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Population density and biomass of Carabidae (Coleoptera) in a forest community

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With 4 figures

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1. Introduction

Carabid beetles constitute one of the major groups of fauna active at the ground's surface and perform an important trophic role in the forest community (LOREAU 1983, 1984c). For a more precise understanding of this role, the quantitative importance of their contribution to the community's metabolism must be known. But data on this subject are particularly scarce or fragmentary in the literature, owing to the methodological difficulties related to the low population density of these insects. A few population density or biomass estimates can be found in van der Drift (1951), Heydemann (1962), Greenslade (1964), Schjøtzb. Christensen (1965), Frank (1967), Dubrovskaya (1970), Weidemann (1971, 1972), Desiere (1972), Manga (1972), Grüm (1971a, 1971b, 1973, 1975, 1976), Kaban-K-Wasylik (1975) and Niesing & Weber (1981).

The present paper purports to define the level of population density and biomass of medium- and large-sized (> 6 mm) adult carabids in a forest community, as preliminaries of a general study on these species' niches, which is summarized in LOREAU (1984b, 1984c). The biotope is a beech forest on acid soil in Lembeek (Belgium), which, together with the characteristics of the carabid community, is described in LOREAU (1984a). Population density is determined here by methods based on pitfall trapping (capture-recapture, catch-effort), for quadrat sampling has proven to be unserviceable for the populations studied. Ten series of estimations were performed over a three-year period (1978, 1970, 1981).

2. Methods

2.1. Capture-recapture

One of the principles guiding the selection of a capture-recapture technique from the very numerous choices, must be its simplicity. Complex techniques give more precision in theory by taking into consideration more parameters, but at the same time introduce more bias in practice (Meunier & Solari 1979). A condition for the application of a simple technique, however, is that the population is "closed". With the highly mobile carabid populations, this condition was ensured by two means:

(1) the populations were isolated by enclosures, suppressing immigration and emigration;
(2) the whole procedure was carried out during a short period of time (from 6 to 10 days), so that natality and mortality were negligible.

The use of enclosures moreover gives the great advantage of allowing population size estimates to be directly converted into population density estimates, as the exact surface covered by the populations studied is known.

An enclosure was made using a series of plastic plates 120 cm long and 25 cm high, sunk a few centimeters into the soil. An empty pitfall trap was placed at each meeting point of two plates, alternatively inside and outside the enclosure. The enclosures in use were as follows: two square enclosures, of 33.4 m² and 28.9 m² respectively, in 1978; two, of 58.6 m² and 69.5 m², in 1980; two, of 70.4 m² each, in May 1981; and one, of 284.9 m², during the rest of 1981. They were set up and

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dismantled at the time of each series of estimations. During this period \((k\) days), the traps were emptied daily, the carabids caught inside the enclosure were individually marked with a microcauterizator (Fig. 1), if not already marked, and then released. At each day \(i\) (for \(i = 2\) to \(k\)), the population estimate was calculated by the well-known Lincoln index with Chapman’s (1951) correction:

\[
\hat{N}_i = \frac{(M_i + 1)(n_i + 1)}{(m_i + 1)} - 1
\]

where

- \(M_i =\) total number of marked individuals in the population before sampling;
- \(n_i =\) number of individuals caught in the sample;
- \(m_i =\) number of marked individuals caught in the sample.

The final estimate is given by the mean of the \(\hat{N}_i\):

\[
\bar{N} = \frac{\sum_{i=2}^{k} \hat{N}_i}{k-1}
\]
with the approximate limits of the confidence interval \((N_1, N_2)\) at the level \(1 - \alpha\):

\[
N_1, N_2 = \bar{N} \pm t_{1-\alpha/2} \frac{s}{\sqrt{k-2}},
\]

where

\(s = \text{standard deviation;}\)

\(t = \text{Student variable with } k-2 \text{ degrees of freedom.}\)

