

THE INDIVIDUAL BEHAVIOUR AND POPULATION DYNAMICS OF SOME CARABID BEETLES OF FORESTS

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ABSTRACT

The development is described of a long-term experiment on the influence on population numbers of the individual reactions of carabid beetles towards surface temperature and humidity under natural conditions. The beetles are individually marked and (re)captured separately every hour during the night with time-sorting pitfalls, whereas at each catch site temperature and humidity of the surface layer (in which the eggs are deposited) is measured and recorded automatically. The processing of the data can be done by computer.

The sizes of the sampled interaction groups of four carabid species from the forest are estimated from capture-recapture data with Jolly's model and compared with the numbers of unmarked (new) individuals caught. These two estimates of population size appear to show a close linear relationship for all four species together, the consequences of which are discussed. All species are night-active with a maximum one or two hours after sunset. *Pterostichus oblongopunctatus* prefers the higher situated places and does not react to local differences in temperature. *Agonum assimile* prefers the lower situated places and reacts positively towards small differences in surface temperature. Many adults of both species reproduce again in a second year and some of them even in a third one. Males of the former species survive better after the first breeding season than females, whereas the latter species does not show differential survival of the sexes. Adults of *Nebria brevicollis* do not usually survive more than one breeding season. Overwintered adults of *Calathus piceus* reproduce again in the next spring, whereas juveniles reproduce for the first time in late summer.

When we realized for the first time, that the dynamics of a population can only be understood via individual reactions and adventures, we planned a long-term field experiment in which both certain aspects of individual behaviour and the fluctuations of numbers in the population could be recorded automatically. We reflected that: if in a small and isolated habitat many individually marked carabid beetles are moving around and repeatedly caught, while at the catch sites some relevant environmental factors are frequently measured, it should not only be possible to follow the numerical changes of the population but also to decide whether, under these natural conditions, the individuals behave randomly or more or less selectively towards these factors.

When investigating the behaviour of the woodlouse *Porcellio scaber* (DEN BOER,

* This (and my other contributions to this volume) were typed by Mrs. G. H. Weijenberg-Boer.

1961) I had already discovered that studying preferences under field conditions may also give some insight into population numbers. I was moreover confronted with the question: What kind of choice situations are actually encountered by the animals in the field? This also means: How carefully should we study the field situation to be able to perform reliable (preference) experiments in the laboratory? Or the other way round: How could we translate the results of laboratory experiments (not only preference experiments) into individual chances of survival and reproduction in the field? In many cases it can hardly be expected that under field conditions there can actually be a choice, e.g. a ground-beetle can take an encountered prey or leave it; but if it has abandoned that prey, what will it meet afterwards? However, also concerning physical factors it is not clear in advance, what the choices are in the field and in what frequencies they occur. At the scale of the sizes of individuals we hardly know anything about spatial distribution and temporal variation of physical factors.

Hence, with the above long-term experiment we planned to find out what the real choice situations in the field were, how carabid beetles react to it, and how this works out dynamically in the population. Concerning the latter point it is specially important to find out what the predictive value is of the established individual reactions, e.g. if eggs are laid at moist places will then these places generally stay moist enough (but not be inundated) during larval development? Ten years ago we started step by step to realize such an experiment in a small and rather isolated deciduous forest close to the Biological Station.

At that time we not only had to start a biological experiment but at the same time we had to solve a number of technical problems*: how far could our wishes be translated into apparatus, which is able to stand up against diverse and often very severe weather conditions? Firstly, we wanted to work with time-sorting pitfalls, viz. 30 pitfalls in which the catches can be kept separately for each hour of the night (or for each two hours of a natural day). Secondly, we wanted to measure repeatedly (e.g. twice an hour, or even more frequently) and continually surface temperature and surface humidity at each catch site, and to record this data automatically.

After a short period (1968–1969) with initial defects the time-sorting pitfalls functioned satisfactorily or even excellently. However, we could only start measuring surface temperatures in 1973 and surface humidities in 1976 (at first only at 10 places, since 1977 at all 30 catch sites). Moreover, the processing of the punched (paper) tapes with data met with great, partly unsolvable difficulties. Since 1976 we have recorded our data on magnetic tape, and these problems have for the greater part disappeared. Although the measuring apparatus will never be foolproof as long as recording occurs in the field (this can only be further improved by recording telemetri-

* Thus this experiment was realized in close cooperation with the TFDL (Technical and Physical Engineering Research Service), Wageningen, which had to develop the greater part of the apparatus and adapt it to our wishes. Special mention should be made of the novel development of a reliable and automatized measuring technique for soil humidity. As far as the time-sorting pitfalls are concerned, the TFDL modified a prototype that had already been developed at the Biological Laboratory of V.U. Amsterdam.



