Life cycles and annual activity patterns of *Pterostichus melanarius* (Illig.) and *P. niger* (Schall.) (Coleoptera: Carabidae) in a Danish beech wood

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The life cycle and the seasonal changes in adult activity of *Pterostichus melanarius* and *P. niger* were investigated in a Danish beech wood by means of pitfall trapping and by the recording of ovarian development in females from the field samples.

Females of both species had a two-year period of development from egg to mature adult, which was presumably caused by the long winters and cool springs in the study period. Newly emerged beetles occurred from late July or early August. Females of this generation hibernated as immatures and reproduced the following year. The main breeding period was June–July for *P. melanarius,* July for *P. niger*. Some females of both species laid eggs in two or more breeding seasons.

Activity started in April or May and lasted until late September; only a very few beetles were still active in October and November. The activity density was at its maximum in the first half of August, when most new beetles had emerged. Females were caught in greater numbers than males, the predominance of females being more considerable in *P. melanarius.*

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Introduction

The carabid beetles *Pterostichus melanarius* (Illig.) and *P. niger* (Schall.) were found by Larsson (1939) to have an annual life cycle and to be autumn breeders, and recent investigations by, e.g., Thiele & Krehan (1969), Krehan (1970) and Witzke (1976) have confirmed this. Both species have a thermic hibernation parapause in the larval stage (Thiele, 1977). The life cycle of Carabidae with this type of development is strongly influenced by climate and may become a two-year cycle in regions with severe winters (Thiele, 1977). Thus *Pterostichus madidus* (Fabr.) is an annual autumn breeder in south and north-east England (Luff, 1973); in a sub-arctic climate, however, W. W. K. Houston (in Luff, 1973) found that all females of *P. madidus* emerged from August to September and then hibernated before breeding for the first time, so that *P. madidus* was here biennial.

During a study of the composition and phenology of the carabid fauna of a Danish beech wood a two-year life cycle was discovered in both *P. melanarius* and *P. niger* (Jørum, 1976 a). This biennial life history is described in greater details in the present paper, and the hypothesis is forwarded that long winters and cool springs in the investigation period caused a delay in metamorphosis resulting in a two-year life cycle in both species. The annual activity patterns of the adult beetles are discussed in the light of their life cycles.

Study area and method

The investigation took place in 1969 and 1970 in Hestehave, at Rønde, 25 km NE of Aarhus, Eastern Jutland, Denmark. The study ares was a ca. 90-year-old beech stand (*Fagus silvatica* L.) on a mull soil. The herb layer included *Anemone nemorosa* L., *Ficaria verna* Huds., *Melica uniflora* Retz., *Asperula odorata* L., *Oxalis acetosella* L., *Carex silvatica* Huds., *Circaea lutetiana* L., *Stellaria holostea* L. and *Hordeum europaeum* L. The carabid fauna was dominated by eurytopic species with autumn reproduction (Jørum, 1976 a).

Carabidae were sampled in pitfall traps, jars 6 cm in diameter and 11 cm deep, containing a 4% formalin solution. Nine and 30 traps were in use in 1969 and 1970 respectively. The traps were emptied at intervals of 8 to 14 days, less frequently in the winter. The number of beetles caught in each trapping period has been adjusted to numbers caught per 100 traps per day (activity density, cf. Thiele, 1977). Some females selected randomly from the pitfall samples were dissected for examination of ovaries and were thereby classified as immature, mature or spent (Gilbert, 1956; Schjøtz-Christensen, 1961; Vlijm & Dijk, 1967). As part of a population study, Carabidae were marked individually and released. From recaptures, some knowledge of the longevity of the imagos has been obtained. Further details about the sampling and marking method are given in Jørum (1976 b).

Temperature recordings were obtained from the meteorological station at Ødum, 20 km from Hestehave.

Results

P. melanarius

The annual pattern of activity of adult *P. melanarius* appears from Fig. 1. In both years the activity started in April. The activity density increased in late April and early May and fluctuated irregularly during the early summer. In late June and in the first half of July there was a slight decrease in activity density, but from late July the activity density increased again and reached a peak in August. This peak was much higher in 1969 than in 1970. From about mid-August the activity density decreased, and from late September onwards only a few beetles were trapped. Females dominated the catch in all months except April and early May 1969 and April 1970. The ratio of males to females for the whole period was 0.34 which differed significantly from a 1 : 1 sex ratio ($X^2 = 529.58$, $P < 0.001$).

