

# DISPERSAL POWER AND SURVIVAL

CARABIDS IN A CULTIVATED  
COUNTRYSIDE



MISCELLANEOUS PAPERS 14 (1977)  
LANDBOUWHOGESCHOOL WAGENINGEN THE NETHERLANDS

E R R A T A :

- p. 13, III<sup>b</sup>, 11<sup>th</sup> line from above: "Populations Replacement" should be: "Population Replacement".
- p. 39, Table 3, column 21: insert on the line of species 66 the reference-mark "7".
- p. 106, insert: GADKIL, M.: Dispersal: Population consequences and evolution. Ecology 52, 253-261 (1971).
- p. 113, insert between 141 and 146: 144. *Stomis pumicatus* Panz.: Moist, deciduous forest. Reproduction in spring. Brachypterous. West-Palearctic species, not far to the North.
- p. 110, species 65: *Bradycellus ruficollis* Steph.
- p. 121, 12<sup>th</sup> line from below: "D(1), E(1), E(1),..." should be: "D(1), E(1), F(1).."
- p. 136, under 1. *Abax parallelepipedus* P & M, the total of '66 should be 75 (in stead of 71).
- p. 142, "34. *Amara Lunicollis*" should be: "34. *Amara lunicollis*."
- p. 147, under 65. *Bradycellus ruficollis* Steph., line '65 (in the middle) "AH" should be "BH".
- p. 189, 9<sup>th</sup> line from below: "of N ind." should be "of N ind. are full-winged".

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(with a mathematical appendix by J. REDDINGIUS)

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## INTRODUCTION AND SUMMARY

During a field investigation into the most important factors governing the distribution of carabid beetles over a number of more or less natural localities in the neighbourhood of Wijster (prov. of Drenthe, the Netherlands), it became soon evident that change and variation rather than stability and homogeneity predominate in the natural situation.

One aspect of the spatial and temporal variation within natural populations – spreading of risk – has already been dealt with several times; cf. DEN BOER (1968a, 1971a) and REDDINGIUS & DEN BOER (1970). In this paper we will treat another aspect: the frequency of natural extinctions and (re)foundings, together with the dominant part played by dispersal in this turnover.

We preferred to treat these topics fundamentally, i.e. we formulated the current opinions upon the predominant effects of dispersal as two opposing sets of hypotheses (the founding hypothesis against the escape and/or overflow hypotheses), and developed a testing procedure that enabled us whether to accept or to reject one of these sets (cf. REDDINGIUS, 1971 b).

During the many discussions on the subject of this paper I experienced that some people – although generally endorsing the results and conclusions – did not think the form in which the matter was treated very enlightening. To remove this difficulty we preface the paper by a survey of the sequence of events that led to our conclusions. This survey will consist of three parts:

- I. The sampling of carabid beetles and the distribution of their numbers over sampling sites.
- II. Dispersal; habitat relations; abundant and sparse species.
- III. Connection of the observations under I with those under II: the effects of cultivation. Summary of the conclusions.

### I. THE DISTRIBUTION OF CARABID BEETLES OVER SAMPLING SITES

#### Ia. *The study area*

When I arrived at Wijster in 1958 to investigate the relations between habitat and numbers I found myself in a highly cultivated countryside. No more than 8% of the surface of Drenthe still consisted of more or less natural habitats (which should decrease still more in the next few years); another 7–8% (former blowing sands) was planted with conifers. For a short survey of the history of this landscape, see: 8.1.1. Most remnants of natural habitat in Drenthe are small (only a few ha) and highly isolated; a notable exception is formed by the nature preserve: Heath of Kralo and Dwingeloo (about 1200 ha). The map in Appendix A. II and also Fig. 5 give some idea of this situation.

I decided first to study the available remnants of natural habitat (deciduous forest, heath, peat moor, secondary bogs, not planted blowing sands), because it was expected that these would show the more original relations between habitat and numbers. Moreover, in most natural sites structural changes will occur more gradually than in cultivated grounds, which makes it possible to study certain natural situations for several years in a nearly unchanged (structural) condition.

In the course of nine years (1959 up to and including 1967) a great part of the more important remnants of natural habitat around Wijster (within a radius of about 10 km, cf. map in Appendix A. II) and a few less natural sites (e.g. coniferous plantations), have been sampled continuously during at least one year, and in many cases during a number of succeeding years. In Appendix A. II each of these 73 sampling sites is shortly described, and placed into one of 4 habitat groups: D, woodland; E, blown sand; F, heath and peat moor; G, instable habitats (see also: Table 1; 3.7 and 4.1).

The data on the quantitative distribution of species derived from these samplings (sampling program) are considered and treated as one block of information. From 1969 onwards hypotheses on the relations between habitat and numbers thus arising are tested both by making new (independent) observations and by performing adequate experiments. On the other hand, independent hypotheses can be tested by 'opening' (working up) this block of information in a new and independent way. One kind of these new observations had thus to be the sampling of man-made habitats (e.g. meadows, orchards, agricultural fields).

#### *Ib. The subject of the study*

From the very beginning we decided to concentrate upon ground-beetles (Carabidae, Coleoptera) because:

- (1) They can be sampled continuously, objectively (i.e. independent of the skill of the student) and rather quantitatively by using pitfalls.
- (2) They can be manipulated (e.g. marked) rather easily and are thus well suited for certain kinds of experiments (e.g. preference experiments).
- (3) They show a rather uniform way of life, that for the majority of the species can be described as: polyphagous predators that move around at the surface of the soil and are univoltine (only one generation in a year); it appeared, however, that in many species part of the individuals again reproduce during one (or even more) following seasons.
- (4) They are a well-known group of arthropods, both taxonomically, autecologically (e.g. THIELE, 1971) and zoogeographically (e.g.: DARLINGTON, 1943; LINDROTH, 1949, 1972), and an interesting one in many respects (e.g. by the occurrence of wing di(poly)morphism).
- (5) The number of species that can be expected to live in some natural locality is both sufficient for different kinds of comparative study, and not as high as to make it necessary to invest too much time into identification.
- (6) It is expected that they – being polyphagous predators – play some part in the

stabilization of numbers among a lot of surface-dwelling arthropods, not only under natural conditions but possibly also in different kinds of man-made sites (e.g. agricultural fields), cf. BASEDOW (1973).

The block of information from our sampling program (cf. I.a) contains data on 148 carabid species. These species are mentioned in Appendix A.I: short descriptions are given of the habitat, reproductive cycle, wing development and distributional area of the 74 more frequently caught ones among them (divided at the median); some information on the 74 species that are only caught incidentally is presented in tabular form.

#### *Ic. Technique and method of sampling*

During the nine years of our sampling program (and in many cases also after that) the technique of sampling has been standardized as far as possible, in order to get results that are comparable in most relevant respects. We used square, metal pitfalls of two types, both with an effective circumference of 100 cm: (1) live traps with perpendicular, smoothly coated, 30 cm high walls; (2) square funnels with a formalin-filled, easily changeable container. Each pitfall, whether live trap or funnel is provided with a draining system, and is freely suspended in an outer container of standardized dimensions. The main function of the latter is to continually drain away excessive rain water from the catch unit; it also enabled us to sample floating vegetations and other very wet places.\* Each sampling site was provided with three such pitfalls: two live traps and one funnel trap (in the middle), buried into the soil at mutual distances of 10 m (as far as possible in a straight line), with the upper rim just at the surface. Each pitfall was equipped with a dazzle-painted roof on four legs, and with a wire-netting (meshes of one square cm) suspended at about 6 cm below the upper rim to keep out litter and predators like shrews, lizards, frogs, toads and birds.

Such a standard set of 3 pitfalls was placed in the centre of each of the study habitats (cf. Appendix A.II), and each week at Wednesday – also in winter (starting in the last week of February) – the animals caught were collected from the live traps, and the container under the funnel was changed. All catches were taken to the laboratory, where the carabid beetles were identified, 'sexed', counted, catalogued, etc. and stored in formalin (or otherwise) for further research (during the first seven years also the other arthropods have been stored).

Combining two live traps and one funnel trap into one standard set originated from the desirability for all samples to keep the possibility at any moment to compare the capture efficiency of two quite different types of pitfalls, and – if necessary – to be able to correct the catches from one type with those from the other. This combination has appeared to be a quite lucky one: middle-sized and big carabid beetles are generally caught better in the live traps (except during the very start and at the end of

\*The traps and outer containers were fabricated by the TFDL (Technical and Physical Engineering Research Service) at Wageningen from undestructable materials.



the reproductive cycle), and small carabid beetles are generally caught better in the funnels (see also: 4.4.3).

After some years already a conjunction of indications changed the supposition (present from the very start) into the firm conviction that for most carabid species (the few exceptions are discussed in 4.4.4) the catches in such a standard set, summed up over the whole period of activity (or a whole catch year) – in the following: year-sample – must give a workable estimate of the relative abundance of that species in the pertinent sample site during that (reproductive) season. From 1968 onwards this conviction was tested in intensive capture-recapture experiments with different species and in different localities. For all cases tested up till now (40 cases concerning 10 very different species) it could be shown that the value of the year-sample is no worse estimator of (relative) abundance than the population size as it can be calculated from the recaptures with the help of different adequate models (cf. SEBER, 1973), and there were even indications that it could be a much better estimator. In BAARS, DEN BOER & VAN DER EIJK (in prep.) these data will be discussed more fully.

BAARS, VAN DIJK & VAN DER EIJK (in prep.) tackled this problem directly by just before the start of reproduction fencing part of a locality at the Heath of Kralo and then trapping all individuals of each of two abundant species present there. A mean density thus obtained could be compared with the value of the relevant year-sample scored during that season with a nearby (20–120 m distant) standard set of pitfalls. This was repeated in several sites and in several years, after which it could be concluded that for each of the two species the year-sample gives a surprisingly accurate (but of course relative) measure of mean density; see 2.1, item (4) for further information.

The high accuracy of this estimator is in accordance with the findings of BAARS (in prep.), who in the field studied the walking pattern of the above species in sufficient details to be able to simulate it in a computer model; with the help of this model he could indeed accurately simulate our pitfall-catches.

Although not yet each of the 74 species has been tested conclusively, the present evidence concerning the above aselect set of carabid species (among which both species of woodland, of heath and of blown sand, and both spring reproducing and autumn reproducing species) admits the conclusion that for the majority of our species we can safely use the values of the different year-samples as – at least approximate – estimates of the level of abundance of that species in the sample sites and/or years concerned. For each of the 74 species in Appendix A.III these relative abundance-values are given for all the year-samples of our sampling program in which the species was represented (j year-samples).

#### Id. *The Distribution of Population Sizes (DPS)*

From the data in Appendix A.III many hypotheses concerning the processes underlying the observed relations between habitat and numbers can be generated.

Most of these – the testing of which is in progress – concern aspects that are unrelated to the subject of this paper, however.

The present theme started with the observation that for some species the frequency histogram of year-samples over geometric abundance classes showed some remarkable features that were different from those of other species. We used geometric classes since more significant changes in the abundance of a population are of an about multiplicative nature (e.g. caused by reproduction or mortality). We preferred  $\times 3$ -classes, because these have the advantage of requiring no splitting of the integer numbers of individuals; cf. 5.1 and WILLIAMS, 1964; perhaps, a ' $\times e$ ' scale would have been – theoretically – more adequate, but the differences with our ' $\times 3$ ' scale –  $e$  being the base of natural logarithms, i.e. 2.71828... – are not very apparent.

Since a logarithmic scale has its origin at minus infinity there should be other classes before class I (with the bounds  $\frac{1}{2}$  and  $1\frac{1}{2}$ , and thus containing the year-samples with only one individual). Because we are unable to distinguish between sample sites where the species is lacking completely and those in which it is so sparse that not even a single catch is realized during a whole year, we put all zero year-samples together in the same class (0) that is placed just before this class I. This zero-class thus contains that part of the distribution that remains hidden below our level of observation. In most species, however, these zero year-samples can for the greater part be considered 'true zeros' (sample sites not occupied by the species); moreover, for most species the few extremely sparse populations that may be among them will have an only low chance to escape early extinction: underpopulation, KLOMP, VAN MONTFORT & TAMMES (1964). Hence, for each of our 74 species such a frequency histogram of abundances contained the same number of year-samples – viz. 175, being the total number in our sampling program.

When looking at the thus obtained frequency histograms we first established that in some species the year-samples apparently show an about log-normal distribution, and, hence – when the frequencies are stepwise cumulated over the successive geometric classes (the highest class thus containing all 175 year-samples) – these species approximately show the well-known, S-shaped (sigmoid), cumulative (log-) normal distribution (a good example is species 136: *Pterostichus niger*). By the use of 'probability paper' for plotting such a cumulated frequency histogram this feature is conveniently visualized: if the cumulated year-samples are about normally distributed over the geometric abundance classes a straight line can be fitted through the class centres (see e.g. LEWIS & TAYLOR, 1967). In the following this line on probability paper (whether straight or not) will be named: the cumulation line of the species.

Such a straight cumulation line means two things: first, that in our study area all kinds of abundances – that are naturally centred around some 'most probable abundance' – seem to be realized without 'preference' (apparently as a result of overall undirected local and/or seasonal conditions), and secondly, that our sampling

program obviously took an about representative set out of the sample space of realized abundances.

Note, that this also holds when such a straight cumulation line starts from a high value in the zero class (which is the more general case), i.e. when part of the log-normal distribution remains 'hidden' in this zero-class (examples are 26: *Amara communis*; 75: *Carabus arvensis*). This simply means that the pertinent species – because of its restricting habitat demands – is living in only a fraction of our 73 sampling sites, but it also means that for the occupied sites the above conditions of 'normality' are still fulfilled. Consequently, the above 'most probable abundance' – which can be considered the result of that combination of conditions tolerable to the species, that is most frequently (both in space and in time) realized in our study area – will be situated somewhat more to the left, i.e. in a lower geometric class.

Many species, however, show a quite different type of cumulation line: viz. a line with a pronounced bend, because it exists of a slowly rising line-part over the lower geometric classes that sharply changes into a steeply rising line-part over the higher classes. This type is pictured in Fig. 2 (A) together with the above straight line (B). As compared with the B-type (straight line) this A-type of cumulation line evidently results from the lower abundance classes being – relative to the higher ones, that show the above B-line – severely underrepresented (good examples are species 70: *Calathus melanocephalus*; 88: *Cymindis macularis*). Note, that this A-type of cumulation line – just as the B-type (see above) – can as well start from a high as from a low value in the zero-class, which also in this case points to either more or less restricting habitat demands.

Many species that mainly occupy sites belonging to one of the habitat groups D (woodland), or E (blown sand) or F (heath and peat moor), see Appendix A. II, appeared to show an A-type of cumulation line, whereas nearly all the species inhabiting instable sites (G group) exhibited the B-type.

The explanatory hypotheses generated by these interesting findings might be tested, when both: (1) we would be able to express the observed differences between A- and B-type cumulation lines in some adequate and standardized measure, and (2) we could make independent observations on the hypothesized phenomena to quantitatively compare them for different groups of species with the relevant values of the above measure.

Because the differences between A- and B-type cumulation lines result from a different ratio between the relative amount of year-samples with low and that with high catches respectively, we preferred a measure in which the contribution of the values of the different year-samples would be adequately scaled, i.e. a high value of that measure when the relative frequency of low catches is high (B-type) and a low value when this frequency is low (A-type). We also preferred a distribution-free measure, i.e. a measure that does not depend on the conditions of some underlying distribution. Because the number of year-samples in the zero-class gives a kind of information that is different from that in the other classes (see above) it seemed better not to include the zero samples into such a measure.

These (and some other) conditions are sufficiently satisfied by the simple and standardized expression for the Distribution of Population Sizes:  $DPS =$

$$1 - \frac{\sum \ln(n_i + 1)}{j \cdot \ln(N + j)},$$
 in which  $n_i$  is the value of the year-sample,  $j$  is the number of year-

samples with catches, and  $N$  is the total number of specimens caught. We add one to each  $n_i$  in order that also year-samples with only one individual contribute to our scaling ( $\ln 1 = 0$ ); because in this way  $j$  times one is added in the numerator, we add  $j$  to  $N$  in the denominator, since  $\sum(n_i + 1) = \sum n_i + j = N + j$ . More about the features of this expression for  $DPS$  can be found in 5.4, whereas the justification of its use is mathematically supported by REDDINGIUS in Appendix B. II. The  $DPS$ -values that thus could be calculated for our 74 species are – together with the composing elements – given in Tabel 7. In Fig. 3 the correspondence is shown between these  $DPS$ -values (abscissa) and the pertinent cumulation lines, from which it appears that this correspondence is indeed very close (cf. 6.1.2) in spite of the fact that the model underlying the cumulation lines is quite different from the mathematics behind the expression for  $DPS$  (cf. Appendix B. II). In my opinion, an important point is, that by using  $DPS$  we could keep the number of assumptions minimal, i.e. we could drop the – apparently unnecessary – assumptions concerning ‘normality’.

For the following it can thus be kept in mind that the most relevant feature that is measured by  $DPS$  is the degree to which sparser populations of the pertinent species were met in our study area as compared with more abundant ones (scaled at the overall level of abundance of that species): the lower the fraction of the year-samples ( $j$ ) with relatively low catches the lower the value of  $DPS$  (which is standardized between 0 and 1).

## II. OTHER FEATURES OF THE CARABID BEETLES

The explanatory hypotheses that were generated by the observed differences between the  $DPS$ -values of different species necessitated the gathering of information on three groups of other features of the species concerned: (a) dispersal capabilities, (b) preferred habitats and (c) overall level of abundance. Because we intended to relate this information with the relevant  $DPS$ -values the former should be independent of the latter, i.e. this information should be essentially the same whether it is derived from the material and data of our sampling program or obtained from a quite different (independent) source. Therefore, we preferably started the classing of our species according to (a) or (b) from the data published by LARSSON (1939) for Denmark and LINDROTH (1945, 1949) for Fennoscandia, since their ecological definitions of species are based on the unified – and quite differently obtained – experiences of a great number of taxonomic collectors.

However, it soon appeared that dispersal capabilities and habitat preferences remain not the same throughout the distributional area of a species, and our very sampling program produced some of the more interesting deviations (see: Appendix A. I, e.g. 17: *Agonum obscurum*; 80: *Carabus problematicus*; 109: *Leistus rufescens*). In all such cases it could easily be shown, however (by consulting other literature, e.g. HORION (1941) and by own experiences), that the data from our sampling program obviously are unbiased as to that, and fit some large-scale – it is true, only poorly known – geographical clines in ecological features. Concerning some of these features (e.g. wing polymorphism, relative abundances in different kinds of habitat) our sampling program soon appeared to have produced some of the most reliable data known so far. This reliability is greatly due to the uniform way of life of most carabids (cf. Ib.: 3), to which our sampling technique is as precisely tuned as possible (see also: Ic, 4.4.3 and 4.4.4).