Photo 1. Our experimental forest, with four rows of time-sorting pitfalls. The central recording station is situated at the right (just out of the picture) November 1978.



Photo 2. A single time-sorting pitfall 'in situ' (covered with a transparent perspex roof). In the background the electronic unit for converting the primary signals concerning surface temperature and humidity.



Photo 3. The same as photo 2, but now the sensor for measuring surface humidity has been uncovered, and the perspex roof has been taken away to show the entrance of the (asymmetrical) funnel of the pitfall with a gitter to keep out litter and animals such as mice, shrews, frogs and toads.



Photo 4. The same as photo 2, but now the time-sorting pitfall has been taken out of its container and laid aside together with the loosened holder containing 13 catch-glasses. Note the asymmetrical outlet of the funnel.

cally in the laboratory), in the course of about ten years we have at least overcome the crucial technical difficulties attendant on such an experiment. At the moment we are greatly occupied in developing the processing of the many data with the help of the computer* and composing the necessary programs to make this possible.

Because of these time-consuming technical developments we do not yet have at our disposal the results of this series of preference experiments in the field, which were interrupted in December 1978 (for a number of years such experiments will be run now at another site and with the species *P. coeruleus* and *C. melanocephalus*). When these results are available, they should enable us to plan supplementary experiments, by which the suggested relations between individual behaviour and the chances to survive and to reproduce will have to be tested and be quantified further.

However, since this experiment intends to connect individual behaviour with population dynamics, I can already report the changes in numbers and composition of the interaction groups of the four carabid species of forest that were studied, viz. *Pterostichus oblongopunctatus* F., *Agonum assimile* Payk., *Nebria brevicollis* F., and *Calathus piceus* Mrsh. I will only mention briefly here some results that are of general interest to carabidologists, whereas a more balanced report will be reserved for more specialized publications.

1. To estimate the size of an animal population, at present the stochastic population model of JOLLY (1965; see also; SOUTHWOOD, 1971 and SEBER, 1973) is generally used. This model is an extension of the well-known Lincoln-index, in which catching, marking and releasing of the individuals is not restricted to a single experiment but is repeated several times. In this way it is possible to also estimate the size of the population several times, and even to estimate (but not very reliably) how many individuals have disappeared from, resp. joined the population (Fig. 1)**.

However, a basal assumption of all mark-recapture-models is, that during the whole sampling period every individual has and will keep the same chance of being caught. We already know that in many cases this assumption is not satisfied: a few individuals are recaptured too frequently (as compared with a Poisson-distribution of recaptures), whereas too many individuals are not recaptured at all during the season (because some of them reappear in the catches of the following year, we know that they have not all

* Our data were at first processed with the CDC-3200 computer of the Department of Mathematics, and later with the DEC-10 system (and next the DEC-1090 system) of the Computing Centre, of the Agricultural University of Wageningen, in which we have been assisted by a number of people (we will only mention here the valuable and often extended help of B. A. Scholte). Thanks to the time-sharing DEC-systems we are able now to directly compose and test our programs and even to read in our magnetic tapes (A. Spee) directly from Wijster.

**A computer-program for this model was at first written for us by G. Sanders (for IBM-1670), revised by C. de Jonge (for CDC-3200), and adapted to DEC-systems by I. Madé Suwetja. Other versions, which can more easily be transformed in order to test the effects of some of the basal assumptions of the model, and which possibly can be corrected for part of these effects, are composed by R. H. van der Eijk and P. J. den Boer.

Estimation of the size (\hat{N}_i) of the population (interaction group) according to Jolly (1965)