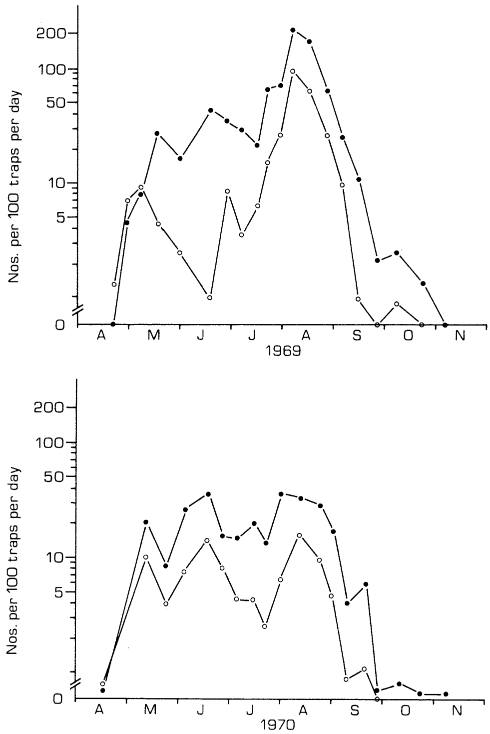

Fig. 1. Activity density (beetles per 100 traps per day) of *P. melanarius* in 1969 and 1970. The total number of beetles caught was 935 in 1969 and 1235 in 1970. Open circles: males, filled circles: females.

Table 1. Ovarian development in *P. melanarius*.

Date	Nos. dis-sected	Nos. imma-ture	Nos. ma-ture	Nos. spent
25–30 Apr. 1969	2	2	0	0
30 Apr.–11 May 1969	8	5	0	3
5–18 May 1970	26	15	1	10
11–21 May 1969	15	10	0	5
21 May–11 June 1969	8	4	4	0
29 May–13 June 1970	12	1	11	0
24 June– 1 July 1970	6	0	6	0
8–16 July 1970	9	0	9	0
5–18 Aug. 1970	14	9	4	1
18–28 Aug. 1970	10	6	2	2
28 Aug.– 6 Sept. 1970	10	6	2	2
6–15 Sept. 1970	5	2	0	3
15–21 Sept. 1970	5	1	0	4

The activity from April to late July was due to hibernating beetles. Most females collected in April and May had immature ovaries (Table 1). They had emerged as adults the previous summer and had hibernated in the prereproductive state. Only about 35% of the dissected females from April and May had spent ovaries and had thus laid eggs in the previous year. The hibernating females oviposited from the end of May until September. In June and July almost every dissected female contained eggs, so these months seem to have been the main breeding period. In three females collected in June the ovaries contained conspicuous corpora lutea and many large oocytes indicating that these were old females which were about to start a second breeding period. When egg-laying was in progress first-time breeders could not be separated from females which had laid eggs in a previous breeding period. The increase in activity density in the late summer was caused by the newly emerged imagos which appeared from late July (1969) or early August (1970). The ovaries of females of this generation were small and showed no sign of egg-development in August and September.

A total of 315 beetles were marked in the spring and early summer of 1969, before the emergence of the new imagos. 11 were recaptured in 1970, and since they must have survived from 1968, they attained at least the age of about two years and probably reproduced in both 1969 and 1970.

P. niger

The activity of *P. niger* began in May, but few beetles were caught in this month (Fig. 2). In 1969 the activity density increased from late June and was at its maximum in early August. In 1970 the increase in activity density started in early June and a peak was reached in late June, after which the activity density decreased until about mid-July. In late July the activity density increased again reaching a second peak in August. This peak was much lower than the corresponding peak of 1969. The activity density decreased during August and September, and from late September very few beetles were caught. The ratio of males to females for the whole period was 0.72, which differed significantly from a 1:1 sex ratio ($X^2 = 19.78$, $P < 0.001$). Females were especially dominating in August and September. Fig. 2 shows a predominance of males in mid-July in both 1969 and 1970, but the difference in number between males and females was not significant (1969: $X^2 = 2.27$, $P < 0.2$; 1970: $X^2 = 3.27$, $P < 0.1$).

