

Occupation of space by the carabid beetle *Abax ater*

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Abstract

The occupation of space by *Abax ater* Villers (Coleoptera, Carabidae) was studied in a near-climax beechwood in Belgium in May-June 1990 using capture-recapture in a grid of 180 pitfall traps.

Population density fluctuated around an average of 2,062 individuals per hectare, a roughly constant value for 13 years as indicated by comparison with previous data. Locomotor activity was weakly correlated with daily temperature, and was higher in males than in females.

The spatial distribution of activity was weakly contagious, and increasingly approached a random distribution at larger scales. The contagious distribution was not explained by a small-scale heterogeneity in either temperature or food quantity.

The movements appeared to conform to a typical random walk over relatively short distances; the mean distance covered per day by males was 1.8 m. "Home range" was estimated at 660 m² on average, but was slightly larger in males than in females. From this it was estimated that an individual is liable to encounter and interact with an average of 543 other individuals in its trivial movements, which suggests a considerable mixing in the population.

Abax ater in the beechwood studied thus provides an example among insects of an equilibrium species in which spatial heterogeneity plays a minor role.

Keywords: Spatial heterogeneity, spatial dispersion, movements, "home range", population density, activity, capture-recapture, Carabidae, *Abax ater*.

Résumé

L'occupation de l'espace par *Abax ater* Villers (Coleoptera, Carabidae) a été étudiée dans une hêtraie proche du stade climax en Belgique en mai-juin 1990 à l'aide d'une technique de capture-marquage-recapture sur une grille de 180 pièges d'activité.

La densité de population a fluctué autour d'une moyenne de 2 062 individus par hectare; cette valeur est restée à peu près constante pendant 13 ans comme l'indique une comparaison avec des données antérieures. L'activité locomotrice était faiblement corrélée avec la température journalière et était plus élevée chez les mâles que chez les femelles.

La distribution spatiale de l'activité était faiblement agrégative et tendait vers une distribution aléatoire à des échelles plus grandes. Le caractère agrégatif de cette distribution ne s'expliquait pas par une hétérogénéité spatiale à petite échelle ni de la température ni de la quantité de nourriture.

Les déplacements individuels se faisaient apparemment au hasard sur des distances relativement courtes; la distance moyenne couverte par jour était de 1,8 m chez les mâles. La taille du « domaine vital » a été estimée à 660 m² en moyenne, avec des valeurs légèrement plus élevées chez les mâles.

que chez les femelles. Ces valeurs ont permis d'estimer qu'un individu est susceptible de rencontrer et d'entrer en interaction avec 543 autres individus au cours de ses déplacements courants, ce qui suggère un mélange considérable de la population.

Abax ater présente donc, dans la hêtraie étudiée, un exemple parmi les insectes d'une espèce à l'équilibre chez laquelle l'hétérogénéité spatiale ne joue qu'un rôle mineur.

INTRODUCTION

Spatial heterogeneity, whether due to the environment or the behavioural or ecological responses of organisms, is today recognized as a key factor promoting the stability and diversity of ecological systems (e.g. SMITH, 1972; HASSELL, 1980; CHESSON & ROSENZWEIG, 1991). Its potential role in the persistence of carabid beetle populations has been emphasized in particular by DEN BOER (1968, 1979, 1981), who proposed that populations exist as interaction groups which frequently go extinct and are refounded by dispersal.