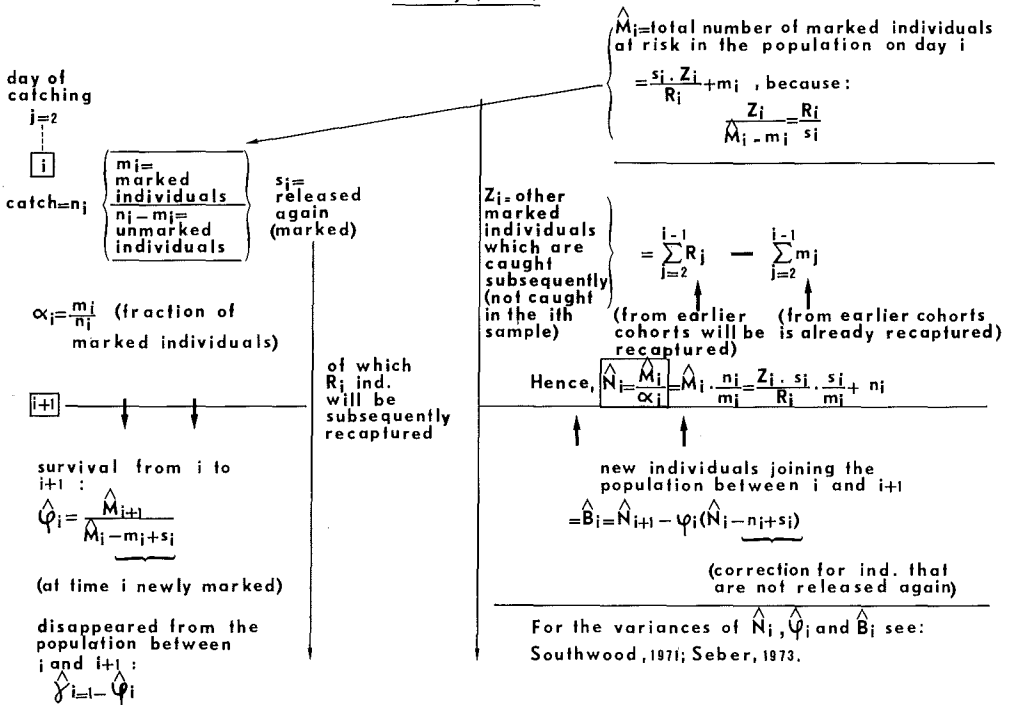


Fig. 1. Outline of the estimation of the running size of the interaction group during a capture-recapture experiment in which several successive samples are taken and all individuals caught are marked individually.

died), viz. about 10% too many in both *P. oblongopunctatus* and *N. brevicollis*. We are now engaged in finding out whether, and how far, this phenomenon will influence our computations.

2. On the other hand we should like to know what kind of behaviour causes the above mentioned effects. It seems probable, that it is connected with differing individual preferences, which will keep some individuals for far too long a period within the catching area of 500 m², whereas others leave it too rapidly. However, when the whole catching area is fenced off – as in 1976 and 1977 – this phenomenon remained at least among young beetles of *N. brevicollis* in 1976 (other cases have not yet been checked). Hence, very variable lengths of the periods of individual activity and/or individually highly diverging intensities of activity apparently can also play a part.

Recently we got many indications (also in other species) which especially favour the latter hypothesis, and it is even probable that the individual level of activity is directly connected – via the frequency of encounters with prey – with the numbers of eggs produced (see also the contributions of VAN DIJK and MOLS).

A picture emerges of an apparently high level of variation of individual activity. To this can be added, that, at least in *P. oblongopunctatus*, old individuals (as far as they can be recognized, i.e. already marked during a preceding season) generally start their activities somewhat earlier in spring than do young ones (hatched last autumn). It seems important to study how far this will influence the amount of reproduction of old and young females respectively (via the influence of different temperatures on egg-production: VAN DIJK, 1979). In the spring of 1978 SZYSZKO (as a guest-worker from Poland) discovered still another behavioural difference between individuals: ♂♂ of *P. oblongopunctatus* dispersed 3–4 times more frequently than ♀♀ into the adjacent pine forest, but also returned 3–4 times as frequently into our catching area, where in general the density of this species is many times higher than in the pine forest (see also: SZYSZKO, 1976).