#### IIa. *Differences in the capability to disperse*

Carabid beetles are well-known (cf. e.g. DARLINGTON, 1943; LINDROTH, 1949) for the existence of both constantly unwinged – or shortly winged – (brachypterous) species, constantly fullwinged (macropterous) and wing di(poly)morphic species. In brachypterous species dispersal can only occur by walking, so the dispersal power (ability to bridge rather great distances) generally will be poor. In many wing di(poly)morphic species with an only very low frequency of fullwinged specimens the powers of dispersal will not be much better. On the other hand, many macropterous species may be expected to possess a high dispersal power, and thus readily to found or refound populations.

But the latter expectation met with some complications: about 1968 (when we became interested in dispersal phenomena) direct observations on flying carabid beetles were remarkably scarce and very incidental (cf. LINDROTH, 1945, 1949). Therefore, we decided to start continuous observations on the frequency of flight activities in carabid beetles. Because carabids drop when hitting an obstacle during flight they soon appeared to be sampled satisfactorily with the help of a window-trap (a large sheet of glass held vertically by a frame at about 80 cm above the vegetation, and provided with a collecting trough containing formalin 4%; see: SOUTHWOOD, 1966 (p. 193); DEN BOER, 1971c (p. 128, and another type at p. 56); VAN HUIZEN, in press). From 1969 onwards and in different localities we continually sample flying carabids in this way. After five years we could establish that 26 of our 74 test species (and 28 of the 74 very sparse ones (cf. Ib): see Appendix A.I) show flight activities. Among these 26 species are 17 constantly macropterous ones and 9 wing di(poly)morphic species. We thus considered these 26 species to form a group with a high – or at least sufficient – dispersal power (in the following: B-species).

To get another estimate of flight capabilities too Mrs. W. DEN BOER – DAANJE measured the wing-surface (relative to the surface of the elytra) in most of these species and compared this measure with that in many of the other macropterous and di

(poly)morphic species. It thus appeared that in 6 macropterous species the wings are much smaller than usual; together with similar notes by LINDROTH (1945) on them we became convinced that individuals of these species will only exceptionally be capable of flying (e.g. when by chance the wings are larger; see note 6 to Table 3). Hence, the dispersal power of these species will be about as poor as that of di(poly)morphic ones with a very low frequency of fullwinged specimens (less than 1%, say). Therefore, we considered these latter species, the above 6 macropterous ones and the constantly brachypterous species together to form a group (of 25 species) with poor – or at least insufficient – powers of dispersal (in the following A-species).

The remaining 23 species (C-species) could not unambiguously be placed concerning their powers of dispersal. During the work on the present paper these C-species have appeared to come close to the A-species. All these observations on the flight capabilities and dispersal power of our 74 species are summarized in Table 3; see further: 4.2. It will be evident that these observations are quite independent of the data derived from our sampling program.

Only one objection seems still to be possible: it might be supposed that the frequency of fullwinged specimens in wing di(poly)morphic species will be underestimated when derived from pitfall-catches, because these specimens could be expected to fly away (cf. DEN BOER, 1970). Since the greater part of pitfall-catches occur during reproduction, however, when in most species the wing-muscles can be expected to be reduced (JOHNSON, 1969; VAN HUIZEN, in press), such an effect – when it occurs at all – must only be a slight one. This is confirmed by the fact that our data on the frequency of fullwinged specimens generally satisfactorily link up with those of LINDROTH (1945, 1949, p. 366–416), that are derived from faunistic collections. Among the few deviations from the data of LINDROTH the most significant one is a case where the frequency of fullwinged specimens is *higher* in Drenthe than in Fennoscandia, viz. *Agonum fuliginosum*, cf. LINDROTH (1945). For the present (this is studied more closely) also the catches from our window-traps suggest that flight activities – at least in di(poly)morphic species, but probably also in most macropterous ones – are restricted to the periods just before and just after reproduction (see also: DEN BOER, 1971b).

#### IIb. *Differences in habitat preference*

Since no species will be randomly distributed over all the available habitats the more or less clear habitat preferences in different species were expected to give the basic information for the investigation mentioned in Ia (see also: DEN BOER, 1968b). Our sampling program was intended to give this basic information. Before making full use of it we had to show that an average individual of a certain species will be caught in different types of habitat and/or in different years with an about similar chance. From Ic can be derived that we will not make a significant error when this is indeed accepted.

This means that the habitat preferences of the different species can be quantified

now from the data in Appendix A. III, e.g. by computing which percentage of N is caught totally in the sites belonging to each of the four habitat groups (D, E, F and G) defined in Appendix A. II (cf. Table 1). The highest ones among these percentages are given in Table 4. Before drawing conclusions from these data we have to take into account that the numbers of year-samples taken from sites of different habitat groups are not similar, and this will influence the fractions of N caught there.

We arrived at the scaling discussed in 4.3. (mean number of ind. in the year-samples of the preferred habitat group is at least four times as high as that in the remaining year-samples) by first comparing the habitat descriptions given by LINDROTH (1945) for Fennoscandia with our own 'definitions' for Drenthe (based on 'general field experience', in which it is tried to reduce the experiences from the pitfalls towards an acceptable proportion), and noting the deviations. These deviations were considered more closely, and it was made sure that these were indeed real geographical deviations (e.g. by comparing with observations from other parts of The Netherlands and from Germany). The resulting 'habitat definitions' are given in Appendix A. I. It then appeared no longer to be difficult to find the best scaling, by which the spreading of the species over the different habitat groups is thus made as independent from our sampling program as possible, without being obliged to make different subjective choices for different species. Species that did not fetch the standard for any of the four habitat groups were placed in a separate H-group: these species are more 'eurytopic' than other ones.

Remembering that man-made sites were hardly incorporated in our sampling program, Table 4 shows that the few species that mainly occupy this kind of localities are adequately placed in the G- or H-group respectively (e.g. the species 22, 31, 35, 54, 60, 104 and 141; cf. Table 2); a species like 139: *Pterostichus strenuus*, that about equally inhabits woodland and weedy vegetations is also adequately placed here in the D-group. Only one point remains to be considered: when comparing the DPS-values of species brought to different habitat groups the different numbers of year-samples that in our sampling program belong to these groups (in the headings of Table 4) might give rise to some bias, because DPS has a slight tendency to increase with increasing j (see 5.4.4 and Appendix B. II, sections 4 and 6). One would suggest for such comparisons to rescale the DPS-values on the highest number of year-samples in such a habitat group, i.e. on 68 as in group D. But the reader can easily make sure – by using expression (III) in 5.4.4 and the values given in Table 7 – that this would change the DPS-values concerned for a few percent only.

Accordingly, none of our conclusions have appeared to depend on whether or not such a rescaling is performed (merely the already significant differences would after rescaling have become somewhat more significant). Since there are as much objections against such a 'correction', however (e.g.: in our study area the sites belonging to each of the four habitat groups are also unequally distributed; most species are not nearly restricted to sites of only one habitat group; therefore, such a 'correction' would in any case be a maximal one), we entirely abandoned it. Because

our DPS-values have appeared to be rather robust against many kinds of moderate deviations – like the above ones – from some ideal sampling program (see also: 6.2.2), conclusions based on the comparing of species of different habitat groups will be sufficiently independent of our sampling program.

### IIc. *Differences in abundance*

When one wants to study the possible effects of differences in the overall abundances of different carabid species, one meets with the problem how to measure 'abundance' comparatively. To clarify this: a certain number of individuals on a square meter, say (mean density) will have a quite different meaning for a species with small individuals than for a species with big individuals. For the former species a much smaller surface should be taken into account than for the latter; but how much smaller?

One should like to measure 'effective abundance', i.e. the chance to interact (mutually between individuals, and/or between individuals and other relevant 'factors', e.g. food). This is exactly what is done with a pitfall: the individuals caught in a pitfall constitute a standardized sample from a single 'interaction group'; hence, in a species with small individuals these interactions will occur on a small surface and in a species with big individuals on a large surface around the pitfall. That is why the pitfall catches give an accurate (relative) estimate of mean density within the same species; cf. Ic, and see further: 1.4 and 2.1, items (4), (5) and (6).

When both capture efficiency (in a standard set of pitfalls) and way of life (especially as far as it is connected with walking activities) would be sufficiently similar for different carabid species our pitfall catches could also be expected to give a workable comparative estimate of the differences in 'effective abundance' between different species. In 4.4 we amply discuss how far the above conditions are answered, and it is concluded there that for most species the N-values (cf. Table 3) can indeed be used for roughly ranking our species from sparse ones towards very abundant ones.

Strictly speaking such a ranking is only valid within our sampling program, but also considering quantitative data from comparable localities elsewhere does not give an essentially different picture: most of our 'abundant' (sparse) species are also abundant (sparse) in surrounding areas. Mainly a few species of man-made habitats (e.g.: 54, *Bembidion lampros*; 141: *Pterostichus vulgaris*) were – quite naturally – ranked too low, but it could be established that they did not influence our conclusions (ch. 7). Hence, the above abundance-ranking of our species can – broadly outlined – be considered sufficiently independent of our sampling program to allow more general conclusions.

It must also be considered whether the DPS-values of abundant species are unbiased with respect to that of more sparse ones, i.e. whether or not there is a systematic relation between the value of N and that of DPS. From Appendix B. II, sections 5 and 6 it appears that when increasing values of N coincide with proportionally



increasing values of  $j$  (see also: 5.4.4) DPS will increase, but Appendix B. II, section 7 shows that increasing values of  $N$ , with the value of  $j$  fixed, will result in decreasing values of DPS. Because it may generally be expected that abundant species will be present in more year-samples than comparable sparse ones (cf. 7.5.1), but also that the  $j$ -values of abundant species will be somewhat less than directly proportionally greater (in respect to the pertinent  $N$ -values) than in comparable sparse ones – owing to the year-samples with high catches that take an important part of  $N$  – there are no special reasons why the DPS-values of abundant species should be systematically different from those of more sparse ones. Hence, when the DPS-values of abundant species would indeed appear to be very different from those of sparse ones there must be special – i.e. biological – reasons for that.

### III. SUMMARY OF THE CONCLUSIONS

#### III a. *Statistical methods used for comparing DPS with the observations in IIa, IIb and IIc*

A statistical analysis on the relations between DPS and dispersal capabilities (IIa), habitat preferences (IIb) and differences in abundance (IIc) respectively may give us now some insight into the processes most probably underlying the differences in DPS-values observed (cf. Table 7). For different reasons we prefer the use of rank-order tests:

- (1) Little or nothing is known about the mathematical distribution form underlying field data.
- (2) In all our work we prefer to make as few assumptions as possible.
- (3) Most field data are somehow relative and/or are used as relative estimates for something that cannot be measured directly (samples), so that we are mainly interested in their being larger or smaller than other equally scaled data.
- (4) Field data can only exceptionally be very precise, so that it seems wise not to attribute much importance on the absolute values of the numbers obtained.

The following statistical methods were used in this paper:

- (1) Where two sets of values on the same property may be considered sufficiently independent their homogeneity was tested by the nonparametric Mann-Whitney U-test or Wilcoxon two-samples test (U-test): SIEGEL (1956, p. 116–127), VAN DER VAART (1950).
- (2) Where the frequencies in discrete categories must be compared between two (or more) independent samples, the Chi square ( $\chi^2$ ) test was used: SIEGEL (1956, p. 104–111, p. 175–179).
- (3) To test whether or not there is a correlation between two sets of values that are connected in pairs the rank correlation method of M. G. KENDALL is used ( $\tau$ ): KENDALL (1962). Since many students are more familiar with the product-moment correlation method in many cases this coefficient ( $r$ ) is given too.

- (4) In a few cases we had to test whether or not two samples of bivariate values belong to the same population. This is performed by the test proposed by WHEELER & WATSON (1964) and by MARDIA (1972, p. 196–201). This powerful test can be considered the nonparametric counterpart of the well-known discriminant function analyses.
- (5) In many cases we had to test whether the regression curve of X on t, say, lies consistently above or below the regression curve of Y on t. In most cases it seemed obvious to compare the lines of least squares according to an analysis of variance (SNEDECOR & COCHRAN, 1967, ch. 14), but the assumptions underlying the linear regression model appeared seldom to be satisfied. Therefore REDDINGIUS proposed to use the nonparametric Median test (SIEGEL, 1956, p. 111) in a manner as described in 5.2.3 (Med.-test). A mathematical justification of this is given by REDDINGIUS in Appendix B. I. To let the reader in contact with more familiar statistics too, the p-values of the analysis of variance on the lines of least squares are also given. The results of the two methods are nowhere conflicting.

### IIIb. *DPS and dispersal power*

As a group, species that show flight activities, i.e. B-species, have DPS-values that are very significantly higher than those of A-species (cf. IIa); the same is true for B-species as compared with A- + C-species (see further 6.1.1). This is also clearly reflected in differences in the relevant cumulation lines (cf. Id): Fig. 3 and 6.1.2.

Hence, A-species (and C-species in a less degree) are characterized by a very low frequency of sparser populations (as compared with B-species). Because sparse populations generally will run a greater risk of extinction than more abundant ones this may point to an insufficient replacement of disappeared populations as a consequence of the poor powers of dispersal of these species. Since a species can only persist in a certain area when (the Realization of) Populations Replacement – in the following RPR – ultimately is about complete, this situation should have arisen rather recently, for otherwise already long ago these species would have disappeared from our study area. This again means that these poor powers of dispersal must have been sufficient in some past situation, i.e. under more natural conditions. Hence, A- and C-species must be considered victims of the rapid extension of cultivation. Once they will have occupied extensive, more or less continuous and rather stable habitats, for only under such conditions RPR can be kept about complete – via refoundings – by walking individuals.

On the other hand should B-species be 'adapted' to environments that also under natural conditions were already small and widely separated and/or only temporarily inhabitable, for under such conditions flight activities will be needed to keep up an about complete RPR.

In this picture the extinction and (re)founding of populations are considered continually occurring processes governing the survival of a species, by which the

main effect of dispersal will be: increasing the chance to (re)found populations and in this way compensating the extinctions.

The above hypothesis was already developed by combining various, and otherwise unrelated observations (cf. DEN BOER, 1970, 1971b), before we could dispose of cumulation lines and adequate DPS-values, so that the above relations between DPS and dispersal power were a first confirmation of this hypothesis. On this base other relations could be predicted and tested. Because these are amply discussed in the present paper in the following they will only be mentioned.

(1) Because big carabids will be able to walk greater distances than will smaller ones, A-species with big individuals can be expected to show higher DPS-values than A-species with smaller individuals. This expectation appeared to be a right one: 6.4.

### IIIc. *DPS and habitat preferences*

Species occupying woodland (D-species), or blown sand fixed by vegetation (E-species), or old heath and/or peat moor (F-species) may be considered species of rather permanent habitats that once covered extensive areas in Drenthe (see also: 3.7 and 4.1). Because unstable habitats generally play an important part among the sites occupied by most H-species (e.g. agricultural fields in 35, 22, 31; weedy grass vegetations in 146, 26, 106; readily inundated places in 76, 30, 79, 118; etc., cf. Table 4) the H-species best match the G-species. Moreover, in many H-species the dispersal capabilities are nicely supplemented by the possibilities to reproduce in very different habitats (a good example is 136: *Pterostichus niger*: cf. 6.7.1); see further under (5).

(2) Species that occupy (or also occupy) instable sites (G- and H-species) can thus be expected to show much higher DPS-values than species inhabiting more permanent localities (D-, E- and F-species). This expectation is very convincingly confirmed (cf. 6.5), whereas – as could be expected – the DPS-values of G-species do not differ from those of H-species (cf. 6.7.1).

(3) The low DPS-values in species occupying permanent habitats are considered to have resulted from the cutting up by cultivation of the preferred habitat into small, widely separated pieces (cf. IIIb). When some rather extensive part of the original landscape would have been left undisturbed by cultivation the species living there should thus have to show a still higher relative frequency of sparse populations than species only living now in small and isolated remnants of natural habitat. The former situation is about realized in our F-species that for the greater part have been sampled at the Heath of Kralo and Dwingeloo (1200 ha; cf. map in Appendix A. II), whereas our D-species have indeed mainly been sampled in small and isolated remnants of forest. Our F-species may thus be expected to show higher DPS-values than the D-species, which expectation is answered (cf. 6.6). In this way we showed the occurrence of the historical process that was supposed to underly the decrease of RPR – and thus of DPS – in species occupying permanent habitats (cf. IIIb, and 3.3).

(4) Among the 26 B-species (cf. IIa) 17 species occupy temporary habitats and 9 spe-

cies permanent ones. In 6.5.1 is shown that the latter 9 species have lower powers of dispersal (that can about be estimated from the catches in window-traps) and correspondingly lower DPS-values (cf. 6.5.3) than the former 17 species, which again fits the picture given above.

(5) Among the H-species A- and C-species have DPS-values that are about similar to those of the pertinent B-species. This illustrates the point made above that 'eurytopy' may supplement rather poor dispersal capabilities, i.e. for the (re)founding of populations eurytopic species generally will have to cover smaller distances than more stenotopic ones. Under more natural conditions this feature will be shifted towards more stenotopic species, a remnant of which is found in our F-species at the Heath of Kralo and Dwingeloo; cf. (3). The DPS-values of these eurytopic A- and C-species are accordingly higher again than those of A- and C-species of permanent habitats (more stenotopic ones); see further 6.7.2, whereas in 6.7.3 and 6.7.4 this is also confirmed by considering still other relations.

#### IIIId. *DPS and differences in abundance*

When it is indeed right that the predominant effect (and thus its 'biological function', so to say) of dispersal is: increasing the chance to (re)found populations it is not expected that abundant species of permanent habitats will show a higher level of dispersal than more sparse ones (rather the reverse), in spite of the fact that in abundant species more individuals will potentially be available for dispersal than in more sparse ones.

(6) It could indeed be shown that the individual chance to disperse is much lower for a specimen of an abundant B-species occupying permanent habitats than for a specimen of a more sparse one (cf. 7.3.1). The absolute number of individuals dispersing (flying away) from populations of such abundant B-species are about the same as those from populations of more sparse ones (cf. Table 12). As a consequence are the DPS-values of all the former species lower than those of any of the latter (cf. 7.5.2): since the  $j$ -values are – very remarkable – about similar for species of both groups, besides an about equal number of year-samples in the lowest classes (mainly newly founded populations) the year-samples with higher catches must therefore in the abundant species be spread over more classes than in the more sparse ones (where the largest populations by definition are smaller). This is equivalent to saying that the RPR of such abundant species is not complete (some medium-sized classes are apparently underrepresented), i.e. these species would have been represented in more year-samples when the powers of dispersal would have been better.

(7) The latter point is confirmed by comparing among these abundant B-species, the F-species with the D-species: Table 12. The lower chance to (re)found populations in the D-species apparently has already resulted in a lowering of the level of dispersal (by natural selection) as compared with that in the F-species (compare (3) and 6.6); cf. 7.5.3. This trend is expected to continue, even – but slower – in the F-species.

(8) The data presented in (6) are again in concordance with the situation among wing di(poly)morphic species occupying permanent habitats: the percentage of full-winged specimens appears to be negatively correlated with abundance (cf. 7.4). As could be expected is such a correlation lacking among the wing di(poly)morphic species occupying temporary habitats.

