

THE REPRODUCTIVE CYCLE AND AGE COMPOSITION OF A POPULATION OF *PTEROSTICHUS OBLONGOPUNCTATUS* (FABRICIUS) IN THE NETHERLANDS (COLEOPTERA: CARABIDAE)

by

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With two plates and four text-figures

ABSTRACT

The reproduction of a Dutch population of *Pterostichus oblongopunctatus* (F.) is analysed. Seasonal variations in egg numbers, "corpora lutea" sizes, the relative positions of eggs in ovarioles and oviducts, and the conditions of the eggs were studied. Three age classes (corresponding with one-, two-, and three-year-old females) could be distinguished by measuring the sizes of the "corpora lutea". The duration of the reproduction and its course could be established. The survival value of a population consisting of more than one age class is discussed.

INTRODUCTION

Previous observations by Den Boer (1968) and Van Dijk (1973) provided information on the heterogeneity of the reproductive cycle which, in some species of carabid beetles, may be important to survival under adverse environmental conditions.

This heterogeneity, which presumably is partly genetically fixed, may contribute to spreading the risk of extinction of the population. Den Boer and Van Dijk observed that not only one-year-old females of *Calathus* species contributed to reproduction, but also two- and even three-year-old ones. These authors observed that in young females at the start of the development of the ovaries no "corpora lutea" (abbreviated c. l.) were present and that only after several weeks the first c.l. could be found. Their results suggest that it would be possible to discriminate between females of the old and the new generation in a field population by means of the c.l. in the ovaria.

The present work was started to investigate the validity of these facts also for *Pterostichus oblongopunctatus*, a carabid beetle common in woods in the Netherlands. The reproductive pattern has been studied by observation of the development of the ovaries and the maturation of the eggs. These features have been studied during a number of successive years in order to unravel the complex dynamics of the population concerned.

The area where the population of *P. oblongopunctatus* has been studied, occupies 2.4 hectares and was planted with oak (*Quercus robur*) about 90 years ago. The oaks are sparsely intermingled with birch (*Betula spec.*) and have formed a dense canopy over a well-developed shrub-stratum. Herbaceous growth is practically non-existent, but a thick layer of partly decomposed leaf-litter (5-10 cm) makes a good hiding place for a rich epedaphic fauna.

MATERIAL AND METHODS

Pterostichus oblongopunctatus (F.), a small bronze-black coloured beetle (9-12 mm) lives as an adult in the superficial layer of leaf-litter, preferably in broadleaved woods. The larvae usually develop in the deeper layers. Reproduction occurs in spring, the eggs are deposited in the litter.

Pitfall traps (Den Boer, 1968) were used for sampling: a plastic funnel (16 cm) fitted to a glass jar filled partially with 4% formaldehyde and dug into the soil, the rim of the funnel being flush with the soil surface. A cover (Ø 25 cm) is placed 5 cm above the funnel to prevent rain from penetrating into the trap and diluting the formaldehyde. Three units of five traps each were dug in. Once a week the jars were changed for fresh ones, and the specimens of *P. oblongopunctatus* selected from the contents of these jars.

Fresh ovaries proved to be preferable for this study to those preserved in formaldehyde, but the former were available only during 1972. The females were dissected carefully and the ovaries (Fig. 1) were taken out. The development of the ovary and the absence or presence of the corpora lutea are a criterion to the age of the female.