A number of studies have been conducted on the spatial structure of carabid populations as revealed by quadrat sampling or, more commonly, the distribution of activity in pitfall traps (GREENSLADE, 1963; GRÜM, 1973, 1990; REISE & WEIDEMANN, 1975; LOREAU, 1984b; LUFF, 1986; NIEMELÄ *et al.*, 1986, 1992; DESENDER, 1988; NIEMELÄ, 1990). They showed that carabid populations are generally aggregated, but sometimes distributed at random in favourable biotopes. Another set of works has been devoted to the dynamical aspect of individual movements using capture-recapture techniques or radioactive marking (GREENSLADE, 1964; GRÜM, 1965, 1971; RIVARD, 1965; BAARS, 1979; RIJNSDORP, 1980; DRACH & CANCELA DA FONSECA, 1990; NÈVE DE MÉVERGNIES & BAGUETTE, 1990). BAARS (1979) thus identified two types of movement in carabids: the random walk, characterized by movements over short distances in random directions, and the directed movement, in which long distances are covered in a more or less constant direction. Most of the other works were mainly concerned with the dispersal of individuals from their point of release. But we still have little information on the actual occupation of space by carabids, combining both these static and dynamical aspects. In particular, we have no direct estimate of the activity or "home" ranges of carabids and the way these ranges overlap.

We addressed this issue in a field study of the occupation of space by *Abax ater* Villers using intensive capture-recapture. We chose *Abax ater* both because it is the dominant species in the forest where we worked and because its ecology and population dynamics had already been extensively investigated there (LOREAU, 1983a, 1983b, 1984b, 1985, 1990).

STUDY SITE AND METHODS

Study site

The work was conducted in a beechwood close to the climax stage at Lembeek, Belgium. This biotope is described in detail in LOREAU (1984a).

Capture-recapture methods

The ground beetles were caught using modified pitfall traps (fig.1). Each trap consisted of a plastic bottle of commercial water 8.5 cm in diameter and cut at mid-height, the upper part of which was turned upside down and served as a funnel to prevent predation by small vertebrates. The bottle slid in a plastic pipe of the same diameter which remained sunk into the ground. This design allowed us to easily collect and replace the bottle, as well as close the trap when necessary (the bottle was then placed upside down in the pipe). The bottom of the bottle was pierced with holes to allow draining of rainwater and thus prevent drowning of the beetles. Four galvanized steel sheets of 50 x 25 cm were sunk a few centimetres into the ground crosswise around the pipe to increase trapping efficiency.

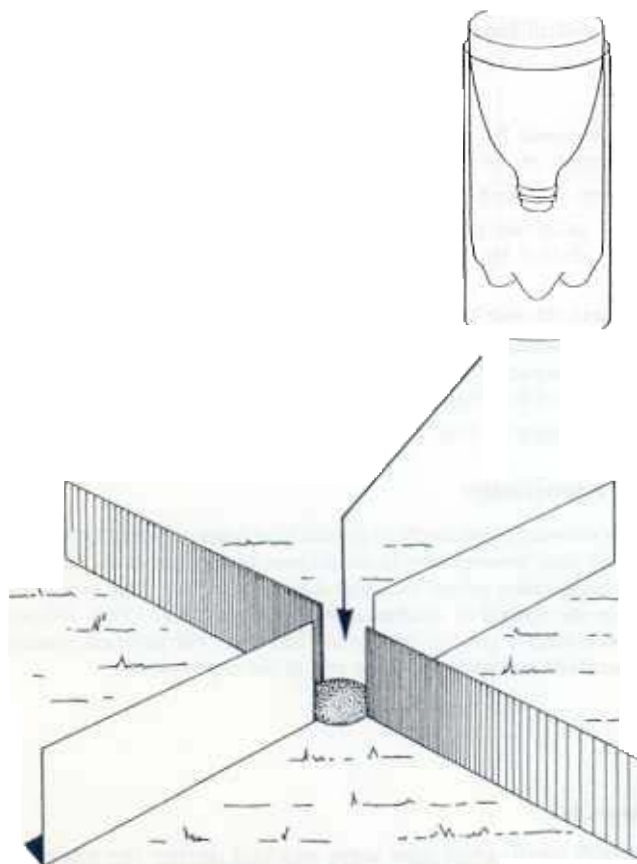


FIG. 1. - Trap used to catch the beetles

180 such traps were placed in a grid of 12 x 15 traps approximately 5 m apart (see fig. 4). Considering each trap as the centre of a square of 5 x 5 m, the area covered by the grid was thus 4,500m².