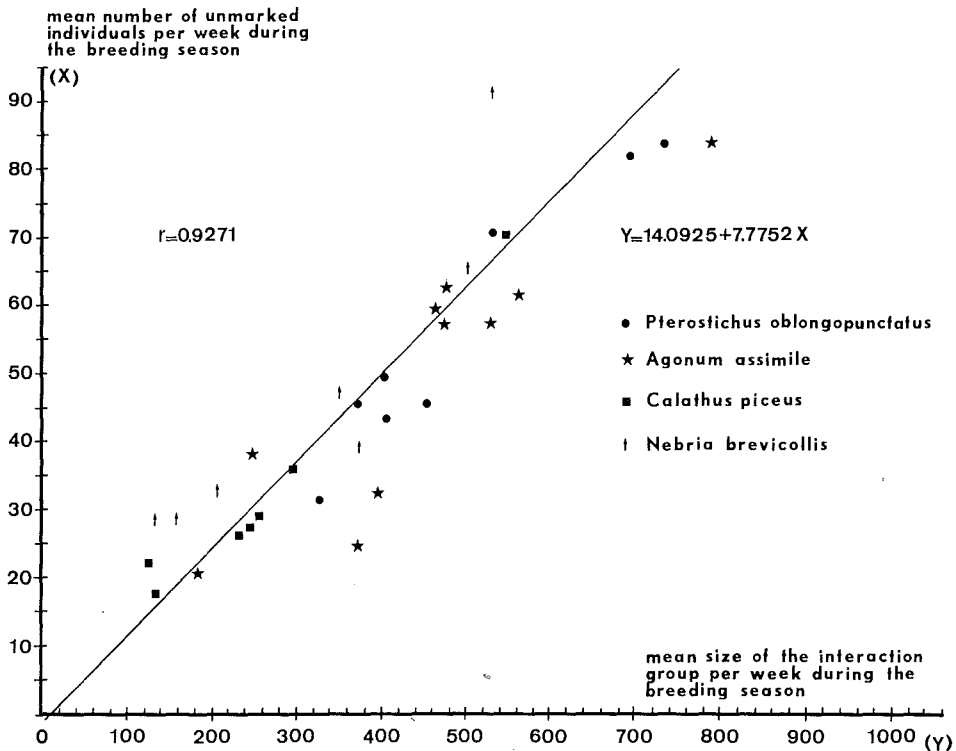


Fig. 2. Relationship between the size of the interaction group as estimated with Jolly's model (version of Sanders-De Jonge-Madé Suwetja) averaged over all weeks of the breeding season (Fig. 1) and the mean number of unmarked individuals (i.e. not captured before) caught during the same weeks. Each point for the pertinent species represents the results from uninterrupted pitfall sampling (see text) during one breeding season. For the different species this capture – recapture experiment was continued for 7–10 years.

3. It is very interesting now to learn that, in spite of the apparent individual differences in activity, the numbers of newly marked individuals totalled over the season gives a reliable relative measure of the size of the population as it can be estimated with JOLLY's model (cf section 1), not only within each species separately but even for all four species together, Fig. 2. This means, that individually determined differences in activity as well as changes of individual behaviour in time, when taken together both for the whole interaction group and over the whole season, work out statistically in such a way that the chance of an average individual being captured at least once does not differ very much between years and even between the species concerned, so that the size of the population is well reflected by the number of individuals caught. This phenomenon is treated more extensively by BAARS (1979). Even comparable data for some species of heathland (among which *P. coeruleescens*, see the previous contribution) fit nicely into the relationship as it is pictured in Fig. 2 for forest species only (see further DEN BOER, 1977; section 4.4, where a few exceptions are also mentioned). In this way, with JOLLY's model we correctly recorded the changes in numbers from year to year on a relative scale. We have only to find out now how far the JOLLY-calculations underestimate or overestimate the actual size of the interaction group. The necessary data for that was collected by enclosing the whole catching area in 1976 and 1977. There are several indications to suppose that JOLLY's model will generally underestimate the size of the population.

4. When we now look at differences and similarities in activity between the four species: they are all night-active, starting locomotory activities immediately after sunset and reaching a maximum (at least in the catches) one to two hours later after which they gradually decrease.

In general, *A. assimile* has a more restricted daily activity period and is more exclusively nocturnal than *P. oblongopunctatus*. However, during a number of nights the activity curves deviate substantially from this general pattern, e.g. in some nights a revival of activity occurs just before sunrise, especially in *N. brevicollis*. Although there are reliable indications that these deviations are connected with weather conditions the causal relations are not yet obvious. Because e.g. egg-production depends highly on the temperatures to which the females have been exposed, it will be important further to unravel these relationships.

5. Further differences and similarities in activity between the species are still hidden in our data on individual preferences, that are now being prepared for computer processings. However, a few provisional results can be mentioned. Although our experimental forest is rather homogeneous the captures are only as an exception distributed randomly (or even more or less equally) over the thirty pitfalls: usually the catches are more or less grouped. For the different species this clustering of the captures generally does not occur in the same part of the sampling area. Our experimental forest shows one spatially heterogeneous feature that time does not alter: There are small

differences in elevation, by which the highest site is situated 27 cm above the lowest one. The two spring breeders apparently react (directly or indirectly) to these small differences in elevation: the catches of *P. oblongopunctatus* generally occur in the higher situated pitfalls, whereas those of *A. assimile* occur for the greater part in the ones situated in the lower sites. Because also the callow beetles in autumn often show this pattern, females of *P. oblongopunctatus* obviously deposit their eggs at other (more elevated) sites than females of *A. assimile*. Although the above pattern can generally be recognized, in different years the distribution of the captures may be quite different, probably because the beetles only react indirectly upon differences in elevation. We have still to find out how far spatial differences in surface temperature and/or humidity are correlated with these differences in elevation (some provisional tests suggest that a clear relationship does not exist).