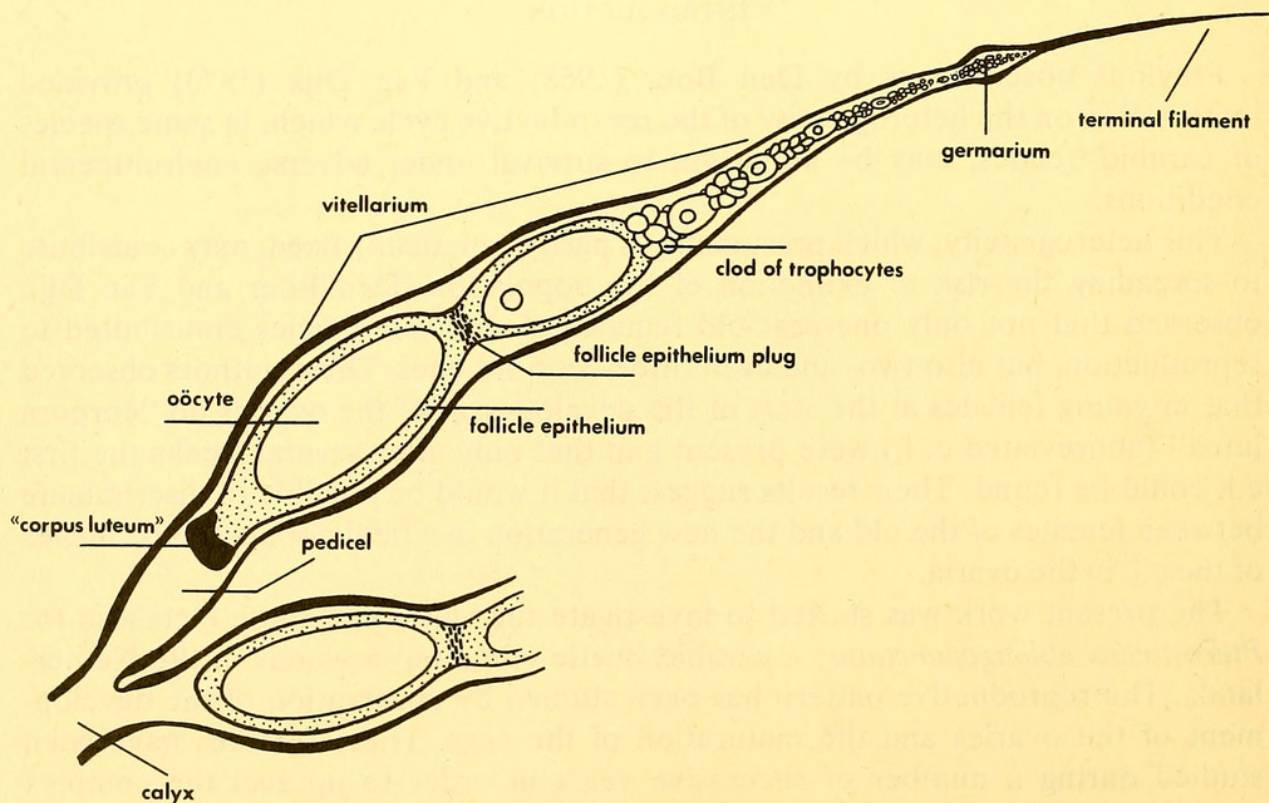


Fig. 1. Ovariole of *Pterostichus oblongopunctatus*, with indication of elements

RESULTS

In the Netherlands, this species has one generation annually. The newly hatched adults hibernate as virgins, and copulate in spring and summer. The new generation appears in autumn. Thus the activity pattern of the population shows two distinct periods in spring and in autumn (Fig. 2). The spring activity starts in

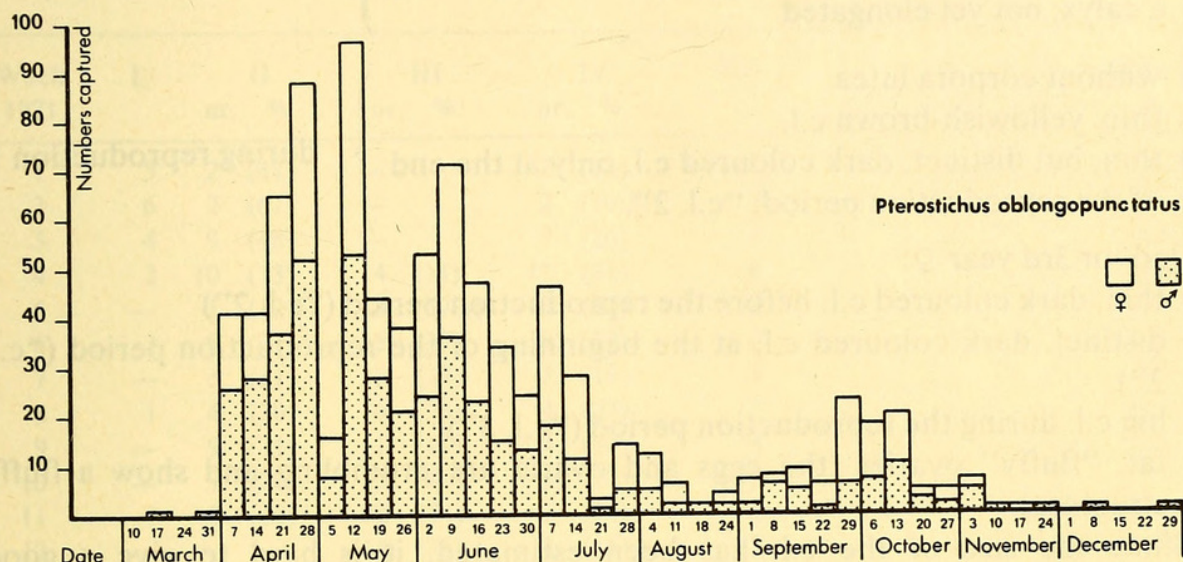


Fig. 2. The activity of *Pterostichus oblongopunctatus* in 1971

approximately the first week of April and is related to reproduction. The number of beetles caught gradually diminishes towards the end of the reproduction period, i.e. the beginning of August. The appearance in September of the new generation probably stands for the major part of the higher catches in autumn. "Spent" females (i.e. those that have oviposited) represent one-third of the specimens trapped, as their activity is low at this time. Until the end of May more males than females are caught (1971: 260 against 189). Presumably the former are more active in this period, in search for a partner. From about the end of May until the first weeks of August the females make up the majority (154 against 186).

The following categories of ♀ in the different stages of development were recognized (Pl. 2):

- Without eggs and without c.l.
- With eggs, without c.l.
- With eggs under the c.l.
- With eggs under and above the c.l.
- With eggs above the c.l.
- Without eggs, with c.l. ("spent").

In the females without c.l. in April, the eggs are still above the calyx, in the ovarioles: a few ♀ (Pl. 2, punctated yellow) have eggs in the calyx, but have c.l. not yet visible. Many ♀ with c.l. are bearing their eggs at this time already under the c.l. in the calyx. The females with c.l. but without eggs may have finished oviposition at this moment ("spent"). The data suggest that at the start of the reproduction season females with c.l. (Pl. 2, gray) may start earlier to reproduce than females without c.l. (i.e. those belonging to the new generation).

