

Apparently, the sample of B-species is more heterogeneous in this respect than the sample of A-species:  $\tau_{B-spp.} = -0.185$  ( $r = -0.1774$ ) n.s.;  $\tau_{A-spp.} = +0.212$ , n.s. ( $r = +0.4054$ ;  $p \approx 0.05$ ), i.e. only the A-species show a weak indication of such a positive correlation between DPS and  $j$ .

6.2.2. In a few (abundant) species the actual change of a single DPS-value, when adding a new collection of 84 year-samples (taken from 1968 until and including 1973), could be compared with the expected change on the base of expression (III) of 5.4.4. These cases are given in Table 8, which shows that the tendency of DPS to increase with an increase of  $j$  is indeed a slight one. In most cases the actual change of DPS hardly deviates from the expected one (only species 34 (*Amara lunicollis*) – and 132 (*Pterostichus versicolor*) in a less degree – shows a notable deviation), i.e. the added collection of year-samples can be considered to be about representative in these cases.

As far as the distribution of the year-samples over relevant groups of habitat (i.e. E, F and G: Table 1) is concerned, this is indeed the case; the 78 year-samples in these groups (only 6 year-samples in the D-group, but woodland species are not represented in Table 8) are distributed as (between brackets the number that would exactly fit the distribution of Table 1): E, 26 (23); F, 39 (36); G, 13 + 6 (19 + 5). However, especially in the E-group only a few sites (6) were sampled, and during 3–6 years (mean: 4.3 year-samples/site; compare: Table 1); in the F-group 12 sites (mean: 3.3 year-samples/site), and in the G-group 7 sites (mean: 1.9 year-samples/site) were sampled. Moreover, the G-sites were quite different from those in the period 1959–'67. Instead of unstable – especially readily inundated – places in natural localities, in the period 1968–'73 were sampled: a neglected orchard, a farm-yard, wet meadows and abandoned arable land.

This illustrates that the resulting DPS-values (Table 7) are rather robust against moderate deviations from a sampling program that intends to be about representative for natural sites (cf. 4.1).

Table 8. Expected and resulting (cf. 5.4.4) DPS-values after the adding of a new collection of 84 year-samples (1968–1973) to the standard-collection of 175 year-samples (1959–1967).

species	$j$ '59–'67	$j$ '68–'73	DPS '59–'67	DPS '59–'73	
				expected	resulting
34	116	72	0.6955	0.7098	0.6729
68	90	67	0.6143	0.6361	0.6463
70	115	74	0.5926	0.6114	0.6203
103	85	56	0.6997	0.7172	0.7037
132	126	79	0.6517	0.6685	0.6400
133	130	61	0.6614	0.6750	0.6660
134	90	64	0.6256	0.6479	0.6445

### 6.3. OTHER TESTABLE EXPECTATIONS

Following the strategy developed in 3.6, in 6.1 we could thus irrevocably reject our null hypothesis (3.2). This also means, that if the thoughts underlying this strategy of testing (cf. 3.3) are generally right, some related phenomena will be influenced in a predictable way. In other words, we should be able to formulate some testable expectations, that should come true (apart from some unexpected – but explicable in retrospect – complications). In the following sections the undermentioned expectations will be tested:

- (1) Since for most A-species many of the distances that must be covered in a cultivated countryside to arrive at (re)founding of populations apparently are unbridgeable (cf. 2.2), this may be expected to be true more completely for A-species with small individuals than for A-species with big individuals, i.e. DPS and size should be positively correlated in A-species: 6.4.
- (2) Because species of temporary habitats will necessarily have a high dispersal power (cf. 3.5.1), for the victims of cultivation – i.e. the species with a decreasing RPR – must mainly be looked for among species of permanent habitats. Hence, both the powers of dispersal and the values of DPS should be lower in species of permanent habitats than in those of temporary ones: 6.5.
- (3) If in two different groups of (permanent) habitat (cf. Table 1) the influences of cultivation have been differently far-reaching – i.e. inhabitable places have generally become less widely separated in habitats of the one group, than in those of the other – for species preferably occupying the least influenced kind of habitat, RPR should be less reduced, than for species preferably inhabiting the most influenced kind of habitat. Hence, in the latter species DPS-values should generally be lower than in the former ones: 6.6.
- (4) It may be expected, that in general the RPR of eurytopic species will have been less reduced by the ‘experiment of cultivation’, than that of comparable – i.e. with about the same powers of dispersal – stenotopic species of permanent habitats. This means, that the DPS-values of eurytopic species should generally be higher than those of comparable stenotopic ones: 6.7.
- (5) It should be possible to show that certain A-species are lacking in sites where populations could be kept: 6.8.

6.3.1. To test (5) it will be necessary to start special investigations. For the testing of the other expectations (items (1) as far as (4) inclusive) it is allowed to make use – as far as possible – of information from our sampling program (Ch. 3): Because during nine years (1959 up to and including 1967) sampling was intended to get a first insight into the most important factors generally governing the distribution of carabid beetles over natural localities, the information produced by it can be considered independent as far as the above (new) questions are concerned.

#### 6.4. DPS AND THE SIZE OF INDIVIDUALS

According to (1) we expect that in A-species size of the individuals (cf. Table 3, column 2) will be positively correlated with DPS (cf. Table 7). Such a correlation is indeed found:  $\tau_A = +0.301$ ,  $p = 0.0207$  (one-sided) ( $r = +0.450$ ;  $0.01 < p < 0.05$ ). In the case of B-species, however, also a significant correlation can be computed:  $\tau_B = +0.401$ ,  $p = 0.00634$  (two-sided) ( $r = +0.503$ ;  $p \approx 0.01$ ). No important correlation is left, when we take A- and B-species together:  $\tau = +0.116$ , n.s. ( $r = +0.145$ , n.s.), i.e. for the A-species the relation between size and DPS is quite different from that for the B-species.

6.4.1. To show this difference, in Fig. 4 we plotted size of the individuals against DPS. From this figure it appears that, firstly: there is a great difference in location between A- and B-points, and secondly: within a wide range of DPS-values the A-

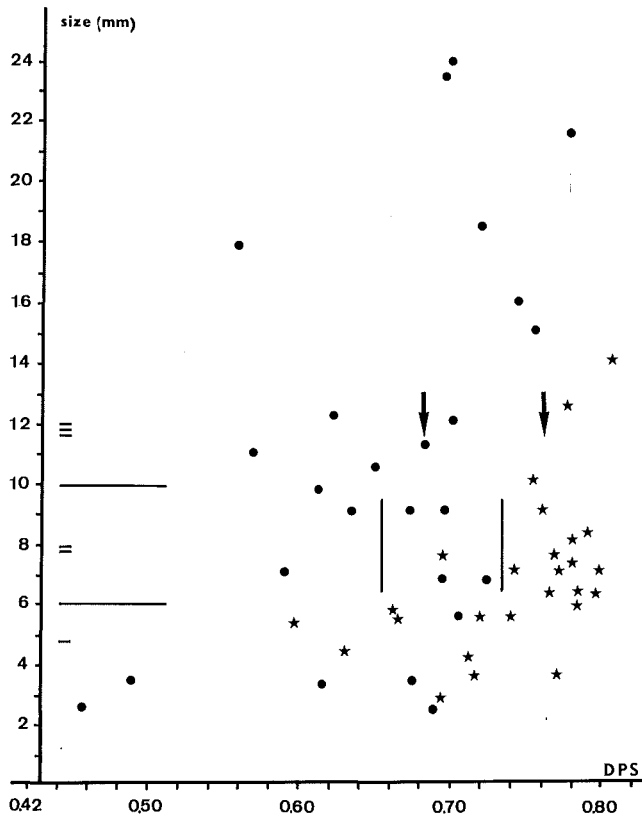


Fig. 4. Relation between size of individuals and value of DPS (cf. 6.4) for A- and B-species respectively (cf. 4.2). ●: A-species; \*: B-species. ↓: median DPS-value of A- and B-species respectively. |: mean DPS-value of A- and B-species respectively. I, II, III: 3 classes in Med.-test.

species are more or less uniformly distributed over the whole range of sizes, whereas the majority of the B-species are concentrated between 5 and 9 mm of size and for the greater part within a narrow range of (high) DPS-values too (in both respects the C-species resemble the A-species). Both differences seem plausible enough. The difference in location (DPS-level) is, of course, an expression of the general difference between A- and B-species that was tested in 6.1.1. The second difference shows that among the A-species each increase in size apparently favourably influences the small chance of bridging rather long distances. Among the B-species this does not seem to be very important. Because in most B-species flying only occurs outside of the reproductive period – when reproducing flight muscles are generally reduced – and then only under favourable weather conditions (that in some years hardly occur in our area; cf. 7.7.4), also in B-species walking may still be of some importance for dispersal. The narrow size-range of the B-species – sizes above 15 mm are not at all realized – may show that the mechanical requirements for an effective dispersal by flight imposes restrictions on size.

6.4.2. We will now try to test whether or not the above differences are significant. It is hardly necessary to test whether the two samples (A- and B-species respectively) belong to the same bivariate population.

When we should like to do this nonetheless, we can best use the nonparametric test proposed by WHEELER & WATSON (1964) and by MARDIA (see e.g.: 1972, p. 196–201), by which the bivariate samples are reduced to circular ones, and the bivariate test is thus reduced to an univariate one. In our case this results in:  $\chi^2 = 24.86$  (d.f. = 2) and  $p \ll 0.001$ . This highly significant difference is thus composed of both the great difference in location and that in kind of distribution of the points.

Testing of the difference in location (DPS-level) is essentially a regression problem, but Fig. 4 shows that the assumptions of the linear regression model will probably not be satisfied. Like in 5.2 we will thus only record that the lines of least squares (regression lines) – like possible regression curves – would run about parallel ( $p \approx 0.50$ )\*, and then apply the Med.-test (cf. 5.2.3). To satisfy the assumption that the size-values of A- and B- species respectively are sets from the same general distribution, we should have to drop the (A-)species with sizes of individuals above 15 mm (which are apparently impossible in B-species). Whether or not we leave out these species with big individuals, however, the result of the Med.-test remains the same:  $Z = 3.05$  ( $p \approx 0.002$ ; 3 classes). Other relevant class-divisions do not alter this result.

To test separately the difference in kind of distribution between A- and B-points (Fig. 4), we shall first have to nullify the general difference in DPS-level between the two samples. Since the lines of least squares for the two samples run parallel, this can sufficiently be reached by moving in Fig. 4 the sample of A-points along the

\* As can easily be seen from Fig. 4 the adjusted means must be very different:  $F = 32.90$  (d.f. 1/48),  $p \ll 0.001$ .

DPS-axis to the right over a distance of 0.08 units (being the difference between the median DPS-values as well as – approximately – between the mean DPS-values of the A- and B-species). Now we can again test whether the B-sample and the new A-sample belong to the same bivariate population, applying the nonparametric test of MARDIA (1972). This results in:  $\chi^2 = 11.17$  (d.f. = 2) and  $0.005 > p > 0.001$ , which will now indeed point to an important difference in kind of distribution between the A- and B-points.

6.4.3. Taking together the discussions and tests of this section we can conclude that the expectation (1) is fulfilled completely, and could even be elaborated by contrasting the A-species with the B-species. The correctness of our expectation is already supported by looking at Fig. 3: The A-species 76, 79, 75, 136, 80 and 78 (5 *Carabus*-species and *Pterostichus niger*) are species with big individuals (cf. Table 3, column 2).

## 6.5. DPS AND THE DEGREE OF PERMANENCE OF THE HABITAT

Following (2) we expect that the DPS-values of D-, E- or F-species will generally be lower than those of G- or H-species (cf. 4.3). Comparing DPS-values with the U-test (cf. 5.2.1), this is indeed shown to be the case for all relevant pairs of groups: Z between 2.72 and 3.73, i.e. p between 0.003 and 0.0001 (one-sided); D- + E- + F-species against G- + H-species even results in (U-test):  $Z = 4.75$  ( $p \ll 0.000033$ ). In 4.3.1 we already demonstrated (Table 5) that the division: permanent habitats (D, E, F) – temporary habitats (G, H), for the greater part also coincides with the division: low powers of dispersal (A, C) – high powers of dispersal (B).

6.5.1. The most important deviation from the above general division of species (Table 5) is found in the B-species: 9 out of 26 B-species have been classified as occupying permanent habitats. Before the start of the 'experiment of cultivation' these 9 species will have inhabited extensive areas: deciduous forest (6 spp.), heath and peat moor (3 spp.) and according to the 'founding' hypothesis (3.4) these may thus be expected to have developed lower powers of dispersal than the 17 B-species occupying temporary habitats. As a rough relative estimate of the powers of dispersal of a B-species we can use the relation between the number of individuals caught in window-traps ( $w$ : Table 3, column 11) and the 'maximal number of potential flyers' ( $f$ : Table 3, column 12), i.e.  $100 w/f$ .

Comparing the values of  $100 w/f$  of the 9 B-species of permanent habitats with those of B-species belonging to the G- or H-group respectively (U-test) indeed suggests the former to have somewhat lower powers of dispersal than the latter: Z (summed, cf. 5.2.1) = 1.78 ( $p = 0.0375$ , one-sided). This can be shown more convincingly by only comparing with the B-species in the H-group:  $Z = 2.09$  ( $p = 0.0183$ , one-

sided), the catches in window-traps of H-species being both more reliable and better comparable than those of G-species with the catches of the B-species of permanent habitats.

The latter statement needs some explanation. Because a window-trap (a vertical sheet of glass of about 0.8 m<sup>2</sup> with a collecting trough ;see: DEN BOER, 1971b, p. 128, Fig. 5) with an only very restricted chance will catch some of the individuals flying away from a population, and this chance will moreover rapidly decrease with an increase of the distance from the pertinent habitat, the majority of the individuals caught will belong to species living close to the trap (see also MEIJER, 1974). Therefore, the higher numbers of individuals given in column 11 of Table 3 will mainly have originated from rather dense populations in the vicinity of the window-traps. In retrospect, in the neighbourhood of most places where window-traps were erected populations of, either some of the B-species occupying permanent habitats, or some of the eurytopic H-species, or both, will have been present; we are less sure, however, of the nearby presence of populations of many of the G-species.