As a first result of our data processing we have already established that *A. assimile* apparently prefers the warmer sites within our catch area – especially during the second part of the reproductive period – in the spring of 1973 to a very significant degree, and in 1974 to a lesser degree. How this preference is related to the higher catches in the lowest situated pitfalls has still to be investigated. These findings are especially interesting in the light of the results of the extensive preference experiments (in the laboratory) by NEUDECKER (1972): he showed convincingly that *A. assimile* is a species that prefers both cold and drought (at least under experimental conditions).

According to THIELE (pers. comm.) this contradiction with our findings can be removed by assuming that *A. assimile* in fact prefers a temperature of about 18°C, whereas in our forest the surface temperatures at night only sometimes exceed 16°C in May and June. Also the recorded drought-preference of this species promises to offer some complications: the densest population of *A. assimile* we ever sampled (during five years) inhabited a very wet site in the centre of a deciduous forest (cf. DEN BOER, 1977).

P. oblongopunctatus did not show any temperature reaction in the spring of 1973, and only a very weak positive reaction in 1974. From a population dynamical point of view it will be especially important to know how individuals of this species – and of *A. assimile* – react upon spatial differences in surface humidity during reproduction. This will be the more so because provisional analyses already show, that even within our experimental forest these humidity differences may be considerable and appear to have a much higher predictive value than spatial differences in surface temperature, with which they generally do not seem to be correlated*.

It will be as important, however, to learn how different individual preferences are, for these differences might contribute greatly to spreading of the risks of larval development and thus to the stabilizing of the numbers of young beetles from year to year (compare: DEN BOER, 1968).

* These provisional analysis (and many others, e.g. those concerning night activity: section 4) have been done by my wife Wil Daanje. They show the kind of relationships that could most probably be expected, which again enables me to program the final computer operations more effectively.

6. Because we individually marked a great number of beetles during a succession of years* we got many reliable data about the survival time of individuals. It thus appeared, that many individuals of *P. oblongopunctatus* and of *A. assimile*, which have reproduced in spring, survive summer, autumn and winter, to reproduce again in a second spring, and sometimes also again in a third one (Table 1). A few individuals even survive a fourth winter.

The lowest estimates in Table 1 were derived from the individuals that could be recognized directly by their mark, whereas in the highest estimates also the chance of being recaptured has been taken into account (since this chance will generally be underestimated – see section 1 – these latter values will be too high). When in 1976 we enclosed the whole catching area, by which nearly all individuals could be recorded and marked, we established that the lowest estimates in Table 1 must be at least 6–8 % too low, whereas many highest estimates appeared to be about 6–8 % too high. Hence, the actual survival of old beetles will be about halfway between the lowest and highest estimates – or still somewhat higher –, i.e. to the second spring in *P. oblongopunctatus* about 30 % in most years, and in *A. assimile* still higher. A still better survival of old beetles (at least in some years) was found in the spring breeder *P. coerulescens* (cf. BAARS, 1979).

Contrary to the spring breeders *P. oblongopunctatus* and *A. assimile* in the autumn breeder *N. brevicollis* survival of beetles until the next reproduction period hardly occurs (Table 1). In this way *N. brevicollis* must also do without the important levelling influence which the survival of old beetles may have on the fluctuations of numbers. Fig. 3 indeed shows that in *N. brevicollis* the numbers tend to fluctuate more violently than in *A. assimile* and *P. oblongopunctatus*; compare the fluctuation characteristics (cf. DEN BOER, 1971), logarithmic range (LR) and variance R (Var R) of these three species: Fig. 3. Without the survival of old beetles (and a somewhat higher production of young beetles, so that the mean density is maintained at about the observed level during these eight years) our spring breeders would also have shown more violent fluctuations of numbers: *P. oblongopunctatus*, LR = 1.0034 (instead of 0.8069) and Var R = 0.265 (instead of 0.1685); *A. assimile*, LR = 1.4473 (instead of 1.1107) and Var R = 1.1213 (instead of 0.3085).

7. *C. piceus* represents a special case: DEN BIEMAN (a student from Wageningen) found that young and old beetles reproduce at different times of the year. Young beetles reproduce soon after hatching, in July–August. Between 7 and 22 % of these young beetles survive the winter (Table 1) and reproduce again in the next spring, in May–June. VAN DIJK (1972) found a comparable – but less extreme – situation in the related

* During almost the whole period of ten years these markings were performed – and maintained often under difficult circumstances – by Arnold Spee (who also took the photographs and did the drawings for this paper). We make use of the technique of brand-marking, which was first described by SCHJØTZ-CHRISTENSEN (1965), and by which many thousands of beetles can be marked individually without loss of marks.