The experiment ran from 4 May to 11 June 1990. From 4 to 21 May, the traps were opened each day only on one half of the experimental site, with a daily alternation of the two halves of the site. This alternation was required by the considerable time taken by marking in the beginning. From 21 May to

11 June, as the proportion of marked individuals increased in the population, all traps were opened and visited daily, except on 2 and 3 June, when the traps were closed because of the exceptional abundance of individuals caught during the night from 1 to 2 June.

The beetles collected in the traps were brought to a nearby field laboratory, where their sex, their mark, their place of capture and their weight (measured to the nearest milligram) were recorded. The individuals captured for the first time were marked individually following the method described in SOUTHWOOD (1978). Pits were ground in the elytra and the pronotum using a pointed grindstone, fitted in a drill-chuck driven by a flexible wire.

The beetles were then released on the day of their capture 1 m from the trap in which they were caught, in the direction of one of the steel sheets surrounding the trap. The direction of the first release was determined at random, while those of the next releases were determined by turning each time 90° clockwise to ensure statistical homogeneity of the directions of release.

Analysis of data

The data were processed by computer using the CMR package of LE BOULENGÉ (1985). This package provided estimates of the following variables:

- (1) Population size, estimated per day by the method of MANLY & PARR (1968).
- (2) Trappability, calculated per day according to MANLY & PARR (1968) as the number of recaptured individuals, divided by the total number of individuals liable to recapture (first and last captures excluded).
- (3) Individual mean distance covered between successive captures.
- (4) "Home range", estimated over the whole sampling period by the method of JENNRICH & TURNER (1969) and MAZURKIEWICZ (1969). This method measures "home range" using a normal bivariate statistical model, as the area of the ellipse corresponding to a probability of the animal's presence of 95%.
- (5) Average and variance of body mass per trap.

Measurement of temperature

Temperature was recorded continuously at ground level using a thermo-hygrograph. To investigate the influence of a small-scale heterogeneity in temperature on the spatial dispersion of *Abax ater*, we measured the average temperature around each trap during the period of the experiment using Pallman thermometers based on the method of saccharose inversion (BERTHET, 1959). 180 such thermometers were placed in the same relative position next to the 180 traps. For technical reasons, however, only 119 of them were recovered and analysed at the end of the experiment.

RESULTS

Demographic aspects

A total of 1,005 adult *Abax ater* were marked during the experiment, and 841 recaptures were obtained. In addition, 135 teneral were caught but could not be marked because of their soft elytra.

The estimates of the total adult population size fluctuated around a mean of 928 ± 117 individuals (95% confidence interval), which corresponds to a population density of $2,062 \pm 260$ individuals per hectare. The male and female populations were estimated at 604 ± 77 individuals and 355 ± 68 individuals respectively. As the experimental site was open, we had to check whether its surface area of $4,500 \text{ m}^2$ was relevant for the estimation of population density. This can be tested

roughly by noting that the smaller the area of the site, the greater the possible overestimation of population density because of individuals from outside the site. Therefore we defined concentric rectangles within our grid of traps and estimated population densities for each of them. We regarded the difference between density estimates per day in two successive areas as a random variable, the mean of which was expected to decrease close to zero when the area was large enough for the bias introduced by peripheral individuals to become insignificant. This was found to be the case between 3,000 and 4,500 m² (fig. 2). Thus our population density estimates can be considered valid.

Trappability as estimated by the Manly-Parr method constitutes a measure of individual locomotor activity. The mean trappability of males was higher than that of females (0.153 against 0.116 over the whole experimental period with all individuals pooled; $\chi^2 = 9.95$, 1 d.f., $P < 0.01$). Trappability (males and females combined) was significantly though weakly correlated with daily mean temperature ($r = 0.437$, 22 d.f., $P < 0.05$), while the log-transformed daily total catch was not ($r = 0.351$, 22 d.f., $P > 0.05$).