According to Vlijm & Van Dijk (1967) it is possible to determine the age of the females by the development of the ovary and the absence or presence of corpora lutea, as follows:

First year ♀:

- | | | |
|--|---|---------------------|
| (1) an ovary in a state of early development | } | before reproduction |
| (2) a small, pointed ovary | | |
| (3) a calyx, not yet elongated | | |
| (4) without corpora lutea | } | during reproduction |
| (5) thin, yellowish-brown c.l. | | |
| (6) thin, but distinct, dark coloured c.l. only at the end of the reproduction period: "c.l. 2". | | |

2nd- or 3rd year ♀:

- (1) thin, dark coloured c.l. before the reproduction period ("c.l. 2")
- (2) distinct, dark coloured c.l. at the beginning of the reproduction period ("c.l. 2")
- (3) big c.l. during the reproduction period ("c.l. 3")
- (4) fat, "fluffy" ovaries (the eggs and ovaria are crumbling and show a fluffy structure).

Since the size of the c.l. has been estimated, it is hard to give a good classification. Especially in specimens with distinct c.l. in the middle of the reproduction period one may be uncertain of their age. In a later stage of research, however, one of us (Blokhuys) used an ocular-micrometer to measure the size of the c.l. Thus more accurate data could be obtained on the difference in size of the c.l. than by mere judgement of their dimension.

The data collected of every female captured in order to judge its stage in the reproduction (Table 1) are as follows:

- (1) the number of ♀ without c.l. or eggs (I)
- (2) the number of ♀ without c.l. with eggs (II)
- (3) the number of ♀ with c.l. and with eggs (III, IV, IVa)
- (4) the number of ♀ with c.l. without eggs ("spent") (V)
- (5) size and colour of the c.l.
- (6) the number of eggs in relation to their position in the ovary
- (7) the condition of eggs and ovaries.

Table 2 shows the relation between the number of eggs per female and the size of the c.l. If the size of the c.l. is a measure for the age of the female, it should be possible to find a relation between age and number of eggs. The number of ovarioles varies between 10-26. The average weekly number is about 15.4-20.0. Probably this number is too low, as counting is made difficult by the "fluffy" ovaries. Three females had few c.l. (resp. 3, 3 and 2) but many ovarioles (14, 18 and 20). In 5 females only one ovary had developed; in 2 females a double c.l. ring could be observed.

Development of the corpora lutea.

As Miss Van Haaften (in 1970) and Blokhuys (1971) obtained almost identical results, these can be summarized as follows:

Table 1. 1971: week 1—4: April; 5—8: May; 9—13: June; 14—17: July; 18—25: Aug.; 22—26: Sept.; 27—30: Oct.; 31—35: Nov.; 36—39: Dec. I, number of ♀ without c.l., without eggs; II, number of ♀ without c.l., with eggs; III, number of ♀ with small c.l. (c.l. 1) with eggs; IV, number of ♀ with distinct c.l. (c.l. 2) with eggs; IVa, number of ♀ with large c.l. (c.l. 3) with eggs; V, number of ♀ with c.l. 1, c.l. 2, c.l. 3 without eggs ("spent"). Between brackets: percentages I-II (without c.l.); III (c.l. 1); IV (c.l. 2); IVa-V (c.l. 3) of the total of animals caught