Table 1. Survival after the first breeding season in four carabid species of forests (lowest estimation–high estimation).

| Spring breeders | | | | |
|------------------------------|--------------------------------------|---------------------------------|---------------------------------|---------------------------------|
| present in the population of | <i>Pterostichus oblongopunctatus</i> | | <i>Agonum assimile</i> | |
| | down to the 2nd breeding season | down to the 3rd breeding season | down to the 2nd breeding season | down to the 3rd breeding season |
| 1968 | 17.0–58.9% | ? | 18.0–41.2% | ? |
| 1969 | 19.2–42.4% | ? | 20.8–36.2% | ? |
| 1970 | 11.0–33.6% | 2.3–7.4% | 16.6–35.0% | 2.1–4.5% |
| 1971 | 14.6–39.4% | 1.1–3.0% | 20.2–44.3% | 1.0–2.0% |
| 1972 | 11.7–30.1% | 0.5–1.3% | 15.5–33.2% | 4.0–8.5% |
| 1973 | 12.4–33.0% | 1.1–2.7% | 16.6–46.4% | 2.2–6.2% |
| 1974 | 13.6–36.4% | 0.7–1.9% | 13.8–35.5% | 2.4–6.1% |
| 1975 | 20.4–54.2% | 0.8–2.1% | 22.2–58.5% | 1.7–4.6% |
| autumn breeder | | | (spring) summer breeder | |
| present in the population of | <i>Nebria brevicollis</i> | | <i>Calathus piceus</i> | |
| | down to the 2nd breeding season | down to the 3rd breeding season | down to the 2nd breeding season | down to the 3rd breeding season |
| 1968 | 3.0– 6.3% | ? | ? | ? |
| 1969 | 2.0– 4.9% | (1.4–3.2%) | 8.3–33.2% | ? |
| 1970 | 2.0– 3.4% | 0.4–0.7% | 4.7–19.5% | 1.2–4.9% |
| 1971 | 2.0– 3.9% | 0 | 6.3–32.0% | 0.7–3.4% |
| 1972 | 5.0– 9.7% | 0 | 4.5–30.6% | 0 |
| 1973 | 3.0– 6.5% | 0.3–0.6% | 2.0–11.6% | 0.7–4.1% |
| 1974 | 0.9– 1.8% | 0 | 2.8–14.6% | 0 |
| 1975 | 6.2–11.6% | 0.4–0.8% | 8.2–37.2% | 0.8–3.5% |

mean size of the
interaction group
per week during
the breeding season
(Jolly)

