

Annual activity and life cycles of carabid beetles in two forest communities

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The annual activity and life cycles of thirteen species of carabid beetles coexisting in two forests in Belgium were studied by recording above-ground activity of adult and larval populations, and by examining the reproductive condition of adults in the course of the year. The cycles were far more complex and diversified than suggested by previous works. Besides typical “spring breeders” and “autumn breeders”, species were found

- with a continuous reproductive period from spring to autumn,
- with several variable breeding periods, part of the population overwintering as adults, part as larvae,
- with a breeding period that begins facultatively in autumn and continues the next spring,
- with a winter reproduction.

Comparison of life cycles in Scandinavia and in Belgium also shows their variability in relation to climate. More flexible and varied cycles are made possible by the milder winters further south. Existing classifications of life cycles of carabids appear unable to account for such a diversity and variability.

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1. Introduction

The annual activity and life cycles of carabid beetles have been studied in several general works, such as those of Larsson (1939), Lindroth (1945), van der Drift (1951, 1959), Scherney (1955), Geiler (1956/57, 1960), Grüm (1959), Kabacik (1962), Lauterbach (1964), Greenslade (1965), Schjøtz-Christensen (1965), Murdoch (1967). Following Larsson (1939) and Lindroth's (1945, 1949) classification, two major types of life cycles were recognized:

- “spring breeders” (or “adult hibernators”), which reproduce in spring or early summer; the larvae develop in summer to give a new adult generation in autumn; they overwinter as adults;
- “autumn breeders” (or “larval hibernators”), which

reproduce in summer or autumn and overwinter as larvae.

A series of works devoted to the regulation of cycles by external factors led Thiele (1977) and Paarmann (1979) to develop and supplement this classification. Nevertheless, the two major types of cycles remained the same, and perhaps the main change was the formal recognition of species with flexible breeding periods and of those requiring more than one year to develop.

Very few attempts, however, have been made to thoroughly describe the whole range of cycles present in a carabid community, and general works have often inferred life cycles from data on activity, since, as a rule, reproduction coincides with the period of maximum activity in these univoltine beetles. The actual variety of cycles may thereby be hidden. In view of this problem,

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the present paper will investigate the annual activity and life cycles of all main species coexisting in two forest communities, as part of a more extensive study of the niches of forest carabid beetles (Loreau 1984b, 1984c). Data from pitfall trapping over a four-year period (1978–1981) were complemented by gonad examination of the adults in order to follow their reproductive condition throughout their period of activity.

2. Methods

The work was carried out in a beech forest and a pine-wood on acid soil in Lembeek (Belgium). The description of these biotopes and of their carabid communities can be found in Loreau (1984a).

The activity of adult and – whenever possible – larval populations was studied using permanent pitfall traps. Each “trap” was composed of two 250 ml pots sunk into the soil at the ends of a plastic plate 120 cm long and 25 cm high. This plate served as an intercepting wall, directing the moving beetles towards the terminal pots, thus increasing trapping efficiency. The pots contained about 100–150 ml of a water solution of picric acid at saturation, of formalin at 4%, and of detergent at 0.1%, which ensured a rapid death of the animals and their later preservation. Small square plates held a few centimeters above prevented rain and dead leaves from falling inside.

Five such traps were in use continuously in each biotope during the four years from 1978 to 1981. They were emptied every month in winter, and every two weeks during the rest of the year. In order to obtain a measure independent of the varying trapping intervals and of the varying number of traps having actually functioned (traps were sometimes disturbed by small mammals, for instance), activity is expressed as the number of individuals caught per 100 traps per day.

The activity graphs describe the mean activity over the four years 1978–81. As trapping periods were not the same from one year to another, annual data were first transformed to give standardized cycles including 24 equal periods in a year, about 15 days long. For this purpose, activity was assumed to be identical for all the days inside a given trapping period; the activity during each new period was recalculated as the mean of the activity values associated to the 15 days it includes. The mean activity cycle over four years was then obtained by taking the mean of the four standardized cycles.

The reproductive condition of the beetles was determined by dissecting the individuals caught in pitfall traps, and examining their gonads. Generally, three phases are distinguished in the maturation of female genital organs:

- a pre-reproductive phase, when the ovaries are not yet developed (immature individuals);
- a reproductive phase, when the developed ovaries contain ripe oocytes (mature individuals);

- a post-reproductive phase, when the ovaries regress and contain corpora lutea (spent individuals).