Hence, it is highly probable, that by column 11 of Table 3, the flight activities of most G-species – especially of the more stenotopic ones – are underrated as compared with those of many other B-species.

6.5.2. In order to avoid a wrong impression: in spite of the above (technical) restriction, flight in carabid beetles has appeared to be of paramount importance for a thorough dispersal, also at greater distances, which is clearly shown by the single specimens caught of species unknown from the environments of Wijster. This is still better illustrated by comparing the catches in window-traps in the centre of the Heath of Kralo and Dwingeloo (a continuous area of 1200 ha) with the catches in the nearby sets of pitfalls: during the 3 years of this sampling experiment between 33 and 56% (mean: 46%) of the (11–18) species present in the catches from the window-traps were not represented in the pitfall-catches. On the other hand, between 55 and 64% (mean: 61%) of those species of the pitfalls (22–28) of which at least part of the individuals caught must have been able to fly (mainly B-species) were not present in the catches from the window-traps. Hence, on the one hand nearly half of the 'window-trap species' (about 5–15% of the individuals caught) have been flying in from outside of the heath area, mainly from arable land; on the other hand, more than half of those species living in the area of which at least 10% of the individuals must have been capable of flying, did not show sufficient flight activities to show up in the relevant window-trap catches. Similar results are reached with the window-traps in other places of our area. In this respect our results do not confirm the conclusions reached by MEIJER (1974), but are in line with the general views of PALMÉN (1944) and LINDROTH (1949), and with the fact that large areas like S-Flevoland (HAECK, 1971) and also the Lauwerszeepolder (MEIJER, 1974) became rapidly populated with a lot of carabid species (cf. 2.2).

6.5.3. Because the 9 B-species of permanent habitats obviously have lower powers of dispersal than other B-species (cf. 6.5.1), next one may wonder whether the drastic reduction by cultivation of the extensive forests, heaths and peat moors (cf. chapter 8) has brought even these species into a position of decreasing RPR. Indeed, the DPS-values of the above 9 B-species are lower than those of the other B-species (U-test):  $Z = 2.21$  ( $p = 0.0136$ , one-sided)\*, and – as should be expected – RPR has already been reduced to a higher degree, when the powers of dispersal of the pertinent species are lower, i.e. in these 9 B-species DPS and 100 w/f are positively correlated:  $\tau = +0.557$  ( $p = 0.022$ , one-sided).

Again in accordance with the ‘founding’ hypothesis, such a positive correlation between DPS and 100 w/f is absent in the case of B-species occupying temporary habitats:  $\tau = +0.058$  (n.s.), for in these species the powers of dispersal are expected to be still sufficient to keep RPR at the level of about complete replacement (cf. 3.3).

6.5.4. However, from 6.5.1 we learned that G- and H-species probably can better be treated separately, as far as 100 w/f is concerned. Within the G-species no correlation between DPS and 100 w/f can be shown to exist ( $\tau = +0.048$ , n.s.), and among the H-spp. a correlation of  $\tau = +0.378$  ( $p = 0.078$ , one-sided) is traced. It is interesting now, to learn that this very weak correlation merely results from the two least eurytopic H-species 34 (*Amara lunicollis*) and 133 (*Pterostichus diligens*), cf. Table 4; when we omit these two species the correlation changes into  $\tau = -0.036$  (n.s.).

Within the habitat group ‘grass’ (Table 4) the species 34 and 133 are less eurytopic than 26 (*Amara communis*) and 106 (*Harpalus rufitarsis*), because the former for the greater part – especially the higher numbers – are restricted to grass vegetations in natural and semi-natural localities (mainly of the F-type), whereas the latter more readily occupy as well various weedy vegetations (that were hardly sampled during the pertinent 9 years): see: Appendix A. III. Because especially *Molinia*-vegetations once covered very extensive areas in heath and peat moor, and a number of these ‘grass’ habitats – above all in those parts of desiccating peat moor that were no longer cultivated (buckwheat and rye) – must have been remarkably stable, the powers of dispersal of species like 34 and 133 may be expected to have become lower than those of other H-species (‘founding’ hypothesis): see also: DEN BOER (1971b: p. 129: 6 and Table 4).

6.5.5. When we take together the results of this section we can conclude that not only the expectation (2) is fulfilled completely, but also that the relation: low powers of dispersal = low values of DPS/high powers of dispersal = high values of DPS, not merely coincides with the division: permanent habitats – temporary habitats. Both the 9 B-species occupying permanent habitats (cf. 6.5.1 and 6.5.3), and the two H-species 34 and 133 (cf. 6.5.4), show that this relation extends unaltered – and in both directions – over the boundary permanent habitats – temporary habitats, i.e. merely

\* On the other hand are the DPS-values of these 9 B-species – expectedly – higher again than those of the A-species of the permanent habitats concerned:  $Z$  (the species in the D- and F-group are tested separately, and summed, cf. 5.2.1) = 1.98 ( $p = 0.0239$ , one-sided).

the relation powers of dispersal/values of DPS fundamentally underlies the phenomena studied in this section. This also means, that it would not have been right to discriminate beforehand between species of permanent habitats and those of temporary ones (cf. 3.5.1 and 3.7).

## 6.6. DPS AND THE PROGRESS OF CULTIVATION

It must be possible to test the expectation (3) by contrasting F-species with D-species, not so much because heath and peat moor should have been less reclaimed by cultivation than deciduous forest, as because 41 of the 52 year-samples from heath and peat moor localities were taken at the Heath of Kralo and Dwingeloo (cf. Appendix A.II). For at present this is the sole heath area of such an extent (more than 1200 ha), that F-species may be expected to live there under spatial conditions that sufficiently approach those prevailing in the whole area of Drenthe before the 'experiment of cultivation' was undertaken. The D-species, on the other hand, were – perforce – for the greater part sampled in small to very small remnants of forest, that are generally very isolated (see also map in Appendix A.II).

6.6.1. There are strong indications that for most of the time, the greater part of the Heath of Kralo and Dwingeloo is more or less inhabitable for most F-species, i.e. barriers unbridgeable for walking individuals will hardly be present. On the other hand, the dimensions of the area are much too large to be covered by walking individuals: the distances covered by a representative sample of individuals of two F-species (70: *Calathus melanocephalus* and 132: *Pterostichus versicolor*) have been studied by BAARS (in prep.): in one year 50–150 m on the average. Therefore, we are pretty sure that the 'interaction groups' (cf. 1.4) of most F-species, as far as these were sampled at different sites of the Heath of Kralo and Dwingeloo, for the greater part must be considered subpopulations; cf. 2.1 item (6).

In this respect, for the D-species the situation must be clearly different: many D-species – at least those with middle-sized or big individuals – will have been sampled as isolated interaction groups (cf. 1.4; i.e. as simple populations).

By this overall difference between the local groups of F- and D-species, our expectation (3) can be reformulated now: Because the chance of the refounding of local groups that have disappeared should generally be higher in F-species – where also refounding by walking individuals is possible – than in comparable D-species, RPR should be less reduced in F-species than in comparable D-species. Hence, the F-species can be considered a relative check on the effects of the 'experiment of cultivation' by which the DPS-values of F-species should generally be higher than that of comparable D-species.

6.6.2. At least among the B-species abundant species ( $N > 2000$ ; cf. 4.4) occupying



permanent habitats have lower DPS-values than sparse ones ( $N < 2000$ ) (cf. 7.5.2). Because the B-species are unequally distributed over the D- (6 spp.) and F-group (3 spp.) respectively, for our present problem comparable DPS-values will be those of about equally abundant D- and F-species (i.e. species with about the same values of  $N$ ; cf. 4.4). Hence, an adequate test of our expectation seems to be: comparing the linear regressions of DPS on  $\ln N$  (to approximate linearity) or on  $\ln(N + j)$  (Table 7). Like in 5.2 and in 6.4.2, and because of the same reasons, we will only record that the regression lines would be fair estimates of the regression curves and would run almost parallel ( $p \approx 0.75$ ) and then apply the Med.-test (cf. 5.2.3):  $Z = -2.75$  ( $p \approx 0.003$ , one-sided; 4 classes of  $\ln N$  or  $\ln(N + j)$ ). Only considering A- + C-species gives about the same results; lines of least squares almost parallel ( $p \approx 0.75$ )\*; Med.-test:  $Z = -2.40$  ( $p = 0.008$ , one-sided; 3 classes of  $\ln N$  or  $\ln(N + j)$ ). Other relevant class-division do not alter these results.

To give at least some impression of the magnitude of the difference between D- and F-species we mention, that from the regression-equations of DPS on  $\ln(N + j)$  (or  $\ln N$ ) can be derived, that at the median value of  $\ln(N + j)$  for F- + D-species – 6.975 – the DPS-value for an F-species would be 0.7157 and for a D-species 0.6742 (only considering A- + C-species this would be: for an F-species 0.7049 and for a D-species 0.6617). A difference of this magnitude is sufficiently important (only slightly smaller than that between the model A- and B-species (5.1); cf. 6.1.2, compare Fig. 3) to suppose that the RPR of D-species has already been reduced considerably more than that of F-species still living in about pre-cultivation conditions for the greater part.

6.6.3. The findings of this section confirm the expectation (3). Because they give a kind of reconstruction – so to say – of the historical process as it was described in 3.3, they most convincingly show that DPS-values are indeed reliable estimates of the Realization of Population Replacement (RPR); compare 6.1.2.

#### 6.7. DPS AND THE 'STENOTOPY' OR 'EURYTOPY' OF SPECIES

When we intend to test expectation (4) we meet with the difficulty, that the concepts 'eurytopic' and 'stenotopic' are as loosely used in ecological literature as to be hardly operational for discriminating between groups of species. Therefore, we opportunistically define the 'degree of stenotopy' of a species within a certain area, as the degree to which the individuals are restrictedly occupying localities of the same kind in that area (by which we will most probably keep close to the – undefined – general use). By 'occupying localities of the same kind' will here be understood: caught with standard-

\* In both cases also the adjusted means are different: all D- and F-species,  $0.025 > p > 0.01$ ; only A- + C-species,  $p \approx 0.025$ .

sets of pitfalls and during a number of years in localities belonging to one of the habitat groups given in Table 1. 'The degree to which the individuals are restrictedly occupying...' will be estimated here by: the percentage of the total number of specimens (N) that is caught in the year-samples from such a habitat group; these values are given in Table 4 (cf. 4.3). Note, that in the latter case also other measures could be used (that may even be 'better'), e.g. the contribution to  $\Sigma \ln(n_i + 1)$ ; we keep to the above one because it is straightforward and in the present case most probably will give about the same possibilities (and difficulties) than more sophisticated measures.

With a glance at Table 4 we will consider the H-species to be 'eurytopic' and all other species to be more or less 'stenotopic' (cf. 4.3).

6.7.1. In accordance with expectation (4) in 6.5 we noted already that the DPS-values of the H-species are higher than those of either D-, E- or F-species (p values between 0.003 and 0.0001; one-sided: U-test). But the DPS-values of the eurytopic H-species do not differ from those of the stenotopic G-species (p = 0.280; two-sided): among the species of both groups the powers of dispersal – however different these may be in the different species – obviously are sufficient to generally keep RPR at the level of about complete replacement (cf. 3.3). Because of the difficulties mentioned in 6.5.1, however, we cannot test this by comparing the powers of dispersal of G- and H-species directly.

We will thus only show here by an example, that a high degree of 'eurytopy' can indeed compensate only moderate powers of dispersal: in our area species 136 (*Pterostichus niger*) can live in all kinds of habitat (it was caught in 164 out of the 175 year-samples). In spite of the fact that it is an A-species (the wings are too small (Table 3) to enable the individuals to fly), albeit with rather big individuals (16–21 mm), it presents a relatively high DPS-value (0.7232) and an almost 'ideal' unbent cumulation line (Fig. 3). The only moderate distances that can be covered by the walking individuals obviously suffice to reach inhabitable sites (that in this species apparently can be found nearly everywhere) and thus to keep RPR at the level of about complete replacement.

6.7.2. We expect that the eurytopic A- and C-species among the H-species will show higher DPS-values than the more stenotopic A- and C-species in the D-, E- or F-groups. This expectation is indeed answered (U-test): D-spp. (p = 0.029), E-spp. (p = 0.006) and F-spp. (p = 0.029). It is not simply a coincidence that all 3 A-species in the H-group (76, 79, 136) have big individuals (> 15 mm), and that the DPS-values of these 3 species apparently are higher than those of the 4 other A-species with big individuals (1, 75, 78, 80): p = 0.05 (one-sided); cf. 6.4. The B-species have already been treated in 6.5. However, within the H-group as a whole the A- + C-species (with the lower powers of dispersal) do not show lower DPS-values than the B-species (with higher powers of dispersal): p = 0.56 (two-sided), i.e. in most of these eurytopic species an about complete RPR is kept up. Hence, also a more close examination of the DPS-values of the H-species – as a rather heterogeneous group of eurytopic species – confirms expectation (4).

6.7.3. Although thus balancing on the bounds of the possibilities of our – only approximate – data, within each group of permanent habitats, we will consider ‘% of N’ (Table 4) to be a workable – relative – estimate of the ‘degree of stenotopy’ of the pertinent species. Hence, following (4), ‘% of N’ is expected to correlate negatively with DPS. This expectation is indeed answered for the D-species:  $\tau = -0.464$ ,  $p < 0.01$  ( $r = -0.488$ ,  $p = 0.01$ ), one-sided, and probably also for the E-species:  $\tau = -0.374$ ,  $p = 0.070$  ( $r = -0.407$ ,  $p \approx 0.1$ ), one-sided. But in the F-species such a correlation is not found at all:  $\tau = +0.029$  ( $r = -0.115$ ; n.s.). This latter result is wholly in accordance with 6.6: The F-species were for the greater part sampled under pre-cultivation conditions and hence, the powers of dispersal of most F-species – whether more or less stenotopic – may be expected still to suffice under these conditions (i.e. only at the Heath of Kralo and Dwingeloo); cf. 3.3.