| Week 1971 | I | II nr. % | III nr. % | IV nr. % | IVa | c.l. 1 | V c.l. 2 | c.l. 3 | IVa + V % |
|--------------|----|-------------|--------------|-------------|-----|--------|-------------|--------|--------------|
| 1 | 5 | 2 (47) | — | 2 (13) | 1 | — | — | 5 | (40) |
| 2 | 6 | 2 (67) | — | 2 (16.5) | 2 | — | — | — | (16.5) |
| 3 | 4 | 9 (48) | — | 7 (26) | 5 | — | — | 2 | (26) |
| 4 | 2 | 10 (33) | 4 (11) | 11 (31) | 6 | — | — | 3 | (25) |
| 5 | — | 1 (12.5) | 3 (37.5) | 2 (25) | 2 | — | — | — | (25) |
| 6 | 3 | 8 (27) | 15 (37) | 8 (22) | 5 | — | 1 | 1 | (14) |
| 7 | — | 5 (31) | 6 (37) | 3 (19) | 2 | — | — | — | (13) |
| 8 | 1 | 4 (30) | 6 (35) | 4 (24) | 2 | — | — | — | (11) |
| 9 | — | 9 (31) | 11 (41) | 4 (14) | 4 | 1 | — | — | (14) |
| 10 | — | 7 (20) | 15 (46) | 6 (17) | 5 | 1 | — | 1 | (17) |
| 11 | 1 | 3 (16) | 12 (54) | 2 (14) | 4 | 1 | 1 | — | (16) |
| 12 | — | — | 14 (74) | 2 (16) | 2 | — | 1 | 1 | (10) |
| 13 | — | — | 6 (55) | 1 (18) | 2 | — | 1 | 1 | (27) |
| 14 | 3 | — (11) | 12 (43) | 4 (21) | 3 | — | 2 | 4 | (25) |
| 15 | 1 | — (6) | 9 (53) | 3 (18) | — | — | — | 4 | (23) |
| 16 | 1 | — (50) | — | 1 (50) | — | — | — | — | — |
| 17 | — | — | 1 (11) | 5 (56) | — | — | — | 3 | (34) |
| 18 | 1 | — (14) | — | 3 (43) | 1 | — | — | 2 | (43) |
| 19 | — | — | 1 (25) | — | — | — | — | 3 | (75) |
| 20 | — | — | — | — | 1 | — | — | — | (50) |
| 21 | 1 | — (50) | — | — | — | — | 1 | — | (50) |
| 22 | 2 | — (40) | — | — | — | — | — | 3 | (60) |
| 23 | 1 | — (50) | — | — | — | — | — | 1 | (50) |
| 24 | 3 | — (75) | — | — | — | — | 1 | — | (25) |
| 25 | 5 | — (100) | — | — | — | — | — | — | — |
| 26 | 13 | — (76) | — | — | — | 2 | — | 2 | (24) |
| 27 | 8 | — (73) | — | — | — | — | 1 | 2 | (27) |
| 28 | 7 | — (70) | — | — | — | 1 | 2 | — | (30) |
| 29 | 1 | — (33) | — | — | — | — | — | 2 | (77) |
| 30 | 1 | — (50) | — | — | — | 1 | — | — | (50) |
| 31 | 1 | — (50) | — | — | — | 1 | — | — | (50) |
| 32 | — | — | — | — | — | — | — | — | — |
| 33 | 1 | — (100) | — | — | — | — | — | — | — |
| 34 | — | — | — | — | — | — | — | — | — |
| 35 | — | — | — | — | — | — | — | — | — |
| 36 | — | — | — | — | — | — | — | — | — |
| 37 | — | — | — | — | — | — | — | — | — |
| 38 | — | — | — | — | — | — | — | — | — |
| 39 | 1 | — (100) | — | — | — | — | — | — | — |
| | 73 | 60 | 115 | 70 | 46 | 9 | 11 | 39 | |

Table 2. 1971. The relation between the number of eggs per ♀ and the size of the c.l.; II, no c.l.; III, small c.l. (c.l. 1); IV, distinct c.l. (c.l. 2); IVa, large c.l. (c.l. 3)

| Number of eggs per ♀ | II | III | IV | IVa |
|----------------------|-----|------|-----|-----|
| 1 | 1 | 2 | 8 | 2 |
| 2 | 1 | — | 17 | 10 |
| 3 | 1 | 1 | 13 | 10 |
| 4 | 3 | 6 | 7 | 4 |
| 5 | 3 | 2 | 6 | 3 |
| 6 | 6 | 11 | 5 | 3 |
| 7 | 5 | 10 | 2 | 1 |
| 8 | 8 | 15 | 1 | 5 |
| 9 | 9 | 16 | 3 | 2 |
| 10 | 3 | 9 | 2 | 1 |
| 11 | 6 | 5 | 1 | — |
| 12 | 6 | 4 | 1 | 1 |
| 13 | 6 | 7 | 1 | 2 |
| 14 | 1 | 9 | — | 1 |
| 15 | — | 4 | 1 | 1 |
| 16 | — | 7 | 1 | — |
| 17 | 1 | 2 | — | — |
| 18 | — | 2 | 1 | — |
| 19 | — | — | — | — |
| 20 | — | 2 | — | — |
| 21 | — | — | — | — |
| 22 | — | 1 | — | — |
| Number of ♀ | 60 | 115 | 70 | 46 |
| Number of eggs | 526 | 1153 | 326 | 243 |
| Mean number of eggs | 8.8 | 10.0 | 4.7 | 5.3 |

In the second week of April females without c.l. still constitute 44-67% of the total catch. Their numbers decrease gradually to zero — after July 14 the results are unreliable. Females with c.l. 1 are observed for the first time in the last week of April. Their share begins with 6—11% and rises to 74% in the third week of June. Later the numbers decline again, but apparently more gradually than is suggested by Table 1, for it has to be corrected by those females which have grown from c.l. 1 to c.l. 2. The resulting decline is probably caused by a decrease of activity. The number of females with c.l. 2 attain a maximum in April (30%). After April 28 their number decreases, because either their c.l. 2 may grow to c.l. 3 or by mortality of the supposed 2nd year individuals. The number of females with c.l. 3: this group is at the onset of the activity represented to 40%, but as April wears on their numbers decrease rapidly to 20%, in May even to 11%. After May 26 an increase takes place again, apparently as a consequence of c.l. 2 ♀ developing into c.l. 3 individuals as they continue to produce eggs. The initial decrease is, obviously, caused by the dying off of the supposed 3rd year generation (Pl. 2). It must be noted that the first females with eggs beneath the c.l. (April) are of the c.l. 3 group, hence, the oldest females apparently take the lead in reproduction, but within a few weeks they are already “spent” again and will probably die off soon,