The same three phases can be distinguished in males, from the condition of the accessory glands of the testicles (Cornic 1973):

- before reproduction, these glands are small and translucent;
- during reproduction, they swell and take on a nacreous colour;
- after reproduction, they become greyish and disintegrate.

A more precise identification of development stages may be obtained from gonad examination (see e.g. Houston 1981), but this was not attempted because of the poor preservation of the beetles. In fact, few individuals were found to be spent. This low proportion reflects an actual decrease in activity after breeding, but in some species it may have been partly due to the difficulty of discerning corpora lutea in animals fixed with picric acid, being entirely impregnated with a yellow colour. Consequently, a confusion may arise between pre- and post-reproductive phases, and the beetles dissected were generally distributed into two classes only, according to whether they were mature or not. Also, the emergence of a new adult generation can be established from the presence of callows, which have soft teguments.

3. Results

Results are given for the thirteen main species in the beech forest, six of which were also the main species in the poorer pine-wood community. Other species were too scarce to provide enough data. Species are presented in decreasing order of dominance in the beech forest community.

1. *Abax ater* Villers

Adult *A. ater* were active from march or April to October or November, depending on the year (Fig. 1). A slight activity was maintained even in winter when temperatures did not drop too low. The period of maximum activity was very long, generally from May to August. Within this period, the precise number of activity peaks was variable (between one and three), and thus did not conform to Löser's (1972) conclusion that the cycles of *A. ater* range from a two-peak cycle in warmer biotopes or years to a single-peak cycle in colder biotopes or years.

The seasonal changes in sex ratio – which are generally considered a species characteristic – were also variable. In the pine-wood, the sex ratio was in favour of males almost throughout the cycle in 1978 and 1981 (so that males were significantly more abundant than females in the yearly catches of 1978 ($\chi^2 = 6.76$, 1 d.f., $P < 0.01$) and of 1981 ($\chi^2 = 16.07$, $P < 0.001$)), in favour of females in 1979 ($\chi^2 = 15.21$, $P < 0.001$), and close to 1:1 in 1980 ($\chi^2 = 0.04$, $0.8 < P < 0.9$). These differences compensated for each other over the four years ($\chi^2 = 1.06$, $0.3 < P < 0.4$). In the beech forest, males always predominated in spring (combined data from the four years: $\chi^2 = 26.07$, $P < 0.001$), but the later changes were not constant.

Although *A. ater* was first considered an autumn breeder by Larsson (1939) and Lindroth (1945), van der Drift (1951, 1959), Murdoch (1967) and Löser (1972) showed that in reality

A. ater reproduces from spring to autumn, and comprises larval as well as adult overwintering individuals. This is fully confirmed by the results in Lembeek. The breeding period extended over the whole period of maximum activity and even further, from April or May to September or October (Fig. 2). The presence of callows in spring and autumn shows that new adults emerged during both these periods. Larvae (Fig. 3) were active throughout the year, except during the coldest months of January and February: the first stage in summer and early autumn; the second stage from the second half of summer to late autumn and, to a lesser degree, in spring; the third stage in autumn and in spring. This succession shows that larval development started in summer and continued until the beginning of the following summer, the new adults appearing from autumn onwards.

A. ater is one of the few species whose reproduction cycle is not fixed by any kind of obligatory dormancy, as Löser (1972) showed experimentally. This peculiarity explains the plasticity of its cycle and the unusual expansion of its period of activity.

2. *Pterostichus oblongopunctatus* Fabricius

The main period of activity of this species extended from March to July, with two constant peaks in April and June (Fig. 4); this period was that of breeding (Fig. 5). After a pronounced decline in summer, during which a few larvae are caught, the activity increased again between August and November with the emergence of a new adult generation. Thus, *P. oblongopunctatus* is a typical spring breeder, in agreement with previous works (Larsson 1939, van der Drift 1951, Paarmann 1966, Penney 1967). A callow caught in April 1981 may have originated from a larva that did not pupate in time and hibernated.

The activity cycle corresponds in its outlines to that described by several authors, though Lindroth (1945) did not mention a summer inactivity, and others recorded only a single peak in spring (Larsson 1939, van der Drift 1951, Paarmann 1966). The double peak only appears in Penney's (1967) results. Yet it was rather typical in the beech forest of Lembeek, and resulted from the activity of males and females being out of step. The former predominated during the first part of the spring activity period (departure of the sex ratio from 1:1 until mid-May, with the combined data from the four years: $\chi^2 = 12.90$, $P < 0.001$), whereas the latter predominated during the second period (departure from 1:1 in June-July: $\chi^2 = 18.85$, $P < 0.001$). Male precocity was also noted by van der Drift (1951).