Among the D- and E-species, however, especially populations of the most stenotopic ones may be expected to live highly isolated. When also the powers of dispersal are low (A- and C-species) the RPR of such species will be decreasing significantly. In line with this, only for the A- and C-species (treated separately) among the D- and E-species (treated separately) the above negative correlation between ‘% of N’ and DPS is still more pronounced:  $\tau = -0.601$  ( $p = 0.0008$ , two-sided); cf. note to 4.4.1.

6.7.4. Rather unexpectedly also the G-species show a negative correlation – but at a much higher DPS-level – between DPS and ‘% of N’:  $\tau = -0.499$ ,  $p \approx 0.05$  ( $r = -0.680$ ,  $0.05 > p > 0.01$ ); two-sided. In this case the correlation has nothing to do, however, with a decreasing RPR in the most stenotopic G-species (compare Fig. 3: 5 out of the 10 cumulation lines of G-species are unbent; in 3 other ones cumulation only slows down over the highest classes (cf. note to 6.1.2)).

The only A-species in the G-group – species 115 (*Metabletus truncatellus*) seems to be an exception (but see also note 8 to Table 3). The DPS-value of this species (supposedly preferring densely overgrown waste and arable land, cf. LINDROTH, 1945\*), however, most probably is liable to an important error, because we surely did not sample its preferred habitat: it was only caught in 4 out of our 175 year-samples ( $N = 72$ ).

In my opinion this correlation results from the presence of some extremely stenotopic ones among the G-species. For such species only a few sites (with very special conditions) will be favourable (with the possibility of dense populations), and most places will be unfavourable (no populations at all). Because consequently in only one (or a few) of the year-samples such a species will have been caught in (relatively) high numbers, the resulting DPS-value will be too susceptible to the chance event of a smaller or greater number of ‘stragglers’ appearing in a smaller or greater number of other year-samples (to be able to survive such species will always dispose

\* In the sea-dunes in the western parts of the Netherlands this species mainly inhabits rather stable natural or semi-natural grass-vegetations, i.e. it would not have been classified there as a G-species.

of high powers of dispersal), i.e. in some cases the DPS-value will come out lower than it ought to be; compare 5.3 item (3).

A good example of such an extremely stenotopic species is 130 (*Pterostichus angustatus*), that only reproduces in localities where wood has been burning. In one year-sample – a locality where the remnants of a peat moor with many tree-stubs has recently been burned down – 984 ind. were caught (out of  $N = 1117$ ). With only one other exception – a site where the branches of felled trees has been burned in the preceding year: 106 ind. – in the other year-samples the species is only represented by one or a few ‘stragglers’: cf. Appendix A. III.

Only omitting the above extremely stenotopic species 130 and the unreliable species 115 reduces the correlation between DPS and ‘% of N’ towards  $\tau = -0.250$  (n.s.). Hence, after all also the G-species seem to fit the general picture developed in this section.

6.7.5. In spite of the disputability of the way in which we provisionally quantified the vague concepts ‘stenotopy’ and ‘eurytopy’, the findings of this section are sufficiently in line with expectation (4) to enable us to conclude that the general idea behind this expectation (dispersing individuals of eurytopic species on the average will have to cover smaller distances to arrive at (re)founding of populations than those of stenotopic ones) is fulfilled. A more thorough comparative analysis into the causes and populational consequences of ‘eurytopy’ and ‘stenotopy’ will be undertaken.

## 6.8. DISAPPEARED POPULATIONS

As was mentioned in 6.3.1 the testing of expectation (5) requires special investigations. A few preliminary founding experiments have already been started, and more are planned. This kind of experiments meet with some difficulties, however:

6.8.1. In spite of a lot of work in that direction, as for most species we are still insufficiently informed about the factors most probably governing their distribution, let alone about the way in which these factors should be ‘translated’ into reliable expectations about the degree of suitability of specified sites for the reproduction and survival of the pertinent species. We have still to add to this that a supposedly suitable site, where the pertinent (A)-species is lacking, most probably not will be a very favourable one: apparently, the population left there from the pre-cultivation period was not able to survive during the last decades, i.e. it may have been an only small (sparse) population. In fact, we are still searching for an efficient strategy to comparatively investigate these habitat relations, and thus to test the reliability of ‘general field experience’.

6.8.2. Because we did not yet solve all the difficulties, at this moment we cannot dispose of the results of adequate founding experiments.

However, it seems relevant to note – as a kind of circumstantial evidence in favour

of expectation (5) – that 3 (out of 5) fenced populations of species 70 (*Calathus melanocephalus*) introduced – for other reasons – BY VAN DIJK (1973) on the experimental field of the Biological Station, Wijster – in a locality where the species had not been caught during the preceding years – increased in numbers during two succeeding seasons (from 19 ind./m<sup>2</sup> in 1970 over 26 ind./m<sup>2</sup> in 1971 towards 31 ind./m<sup>2</sup> in 1972). This is the more remarkable since the fenced surfaces were very small each (4 m<sup>2</sup>) and the densities more than 20 times higher than those of natural open populations at the Heath of Kralo in the same years.

Apart from illustrating that sometimes founding experiments may succeed by chance – i.e. without consciously having solved the difficulties noted in 6.8.1 – this observation teaches us that even for the most abundant carabid species in our study area (70), in certain localities the ‘carrying capacity’ may lie many times higher than the highest densities actually found within the same period in nearby and evidently favourable habitats. We have indeed the impression that in general the densities of carabid beetles only seldom reach ‘carrying capacity’ (whatever that exactly may be in these kinds of species), i.e. the relation between the frequency, magnitude and spatial pattern of the influence on density of independent factors (e.g. weather conditions) on the one hand, and the time required to build up density ‘freely’ on the other hand, is supposed to be such that the latter will only seldom be completed.

6.8.3. Because only a small part of the active individuals will be caught in a standard set of pitfalls our sampling program cannot give direct evidence on the extinction and (re)founding of populations (cf. 1.3). On the other hand we rather frequently come across circumstantial evidence on the occurrence of these processes. Some of these data – more are available – are given in Table 9.

Guided by ‘general field experience’ we are inclined to set some value on this kind of evidence. The more so because it is in line with the more convincing observations of BOYCOTT (1936); p. 125: ‘In 1915, 69 of the 84 closed ponds which survived till 1925 contained Mollusca of 18 species, the total occurrences being 173; ... A re-examination of the same ponds in 1925 gives us perhaps some idea of what is going on now. Only 65 of them yielded Mollusca; there were 64 disappearances and 93 fresh appearances (...), so that the total number of occurrences had risen to 202’.

Possibly a thorough examination of the literature will produce still more direct evidence supporting the general conclusion from our indirect investigations: the extinction and (re)founding of populations are inevitable natural processes determining the ultimate survival of all kinds of species (founding hypothesis of dispersal), i.e. including species of permanent or stable (natural) habitats in the centre of distribution (for the latter point, see also: 8.2). Only very recently (e.g. SIMBERLOFF, 1974; DIAMOND, 1975) this conviction begins to gain ground, although the work of SIMBERLOFF (1974) will mainly concern species of temporary habitats. See also: ANDREWARTHA & BIRCH (1954).

Table 9. Circumstantial evidence on the disappearance and/or (re)founding of local groups from sites where pitfall-catching was continued during a number of successive years.

spe- cies	site*	number of ind. in year-samples											
		1959	'60	'61	'62	'63	'64	'65	'66	'67	'70	'71	'72
114	N	3	5	13	30	6	-	-	-	-	-	-	4
	Z		-	3	10	3	-	-	1	1	12	9	
	P	3	20	-	-	-							
118	N	41	23	29	38	6	1	-	-	-	-	-	
	P	2	5	-	-	-							
69	X		3	3	9	3	-	-	-				
68	N	205	110	32	33	13	23	3	-	31	98	26	
112	N	-	-	-	5	3	2	2	-	-	-	-	
121	Z		-	9	6	6	1	-	-	-	2	-	
124	C	-	-	2	8	23	16	29	31			40	
17	N	-	-	1	21	10	87	9	38	-	1	7	
56	Z		-	-	4	4	24	11	14	3	19	190	
9	M	-	-	4	2	5	9	11	9				
94	AZ						-	29	45	150			

\* cf. Appendix A. II.

## 6.9. OTHER TESTS OF OUR HYPOTHESES

The testing of our hypotheses as performed in this chapter was based on a division of our 74 species (cf. 4.1), in which some arbitrariness could not be avoided (cf. 4.2). The B-species form a 'natural' group based on catches in window-traps (cf. 4.2.1), but the A-species had to be separated by making use of three (reasonable) criteria (cf. 4.2.2). The different sections of this chapter showed, however, that the group of B-species apparently is more heterogeneous than the group of A-species, which is also supported by the C-species being more related to the A-species than to the B-species, i.e. the transition from species with a still sufficient dispersal power to species with an insufficient dispersal power obviously is running somewhere through the group of B-species (cf. 6.5). Hence, it seems worth while to try whether or not some other reasonable divisions of our 74 species support the results arrived at in 6.1.

6.9.1. Only in monomorphic brachypterous species one can be absolutely sure that dispersal by flight will never occur. Therefore we can compare the DPS-values of this group of species with those of the other extreme, i.e. that B-species in which the value of  $100 w/f$  (cf. 6.5.1) exceeds a certain level, 3.5% (say). We are thus testing the 13 A-species: 1, 8, 56, 75, 76, 78, 79, 80, 115, 134, 144 and 148 against the 13 B-species: 9, 22, 26, 30, 31, 35, 60, 64, 82, 86, 135, 139 and 140. The DPS-values of these new B-species are again significantly higher than those of the new A-species (U-test):  $Z = 3.33$  ( $p = 0.00043$ , one-sided).

The same result is reached when taking our two groups less extremely, e.g. comparing species with  $f$  (the maximal number of potential flyers: Table 3)  $\leq 70$  ind. – i.e. all A-species + the C-species 33, 89, 109, 121, 122, 141 and 146 ( $n = 32$ ) – with species with  $f > 300$  ind. – i.e. all B-species + the C-species 66, 102, 105, 110, 117, 118, 124 and 130 ( $n = 34$ ) – U-test:  $Z = 3.35$  ( $p = 0.0004$ ; one-sided).

Even when testing only among dimorphic species (on the assumption that the fullwinged specimens in dimorphic species are the ‘diaspores’, cf. DEN BOER, 1970), e.g. dimorphic species with  $< 5\%$  macropterous ind. (Table 3) – the species 17, 33, 68, 69, 70, 95, 114, 119, 121, 133, 141 and 146 ( $n = 12$ ) – against dimorphic species with  $> 10\%$  macropterous ind. – the species 9, 54, 60, 62, 64, 73, 86, 120, 125, 135 and 139 ( $n = 11$ ) – the differences between the pertinent DPS-values again point in the same direction,  $Z = 2.43$  ( $p = 0.0075$ ; one-sided).

6.9.2. Up till now we tested our hypotheses by first defining two groups of species with very different powers of dispersal, and then computing how different the DPS-values are between these two groups. We can also reverse this procedure, i.e. first dividing the 74 species into one group with low and another group with high DPS-values and then testing how different the composition of these two groups is concerning the numbers of A-, B- and C-species respectively.

Taking the median DPS-value as a divider we should separate our two groups at  $DPS = 0.7070$ ; because – by chance – two species (80, 125) show this value (Table 7) we accepted the nearest DPS-value – i.e. 0.7069 – as a divider. The composition of each of the two DPS-groups obtained in this way is given in Table 10. Comparing with the Chi-square-test results in  $\chi^2 = 14.31$  (d.f. 4),  $p \approx 0.005$ , i.e. the group with low DPS-values mainly includes A-species and the half of the C-species, whereas the group with high DPS-values mainly includes B-species and the other half of the C-species. Moreover, 5 of the 6 A-species in the ‘high-group’ are exceptional so far as the mean size of individuals of these species is above 15 mm (cf. 6.4), whereas the 6 B-species in the ‘low-group’ are ‘abundant’ ( $N > 2000$ ; cf. 4.4) and it will be shown in chapter 7 that in some way these are also exceptional.

Table 10. Composition of a group of species with high DPS and of a group of species with low DPS respectively, according to 3 different levels of dispersal power.

DPS \ Dispersal power:	A-spp.	B-spp.	C-spp.	total
$> 0.7069$	6	20	12	38
$\leq 0.7069$	19	6	11	36
total	25	26	23	74

$\chi^2 = 14.31$  (d.f. 4);  $p \approx 0.005$

## 6.10. GENERAL CONCLUSIONS

When reviewing this chapter we may first conclude, that we could not only reject our null hypothesis (3.2) following the strategy developed in 3.6 (cf. 6.1), but also following other reasonable divisions of our 74 species (cf. 6.9). Secondly, a number of expectations (6.3) resulting from the acceptance of hypothesis 3.4 were answered (6.4 as far as 6.7 inclusive).

This means that the phenomena evoked by the 'experiment of cultivation' (cf. 3.3), as these are predicted by the founding hypothesis of dispersal (3.4), must be very pronounced, because the chance of committing a type II error can be expected to be rather high when comparing data troubled with so many sources of error (cf. 3.1, 5.1.3 and 5.2.5).

Hence, our general conclusion can now be formulated as: the differences between species in the relative frequency of sparse populations, as these are measured as differences in DPS-value, can only be brought into line with all the evidence presented, when they are assumed to result from the influence of the 'experiment of cultivation' on the RPR of species with pre-existing differences in dispersal power (i.e. differences in dispersal power that were evolved under pre-cultivation conditions).