(9) If the explanation of the systematic difference between the DPS-values of abundant and more sparse B-species of permanent habitats – as it is given in (6) – is the right one, the DPS-values of abundant A- (and also C-) species should not be as systematically smaller than those of the more sparse ones: because of the poor powers of dispersal both abundant and sparse A- (and C-) species will have been severely influenced by the progress of cultivation. Accordingly are the DPS-values of these abundant A- (and C-) species hardly different from those of the more sparse ones (cf. 7.6.1): most of the DPS-values concerned are low. Hence, among the species of permanent habitats the RPR of sparse B-species (i.e. the species 9, 86, 112 and 139: cf. Table 12) has least severely been influenced by the progress of cultivation, which is also illustrated by the fact that these sparse B-species have DPS- (and also j-) values that are similar to those of B-species of temporary habitats, but at the same time they show both significantly higher j-values and significantly higher DPS-values than sparse A- (or C-) species of permanent habitats (cf. 7.6.2).

(10) Why have during the progress of cultivation the dispersal capabilities of sparse B-species occupying permanent habitats not severely been reduced by natural selection because of the growing island-distribution of the preferred habitats?

In my opinion the answer must be: because in these species flight activities are more integrated into the way of life than in abundant carabid species (where flight activities – as far as these are possible – are only ‘functional’ as means to disperse). Hence, these sparse B-species are supposed to show a more or less ‘nomadic’ way of life. For more information on this point, see: 7.6.3.

### IIIe. *Carabid species in the centre and at the fringes of distribution*

It is often supposed that the dynamics of populations should be quite different at the fringes than in the centre of distribution of a species (cf. NICHOLSON, 1958). Because 19 of our 74 species are living here at the fringes of their distribution (cf. Appendix A. I and Table 13) we may expect that these 19 species would be different from the 55 ‘centre’ species in one or more of the features studied. In 8.2.1 is shown, however, that among the ‘centre’ species there are no more abundant ones, no more A-species, and no more species of permanent habitats than among the ‘fringe’ species. Moreover are the DPS-values of ‘fringe’ species similar to those of ‘centre’ species. Fringe species are only caught in somewhat less year-samples (mean 50) than centre species (mean 68), although they apparently are *not* more stenotopic. Hence, the only difference that could be traced, could be something like: ‘fringe’ species seem to react somewhat more ‘heavily’ (in their changes of numbers) than do ‘centre’ species concerning conditions that are not overall favourable, by which

the chance of extinction of those populations of 'fringe' species that live in sub-optimal habitats may be somewhat higher than that of 'centre' species. For the time being it is supposed that this slight difference (when it appears to be consistent) not so much results from a being different of the animals but more from a being different of the pattern of temporal fluctuations of some environmental – probably physical – factors at the fringes of geographical distribution.

### III f. *Other opinions on the predominant effect of dispersal*

Up till now the opinion that the predominant effect of dispersal should be: increasing the chance to (re)found populations (founding hypothesis) – and that emerged from our sampling program, cf. III b –, has only been put forward by DEN BOER (1970, 1971b, this paper), although also in the views of ANDREWARTHA & BIRCH (1954) and BIRCH (1957, 1971) it seems to be an understood thing. Other opinions on the significance of dispersal (that are only incidentally expressed explicitly) can be brought under two headings: (a) dispersal capabilities enable the individuals to escape from 'currently adverse conditions'. According to JOHNSON (1969) this view seems especially to be favoured by entomologists, and he does already note some objections (see e.g. p. 637–639): escape hypothesis; (b) dispersal results from overcrowding, i.e. from exceeding 'carrying capacity' (favoured in population biology): overflow hypothesis.

Especially SOUTHWOOD (1962) tries to find the evolutionary significance of dispersal, but his conclusions mainly apply to species living in unstable environments. DEMPSTER (1975) combines the views of SOUTHWOOD (1962) with the idea of 'overflow', and therefore is his definition of dispersal (cf. 7.1) an adequate starting point for the formulation of a testable null hypothesis. GADKILL (1971) is mainly concerned with the 'overflow' aspect of dispersal. To make completely clear that all the conclusions mentioned above can only be brought into line with each other under the founding hypothesis we preferred to treat the whole matter as a testing of the founding hypothesis against the escape and overflow hypotheses.

Moreover, in our opinion one can only correctly judge the import of a set of conclusions when one has fully considered the possible alternatives (see also: REDDINGIUS, 1971b). The above hypotheses are amply discussed and put in a testable form in chapter 3, and tested in the chapters 6 and 7; especially in section 7.7 we try to place our conclusions back again in the context of the more general knowledge on dispersal.

The founding hypothesis must be considered a necessary corollary of the conclusion (from our abundance histograms; Id) that the extinction and (re)founding of populations must be considered continually occurring processes. The – nearly inescapable – preoccupation of population dynamics with dense and/or large populations prevented the discovery of this 'biological function' of dispersal (cf. 7.8), so that the attention was drawn by phenomena that in most cases will only be marginally connected with dispersal: 'escape' and 'overflow'. This was again facilitated by

the general opinion among population biologists that natural extinctions only occur exceptionally, which again resulted from the above preoccupation with dense populations (cf. WATT, 1971).

When the text of the present paper was already fixed we came across some new papers (SIMBERLOFF, 1974; DIAMOND, 1975) – see also 1.1 – in which extinction and (re)founding are evidently considered processes continually occurring on a time-scale of decennia (or even years). It is a pity, however, that this is connected with the – in my opinion quite unnecessary – assumption of the existence of some ‘mechanism’ that should maintain an ‘equilibrium’ between the number of extinctions and that of refoundings (cf. 8.5.2). Apparently have the thoughts on the ‘regulation of population numbers’ (cf. NICHOLSON, 1933, and 1.1) recently been extended towards the level of ‘numbers of species’; in fact, this possibility was already indicated in the work of PRESTON (1962) and has been used in this sense by MAC ARTHUR & WILSON (1967).

### IIIg. *The survival of carabids in a cultivated countryside*

On the base of conclusion (3) we could consider the indirect effects of the progress of cultivation as these will have occurred at two separate points on the time-scale (about 50–100 years apart) to be shown by the D- and F-species respectively. From this model we could estimate that at least 14% of the populations of the pertinent (D-)species must have been disappeared unreplaced, exclusively as a result of a growing island distribution of the remnants of natural habitat during a period of 50–100 years (cf. 8.1.3). There are several reasons to suppose that this will be an underestimation, even apart from the direct losses by the reclamation of the greater part of natural areas, by which not only the number of populations but also the number of potential dispersers will have decreased significantly (cf. 8.1.4). We thus expect that within a few centuries – and probably even earlier – the majority of our (carabid) species now occupying remnants of permanent natural habitat will become extinct. Although it may also be expected that in the (very) long run some other species with still sufficient powers of dispersal will gradually succeed in occupying part of these emptying habitats, for the time being the net result will be a significant impoverishment of our (carabid) fauna (cf. 8.3. and 8.4). However, it seems not inevitable to await this impoverishment. It seems possible to take some measures – if accompanied by intensive investigations into the powers of dispersal and dynamics of the species concerned – that might counteract these processes:

- (1) First of all it will be necessary to preserve – or even ‘create’ – a few extensive ‘natural’ areas (like the Heath of Kralo and Dwingeloo).
- (2) Certain waste sites, gardens, hedgerows, roadside verges, railway embankments may be made – by adequate measures – in an important way to participate in the linking together of remnants of natural habitat (cf. ELTON, 1958).
- (3) We will have to create ‘stepping stones’ at places where apparent bottlenecks for

the dispersal of many species occur, and we will have regularly to test – and probably to adapt – the suitability of these ‘stepping-stones’.

- (4) Last but not least for the time being, i.e. during the decennia in which the countryside is made suitable for the survival of part of its inhabitants, we will have regularly to repopulate remnants of natural habitat with part of its original species that already disappeared during the progress of cultivation. See further: 8.5, DEN BOER (1970), DIAMOND (1975).



## 1. STATING THE PROBLEM

1.1. Since the discussions between THOMPSON (1929, 1939) and NICHOLSON (1933), diverging ideas concerning the concept 'animal population' have been at the root of many controversies in population dynamics. Analogous to the 'holistic' views of CLEMENTS (1916), FRIEDERICHS (1930), TANSLEY (1935), ALLEE c.s. (1949), and others, concerning 'biocoenosis' and 'ecosystem', NICHOLSON (1933, 1954) and e.g. WILBERT (1962, 1971) apparently consider an animal population to be 'a real entity', and consequently attribute to it the power of selfregulation; see also BAKKER (1964). The ideas of many other authors probably still go in a similar direction, because – most characteristically – they generally speak of population 'mechanisms' and preferably adhere to equilibrium theories and models (see e.g. WILSON & BOSSERT, 1971; WILLIAMSON, 1972; VARLEY, GRADWELL & HASSELL, 1973; SOLOMON, 1976).

Many of such investigators hardly allow for the extinction of populations under natural conditions. But see also: MACARTHUR & WILSON (1967, ch. 2 & 3) and SIMBERLOFF (1974) concerning extinctions on islands.

According to THOMPSON (1956) 'the population... as an entity it exists only in the mind, having merely the status of a concept... the only real beings that exist in the real world are individual organisms'. In fact, THOMPSON (1929, p. 275) has a more analytic and probabilistic starting point, which is also advocated by e.g. ANDREWARTHA & BIRCH (1954), ANDREWARTHA (1957), BIRCH (1957), DEN BOER (1968a, 1973), REDDINGIUS (1971a).

From the latter point of view with a probability of one, each population will become extinct at some time, and consequently THOMPSON (1956), ANDREWARTHA & BIRCH (1954), BIRCH (1957, 1971) discuss some examples of the natural extinction of local populations. NICHOLSON (1958), however, still tries to explain the known examples of population extinction as phenomena only occurring near the fringes of distribution of a species, where 'density-governing reaction must be slight and inconspicuous'; on the other hand, in the centre of distribution 'density-governing reaction permits a species to persist indefinitely in all favourable places' (but see also: WILSON, 1968).

At this point one wonders whether it might be shown that the natural extinction of populations is a phenomenon occurring frequently enough to be traced in field investigations, not only at the fringes of distribution of species, but in fact everywhere. And as an immediate corollary of this a prominent place will have to be attributed to studying of the effects of dispersal. To develop a relevant strategy we will first have to consider some points.

1.2. First of all, one realizes that no population can exist longer than the locality in

which it is living, i.e. plant and animal species of temporary habitats\* will necessarily live in populations that are continually disappearing and being refounded.

Following NICHOLSON (1958) such species might be living throughout the whole area of distribution under circumstances thought by him to be restricted to the fringes of distribution. A necessary condition for the survival of such species is, of course, that the powers of dispersal\*\* suffice to keep up a rate of (re)founding of populations, which in the long run, at least keeps pace with the rate of disappearance of populations.

In fact, the above condition must be a necessary one for the ultimate survival of all species. It may be expected, however, that the powers of dispersal required to satisfy this condition will show great differences between species, being not only related to the rate of disappearance of populations but also to the availability and pattern of distribution of suitable localities. Therefore, even in a species area with many generally long-living populations in permanently inhabitable localities at comparatively short mutual distances, some dispersal will still be required to compensate for the assumed infrequent population extinctions by some infrequent (re)foundings. But in the latter case, the required minimal level of dispersal may happen to be so low that it might be difficult to establish its existence or to separate it from 'trivial movement' (compare SOUTHWOOD, 1962).

From a review of the literature on the migration of terrestrial arthropods, SOUTHWOOD (1962) concludes that the level of migratory movement (= kind of movement that carries the individual away from its population, i.e.: dispersal) is positively correlated with the degree of impermanence of the habitat, being high in species of temporary habitats and being low in species of permanent habitats. He supposes that the level of migratory movement in any species will be geared by natural selection to the rate of change of its habitat. Conceiving 'habitat' as in the first note and taking into account the above condition for the survival of species, his conclusion can be reformulated now: The level of dispersal of any persisting species can be expected to be positively correlated – and probably be geared so by natural selection – with

\* To avoid confusion: 'habitat' is conceived as is customary in ecology, i.e. as 'a place in which to live' (ANDREWARTHA & BIRCH, 1954). Hence, in this concept the main aspects of physiography, structure of vegetation, structure, composition and inclinations of soil, etc. are grasped, including e.g. frequency of inundation, frequency of covering with blown sand. There must be warned against incorporating too much into 'habitat', e.g. also 'weather' and 'enemies', by which 'habitat' would approach 'all factors that influence numbers', and a useful discrimination like that between stable and unstable habitats would become meaningless.

\*\* By 'dispersal power' is understood the ability of individuals to bridge comparatively great distances, and by doing so to found or refound populations. Therefore, the powers of dispersal of a population or species do not only depend on the kind of dispersal – flying or walking – but also on the level of dispersal, i.e. the number of individuals dispersing. In this paper by 'dispersal' is meant: that kind of – generally differently released, see e.g. DEN BOER (1961) and 7.7.4 – movement that results in leaving of the population area (compare, e.g. ODUM, 1973; CLARK, GEIER, HUGHES & MORRIS, 1967, p. 22–24).

the overall degree of instability of its populations (see: DEN BOER, 1971b).

In this formulation we have assumed that, firstly: In many species the causes of population disappearance are indeed closely related to the conditions that determine the degree of instability or impermanence of habitats (see: 2.2), and secondly: Within a high – but restricted – number of generations, the chance of extinction of populations is generally less for species living in permanent habitats than for comparable species living in more temporary habitats. Note, that it is thus supposed – apparently contrary to the ideas of SOUTHWOOD (1962) – that in permanent habitats the causes of population extinction will generally not be closely related to the conditions that determine the permanence of the habitat (e.g.: aspects of the spatial structure of the habitat).

Good examples of local groups that become extinct independent of structural changes of the locality can be found in the Western Tent Caterpillar: WELLINGTON (1960, 1964).

1.3. It is not surprising that most population students are convinced that the extinction of a population must be a very rare event. For practical reasons each of us studies one or a few large and/or very dense populations in permanent habitats, which are less likely to die out within the relatively short period of observation than most others (see also: ANDREWARTHA & BIRCH, 1954, p. 664; REDDINGIUS, 1971a, p. 82). In this respect the current ideas on populations must be greatly biased, because by far most populations are sparse (see e.g. WILLIAMS, 1964). Therefore, there is a great need to study the dynamics of sparse populations, at least as far as their frequency of extinction and refounding is concerned.

In many species, however, particularly when populations are to be studied by taking samples, it will be very difficult to establish population extinctions with certainty. Even when in continuous sampling during some successive generations not a single specimen is observed, it can not be excluded that a very sparse population is still present. But for a number of purposes, the investigator will feel justified – depending on the kind of animal and on the intensity of sampling – in practically considering such populations to be extinct, because in many of such cases the chance of recovery will largely depend on the occurrence of sufficient immigration (underpopulation: KLOMP, VAN MONTFORT & TAMMES, 1964), and such a situation hardly differs from complete refounding. When, on the other hand, sampling is not continued during many successive generations (e.g. samples are only taken during each fourth year, say) possible population extinctions may easily escape attention when repopulating happens to occur rather early.

Largely to avoid such ambiguities, and also so as not to lean too heavily on a few special cases, a comparative and more indirect strategy for investigating the relations between survival and dispersal was developed. Before discussing this strategy a last point will have to be cleared up.

1.4. 'Population' in fact is an opportunistic working-unit, and depending on the problems being studied, 'populations' may thus be groups of individuals on very different scales. If 'populations' can merely be considered sample spaces of individuals (compare the statistical working-unit 'population') the necessary conditions for circumscribing a 'population' will generally not be very restrictive, as long as we are able to sample our 'population' representatively. But if we intend to study population processes that depend on some kind of interaction between individuals (e.g. frequency of copulations, degree of some kind of intraspecific interference), we must have some notion of the magnitude of the distances at which the individuals may be expected still to have a reasonable chance to interact in the pertinent way. For in that case the results of our study will be greatly influenced by the scale at which we delimited our (animal) 'populations' (cf. BAKKER, 1971). We should be virtually able then to study single 'interaction groups', i.e. groups of individuals living in places with spatial dimensions that do not substantially exceed the distances normally covered by the individuals in the relevant patterns of activity, during their lifetime; see Fig. 1A. With some knowledge about these distances the population student may be able to roughly delimit in the field more or less isolated localities of about the right order of dimensions for accomodating such an interaction group (simple population).

Because interactions (or the lack of interactions) between individuals generally also matter in the processes of population extinction and (re)founding, whereas the frequencies of extinctions and (re)foundings will be highly scale-dependent, a comparative study on these phenomena should deal with relevant and comparable groups of individuals, i.e. with interaction groups as far as possible. In 2.1 items (5)

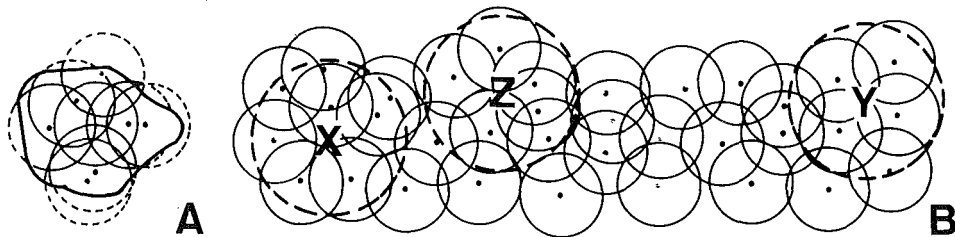


Fig. 1. Diagram of interaction groups.

Each dot represents a place where an individual is supposed to be born, and is the centre of a circle delimiting the maximal distances that can be covered by that individual in the normal patterns of activity, during its lifetime. Only a few individuals are pictured, of course.

A. A separate interaction group at a more or less isolated site of about the right dimensions. Such a group of individuals represents a case for the most correct use of 'interaction group': simple population.

B. A continuum of interaction groups. Starting from each point an interaction group can be defined (dotted circles), e.g. starting from the points X, Y or Z. Although such 'subpopulations' often cannot be independently separated from other ones, in many investigations it is useful to distinguish between different 'subpopulations' living under different local conditions, and being parts of a composite population.

and (6) it will be expounded how this necessary condition is satisfied. But also in many other cases it would be important – whenever possible – to take account of the approximate spatial dimensions of ‘interaction groups’ of the relevant organisms.

To illustrate this: Because in the case of Fig. 1B, the individuals at site X cannot interact with those at site Y, at these sites possible interaction processes are running independently of each other, i.e. the effects of these processes at site X may be very different from those at site Y (differences in the effects of relevant local conditions are not levelled and will thus work maximally).

The same applies to site Z as compared with site Y, and to many other sites within the area of this ‘large’ (composite) population. However, it is only true for the greater part for site Z as compared with site X, some individuals that just live between and partly within both these two sites, to some extent ‘connecting’ site Z with site X. Whereas in the case of Fig. 1A (simple population) possible interaction processes might be studied correctly, without taking account of the spatial scale at which interactions between individuals operate, in the case of Fig. 1B (composite population) a similar strategy of investigation would mainly result in gathering information on the overall effects of the spatial heterogeneity in local conditions: spreading of risks (cf. DEN BOER, 1968a, 1971a).