### 2.2. Catch-effort

Another method was applied to estimate the population size using the same data: the Leslie & Davis’s (1939) catch-effort method. Here the individuals caught are not released but eliminated from the population. Whereas, for a constant “catch-effort”, a constant fraction of the remaining population is expected to be caught each day, the figure for the daily capture must decrease linearly as a function of the previous total capture. When it tends towards zero, the total capture tends towards the population size, which can thus be estimated by the intercept on the x-axis of the regression line of \(y\) on \(x\), with \(y = \text{daily capture, and } x = \text{previous total capture.}\)

In the present case, the marked individuals were simply considered as “eliminated” in the calculations. This method moreover has the advantage that the proportion of the newly caught individuals may be used instead of their absolute number. In fact, the activity of carabids being variable according to the climatic conditions, the capture efficiency fluctuates from day to day. Thus, it is more correct to divide the number of newly caught individuals \((n - m)\) by the total activity measured by \(n\). The calculated regression line is then:

\[
y = ax + b, \text{ with } y = \frac{n - m}{n} \text{ and } x = M.
\]

Hence \(x(0) = N = \frac{b}{a}\).

The confidence interval of \(\hat{N} = (N_1, N_2) = (x_1, x_2)\), can be obtained by calculating the roots of the following quadratic equation:

\[
a'(x - \bar{x})^2 + b' (x - \bar{x}) + c' = 0
\]

with

\[
a' = a^2 - \frac{\sigma^2 \bar{y} \cdot x}{\sum (x_i - \bar{x})^2}
\]

\[
b' = 2a\bar{y}
\]

\[
c' = \bar{y}^2 - \frac{\sigma^2 \bar{y} \cdot x}{k}
\]

\[
\hat{\sigma}^2 \cdot x = \frac{(1 - r^2) \sum (y_i - \bar{y})^2}{k-2}
\]

\(t = t_{1-\alpha/2}, \text{ Student variable with } k-2 \text{ degrees of freedom (after Seber 1982).}\)

Hence \(x_1, x_2 = \frac{-b' \pm \sqrt{b'^2 - 4a'c'}}{2a'} + \bar{x}.

### 2.3. Estimation of the biomass

The biomass of each species was calculated by multiplying the population density estimate by the mean individual fresh mass (this being the mean of the values obtained separately for males and females). To obtain the individual masses, carabids were caught by pitfall traps during the night, anaesthetized with ethyl acetate the next morning, then weighed separately with the assistance of a Mettler type H16 balance, sensitive to a hundredth of milligramme. As individuals were caught on several occasions from May to October, the resulting means roughly reflect the mean mass of each species during the course of its whole activity period.

### 3. Results

#### 3.1. Verification of the conditions of application of the methods

#### 3.1.0. General

Application of the estimation methods described requires two main conditions:

- an equal probability of capture for all the individuals of a species;
- a “closed” population.
Fig. 2. Evolution of the proportion of the *Pterostichus oblongopunctatus* marked on the first day (18/5), in the captures of the following days. Results from enclosures a and b in May 1978.

Fig. 3. Evolution of the proportion of the *Abax aler* marked on the first day (22/6), in the captures of the following days. Results from the enclosure in June 1981.

In order to judge the reliability of the methods, it is useful to verify at least some aspects of these conditions, i.e.:
- whether released individuals distribute themselves randomly in the population;
- whether marked animals suffer an abnormal mortality on account of the marking;
- whether the enclosure is effective in isolating the population.

### 3.1.1. Distribution of marked individuals

A simple means of verifying whether the beetles distribute themselves randomly in the population, is to determine whether those marked on the first day, and released in the centre of the enclosure, are always present in the same proportion in the captures of the next days. The expected result of poor dispersal is that they will be present in lower proportions in the captures, which are made at the periphery of the enclosure, during the first days. Figures 2 and 3 show, for two abundant populations as examples, that the proportion of the individuals marked on the first day remains quite stable, given the random variations due to the small numbers involved (e.g., only 5 individuals caught on the 27/6 in Fig. 3). One may conclude from this that the first condition is roughly fulfilled.