A corollary to this conclusion is, that the natural extinction of populations occurs frequently enough (also in permanent habitats) to enable the investigator to evaluate the results of the 'experiment of cultivation', and also that generally there must have been a close relation between the powers of dispersal of a species and the frequency of the natural extinction of its populations. It can hardly be imagined how such a close relation would have been supported by unrelated phenomena like 'overflow' or 'escape', which under natural conditions can only be expected ultimately to match the frequency of population disappearances by (re)foundings when in very different kinds of species and in many kinds of environments both the general level of 'overflow' (escape) and the resulting kind of dispersal would be such as at least continually to keep up a complete RPR. But in that case the 'experiment of cultivation' could not have resulted in distinctly different results for different groups of species, what was to be proved.

All the evidence presented in this chapter points towards the conclusion that under pre-cultivation conditions natural selection must have influenced the powers of dispersal of each species (also of species occupying permanent habitats, compare SOUTHWOOD, 1962) in such a way that the disadvantages of the leaving of a still favourable habitat are about matched by the possibilities to ultimately realize a sufficient replacement of disappeared populations (RPR): founding hypothesis.



## 7. ABUNDANT AND SPARSE SPECIES

In 3.1 we concluded that within species the 'overflow' hypothesis of dispersal will either not predict special relations between the level of dispersal and the frequency distribution of population sizes (DPS) or there might be reasons to expect the higher levels of dispersal in species with a relatively high frequency of dense populations. From the latter point it may therefore be interesting to compare directly – as far as possible (cf. 4.4) – abundant with sparse species. For this gives a possibility to test a statement that seems to be in the background of many thoughts about dispersal (see e.g. GADKIL, 1971): within a given area the chance to exceed carrying capacity (overcrowding) may be expected generally to be higher for abundant populations than for comparable sparse ones. Under the 'founding' hypothesis of dispersal such a difference between abundant and sparse species will generally not be relevant (but see 7.7.2).

### 7.1. DISPERSAL AS OVERFLOW

The current views on dispersal are most concisely expressed by DEMPSTER (1975, p. 12): 'The main evolutionary advantage of migration lies in it enabling a species to keep pace with changes in the location of suitable habitats. Dispersal may be obligatory for these animals, but for others it is facultative and is triggered off by unsatisfactory conditions. Overcrowding can act in this way, so that dispersal may be density-dependent'. In his chapter 3, DEMPSTER (1975) illustrates this view by two examples in which dispersal by flight is stimulated by population numbers apparently exceeding the possibilities of a limited resource. At least one of the species seems to be very numerous.

Another case is described by MURAI (1975), in which long-winged adults of an abundant sugar cane bug disperse by flying from a population with high density to populations with lower densities.

Although phenomena like these look rather sensible, chapter 6 of the present paper suggests that in general dispersal should be a quite different phenomenon (cf. 3.3). Hence, we shall have to investigate whether such 'overflow dispersal' occurs frequently enough to be traced in our data as an evident departure from the views developed in the preceding chapters. In our case it should thus be supposed that within a group of polyphagous predators with a rather uniform way of life – like most carabid beetles – the chance to meet with cases of 'overflow dispersal' will generally be higher when dealing with species that are actually abundant within the study area than in the case of sparse ones. Therefore, as a supplement to chapter 6 in the following we will try to compare the degree of dispersal – and its results – of abundant with that of sparse carabid beetles.

## 7.2. TESTABLE EXPECTATIONS

In 4.4 we showed already that for the majority of our 74 species the N-values of Table 3 can be considered rough indications of the relative abundances of the pertinent species within our study area. On the base of the overflow hypothesis (3.2) we will now formulate some expectations about the results of a comparison of abundant with sparse species, that can be tested against the founding hypothesis (3.4).

(1) Because dense populations generally will have a greater chance sometimes to exceed 'carrying capacity' than comparable sparse ones, under hypothesis 3.2 may be expected that the average individual of an abundant species often will have a greater – or at least not lower – chance to disperse from its population – especially from the dense ones that also contain the majority of the individuals – than the average individual of a more sparse species (other things being equal); if anything, under hypothesis 3.4 rather the reverse should be expected. This will especially apply to species occupying permanent habitats, because under both hypotheses for the individuals of species of temporary habitats – whether abundant or sparse – dispersal generally will be obligatory: cf. 7.3.

(2) According to DEN BOER (1970) the fullwinged specimens of a dimorphic species should be considered to represent the 'dispersal morph'.

Under hypothesis 3.2 and combined with (1) it may thus be expected that among dimorphic species of stable environments the percentage of macropterous individuals (in the following: % macr. ind.) will be the higher (or at least not the lower) the more abundant the species concerned. As far as dimorphic species are able to live in unstable environments, under neither hypothesis can be expected that the percentage of fullwinged individuals will show some relation with abundance, viz. this percentage will generally be high: cf. 7.4.

(3) If the degree of dispersal of abundant B-species occupying permanent habitats would indeed be high, see (1), these species would generally be capable (even under the 'experiment of cultivation') easily to found populations in more or less suitable places, i.e. the DPS-values of these species will be high (hypothesis 3.2). Under hypothesis 3.4 neither high degrees of dispersal nor high DPS-values are expected in these species: cf. 7.5.

(4) Because all A-species are defined as to have poor powers of dispersal (cf. 4.2.2), hypothesis 3.2 does not predict testable features for abundant or sparse A-species respectively: the necessary 'overflow' can always occur by walking, but this kind of dispersal was not directly measured. However, under hypothesis 3.4 the RPR of both abundant and sparse A-species may be expected to have been profoundly affected by the 'experiment of cultivation', i.e. the DPS-values of all A-species will be about equally low: cf. 7.6.

7.2.1. Since the relative frequencies of abundant and sparse species among the A-species are not similar to that among the B-species (Table 3), in the light of the present

questions it might be wondered whether or not the test results as obtained in 6.1.1 would be changed when allowing for the influence of differences in the abundance of the pertinent species. An adequate test to check the robustness of the results of 6.1.1 against such effects seems to be: comparing the linear regression of DPS on  $\ln N$  (to approximate linearity) or on  $\ln(N + j)$  (Table 7) for A-species with that for B-species. Because of the same reasons as in 5.2, 6.4.2 and 6.6.2 we prefer to apply the Med.-test (cf. 5.2.3). As for the assumptions: for both A- and B-species the values of  $\ln N$  or  $\ln(N + j)$  can be considered samples from the same universe; the regression lines will be fair estimates of the regression curves, and although they do not run parallel ( $0.10 > p > 0.05$ )\*, they do only intersect outside of the actual range of  $\ln N$  or  $\ln(N + j)$ ; see Appendix B.I. The Med.-test now results in  $Z = 3.14$  ( $p = 0.00084$ , one-sided; 3 classes of  $\ln N$  or  $\ln(N + j)$ ). Hence, the testing of our hypotheses 3.2 and 3.4 – as it is performed in 6.1 – was adequate, i.e. the results are not altered by allowing for the possible effects of differences in the abundance of the pertinent species. This again means that the general difference between the DPS-values of A- and B-species is only determined by the differences between the powers of dispersal of these two groups of species.

### 7.3. ABUNDANCE AND DISPERSAL BY FLIGHT

Following (1) we will compare the degree of dispersal of abundant B-species occupying permanent habitats with that of sparse ones.

7.3.1. Because especially in B-species  $f$  and  $N$  are highly correlated (cf. Table 3) – if not identical – comparing  $100 w/f$  (as an estimate of the powers of dispersal; cf. 6.5.1) with  $N$  (as an estimate of abundance; cf. 4.4) can only be used in special cases for treating these problems.

Only when in a not too small sample of species  $100 w/f$  and  $N$  (varying over a wide range) are not significantly correlated this may point to  $w$  varying among different species about directly proportionally to  $f$  (or  $N$ ), i.e. the individual chance to disperse is about the same for abundant and for sparse species. Whenever  $w$  increases less with an increase of  $f$  (or  $N$ ), however,  $100 w/f$  and  $N$  will be highly and negatively correlated.

Among the 9 B-species of permanent habitats  $w$  and  $f$  are not significantly correlated:  $\tau = +0.141$  ( $p = 0.70$ , two-sided), i.e. the 5 numerous ones ( $N > 2000$  or  $N > 1200$ ) among these species score about the same  $w$ -values as the 4 more sparse species, U-test:  $p = 0.64$  (two-sided). Hence, an individual of an abundant B-species of permanent habitats generally has a smaller chance to disperse than an individual of a sparse one, which is also indicated by the significantly negative correlation between  $100 w/f$  and  $N$ :  $\tau = -0.611$  ( $p = 0.012$ ; one-sided).

\* The adjusted means of A- and B-species are very different:  $F = 13.45$  ( $p < 0.001$ ).

7.3.2. The above findings are in line with the founding hypothesis (3.4): under this hypothesis it is reasonable to suppose that many populations of abundant species occupying permanent habitats (especially the dense ones) generally will have a lower – or at least not higher – chance of extinction than many populations of more sparse species of permanent habitats (other things being equal), by which a higher degree of dispersal in such abundant species than in comparable sparse ones would not be ‘adaptive’.

Although it will not be difficult to score exceptions from the above broad generalization, during the many years that we are sampling flying carabid beetles with the help of window-traps (cf. 4.2.1), we never observed phenomena that even resemble those given by DEMPSTER (1975: his Tables V and VI, p. 29: e.g. in 1961 during the reproductive period of the psyllid *Arytaina spartii*, DEMPSTER sampled 10572 ind. in suction-traps against 7792 ind. in the population which was evidently ‘overcrowded’).

In this connection it must be noted that the high catches in window-traps in the species 35 and 64 (Table 3, column 11) are quite different from the high catches in suction-traps as given by DEMPSTER (1975). In species 35 (*Amara plebeja*) dispersal is only connected with an obligatory habitat change (migration to a reproduction habitat and back): cf. VAN HUIZEN (in press). In species 64 (*Bradycellus harpalinus*) dispersal only occurs in August, i.e. outside the reproduction period that is in winter: cf. DEN BOER (1971b: Table 3): JOHNSON (1969).

As far as B-species of temporary habitats are concerned, we showed already in 6.5.1 that the individual chance to disperse is generally higher in such species than in B-species occupying permanent habitats, which points more towards the ‘escape’ hypothesis s.l. (3.1) than towards the ‘overflow’ hypothesis.

#### 7.4. ABUNDANCE AND THE % MACR. IND. IN DIMORPHIC SPECIES

In line with (2) we should expect that among the wing dimorphic species of permanent habitats the % macr. ind. will be positively correlated with N, and that among those occupying temporary habitats such a correlation will not be found: Table 3.

7.4.1. However, among the 18 wing dimorphic species occupying permanent habitats the % macr. ind. is negatively correlated with N:  $\tau = -0.354$  ( $p = 0.022$ , one-sided). Probably this is even more convincing so when we only consider the F-species:  $\tau = -0.571$  ( $p = 0.031$ ,  $n = 8$ ), being the group of species among which we may expect to find the more original relations between dispersal power and abundance (cf. 6.6). Hence, also this result, like that of section 7.3, is only in line with the founding hypothesis of dispersal.

Among the 7 dimorphic species of temporary habitats a correlation between % macr. ind. and N is indeed lacking:  $\tau = +0.048$  (n.s.). In dimorphic populations apparently not all fullwinged individuals are equally inclined to fly away: in some rather abundant dimorphic species with a not too low % macr. ind. – i.e. in 54, 73, 120 and 133 – comparatively (and often also absolutely) fewer macropterous individ-

uals are found outside their populations (stragglers) than are macropterous individuals of more sparse dimorphic species – i.e. of 9, 89, 122, 125 and 139 – cf. DEN BOER (1971b: Table 1). This is completely in line with the founding hypothesis (3.4).

7.4.2. When we rank the 25 dimorphic ones among our 74 species according to the % macr. ind., with only one exception – species 120 (*Notiophilus biguttatus*) with 79% macr. ind. and with  $N = 4020$  (Table 3), but see: DEN BOER (1970: 2.2) – all species with % macr. ind.  $\geq 5.8\%$  (the median value) have  $N$ -values  $< 1300$ . The species with % macr. ind.  $< 5.8\%$  are distinctly clustered in two groups, one group of 7 species with  $N$ -values  $< 2000$  and another group of 5 species with  $N$ -values  $> 5000$ . Together with the conclusion from 4.4.5 item (5)  $N = 2000$  seems thus to be both a convenient and a rather natural divider between abundant and sparse species. When looking at Fig. 3 we can add still another argument: among the B-species  $N = 2000$  also appears to be a divider between the species with unbended cumulation lines and the species with distinctly bended cumulation lines, viz. the species 149, 34, 65, 25, 133, 150 and 120 all have  $N$ -values  $> 2000$  (cf. Table 3); about the only exception, species 64, in 4.4.4 we learned already that its  $N$ -value (878) will severely underestimate its relative abundance.

#### 7.5. DPS AND THE ABUNDANCE OF B-SPECIES

Before being able to test the expectations (3) and (4) adequately we will have to deal with a complication.

From 5.4.4 and section 6 of Appendix B.II can be learned that DPS will have a general tendency to increase with  $j$ . Hence, when among some group of species  $j$  would increase with  $N$ , merely this tendency could already result in abundant species having higher – or at least not lower, cf. 6.2.2 and Table 8 – DPS-values than sparse ones.

7.5.1. Among all three groups of species, A-species, B-species and C-species  $j$  indeed appears to increase with  $N$ : Table 11, left part. Both among the A-species and among the C-species this relation is due to the species occupying permanent habitats: Table 11, left part.

However, among the B-species the above correlation only results from the 17 species occupying temporary habitats: Table 11, left part. Contrary to the A- and C-species among the 9 B-species of permanent habitats the 5 abundant ones ( $N > 2000$  or  $N > 1200$ ) show the remarkable fact not to have been found in more year-samples than the 4 sparse species:  $p = 0.50$  (U-test) (among the 17 species of temporary habitats the three species with  $N > 1200$  also have the three highest  $j$ -values, in the right order).