Table 3. 1972. Size of the c.l. measured in μ

| From 30 March to 12 April | | From 31 May to 14 June | |
|---------------------------|----------|-------------------------|----------|
| Size | Number ♀ | Size | Number ♀ |
| — ¹⁾ | 19 | — | 2 |
| 82 μ | 2 | 23 μ | 1 |
| 85 μ | 2 | 31 μ | 3 |
| 108 μ | 2 | 42 μ | 1 |
| 112 μ | 1 | 45 μ | 2 |
| 123 μ | 1 | 46 μ | 4 |
| | | 49 μ | 1 |
| | | 77 μ | 2 |
| | | 88 μ | 1 |
| | | 92 μ | 2 |
| | | 97 μ | 1 |
| From 12 April to 26 April | | From 14 June to 28 June | |
| Size | Number ♀ | Size | Number ♀ |
| — | 80 | — | 2 |
| 31 μ | 1 | 29 μ | 1 |
| 49 μ | 1 | 31 μ | 1 |
| 54 μ | 3 | 40 μ | 1 |
| 62 μ | 2 | 46 μ | 1 |
| 120 μ | 1 | 49 μ | 1 |
| | | 50 μ | 1 |
| | | 54 μ | 1 |
| | | 55 μ | 1 |
| | | 57 μ | 1 |
| | | 62 μ | 10 |
| | | 69 μ | 3 |
| | | 72 μ | 1 |
| | | 77 μ | 7 |
| | | 108 μ | 1 |
| | | 123 μ | 2 |
| | | 131 μ | 1 |
| From 26 April to 10 May | | From 28 June to 12 July | |
| Size | Number ♀ | Size | Number ♀ |
| — | 9 | — | 0 |
| 28 μ | 1 | 46 μ | 1 |
| 31 μ | 3 | 69 μ | 1 |
| 54 μ | 1 | 77 μ | 4 |
| 62 μ | 2 | 123 μ | 1 |
| 69 μ | 1 | | |
| 77 μ | 1 | | |
| From 10 May to 31 May | | | |
| Size | Number ♀ | | |
| — | 11 | | |
| 31 μ | 2 | | |
| 38 μ | 1 | | |
| 42 μ | 1 | | |
| 58 μ | 1 | | |
| 62 μ | 2 | | |
| 69 μ | 1 | | |
| 92 μ | 3 | | |
| 108 μ | 1 | | |

¹⁾ — = without c.l.

according to their disappearance in May (Pl. 2). A postponed reproduction of the preceding year may be possible, so that 2nd year ♀ may die when they are two years old and only those ♀ which failed to reproduce the previous year would reach their 3rd year (Vlijm & Van Dijk, 1967, have supposed this to be the case in *Calathus melanocephalus*).

Measurements of corpora lutea.