The activity from May until the end of July was due to hibernating beetles. In May and June most hibernating females had immature ovaries; only a few had spent ovaries and had accordingly laid eggs in the previous year (Table 2). Females with ripe eggs were found from June to September, mainly in July when almost 95% of the dissected beetles contained eggs. This and observations of copulation and oviposition in July suggest that July was the main breeding period. Mature females from June to the begin-

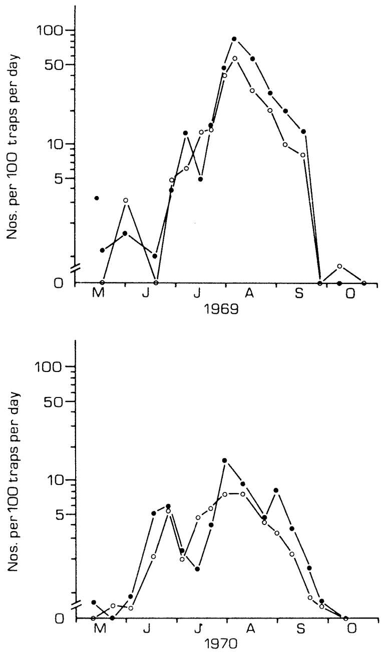

Fig. 2. Activity density (beetles per 100 traps per day) of *P. niger* in 1969 and 1970. The total number of beetles caught was 402 in 1969 and 326 in 1970. Open circles: males, filled circles: females.

Table 2. Ovarian development in *P. niger*.

Date	Nos. dis-sected	Nos. imma-ture	Nos. ma-ture	Nos. spent
11–21 May 1969	1	0	0	1
21 May–11 June 1969	3	1	0	2
29 May–13 June 1970	4	4	0	0
11–22 June 1969	1	1	0	0
13–24 June 1970	12	7	5	0
22 June– 1 July 1969	3	0	3	0
24 June– 1 July 1970	12	3	9	0
1– 8 July 1970	5	0	5	0
1–10 July 1969	10	0	10	0
8–16 July 1970	4	0	4	0
10–17 July 1969	3	0	3	0
17–25 July 1969	7	0	7	0
16–25 July 1970	10	0	10	0
25 July– 5 Aug. 1970	9	2	6	1
18–28 Aug. 1970	13	1	11	1
28 Aug.– 6 Sept. 1970	19	7	9	3
6–15 Sept. 1970	10	2	6	2
15–21 Sept. 1970	2	2	0	0

ning of August had no or very small corpora lutea, but a few females from the last half of August and September contained conspicuous corpora lutea and large oocytes, indicating that these were spent females which were about to start a new breeding period. The increase in activity density from late July to early August was due to the appearance of newly emerged imagos. The ovaries of females of this generation were small, without any sign of egg-development in August and September.

Only 27 beetles were marked before the emergence of the new generation in 1969. Two were recaptured in 1970, and since they had survived from 1968, they lived at least for about two years.

Temperature recordings from the meteorological station at Ødum are shown in Fig. 3. The mean weekly temperatures from January to May for 1969 and 1970 are compared with the mean values for the period 1965–1974. It appears that the temperatures in the first part of 1969 and 1970 were lower than normal, i.e. the winters of 1968/69 and 1969/70 both were long and both were followed by a cool spring.

Discussion

Callow beetles of *P. melanarius* and *P. niger* appeared in late July and early August. The time needed for the new generation of *P. melanarius* to reach sexual maturity is at least three weeks at 20 °C (Thiele, 1969; Krehan, 1970), in the field it probably takes longer (Hůrka, 1975). Presumably, *P. niger* needs about the same time to become mature. Thus, if the new generation had reproduced in the year when it emerged, a period of high activity would have been expected in late August and September. At this time, however, the activity density was low. Moreover, females of the new generation showed no egg-development in August and September. These facts and the occurrence of many immature females in the spring show that females of the new generation hibernated without reproducing; they resumed activity and laid eggs the following year. Thus, females of both species were biennial. However, it cannot be excluded that some females which appeared early reproduced in the year of their emergence. Examinations of gonads were not carried out in males, so it is not known whether they had a similar life cycle.