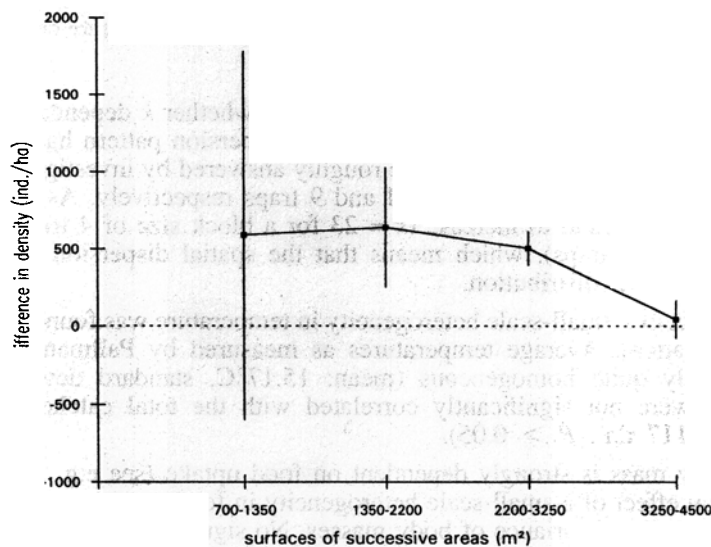


FIG. 2. – Test of the validity of the population density estimates: differences in the density estimates in successive concentric rectangles as a function of the surface areas of the latter (mean \pm standard error).

Spatial dispersion pattern

The spatial distribution of activity, as revealed by the total numbers of catches in the traps over the whole experimental period, deviated from a random distribution: the variance-to-mean ratio, which was used to test this deviation (SOUTHWOOD, 1978), was significantly higher than 1 (1.753; $\chi^2 = 313.81$, 179 d.f., $P < 0.00001$), which indicates a contagious distribution. A negative binomial distribution with a value of the dispersion parameter $k = 14.5$, was fitted to the frequency distribution of catches in the traps. As figure 3 shows, the agreement is quite good ($\chi^2 = 6.52$, 13 d.f., $P > 0.9$).

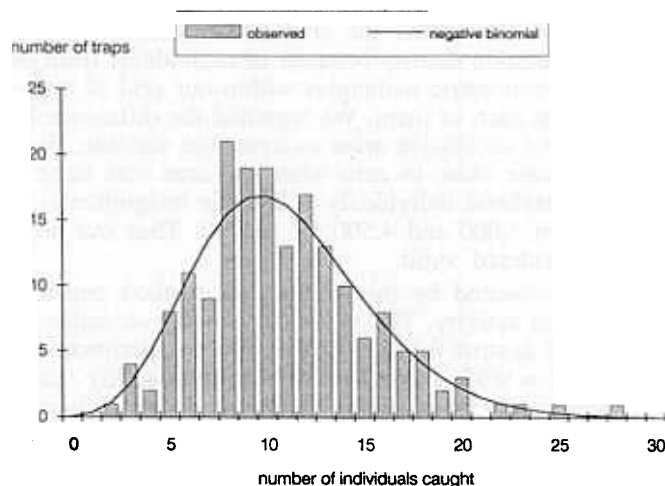


FIG. 3. – Observed and theoretical (negative binomial) frequency distributions of the catches in the traps.

An interesting question that can be raised is whether k depends on the spatial scale of sampling: what would have been the dispersion pattern had activity been recorded at a larger scale? This can be roughly answered by investigating the effect of pooling the catches by blocks of 4 and 9 traps respectively. As the block size increased, k was found to increase ($k = 23$ for a block size of 4 traps, and 30 for a block size of 9 traps), which means that the spatial dispersion pattern tended towards a random distribution.

No effect of a small-scale heterogeneity in temperature was found on the spatial dispersion pattern. Average temperatures as measured by Pallman thermometers were spatially quite homogeneous (mean: 15.17°C, standard deviation: 0.50°C only), and were not significantly correlated with the total catches in the traps ($r = 0.163$, 117 d.f., $P > 0.05$).