Table 11. Correlations of abundance (N) with the number of year-samples (j) and with DPS respectively for different groups of species.

group of species	number of spp.	correlation between N and j	correlation between N and DPS
all B-species	26	$\tau = +0.570^{**} (+0.644^{**})$	$\tau = -0.524^{**} (-0.735^{**})$
B-spp. of permanent habitats	9	$\tau = +0.111 (+0.043)$	$\tau = -0.722^{**} (-0.844^{**})$
B-spp. of temporary habitats	17	$\tau = +0.691^{**}$	$\tau = -0.323$
all A-species	25	$\tau = +0.514^{**} (+0.674^{**})$	$\tau = -0.253 (-0.100)$
only A-spp. of permanent hab.	21	$\tau = +0.616^{**} (+0.771^{**})$	$\tau = -0.295^{*} (-0.355)$
all C-species	23	$\tau = +0.488^{**} (+0.728^{**})$	$\tau = -0.166 (-0.024)$
only C-spp. of permanent hab.	18	$\tau = +0.625^{**} (+0.872^{**})$	$\tau = -0.189 (-0.048)$

\*\* (in italics):  $p < 0.001$  (one-sided).

\* :  $p \approx 0.05$  (one-sided), just below or just above.

all other correlations: not significant.

between brackets: product-moment correlation coefficient with  $\ln N$ .

7.5.2. The above remarkable finding concerning the j-values of the B-species of permanent habitats can hardly agree with expectation (3) (under hypothesis 3.2). Table 11 (right part) indeed shows that exactly the reverse relation is realized, the 5 abundant B-species ( $N > 2000$  or  $N > 1200$ ) of permanent habitats all having lower DPS-values than any of the 4 sparse ones (see also: Table 12 and Appendix B.II, section 7). In the same line (under the founding hypothesis) one could already expect these 5 abundant species also to have the poorer powers of dispersal. Although the individual chance to disperse is indeed smaller in the 5 abundant B-species than in the 4 sparse ones (cf. 7.3.1) – which already contradicts the overflow hypothesis of dispersal – the absolute numbers of individuals dispersing (w in Table 3, column 11) apparently do not differ (cf. 7.3.1; see also: Table 12). We therefore assume that the chance to (re)found a population will not differ either between abundant and sparse B-species – which is not necessarily true, of course.

It will be clear that the lower DPS-values in these 5 abundant species must go with a proportional distribution of numbers over year-samples that is quite different from that in the 4 sparse species (cf. Appendix B.II, and 5.4.4). Notably somewhere between the few samples from small populations (newly founded) and those from larger ones this distribution can be expected to steepen less in such an abundant species than in a more sparse one, i.e. in these abundant species especially some groups of small- to medium-sized populations will be relatively underrepresented. This is also distinctly expressed by the bended cumulation lines in Fig. 3.

Table 12. Relation between abundance, number of year-samples, catches in window-traps and DPS in some B-species occupying wood-like (D) or heath-like (F) habitats respectively.

habitat group <sup>1</sup>	species <sup>2</sup>	N <sup>3</sup>	wing develop-ment <sup>3</sup>	f <sup>3</sup>	j <sup>4</sup>	w <sup>3</sup>	DPS <sup>4</sup>	
F	149	2124	macr.	2000	84	62	0.7175	abundant species
D	150	2390	macr.	>2000	66	35	0.6312	
F	65	3219	macr.	>3000	103	54	0.6953	abundant species
D	25	2926	macr.	3000	42	1	0.6659	
D	120	4020	d. 79%	>3000	74	3	0.5971	
F	86	208	d. 90%	186	65	32	0.7846	sparse species
D	139	651	d. 23%	150	67	14	0.7415	
D	9	286	d. 28%	80	71	3	0.7664	sparse species
D	112	1045	macr.	1000	134	13	0.7712	

<sup>1</sup> Table 1    <sup>2</sup> Table 2    <sup>3</sup> Table 3    <sup>4</sup> Table 7

Only in this way it can be understood that the year-samples of the abundant B-species do not outnumber those of the more sparse ones (see also Table 12). In my opinion this is equivalent, however, to saying that the RPR of the abundant species is not complete, i.e. these species would have been represented in more samples when the powers of dispersal would have been better. See further 7.5.4.

7.5.3. In line with the founding hypothesis the above conclusion would also imply that among these 5 abundant species, following 6.6, F-species – that partly live under pre-cultivation conditions – would still have to do better than D-species with similar N-values. The relevant data are summarized in Table 12 (in which the 4 sparse B-species are also given). The values of j and DPS – the w-values seem to be somewhat less reliable – especially of the species 149 and 150, clearly show that among the abundant species the supposed incomplete RPR has already affected the D-species more than the F-species (among the sparse species such an effect is less clear). This is an important finding in favour of the founding hypothesis of dispersal. See further 7.5.4.

Not only concerning the N-values (Table 12) are the two taxonomically closely related species 149 and 150 (*Trichocellus cognatus* and *placidus*) the best comparable species one could wish, but also in nearly all other relevant respects, e.g. sample situations both of pitfalls and of window-traps; way of life, reproductive period; size, wing development (Table 3).

Probably, the w-values in Table 12 indeed indicate that since the start of the 'experiment of cultivation' the powers of dispersal have already been reduced more by natural selection among the D-species than among the F-species (compare: DEN

BOER, 1970). For species of both groups the favourable situation of being enabled to optimally inhabit rather extensive and nearly continuous areas with only moderate powers of dispersal has irreparably disappeared, for the D-species for a rather long time already, for the F-species only recently (cf. 8.1).

7.5.4. The findings of this section are both contradicting expectation (3) (under the overflow hypothesis) and sufficiently in line with the founding hypothesis: the chance to disperse is lower for individuals of abundant B-species occupying permanent habitats than for those of more sparse ones (cf. 7.3), and this adequately coincides with lower DPS-values in these abundant B-species (cf. 7.5.2 and Appendix B.II, section 7). As already noted in 7.5.2 this implies that, in order to reach a complete RPR, the absolute numbers of individuals dispersing should be higher in abundant B-species than in sparse ones, and this seems generally not to be realized (cf. Table 12). Although I suppose that under pre-cultivation conditions also the abundant B-species of permanent habitats will have reached an about complete RPR (to which walking individuals will have significantly contributed), the present reduced RPR is not expected to endanger the survival of these species for the time being. This expectation is based on the consideration that in many abundant species the chance of extinction of the largest populations will often be smaller than in comparable more sparse species (in which the largest populations – by definition – are smaller), other things being equal. Since the latter phenomenon goes together here with an apparently insufficient dispersal the low DPS-values of these abundant B-species mainly result from a too great difference between the realization of extinction – with incomplete replacement – of the largest and that of the smallest populations as compared with the much smaller difference in the more sparse species – where it goes with accordingly higher DPS-values.

In the long run, however, this situation will unfavourably influence the survival of these abundant B-species too, because it will incorporate a positive chance of a further reduction of dispersal power by natural selection (cf. DEN BOER, 1970). The reality of this process is already shown by the differences between abundant D- and F-species as discussed in 7.5.3 and illustrated by Table 12.

The latter point in fact also rules out an alternative explanation for the low DPS-values of abundant B-species as compared with more sparse ones, viz.: our fixed set of 175 year-samples is too small to include also a representative distribution of year-samples for the most abundant species (in which  $j$  is expected to reach its highest values, cf. 7.5.1), by which particularly the supposedly large group of smaller populations would have to be relatively underrepresented.

Moreover, this alternative explanation would imply that the significant and negative correlation between DPS and  $N$ , as it is found in B-species would also exist in A-species and in C-species. This appears not to be the case, however: Table 11, right part.



## 7.6. DPS AND THE ABUNDANCE OF A- (AND C-)SPECIES

From 7.5.1 and Table 11 (left part) we know already that – contrary to the situation in the relevant B-species – among the A-species occupying permanent habitats  $j$  appears to be highly correlated with  $N$ , and that the same applies to the pertinent C-species.

7.6.1. On the one hand, the above correlation could result in DPS increasing with  $N$  (compare 7.5), but on the other hand – under the founding hypothesis – we may also expect the phenomenon discussed in 7.5.4 to play some part, viz. the increasing difference between the realization of extinction – with little replacement – of the largest and that of the smallest populations with increasing  $N$  will for A-species – and most probably also for C-species – result in a tendency of the DPS-values to decrease with increasing  $N$  – other things being equal. Together, for the 21 A-species of permanent habitats these will most probably result in no or an only weak, negative correlation between DPS and  $N$ : Table 11 (right part). The DPS-values of the 8 A-species of permanent habitats with  $N > 2000$  are accordingly only slightly lower than those of the 13 A-species with  $N < 2000$ , U-test:  $Z = 1.84$  ( $p = 0.033$ , one-sided); with  $N = 1200$  as a divider even this weak difference disappears, U-test:  $Z = 0.67$  ( $p = 0.2514$ , one-sided). Leaving out the A-species with sizes of individuals above 14–15 mm (cf. 6.4) does not alter the situation (U-test): with  $N = 2000$  as a divider,  $Z = 1.69$  ( $p = 0.046$ , one-sided), and with  $N = 1200$  as divider,  $Z = 0.78$  ( $p = 0.218$ , one-sided).

Among the pertinent 18 C-species even this indication of a correlation has disappeared (Table 11, right part), because abundant C-species are almost absent.

7.6.2. Following the above considerations we can expect that especially sparse A-species of permanent habitats will have been found in a smaller number of year-samples (extinctions with only little replacement) than comparable B-species (extinctions with much replacement). This expectation is indeed fulfilled; with  $N = 2000$  as a divider we find (U-test)  $Z = 1.87$  ( $p = 0.0307$ , one-sided), and with  $N = 1200$  as a divider  $Z = 2.33$  ( $p = 0.0099$ , one-sided).

Of course, the DPS-values of these A-species are also lower than those of the relevant B-species; with  $N = 2000$  as a divider (U-test):  $Z = 2.78$  ( $p = 0.0027$ , one-sided), and with  $N = 1200$  as a divider:  $Z = 2.62$  ( $p = 0.0044$ , one-sided). Compare: 6.1 and 7.2.1. Also in these respects – as in most other ones, cf. 6.1.1 and Table 11 – the C-species resemble the A-species, the sparse C-species of permanent habitats showing lower  $j$ -values than the relevant B-species (U-test): with  $N = 2000$ :  $Z = 2.42$  ( $p = 0.0078$ , one-sided), with  $N = 1200$ :  $Z = 2.30$  ( $p = 0.0107$ , one-sided), and accordingly lower DPS-values: with  $N = 2000$ :  $Z = 2.91$  ( $p = 0.0018$ , one-sided), with  $N = 1200$ :  $Z = 2.85$  ( $p = 0.0022$ , one-sided).

### 7.6.3. *Nomadic and sedentary species*

When taking into account the phenomenon discussed in 7.5.4 and 7.6.1 we can conclude that the findings of this section are in line with expectation (4) under the founding hypothesis. Together with section 7.5 the present section confirms one of the conclusions from chapter 6: the transition from species with a still sufficient dispersal power to species with an insufficient dispersal power is obviously running somewhere through the group of B-species (cf. 6.9). We can now supplement this conclusion with: this transition is apparently running between the abundant B-species ( $N > 2000$ ) of permanent habitats (cf. 7.5.2) and the sparse B-species of permanent habitats (cf. 7.6.2). This is supported by the fact that the DPS-values of the sparse B-species of permanent habitats ( $N < 2000$ ) do not differ from those of the sparse B-species of temporary habitats (U-test:  $Z = 0.75$ ,  $p = 0.4524$ , two-sided), and that about the same can be said about the relevant  $j$ -values ( $Z = 1.55$ ,  $p = 0.121$ , two-sided); compare 6.5.2.

I have the impression that this transition about coincides with a transition from a more or less 'nomadic' way of life to a more sedentary one. It is supposed that in the 'nomadic' species individual reactions to relevant environmental variables are such that the individuals are generally kept more or less spread over the whole inhabitable area, whereas in the sedentary species these reactions will generally result in a tendency of the individuals to cluster – often only during part of the reproductive period – in sites that are opportunistically experienced to be 'favourable' (e.g. preferred temperatures, concentrations of food).

In 'nomadic' carabid species the supposed spreading of individuals will generally occur by flight activities – which will also keep up a certain degree of dispersal – although in some (or even many) cases also walking activities may contribute to it. Hence, 'nomadic' species will generally be fullwinged (or dimorphic with a high % macr. ind.). With our procedure of sampling such species will necessarily come out as sparse ones. See also: DEN BOER (1971b).

In more sedentary carabid species the clustering of individuals will in most cases occur by walking activities, by which dispersal by flight generally will be a quite different phenomenon (e.g. only occurring outside of the reproductive season). Hence, sedentary species will be more susceptible to selection against flying ind. and will thus often be A-species (among which are indeed many abundant species; cf. Table 3). When sampling, many of such species will come out as abundant ones (at least locally).

In connection with the latter phenomenon it must be noted that a representative distribution of population sizes of sedentary species can only be obtained by sampling many suitable sites in many years. We assume to have satisfied this condition (cf. 2.1).

The above classification is not only suggested by 'general field experience', but it is also supported by theoretical considerations: The 'nomadic strategy' is expected to be a favourable one for species occupying vast and heterogeneous – but in most places more or less suitable – natural areas. Under these conditions, 'dispersal

losses' need not be very high (DEN BOER, 1970), whereas the widely spread individuals (also – indirectly – in less mobile stages) will both experience an important spreading of the risks from unpredictable local conditions – resulting in a significant stabilization of numbers, cf. DEN BOER (1968a, 1971a), REDDINGIUS & DEN BOER (1970) – and experience some 'protection' from severe predation (cf. DEN BOER, 1971a).