The most detailed description of the life history of *P. melanarius*, based on examination of gonads, has been given by Krehan (1970). He found callow beetles at the end of June and in July; reproduction took place from the end of June to the beginning of September. Third instar larvae hibernated, but in addition, a number of old beetles which had reproduced hibernated and entered a second breeding period in the following year. These results agree with those of Briggs (1965), who found newly emerged beetles mainly in late May and early June. They reproduced from July to September, and most died subsequently; only a small number hibernated and resumed activity in the following year. Larsson (1939) and Lindroth (1945), on the other hand, found large numbers of hibernating imagos. Since their results were not based on examination of gonads, it seems possible that the hibernating adults comprised both immature and spent individualt. The results of the present study do not agree with those of Krehan (1970) and Briggs (1965). However, like Krehan, I found that some females, which had laid eggs in one season, hibernated and reproduced again in the next.

Witzke (1976) described the life cycle of *P. niger*. Newly emerged imagos appeared from May to July and reproduced in August and the first half of September. Third instar larvae hibernated, but in addition, a number of old beetles hibernated and reproduced a second time. In the laboratory one hibernating female laid eggs from May to July. An annual life cycle with autumn reproduction was also described by Larsson (1939) and Lindroth (1945). These results are not in agreement with those of the present study. However, Witzke's (1976) observation that some beetles may reproduce in more than one season, was confirmed by me. From the extent of adult hibernation, Greenslade (1965) assumed that the species may either breed in two seasons, or those individuals emerging late in one season will not breed until the next. The present study and Witzke's show that both assumptions may be valid. Also Larsson (1939) and Lindroth (1945) found many hibernating adults, and it seems possible, as in the case of *P. melanarius*, that these overwintering beetles may have included immature as well as spent animals.

Larval development in both *P. melanarius* and *P. niger* is controlled by temperature. Thiele & Krehan (1969) and Hůrka (1975) found a temperature governed dormancy ("thermic parapause") in larvae of *P. melanarius*. Thiele & Krehan showed that at the end of the second instar it is essential that the larvae are exposed to cold. In addition, a long period of low temperature is necessary for a normal development of the third instar. However, the larvae need a final period of high temperature to complete the development. Krehan (1970) found that the third larval instar is fully developed after a period of three and a half months of cold, followed by an exposure to 14 °C for two months. Larvae of *P. niger* also need a period of cold, followed by a rise in temperature, to ensure a succesful development (Witzke, 1976). When larvae were kept at 20 °C from November onwards, growth was arrested after three months, and subsequently the larvae died. When low temperature from November to February was followed by a period of high temperature (20 °C), pupation occurred in May.

A probable consequence of this is that a short winter followed by a rise in temperature early in the spring will cause the emergence of callow beetles in the spring or early summer, and reproduction will then follow in the autumn (annual life cycle). On the other hand, a long winter followed by a cool spring will prolong the life of the third larval instar and postpone the emergence of callow adults till about August. The newly emerged imagos will then hibernate as immature beetles and reproduce the following year (biennial life cycle). The long cold winters in the study period were the probable cause of the biennial life cycles in *P. melanarius* and *P. niger* in Hestehave (Fig. 3). If this hypothesis is correct, an annual life cycle is to be expected at

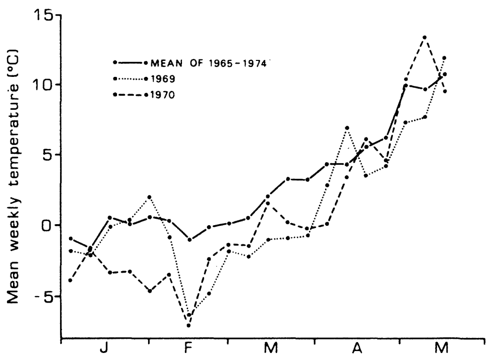

Fig. 3. Mean weekly temperatures of 1969 and 1970 compared with the mean values for the period 1965–1974. The temperatures were recorded at the meteorological station at Ødum, 20 km from the study area.

the same site in years following a short winter and high temperatures in the early spring.