The estimate of the size of the c.l. being not quite reliable, those of freshly

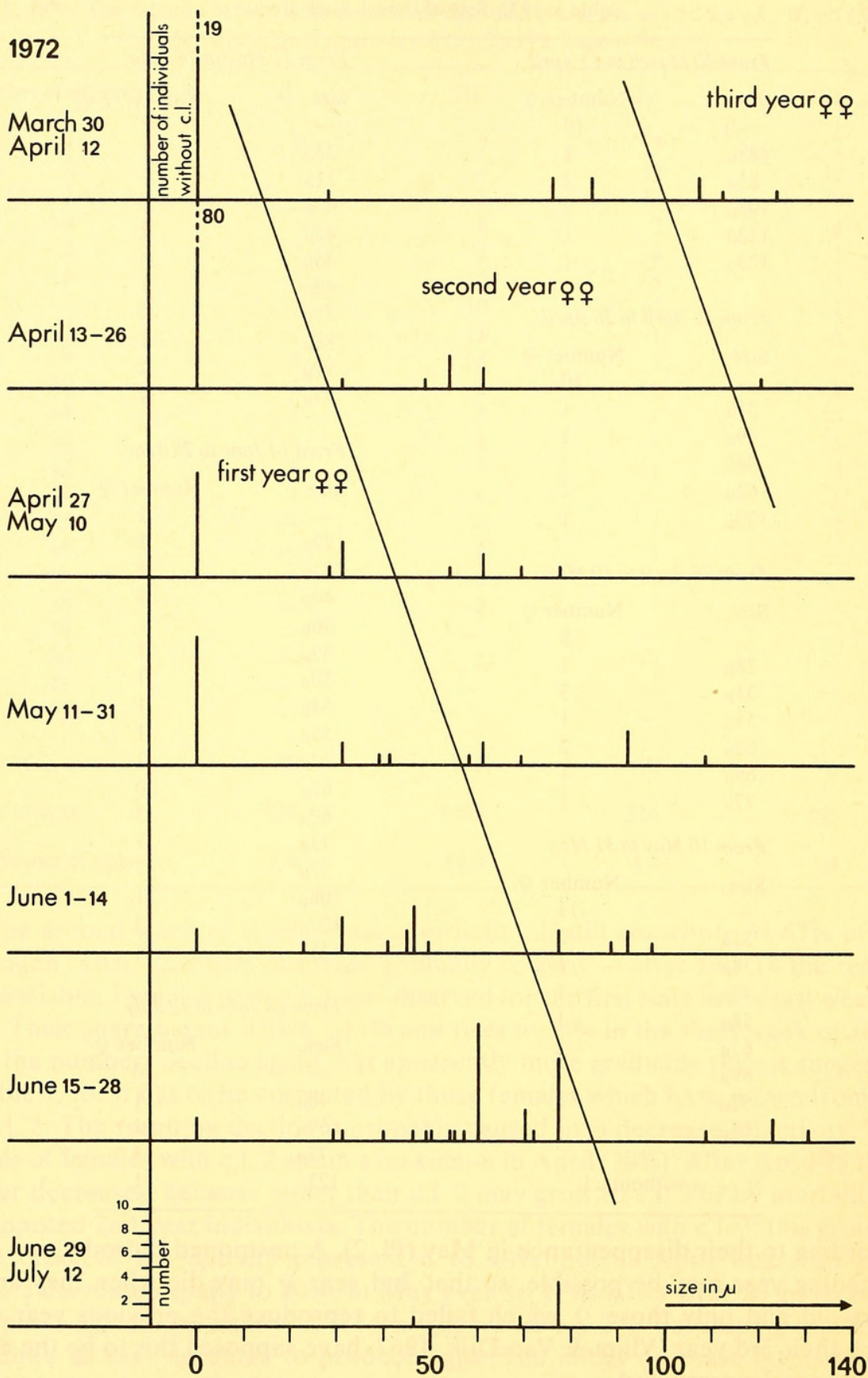


Fig. 3. Size of corpora lutea in 1972

caught ♀ were measured by Blokhuis in 1972 by means of an ocular micrometer at a magnification of $100\times$ (Table 3). In the first weeks of April 1972 only females with c.l. 3 ($108\text{--}124\mu$) or large c.l. 2 ($77\text{--}85\mu$) were present. One female with a c.l. of 28μ probably reproduced only a short time during the preceding year. In the second half of April only one ♀ with c.l. 3 was captured, but females with small c.l. 2 made their first appearance ($50\text{--}60\mu$). No females with c.l. 3 could be caught during the first part of May but the c.l. of the c.l. 2 females tend to be bigger ($55\text{--}80\mu$) and it is in this period that females with c.l. 1 have been collected for the first time. During the second part of May, in June and the first two weeks of July the c.l. 2 have reached the size which the c.l. 3 showed in April, and the c.l. 1 those of the c.l. 2. During 7 weeks (April 26–June 14) not a single female with c.l. 3 had been caught. Hence, we may conclude that females with c.l. 3 at the onset of the breeding season (first half of April) die after oviposition. The new 2nd year females take their place at the end of June. These data are a confirmation of the hypothesis that more generations are involved in reproduction (Fig. 3).

A check in 1973 on individuals of the 1971 generation which were marked as young females in 1972, showed a size of the c.l. corresponding with those of second year ♀ (cf. Fig. 4). Consequently the age of a female can be estimated approximately by these figures though a certain overlap exists. It is evident that at a certain moment of development, 1st year c.l. 2 and 2nd year c.l. 2 do not differ in