When the suitability of sites is more pronounced (or the individuals show more pronounced preferences) a 'clustering strategy' may be favourable, particularly when such suitable sites – although they may change places – are generally within travelling distances for – in carabid beetles – walking individuals. Because also less mobile stages (e.g. larvae) will be more or less clustered in a restricted number of places that were preferred by the more mobile ones (e.g. adults), the general unpredictability of future conditions (e.g. weather) may thus result in important fluctuations in numbers, viz. the risks are not maximally spread. Therefore, this 'strategy' will be more 'safe' for abundant species than for more sparse ones. As soon as the more or less continuously inhabitable natural area becomes severely interrupted sedentary species will be among the first ones to show a reduced RPR, i.e. to show the phenomenon described in 7.5.4.

It will be clear, that the way of life of the majority of carabid species will be somewhere between the above 'strategies'. The same applies to the suggested relations between any 'strategy' and abundance, that are of a statistical kind only. Nevertheless is it expected that especially the majority of the 'nomadic' carabid species will be among the 50% most sparse ones of the 148 species caught, and that were excluded from the present operations (cf. 4.1, and Appendix A.I); only a minority of the 'nomadic' species is expected to be found among our 74 test species, primarily among the sparse B-species of permanent habitats, but possibly also among the pertinent C-species, and perhaps even among the A-species with big individuals (walking 'nomads'). Especially among the B-species the 'nomadic' way of life apparently gradually merges into that of species occupying temporary habitats.

## 7.7. 'OVERFLOW' DISPERSAL IN CARABID BEETLES

We shall now have to evaluate the findings of this chapter with regard to the question whether or not the kind of 'overflow' dispersal that is described in 7.1 occurs frequently enough to be traced in our data as a departure from the general views as these were developed in chapter 6.

7.7.1. Although some interesting phenomena emerged from comparing abundant with more sparse carabid species nothing is found that could support such an 'overflow' hypothesis of dispersal. On the contrary, the individual chance to disperse is smaller in abundant (B)-species than in more sparse ones (cf. 7.3) – which is con-

firmed by the smaller % macr. ind. in abundant than in more sparse wing dimorphic species (cf. 7.4) – and the DPS-values of abundant (B)-species are lower than those of more sparse ones (cf. 7.5).

If (overflow) dispersal would occur more frequently in abundant than in comparable sparse species, populations would be more easily (re)founded in abundant than in sparse species, i.e. together with the (supposed) comparatively low chance of extinction of many dense populations this would have to result in a higher chance to keep up an about complete RPR in abundant than in sparse species. In 7.5.4 we showed that we can only arrive at the opposite conclusion. Hence, our general conclusion can be about the same as that from chapter 6 (cf. 6.10): the differences between species as far as the relations between abundance on the one hand and the degree of dispersal, the numbers of year-samples with catches (j) and the values of DPS on the other hand are concerned, can only be brought into line with all the evidence presented, when they are assumed to result from the influence of the ‘experiment of cultivation’ on the RPR of species with pre-existing differences in dispersal power (i.e. differences that were ‘adapted’ to quite different spatial relations).

7.7.2. The above conclusions do not mean, however, that in carabid beetles dispersal will never be released by overcrowding (cf. 7.1). In fact, we did not directly investigate this point. We can thus only state, that the frequency of occurrence of such dispersal is apparently so low, that it is unable by and large to compensate for the reducing RPR of abundant B-species of permanent habitats (cf. 7.5.4), nor to manifest itself in some other way in our data. As already mentioned in 6.8.2, moreover we have the impression that ‘carrying capacity’ is only seldom reached in carabid beetles. Possibly ‘carrying capacity’ – and by it dispersal released by ‘overcrowding’ – is more readily reached in a number of phytophagous insects, by which we must keep in mind, however, that many of the more spectacular cases are shown under highly artificial conditions, e.g. in many agricultural pests.

However, also the commonness of a loss of dispersal power in highly isolated populations (islands, mountains) of all kinds of organisms (see e.g. DARLINGTON (1943) for carabid beetles and CARLQUIST (1966) for plants) does not say much for a general validity of an ‘overflow’ hypothesis of dispersal: If dispersal would generally relieve the pressure from too high densities (cf. 7.1), during the process of decrease of dispersal power such isolated populations might thus progressively be confronted with the serious drawbacks of overcrowding, and could eventually be driven to extinction. Hence, the loss of dispersal power can hardly be understood from this point of view, whereas it is completely in line with the ‘founding’ hypothesis: dispersal has lost its function, viz. increasing the chance to (re)found populations. See also: DEN BOER (1970).

Therefore, we had to study quite different processes when we wanted to know what kind of phenomenon dispersal is in general, and we hope to have shown that dispersal can only be generally understood in terms of the ‘founding’ hypoth-

esis (3.4). It must be stressed, however, that this does not exclude the possibility that in some or even in many cases dispersal could be density-dependent (cf. ZIEGLER, 1976) and/or is released by 'overcrowding' (cf. DEMPSTER, 1975): the only relevant point is, that the overall degree of dispersal suffices to keep up an about complete RPR, and it may be expected that in different organisms this will be reached in different ways.

7.7.3. For some students (see e.g. VLIJM, 1971) a remarkable feature of the 'founding' hypothesis (3.4) will be, that the interest is not concentrated upon the question by what causes an individual starts dispersing. Because for the time being we are mainly interested in the amount of dispersal, in dispersal power and in the effects of dispersal, for the present it suffices to suppose that a smaller or greater part of the individuals (or even all individuals, e.g. in many species of temporary habitats) will potentially be inclined to disperse and that the majority of these individuals will generally come across the stimuli that actually start dispersal. Otherwise, we have already some knowledge about the direct causes of dispersal (cf. 7.7.4) and it will be studied further. In fact, the above situation is like the population ecologist's interest in reproduction (which will be clear when in the above 'dispersal' is replaced by 'reproduction').

7.7.4. Following 7.7.2 we will now consider the more general statement that dispersal is released by unsatisfactory conditions (cf. 7.1). The available observations suggest that during the reproductive period of most carabid beetles unsatisfactory conditions are evaded by walking, also in macropterous species (the more so because in many species the flight-muscles are then reduced). These locomotory activities – which can as well be considered searching for more satisfactory conditions – will in the first place contribute to a continuous redistribution of individuals throughout the population area, but in many species these will also contribute to some dispersal over short distances. Hence, this kind of dispersal is completely integrated in the general pattern of locomotory activities, and its level will thus depend both on the general level of locomotory activities and on the way of life of the pertinent species.

On the (small) scale of interaction groups (cf. 1.4) we can indeed observe that locomotory activities will sometimes result in the vacating of a small site that apparently has become 'unsatisfactory', but on a larger scale this will merely be considered to be part of the continuous redistribution of individuals throughout the population area. Dispersal by flight, however, which in the present study is the more significant kind of dispersal, is a quite different phenomenon. In most carabid species it only occurs outside of the reproductive period (cf. DEN BOER, 1971b; VAN HUIZEN, in press), and it is released by fine weather conditions (sunny, not too windy, temperature above a certain level), not only in species showing obligatory habitat change (VAN HUIZEN, in press), but to a higher or lower degree in all kinds of species.

Nothing whatever in this phenomenon suggests an escape from currently adverse

conditions. Also the work of RICHTER (1971) on the 'tip-toe' behaviour of spiders clearly shows that we have to do here with a distinct kind of behaviour that is released by such a set of physical conditions that obviously an effective dispersal is facilitated. The data compiled by JOHNSON (1969) show, that this situation is not restricted to carabid beetles and spiders.

In wingless species an effective dispersal over short distances may probably be reached – at least under natural conditions – by intensifying some aspects of the normal locomotory activities. We have indications that this may indeed be the case in some brachypterous carabid species, e.g. in species 80: *Carabus problematicus* (cf. DEN BOER, 1970). It evidently occurs in the woodlouse *Porcellio scaber*, where the whole pattern of locomotory activities is dominated by a search for more satisfactory air humidities (or escaping from unsatisfactory ones): DEN BOER (1961). By this active regulation of the water-balance a very high level of dispersal over short distances is kept up. In 1954 it was observed – and confirmed by PALMÉN (pers. comm.) to be the normal process – that *Porcellio scaber* is effectively dispersed throughout the Tvärminne-archipelago (Finland) because of its habit to shelter under *Fucus*-heaps. These *Fucus*-heaps, namely, are washed ashore, taken away to sea in each spring, transported, and washed ashore again in some other place, by which the woodlice – and other arthropods – can indirectly cover rather long distances. We must allow for the possibility that among other wingless species that survived under natural conditions many different kinds of such a substitution for dispersal by flight will occur (in fact the aeronautic behaviour of spiders is a nice example of such a substitution).

Again, different organisms will reach in different ways, that the overall degree of dispersal will suffice to keep up an about complete RPR, and in some or even many cases also an escape from currently adverse conditions may contribute to this.

## 7.8. BIAS IN OUR IDEAS ON POPULATIONS

The current ideas on populations are largely influenced by data on a small number of comparatively dense populations (see also: WATT, 1971). Are these sufficiently representative to give a reliable impression of the processes that are of general importance for all kinds of populations? If not, our ideas on populations might be highly biased. Because in this chapter we compared abundant with more sparse carabid species, we might have obtained some indication on the possible occurrence of such a bias.

7.8.1. In the sections 7.3 and 7.4 we showed that the chance to disperse is much smaller for an individual of an abundant (B)-species occupying permanent habitats than for an individual of a more sparse one. When this would be a more general phenomenon, this may indeed give rise to an important bias in our ideas. When only

studying very abundant species we will be confronted either with species that show very pronounced dispersal activities (or even migration), i.e. species of unstable or temporary habitats – among which most of the species of economic importance – or with species that apparently do not show dispersal activities, i.e. the percentage of individuals dispersing is generally so low, that most students will not be inclined to attribute any importance to it, if they observe and mention it at all (compare e.g. the % macr. ind. in the most abundant dimorphic carabid species: Table 3: 68, 70, 95, 119). This situation may have brought SOUTHWOOD (1962) to his conclusion that the level of migratory movement (= dispersal) is positively correlated with the degree of impermanence of the habitat (cf. 1.2). Yet, the absolute numbers of individuals dispersing need not be very different in abundant and comparable sparse species of permanent habitats (cf. 7.5), and these may still enable some very abundant dimorphic carabid species – viz. 70, 95 – to found populations: DEN BOER (1970).

Hence, by only studying very abundant species we are not in a position to recognize the general significance of dispersal power.

7.8.2. The bias mentioned in 7.8.1 implies another one: A certain number of individuals dispersing in each generation from a very dense population occupying a permanent habitat will hardly influence the numbers of this population, whereas the same applied to a comparable sparse species will in many cases result in a profound influence on the numbers of the parent population. This is equivalent to saying that the dynamics of such very dense populations will hardly be influenced by dispersal, whereas in many sparse species dispersal will be a chief process in the dynamics of populations. Hence, the way of life of many sparse species – especially of those occupying permanent habitats – can be expected to be quite different from that of comparable abundant ones, viz. the way of life of many sparse species will inevitably be a more or less 'nomadic' one (cf. 7.6.3).

When we take into account that by far most populations are sparse (see e.g. WILLIAMS, 1964) – only 17 out of our 148 carabid species ( $11\frac{1}{2}\%$ ) have N-values > 2000, and only 5 species have N > 10,000: Table 3 – we get some idea of the possible importance of this bias in our way of thinking about populations; see also: WATT (1971), and other remarks on 'sparse populations' and 'rarity' – by consulting the index under these items in 'Dynamics of Populations' (DEN BOER & GRADWELL, 1971).

Because the sparseness of populations from which a high percentage of the individuals is dispersing will be accentuated by this very dispersal, it seems possible that among some groups of organisms the transition from a more or less 'nomadic' way of life to a more 'clustering' or sedentary one (cf. 7.6.4) may be about estimated from the sampling numbers. In 7.4.2 we argued for the carabid species of our sampling program to have preliminary found such a transition at about N = 2000 (see 4.4.5 and 7.6.3). We hope once to compare the dynamics of some of the species with N > 2000 with those of related species with N < 2000 to support the above considerations.

## 8. SURVIVAL OF CARABIDS IN A CULTIVATED COUNTRYSIDE

In the preceding chapters we (indirectly) showed that natural extinctions will occur everywhere (compare also: MAC ARTHUR & WILSON (1967: ch. 2 & 3) for extinctions on islands) – i.e. not only (necessarily) in species of temporary habitats (cf. 1.2), but also in species of permanent ones (cf. chapters 6 and 7) – and even frequently enough to be studied. As a consequence of this a power of dispersal sufficient to replace populations which have disappeared is a necessary condition for the ultimate survival of all species, by which the significance of the effects of dispersal appears to be comparable with that of reproduction.

### 8.1. POPULATIONS LOST FROM OUR STUDY AREA

We could show in different ways (ch. 6 and 7) that by a major environmental change like cultivation the relative frequency of sparse populations is the more reduced the poorer the pre-existing powers of dispersal of the species concerned. Hence, in our cultivated countrysides these species – particularly those occupying the remnants of permanent natural habitat – have entered a process of accelerated extinction (cf. DEN BOER, 1970: 6.4). We will now try to estimate how far this process has already progressed.

8.1.1. A survey of the history of the landscape of our study area, Drenthe (WATERBOLK, 1951) shows, that at the start of the Christian era the conditions for the survival of most (carabid) species inhabiting natural localities must generally have been very favourable. At that time the area was already occupied during some 1500 years by a sparse agricultural population practising exhaustive cultivation, by which rather large areas of heath and/or blown sand were maintained. The greater part of the primeval (deciduous) forest, however, was still present, whereas the area was surrounded by vast peat moors and studded with smaller ones. This situation did not alter fundamentally until the Eighty Years' War (16th century) during which great parts of the primeval forest were destroyed. Yet, some 200 years ago a number of the old forests will still have been present (see Fig. 5), and it is only somewhat over a century since the last greater forests disappeared in Drenthe. Some hundred years ago both the planting (with conifers) of the blown sand areas and the reclamation of the vast heath and peat moor areas started; it is only 25–50 years since these reclamations neared completion.