Although keeping as far as possible to the interaction concept of ‘population’ (BAKKER, 1971), it cannot be avoided also to use ‘population’ as a general descriptive term. Therefore, when we want to indicate that interactions are taken into account, spatially isolated interaction groups (the case of Fig. 1A) will indeed be named ‘interaction groups’, whereas interaction groups that gradually merge into other ones (the case of Fig. 1B) will be named ‘subpopulations’. When we are not certain whether we are dealing with ‘interaction groups’ or with ‘subpopulations’, we will speak of ‘local groups’.

## 2. CARABID BEETLES AS AN OBJECT OF STUDY

2.1. For a comparative study of the rate of extinction of local groups in relation with the question whether or not dispersal might compensate these extinctions by (re) foundings, carabid beetles form an adequate object of study, because:

(1) Within the occupied area the normal means of locomotion of most carabid beetles is walking (exceptions are *Cicindela*-species and some *Bembidion*-species), and therefore virtually all flight of carabids takes the individual away from its habitat, i.e. can be considered 'dispersal' (see also: GREENSLADE & SOUTHWOOD, 1962). This enables one to compare, in different species, the amount of dispersal by flight in its relation to the distribution of populations and to the way of life.

Note, that this does not mean that walking will never contribute to dispersal; especially in species with big individuals – e.g. *Carabus*-species – walking can take a number of individuals far away from their habitat (see DEN BOER, 1970, 1971b).

(2) The occurrence of monomorphic macropterous, di(poly)morphic and monomorphic brachypterous carabid populations within the same localities gives an almost ideal opportunity for the above comparison: Monomorphic brachypterous species can be contrasted with those monomorphic macropterous ones in which dispersal by flight occurs frequently.

(3) Carabids overall offer many advantages for a comparative study. In spite of a rather uniform way of life among most species of this group, one can compare stenotopic with eurytopic species, euryphagous with stenophagous species, species of temporary habitats with species of permanent habitats, species with usually sparse populations with species with usually dense populations, spring reproducing with autumn reproducing species, macropterous with brachypterous species (see e.g. LINDROTH, 1949), etc.

(4) Nearly all vital functions (e.g. copulating, hunting, egg-laying) are in most carabid beetles accompanied by walking activities at the surface of the soil, through which they can be conveniently sampled by means of pitfalls. Moreover, both from direct measurements, and from capture-recapture experiments it could be concluded that in general the catches from continuous pitfall-sampling summed over the whole period of activity themselves give a useful comparative measure of the population size (within species).

This conclusion was reached in the following way:

In different localities (at the heath of Kralo) and in different years BAARS, VAN DIJK & VAN DER EIJK (in prep.) compared the density of the reproducing population – by trapping all individuals within a fenced site – with the annual catches in an adjacent standard set of pitfalls, for two of our species: 70 (*Calathus melanocephalus*) and 132 (*Pterostichus versicolor*). Over a wide range the densities appeared to show a perfect linear relationship with the pitfall-catches:  $r$  (product-moment correlation coefficient) = 0.978 ( $n = 7$ ) in the case of 70;  $r = 0.998$  ( $n = 6$ ) in the case of 132.

Moreover, in 26 cases (5 other species), in which the size of the interaction group in the next year was predicted from that in the present year (calculated on the base of the stochastic model of JOLLY, 1965), by multiplying the latter with the quotient of the seasonal pitfall-catches in the next and the present year respectively, the mean deviation of these predictions from the Jolly-estimations for the next year amounted only to 20% (between 3 and 50%) of the estimates, nearly all deviations being insignificant. Similar results are obtained when comparing, within the same year, pitfall-catches and group sizes in two different sites. Some of these cases are preliminary shown in DEN BOER (1971a: Table 2); more cases will be published separately in a more elaborated version. See further: 4.4.

(5) When thus estimating the relative sizes of carabid populations (within species) by continuous pitfall-catching, in all cases one actually samples interaction groups (cf. 1.4), because the frequency by which individuals happen upon the fixed site of a pitfall – i.e. the number caught – can be assumed to be approximately proportional to the ‘chance to interact’. Sampling carabids by means of pitfalls gives still another advantage, viz. by doing so the area of the interaction group belonging to that set of pitfalls is naturally adjusted by the movements of the catchable individuals: Most carabid beetles do not show ‘home range’ behaviour (unpublished results), by which in the course of their lifetime the individuals are shifted by the normal patterns of activity throughout that ‘catch area’.

(6) Hence, when a set of pitfalls is placed in the centre of a structurally reasonably uniform and well-bounded locality, one will sample isolated interaction groups (simple populations, cf. 1.4) of those carabid species of which the distances covered by individuals approximately coincide with – or surpass – the spatial dimensions of the locality. At the same time one will sample arbitrary interaction groups (i.e. ‘subpopulations’ that are spatially defined by the fixed sites of the pitfalls) – which gradually merge into other ones – of those carabid species of which the distances covered by individuals are much smaller than the dimensions of the locality. Although in both cases interaction groups are sampled, in respect to our strategy these are not similar, i.e. in the latter case – subpopulations – the chance of refounding by walking individuals will generally be much higher than in the first case (see Fig. 1A, 1B). For comparative purposes, however, the above mixed situation – indicated by ‘local groups’ – is the most workable approximation of ‘population’ one can expect to find in the field. The degree of comparability will be the better, the greater the number of different localities of different dimensions, that is sampled in the same way, i.e. by means of a highly standardized technique of sampling (cf. 4.1).

2.2. DEN BOER (1970) discusses the dispersal power of monomorphic macropterous, di(poly)morphic and monomorphic brachypterous carabid populations in a cultivated countryside like Drenthe. From observations on the founding of carabid populations in the recently reclaimed ‘Zuiderzee’-polder, E-Flevoland, it could be

concluded that fullwinged individuals of both monomorphic macropterous and di (poly)morphic species potentially have a high power of dispersal, i.e. the flight activities of such individuals may appreciably increase the chance of (re)founding of populations.

Although it was clear that particularly individuals of species from temporary or unstable environments take part in flight activities (see also GREENSLADE & SOUTHWOOD, 1962; HAECK, 1971), it also appeared that this is not restricted to such species.

A number of species from more stable or permanent environments – especially some species living there in sparse populations – do show flight activities (see also DEN BOER, 1971b). HAECK (1971) directly shows that a newly reclaimed polder (S-Flevoland) is at first mainly invaded by carabid species from unstable environments, and that a number of monomorphic macropterous and di(poly)morphic species from more stable environments can be expected to follow within a few years. From the observations of both DEN BOER (1970, 1971b) and HAECK (1971) it can also be concluded, that the founding of populations by monomorphic brachypterous species is seriously hampered when suitable localities are not within travelling distances of walking individuals (see also: MEIJER, 1974).

If monomorphic brachypterous species are living in a vast natural area consisting of more or less suitable sites which gradually merge into one another, walking individuals may substantially contribute to dispersal (over short distances), and thus contribute to an exchange of individuals between interaction groups (1.4) and to the chance of the refounding of extinct populations: spatial spreading of the risk of extinction between populations (DEN BOER, 1968; REDDINGIUS & DEN BOER 1970). By some examples it is shown (DEN BOER, 1970), that brachypterous individuals of both di(poly)morphic and monomorphic brachypterous populations may indeed participate in dispersal.

When such a vast natural area has for the greater part been reclaimed for cultivation, however, natural localities generally will be small to very small and usually widely separated. Because walking individuals are unable to bridge even moderate distances, in a cultivated countryside most populations of monomorphic brachypterous species from natural areas will thus be both small – i.e. inhabiting small localities – and highly isolated. It may be expected that such populations will become extinct in the long run, one after another, without a chance of founding new ones. Many di(poly)morphic species with an only low frequency of fullwinged individuals may be expected to suffer a similar fate, the more so because flying away from a highly isolated population will mean selection against flying individuals to a high extent (compare DARLINGTON, 1943).

On the other hand, the above cited observations in the Flevoland-polders show that many of the monomorphic macropterous and di(poly)morphic species of natural areas which show a high frequency of flight activities can be expected in many situations to be able by and large to compensate population extinctions by (re)foundings, probably even in a cultivated countryside like Drenthe.



### 3. THE FORMULATION OF A SET OF HYPOTHESES

The observations surveyed in 2.2 suggest that the general significance of dispersal would be: *increasing the chance to (re)found populations*, not only for species living in temporary or unstable environments – for which this is self-evident, cf. 1.2 – but apparently also for species living in more stable environments (founding hypothesis). See also JOHNSON (1969, p. 637–639).

#### 3.1. ESCAPE AND OVERFLOW AS EFFECTS OF DISPERSAL

From the review by JOHNSON (1969, e.g. p. 207), however, it appears that according to the general opinion among entomologists the significance of dispersal would be: the possibility to escape from ‘currently adverse conditions’ (escape hypothesis). This is especially thought to apply to species living in unstable environments (cf. SOUTHWOOD, 1962). As far as dispersal from species living in more stable places is considered too, it seems generally to be supposed – especially by population biologists – that it results from too high densities – a kind of ‘overflow’ (see GADKIL, 1971, and e.g. DEMPSTER, 1975, p. 12); cf. 7.1.

DEN BOER (1971b) preliminarily contrasted the ‘founding’ hypothesis of dispersal with the above ‘overflow’ hypothesis; in the following chapters this is done more conclusively. For the present discussion it suffices to establish that under this ‘overflow’ hypothesis significant dispersal might especially be expected to occur in those species of permanent or stable habitats that are generally living there in comparatively – depending on the kind of species and on the kind of habitat – dense populations (i.e. populations whose numbers are often approaching or exceeding ‘carrying capacity’). This will be the more so because more individuals will potentially be available for dispersal from dense than from sparse populations. DEN BOER (1971b) showed, however, that in the case of carabid beetles these expectations are probably *not* answered; more evidence on this point will be discussed in chapter 7.

As a widening of the more general ‘escape’ hypothesis (see above) an apparent source of dispersal from populations living in permanent or stable habitats might also be: the incidental occurrence of short runs of less favourable conditions in these generally ‘favourable’ environments, supposedly without thus increasing the chance of extinction of the pertinent populations. If one wants to bring this under the viewpoint of ‘overflow’ too, one might think this to be caused by fluctuations of the value of  $K$  (total carrying capacity)\*; see also GADKIL (1971); cf. 7.7.4. Because, of course,

\* This point of view can be traced back to the – still very general – conviction that the dynamics of populations could be approximately described as: ‘reactions to disturbances about the positive equilibrium density’, which is thought to coincide with ‘carrying capacity’ that is symbolized by  $K$  in the differential equation of logistic population growth and related equations (see e.g. WILSON & BOSSERT, 1971).

such short runs of unsatisfactory conditions will not only occur in the environments of dense populations, but also in that of more sparse ones (e.g. because  $K$  is supposed to be very different both for different species and in different environments; but see also 6.8.2), the 'escape' hypothesis s.l. will not predict some general relation between the levels of dispersal of the respective species and the overall densities of the populations concerned.

Therefore, when concentrating upon differently abundant populations of the same species, the above considerations can also be applied to the specific frequency Distribution of Population Sizes (in the following : DPS) as it may be derived in some suitable area for each separate species from the sampling data (cf. 2.1): some relation between the frequency of occurrence of dense populations – as compared with that of sparse ones – and the level of dispersal is either not expected to be found (escape hypothesis), or: the greater the relative frequency of dense populations in such a species, the higher will be the overall level of its dispersal (overflow hypothesis); see e.g. DEMPSTER (1975, ch. 3). These hypotheses could also have emerged from the model of GADKIL (1971).

Because under these hypotheses especially the dispersal from permanent or stable (natural) habitats is considered to result from 'overflow' (or escape) there is neither a necessary relation between the powers of dispersal and the degree to which extinct populations have to be replaced by (re)foundings (in the following RPR: the degree of Realization of Population Replacement), the more so because in stable environments natural extinctions are generally considered (by population biologists) to occur only exceptionally. Hence, even in a cultivated countryside the original species will be expected generally to survive in the remaining natural localities as long as these stay suitable (but see also : DIAMOND, 1975). In other words: the generally much increased distances between inhabitable places in cultivated areas, will – at least for a considerable period – not be expected to influence the survival of the pertinent species substantially; for the time being the most relevant point will be how many 'favourable' places are still present in such a cultivated countryside.

On this basis we can formulate a testable null hypothesis.

### 3.2. THE NULL HYPOTHESIS

As far as dispersal occurs from populations of species living in permanent or stable natural habitats within a cultivated countryside, some measure for the frequency of sparse populations – as compared with that of the more dense ones – will between species either not show any relation with the levels of dispersal (power) concerned, or such a relation will be: the greater the relative frequencies of dense populations, the higher will be the pertinent levels of dispersal (power).

Although somewhat schematized this null hypothesis – i.e. dispersal is a response

to currently adverse conditions – gives a fair idea of the *consequences* of the above (3.1) lines of thought – that are still generally accepted in population biology – because from such a point of view the concept RPR (degree of Realization of Population Replacement) will hardly be a relevant one for species of permanent or stable habitats. In other words: ‘population replacement’ will be supposed to occur only exceptionally (or not at all, cf. NICHOLSON, 1958) in these ‘favourable’ environments, whereas relieving the pressure from too high densities will be considered the main effect of dispersal there (‘overflow’ hypothesis: DEN BOER, 1971b), by which it will only accidentally result in the founding of populations.

### 3.3. FOUNDING AS AN EFFECT OF DISPERSAL

Our alternative hypothesis will be based on more probabilistic lines of thought, in which the extinction and (re)founding of populations are considered natural processes governing the survival of all species, i.e. from such a point of view the main effect of dispersal is supposed to be: increasing the chance to (re)found populations, and thus by and large to compensate for the disappearance of populations (‘founding’ hypothesis: DEN BOER, 1971b), not only for species of temporary or unstable environments, but also for species living under more stable conditions.

Among species that survived under long persisting natural conditions, prevailing in some extensive natural area, features – like mean, variance, kurtosis – characterizing for each species the frequency Distribution of observed Population Sizes (DPS), are generally not expected to show differences between species that are highly correlated with differences in the levels of dispersal power concerned (in this respect we do not contradict the escape hypothesis s.l., cf. 3.1). For the very survival of these species under these conditions shows, that in all species observed the powers of dispersal obviously suffice by and large to compensate – by (re)foundings – for (even frequent) extinctions – both in species with a low and in that with a high dispersal power –, i.e. for each of the pertinent species DPS will be a fair reflection of the overall pattern of temporal variation in relevant conditions as it is distributed over the inhabitable places. In fact, on statistical grounds it may be expected that under such conditions, in different species DPS will be quite similar qualitatively, and for many – not extremely stenotopic – species will more or less resemble a log-normal distribution (cf. ch. 5).

When such a more or less continuous natural area is for the greater part reclaimed for cultivation, however, the availability and pattern of distribution of inhabitable localities will be altered to such an extent, that under the founding hypothesis the powers of dispersal of many species will no longer suffice to keep pace with the rate of disappearance of populations. In other words: because a fundamental difference between our hypotheses is the supposed frequency of natural extinctions these hypotheses will – by differently appreciating the main effect of dispersal – predict

different effects from a major environmental change. The founding hypothesis will predict secondary changes generally to occur in the course of decennia (or centuries at most), whereas our null hypothesis will mainly allow for secondary changes on a more geological time-scale. Because sparse populations of a certain species generally will run a greater risk of dying out than comparable dense ones (other things being equal), in a cultivated countryside the DPS of species with a low dispersal power are expected to show relative frequencies of sparse populations that decrease with time, i.e. the DPS of such species will increasingly deviate from that of species with a still sufficient dispersal power (in many of the latter cases still an about log-normal DPS may be found). Under the overflow (escape) hypothesis such changes are not expected for the time being (cf. 3.1).

Hence, under the founding hypothesis DPS is expected to be a fair relative estimate of RPR (degree of Realization of Population Replacement) under these conditions. We may thus consider the intensive cultivation of a more or less continuous natural area to represent a critical experiment on the significance of dispersal.

After a running-time of a lot of decades the results of the 'experiment of cultivation' can be evaluated, i.e. we can formulate our expectations about these results in the light of the 'founding' hypothesis of dispersal, and test these against our null hypothesis (cf. 3.2).

#### 3.4. THE ALTERNATIVE HYPOTHESIS

The considerations of 3.3 thus lead to the following alternative hypothesis: In a cultivated countryside, species with a low dispersal power (e.g. carabid species without or with only infrequent flight activities) generally will not realize sufficient population replacements (low RPR), by which the pertinent DPS will show a relative shortage of sparse populations, as compared with those of species showing a high dispersal power (e.g. carabid species with a high frequency of flight activities) and a high RPR. In other words: greater relative frequencies of dense populations will coincide with lower levels of dispersal power.

Hence, in the course of time the generally widely separated inhabitable localities within a cultivated countryside are assumed to lead to growing differences in DPS between different species, the changes in DPS – i.e. the preferential disappearance of more sparse populations – being the greater the lower the powers of dispersal, by which under these new spatial conditions, after some time DPS will be a reliable relative estimate of RPR. Because of the still short history of cultivation, it is not expected that the powers of dispersal of species living in the remaining natural localities will already show some 'adaptation' to the new situation, and as far as carabid beetles are concerned, it may even be wondered whether in the future 'adaptation' will often occur (see also: chapter 8).

### 3.5. CONDITIONS FOR TESTING

Our testing procedure boils down to: demonstrating that, within a group of comparable species that show great differences in dispersal power and are living in the remaining natural localities within a cultivated countryside (with a history of intensive cultivation of at least some decades), higher relative frequencies of dense populations significantly coincide with lower powers of dispersal (alternative hypothesis), or do not so (null hypothesis).

3.5.1. Species of temporary natural habitats are not expected to disturb the testing of our hypotheses significantly, because such species in fact fit both hypotheses, i.e. they will necessarily show both a high rate of population extinction and a high dispersal power (founding hypothesis and escape hypothesis s.s.). These processes will moreover hardly be negatively influenced by cultivation as long as favourable localities – that are often unsuited for cultivation – are available. Such species will thus belong to a group in which a ‘normal’ (to high) frequency of sparse populations is expected. Under the alternative hypothesis (3.4) these species will naturally fit into the general picture as part of the group with a high RPR and a corresponding DPS, and thus contrast adequately with the group with a low RPR. Under the null hypothesis I see no special reasons to suppose that the relative frequency of sparse populations would generally be lower for species of permanent habitats than for species of temporary ones (in fact, many species of permanent habitats are relatively sparse in many places: WILLIAMS, 1964). One might even take the opposite stand: species of temporary habitats will have a relatively high reproductive capacity and therefore will be able rapidly to build up dense populations – consider for instance, insects of agricultural fields, insects reproducing in carrion, etc. – so that if testing would result in disproving the null hypothesis we will keep on the safe side.

### 3.6. METHOD OF INVESTIGATION

Our strategy of investigation will be clear now. In a representative – i.e. rather high – number of different natural localities within a cultivated countryside, and in different years, the sizes of the interaction groups of a number of carabid species are estimated by standardized and continuous pitfall-sampling; cf. 2.1, items (4), (5) and (6).