As body mass is strongly dependent on food uptake (see e.g. LOREAU, 1990), the potential effect of a small-scale heterogeneity in food quantity was investigated using an analysis of variance of body masses. No significant difference among the mean body masses in the various traps was found, either in males ($F = 1.13$, 179 and 1,250 d.f., $P > 0.05$) or in females ($F = 0.93$, 164 and 297 d.f., $P > 0.05$).

Movements and “home range”

The movements recorded by capture-recapture data appeared to conform to a typical random walk over relatively short distances; Figure 4 shows the trajectories of two individuals as examples. The mean distance covered between two successive captures was 14.2 m in males and 13.1 m in females. The frequency distribution of the mean distances travelled per day for the 105 males which were caught at least 4 times was roughly log-normal with a mean at 1.8 m/day (fig. 5). This distribution was not established for females because only 18 of them were caught at least 4 times.

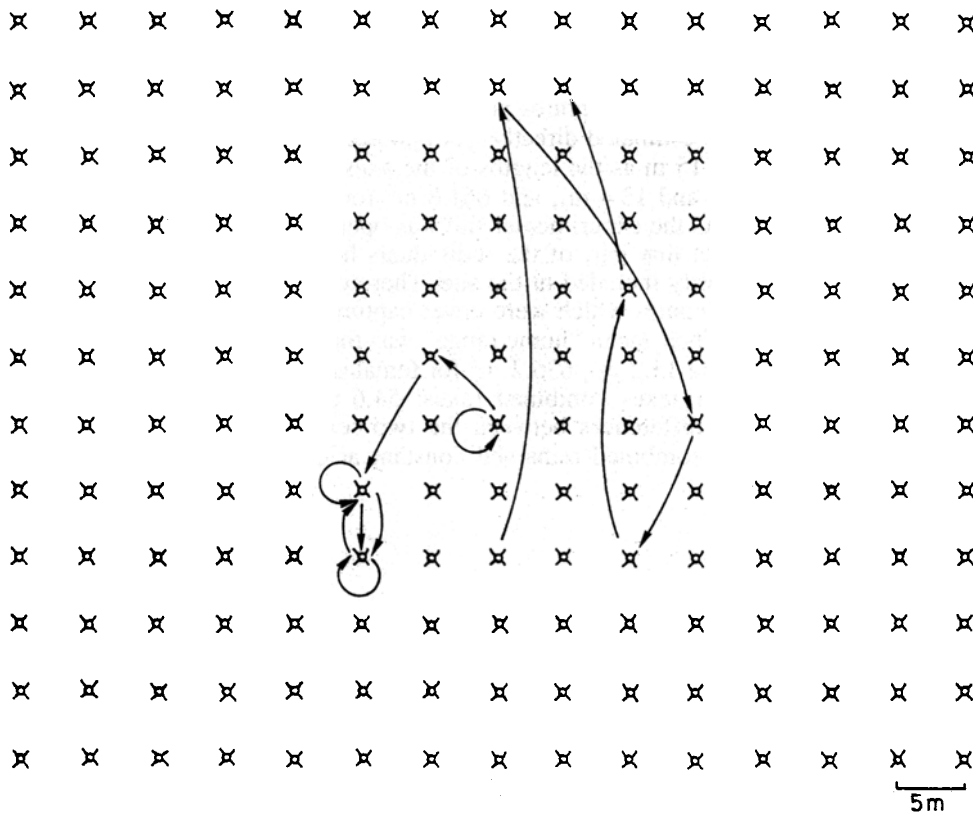


FIG. 4. - Trajectory recorded by capture-recapture in the experimental site for two selected individuals.