8.1.2. Therefore some 100 years ago for many (carabid) species occupying per-



manent habitats, the availability and pattern of distribution of suitable localities probably still was such that the powers of dispersal generally met the needs of population replacement. For sand (E)- and especially heath (F)-species these favourable conditions may have lasted for several decades longer (cf. BROUWER, 1968), whereas for woodland (D)-species, these will have become unfavourable earlier already. On the other hand, both the numerous hedgerows bordering the fields and pastures and the oak-groups in and around the villages, part of which disappeared only in the last decades – e.g. by re-allotments – might long have functioned as an important network of ‘stepping-stones’ (cf. DEN BOER, 1970) facilitating the dispersal of many woodland-species. For only a minority of these species (e.g. *Carabus problematicus* (80), *Notiophilus biguttatus* (120) and *Pterostichus oblongopunctatus* (138)) the coniferous plantations in blown sand areas meant an actual increase of the number of inhabitable localities (compare: DEN BOER, 1968b; Fig.’s 1 and 2; see also Appendix A.III). If we assume that the situation in which our heath (F)-species were sampled – i.e. with many year-samples from rather large ‘natural’ localities, in this case represented by the Heath of Kralo and Dwingeloo – resembles the situation in which one or two centuries ago also most other (carabid) species of natural localities would have been found in Drenthe, the findings of 6.6 give us a conservative estimate of the degree to which for the majority of these species the realization of population replacement (RPR) might have decreased during the last hundred years, say\*.

Because the Heath of Kralo and Dwingeloo is the only extensive heath area left in Drenthe for the present time our F-species were sampled partly in an exceptionally favourable situation. If for the F-species also, sampling had been attuned to the present pattern of availability and distribution of suitable localities the situation should have appeared not to be very much better than that for the D- and E-species. But in that case the pertinent comparison would hardly have been possible.

8.1.3. Because for D-species comparatively fewer small populations will have been cumulated in  $\sum \ln(n_i + 1)$  than for F-species (cf. 5.4.1), the same value of  $\sum \ln(n_i + 1)$  will for a D-species correspond with a lower number of year-samples (j) than for an F-species. Hence, comparing the relations between j and  $\sum \ln(n_i + 1)$  for F- and D-species respectively may give us some idea of the number of local groups that might have been lost only by changing the pattern of distribution of suitable sites – during some hundred years, say – from the kind of F-species – large continuous areas – to that of D-species – small isolated areas – (cf. 6.6), i.e. without incorporating the actual loss of many inhabitable localities.

From some regressions – none of which do unadmissibly violate the assumptions of the linear regression model (cf. 5.2.2) – of  $\sum \ln(n_i + 1)$  on j, or of  $\sum \ln(n_i + 1)$  on

\* This argument is not influenced by the fact that some F-species (e.g. 86, 132, and to a less extent 70, 119) also live in agricultural fields and other man-made sites, because the same is true for some D-species (e.g. 78, 112, 117, 139). For the majority of both the F- and the D-species this argument remains valid.

$j^2/100$  (to better approximate linearity) for F- and D-species respectively, both with B-species included and B-species excluded, it can be derived that at the median value of  $\Sigma \ln(n_i + 1)$  for F- + D-species,  $j_D$  is 12–16% (of  $j_F$ ) lower than  $j_F$  (the different regressions not scoring very different results). When taking other values than the median one – especially in the case of  $j^2/100$  – the results do not change significantly. Hence, we arrive at a probable relative loss of about 14% of the local groups, exclusively resulting from an increasingly unfavourable change of the pattern of distribution of persisting suitable sites during the last hundred years, say. It can only be a relative loss, because it resulted from the difference between D- and F-species concerning the overall contribution of sparse and more dense populations respectively to  $\Sigma \ln(n_i + 1)$ , i.e. when also a few dense populations – especially of D-species – have become extinct (without destruction of the pertinent localities) we will severely underestimate the fraction of local groups that probably disappeared.

8.1.4. The estimations in 8.1.3 do not take into account the very important direct losses by the reclamation of the greater part of natural areas. The reclamations not only resulted in a highly unfavourable distribution of persisting suitable sites, but also in a drastic reduction of the numbers of potential dispersers. The latter effect alone will already have led to an important lowering of the chance to (re)found populations. Adding to this the simultaneously growing ‘island-effect’ of the distribution of persisting suitable sites (compare also: Fig. 5) will give us some idea of the extent to which the pre-existing powers of dispersal of the majority of (carabid) species of permanent habitats must have increasingly failed to keep up with the progress of cultivation. This situation still deteriorated by an increased selection against dispersing individuals – via a lowered chance to (re)found populations leading to a decreased production of dispersing individuals, etc. ... cf. DEN BOER (1970: 6.4). In Fig. 5 for different groups of carabid species we tentatively pictured the growing deviations from an about complete RPR as these might have occurred during the period of greatest intensification of cultivation (20th century), the present results of which could be estimated from our present knowledge. For convenience only, we assumed that for all groups these RPR-reductions rather suddenly started at about 1900 (cf. 8.1.2). We generally expect the present trend to continue, ultimately resulting in the regional extinction of the majority of our (carabid) species occupying permanent natural habitats, particularly of those with poor powers of dispersal (continued in 8.3).

## 8.2. CARABID SPECIES IN THE CENTRE AND AT THE FRINGES OF GEOGRAPHICAL DISTRIBUTION

Some students possibly will be inclined to mainly restrict the above pessimistic vision to species that are living here already near their fringes of (geographical)

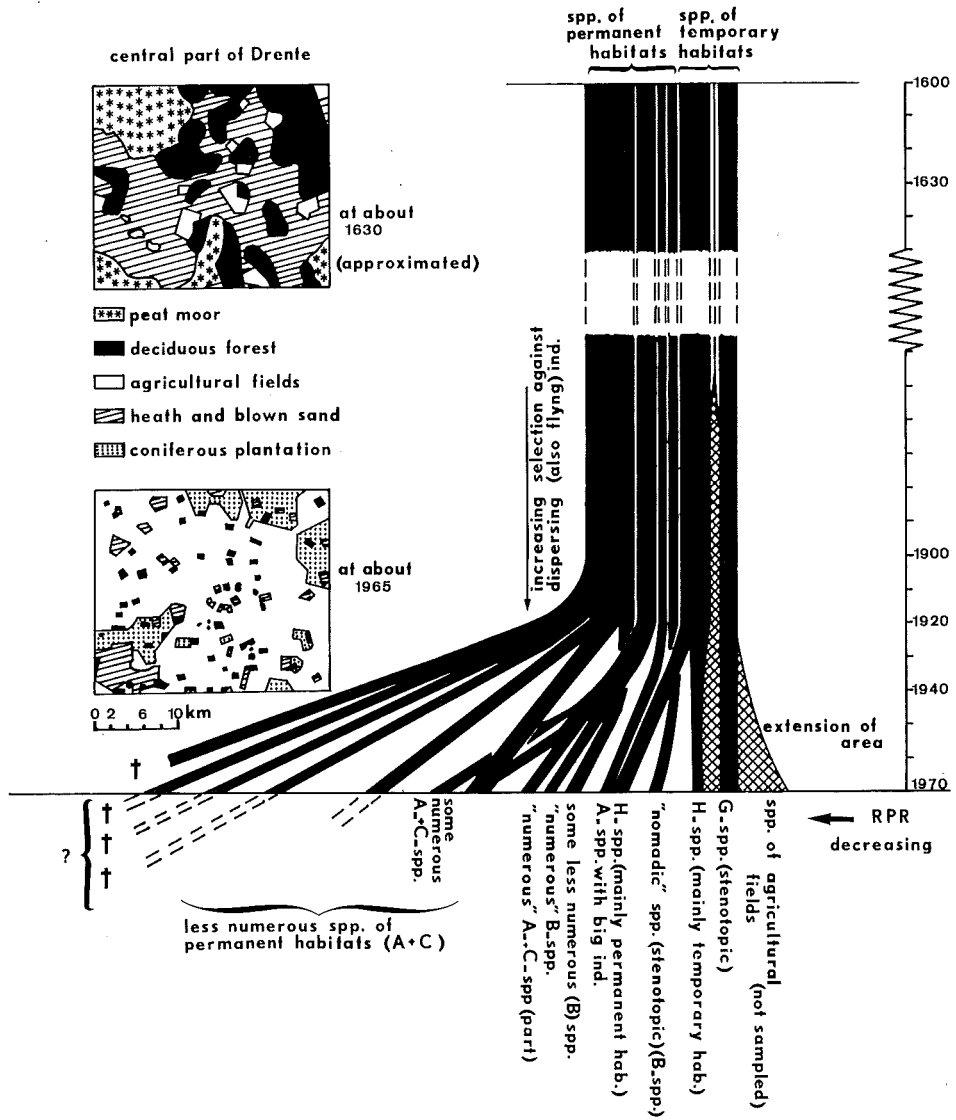


Fig. 5. Probable changes of RPR (degree of Realization of Population Replacement; cf. chapter 5) of 74 carabid species, as these are supposed to have resulted from important changes in the accessibility and pattern of distribution of suitable sites in the study area (central part of Drenthe) between 1630 and 1965 (arbitrarily supposed to have mainly occurred during the last decades) cf. 8.1.4 and 8.4.1.

distribution, i.e. they will assume such populations to live here – also without cultivation – under generally unfavourable conditions and consequently in rather unstable and often relatively sparse populations, which are thus more open to extinction than other ones.

8.2.1. The suggestion that species living here near the fringes of (geographical) distribution might be more endangered by cultivation than those living here more in the centre of distribution is an interesting one, because in a less rigid way it refers to the point made by NICHOLSON (1958); cf. 1.1. Without necessarily assuming that in the centre of geographical distribution ‘density-governing reaction permits a species to persist indefinitely in all favourable places’ (NICHOLSON, 1958), at first sight it seems not unreasonable to suppose that generally – i.e. for a greater part of time and/or a higher number of places conditions might be more favourable in the centre than near the fringes of (geographical) distribution of a species (compare 3.1). Of our 74 test species 19 are not (or hardly) known from the countries neighbouring the Netherlands either in the South, or in the North (Scandinavia), or in the West (British Isles), or in the East (Central Germany and still more eastern); cf. Appendix A.I. Hence, these species – given in Table 13 – are apparently living in our study area near the fringes of their geographical distribution (cf. HORION, 1941; LINDROTH, 1945), and we are thus in a position to test the above hypothesis.

Under this hypothesis one would expect to find relatively more dense populations among the ‘centre’-species than among the ‘fringe’-species, i.e. ‘centre’-species

Table 13. Carabid species that are living in the Netherlands near the fringes of geographical distribution.

near the ... fringe	species (cf. Appendix A.I)	number of species
South or SW (subboreal)	8, 25, 38, 56, 89, 105, 109, 149, 150	9
North or NW (south-continental)	1, 37, 106, 124	4
West (continental)	30, 76, 88, 102, 110	5
North-East (amphi-atlantic)	73	1
near the ... fringe	Out of 74 species with $N \geq 70$ (cf. 4.1):	19 spp.
South or SW (subboreal)	16, 116	2
North or NW (south-continental)	3, 43, 47, 48, 71, 83, 101, 111, 113, 142, 143	11
West (continental)	11, 53	2
North-East (west-european)	91	1
	Out of 74 species with $N < 70$	16 spp.

should generally be sampled in higher numbers than 'fringe'-species (cf. 4.4). Taking again the dividing value  $N = 2000$  (cf. 7.4.2) 4 out of 19 'fringe'-species and 13 out of 55 'centre'-species respectively appear to be abundant:  $\chi^2 = 0.0073$  (d.f. = 1),  $p \approx 0.90$ ; hence, expectations are not fulfilled. Taking another divider, e.g.  $N = 1200$  (6 'fringe'-species and 17 'centre'-species abundant) does not change our conclusions:  $\chi^2 = 0.0544$  ( $p \approx 0.85$ ). When 'fringe'-species are indeed more endangered by cultivation than 'centre'-species one would expect the former generally to have lower DPS-values than the latter. Such a difference can not be shown to exist anymore (U-test):  $Z = 0.084$  ( $p = 0.200$ ; one-sided), no more when only species of permanent habitats – 15 'fringe'-species and 33 'centre'-species – are considered:  $Z = 1.22$  ( $p = 0.1112$ ; one-sided), or when the D- (8 'fringe'-species), E- (3 'fringe'-species) and F-species (4 'fringe'-species) are tested separately (the 3 U-tests summed:  $Z = 0.65$ ;  $p = 0.2578$ , one-sided).

In fact, between 'fringe'- and 'centre'-species we can not show that any of the differences discussed in the preceding chapters do exist; e.g. the distribution over A- and B-species respectively – in both groups 5 'fringe'-species – is an equal one ( $\chi^2 = 0.0805$ ; d.f. 1;  $p \approx 0.800$ ), and that over permanent and temporary habitats does not differ either ( $\chi^2 = 1.4698$ ; d.f. 1;  $p \approx 0.250$ ).

Hence, 'fringe'- and 'centre'-species respectively are proportionally equally represented among abundant and less abundant species, among species with a very low and those with a high dispersal power, and among species occupying permanent and those occupying temporary habitats.

Accordingly, these two groups of species do not show different DPS-values and therefore will not produce any consistent difference concerning the degree to which the replacement of disappeared populations is realized (RPR), i.e. they will be about equally endangered by cultivation. In only one respect 'fringe'-species differ weakly from 'centre'-species: on the average 'fringe'-species are caught in less year-samples (mean 50) than 'centre'-species (mean 68), U-test,  $Z = 1.91$  ( $p = 0.028$ , one-sided). This means that on the average 'fringe'-species are found in somewhat less places than 'centre'-species, i.e. ecological conditions are apparently more critical for 'fringe' species, although 'fringe'-species are not more 'stenotopic' ( $\chi^2 = 0.221$ ,  $p \approx 0.60$ ; cf. 6.7) than 'centre'-species.