For each species, DPS is estimated by some standardized measure in which the relative frequency of sparse groups is weighted adequately (cf. 3.1 and 3.3): chapter 5.

For each species, the development of the wings is studied in a representative number of individuals caught, and the species are thus divided in monomorphic brachypterous, di(poly)morphic and monomorphic macropterous ones respectively (cf. 2.2).

The relative frequency of flight activities of monomorphic macropterous and of di(poly)morphic species is estimated by sampling with window-traps during a number of years (DEN BOER, 1971b; HAECK, 1971; MEIJER, 1971).

On the basis of wing development and frequency of flight activities – i.e. independent criteria – species with a low dispersal power (A) and species with a high dispersal power (B) are separated: 4.2. Our hypothesis (3.4) can now be tested against the null hypothesis (3.2) by contrasting the DPS-values for A-species with the DPS-values for B-species by some adequate statistical method of testing.

3.7. In the first instance, we will not discriminate between species of permanent habitats and those of temporary ones when testing, because in our opinion such a separation is hardly given in nature and would therefore be somewhat arbitrary (see also: 3.5). Although the extremes are evident, and some species can safely be classified as species of temporary habitats and some other ones as species of permanent habitats, the majority of carabid species can only be brought to one or the other habitat group by rigorously applying the following rule:

Sampling sites that (at least) during the 9 years of our study (cf. 4.1) did not show major structural changes and became not inundated for at least some months were considered to represent permanent habitats. All other sampling sites were temporary ones. By applying these criteria some natural habitats appeared to be less permanent or stable than might be expected at first sight. Some parts of the heath especially may gradually become overgrown by young trees or become inundated rather frequently. On the other hand, some blown sand areas, when partly fixed by vegetation, and most old peat moor appear to represent remarkably stable habitats, both structurally and with respect to soil humidity.

Because already in separating species with a low dispersal power (A-species) from species with a high dispersal power (B-species) some arbitrariness can not be circumvented (see 4.2) it will be necessary – in order to avoid some kind of circular reasoning – not to complicate our testing procedure beforehand by adding another (even more) arbitrary classification. But after having treated our problem more generally we can reliably compare different species as classified by some procedure of division into different habitat groups (cf. 4.3). In this way we will also be able to judge whether the assumption made in 3.5 – i.e. species of temporary habitats will not significantly disturb the testing of our hypotheses – is right or not: 6.5.

## 4. RELEVANT INFORMATION ON THE CARABID BEETLES OF DRENTHE, AND HOW IT WAS OBTAINED

### 4.1. RELATIVE POPULATION SIZES

From a field investigation into the most important factors governing the distribution of carabid beetles over natural localities in the neighbourhood of Wijster (prov. of Drenthe) an adequate amount of independent data on relative – within species – population sizes (local groups) in different sites and years (cf. 2.1) of a number of carabid species is available. These were estimated by uninterrupted sampling with standardized sets of pitfalls. The total catch of a single species in one standard set of pitfalls during a whole year (year-sample) – covering one reproductive season – gives a reasonable approximation: 2.1. In this way the year-catch from one set of pitfalls gives estimates of the relative – within species – sizes of the local groups of between 6 and 63 carabid species at a time.

Between-species comparisons of group sizes will only be used in this paper to distinguish abundant species from sparse ones (ch. 7). In a few cases in which it could be tested, it appeared that the reliability of such between-species comparisons can be satisfactory (cf. 4.4). In order to include as well as possible also a whole reproductive season of winter reproducing species – e.g. the species 33, 56, 62, 64, 65, 149, 150 of Appendix A. I. – the ‘carabid-year’ had to be started in the last week of February.

For the calculation of DPS-values (chapter 5) we will use all relevant data of the available 175 year-samples taken from 73 different natural sites (cf. Appendix A. II) during nine years (1959 up to and including 1967) covering more than 176,000 carabid individuals belonging to 148 species.

A number of these sites (44) was only sampled during one ‘carabid-year’, others (29) during two or more (up to 8) years. Both years and sites were sampled about equally, i.e. within each group of habitat the year-samples are about equally distributed over many sites that were sampled during 1 to 3 (4) years (more than half of them in the one-year group) and a few sites that were sampled during 4 (5) to 8 years. In Appendix A. II the sites are described and in Table 1 the frequency of the year-samples and sites in different groups of habitat is given. This frequency distribution of sites sampled roughly reflects the relative surfaces in which these different habitat groups are represented now in the surroundings of Wijster\* ; it was not tried, however, to reach this agreement exactly.

It is hardly possible at the moment – with only a few exceptions – to judge in what

\*The greater part of the woodland, however, consists nowadays of coniferous plantations, that are unsuited for most woodland-species (cf. 8.1 and Fig. 5). Therefore, most of the year-samples from woodland had to be taken from remnants of deciduous forest.

Table 1. Frequency of year-samples (catching with a standard-set of pitfalls during one year) in different habitat groups within natural localities: 1959 up to and including 1967. See also: Appendix A.II.

type of habitat	number of sites	number of year-samples	mean number of year-samples/site
D. Woodland	32	68	2.1
E. Blown sand (fixed)	12	33	2.7
F. Heath and peat moor in both D and E	17 (1)	52 (6)	3.0
Total in permanent habitats	60	147	2.4
G. Instable habitats (i.e. only temporarily inhabitable)	13 (+5)	28 (+8)	1.8-2.0
in both D and G	(1)	(1)	
in both E and G	(1)	(1)	
in both F and G	(3)	(6)	
Total in all habitats	73	175	2.4

Between brackets: number of sites and year-samples that had to be brought under more than one habitat group.

cases separate interaction groups and in what cases 'subpopulations' (cf. 2.1) of a certain species have been sampled (but see: 6.6). Since in all habitat groups, and thus for all species, sampling occurred in many sites of very different dimensions, we expect that in most – not very sparse – species all kinds of local groups will be represented. Therefore, we may assume that as far as this mixed situation can be expected to influence our results such an influence will be a levelling or masking one, by which at most our null hypothesis (3.2) might be accepted wrongly. At several places we will return to this point.

Because we want to compare the relative frequency of occurrence of sparse with that of dense local groups between different species, no relevant information can be expected from species of which in total only a small number of specimens was caught. Therefore, we divided our 148 species at the median and only the 50% more abundant species are taken into account, i.e. all year-samples of the 74 species of which 70 or more (up to 30,887) individuals were caught in total (N in Table 3). These data are given in Appendix A. III whereas the 'ecology' of the species is shortly described in Appendix A. I.

These 74 species comprise 99.37% of the carabid-individuals caught and are each represented in between 4 and 166 of the 175 year-samples (mean: 63.8 year-samples/species, i.e. on the average we possess 63.8 estimates of relative group sizes per species). The 74 very sparse species are mentioned in tabular form in Appendix A. I.



Table 2. Carabid species ( $\geq 70$  ind. caught) divided according to dispersal power. See also Appendix A.I.

A-species: low dispersal power	B-species: high dispersal power	C-species: dispersal power uncertain
1. <i>Abax parallelepipedus</i> P & M	9. <i>Agonum fuliginosum</i> Panz.	33. <i>Amara infima</i> Dfts.
6. <i>Agonum assimile</i> Payk.	18. <i>Agonum sexpunctatum</i> L.	37. <i>Amara pseudo-communis</i> Burak
8. <i>Agonum ericeti</i> Panz.	22. <i>Amara apricaria</i> Payk.	38. <i>Amara quenseli</i> Schönh.
17. <i>Agonum obscurum</i> Hbst.	25. <i>Amara brunnea</i> Gyll.	62. <i>Bradycellus collaris</i> Payk.
29. <i>Amara equestris</i> Dfts.	26. <i>Amara communis</i> Panz.	66. <i>Brosicus cephalotes</i> L.
56. <i>Bembidion nigricorne</i> Gyll.	30. <i>Amara famelica</i> Zimm.	73. <i>Calathus piceus</i> Marsh.
68. <i>Calathus erratus</i> Sahlb.	31. <i>Amara familiaris</i> Dfts.	84. <i>Cicindela hybrida</i> L.
69. <i>Calathus fuscipes</i> Goeze	34. <i>Amara lunicollis</i> Schiödte	89. <i>Cymindis vaporariorum</i> L.
70. <i>Calathus melanocephalus</i> L.	35. <i>Amara plebeja</i> Gyll.	94. <i>Dyschirius thoracicus</i> Rossi
75. <i>Carabus arvensis</i> Hbst.	54. <i>Bembidion lampros</i> Hbst.	102. <i>Harpalus fuliginosus</i> Dfts.
76. <i>Carabus cancellatus</i> Illig.	60. <i>Bembidion tetracolum</i> Say	105. <i>Harpalus quadripunctatus</i> Dej.
78. <i>Carabus nemoralis</i> Müll.	64. <i>Bradycellus harpalinus</i> Serv.	109. <i>Leistus rufescens</i> F.
79. <i>Carabus nitens</i> L.	65. <i>Bradycellus ruficollis</i> Steph.	110. <i>Leistus rufomarginatus</i> Dfts.
80. <i>Carabus problematicus</i> Hbst.	82. <i>Cicindela campestris</i> L.	117. <i>Nebria brevicollis</i> F.
88. <i>Cymindis macularis</i> Dej.	86. <i>Clivina fossor</i> L.	118. <i>Nebria salina</i> Fairm.
95. <i>Dyschirius globosus</i> Hbst.	104. <i>Harpalus rufipes</i> de Geer	119. <i>Notiophilus aquaticus</i> L.
103. <i>Harpalus latus</i> L.	106. <i>Harpalus rufitarsis</i> Dfts.	121. <i>Notiophilus germinyi</i> Fauv.
114. <i>Metabletus foveatus</i> Fourcr.	112. <i>Loricera pilicornis</i> F.	122. <i>Notiophilus palustris</i> Dfts.
115. <i>Metabletus truncatellus</i> L.	120. <i>Notiophilus biguttatus</i> F.	124. <i>Notiophilus rufipes</i> Curt.
132. <i>Pterostichus versicolor</i> Sturm	133. <i>Pterostichus diligens</i> Sturm.	125. <i>Olisthopus rotundatus</i> Payk.
134. <i>Pterostichus lepidus</i> Leske	135. <i>Pterostichus minor</i> Gyll.	130. <i>Pterostichus angustatus</i> Dfts.
136. <i>Pterostichus niger</i> Schall.	137. <i>Pterostichus nigrita</i> Payk.	141. <i>Pterostichus melanarius</i> Illig.
138. <i>Pterostichus oblongopunctatus</i> F.	139. <i>Pterostichus strenuus</i> Panz.	146. <i>Trechus obtusus</i> Er.
144. <i>Stomis pumicatus</i> Panz.	140. <i>Pterostichus vernalis</i> Panz.	
148. <i>Trechus secalis</i> Payk.	149. <i>Trichocellus cognatus</i> Gyll.	
	150. <i>Trichocellus placidus</i> Gyll.	

Nomenclature according to LINDROTH (1974) as far as possible.

## 4.2. DISPERSAL GROUPS

Next, on independent criteria we will have to separate from the above 74 more abundant species a group of species with a high dispersal power and a group with a low dispersal power (cf. note to 1.2). From the observations surveyed in 2.2 it could be derived that species with a high dispersal power are species showing a high frequency of flight activities, and species with a low dispersal power are species showing no or only very infrequent flight activities.

4.2.1. To get some independent data on the frequency of flight activities in different species, during five years (1969 up to and including 1973) flying carabids were sampled with the help of window-traps (SOUTHWOOD, 1966); cf. 2.2.

During 27 'trap-years' (one window-trap functioning during one year) in 3 different localities 4337 carabid individuals were caught belonging to 64 species. Among these species, demonstrably capable of flying, 26 of our 74 test-species (cf. 4.1) are represented with a total of 3748 individuals.

These 26 species can thus be considered species with a comparatively high dispersal power (B-species): Tables 2 and 3.

Comparing the columns 11 and 12 (max. number of potential flyers) of Table 3 shows that there must still be great differences among these species (compare e.g. species 25 and 120 with species 31, 35 and 64). Column 10 (Table 3) shows that as far as individuals of di(poly)morphic species were caught in window-traps, with the exception of the abundant species 133 (3.7%), species with a rather high percentage of macropterous individuals (17% or higher) are concerned.

To get some idea of the relative dimensions of the wings of species that show flight activities, in samples of the relevant species the greatest length and width of the expanded wing were measured and compared with the same values for the elytrum by Mrs. DEN BOER-DAANJE. Comparison with some planimeter measurements of wing and elytrum showed that the quotient

$$\frac{\text{greatest length of wing} \times \text{greatest width of wing}}{\text{greatest length of elytrum} \times \text{greatest width of elytrum}}$$
 generally gives a reliable estimate (somewhat too large) of the relative wing surface:  $\frac{\text{surface of wings}}{\text{surface of elytra}}$ .

For a number of critical species the mean values of these quotients (with the standard deviation of the individual measurements) were estimated and given in column 14 (Table 3), from which it appears that for most species this quotient exceeds 2.0.

That this quotient gives some indication for flight capacities is supported by the fact, that in the two species for which it is lower than 2.0, the few individuals caught in window-traps all have values above the mean: in species 25 the value 2.034 and in species 9 the values 3.145, 2.694 and 1.838 respectively.

4.2.2. To contrast with the 26 species with a comparatively high dispersal power (B-species: 4.2.1) we should like to separate from the remaining species a group with

Table 3. Data on the dispersal power of 74 carabid species (cf. 4.2).

A-species: low dispersal power							B-species: high dispersal power			
species (see Table 2)	size of ind. (mm)	wing de- velop- ment <sup>1</sup>	N and (max. number of poten- tial flyers = f) <sup>2</sup>	wings studied in ... ind. <sup>3</sup>	surface wings surface elytra with S.D.	notes on dispersal <sup>4</sup> by LINDROTH (1945, 1949)	spe- cies (see Table 2)	size of ind. (mm)	wing de- velop- ment <sup>1</sup>	number of ind. caught in window traps = w
1	2	3	4	5	6	7	8	9	10	11
1	17-19	brach.	719(-)				9	6-6½	d. 28%	3
6	10-12½	(macr.)	1853(?)	(100)	1.284 ± 0.135	L.1.	18	7-9½	macr.	4
8	6½-7	brach.	962(-)	658		L(d).(1).	22	6½-7½	macr.	66
17	5-6	d.0.12%	1787(2)	815		L(!)	25	5½	macr.	1
29	7-11	(macr.)	1082(?)	(100)	1.374 ± 0.203	L(1)	26	6-8	macr.	43
56	3-3½	brach.	3528(-)	1469		L.d.	30	7½-8½	macr.	16
68	8½-11	d.0.2%	10882(21)	971		L(!)	31	5½-7	macr.	191
69	10-14	d.0.85%	453(4)	351		L.br.(1).	34	7-8	macr.	38
70	6-8	d.0.23%	30887(70)	> 5000		L(!) <sup>5</sup>	35	6-6½	macr.	638
75	12-20	brach.	680(-)				54	3-4	d.17%	4
76	19-24	brach.	365(-)				60	5-6	d.39%	2
78	21-26	brach.	515(-)				64	3¾-4½	d.78%	2468
79	14-16	brach.	268(-)				65	2½-3	macr.	54
80	21-27	brach.	1578(-)				82	11-14	macr.	10
88	8½-9½	brach.	308(-)	171		L.d.	86	5½-6½	d.90%	32
95	2-2¾	d.0.11%	9666(11)	1882		L.br.(1). <sup>5</sup>	104	13-15	macr.	3
103	8-10	(macr.)	3647(?)	(100)	1.491 ± 0.173	L.2(1).	106	8-10	macr.	4
114	3-3¾	d.0.23%	1108(3)	439		L.br.	112	7-8	macr.	13
115	2½-3	brach. <sup>8</sup>	72(-)	20		L.d.(1)	120	5-5½	d.79%	3
132	9-12	(macr.)	15796(?)	2810(100)	1.426 ± 0.170 <sup>6</sup>	L.3(1)	133	5½-6	d.3.7%	7
134	11-13½	brach.	4655(-)	1950		L.d.	135	7-7½	d.95%	12
136	16-21	(macr.)	2569(?)	(100)	1.291 ± 0.232	L.3.	137	9-11	macr.	4
138	10-12	(macr.)	12839(?)	(100)	1.266 ± 0.191 <sup>6</sup>	L(1).	139	5-6	d.23%	14
144	6-7½	brach.	83(-)	85			140	6½-7½	macr.	21
148	3-4	brach.	908(-)	> 200			149	3½	macr.	62
							150	4-4½	macr.	35

<sup>1</sup> brach. = brachypterous (wings smaller than elytra). macr. = macropterous (large wings). d. 0.12% (d. 28%) = di(poly)morphic wings, 0.12% (28%) of the individuals studied with large wings, i.e. about twice as large as the elytra. (macr.) = wings relatively small, i.e. < 1.5 times the surface of the elytra (cf. 4.2).

<sup>2</sup> N = total number of ind. caught in pitfalls in 175 year-samples; between brackets: the maximal number of ind. (of N), that potentially could have been able to fly, only judging the development of the wings (the fact that some fullwinged ind. might have shown reduced wing-muscles is not considered).

<sup>3</sup> between brackets: number of ind. in which wings and elytra are actually measured (in polymorphic species only macr. ind.); otherwise the development of the wings is judged by eye; when no number is mentioned the species is either evidently brachypterous or evidently macropterous (i.e. wings > 2 times surface of elytra).

<sup>4</sup> L.1, L.3 = number of observations on spontaneous flight known to L. (mostly from literature); L.0 = no observations on flight known to L; L.(1) = number of indirect observations on flight, e.g.