3. *Cychrus attenuatus* Fabricius

The yearly cycle of this species has not previously been described. Activity started in May-June, but only reached a clear-cut peak in September (Fig. 6). After a decline in October it rose again in November, and eventually disappeared in December. Reproduction took place from August to early November (Fig. 7). All individuals caught earlier were immature, whereas all individuals caught later were spent. A few larvae were caught in winter. *C. attenuatus* is a typical autumn breeder.

As in *Pterostichus oblongopunctatus*, the activity of the two sexes were not synchronized. Whereas males were responsible for the main peak in September, females reached their maximum activity later, and so there was a significant change in sex ratio between May-September and October-December (combined data from the four years: $\chi^2 = 34.37$, 1 d.f., $P < 0.001$). Females also remained mature a month later than did males.

4. *Carabus problematicus* Herbst

In the beech forest (Fig. 8B), a first period of activity in April-June was always followed by a phase of inactivity, generally in

June. Activity started again around July and reached a maximum throughout September, to fade away in November. In the beech forest, females were almost constantly more active than males (over the four-year period, $\chi^2 = 11.13$, $P < 0.01$), but in the pinewood they were so only in 1979 ($\chi^2 = 13$, $P < 0.01$ vs $0.3 < P < 0.5$ during the other years).

As shown by gonad examination (Fig. 9), the first period of activity in spring was due to old adults having overwintered; the new adult generation emerged in July and bred during the main period of activity. A slight larval activity was then recorded from late October to late May. *C. problematicus* is also an autumn breeder, but with part of the population hibernating as adults and probably reproducing once again during the next summer. The same life cycle was found in the Netherlands (van der Drift 1951, 1959, Rijnsdorp 1980) and in England (Green-slade 1965).

However, van der Drift (1951, 1959) mentioned an aestivation period in August, which was hardly apparent in the beech forest. In the pinewood (Fig. 8P), it was entirely lacking, and the autumn activity peak regularly occurred nearly a month earlier, in August. This shift in activity peak is probably explained by the fact that the pinewood is more favourable for adult life, and the beech forest more favourable for egg-laying and larval development. The relative proportions of adult and larval activity are significantly different in the two biotopes ($\chi^2 = 11.27$, 1 d.f., $P < 0.01$).

The lifecycle of *C. problematicus* can vary to a large extent; Larsson (1939) and Lindroth (1945) placed the species among spring breeders in Scandinavia, and Houston (1981) showed a biennial life cycle under subarctic conditions in northern Great Britain.

5. *Leistus rufomarginatus* Duftschmid

Few references are to be found in the literature concerning *L. rufomarginatus*. Yet this species is of particular interest because of its unusual cycle. In Scandinavia, it was classed as an autumn breeder, with a maximum activity in July (Lindroth 1945) or in August-September (Larsson 1939). In Lembeek, it exhibited a quite different cycle. There were two completely separate periods of activity, one in summer and the other in winter, their relative importance being different in the two forests (Fig. 10). Figure 11 shows that the first period corresponded to the emergence of a new adult generation. This then entered a long dormancy, and bred during the second period from November to January. Spent individuals were found in January and February. Larvae occurred during winter and spring (Fig. 12), the first stage from December to April, the second from February to May, the third - which is very active on the surface of the soil - from March to May.

All this establishes that *L. rufomarginatus* is neither a spring breeder nor really an autumn breeder, but rather a winter (or late autumn) breeder, which is distinguished by the lack of a specific hibernation pattern since no break occurs in the cycle in winter, when both adults and larvae are active. The single period of activity recorded in Scandinavia is most likely due, on the one hand to the breeding period being brought forward because of the cold winter, and on the other hand to the use of normal collection material by Larsson (1939) and Lindroth (1945), which may give misleading results since beetles can be collected by hand under stones during their aestivation.

There was a striking change in sex ratio in the beech forest, where females predominated in summer (with the combined data from the four years, $\chi^2 = 9.8$, $P < 0.01$), and males in winter (though not significantly so: $\chi^2 = 2.61$, $0.1 < P < 0.2$). This pattern was not found in the pinewood.