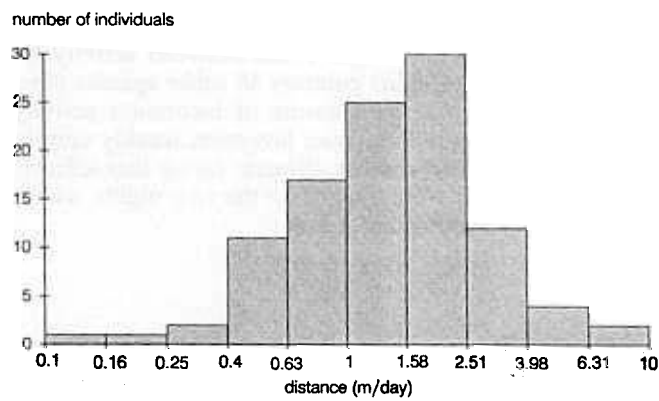


FIG. 5. - Frequency distribution of the mean distances covered per day by those males which were caught at least 4 times.

The calculation of "home range" requires at least 3 captures in 3 different traps per individual, which was the case for 179 males and 22 females. Separate estimates of their individual "home ranges" are not very informative because of the relatively low numbers of captures per individual; therefore we only give their mean "home range" as estimated directly from pooled data. This was 674.5 m² for males (with 57 m and 15 m as the lengths of the axes of the ellipse), 554.2 m² for females (axes: 52.6 m and 13.4 m), and 661.8 m² for both sexes combined (axes: 56.6 m and 14.8 m). As the experimental site was open, these estimates might have been biased by the fact that part of the individuals had a "home range" that was peripheral and only partly included in the site. Therefore, we recalculated them for the 82 males and 12 females which were never captured in one of the traps on the perimeter of the site. Their mean "home range" was then estimated at 661.7 m² for males (axes: 55.6 m and 15.2 m), 635.2 m² for females (axes: 48.4 m and 16.8 m), and 659.5 m² for both sexes combined (axes: 54.6 m and 15.4 m). These new estimates reduced the differences between the two sexes, but the average "home range" for both sexes combined remained constant at 660 m².

DISCUSSION

Demographic aspects

Although the focus in this study was on spatial patterns and dynamics, not demography, some demographic aspects are worth of interest. The population of *Abax ater* in the beechwood of Lembeek reached the same density in 1990 as during the years 1978 to 1987, which indicates a remarkable stability in this population (LOREAU, 1990). Males were both more active and more abundant than females, which is in keeping with previous results indicating a biased sex ratio in favour of males in the spring (LOREAU, 1985).

Also, the lack of correlation between daily catch and mean temperature confirms the complex and variable response of *Abax ater* to climatic factors over short periods of time which was found previously (LOREAU, 1983a), and contrasts with the strong correlation that exists between activity and temperature over a whole season (LOREAU, 1983a) contrary to other species (OLSZEWSKI, 1979). Trappability, which provides a better measure of locomotor activity because it is independent of all density fluctuations, was, however, weakly correlated with daily temperature. Rainfall is certainly another climatic factor that affects activity, since massive numbers of *Abax ater* were caught on the two nights when heavy rainfall occurred after several dry days.

Spatial dispersion pattern

Spatial distribution of activity has been found to be contagious in most carabid populations (LUFF, 1986; NIEMELÄ *et al.*, 1986, 1992; DESENDER, 1988; NIEMELÄ, 1990), and this was also the case to some extent for the *Abax ater* population studied. However, the latter was only weakly aggregated, since a value over 8 of the dispersion parameter k of the negative binomial distribution is classically regarded

as an indication that the distribution is approaching a Poisson series (SOUTHWOOD, 1978). Moreover, k increased further with increasing spatial scale of sampling. Thus the departure from a random distribution is likely to be due to a small-scale heterogeneity of the environment, but at larger scales *Abax ater* tends in its activity to occupy the whole available space, as was found previously using pitfall trapping at a large scale (LOREAU, 1984b). These results are consistent with those of GRÜM (1973), who found that the large-scale distribution of activity of *Carabus arvensis* was random or near-random in the most homogeneous and favourable biotope. The tendency towards a large-scale random distribution of activity seems to be a feature of dominant species in favourable biotopes, and to indicate a tendency towards the "saturation" of a biotope by a species (LOREAU, 1984b).