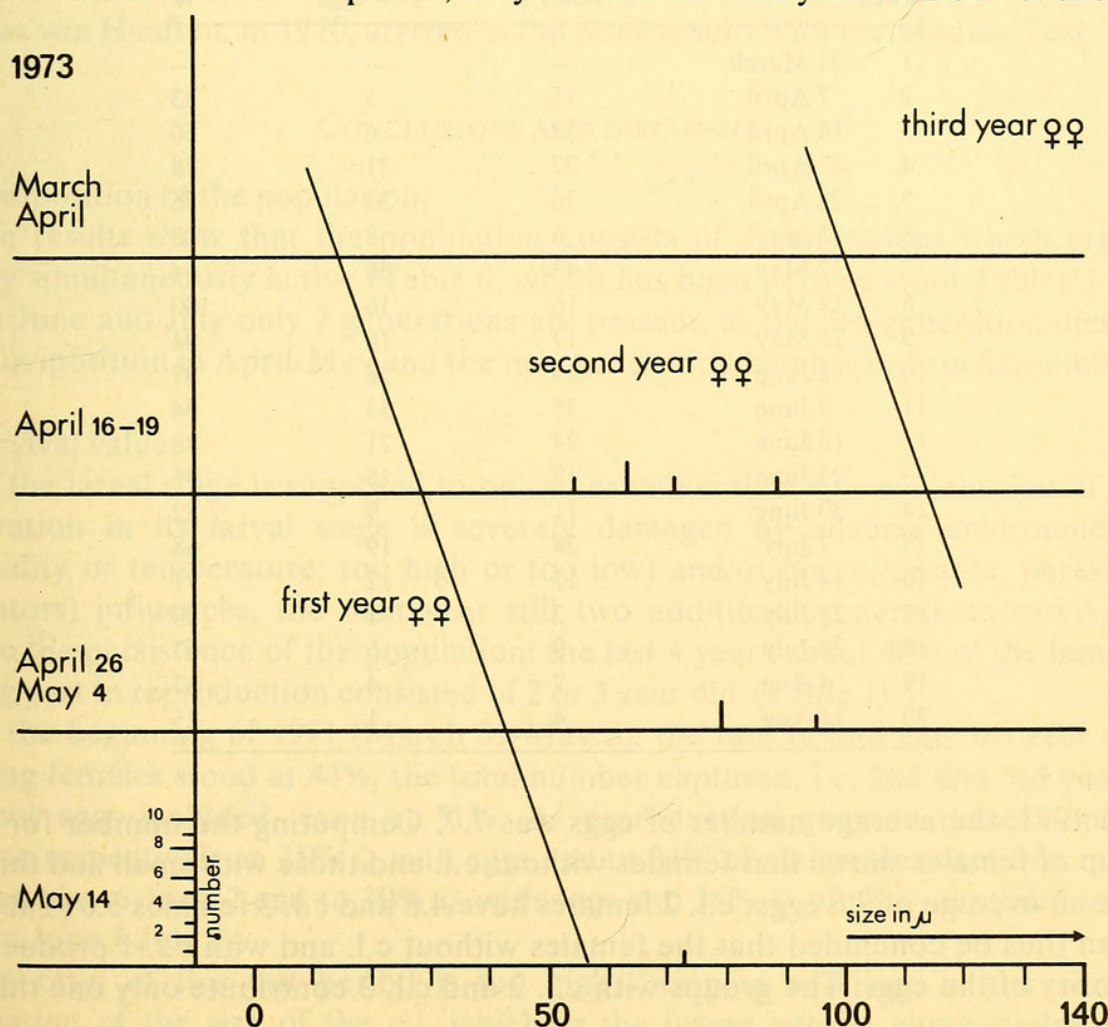


Fig. 4. Size of the corpora lutea of individuals marked in 1972, recaptured in 1973

size. A more accurate way to determine the ages of the ♀ taking part in reproduction is the marking-recapture method which we intend to use in the future.

A serious obstacle in the interpretation of "corpora lutea" (sizes as well as numbers) as indicators of age is the phenomenon of egg resorption (Joly, 1949, and others). The precise origin of the c.l. seems to be unknown.

Egg production.

When dissected, only 6 out of the 291 egg-bearing females appeared to have white, glossy, elastic eggs, one female had brown, hard, malformed eggs. The eggs of all the other females proved to be "fluffy" and soft and were coloured light yellow to orange. It is possible that this coloration is due to the preservation agent, i.c. formaldehyde.

In the first week of May all females are bearing eggs. This situation is reached within one month. Decrease to zero takes more time: it takes more than 3 months before the last egg has been deposited (Table 4).

Table 4. 1971. The number of egg bearing ♀. Week nr. 1: March 31-April 7. Week nr. 20: August 11-August 18

| Week | Total ♀ | ♀ + eggs | % |
|------------|---------|----------|-----|
| 1 31 March | — | — | — |
| 2 7 April | 15 | 5 | 33 |
| 3 14 April | 12 | 6 | 50 |
| 4 21 April | 27 | 21 | 78 |
| 5 28 April | 36 | 31 | 86 |
| 6 5 May | 8 | 8 | 100 |
| 7 12 May | 43 | 36 | 84 |
| 8 19 May | 16 | 16 | 100 |
| 9 26 May | 17 | 16 | 94 |
| 10 2 June | 29 | 28 | 97 |
| 11 9 June | 35 | 33 | 94 |
| 12 16 June | 24 | 21 | 88 |
| 13 23 June | 19 | 18 | 95 |
| 14 30 June | 11 | 9 | 82 |
| 15 7 July | 28 | 19 | 68 |
| 16 14 July | 17 | 12 | 71 |
| 17 21 July | 2 | 1 | 50 |
| 18 28 July | 9 | 6 | 67 |
| 19 4 Aug. | 7 | 4 | 57 |
| 20 11 Aug. | 4 | 1 | 25 |

In 1971, the average number of eggs was 7.7. Computing the number for each group of females shows that females without c.l. and those with small and thin c.l. have an average of 9.6 eggs; c.l. 2 females have 4.6 and c.l. 3 females 5.8 (Table 5). It can thus be concluded that the females without c.l. and with c.l. 1 produce the majority of the eggs. The groups with c.l. 2 and c.l. 3 contribute only one third of the total.

By means of Wilcoxon's Two Sample Test the zero-hypothesis of a similar egg-

Table 5. The average number of eggs in 1970 and 1971

| | 1970 | 1971 | Corrected average numbers (1971) |
|-------------------|------|------|--|
| Generation 1967 } | 5.5 | 5.8 | (6.3 for c.l. 3-group ♀ in April) |
| Generation 1968 } | | | |
| Generation 1969 | 4.3 | 4.6 | (4.7 for c.l. 2-group ♀ and c.l. 3-group ♀ without in April) |
| Generation 1970 | — | 9.6 | |

N.B. Generation 1968 corresponds with the c.l. 3 group in April 1971. Generation 1969 corresponds with the c.l. 2 group and the c.l. 3 group together, without the individuals with c.l. 3 caught in April. Between brackets the corrected averages of the number of eggs. After April the c.l. 3 group should be added to the c.l. 2 group because of the development of c.l. 2 to c.l. 3 in the course of the summer. The average of 5.5 has been computed by adding the number of eggs of the generations 1967 and 1968 which until that time could not yet be discerned. Only the c.l. 3 ♀ caught in April probably have an age of three years (or more).

production in two groups is tested against the alternative hypothesis of a different egg-production ($\alpha = 0.05$; $u = 1.96$). It can be concluded that group II and III do not differ significantly. This could be expected as these groups belong to the same generation: 1970-groups II and IV differ significantly ($u = 6.4$; $p < 0.0001$) as do groups II and IVa ($u = 4.76$), but groups IV and IVa do not differ significantly ($u = 1.22$).