### 3.1.2. Influence of marking on mortality

In order to test the influence of marking on mortality, two groups of *Pterostichus oblongopunctatus*, one of 28 marked individuals and the other of 30 non-marked individuals, were maintained under identical conditions in the laboratory. After five months, the mortality was quite low in both groups, and even slightly (but non-significantly) greater among non-marked individuals (27% against 14%, new generations of beetles excluded) (Fig. 4). Most other authors similarly find that marking does not increase mortality, whether it is performed with a petroleum-based glossy dope (Greenstreet 1964) or with a microcauterizator (Schjøtz-Christensen 1965).

### 3.1.3. Efficiency of population isolation by enclosure

Experiments with contiguous enclosures have shown that as long as pitfall traps are functioning, very few *Pterostichus oblongopunctatus* escape from the enclosures, whereas when traps are non-functional the escape rate is much higher. Under the latter condition, the carabids probably eventually escape at the junction between two plates. If such is the case, the escaped animals are most likely to be caught by the trap located just on the other side. The number of individuals found in the external traps during the population estimations
would consequently indicate an escape rate of a few per cent (≈ 3%) of the enclosed population during one week, a quite low proportion, given the degree of accuracy of the estimation methods.

Amongst the other species, only Leistus rufomarginatus is likely to have escaped more frequently, owing to its smaller size and the greater ability of the males to climb rough surfaces. Thus in general, populations were well isolated by the enclosures. This conclusion is supported by figures 2 and 3, since in case of large immigration, one should expect after a few days a gradual decrease in the proportion of animals marked on the first day.

3.2. Population density

Table 1 describes a population estimation as an example. One notes that both capture-recapture and catch-effort methods give the same estimate, with a good degree of precision as shown by the narrow confidence interval. This is a general feature, which results from the good fulfillment of the conditions of application of the methods, and from the high rate of capture compares with the population. However, as soon as the correlation between the rate of new captured and the previous total capture grows weak, the precision of the catch-effort method falls rapidly. Indeed, the population estimate is given by the abscissa of a

Table 1. Estimation of the population of Pterostichus oblongopunctatus from enclosure a in May 1978 (18-23/5)

<table>
<thead>
<tr>
<th>i</th>
<th>$M_i$</th>
<th>$n_i$</th>
<th>$m_i$</th>
<th>$n_i - m_i$</th>
<th>$\hat{N}_i$ (CHAPMAN)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0</td>
<td>25</td>
<td>0</td>
<td>1</td>
<td>—</td>
</tr>
<tr>
<td>2</td>
<td>25</td>
<td>29</td>
<td>15</td>
<td>0.48</td>
<td>47.8</td>
</tr>
<tr>
<td>3</td>
<td>39</td>
<td>17</td>
<td>11</td>
<td>0.35</td>
<td>50</td>
</tr>
<tr>
<td>4</td>
<td>45</td>
<td>19</td>
<td>18</td>
<td>0.05</td>
<td>47.4</td>
</tr>
<tr>
<td>5</td>
<td>46</td>
<td>20</td>
<td>18</td>
<td>0.1</td>
<td>50.9</td>
</tr>
<tr>
<td>6</td>
<td>48</td>
<td>17</td>
<td>15</td>
<td>0.12</td>
<td>54.1</td>
</tr>
</tbody>
</table>

CHAPMAN: $\bar{N} = 52 \; (46, 58)$
CATCH-EFFORT:
$y = -0.019 \; x + 0.995$
$\hat{N} = 52 \; (47, 60)$

Symbols: see text. The 95% confidence interval of the estimates is indicated in brackets.
Table 2. Population density estimates, in individuals m\(^{-2}\)