6. *Nebria brevicollis* Fabricius

N. brevicollis had a cycle very similar to that of *L. rufomarginatus* but earlier in time, so that it can be classed among autumn breeders. The first period of activity from April to July

again coincided with the appearance of a new adult generation, which, after a period of dormancy, reproduced during the second period of activity in autumn (Figs 13 and 14). Larvae developed in winter; the third stage was caught from December to April (Fig. 15).

This cycle corresponds to that described by several British authors (Williams 1959, Greenslade 1965, Penney 1966). But here again, summer dormancy was not recorded by Larsson (1939) and Lindroth (1945), who found a single activity peak in summer.

7. *Abax parallelus* Duftschmid

The life cycle of *A. parallelus* was particularly complex. There were two distinct periods of activity (Fig. 16), but the apparent continuity of the April-August period results from the combination of data from four years. In reality, there seemed to be two periods of activity in spring, one in April-May, the other in June, which corresponded to the period of reproduction (Fig. 17), in agreement with Löser (1972). The callows emerging in autumn thus constituted the resulting new generation. But an immature female was found in July 1981 and a male ready to reproduce in October 1978. Thus, part of the population might breed in autumn and overwinter as larvae. Again, captures in 1979 did not accord with this scheme, since mature individuals were present in May-June, then again in August. The low number of individuals caught does not allow a reliable conclusion to be drawn from these results, but they would indicate that the Lembeek populations of *A. parallelus* exhibit a variable or complex life-cycle. They thus differ from those of van der Drift (1951), Lauterbach (1964) and Löser (1972), who all considered *A. parallelus* a simple spring breeder.

Males were always markedly predominant in the catches (over the four-year period, $\chi^2 = 8.89$, $P < 0.01$).

8. *Trichotichnus laevicollis* Duftschmid

T. laevicollis was active from April to August (Fig. 18). Reproduction took place during the period of maximum activity, in June-July (Fig. 19). The individuals caught earlier were immature, and those caught later seemed to be spent. This cycle appears to be that of an early "autumn breeder" or, more exactly, of a species hibernating as larvae. But further studies would be necessary to verify this hypothesis; no other work has so far dealt with this species.

9. *Asaphidion flavipes* Linné

A. flavipes is a typical spring breeder. Reproduction occurred during the main period of activity in spring; the individuals caught in autumn and winter were immature (Figs 20 and 21). A few first- and second-stage larvae were present in traps in June-July. The cycle concurs with that described by Geiler (1956/57); the activity peak took place a month earlier than in Scandinavia (Larsson 1939, Lindroth 1945).

10. *Carabus purpurascens* Fabricius

In agreement with the findings of van der Drift (1959), *C. purpurascens* was active in summer, with a maximum in August (Fig. 22). Reproduction occurred at this time (Fig. 23). A callow was found just before, and suggests that adults emerging after metamorphosis mature quickly. Thus, *C. purpurascens* appears to be an "autumn breeder". But as a third-stage larva was caught in late August 1980, the cycle may be more complex.

11. *Notiophilus biguttatus* Fabricius

The main period of activity of this species covered the spring, although it sometimes began as early as February and did not end until July (Fig. 24). The maximum, generally in May, occurred a month earlier than in Scandinavia (Larsson 1939, Lindroth 1945). Surprisingly, in two of the years (1978, 1979) a second important period of activity took place in autumn, from September to November, whereas it was lacking in the other two (1980, 1981). Females had a higher activity than males in spring (with the combined data from the four years, $\chi^2 = 7.05$, $P < 0.01$), whereas males predominated in autumn (though not significantly so: $\chi^2 = 1.67$, $0.1 < P < 0.2$). Larvae were numerous in traps from May to July, the three stages often occurring at the same time (Fig. 26).

At first sight, the cycle of *N. biguttatus* is typical of a spring breeder with a facultative autumn activity. Such was the conclusion of almost all authors (Larsson 1939, Lindroth 1945, Williams 1959, Greenslade 1965). Yet the examination of gonads brings a surprise (Fig. 25). After new adults had emerged in September, another breeding period followed immediately in October-November. Already van der Drift (1959) noticed that *Notiophilus* species bore ripe eggs throughout the year. It must be concluded that part of the population had two generations in the same year. The facultative nature of autumn activity and the sensitivity of the cycle to low winter temperatures (the cold winter 1978-79 inhibited all activity, but the milder winter 1979-80 stopped it only for a month) suggest that the annual breeding period in fact begins in autumn and continues the next spring, with a winter quiescence induced by low temperatures.