A number of Carabidae have been found to have a two-year period of development; a survey is given in Lampe (1975). Most of these species seem to have a facultative biennial life cycle and are accordingly biennial only under unfavourable conditions such as cold winters or cool summers. In *P. madidus* most beetles reproduced shortly after emergence, but females emerging late in the summer hibernated as immature, and did not breed until the next season (Greenslade, 1965). The earlier in the year the conditions become unfavourable, the more beetles will reproduce in the year after hibernating as shown in *Calathus melanocephalus* (L.) (Dijk, 1972). An obligatory biennial life cycle has so far been described only in *Abax ovalis* (Dft.) (Lampe, 1975), but is likely to occur also in *Pterostichus metallicus* (Fabr.) (Weidemann, 1971). Both are mountain-dwelling Carabidae, and the obligatory biennial life cycle may be considered an adaptation to a permanently unfavourable climate (Thiele, 1977).

In both *P. melanarius* and *P. niger* the activity density in the late summer of 1970 was much lower than in 1969 because of a decrease in the density of both populations (Jørum, unpubl.). This decrease was presumably a result of the dry summer of 1969 which may have caused a low recruitement of new adults in 1970; the drought of 1969 also gave rise to a reduction in the density of a population of *Nebria brevicollis* (Fabr.) (Jørum, 1976 b).

Females of both species were trapped in significantly greater numbers than males. Formalin traps are known sometimes to capture more females than males (Luff, 1968; Skuhravý, 1970), so the slight predominance of females in *P. niger* may be due to this alone. In *P. melanarius,* however, the predominance of females was very great and was chiefly a result of a considerably greater density of females than of males (Jørum, unpubl.). According to Heydemann (1962) and Müller (1968) females often predominate in habitats which are optimal to a species. In sugar beet fields, males of *P. melanarius* were more numerous in formalin traps than females (Novák, 1967), whereas Ericson (1977, 1978) found a very great dominance of females in a winter wheat field. *P. melanarius* is generally considered an eurytopic species, mainly associated with grassland and arable land (Lindroth, 1945; Thiele, 1964;

Greenslade, 1965), so the great predominance of females in Hestehave is surprising and does not support the idea of using the sex ratio of Carabidae as an ecological indicator, as suggested by Müller (1970).

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Sammendrag

Livscyklus og årligt aktivitetsmønster hos *Pterostichus melanarius* (Illig.) og *P. niger* (Schall.) (Coleoptera: Carabidae) i en dansk bøgeskov.

Som et led i en undersøgelse af løbebillefaunaens sammensætning og sæsonaktivitet i et bøgeskovsområde i Hestehave ved Rønde, 25 km nord-øst for Århus, er livscyklus og det årlige aktivitetsmønster hos

Pterostichus melanarius og *P. niger* blevet studeret i årene 1969 og 1970. Hovedtrækkene i de to arters livscyklus og sæsonaktivcitet er beskrevet tidligere (Jørum, 1976 a); nærværende artikel indeholder en mere indgående redegørelse for undersøgelsens resultater.

Billerne blev indsamlet ved hjælp af faldgrubefælder med en formalinopløsning. Fælderne blev i størstedelen af året tømt med 8–14 dages mellemrum. En del af de indsamlede hunner blev dissekeret med henblik på en undersøgelse af ovarietilstanden og blev på basis heraf inddelt i umodne hunner, der endnu ikke havde udviklet æg, modne hunner, som indeholdt æg, og gamle hunner, som havde lagt æg tidligere. Oplysningerne om billernes levetid blev tilvejebragt gennem individuel mærkning af imagines. Flere detaljer om metodikken findes hos Jørum (1976 b).

Imagoaktiviteten strakte sig fra april eller maj til sidst i september; kun ganske få biller var endnu aktive i oktober eller november.

Undersøgelsen viste, at *P. melanarius* og *P. niger* i Hestehave havde en anden livscyklus end den hidtil antagne, idet i al fald hunnerne af begge arter var to år om at udvikle sig fra æg til kønsmodne biller. Nyklækkede imagines fremkom i slutningen af juli eller i begyndelsen af august. Hunnerne af denne generation overvintrede som umodne og lagde først æg den følgende sæson, hovedsagelig i juni og juli. Nogle hunner lagde æg flere sæsoner.