8.2.2. The above data seem to suggest that in the centre, the distribution in space and time of both favourable and unfavourable conditions, need not to be strikingly different from that at the fringes of the (geographical) distribution of a species (see also: WILSON, 1968), although the conditions for 'favourable' may be somewhat more critical at the fringes. This is in agreement with our (probabilistic) starting point, but gives no arguments in favour of the assumption of NICHOLSON (1958) that the dynamics – as far as these are relevant for the chance of survival – of populations living at the fringes of distribution would be quite different from that of populations in the centre of distribution, i.e. marginal ecologically may not be the same as marginal

geographically. In other words, marginal (ecological) conditions will be found throughout the distributional area of a species. Hence, for our general insight into the survival of populations and species, the population processes studied by e.g. ANDREWARTHA & BIRCH (1954) and BIRCH (1971) will be as relevant as those studied by e.g. KLOMP (1966).

### 8.3. POSSIBLE ADAPTATION TO THE CONDITIONS OF CULTIVATION

Continuing now the discussions of 8.1 one will wonder whether in the long run natural selection should not enable some of the species endangered by cultivation to 'adapt' the powers of dispersal and/or the habitat requirements to the new situation.

8.3.1. The possibilities of a direct 'adaptation' of the powers of dispersal are very remote indeed. Monomorphic brachypterous (carabid) species are not expected ever to redevelop wings, because within Pterygote insects the loss of flight seems always to be secondary (see e.g. IMMS, 1960). As far as wing di(poly)morphic (carabid) species are concerned, it can only be expected that in isolated populations persisting for a number of generations in our cultivated countrysides – i.e. in permanent natural habitats – the percentage of fullwinged individuals will still more decrease (cf. 8.1.4 and DEN BOER, 1970). As soon as the overall production of 'diaspores' in newly (re) founded populations does no longer by and large compensate for the overall loss of individuals the net effect of flying away from existing populations will be natural selection against flying individuals. Even a number of the monomorphic macropterous (carabid) species of permanent natural localities may be subject to such a net selection against dispersing individuals under the present cultivation conditions.

8.3.2. An indirect 'adaptation' of the powers of dispersal in some of the endangered species cannot be wholly excluded, however. When some species occupying permanent habitats – and in which the powers of dispersal are not yet reduced too much – become increasingly able also to reproduce in some of the highly accessible man-made habitats, they may perhaps significantly restore the production of 'diaspores'. This will particularly work when the pertinent man-made habitats are sufficiently unstable to keep up the thus obtained level of dispersal power.

Such a situation might be about realized in species 139 (*Pterostichus strenuus*), which is able to reproduce now both in moist deciduous woodland (23% macr. ind.: Table 3) and in different kinds of moist man-made habitats with a dense vegetation, e.g. pastures (60–90% macr. ind.), grass-covered waste lands (40% macr. ind.); see also DEN BOER (1970: 4). Although the production of fullwinged individuals is thus kept high in this species (fullwinged migrants are caught frequently both in pitfalls and in window-traps) the net selection against flying individuals seems to be still apparent in – expectedly – long-persisting populations: in old forest 12% macr. ind. as

compared with young forest, 39% macr. ind.: DEN BOER (1970: Fig. 3). On the other hand the present % macr. ind. is in Drenthe generally higher than in Fennoscandia, cf. LINDROTH (1949, p. 396).

The surprisingly high % macr. ind. (79%: Table 3; see also 7.4.2) in species 120 (*Notiophilus biguttatus*) in Drenthe possibly may be understood in a comparable way: it is the only non-brachypterous woodland-species that also reproduces about normally in the different kinds of coniferous plantations nowadays covering extensive areas in Drenthe (former blowing sands, cf. 8.1.1): DEN BOER (1968b: Fig's 1 and 2); see also: DEN BOER (1970, p. 6), LINDROTH (1949, p. 407-409) and the discussion after the paper of HAECK in DEN BOER (1971c).

A few more species of permanent habitats may thus be on the way to escape from the more severe consequences of the 'experiment of cultivation' too, e.g. 86 (*Clivina fossor*), 112 (*Loricera pilicornis*) and 117 (*Nebria brevicollis*).

Whether also some species, in which dispersal by flight has completely or practically (very low % macr. ind.) disappeared, will ultimately be able to persist in a comparable way in our cultivated countryside, may be doubted. We may have hope for some of the very abundant ones among these species of permanent habitats, e.g. 70 (*Calathus melanocephalus*), 119 (*Notiophilus aquaticus*) and 132 (*Pterostichus versicolor*), because these are also able to reproduce in arable land (cf. 8.4.4).

8.3.3. Taking together the discussions in 8.3.1 and 8.3.2 it must be expected that, with the probable exception of rather extensive 'natural' areas – like the Heath of Kralo and Dwingeloo (cf. 8.1.2) – most remnants of natural habitat will gradually become deprived of many of the most characteristic – viz. stenotopic – (carabid) species. What fraction of our (carabid) fauna is actually endangered or has already disappeared from the area can only be guessed at the moment, because historical data are lacking.

#### 8.4. CARABID SPECIES FAVOURED BY CULTIVATION

As a counterpart to the preceding sections it must be noted, however, that the 'experiment of cultivation' has also added a number of species to our fauna (cf. DEN BOER, 1962), and probably will continue to do so in the future (cf. LINDROTH, 1972).

8.4.1. When the greater part of natural areas has been reclaimed for cultivation most species of arable land and other man-made sites have entered a highly favourable situation, viz. the reverse of that described in 8.1.4 for most species of permanent natural habitats. Because of an important extension and linking together of suitable sites these species – with generally high powers of dispersal – will be subject to a decreased selection against flying individuals, whereas the chance to (re)found populations will be highly increased, thus leading to an increased production of

dispersing individuals, etc. ... and ultimately to an expansion of the geographical range (DEN BOER, 1970): Fig. 5. The latter phenomenon is nicely illustrated by *Amara majuscula* Chaud. and *Amara ingenua* Dfts. (cf. DEN BOER, 1962; LINDROTH, 1949, 1972).

8.4.2. Because most man-made sites are comparatively unstable the powers of dispersal of these weedy species (cf. 8.4.1) will generally be kept at a high level (compare 8.3.2), by which the high chance also frequently to invade the remnants of natural habitat will persist in these species. In fact, during our sampling program such invaders from arable land were caught repeatedly in all kinds of natural habitat. A few of these species are naturally capable of reproducing there (e.g. 54, 104 and 106 in heath; 60 and 141 in some remnants of forest), and others may be expected increasingly to develop such a capability (e.g. 22 and 31, and many of the species that were not incorporated in our program: 4.1).

8.4.3. The invasions into the new 'IJsselmeer'-polders (cf. MOOK, 1971), especially those of carabid beetles with high powers of dispersal (cf. HAECK, 1971) clearly illustrate the point made in 8.4.2. Moreover, they demonstrate how fast new suitable sites can generally be occupied by such species. The same is shown by MEIJER (1974) for a more specialized group of carabid beetles (species that can tolerate salt) immigrating into the new 'Lauwerszee'-polder. Although practically all these species are generally occupying temporary and/or unstable habitats, DEN BOER (1970) showed that under these exceptionally favourable conditions – viz. extensive more or less suitable areas and thus a relatively high chance to land there – even some species with comparatively low powers of dispersal (low % macr. ind.) were able to found populations there, albeit only after some years in most cases: HAECK (1971: Table 6).

We may hardly hope, that among the latter species there will also be some highly endangered ones, and that some of these will be capable of developing such high numbers of fullwinged individuals there, that both part of the populations in the 'old' land can be reinforced by it, and some localities that have been left empty and highly isolated by cultivation can be repopulated, but one never can tell.

For future research concerning the above problems something can be learned from considerations on island biogeography (e.g. in MAC ARTHUR & WILSON, 1967: ch. 2 and 3), in which the number and turnover (extinctions and colonizations) of species are brought in relation to the area of the island and to distance. It is a pity that differences in dispersal power and the time-scale of turnover are hardly incorporated in these considerations; this is changing, however, during the last years (see e.g. DIAMOND, 1975).

8.4.4. Some 3000 years ago a comparable process (cf. 8.4.3) will have been started in Drenthe when the sparse human population practised exhaustive cultivation there (cf. 8.1.1). I guess that some of the species then mainly occupying agricultural fields



will have invaded the growing heath areas and became increasingly capable of reproducing there. After the change-over to more intensive agricultural practices the heath areas have been kept stable by sheep grazing, and the pertinent species will have increasingly lost their high powers of dispersal. Particularly the species 17, 70, 95, 119 and 132 – which are still able to reproduce in arable land – may be considered to belong to this group (3 of these – 17 (*Agonum obscurum*), 70 (*Calathus melanocephalus*), 95 (*Dyschirius globosus*) – were also able to found populations in the new ‘IJsselmeer’-polders: DEN BOER (1970).

It is tempting to assume that some other species of heath areas, which now have a sibling partner in forest (e.g. 149/150 (*Trichocellus cognatus/placidus*); 118/117 (*Nebria salina/brevicollis*), should have originated from these early agricultural practices.

8.4.5. The latter point refers to events that are supposed more generally to occur on a larger time-scale. When we project the kind of processes that are treated in the different parts of this chapter on a large – geological – time-scale, we get some idea how major environmental changes – as these occurred repeatedly during the history of life – ultimately resulted in an ‘outburst’ of new taxa. I guess that in many of such cases the ‘old’ species entered a process of accelerated extinction because the powers of dispersal had become insufficient to reach more distant suitable areas\*, whereas a number of species with high powers of dispersal could increasingly settle in such changing areas and evolve there into a number of new taxa. Given enough time, along the above lines the ‘experiment of cultivation’ may also lead to the appearance of some new taxa.

8.4.6. Returning to our present cultivated countryside in Drenthe we may thus expect that in the long run the remnants of natural habitat will gradually be occupied by ‘new’ species (cf. 8.4.2). However, this process will demand much time, and on the ground of the preceding chapters of this paper we may be quite sure that the process of the disappearance of ‘old’ species will run too fast (cf. section 8.1) to prevent a net impoverishment of many of our natural habitats – particularly the small and highly isolated ones – at least for a considerable period.

## 8.5. POSSIBILITIES OF NATURE MANAGEMENT

When we do not have the patience to await the results of the evolutionary processes

\* Note, that this may already originate from a reduced tendency to leave the preferred habitat, even in animals that are capable of flying very well. This being apt to use the flight capabilities mainly to keep to the habitat has been noticed among some groups of birds, among some groups of butterflies, among bumble-bees, etc. (cf. LINDROTH, 1949). For carabid beetles LINDROTH (1949, p. 590) mentions a case in *Cicindela maritima* and another one in *Bembidion litorale*. Probably comparable cases: in the C-species 102, 110, 117, 118 and 124 the individuals are apparently hardly inclined to fly in spite of the occurrence of well-developed wings (cf. Table 3: column 20).

mentioned in 8.4.5, or are not easy about these results, we will be highly motivated to slow down the process of the disappearance of 'old' species (cf. 8.4.2) to such an extent that both some of these species is given the opportunity to 'adapt' the powers of dispersal and/or the habitat requirements (cf. 8.3.2) and the 'new' species can keep pace with the rate of these disappearances. What kind of strategy should be followed to gain this object?

8.5.1. Apart from the *evident necessity* to preserve – or even to 'create' – a few extensive 'natural' areas (cf. 8.1.2 and 8.1.3), I expect that especially certain waste sites, gardens, hedgerows, roadside verges, railway embankments, etc. can be made in an important way to participate in the linking together of remnants of natural habitat (cf. ELTON, 1958), particularly when suitable conditions for a number of species can be maintained and/or created there by an adequate management; see also: DEN BOER (1970). The degree of suitability of these 'stepping-stones' will have to be tested by founding experiments (cf. 6.8). At places where apparent 'bottlenecks' for the dispersal of many critical species occur we will have to (re)construct adequate 'stepping-stones'.

Highly endangered species should be given an opportunity – by adequate founding experiments – to repopulate suitable sites from which they obviously disappeared during the 'experiment of cultivation'.

Such measures will only have a high chance to succeed when they are integrated in – and regularly adapted with the help of the results of – intensive and long-term investigations into the dynamics of the spatial distribution of populations. If we should be able to reconstruct our cultivated countryside in such a way that the greater part of the natural sites become interlinked by a network of more or less adequate 'stepping-stones', and that these sites are again occupied by most of the species belonging to them (if necessary, via artificial refoundings) we may hope to sufficiently slow down and in the long run even to stop the process of accelerated extinction that is started by the 'experiment of cultivation', and thus to preserve at least part of the present diversity of nature for a long time.

8.5.2. Starting from the – unproved, and in my opinion unnecessary – assumption that each habitat will eventually contain an 'equilibrium' number of species\* (kept up again by processes that 'try to maintain' such an equilibrium between (re)foundings and extinctions; cf. MAC ARTHUR & WILSON, 1967), DIAMOND (1975) arrives at ideas concerning the survival of birds and mammals in isolated areas that in many respects resemble those exposed in this chapter. He too points to the effects of differences in dispersal power, and to the effects of the area and the degree of isolation of the suit-

\* This opinion probably originates from the idea that for the greater part of time each species should about 'fill up' its habitat until 'carrying capacity' (cf. 3.1), by which each habitat can only contain a certain number of species that apparently fit a highly determined pattern of (fundamental) 'niches': cf. MAC ARTHUR & WILSON (1967).

able habitats (compare: 6.6). His advices concerning nature management consequently go into a similar direction as ours.

There is one important difference, however: according to DIAMOND (1975) a remnant of natural habitat left isolated in a cultivated countryside will lose species by natural extinctions until a new (lower) 'equilibrium number' of species is reached. In our opinion irreplaceable extinctions will continue for all species in which the powers of dispersal in the new situation do no longer suffice for an adequate replacement (cf. 8.1), i.e. this prediction concerns separate species, and has nothing to do with the number of species still present in the pertinent remnants of natural habitat. See also: 8.3 and 8.4. We hope to return to these points in following papers.

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