<table>
<thead>
<tr>
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<tbody>
<tr>
<td></td>
<td>18—23/5 8—17/7</td>
<td>20—27/9 22—28/7</td>
<td>31/7—4/8 22—30/9</td>
<td>11—18/5 22—28/6 31/8—6/9 25/9—1/10</td>
</tr>
<tr>
<td>Abax ater</td>
<td>(a) .27  .15</td>
<td>.18  .07</td>
<td>.07  .12</td>
<td>.23  .30  .07  &gt;.03</td>
</tr>
<tr>
<td></td>
<td>(b) .14  .28</td>
<td>.04  .03</td>
<td>.03  .07</td>
<td>.16</td>
</tr>
<tr>
<td>Pterostichus oblongopunctatus</td>
<td>(a) 1.56  .15</td>
<td>.18  .06</td>
<td>&gt;.03  .04</td>
<td>.27  &gt;.03  &gt;.004</td>
</tr>
<tr>
<td></td>
<td>(b) 1.28  .38</td>
<td>.07  .05</td>
<td>&gt;.08</td>
<td>.26  &gt;.02  &gt;.004</td>
</tr>
<tr>
<td>Leistus rufomarginatus</td>
<td>(a) &gt;.06  .18</td>
<td>&gt;.04  &gt;.01</td>
<td></td>
<td>.03  &gt;.02</td>
</tr>
<tr>
<td></td>
<td>(b) —  .69  &gt;.17</td>
<td>.10  &gt;.03</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyphrus attenuatus</td>
<td>—  .03  .03  .01</td>
<td>.02  .02</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carabus problematicus</td>
<td>—  .02  —  .02</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nebria brevicollis</td>
<td>&gt;.02  .05  .02</td>
<td></td>
<td>.01</td>
<td></td>
</tr>
<tr>
<td>Abax parallelus</td>
<td>&gt;.05  .02  .02  .01</td>
<td></td>
<td>&gt;.04  &gt;.004  &gt;.004</td>
<td></td>
</tr>
<tr>
<td>Badister bipustulatus</td>
<td>&gt;.23  —  —  .02</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Others</td>
<td>&gt;.05  —  .03  .02</td>
<td></td>
<td>.01  &gt;.004  &gt;.01</td>
<td>&gt;.01</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>&gt;2.01 1.00  &gt;.42  .24  &gt;.15  .17</td>
<td>.48  &gt;.38  &gt;.13  &gt;.08</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

When two enclosures (a and b) were functioning simultaneously, separate estimates are given for the three most abundant species. For the other species, the estimates are means over the two enclosures.

Table 3. Biomass estimates (fresh mass), in mg m\(^{-2}\)

<table>
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<tr>
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</thead>
<tbody>
<tr>
<td></td>
<td>18—23/5 8—17/7</td>
<td>20—27/9 22—28/7</td>
<td>31/7—4/8 22—30/9</td>
<td>11—18/5 22—28/6 31/8—6/9 25/9—1/10</td>
</tr>
<tr>
<td>Abax ater</td>
<td>53  53</td>
<td>29  14</td>
<td>14  24</td>
<td>49  76  19  &gt;6</td>
</tr>
<tr>
<td>Pterostichus oblongopunctatus</td>
<td>86  15</td>
<td>8  3</td>
<td>&gt;.2  1</td>
<td>16  &gt;2  &lt;-.2</td>
</tr>
<tr>
<td>Leistus rufomarginatus</td>
<td>&gt;.08  11</td>
<td>&gt;.2  2</td>
<td>&gt;.06 —</td>
<td>0.4 &gt;.0.5 —</td>
</tr>
<tr>
<td>Cyphrus attenuatus</td>
<td>—  6</td>
<td>6  2</td>
<td>3  5</td>
<td>—  &gt;4  7  6</td>
</tr>
<tr>
<td>Carabus problematicus</td>
<td>—  8  —  8</td>
<td>—  —</td>
<td>—  —</td>
<td>—  2  —  —</td>
</tr>
<tr>
<td>Nebria brevicollis</td>
<td>&gt;1  3</td>
<td>1  —</td>
<td>—  0.5</td>
<td>—  —  —  &gt;.2</td>
</tr>
<tr>
<td>Abax parallelus</td>
<td>&gt;.7  2</td>
<td>2  1</td>
<td>—  1</td>
<td>—  &gt;.0.5  —-.5</td>
</tr>
<tr>
<td>Badister bipustulatus</td>
<td>&gt;.3  —  —  —</td>
<td>—  —</td>
<td>—  —</td>
<td>—  —  —  —</td>
</tr>
<tr>
<td><strong>Total 8 species</strong></td>
<td>&gt;151 98</td>
<td>48 30</td>
<td>20 32</td>
<td>65 &gt;85 &gt;27  &gt;12</td>
</tr>
</tbody>
</table>


point distant from the mean point \((\bar{x}, \bar{y})\) whereas the confidence area of a value estimated using a regression line is limited by two branches of hyperbola which diverge either side of the mean point (Dagnelie 1970). In many cases, it was possible to obtain an exact evaluation of the enclosed populations form the total number of individuals caught, because these were rapidly found to be all marked.