The great homogeneity of the beechwood from the point of view of *Abax ater* is further indicated by the low spatial variability of temperature, the lack of correlation between catch number and local temperature, and the spatial homogeneity of body mass. Small-scale heterogeneity in either microclimatic conditions or food quantity does not seem to be responsible for the small-scale contagious distribution of *Abax ater*. The factor most likely to explain it is the spatial structure of the environment, such as the presence of dead trees, the thickness and compactness of the litter and the associated variations in soil moisture, which can influence the movements and rest sites of carabids at small scale. But other factors, such as active aggregation by attraction (LUFF, 1986) or the distribution of some preferred prey types (i.e., food quality), may also be involved. Unfortunately, we did not collect quantitative data to test these hypotheses.

Movements and "home range"

The pattern of movement of *Abax ater* was apparently a typical random walk. As a result, the movements recorded by capture-recapture data certainly underestimate the actual mobility to a large extent, since they only record distances travelled along a straight line between two traps, i.e., they reduce a complex random walk into a resultant directed movement. Nevertheless, they are useful for comparative purposes. The mean distance of 1.8 m/day covered by male *Abax ater* thus appears to be distinctly lower than that of some larger *Carabus* species (RIJNSDORP, 1980; DRACH & CANCELA DA FONSECA, 1990; NÈVE DE MÉVERGNIES & BAGUETTE, 1990).

The present work provides the first estimate of a "home range" in carabids. Although the term is questionable and therefore is put in quotes here (there is no evidence so far that carabids have anything like a "home"), the notion of "home range" as the area over which an animal engages in trivial movements (foraging, search for mates, rest) is not specific to vertebrates and can be applied to insects (SOUTHWOOD, 1978). Despite the relatively low mobility of *Abax ater*, its "home range" was estimated at about 660 m². Given the population density, an average of 135 other individuals are included in the "home range" of any individual. However, they themselves move and change with time. A rough estimate of the number of other individuals whose "home range" overlaps with that of a given individual is provided by the number of individuals in an ellipse of which the axes are twice longer than the ellipse defining the "home range", and thus the surface area is 4 times larger. This was found to be 543 individuals. This means that an individual

is liable to encounter and interact with an average of 543 other individuals in its trivial movements, and thus that a considerable mixing occurs in the population.

It must be noted that the "home range" estimate may be dependent on the length of the experimental period. As carabids move freely, their activity area may be constantly changing, so that the "home range" estimate would increase with the duration of the observation. Longer experimental periods would be necessary to verify this hypothesis.

The role of spatial heterogeneity

Although DEN BOER (1968, 1979, 1981) emphasized the universality of the phenomena of subpopulation extinction and colonization by dispersal due to the mosaic nature of populations and their environment, their frequency is likely to strongly decrease in the predictable and homogeneous climax environments (BLONDEL, 1986). Spatial heterogeneity appears indeed to play a minor role in the *Abax ater* population of the near-climax beechwood at Lembeek. The spatial distribution of activity was only weakly contagious at small scale and increasingly approached a random distribution at larger scales. Individual "home ranges" overlapped widely, ensuring a sizeable mixing of the population. In such a population, there is no objective basis for the distinction of different interaction groups. Only significant discontinuities in the environment at yet larger scales, such as changes in the vegetation type, are likely to subdivide or isolate it. But the population was also found to be remarkably stable. Therefore, at such large scales, the size of the population makes the probability of a population extinction extremely low.

Abax ater in the beechwood of Lembeek thus provides an example among insects of an equilibrium species with features of a *K*-strategist. More generally, these features are likely to be those of dominant species in climax environments: the latter are generally more buffered, predictable and homogeneous, so that some successful species like *Abax ater* can be adapted to the overall conditions of the environment, occupy space widely and stabilize their populations by regulatory processes (LOREAU, 1990). But for most other species with more specific requirements, and in other biotopes, spatial heterogeneity and temporal fluctuations are likely to be much more significant, as has been observed in other carabids.

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