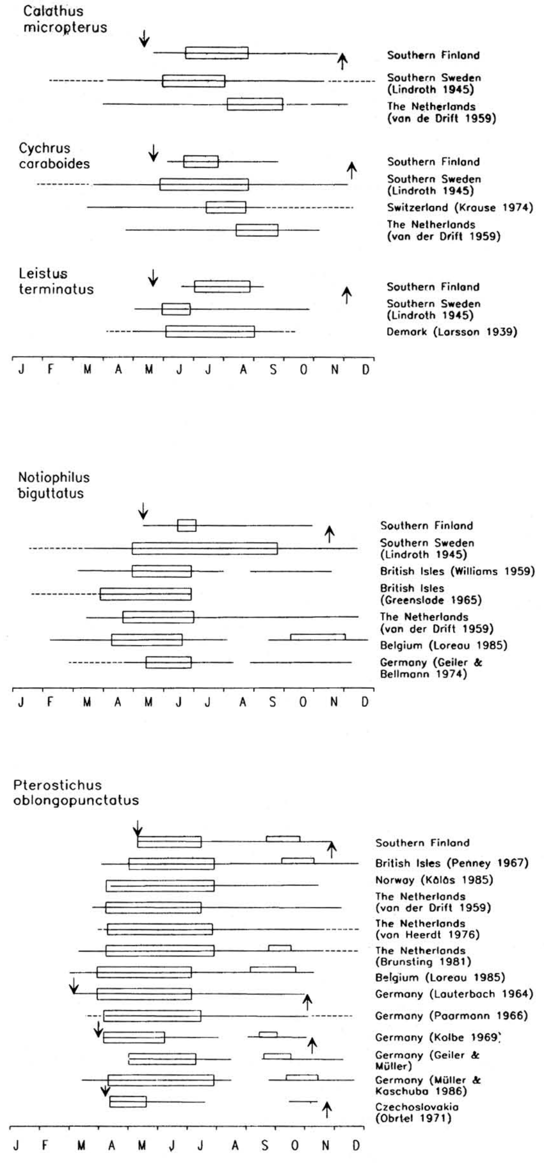

Fig. 2. The activity patterns of the five most abundant species in our study (southern Finland) and in some studies from other parts of Europe. The solid line indicates the period when the species was continuously found and the interrupted line the period when only occasional individuals were found. The high rectangles indicate periods of peak activity and the lower rectangles secondary peaks. The arrows show the start and end of the sampling period; studies without arrows covered the whole year.

young beetles which had hatched during the summer. This suggestion was also made by Lindroth (1985). On the other hand, Loreau (1985 and pers. comm.) believed that there may be two successive generations in the same year. In central Europe there is a gap between two activity peaks, but in the north this interval may have reduced resulting in a more uniform activity pattern.

Most of the other species in our study were scarce, and the activity patterns were difficult to interpret. *Amara brunnea* was caught from May to August, with its peak in July. *Carabus glabratus* occurred only from early June to mid July, and exhibited a peak in late June. The closely related *Carabus hortensis* had a similar occurrence, but some individuals were also found in the late autumn. *Notiophilus reitteri* occurred in low numbers throughout the season, even in the autumn. All the six individuals of *Bradycellus caucasicus* were caught in October and November. Eight individuals of the typical taiga species, *Agonum mannerheimii*, were caught mainly in the spring and early summer. A detailed study on the habitat preferences and seasonal activity pattern of *A. mannerheimii* are presented in Niemelä et al. (1987).

4. Discussion

The activity cycles of the species in our study seem to be quite similar to those in more southern areas, but some differences were observed. Below we discuss our observations in relation to those made in other parts of Europe.