C-species: dispersal power uncertain

N and (max. number of potential flyers = f) <sup>2</sup>	wings studied in ... ind. <sup>3</sup>	surface wings surface elytra with S.D.	species (see Table 2)	size of ind. (mm)	wing development <sup>1</sup>	N and (max. number of potential flyers = f) <sup>2</sup>	wings studied in ... ind. <sup>3</sup>	surface wings surface elytra with S.D.	notes on dispersal <sup>4</sup> by LINDROTH (1945, 1949)
12	13	14	15	16	17	18	19	20	21
286(80)	183 (11)	1.729 ± 0.268	33	4½-5	d.1.3%	799(10)	675		L.0.
276(276)	(39)	2.058 ± 0.242	37	6-8	macr.	162(162)			
178(178)			38	7-8	macr.	79(79)	49		L.(1).
2926(3000?)	(100)	1.824 ± 0.169	62	3-3½	d.15%	866(130)	93		L.5(2).
546(546)			66	18-21	macr.	490(490?)			L.0.?
425(425)			73	8½-10	d.93%	1264(1100?)	335(100)	1.808 ± 0.161	L.(1).
119(119)	(122)	2.307 ± 0.144	84	12-15	macr.	100(100)			L.!
16672(16000)	334(100)	2.113 ± 0.153	89	8-9	d.5.8%	148(9)	87		L.1.
357(357)	(122)	2.313 ± 0.139	94	4-4½	macr.	230(230)			L.1.
882(150)	385		102	8¾-10	macr.	461(461)	(100)	2.355 ± 0.175	L.0.
124(48)	183(62)	2.808 ± 0.258	105	10-11½	macr.	325(325)	(43)	2.169 ± 0.226	L.0.
878(685)	281(170)	3.070 ± 0.254	109	6-6½	(macr.)?	335(?)	336(47)	1.503 ± 0.211	L.br.?
3219(> 3000)	(128)	2.177 ± 0.201	110	8-8½	macr.	1110(1000)	638(100)	2.336 ± 0.202	L.(d).(1).
70(70)			117	10-12	macr.	907(900)	(100)	2.105 ± 0.141	L.1(1).
208(186)	202(73)	2.700 ± 0.467	118	10-12	macr.	376(376)			L.0.
385(385)	(50)	2.852 ± 0.208	119	4½-6	d.1.2%	9491(1100)	3153		L.1.
124(124)	(50)	2.438 ± 0.205	121	4½-6	d.2.6%	811(21)	267		L.0.
1045(1000)			122	4½-6	d.7%	252(18)	143		L(!)
4020(> 3000)	556(100)	2.497 ± 0.266	124	5-6	macr.	1679(1500)	100	2.353 ± 0.246	L.0.
5945(220)	2210		125	6-7	d.21%	555(116)	305		L.(1).
274(261)	263		130	8-10½	macr.	1117(1000)			L.0.
1799(1700)			141	13½-17½	d.2%	119(2)	108		L.0. <sup>5</sup>
651(150)	701	<sup>5</sup>	146	3½-4	d.2.8%	332(9)	289		L.br. <sup>5</sup>
143(140)	124								
2124(2000)	(50)	2.408 ± 0.185							
2390(> 2000)	(50)	2.108 ± 0.180							

ind. floating on water, ind. of inland species observed on the shore (drifted ashore?), generally not wholly convincing; L. (!) = convincing indirect observations on flight, e.g. macr. ind. of a di(poly) morphic species drifted ashore (PALMÉN, 1944).

L. br., L.d. = brach. or di(poly)morphic respectively in Fennoscandia according to L.; L. (d). = notes in literature suggesting wing-dimorphism in some other part of the distributional area.

<sup>5</sup> compare DEN BOER (1970): 2.2, where is shown that the species is able to found a population in a newly reclaimed polder by flying ind.

<sup>6</sup> one specimen is found in a special type of window-trap that was only used incidentally, and in which crawling into the catch-jar could not be avoided completely; comparable with L ( ) observations, i.e. not wholly convincing indication for flying. In 1976, however, in such a window-trap a specimen of 132 was caught with surface wings/surface elytra = 1.81.

<sup>7</sup> observations on flight in BRAKMAN (1950-'51).

<sup>8</sup> after closing of the manuscript, in 1976 some fullwinged specimens of species 115 were caught in window-traps; see also 6.7.4.

comparatively low powers of dispersal (A-species), i.e. species showing no, or only very infrequent flight activities.

First of all, the monomorphic brachypterous species will belong to this group, i.e. 13 species. But also di(poly)morphic species with a very low frequency of macropterous individuals will have a comparatively low dispersal power. We decided to consider the species with less than 1% of individuals macropterous – by which the maximum number of potential flyers does not exceed 70 individuals, column 4 of Table 3 – to belong also to the group of A-species, i.e. 6 species. A number of monomorphic macropterous species, in which the wings are rather small are generally considered to be hardly able to fly.

In one of these species (6: *Agonum assimile*) it is observed – under laboratory conditions – that some individuals may use their wings in making some kind of short (a few cm's) 'parachute-jumps' (NEUDECKER & THIELE, pers. comm.); perhaps there is a small chance that such a 'jumping' individual is borne away by a sudden air current and thus becomes a 'flying' one. See also: note 6 to Table 3.

Mrs. DEN BOER-DAANJE estimated  $\frac{\text{surface of wings}}{\text{surface of elytra}}$  (cf. 4.2.1) in samples of the pertinent species (LINDROTH, 1945): column 6 of Table 3. On the base of these measurements, species in which the average value of this ratio is lower than 1.5 are also incorporated into the group of species with a low dispersal power, i.e. 6 species.

Together these make 25 A-species (Table 2) of which we can be sure that the dispersal power will generally be substantially lower than in the 26 B-species.

4.2.3. The dispersal power of the remaining 23 species (C-species) is uncertain. In general, the fact that no specimens were caught in window-traps can only mean that the dispersal power is low; for a few species only this can be the result of a highly localized distribution, e.g. for the species 38, 84, 94, 130. In many di(poly)morphic C-species the percentage of macropterous specimens is rather low, e.g. in the species 33, 119, 121, 141, 146 (column 17 of Table 3); in some other species the wings are rather small, e.g. in 73 and 109 (column 20 of Table 3). Hence, the majority of the C-species seem to be more related to the A-species than to the B-species. Therefore, in some critical cases we will also contrast A- + C-species with B-species. Moreover, when testing reliable DPS-values some other reasonable arrangements of the 74 species of Table 2 will be tested too (cf. 6.9).

#### 4.3. HABITAT GROUPS

To be able both to compare the powers of dispersal and the pertinent DPS-values between groups of carabid species of permanent habitats, and to compare these with those of species of temporary habitats, we will have to place each of our carabid species in one or the other habitat group depending on where the majority of indi-

viduals was caught. Starting from the classification as given in Table 1 (cf. 3.7 and 4.1), an independent – but somewhat arbitrary – distribution of the 74 species (cf. 4.1) over these habitat groups could be reached by rigorously applying the rule, that a species is considered to fit – i.e. to be able to keep comparatively dense populations in – a certain kind of habitat, when the mean number of individuals present in the year-samples of that habitat group (Table 1) is at least four times as high as that in the remaining year-samples (X). This means, that at least Y % of the total number of specimens caught (N of Table 3) should be present in the k year-samples of the habitat group concerned, where

$$Y = \frac{4.kX}{4.kX + (175 - k)X} \times 100 = \frac{400 k}{175 + 3 k}.$$

The results of this division procedure are shown in Table 4. The species in the groups D, E and F can be considered species of ‘permanent’ habitats (48 species), whereas the 10 species of the G-group are species of ‘temporary’ habitats. These 58 species are more ‘stenotopic’ (for a definition, see 6.7) than the 16 H-species, because the latter ones without much preference inhabit localities belonging to more than one habitat group. Local groups of many H-species can be found both in temporary habitats and in some kind of permanent ones (e.g. the species 136, 146, 30, 79, 82, 118, 31); the species in the habitat group ‘grass’ (26, 34, 106 and 133) probably also show this pattern, because most natural localities dominated by grasses are either only temporarily inhabitable – e.g. most vegetations of *Molinia* only during dry periods – or change within a number of years – e.g. localities whose structure has recently been influenced by human activities. Hence, the group of H-species apparently is most related to that of the G-species, the species of the first group being mainly more ‘eurytopic’ (cf. 6.7).

It should be noted, that the above division key is not very restrictive. If we had taken

$$Y = \frac{500 k}{175 + 4 k} \text{ or } Y = \frac{300 k}{175 + 2 k}$$

the values of Y would only have been a few percent higher or lower respectively, and only two or three species would have been placed in a different group. The division key used here (Table 4) is preferred, because the resulting distribution of species agrees better with data from literature and with ‘general field experiences’ than other ones, by which it is an independent division. Moreover, it shows the eurytopic character of the H-group to better advantage (for the apparent exception of species 35 see VAN HUIZEN, in press).

4.3.1. To simplify future discussions we will already establish at this place what are the frequencies of the A-, B- and C-species (cf. 4.2) within these habitat groups: Table 5. As could be expected because of the necessarily high dispersal power in species of temporary habitats (compare 2.2 and SOUTHWOOD, 1962), most B-species (17 out of 26) are found in the G- and H-groups.

Table 4. Division of 74 carabid species into 5 groups (compare: Table 1), based on the % of the total number of specimens caught (N) that is present in the year-samples of the concerning habitat group (for the computation of Y cf. 4.3).

D-species 68 year-samples Y = 72%		E-species 33 year-samples Y = 48%		F-species 52 year-samples Y = 63%		G-species 33 year-samples Y = 48%		H-species (= remaining spp.)					
								% of N in year-samples of the habitat group <sup>2</sup>					
species <sup>1</sup>	% of N <sup>2</sup>	species <sup>1</sup>	% of N <sup>2</sup>	species <sup>1</sup>	% of N <sup>2</sup>	species <sup>1</sup>	% of N <sup>2</sup>	species <sup>1</sup>	D	E	F <sup>3</sup>	G	grass <sup>4</sup>
1	99.6	33	93.0	8	87.2	18	51.8	35	60.0	13.0	14.0	13.0	16.0
6	99.5	38	100	17	72.7	54	70.8	109	53.0	23.9	34.0	10.7	18.8
9	73.1	56	76.7	29	88.3	60	63.7	136	48.9	12.9	21.4	32.8	27.1
25	98.2	66	95.0	62	74.0	104	63.7	146	57.5	–	2.7	40.0	
37	96.9	68	80.9	65	76.2	115	100						
73	99.4	69	73.4	70	78.4	130	98.8	22	2.8	47.1	44.9	6.2	29.2
78	87.6	84	100	75	76.0	135	59.2	64	3.2	33.8	52.7	14.7	16.1
80	88.3	88	93.5	86	68.2	137	60.9	76	7.1	34.8	41.9	29.1	21.1
105	99.1	94	100	89	89.2	140	48.2						
110	99.5	114	67.8	95	94.6	141	65.5	30	2.6	5.9	55.2	40.7	
112	75.0	121	84.8	102	77.7			79	.4	26.8	50.0	36.6	
117	87.0			103	93.3			82	–	13.0	57.0	37.0	
120	93.9			119	70.9			118	2.7	5.8	51.6	40.4	
122	75.0			125	77.3								
124	99.6			132	73.0			31	27.7	22.7	12.6	39.5	
138	99.5			134	66.1								
139	90.0			149	74.2			26	16.0	2.2	(63.0)	32.0	85.1
144	96.4							34	.4	7.8	(78.2)	14.5	71.4
148	90.2							106	2.4	16.1	(76.5)	3.2	71.0
150	95.3							133	2.9	3.9	(65.6)	33.0	54.6
20 spp.		11 spp.		17 spp.		10 spp.		16 spp.					

<sup>1</sup> see: Table 2.

<sup>2</sup> see: Table 3.

<sup>3</sup> between brackets: 4 species that were not brought to the F-group, because they highly prefer grass vegetations (within our sampling program these were mainly found among the F-habitats); see also: 6.5.4.

<sup>4</sup> 37 year-samples (Y = 52%) from localities with a vegetation structure highly dominated by grasses; all these year-samples are overlapping, either some localities of D, E, F or G.

Table 5. Frequency of A-, B- and C-species within different habitat groups (cf. Table 4).

Dispersal type:	A-species	B-species	C-species	total	
D-species	7	6	7	20	permanent habitats
E-species	5	0	6	11	
F-species	9	3	5	17	
	21	9	18	48	
G-species	1	7	2	10	temporary habitats
H-species	3	10	3	16	
	4	17	5	26	
Total	25	26	23	74	all habitats

Because in temporary habitats populations will only be able to persist during one or a few generations, even under the founding hypothesis the frequency of population disappearances must be supposed generally to be much lower in permanent habitats than in temporary ones (cf. 1.2). The dispersal power of species of permanent habitats might thus be assumed (although not necessarily so) to be accordingly lower than that of species of temporary ones.

In accordance with this, most A-species (21 out of 25) are found in the D-, E- and F-group (Table 5). Note, that the distribution of the C-species over the different habitat groups closely resembles that of the A-species (Table 5), which corroborates our supposition that the C-species are more related to the A-species than to the B-species (compare: 4.2.3). As could be expected, the distribution of A- B- and C-species over 'permanent habitats' differs very significantly ( $\chi^2 = 16.27$ ; d.f. = 2;  $p \ll 0.005$ ) from that over 'temporary habitats' (Table 5). Hence, for future discussions it can be kept in mind that the distribution of our 74 carabid species over 'temporary habitats' and 'permanent habitats' respectively can be mainly – but not completely, and that is an interesting point – reduced to a distribution according to differences in dispersal power.

#### 4.4. ABUNDANCE GROUPS.

To be able to test the 'overflow' hypothesis of dispersal s.s. in every respect (cf. 3.1), it would be helpful also to know how abundant species can reliably and independently be distinguished from sparse ones.

4.4.1. In 2.1 we mentioned how the individuals caught by continuous pitfall sampling and summed over the whole period of activity give a reliable comparative measure – within species – of the population size. This could be checked among others



by comparing these values with the data from extensive capture-recapture experiments on a number of these species and made in different sites and years. From the latter experiments the actual population sizes (in the sense of the sizes of the interaction groups concerned; cf. 1.4) could be estimated on the base of the stochastic model of JOLLY (1965); see further: BAARS, DEN BOER & VAN DER EIJK (in prep.), in which also will be shown that some drawbacks of the Jolly-model are unimportant in the present operations. By so doing it was found that also among different species the Jolly-estimates for the respective main periods of reproduction were closely and linearly related with the numbers of first (pitfall-)catches of individuals (i.e. the recaptures of these individuals not included), summed over the same periods.

First of all this appeared to be perfectly true for some species with about equally sized individuals and occupying the same habitat (i.e. the species 6 (9 years), 73 (6 years) and 138 (7 years)), but adding some other species with differently sized individuals (e.g. species 80 with the largest individuals: 21–27 mm), and/or occupying different habitats, and/or studied in other years, did hardly alter this relation. After all, in 34 cases concerning 8 species (6, 34, 73, 80, 117, 132, 134 and 138) the Jolly estimates and the pertinent pitfall-catches showed a correlation of:  $\tau = +0.767$ ,  $Z$  (standardized normal deviate) = 6.35,  $p \ll 0.00003$  ( $r = +0.961$ ;  $p \ll 0.01$ ); the same correlation is found when each year is treated separately and the results are added:  $\bar{\tau} = +0.770$  ( $p \ll 0.00003^*$ ). Note, that among these species there are 4 spring reproducing (6, 34, 132, 138), 2 summer reproducing (73, 134) and 2 autumn reproducing (80, 117) species, and there are 5 D-species, 2 F-species and one H-species (cf. Table 4).

Hence, within our study area the N-values of these 8 species (Table 3) will be representative and independent (i.e. checked by independent experiments) estimates of their relative abundances. It now appears from Table 3 that 34, 132 and 138 must anyhow be considered abundant species (they belong to the 5 species with N-values > 10,000), and that 6, 73, 80 and 117 are more sparse species (N-values < 2000, say).

4.4.2. Similar capture-recapture experiments were made with two more species – 68 and 70 – so that similar comparisons between Jolly-estimates and first catches of individuals were possible. These 2 species, however, appear to deviate from the general relation given above for 8 other species.

As far as species 68 (*Calathus erratus*: 4 cases) is concerned, the first catches of individuals only amount to about half – or somewhat lower – the value they should

\* We preferably use rank correlations:  $\tau$  (KENDALL, 1962), but in many cases between brackets the product-moment correlation coefficient  $r$  will be given too. Rank correlations can be combined ( $\bar{\tau}$ ) by adding the corresponding values of  $S$  and dividing by the added denominators of the parent  $\tau$ 's. The significance of  $\bar{\tau}$  can be tested against the sum of the variances of the individual rankings (the variance of the sum of independent variables is the sum of their variances): KENDALL (1962, p. 65).

have reached according to the above relation (cf. 4.4.1). From unpublished work done by TJALLINGII in 1969, it appeared that the capture efficiency of our pitfalls (and also of 3 other types of traps) was low for this species: 28% (viz. only 55 out of 197 encounters with a pitfall resulted in catches). LUFF (1975), who in about the same way studied the capture efficiency for a lot of other carabid species, reached values between 53 and 80% (his Table 7), i.e. more than twice as high as in our case of species 68. One out of the 8 species that fit the above 'general relation' – viz. 117 (*Nebria brevicollis*) – was also among the species studied by LUFF, and reached there a capture efficiency of 71%. Hence, the degree to which species 68 deviates from the above relation about agrees with the extent to which its capture efficiency deviates from the values given by LUFF (1975) so that the latter deviation most probably will have been the cause of the former one. In the same time this means, that the other species mentioned in LUFF's Table 7 probably will also fit our 'general relation' (cf. 4.4.1), i.e. besides 117, our species 104, 136 and 141 (cf. Table 3).

In species 70 (*Calathus melanocephalus*; 2 cases) the sums of the first catches of individuals are about five times lower than predicted from our 'general relation'. See further: BAARS, VAN DIJK & VAN DER EIJK (in prep.). Up till now we did not directly study the capture efficiency for species 70, but different other observations strongly suggest that it is indeed very low.

Hence, the N-values (Table 3) of both species 68 and species 70 will underestimate their respective relative abundances. However, these species will anyhow be considered to be very abundant because they already have N-values > 10,000.

4.4.3. The extent to which beetles can escape from our pitfalls will generally not be an important cause of misinterpreting the N-values of Table 3, because our pitfalls are deep (30 cm) and smoothly coated.

Retaining efficiency was tested in the field for 15 out of the 30 species with large individuals ( $\geq 9$  mm) and for 16 out of the 26 species with medium-sized individuals (5.5–8.5 mm; cf. Table 3). For weekly periods (the frequency of sampling from the pitfalls) and under all kinds of weather conditions, for the first group of species retaining efficiency amounted to 92.4% (88 out of 1149 marked ind. escaped), and for the second group of species to 84% (63 out of 395 marked ind. escaped). Because not all catches will occur during the first day of a sampling week, and because one out of the 3 pitfalls of a standard set has a formalin-filled container, in our routine sampling retaining efficiency will have been still higher, i.e. – after correction – about 97% for the species with large ind., and about 94% for the species with medium-sized ind. Compare also LUFF (1975).

Although it was not tested, incidental observations suggest that retaining efficiency must be substantially lower for most of the 18 species with small individuals (< 5.3 mm; cf. Table 3); many small carabids are able to climb a wetted surface. When species with N-values > 2000 are considered to be 'abundant' ones, however – and there are good reasons to do so (see: 7.4.2) – retaining efficiency for the above

18 species should be lower than 50% (which seems to be a too low value) to get a first 'misclassification', viz. the next lower N-value under 2000 is 1108 (species 114): Table 3.

4.4.4. Carabid beetles in which the way of life deviates from the general pattern: 'predators that walk around at the surface of the soil' are generally expected to score too low N-values (Table 3). Among our 74 species such an underestimation of the relative abundance could possibly occur in the species 66, 86, 94 and 95 (burrowing species), the species 82 and 84 (flying hunters) and the species 31, 35 and 64 (phytophagous species that often climb plants to feed on the seeds: LINDROTH, 1945).

Among the above species, 64 (*Bradycellus harpalinus*) is the most probable candidate for a 'misclassification'. The very high numbers that are caught in window-traps (Table 3: column 11) do suggest that it is an abundant species in our area. Although we sufficiently sampled its preferred habitat – heath-like localities – its N-value is undoubtedly too low for this (Table 3: column 12). The latter may be accentuated by its being one of the 18 species with small individuals too (cf. 4.4.3).