It is interesting to note that autumn activity occurred in 1978 and 1979 after abundant larval generations, and was followed by a subsequent high spring activity (in 1979 and 1980), whereas it was lacking in 1980 and 1981 after poor larval generations. Thus, the abundance or the rapidity of breeding of an adult generation might be related to the abundance of larvae and result from a regulating mechanism like that described by Murdoch (1966), i.e. under favourable conditions (e.g. abundant food) females lay more eggs and larvae develop better, so that the next adult generation is more abundant and able to take advantage of such conditions.

12. *Badister bipustulatus* Fabricius

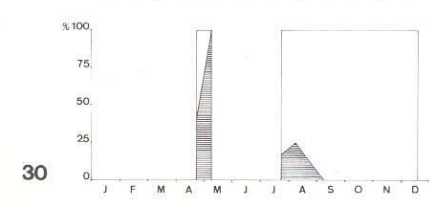
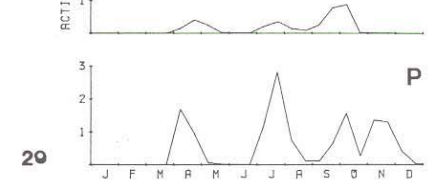
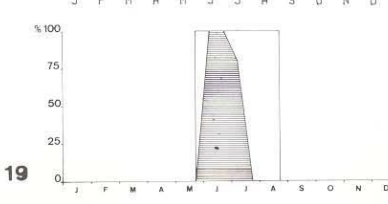
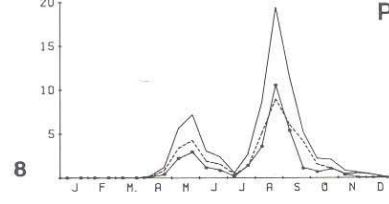
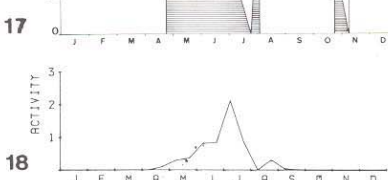
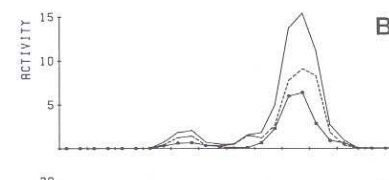
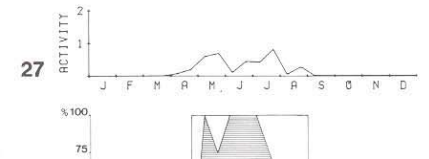
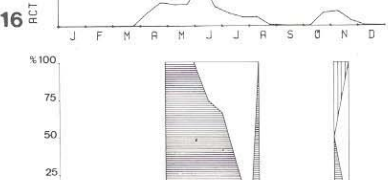
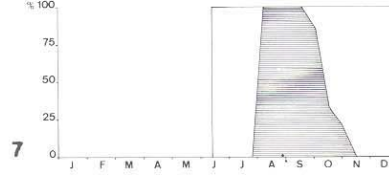
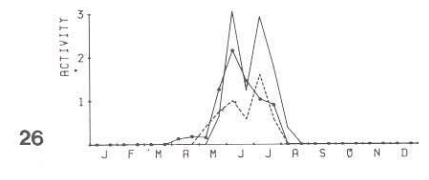
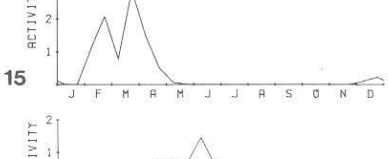
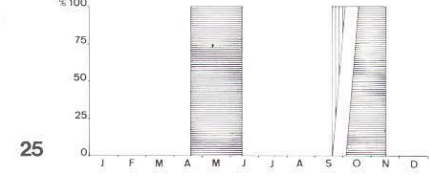
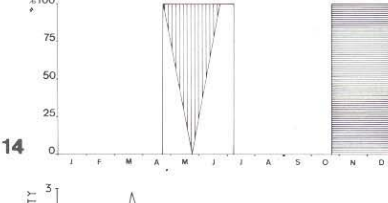