The resulting population density estimates are summarized in Table 2. A series of values (preceded by the sign \(>\)) are minimal estimates from the total number of individuals caught, when few recaptures were made.

Population density is obviously variable between enclosures; in almost all cases, however, the differences are not statistically significant. The total density of the carabid community declines between 1978 and 1981 from about 2 individuals m\(^{-2}\) to 0.5 m\(^{-2}\) in May, and from about 0.4 m\(^{-2}\) to 0.1 m\(^{-2}\) at the end of September. This reduced population density, however, only affects some abundant spring species with highly variable populations (in particular *Pterostichus oblongopunctatus*), whereas other species (such as *Abax ater*) maintain, or even increase, their population densities. Similar changes have been found in activity, and are explained by variations in climatic conditions, particularly increased rainfall above mean levels from 1978 to 1981, which differentially affects the carabid species (Loreau 1984a). Note that the estimates mentioned in Table 2 are not suitable for performing precise year-to-year comparisons for all species, since the periods of estimation are variable and do not regularly coincide with the periods of maximum activity in some species (e.g. *Leistus rufo-mARGINatus*, *Abax parallellus* and *Nebria brevicollis*).

The parallelism between important changes in population density and in total annual activity is worth emphasizing, given the controversies in the literature about the density-activity relation. However, if more precise comparisons are made, the linear relation between these two parameters, proposed by Baars (1979), is not found to be verified. In particular, for species with variable populations, total activity varies less than density: thus, the population of *Pterostichus oblongopunctatus* diminishes by a factor of 5.4 between 1978 and 1981, whereas its total activity diminishes only by a factor of 2.8 (Loreau 1984a). A phenomenon of compensation between population density reduction and increase in individual activity is likely to occur (Kaczmarek 1963).

### 3.3. Biomass

Biomass estimates are shown in Table 3. The total carabid biomass reaches a maximum of about 150 mg m\(^{-2}\) (fresh mass) in 1978 and 85 mg m\(^{-2}\) in 1981 — far less divergent values than those for population density. In 1980, the lack of an estimate before the end of July does not allow this maximum to be calculated.

The dominance relationships studied in Loreau (1984a) using results of annual activity appear to be related to the interspecific differences in biomass. The dominant species *Abax ater* maintains a distinctly higher biomass than the other species (except in May 1978). Among the subdominant species, however, the vernal *Pterostichus oblongopunctatus* reaches a much higher biomass than the autumnal *Cychrus attenuatus* and *Carabus problematicus*. This difference probably reflects a difference in “strategy”: the strategy of the spring species could be centred on abundance, because of the presence of more or less abundant small and not very mobile prey; that of the autumn species, on mobility, corresponding to the presence of larger and more mobile but scarcer prey.

### 4. Discussion

The methods based on pitfall trapping of carabids within enclosures, which were used here, provide accurate estimates of the enclosed populations. But they also have drawbacks which limit their efficiency. Firstly, they do not allow precise estimates to be obtained on the scale of the whole biotope, because of the spatial variations in population density and the difficulty of setting up a great number of large enclosures. Secondly, the enclosures used may be still too small for the large, very mobile species *Carabus problematicus*, which was sometimes distinctly more abundant in the external traps than in the inner ones.
In interpreting the results, it is necessary to bear in mind that they represent estimates of active adult populations. The values obtained for biomass do not express the total biomass of the carabids present, partly because the larval stages are not included here, but also because a fraction of the adult populations subsists in the soil in an inactive state. In particular, the decline of the active populations after their maximum activity period does not reflect real population trends, since some animals survive till the following year, thus ensuring a certain population stability from year to year (see e.g. Van Dijk 1972). Also, results for the smallest species are lacking, but comparative observations with other, more open biotopes revealed that these species (including, among others, Notiophilus, Asaphidion and Bembidion species) are scarce in the beech forest, and do not contribute much biomass.