The distinction between the two major types of carabid activity cycles, "spring breeders" and "autumn breeders", was less clear in our data than in many studies in the temperate region (e.g. Larsson 1939, van der Drift 1959). The decreasing length of the growing season in the north may force carabids to concentrate their activity at the middle of the summer (Loreau 1985). This leads to high overlaps in the activities among the species and to a high overall abundance of carabids in the middle of the summer. On the other hand, the two classical categories of activity types may not cover all the diversity in activity cycles of carabids. For instance, activity patterns detected in central Europe may change radically along a latitudinal gradient to Fennoscandia (Loreau 1985, Andersen 1984, Butterfield 1986, Refseth 1988).

The activity peak of some species in our study differed somewhat from that in the more southern regions. *Calathus micropterus* and *Cychrus caraboides*, active in the mid- and/or late summer (autumn breeders), tended to occur earlier. This geographical variation in the annual activity is most likely due to climatic differences along a south-north gradient as mentioned above. Van der Drift (1959) observed that many species overwintering as larvae (e.g. *Calathus micropterus*, *Cychrus caraboides*) peaked earlier in the summer with decreasing length of the growing season (from the Netherlands to southern Sweden). He assumed that the earlier reproduction gives the larvae enough time to reach the right stage (even the adult stage) for overwintering. Furthermore, depending on the climate species may hibernate in different developmental stages. For instance, *Calathus micropterus* overwinters mainly as an adult in Scandinavia (cold winter), but as a larva in central Europe (mild winter) (Lindroth 1949, Larsson 1939, van der Drift 1959, see also Thiele 1977). The problems with the timing of the life cycles (for instance that of the onset of hibernation) have been the focus of several theoretical studies (e.g. Dingle 1986, Taylor 1986).

A positive correlation between temperature fluctuations and carabid activity has been found in many studies in central Europe (e.g. van der Drift 1959, Lauterbach 1964, Heessen 1980, Brunsting 1983). Grüm (1959), Lauterbach (1964) and Brunsting (1981) observed that the effect of temperature on carabid catches is especially pronounced in the spring. In our data the very close correlation between the carabid sample and temperature in the spring was mainly due to the fluctuation of one species, *P. oblongopunctatus* (see Fig. 1).

The increase in total sample size, species richness and diversity was rapid in early summer, whereas the decrease in these parameters was slower in the autumn. A similar pattern was found in the mountaineous area of western Germany (Lauterbach 1964) and southern Europe (Brandmayer & Brandmayer 1986), and in several habitats in Denmark (Larsson 1939). We do not know whether the lack of abundant species in the late summer in our study is a habitat effect (i.e. northern coniferous forests may be unsuitable habitats for "autumn breeders") or due to the short growing season (see van der Drift 1959). In a more luxuriant habitat type (spruce dominated lush forest) on the Åland Islands (about 60°N) the highest total carabid abundance was reached in the late summer, when *Trechus secalis* and *Patrobus atrorufus* peaked (Niemelä et al. 1985). Lauterbach (1964) discovered that in cooler habitats the activity peak was reached later (all species pooled) than in warmer ones. He also observed that the two-peak activity pattern (May and July) of *Abax ater* in warmer forest habitats was reduced to a single peak in July–August in cooler forests. Similarly, van der Drift (1959) observed that in habitats with a higher ground temperature (pine forest) the first individuals of *Pterostichus oblongopunctatus* were caught earlier and the newly hatched adults emerged earlier than in cooler habitats (oak forest).

Studies in different habitats in the same climatic region and in similar habitats in different regions are needed to reveal whether the activity patterns vary among habitats (perhaps due to microclimatic differences) and/or whether the activity periods are determined by macroclimatic differences among regions. Climate may also cause the above differences among habitats and among geographic regions indirectly through affecting the availability of food to carabids (Obrtel 1971, Szujecki 1987).

Our conclusions were based on a one-year study, but several authors have concluded that the seasonal activity patterns of the species remain similar in spite of fluctuations in their abundance among years (van der Drift 1959, Penney 1966, 1967, Kolbe 1969, Refseth 1980, 1988, Brunsting 1981, Müller & Kaschuba 1986). To examine the effect of between-year variation in weather conditions on carabid populations long term studies are clearly needed.

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