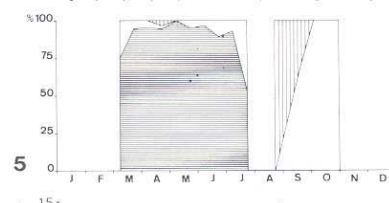
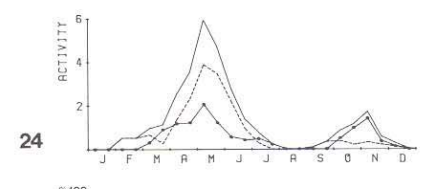
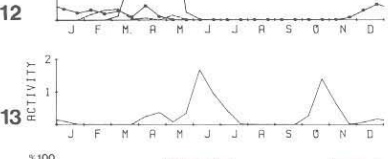
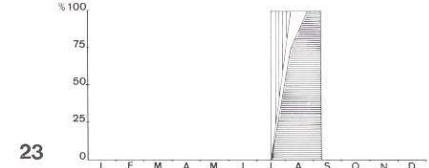
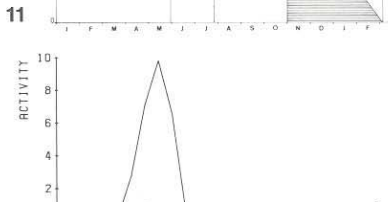
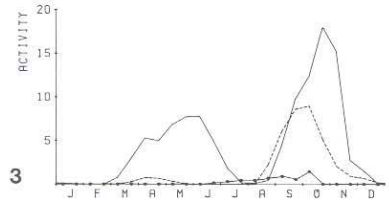
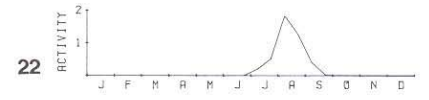
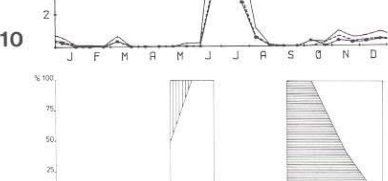
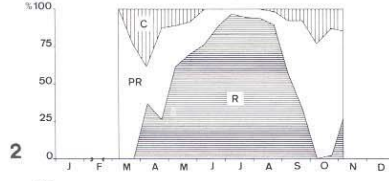
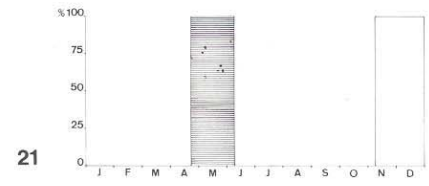
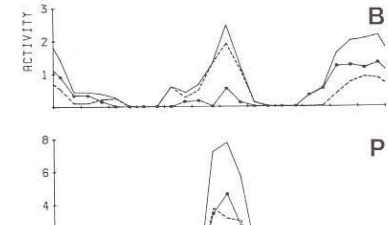
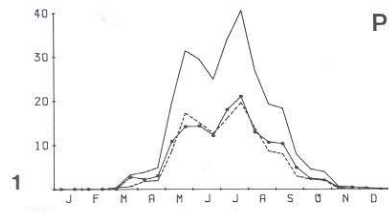
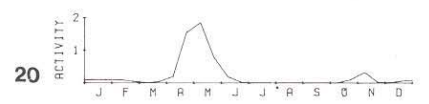
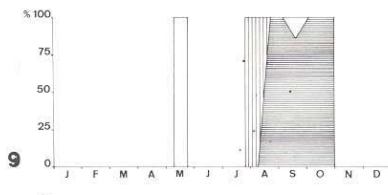
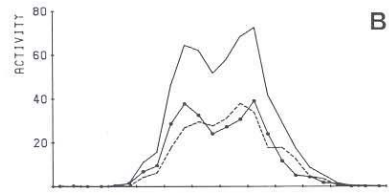
B. bipustulatus was active from April to August (Fig. 27) and bred from May to July (Fig. 28). According to Larsson (1939) and Lindroth (1945) it overwinters as adults.

13. *Lorocera pilicornis* Fabricius

In the pinewood (Fig. 29), *L. pilicornis* exhibited a succession of four activity peaks. In the beech forest, the last peak was absent and the second one much less apparent. The cycle of this species seems rather variable, since other authors reported cycles with a single peak, at different times of the year (Lindroth 1945, Geiler 1956/57, 1960, Greenslade 1965).