Årsagen til det toårige udviklingsforløb i Hestehave formodes at være de kølige forår i både 1969 og 1970, som ved at forlænge varigheden af 3. larvestadium kan have forsinket fremkomsten af den nye imagogeneration, således at den for arterne normale efterårsforplantning ikke kunne gennemføres.

Aktivitetstætheden i eftersommeren 1970 var hos begge arter mindre end på samme tid i 1969 som følge af en nedgang i populationstæthed. Denne nedgang var utvivlsomt en følge af den tørre sommer i 1969.

Aktivitetstætheden hos hunnerne var gennemgående større end hos hannerne. Hos *P. niger* kan årsagen hertil have ligget i indsamlingsmetoden, men hos *P. melanarius* var forklaringen først og fremmest, at hunnernes populationstæthed var langt større end hannernes.

Anmeldelse

Lohm, U. & T. Persson (eds), 1977. Soil organisms as components of ecosystems. Proc. 6th. Int. Coll. Soil Zool., Uppsala June 1976. Ecol. Bull. (Stockholm) 25. 614 pp. Pris 140 sv. kr.

Det sjette i rækken af kollokvier arrangeret af jordbundszoologikomitéen under International Society of Soil Science (I.S.S.S.) blev afholdt i juni 1976 i Uppsala. Nærværende bog indeholder de arbejder, der blev præsenteret under dette veltilrettelagte møde i form af foredrag (53 afhandlinger) eller små udstillinger, »posters« (41 afhandlinger).

Disse kollokvier har udviklet sig til i nok så høj grad at være jordbundsøkologiske som i egentlig forstand jordbunds*zoologiske* – på trods af navnet. Foruden arbejder, der beskæftiger sig med jordbundsdyrenes økologi, udgør afhandlinger, der overvejende omhandler jordbundens mikroflora eller de højere planters rødder ofte vigtige indslag i kollokvierne. Blandt de zoologiske afhandlinger, der trods alt er i overtal i nærværende bind, dominerer undersøgelser vedrørende regnorme sammen med arbejder, hvor en eller flere arthropodgrupper er studieobjektet. For den økologisk interesserede entomolog vil mange afhandlinger derfor være værd at stifte bekendtskab med.

Sessionernes emner reflekterer nogle af de problemkredse, der i disse år i særlig grad har økologernes opmærksomhed. I den afdeling, der beskæftiger sig med organismesamfundenes struktur, er det værd at fremhæve J. Andersons diskussion af dyresamfundenes opbygning i jordbundssystemet belyst ved hjælp af oribatiderne; Parkinson, Visser og Whittakers påvisning af, at en collembolart ved selektiv ædeaktivitet kan forskyde konkurrenceforholdet mellem to svampearter, samt MacLean, Douce, Morgan og Skeels beskrivelse af enchytræers, collembolers og miders samfundsstruktur i relation til mikrohabitater i Alaskas tundra.

I en session, der behandler jordbundsorganismernes rolle i økosystemernes mineralkredsløb kan nævnes van der Drift og Jansens laboratorieeksperimenter, der demonstrerer, at collemboler ved deres konsumption af mikrosvampe kan stimulere disses vækst og iltoptagelse og dermed indirekte accellerere nedbrydningsprocessen. Ausmus og Swift diskuterer i to interessante indlæg arthropoders og anneliders betydning for mineralomsætningen i forbindelse med nedbrydningen af døde træstammer og grene. Relationerne mellem planterødder og jordbundens dyreliv er emne for en række afhandlinger. Heriblandt finder entomologer nok størst interesse i Schauermanns arbejde om rhizophage insekters produktionsbiologi og Curry og Ganleys analyse af mikroarthropodsamfundenes relation til bestemte plantearter i en permanent engvegetation.

Også under temaet »Modeller for jordbundsorganismer og deres miljø« og blandt de mange korte artikler, der under kollokviet blev præsenteret som »posters«, er mange bidrag entomologisk relevante. I det hele taget udgør denne kollokvieberetning en værdifuld og allerede hyppigt citeret kilde til den nyeste forskning indenfor jordbundsorganismernes økologi, som kan anbefales også for den økologisk interesserede entomolog.

Henning Petersen