The total population density and biomass recorded in the beech forest of Lembeek are rather low compared with the few results given in the literature. Carabid populations seem to be highly variable according to the kind of biotope, and generally larger in fields than in forests. Heydemann (1962) and Dubrovskaya (1970) both estimate the population density in fields at tens of individuals m\(^{-2}\), equivalent to a biomass of more than 1.5 g m\(^{-2}\) according to Heydemann (1962). However, Karacik-Wasylk (1975) gives values about ten times lower. Wide variations in population density may be characteristic of open biotopes, as suggested by Baars’s (1979) results. Estimations made in forests (Van der Drift 1951; Weidemann 1971, 1972; Desiere 1972; Grum 1971b, 1973, 1975, 1976) seem more homogeneous. They only concern medium- and large-sized species, which makes the comparison with the present work easier. The maximum total population density of communities reaches a few individuals m\(^{-2}\) — thus values of the same order as the present results, but generally higher. Only Frank’s (1967) estimates are abnormally high, but they are doubtful, given that 10 marked individuals of each large species were released in an enclosure as small as 1/2 m\(^2\) and yet few were recaptured.

The low abundance of carabids in Lembeek results from both a low population density of each species and a limited number of species. This relative poverty is explained by the rather extreme conditions of the biotope caused by the high acidity of the soil, which must have repercussions on the carabid community in terms of the availability of prey species (earthworms, molluses, etc.; Loreau 1984a).

5. Résumé

Densité de population et biomasse des Carabidae (Coleoptera) dans un peuplement forestier

Six séries d’estimations de la densité de population et de la biomasse des carabides adultes de taille grande et moyenne présents dans une hêtraie furent réalisées à l’aide de techniques de capture-recapture et d’effort de chasse au sein d’enclos.

Ces méthodes fournissent des estimations précises des populations, dues au taux élevé de captures et à la bonne réalisation des conditions d’application: en particulier, une distribution aléatoire des individus marqués, une absence d’influence du marquage sur la mortalité, un bon isolement des populations par les enclos.

La densité de population totale du peuplement de carabides atteint 0.5 à 2 individus m\(^{-2}\) selon les années, ce qui équivaut à une biomasse de 85 à 150 mg m\(^{-2}\) (masse fraîche). Une diminution générale de la densité de 1978 à 1981 est causée par une augmentation constante de la pluviosité au-dessus de la normale, qui affecte quelques espèces printanières abondantes à populations très variables. L’espèce dominante Abax ater maintient une biomasse supérieure à celle des autres espèces.

Par comparaison avec d’autres milieux, la densité de population et la biomasse trouvées s’avèrent basses. Ceci s’explique vraisemblablement par la forte acidité du sol.

6. References


276


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Synopsis: Original scientific paper


Ten series of population density and biomass estimations of medium- and large-sized adult carabids in a beech forest were performed using capture-recapture and catch-effort techniques within enclosures.

These methods give precise estimates of the enclosed populations, owing to the high proportion of individuals captured and to the conditions of application being fulfilled, i.e. a random distribution of marked individuals, an absence of influence of marking on mortality, and a good isolation of the populations by the enclosures.

The total population density of the carabid community reaches from 0.5 to 2 individuals m$^{-2}$, depending on the year, corresponding to a biomass of 85 to 150 mg m$^{-2}$ (fresh mass). A general decrease in density from 1978 to 1981 is caused by a constant increase in rainfall above mean levels, which affects some abundant spring species with highly variable populations. The dominant species *Abax aler* maintains a higher biomass than the other species.

Compared with other biotopes, the population density and biomass found appear to be low. This is most likely a consequence of the high acidity of the soil.

Key words: Carabidae, population density, biomass, forest, soil, enclosures.