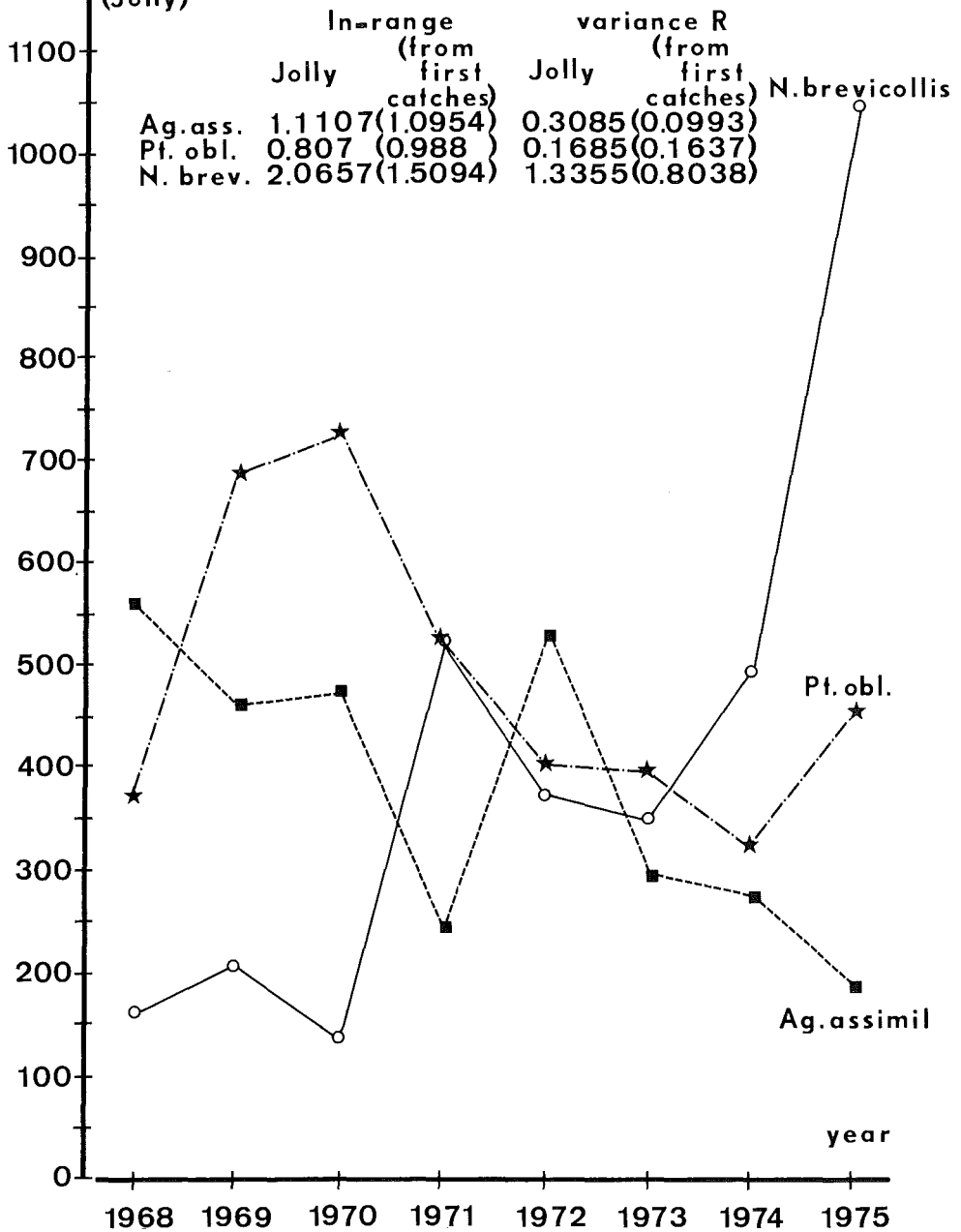


Fig. 3. Changes in the size of the interaction group (averaged per week over the breeding season) during eight years for three carabid species of forest. The magnitude of the fluctuation of numbers is compared with ln-range (= ln greatest size minus ln smallest size) and with variance R (= variance net reproduction, i.e. variance of: size in year n/size in year n-1), both for Jolly-estimations and from first catches of individuals (compare Fig. 2).

C. melanocephalus on Schiermonnikoog: on the average overwintered individuals reproduce about one month earlier than young ones (in Drenthe in most years this difference is less, in *C. melanocephalus*). A further peculiarity of *C. piceus* is, that the reproductive season of the old beetles is nearly completely separated in time from that of the young beetles: when the young individuals start reproduction the few old beetles, that are still active, are already 'spent' again. Larvae born from eggs, that were laid early in spring, apparently have an uninterrupted development: at the end of August, when the young, reproducing beetles have already hardened their elytra, in most years once again a few callow beetles are caught. This somewhat unusual life-cycle among carabids may be connected with the fact, that *C. piceus* most probably is a comparatively new species in our regions (DEN BOER, 1962).

8. Among the four forest species studied *N. brevicollis* is remarkable because of the high level of locomotory activities shown by the non-reproducing stages (in this – and some other – respects it resembles the less abundant *Leistus rufomarginatus* Dfts., and possibly some other Carabinae). The first young individuals of this late-autumn breeder already hatch in May–June and are very active, allowing many hundreds to be caught and individually marked. After aestivation only about 40% of these young beetles are recaptured, whereas in average 70% of the individuals caught during the breeding period are still unmarked. Apparently, individuals of *N. brevicollis* are moving around in a much larger area than our experimental forest, and therefore the young beetles might make an important contribution to a thorough dispersal of the species. This was supported by enclosing the catching area in 1976: 58.6–68.4% of the young individuals marked in spring were recaptured in autumn, whereas only 9.7% of the beetles reproducing within the enclosed area were then unmarked.

Also the larvae – especially in the third stage – show a remarkably high level of locomotory activities, in this case during the winter. Part of the third stage larvae actively leave the forest, to return again early in spring (NELEMANS). To understand the life-cycle of *N. brevicollis* it may be important to note, that most other *Nebria*-species live under arctic and/or alpine conditions (see also: THIELE, 1969; TOPP, 1975).