Miss van Haaften, in 1970, arrived at the same results with the Median Test.

CONCLUSIONS AND DISCUSSION

Composition of the population.

The results show that the population consists of 3 generations which are all nearly simultaneously active (Table 6, which has been derived from Tables 1 and 5). In June and July only 2 generations are present, as the 3rd generation dies off after oviposition in April-May and the new generation hatches only in September.

Survival value.

As the larval stage is supposed to be rather vulnerable, it is evident that, if one generation in its larval stage is severely damaged by adverse environmental (humidity or temperature: too high or too low) and/or biotic (disease, parasites, predators) influences, the next year still two additional generations survive to assure the persistence of the population: the last 4 years about 40% of the females taking part in reproduction consisted of 2 or 3 year old (Table 7).

At the beginning of 1971 (March 31-May 5), the rate of 2nd and 3rd year egg-bearing females stood at 44%, the total number captured, i.e. 2nd and 3rd year ♀ without eggs included, even at 51%. As reproduction goes on these numbers decline respectively to 25% ♀ with eggs and to 24% of all females captured in the period May 6-June 2 and to 30% ♀ with eggs and 36% ♀ of all ♀ captured in the period June 3-July 7.

The ratio of this last period is too high owing to a failure in the correct estimation of the size of the c.l. which in the future can be eliminated by the micrometer method (cf. p. 9).

Table 6. Reproductive activity in 1971

| Date | Age | Reproductive activity | Generation |
|-----------|--------------------------------|------------------------------|------------|
| April | 1st year | without c.l., without eggs | 1970 |
| | 1st year | without c.l., with eggs | 1970 |
| | 1st year | with c.l. 1, with eggs | 1970 |
| | 2nd year | with c.l. 2, with eggs | 1969 |
| | 3rd year | with c.l. 3, with eggs | 1968 |
| | 3rd year | with c.l. 3, "spent" | 1968 |
| May | as April | but 3rd year ♀ disappear | |
| June | 1st year | with c.l. 1, with eggs | 1970 |
| | 1st year | spent with c.l. 1 and c.l. 2 | 1970 |
| | 2nd year | with c.l. 3 and eggs | 1969 |
| | 2nd year | spent with c.l. 3 | 1969 |
| July | 1st year | with c.l. 1, c.l. 2 and eggs | 1970 |
| | 1st year | spent with c.l. 2 | 1970 |
| | 2nd year | spent with c.l. 3 | 1969 |
| August | 1st year | with c.l. 2 and eggs | 1970 |
| | 1st year | spent with c.l. 2 | 1970 |
| | 2nd year | spent with c.l. 3 | 1969 |
| September | Hatching of the new generation | | 1971 |
| | 1st year | spent with c.l. 1 and c.l. 2 | 1970 |
| | 2nd year | spent with c.l. 3 | 1969 |
| October | New generation | | 1971 |
| | 1st year | spent with c.l. 1 | 1970 |
| | 2nd year | spent with c.l. 3 | 1969 |

The first year generation (1970) produced a large number of eggs (average 9.6). The second year generation (1969) had an average production of 4.7, the third year generation (1968) one of 6.3. According to Miss Van Haaften, the generations of 1969 and 1968 produced about the same average (4.3 and 5.5, respectively). Data of 1972 have already confirmed that the population increased with about 10%: the generation of 1970 may have had a big part in this increase.

Survival, however, is not dependent of meteorological factors only: predation, disease and the available amount of food will be important too, but reliable data are, thus far, lacking.

Comparison with other carabid beetles.

It is a special advantage that Van Dijk (l.c.) studied the age composition of *Calathus melanocephalus* (L.) which is, contrary to *P. oblongopunctatus*, a "winter

Table 7. Composition of the population in 1969, 1970 and 1971

| Year | Locality | % more than one year old | Method |
|------|----------|-----------------------------|---|
| 1969 | Baarn | 49% | by estimating the size of the c.l. (by De Bruyn) |
| 1970 | Baarn | 32% | by estimating the size of the c.l. (by Van Haaften) |
| 1971 | Baarn | 39% | by estimating the size of the c.l. (by Blokhuis) |
| 1969 | Wijster | 37% | capture-recapture (Van Dijk, personal communication) |

breeder" (i.e. the larvae develop during winter time). In the former species young adults hatch in spring and only mature in the course of July, while in *P. oblongopunctatus* the adults hatch in September, mature in the course of the autumn and start oviposition towards the end of April. In *P. oblongopunctatus*, egg-production by 1st year females as well as by 2nd and 3rd year females starts earlier in the season but finishes about July 21, whereas in *C. melanocephalus* it continues well into September. As a matter of fact, *P. oblongopunctatus* has a lead over *C. melanocephalus* as at a certain moment (end of April, beginning of May) three generations may reproduce simultaneously, contrary to *C. melanocephalus* where at best two generations do so.

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