L. pilicornis was an exception from the normal pattern in that maximum activity was not associated with reproduction. Most individuals caught were immature (Fig. 30). Nevertheless, a first breeding period appeared to occur in April-May, and a second, less important one in July-August. There were obviously two groups in the population, the largest of which was made up of spring breeders, and the other of "autumn breeders". The species has previously been considered a spring breeder (Larsson 1939, Lindroth 1945, Greenslade 1965), though Larsson (1939) and Lindroth (1945) mentioned exceptional cases of overwintering larvae.

- Fig. 1. Annual activity cycles of adult *Abax ater* in the beech forest (B) and in the pinewood (P). Means for the four years 1978 to 1981. Dashed lines: females; solid lines with circles: males; solid lines without circles: sexes combined.
- Fig. 2. Seasonal changes in the reproductive condition of adult *Abax ater* in the beech forest: combined results from the years 1978 and 1981 (number of individuals examined, N = 856). Throughout the period of activity, the diagram shows the respective proportions of the individuals found to be in the reproductive phase (R: surfaces with horizontal lines); in the pre- or post-reproductive phase (PR: empty surfaces); callows (C: surfaces with vertical lines).
- Fig. 3. Annual activity cycles of the three larval stages of *Abax ater* in the beech forest. Means for the four years 1978 to 1981. Solid lines with circles: first stage; dashed lines: second stage; solid lines without circles: third stage.
- Fig. 4. Annual activity cycle of adult *Pterostichus oblongopunctatus* in the beech forest. Legend as in Fig. 1.
- Fig. 5. Seasonal changes in the reproductive condition of adult *Pterostichus oblongopunctatus* in the beech forest: combined results from the years 1978 and 1981 (N = 143). Legend as in Fig. 2.
- Fig. 6. Annual activity cycle of adult *Cychrus attenuatus* in the beech forest. Legend as in Fig. 1.
- Fig. 7. Seasonal changes in the reproductive condition of adult *Cychrus attenuatus* in the beech forest in the course of the year 1978 (N = 64). Legend as in Fig. 2.
- Fig. 8. Annual activity cycles of adult *Carabus problematicus* in the beech forest (B) and in the pinewood (P). Legend as in Fig. 1.
- Fig. 9. Seasonal changes in the reproductive condition of adult *Carabus problematicus* in the beech forest in the course of the year 1978 (N = 35). Legend as in Fig. 2.
- Fig. 10. Annual activity cycles of adult *Leistus rufomarginatus* in the beech forest (B) and in the pinewood (P). Legend as in Fig. 1.
- Fig. 11. Seasonal changes in the reproductive condition of adult *Leistus rufomarginatus*: combined results from the beech forest and the pinewood, and from the years 1978 and 1979 (N = 58). Legend as in Fig. 2.
- Fig. 12. Annual activity cycles of the three larval stages of *Leistus rufomarginatus* in the beech forest. Legend as in Fig. 3.
- Fig. 13. Annual activity cycle of adult *Nebria brevicollis* in the beech forest.
- Fig. 14. Seasonal changes in the reproductive condition of adult *Nebria brevicollis* in the beech forest: combined results from the four years 1978 to 1981 (N = 18). Legend as in Fig. 2.
- Fig. 15. Annual activity cycle of *Nebria brevicollis* larvae (third stage only) in the beech forest.
- Fig. 16. Annual activity cycle of adult *Abax parallelus* in the beech forest.
- Fig. 17. Seasonal changes in the reproductive condition of adult *Abax parallelus*: combined results from the beech forest and the pinewood, and from the four years 1978 to 1981 (N = 22). Legend as in Fig. 2.
- Fig. 18. Annual activity cycle of adult *Trichotichnus laevicollis* in the beech forest.
- Fig. 19. Seasonal changes in the reproductive condition of adult *Trichotichnus laevicollis*: combined results from the beech forest and the pinewood, and from the four years 1978 to 1981 (N = 21). Legend as in Fig. 2.
- Fig. 20. Annual activity cycle of adult *Asaphidion flavipes* in the beech forest.
- Fig. 21. Seasonal changes in the reproductive condition of adult *Asaphidion flavipes*: combined results from the beech forest and the pinewood, and from the four years 1978 to 1981 (N = 26). Legend as in Fig. 2.
- Fig. 22. Annual activity cycle of adult *Carabus purpurascens* in the beech forest.
- Fig. 23. Seasonal changes in the reproductive condition of adult *Carabus purpurascens* in the beech forest: combined results from the four years 1978 to 1981 (N = 12). Legend as in Fig. 2.
- Fig. 24. Annual activity cycle of adult *Notiophilus biguttatus* in the pinewood. Legend as in Fig. 1.
- Fig. 25. Seasonal changes in the reproductive condition of adult *Notiophilus biguttatus* in the course of the year 1978: combined results from the beech forest and the pine-wood (N = 22). Legend as in Fig. 2.
- Fig. 26. Annual activity cycles of the three larval stages of *Notiophilus biguttatus* in the pinewood. Legend as in Fig. 3.
- Fig. 27. Annual activity cycle of adult *Badister bipustulatus* in the beech forest.
- Fig. 28. Seasonal changes in the reproductive condition of adult *Badister bipustulatus* in the course of the year 1978: combined results from the beech forest and the pinewood (N = 16). Legend as in Fig. 2.
- Fig. 29. Annual activity cycles of adult *Lorocera pilicornis* in the beech forest (B) and in the pinewood (P).
- Fig. 30. Seasonal changes in the reproductive condition of adult *Lorocera pilicornis*: combined results from the beech forest and the pinewood, and from the four years 1978 to 1981 (N = 50). Legend as in Fig. 2.