The species 31 (*Amara familiaris*) and 35 (*Amara plebeja*) – also high numbers in the window-traps (cf. Table 3: column 11) – are different in that their preferred habitats – arable and waste land, see e.g. VAN HUIZEN (in press), from which they are obviously flying in abundantly – were not incorporated in our program; within the localities of our sampling program these will not have been abundant species, however (although probably underrated by their N-values). In this connection must be noted that many other *Amara*- (and *Harpalus*-)species are not phytophagous, e.g. the species: 25, 33, 38, 104 and 105 (HENGEVELD, in prep.), and are therefore not expected to be importantly underrated by their N-values.

The N-values of the other species mentioned in this section are either too low (66, 86, 94, 82, 84) or too high (95) to consider an important chance of 'misclassification' when species with  $N > 2000$  are considered 'abundant'.

4.4.5. Reviewing the parts 4.4.1 up to 4.4.4 inclusive we can conclude about the N-values of Table 3:

- (1) Among many carabid species the N-values obviously are reliable and independent estimates of their relative abundances within interaction-groups (cf. 4.4.1).
- (2) Compared with the species fitting the 'general relation' of 4.4.1, not-tested carabid species apparently will either also fit this relation (cf. LUFF, 1975), or underestimate – by various causes – their relative abundances by giving too low pitfall-catches (cf. 4.4.2).
- (3) Because of (2), species with a high N-value –  $> 2000$ , say – will anyhow be comparatively abundant.
- (4) Sparse species will anyhow score low N-values.
- (5) When we take  $N = 2000$  as a divider to separate abundant from sparse species (more arguments for this will be given in 7.4.2) the chance to 'misclassify' any species is apparently small (cf. 4.4.3 and 4.4.4). To show that the above division is not very restrictive, however, in most cases (ch. 7) there will also be tested with  $N = 1200$  as a divider.

Because the N-values of Table 3, as rough indicators of the order of magnitude of the relative abundances of the pertinent species, thus appear not to be so much worse than many other field estimators, significant correlations with the N-values may generally be considered to give a reliable impression of the actual trends that go with the abundances of the pertinent species.

## 5. HOW TO ESTIMATE THE DEGREE OF REALIZATION OF POPULATION REPLACEMENT (RPR)?

In 3.3 we concluded that DPS, i.e. the frequency of occurrence of sparse populations – as compared with that of dense ones – in the natural localities of a cultivated area would be an estimate of RPR. In 2.1 it is indicated why the summed catches from continuous pitfall-sampling in a locality (year-sample: 4.1) gives a workable estimate of the relative size of the local group of the species concerned.

Hence, we will now consider, how, for each species, the catches in the 175 year-samples (cf. 4.1) can be grouped to an adequate frequency distribution (i.e. DPS). Next, we will have to look for a method by which such a distribution can be reduced to a single value, in such a way that the resulting DPS-value can be expected to be the best possible estimate of RPR. Then we will be able to compare these DPS-values for different groups of species – in the first place for A- and B-species respectively – and thus to test our hypotheses (ch. 3): chapter 6.

### 5.1. A MODEL OF DPS

Because most aspects of the changes in numbers of a local group (e.g. reproduction, mortality) can be considered to be of an approximate multiplicative nature relative population sizes have to be compared in the form of their logarithms (see e.g.: WILLIAMSON, 1972). Hence, for each species we will have to distribute the year-samples over a set of geometric classes.

To work with convenient class-bounds we will use  $\times 3$ -classes, i.e. class 0 has the upper bound  $\frac{1}{2}$  and will thus contain all year-samples in which the species is not represented; class I will contain those with a single specimen, viz. with the bounds  $\frac{1}{2}$  and  $1\frac{1}{2}$ ; class II will have the bounds  $1\frac{1}{2}$  and  $4\frac{1}{2}$  ( $= 3 \times 1\frac{1}{2}$ ) and contain all year-samples with 2, 3 or 4 specimens; etc. (cf. WILLIAMS, 1964), see Table 6.

To get some insight into the kind of differences that can be expected to be found between the distributions of year-samples over such geometric classes for A-species and B-species respectively, we will first consider a model.

5.1.1. We consider a B-species in which the dispersal power is supposed to be high enough to realize early (re)founding of local groups in nearly all places that are suitable, i.e. a species with an about complete RPR, even in a cultivated countryside. When a collection of year-samples of such a B-species is available in which each kind of natural locality and each kind of year is sufficiently represented, it is convenient to assume for the moment that the distribution of these year-samples over adequate geometric classes will approach a normal one. Note, that this assumption – although

Table 6. Model of the distribution of year-samples (starting from 1000) over  $\times 3$ -classes of catch sizes; B: complete replacement of extinct populations; A: no significant replacement.

class	bounds of $\times 3$ -classes	class-mark = n between brackets: $\ln(n + 1)$	B: j, normally distributed <sup>1</sup>	$\lambda^n$ : chance of extinction	A: j, with extinction <sup>1</sup>
0	– 0.5	0	(4)		(357)
I	0.5– 1.5	1 (0.6931)	36	0.92	3
II	1.5– 4.5	3 (1.3861)	160	0.779	35
III	4.5– 13.5	9 (2.3025)	340	0.472	179
IV	13.5– 40.5	27 (3.3321)	310	0.105	277
V	40.5– 121.5	81 (4.4068)	125	0.011	124
VI	121.5– 364.5	243 (5.4971)	23	$0.14 \times 10^{-5}$	23
VII	364.5–1093.5	749 (6.5931)	2	$<0.1 \times 10^{-8}$	2
			B	A	
j: number of year-samples with catches			996	643	
N: total number of ind.			29,118	26,329	
$\frac{N}{j}$ = mean number of ind. per year-sample			29.2	40.9	
$\Sigma \ln(n_i + 1)$			2752.997	2071.795	
$\frac{\Sigma \ln(n_i + 1)}{j}$			2.764	3.222	
$(n_i$ : number of ind. in year-sample i)					

<sup>1</sup> between brackets: number of year-samples without catches.

probably reasonable – is not restrictive, cf. 5.1.2. Suppose this collection covers 1000 year-samples, that are distributed over  $\times 3$ -classes as given in Table 6, column B.

We now consider a comparable A-species in which the dispersal power is supposed to be so low that in an intensively cultivated countryside no significant replacement of extinct populations is realized anymore. When the running time of the 'experiment of cultivation' has been sufficiently long – a century, say – many sparse populations will have disappeared already, by which a collection of 1000 year-samples from such an area will show many zero samples and a skew distribution of the remaining ones, concerning our A-species. We assume – modified from PIELOU (1969: p. 17) – that the chance of extinction of a local group is:  $P_n = \lambda^n$ , in which n is the catch size in the year-sample concerned, and consequently  $\lambda = \lambda^1$  is assumed to be the chance of extinction of a group that is so sparse, that only a single specimen is caught during a whole year. For simplicity is supposed that  $P_n$  has the same value for all local groups

within the same  $\times 3$  class of catch sizes. When we arbitrarily assume  $\lambda$  to be 0.92, the distribution of such an A-species over  $\times 3$ -classes can be derived now from that of the B-species, and is thus as given in Table 6, column A. It will be evident, that in the A-species – with the exception of the 0-class – the lower classes will be under-represented as compared with the B-species, i.e. the relative frequency of sparse populations will be lower in the A-species than in the B-species of our model.

This is clearly illustrated by Fig. 2, in which the year-samples are cumulated over  $\times 3$ -classes – as the percentage of the total number of year-samples – and plotted on a probability-scale. The B-species cumulates – by definition – linearly over the whole range of  $\times 3$ -classes. The A-species, after a high start in the 0-class, cumulates very slowly over the lower classes, to turn then to about the same rate of cumulation over the higher classes as the B-species.

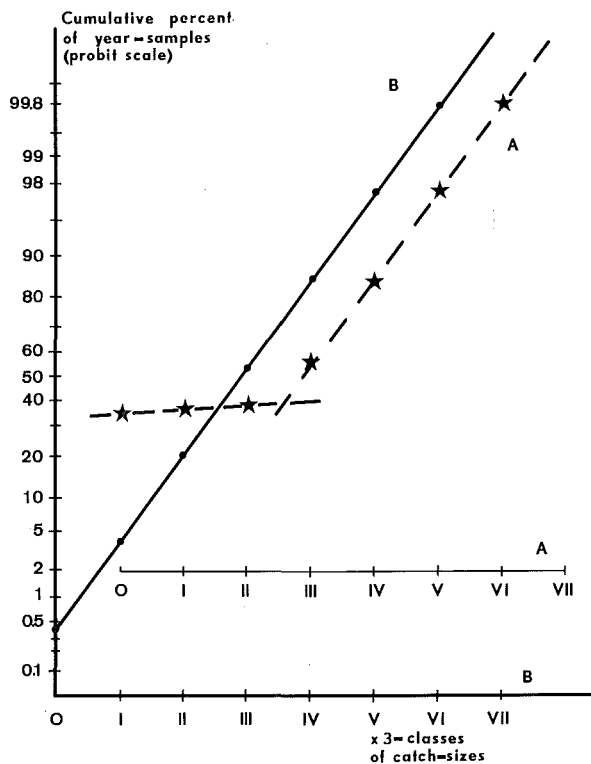


Fig. 2. Cumulated distribution of year-samples over  $\times 3$ -classes (plotted on a probability scale as the percentage of the total number of year-samples) for two model species: a species with an about complete replacement of populations which have disappeared (B-species) and a species without significant replacement and a chance of extinction of local groups of  $P_n = \lambda^n$  (A-species); cf. 5.1.1., Table 6. Note, that for the sake of clearness the scale of classes for the A-species is moved one class to the right. ●: B-species; \* : A-species.

5.1.2. Apart from some special properties – such as the exact value of  $P$  and the exact form of the distribution in the B-case – the main features of the model discussed in 5.1.1 give some idea of the kind of differences that can be expected to be found when comparing species with a high RPR with species with a low RPR (cf. 3.3); lower part of Table 6.

Hence, species with a comparatively low frequency of sparse populations will show a relatively high value of  $N/j$  and of  $\sum \ln(n_i + 1)/j$  ( $N$ : total number of ind.;  $j$ : number of year-samples with catches;  $n_i$ : number of ind. in year-sample  $i$ ). Concerning these main features the model of 5.1.1 will be rather robust; these features will e.g. hardly depend on whether or not in species with a high dispersal power the distribution of year-samples over  $\times 3$ -classes will indeed approach a normal distribution. On the other hand, Fig. 3 (6.1) will show, that the cumulation lines of a number of carabid species remarkably resemble one of the cumulation lines of Fig. 2. Hence, our convenient starting point (cf. 5.1.1) – an about normal distribution of the logarithms of catch sizes in B-species – seems to be close to the mark.

5.1.3. It is generally not expected that catch intensity – as long as it is the same (and not too low) in all cases compared – will substantially influence the form of the distribution of year-samples over classes of catch sizes (DPS). The reader can easily make sure that, when in the model B-species (cf. 5.1.1 and Table 6) the supposed catch intensity is lowered to one third, say, class I will be added to the zero class and as a consequence the whole distribution will move up one class. However, shape and slope of the cumulation line, as given in Fig. 2, will not be altered by this. In the model A-species this is somewhat different, however. Lowering catch intensity to one ninth of the modeled one, say, will move up the distribution two classes, by which both class I and class II will be added to the zero class, i.e. that part of the distribution that gives information on the relatively low frequency of small population sizes, will for the greater part be hidden under the zero class.

In the present investigation, in which catching was standardized as far as technically possible (cf. 4.1), it is assumed that catch intensity was still sufficiently high to show at least part of the expected differences between A- and B-species. But if this assumption would not hold to a sufficient degree, we will not be able to reject our null hypothesis (cf. 3.2), and thus we will keep on the safe side, when testing results in accepting our alternative hypothesis (cf. 3.4).

## 5.2. A PRELIMINARY TEST OF OUR HYPOTHESES

If for the moment we accept the kind of differences between the model A- and B-species, as shown in the lower part of Table 6, to be sufficiently workable measures of DPS, we can already perform some preliminary tests of our hypotheses 3.2 and 3.4.



5.2.1. Because the properties of collections of year-samples from different places and/or years may generally be considered to be sufficiently independent in different species, we can perform a comparison of the values of one such property in two samples of different species by the non-parametric Mann-Whitney U-test or Wilcoxon two-samples test – in the following U-test – see e.g. SIEGEL (1956; p. 116–127), VAN DER VAART (1950). The U(S)-values of a number of U-tests on the same property but from different – although comparable – pairs of samples can be combined (SIEGEL, 1956), by which irrelevant differences between the sample pairs (e.g. effectuated by different levels of numbers) are left out.

As first relevant features of DPS we consider  $N/j$  and  $\sum \ln (n_i + 1)/j$  (Table 6). Both appear to be significantly higher (U-test) in the 25 A-species than in the 26 B-species (cf. 4.2):  $Z$  (standardized normal deviate) = 2.94 ( $p = 0.0017$ , one-sided) and  $Z = 3.45$  ( $p = 0.00025$ , one-sided). Similar results are obtained when testing A- + C-species against B-species.

5.2.2. Because quotients like  $N/j$  may have a different meaning in abundant species than in sparse ones (cf. 4.4), it seems better to treat the above comparisons as bivariate problems. It seems obvious here to regress total catch on the number of year-samples – i.e.  $\ln N$  on  $\sqrt{j}$  (to approximate linearity), or  $\sum \ln (n_i + 1)$  on  $j$  – and to compare the regression lines for the A- (or A- + C-) species with that for the B-species (cf. SNEDECOR & COCHRAN, 1967, Ch. 14). In all cases the regression lines concerned appear to run parallel ( $p \approx 0.75$ ), whereas the adjusted mean for A-species (or A- + C-species) is always significantly higher than that for B-species ( $p \approx 0.005$ ).

When we consider to what degree the assumptions underlying the linear regression model are satisfied, it appears that in the case of  $\ln N$  on  $\sqrt{j}$  these are not violated too much, but in the case of  $\sum \ln (n_i + 1)$  on  $j$  the variance of  $y$  increases when  $x$  increases. Because similar difficulties were met several times during the present study I looked for nonparametric bivariate tests that could do the job. A standard test that could be applied to the above – and a number of similar – cases was not found, however. Following a proposal by REDDINGIUS, the Median Test was used in the manner described below. A mathematical justification of this procedure is given by REDDINGIUS in Appendix B.I.

5.2.3. Suppose we have two bivariate samples, say  $(t_{11}, X(t_{11})), (t_{12}, X(t_{12})), \dots, (t_{1n}, X(t_{1n}))$ , and  $(t_{21}, Y(t_{21})), (t_{22}, Y(t_{22})), \dots, (t_{2m}, Y(t_{2m}))$  where  $t_{11}, t_{12}, \dots, t_{1n}$  and  $t_{21}, t_{22}, \dots, t_{2m}$  are from about the same interval, and suppose we wish to test whether the regression curve of  $X$  on  $t$ ,  $f(t)$ , say, lies consistently above or below the regression curve  $g(t)$  of  $Y$  on  $t$ , then in many cases we may treat  $X(t_{11}), \dots, X(t_{1n})$  and  $Y(t_{21}), \dots, Y(t_{2m})$  as just two independent samples and test the null hypothesis whether they were drawn from populations with the same median by means of the Median Test (SIEGEL, 1956, p. 111). This procedure is justified under, e.g., the following conditions:

- (a) The  $X$  and  $Y$  variates either are measured at the same values of the independent variable  $t$ , or else  $(t_{11}, t_{12}, \dots, t_{1n}), (t_{21}, \dots, t_{2m})$  are two independent random samples from the same universe.
- (b) The regression curves  $f$  and  $g$  are either both monotonically increasing, or both monotonically decreasing. (They need not be linear).
- (c) For any given  $t$ , the residuals  $X(t) - f(t)$  and  $Y(t) - g(t)$  have the same probability distribution (which may depend on  $t$ ); this distribution is continuous and the probability density function is symmetrical about zero and has a unique maximum at zero.

If the interval of t-values considered is rather large, we might doubt if assumptions such as these are even approximately true; moreover in such cases the test presumably is not very powerful. Therefore it is better then to divide the range of t-values into a number of classes in such a way that in each of these classes the dependent variables do not show very obvious trends, and the values of the independent variables are distributed in about the same fashion for both sets of values of the dependent variables within each class. Within each class, a common median of the X and the Y-sample is estimated. Suppose we have p X-values and q Y-values, and let  $p + q = m$ . We now count the number of X-values which are not greater than the common median; let this number be a, and let  $b = p - a =$  number of X values greater than the median. Let c = number of Y-values which are not greater than the median, let  $d = q - c$ ,  $r = a + c$ , and  $s = b + d$ . We now compute

$$U = \left( a - \frac{rp}{m} - \frac{1}{2} \right) / \sqrt{\left( \frac{pqrs}{m^2(m-1)} \right)} = \left( am - rp - \frac{m}{2} \right) \sqrt{\frac{m-1}{pqrs}}$$

Let  $U_i$  denote the U thus computed in the i-th class, and suppose there are k classes. We then compute  $Z = \sum_{i=1}^k U_i / \sqrt{k}$ .

Under the null hypothesis, and assuming that the  $U_i$  are independent, Z is approximately a standardized normal variate, and the null hypothesis is rejected when the value of Z differs significantly from zero according to the standard normal distribution.

5.2.4. When applying the median test described above (in the following Med.-test) to our problem of 5.2.2, we can first ascertain that the assumptions of this Med.-test are satisfied: for all samples (A-, A- + C- or B-species) the j- (or  $\sqrt{j}$ -) values belong to about the same distribution (all kinds of species can theoretically reach all kinds of j-values; the j-values found are considered to be those only realized by our sampling program); the regression lines of the dependent variables on j (or  $\sqrt{j}$ ) seem to be fair estimates of the regression curves, and they run almost parallel. The results are now:  $\ln N$  on  $\sqrt{j}$ ,  $Z = -3.54$  ( $p \approx 0.0002$ , one-sided; 3 classes of  $\sqrt{j}$ );  $\Sigma \ln(n_i + 1)$  on j,  $Z = -3.05$  ( $p \approx 0.002$ , one-sided; 4 classes of j). Other relevant class divisions give about the same results.

5.2.5. The features of DPS tested in 5.2.1, 5.2.2 and 5.2.4 are only rough approximations of RPR, which means that possible differences in RPR between the groups of species compared may be expected to be expressed only imperfectly by them. Hence, the chance of committing a type II error – accepting the null hypothesis wrongly – can be expected to be rather high. The more remarkable, that the results of these tests already point towards rejecting of our null hypothesis (cf. 3.2).

To exclude the very low chance that the above test-results have exactly arisen from the imperfections of the DPS-features used, we should prefer to base our testing on a more elaborate measure of DPS, i.e. some measure in which the relative frequency of sparse populations is made comparable for different species. We should like to dispose of a single value that can be considered the best possible estimate of RPR.

### 5.3. CONDITIONS FOR A SINGLE VALUE OF DPS

Which requirements should be met by such a reliable measure of DPS? First: to be able to compare all kinds of species on the same scale, DPS should be standardized, e.g. with 0 and 1 as the extreme values. Some further requirements are formulated below.