9. As compared to the situation in *N. brevicollis* (section 8) the callow beetles of the spring breeders *P. oblongopunctatus* and *A. assimile* hardly show appreciable activities: in most autumns only some tens of callow individuals (of even less) are caught and marked (see also Table 2). Accordingly, the number of the young beetles that are then active is hardly correlated with the size of the population in the following spring. In order to find the significance of these locomotory activities it may be useful to note, that in most autumns also some marked individuals that have already reproduced in spring are moving around again. The latter are apparently unable to await inactively the next spring, possibly because they did not make enough fat (?). In any case – at least in *A. assimile* – the number of callow beetles active in autumn is positively correlated with the fraction of the old beetles that then reappear: $\tau = +0.67$ ($p = 0.025$, 7 years). There is

Table 2. Survival of the sexes.

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| <i>Pterostichus oblongopunctatus</i> | | | | | | | | | | |
|---|------------|------|----------------------|-------|---|------|-------------------------|------|---|-------|
| young beetles immediately after hatching in year n | | | | | the same young beetles during their first breeding in year n + 1 | | | | individuals in their 2nd (or later) breed- ing season in year n | |
| year | estimation | | recognized as callow | | estimation | | recognized individually | | recognized individually | |
| (n) | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| 1968 | 159 | 166 | 104 | 110 | 67 | 65 | 44 | 54 | 23 | 13(*) |
| 1969 | 100 | 80 | 18 | 16 | 35 | 33 | 4 | 4 | 71 | 37** |
| 1970 | 32 | 36 | 9 | 17 | 14 | 9 | 5 | 3 | 101 | 39*** |
| 1971 | 58 | 46 | 37 | 26 | 10 | 8 | 7 | 5 | 115 | 63*** |
| 1972 | 28 | 54** | 19 | 35(*) | 6 | 10 | 5 | 6 | 87 | 27*** |
| 1973 | 31 | 22 | 19 | 9(*) | 7 | 5 | 5 | 2 | 58 | 30** |
| 1974 | 21 | 26 | 19 | 19 | 3 | 9(*) | 2 | 8(*) | 56 | 25** |
| 1975 | 51 | 52 | 23 | 28 | | | | | 76 | 33*** |
| <i>Agonum assimile</i> | | | | | | | | | | |
| young beetles immediately after hatching in year n | | | | | the same young beetles during their first breeding in year n + 1 | | | | individuals in their 2nd (or later) breed- ing season in year n | |
| year | estimation | | recognized as callow | | estimation | | recognized individually | | recognized individually | |
| (n) | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| 1968 | 58 | 66 | 36 | 36 | 20 | 16 | 11 | 9 | 67 | 80 |
| 1969 | 63 | 65 | 18 | 15 | 27 | 27 | 3 | 7 | 90 | 105 |
| 1970 | 8 | 11 | 4 | 5 | — | 3 | — | 1 | 82 | 72 |
| 1971 | 30 | 31 | 14 | 18 | 7 | 14 | 3 | 8 | 92 | 70 |
| 1972 | 49 | 47 | 12 | 5 | 8 | 9 | 2 | 1 | 36 | 35 |
| 1973 | 15 | 17 | 7 | 4 | 4 | 8 | 1 | 2 | 72 | 72 |
| 1974 | 4 | 7 | 1 | 3 | 2 | 2 | — | 2 | 28 | 39 |
| 1975 | | | | | | | | | 41 | 33 |

(*) Nearly significantly different; * $p \approx 0.05$; ** $p \leq 0.005$; *** $p \leq 0.0005$

even a weak indication that this phenomenon is more apparent after a warm than after a cool summer ($\tau = +0.43$; $p = 0.119$).

10. In autumn equal numbers of young males and females are caught and marked of both *P. oblongopunctatus* and *A. assimile*: Table 2. During their first breeding period the sex ratio is still 1/1 in both species. Between the first and second breeding season, however, twice as many males as females of *P. oblongopunctatus* survive, whereas in *A. assimile* the survival of the sexes is then still similar: Table 2. It will be interesting to learn what causes this different mortality of the sexes in *P. oblongopunctatus*, since it may be connected with processes that significantly influence fluctuations of numbers. SZYSZKO (1976) suggests that the sex ratio in this species, which may again be different in different localities, might be connected with the favourability of the habitat. '.

The above are provisional notes on the population dynamics of four carabid populations studied for eight years, and we have discussed some first observations on relevant individual activities and preferences. During the same years VAN DIJK prepared the 'tools' with which these investigations will have to be continued, i.e. he developed the methods by which the egg-production of individual females and the survival of larvae can be measured under different sets of conditions (see his contribution to this volume, and VAN DIJK, 1979). First our observations on individual preferences will have to be worked out completely, and the experiments performed by which these reactions can be translated into individual chances to reproduce and survive (the latter especially during larval development). Then we can try to integrate all this data into simulation models which will have to produce the numerical changes of the interaction groups concerned as they were observed under the recorded field conditions.

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