4. Discussion

The life cycles of carabids within the two forest communities in Lembeek appear to be far more complex and diversified than suggested by previous works. Species that did not fit in with the classical division between "spring" and "autumn" breeders were not merely exceptions, but constituted a significant proportion of the species studied. One can classify *Pterostichus oblongopunctatus*, *Asaphidion flavipes*, and perhaps *Badister bipustulatus* as spring breeders; *Cychrus attenuatus*, *Carabus problematicus*, *Carabus purpurascens*, *Nebria brevicollis*, and perhaps *Trichotichnus laevicollis* as autumn breeders. Among these one could further distinguish some that only have one period of activity at the time of breeding, and others that have two periods of activity separated by a dormant period (Thiele 1977). The other species showed several different types of cycles:

- *Abax ater* reproduced continuously from spring to autumn, and overwintered both as larvae and adults;
- *Abax parallelus* and *Lorocera pilicornis* possessed several variable breeding periods, part of the population overwintering as adults, part as larvae;
- *Notiophilus biguttatus* started reproducing facultatively in autumn and continued the next spring; part of the population probably had two breeding generations in the same year;
- *Leistus rufomarginatus* was a winter breeder.

This diversity allows an important temporal niche differentiation between coexisting species (Loreau 1984b).

Although unexpected, the results presented here are unlikely to be exceptional. In a detailed study on a few carabid populations in Denmark, Schjøtz-Christensen (1965) found half of the species to possess two sections within the population with different breeding periods. The conclusion to be drawn from this is that the life cycles of most carabids are not yet thoroughly understood. Though Larsson (1939) and Lindroth's (1945) classical subdivision remains wholly valid for distinguishing the two main types of cycles, it is inadequate to account for all the diversity in life cycles of ground beetles. Thiele (1977) and Paarmann's (1979) new classification, based on types of dormancy, still seems incomplete; more investigations on the regulation of cycles by external factors would doubtless result in its enrichment or modification. It is true that species that do not strictly fit in with the categories "spring breeders" or "autumn breeders" could be classed among "species with unstable conditions of hibernation", but this category would then probably become meaningless because of its heterogeneity.

The present results also stress the variability of the cycle in several species, in particular along a latitudinal gradient. *Carabus problematicus*, for instance, seems to turn from a biennial autumn breeder in a subarctic climate into a spring breeder in Scandinavia, and again into an autumn breeder in the more southern countries. Early autumn breeders in Scandinavia such as *Nebria*

brevicollis and *Leistus rufomarginatus* become late autumn or even winter breeders in Belgium, reproduction being delayed by a long dormancy after metamorphosis. The spring breeding period of *Asaphidion flavipes* occurs a month earlier, and that of *Notiophilus biguttatus* may be brought forward so far that it starts before winter. Generally speaking, a spread of the periods of activity occurs in Belgium compared with Scandinavia; Greenslade (1965) has already pointed out that this spread occurs also in Great Britain. While the Nordic winter forces carabids to concentrate their activity towards summer and to conform to a rather strict life cycle pattern, the milder winter climate further south allows cycles to be more flexible and more evenly distributed throughout the year. Thus, it is evident that the clear-cut classical categories may not be adapted to describing variations in cycles. Further detailed studies on a larger number of species and on a wider geographical scale would provide important data for clarifying this issue, and for eventually drawing up a more suitable classification of life cycles of carabid beetles.

5. References

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