- (1) The higher the relative number of year-samples with low catches (sparse populations) the higher should be the value of DPS. The most extreme case will be a species with only one dense population – manifested by a single year-sample with high catches – and many very sparse populations – indicated by a high number of year-samples each with a single specimen. Such a species would indeed give evidence of an extremely high dispersal power, and consequently should DPS (RPR) reach a maximal value in such a case.
- (2) The higher the relative number of year-samples with high catches (dense populations) the lower should be DPS. In the most extreme case there will be no sparse populations (low catches) at all, and all year-samples will show catch sizes of about the same – relatively high – order of magnitude. Hence, when the catch size would be the same for all year-samples, DPS (RPR) should reach a minimal value, which should be the lower the higher that catch size.
- (3) In general, starting from an already high level of the total number of individuals caught ( $N$ ), the addition of some year-samples with low catches should increase the value of DPS, because in such a case the relation between the number of dense and that of sparse populations is changed in favour of the latter ones, i.e. in favour of a higher population replacement (RPR) as a result of a high dispersal power. On the other hand, with high values of  $j$ , DPS should not necessarily be high, i.e. especially in very abundant and eurytopic species it should be possible that DPS (RPR) reaches a relatively low value – depending on the proportion of the year-samples that show relatively low catches.

### 5.4. AN ADEQUATE MEASURE OF DPS

After having considered the necessary requirements that should be met by a reliable measure of DPS (cf. 5.3), one realizes that the cumulation lines of Fig. 2 in fact about visualize the features we want of DPS. Hence, a promising strategy seems to be: trying to standardize the main quantitative properties of such a cumulation line, without leaning on the underlying normality model.

5.4.1. Because in the model of Fig. 2 (cf. 5.1) the sizes of the year-samples are cumulated over logarithmic classes,  $\sum \ln(n_i + 1)$  can be considered the result of such a cumulation process, a result that is independent of the kind of distribution of the year-samples. Also year-samples with relatively low catches will appreciably contrib-

ute to  $\sum \ln (n_i + 1)$ , which is a necessary condition if one intends to compare the frequency of occurrence of sparse and of dense populations. Of course, it makes all the difference whether a certain value of  $\sum \ln (n_i + 1)$  has been cumulated from a low number or from a high number of year-samples with catches ( $j$ ). Because the level of  $N$  (total catch) is to a large extent determined by the high catches (year-samples from dense populations), the value of  $N$  – in some adequate transformation – together with that of  $j$  should be used to scale the contribution of low and of high catches respectively to the value of  $\sum \ln (n_i + 1)$ . The above conditions are satisfied by the standardized expression  $DPS = 1 - \frac{\sum \ln (n_i + 1)}{j \cdot \ln (N + j)}$ ; because in the numerator  $j$  times one is added in  $\sum \ln (n_i + 1)$ , in the denominator  $j$  is added to  $N$  in  $\ln (N + j)$  since  $\sum (n_i + 1) = \sum n_i + j = N + j$ .

5.4.2. In Appendix B.II it is mathematically shown by REDDINGIUS, that our equation for the reduction of DPS to a single value does indeed satisfy the above conditions, as well as the requirements to be met by the best possible estimate of RPR (cf. 5.3). In the following we will only briefly deal with the main points of the argument; for a more rigorous discussion the reader is referred to the Appendix (B.II).

5.4.3. The requirement (1) will result in an extreme (maximal) value of DPS, when for  $\sum \ln (n_i + 1)$  can be written  $(j-1) \ln 2 + \ln [(N - (j-1)) + 1]$  and thus for DPS:  $1 - \frac{(j-1) \ln 2 + \ln (N - j + 2)}{j \cdot \ln (N + j)}$  (I). With  $N$  fixed, an increasing value of  $j$  – i.e.

more year-samples with a single specimen – will have a relatively greater influence in the denominator than in the numerator, by which the value of DPS will increase; e.g. with  $N = 1000$ ,  $DPS = 0.810$  for  $j = 10$ , and  $DPS = 0.892$  for  $j = 100$ .

The requirement (2) will result in an extreme (minimal) value of DPS, when  $DPS = 1 - \frac{j \cdot \ln (N/j + 1)}{j \cdot \ln (N + j)} = \frac{\ln j}{\ln (N + j)}$  (II). The higher  $N$  as compared to  $j$  – i.e. the higher the catch size/year-sample – the lower the value of DPS. Hence, with  $N$  fixed, a decreasing value of  $j$  will mean a decreasing value of DPS; e.g. with  $N = 1000$ ,  $DPS = 0.657$  for  $j = 100$ , and  $DPS = 0.333$  for  $j = 10$ ; in all cases for  $j = 1$ ,  $DPS = 1 - \frac{\ln (N + 1)}{1 \cdot \ln (N + 1)} = 0$ .

The requirement (3) will be satisfied when the addition of some year-samples will have a proportionally greater influence in the denominator than in the numerator. Assuming that such an addition has only a small influence on  $\ln (N + j)$ , this will generally be the case when for the added year-samples the value of  $\ln (n_i + 1)$  is lower than that of  $\sum \ln (n_i + 1)/j$ , i.e. when we add year-samples with relatively low catches. When, on the other hand, year-samples are added for which the value of

$\ln(n_i + 1)$  is much higher than that of  $\sum \ln(n_i + 1)/j$ , the value of DPS will generally decrease, if  $\ln(N + j)$  is not influenced too much. This also means that with high values of  $j$ , DPS will not necessarily be high, because the value of DPS will especially depend on the relation between the number of year-samples with low catches – i.e.  $\ln(n_i + 1) \ll \sum \ln(n_i + 1)/j$  – and that with high catches – i.e.  $\ln(n_i + 1) \gg \sum \ln(n_i + 1)/j$ .

5.4.4. This latter dependence indeed appears to be more significant than the tendency of DPS to increase slightly with a substantial increase of the number of representative year-samples (cf. 6.2), i.e. an increase by which the distribution of year-samples over classes of catch size is not altered proportionally. If in such a case the number of representative year-samples increases  $t$  times ( $t > 1$ ) the new value of DPS will be:

$$1 - \frac{t \cdot \sum \ln(n_i + 1)}{t \cdot j \cdot \ln(t \cdot N + t \cdot j)} = 1 - \frac{\sum \ln(n_i + 1)}{j \cdot \ln t + j \cdot \ln(N + j)} \quad \text{(III)},$$

i.e. only the denominator increases, and by it the value of DPS. In 6.2 will be shown that within our collection of 175 year-samples this tendency is generally surpassed by differences between species concerning the distribution of year-samples over classes of catch size, i.e. by the supposed differences in the level of dispersal power. In this connection it must be noted that the above tendency of DPS does not disagree with the requirements that should be met by a reliable estimate of RPR: to understand this we suppose for the moment that in a certain area many year-samples have been taken to compare the DPS-values of two species with the same kind and degree of dispersal. It is known that for species 1 generally more favourable places are available in the area than for species 2, by which more dense populations of species 1 than of species 2 will have been sampled (high catches). Because in species with the same degree of dispersal the number of dispersing individuals will generally be the higher the more individuals are available (other things being equal) the chance of (re)founding of populations in less favourable and/or only temporarily favourable places will be higher for species 1 than for species 2. Therefore, species 1 will not only be represented in more year-samples with high catches but also in more year-samples with low catches, than is the case in species 2. Hence, when in this case the many year-samples of species 1 appear to show a proportionally similar distribution over the classes of catch size as the fewer year-samples of species 2 (which is possible, but not necessary, of course) the DPS-value of species 1 should nevertheless be higher than that of species 2, because RPR will be higher in species 1. Above we showed that this will indeed be the case.

5.4.5. We learned already that for  $j = 1$ ,  $DPS = 0$ , and because in our investigation  $N \geq 70$ , this would indeed point to a case in which the replacement of extinct populations is apparently lacking completely. It must be noted here, that DPS

cannot reach 1 – although it might run close to it – because  $\frac{\sum \ln(n_i + 1)}{j \cdot \ln(N + j)}$  cannot reach 0.

## 6. TESTING OF THE HYPOTHESES 3.2 AND 3.4

Now we arrived at a single value for the frequency distribution of population sizes (DPS) that meets the requirements to be the best possible estimate of the degree to which disappeared populations are replaced (RPR) – cf. 5.3 and 5.4 – and that does not show any odd mathematical properties (cf. Appendix B.II), we can test our hypotheses (3.2 and 3.4) to a more conclusive degree than in 5.2. Therefore, in the following the term DPS will only refer to the expression:  $1 - \frac{\sum \ln(n_i + 1)}{j \cdot \ln(N + j)}$ .

### 6.1. RESULTS OF THE TEST

Our testing procedure can be formulated now: we will have to demonstrate that within a group of comparable species living in natural localities within a cultivated countryside (with a history of cultivation of at least some decades), and among which species with low powers of dispersal (A-species) can be distinguished from species with high powers of dispersal (B-species), lower DPS-values – i.e. lower frequencies of sparse populations as compared with those of dense ones – significantly coincide with lower powers of dispersal (i.e. are mainly found among A-species): alternative hypothesis (3.4) or do not so: null hypothesis (3.2). In other words: according to our alternative hypothesis (3.4) we will have to show that the DPS-values of our 25 A-species (cf. 4.2.2) are significantly lower than those of the 26 B-species (cf. 4.2.1). The DPS-values that will be tested – together with the composing elements – are given for A-, B- and C-species respectively in Table 7.

6.1.1. Performing the U-test (cf. 5.2.1) for A-species against B-species results in highly corroborating our expectation:  $Z = 3.93$  ( $p = 0.000042$ ; one-sided); see also: 7.2.1. A similar result is reached when testing A- + C-species against B-species:  $Z = 3.86$  ( $p = 0.000057$ ; one-sided). In 4.2.3 and 4.3.1 we suggested that the C-species may be more related to the A-species than to the B-species. Accordingly the B-species appear to show significantly higher DPS-values than the C-species (U-test):  $Z = 2.69$  ( $p = 0.00357$ ; one-sided), whereas the DPS-values of the C-species are only slightly higher than those of the A-species:  $Z = 1.82$  ( $p = 0.0344$ ; one-sided).

6.1.2. The above relations are also clearly illustrated by Fig. 3, in which the cumulation lines (cf. 5.1.1 and Fig. 2) for all the 74 species – divided into B-, A- and C-species respectively – are arranged as well as possible according to the corresponding DPS-values (abscissa): the DPS-range in which the majority of the cumulation lines for the

Table 7. DPS-values and the composing elements for 74 Carabid species divided into 3 groups according to dispersal power (cf. 4.2).

A-species				B-species				C-species						
sp.	j	$\ln(N+j)$	$\Sigma \ln(n_i+1)$	DPS	sp.	j	$\ln(N+j)$	$\Sigma \ln(n_i+1)$	DPS	sp.	j	$\ln(N+j)$	$\Sigma \ln(n_i+1)$	DPS
1	34	6.62	98.382	0.5629	9	71	5.88	97.508	0.7664	33	43	6.74	87.265	0.6987
6	44	7.55	104.252	0.6862	18	66	5.83	79.915	0.7923	37	29	5.25	40.026	0.7372
8	50	6.92	104.904	0.6968	22	49	5.42	60.311	0.7729	38	10	4.49	17.855	0.6022
17	110	7.55	243.417	0.7069	25	42	8.00	112.243	0.6659	62	76	6.85	146.113	0.7193
29	52	6.96	117.601	0.6751	26	62	6.41	101.535	0.7445	66	39	6.27	73.843	0.6981
56	45	8.18	141.133	0.6166	30	57	6.18	76.466	0.7829	73	56	7.19	133.034	0.6694
68	90	9.30	322.849	0.6143	31	48	5.12	49.610	0.7981	84	13	4.73	22.096	0.6405
69	32	6.18	58.426	0.7045	34	116	9.73	343.727	0.6955	89	45	5.26	55.681	0.7649
70	115	10.34	484.315	0.5926	35	102	6.13	133.872	0.7859	94	5	5.48	14.955	0.4522
75	86	6.64	143.683	0.7484	54	63	6.85	97.844	0.7733	102	48	6.23	78.936	0.7361
76	97	6.14	128.987	0.7834	60	20	4.97	27.750	0.7208	105	48	6.16	79.672	0.7197
78	55	6.35	104.057	0.7020	64	83	6.87	163.500	0.7133	109	79	6.03	109.098	0.7708
79	63	5.80	87.871	0.7595	65	103	8.11	254.564	0.6953	110	49	7.06	118.809	0.6563
80	90	7.42	195.002	0.7070	82	34	4.64	34.659	0.7803	117	74	6.89	140.718	0.7277
88	29	5.80	60.959	0.6376	86	65	5.61	78.525	0.7846	118	41	6.03	59.188	0.7607
95	108	9.19	307.355	0.6902	104	72	6.12	83.394	0.8109	119	110	9.17	377.047	0.6262
103	85	8.22	209.790	0.6997	106	32	4.83	38.211	0.7635	121	65	6.78	130.640	0.7034
114	63	7.07	143.368	0.6781	112	134	6.95	216.758	0.7712	122	49	5.71	72.664	0.7402
115	4	4.33	9.379	0.4585	120	74	8.30	248.081	0.5971	124	57	7.46	143.410	0.6627
132	126	9.68	424.668	0.6517	133	130	8.69	383.373	0.6614	125	58	6.42	109.086	0.7070
134	90	8.46	285.102	0.6256	135	40	5.62	50.018	0.7825	130	14	7.03	23.689	0.7593
136	164	7.91	359.064	0.7232	137	166	7.50	304.001	0.7584	141	31	5.01	32.658	0.7897
138	86	9.47	348.923	0.5716	139	67	6.48	113.915	0.7415	146	20	5.86	40.550	0.6542
144	27	4.70	34.566	0.7276	140	56	4.97	59.317	0.7998					
148	9	6.82	31.239	0.4911	149	84	7.66	182.745	0.7175					
					150	66	7.78	190.045	0.6312					

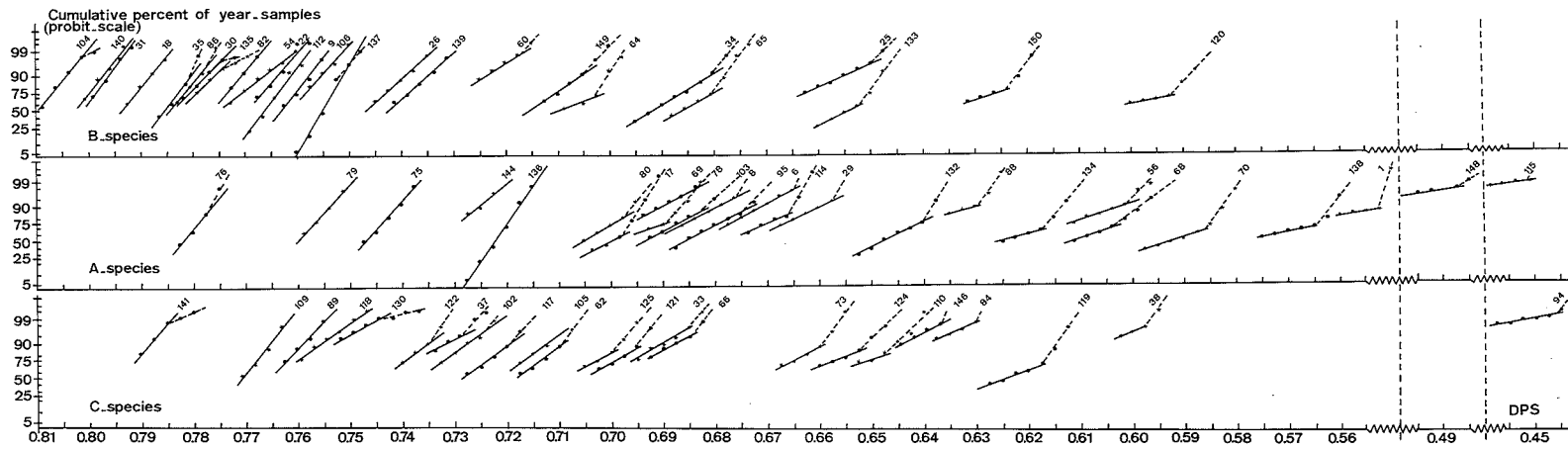


Fig. 3. Cumulation lines (compare Fig. 2) for 74 carabid species (divided into B-, A- and C-species respectively; cf. 4.2), arranged according to the corresponding DPS-values: abscissa (Table 7); cf. chapters 5 and 6. The numbers refer to Table 2.



B-species is quite different from that of the majority of the lines for the A-species, whereas the C-species are intermediate in this respect.

Fig. 3 also shows that the general shape of a cumulation line indeed gives information about the order of magnitude of the corresponding DPS-value (compare: 5.4): from high to low DPS-values (left to right) the slope of the cumulation lines gradually decreases, in most cases mainly in the lower classes of catch size – by which the lines concerned exhibit a bend – in some cases also in higher classes\*. In this respect too, the B-species are clearly different from the A-species: the majority of the B-species (17–19 out of 26) show unbended cumulation lines with a relatively steep slope, whereas the majority of the A-species (20 out of 25) show bended cumulation lines with a relatively feeble slope – at least in the lower classes.

Note, that this agreement between shape of cumulation lines and values of DPS is not self-evident, because the underlying models are quite different, e.g. the cumulation lines are based on a log.-normal distribution in which also the zero-catches are taken up. With the help of different sets of assumptions this agreement can be understood. Because the cumulation lines are only used as illustrations, however, this can be left to the reader. For the present, it suffices to ascertain that Fig. 3 convincingly shows both, that A- and B-species importantly differ as regards the distribution of year-samples over classes of catch size, and that the values of DPS represent fair estimates of the magnitude of these differences.

## 6.2. THE INFLUENCE OF $j$ ON THE VALUE OF DPS

In 5.4.4 it is shown that DPS has a tendency to become greater with an increase of the number of representative year-samples, which might have influenced our test result (cf. 6.1) to some extent.

6.2.1. When the general distribution of year-samples over classes of catch size is proportionally about the same for species with a low value of  $j$  and for species with a high value of  $j$ , DPS and  $j$  are thus expected to be positively correlated. Such a correlation appears to be absent in the case of A- + B-species:  $\tau = +0.023$  ( $r = +0.1709$ ), n.s. This suggests that differences in the distribution of year-samples between different species (see Fig. 3) more importantly determine the relevant values of DPS than differences in the number of year-samples.

This is also illustrated by our model-species (Table 6): if we should replace the value of  $j$  (643) of the model A-species by that of the model B-species (996) using expression (III) (cf. 5.4.4) the DPS-value of the A-species would only increase from 0.6842 to 0.6972, which is much less than the conceived DPS-difference between the two species (0.6842 and 0.7320 respectively).

\* The few species in which cumulation seems especially to slow down over the highest classes – e.g. 135, 141, 130 – are hardly sampled in the ‘optimal’ habitat, either because sampling is technically difficult there (floating *Sphagnum*: 135), or because it is very rare (burned wood: 130), or because sampling was not planned there (arable land: 141).