



The Survival Value of Dispersal in Terrestrial Arthropods*

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ABSTRACT

Dispersal in terrestrial arthropods cannot merely be a means to 'escape from adverse conditions'. During the 'dispersal phase' aeronautic behaviour of insects and spiders is made possible by suitable weather, often resulting in airborne 'plankton', the washing ashore of large numbers of winged insects, regular catches on 'window' traps, and in the rapid colonization of new polders. Therefore, the primary biological significance of dispersal will be the maintenance and extension of the presence of a species in space by (re)founding and supplementing local populations. Accordingly, dispersing individuals of some species show a higher egg production than those which do not disperse. Depending on the spatial relationships between habitats natural selection will 'manipulate' the powers of dispersal of many species. In a cultivated area this will endanger poorly dispersing species by increasingly isolating them in remnants of the 'old landscape'. In carabids mean survival times of such local populations were estimated to be some decades, but not to exceed a few centuries. Therefore, for a species to survive, a complete turnover (extinction/(re)founding) of local groups must be maintained by sufficient dispersal. Carabids adapted to extensive, stable habitats usually live there in heterogeneously structured metapopulations. Spreading the risk of extinction over interconnected and differently fluctuating local groups will then result in almost unrestricted survival of the species. The reclamation of such areas breaks up these metapopulations into isolated fragments, which will usually no longer be favoured by this kind of risk spreading. The local populations which remain are confined to small localities and without replacement are

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eventually likely to become extinct. This process also applies to other organisms, such as poorly dispersing bird species which became extinct on Barro Colorado Island following the creation of the Panama Canal.

INTRODUCTION

The biological significance of dispersal (here defined as the undirected movement away from the habitat of origin) has often given rise to misunderstanding. On the one hand, in sessile organisms, plants and many marine and freshwater animals, dispersal coincides with reproduction, diaspores, eggs, or young larvae being passively taken away from the site of origin. As some parent organisms are able to survive reproduction, and to reproduce more than once, dispersal will considerably extend the presence of the species in space. Although some plant species can persist during many generations at a single site the chances of survival of the species will be greatly increased if its area of distribution is not continually restricted to that unique locality. The production of diaspores evidently has survival value. The same value can be seen in the dispersal of the plankton larvae of marine invertebrates.

On the other hand, in terrestrial animals full-grown, though often very young, individuals disperse. This means that, contrary to the situation in sessile organisms, dispersal implies some loss of reproductive potential from the parent population. Some entomologists will, therefore, give priority to the view expressed by Carl Lindroth: 'It can hardly be favourable to an individual insect to fly away from a locality where its life is not threatened, i.e. where feeding, reproduction and hibernation are still possible; the chance of dying before reproduction will generally be much greater in dispersing individuals than in individuals staying in the population, especially when the habitat is rather isolated' (Den Boer (ed.), 1971: 136). Such scientists may thus prefer hypotheses which relate dispersal to 'adverse conditions' in the habitat, such as food shortage or overcrowding.

Unfortunately, the discussion has become confused, because some authors do not discriminate between 'migration' and 'dispersal'. In typical cases of 'migration' the movements are connected with an obligatory change of habitat, and can be considered an alternative to entering diapause (Dingle, 1978). But such a change in conditions is often not predictable, so that 'migration' and 'dispersal' cannot always be separated unambiguously. As a result, sometimes all movements of insects away from the habitat of origin are called 'migration' (e.g. Southwood, 1962, 1977), but in other cases specific movements are excluded as 'adaptive dispersal' (Johnson, 1969). Others consider dispersal to be the principal phenomenon with migration as a

special case (e.g. Andrewartha & Birch, 1954; Udvardy, 1969). The last view has become more fashionable during recent decades (e.g. Rose, 1972; Roff, 1977; Harrison, 1980).

In the following I will try to show that, in spite of the fact that it can be safely assumed that all animals will try to flee from sites where conditions are becoming adverse, in terrestrial arthropods dispersal cannot merely be an 'escape from adverse conditions'.

THE UNIVERSALITY OF DISPERSAL IN TERRESTRIAL ARTHROPODS

The universality of dispersal is demonstrated not only by the existence of airborne 'plankton' (Glick, 1939), including surprisingly high numbers of small spiders (Duffey, 1956; Greenstone, 1982), but also by the observations of Palmén (1944) of hundreds of thousands of winged insects washed ashore in the Gulf of Finland.

At the Wijster Biological Station we compared the 93 carabid species represented in catches from 'window' traps in the course of 16 years (1969 through to 1984) (see Den Boer, 1971; Van Huizen, 1980*a*) with those in the different kinds of habitat in the province of Drenthe (the area around Wijster). We concluded that a few or many individuals of all carabid species with functional hind wings—including wing di(or poly)morphic species—use their wings for flight, and during at least part of the life cycle can thus be caught in window traps (Van Huizen, 1979, 1980*b*). Otherwise all movements of these beetles (except *Cicindela* spp.) within the habitat (to feed, mate, lay eggs or shelter) occur by walking. We can be sure that the same applies to the 111 species of carabids that were washed ashore near Tvärminne (Palmén, 1944), since only full-winged specimens of wing di(poly)morphic carabid species were represented.

Although both airborne arthropods and insects that are washed ashore may be considered to be no more than victims of accidents, this cannot occur without dispersal as the initiatory process. Therefore, dispersal might be as universal among terrestrial arthropods as it is among sessile organisms. This suggestion is confirmed by our window trap catches: just as in plants and sessile marine animals dispersal only occurs during a specified period, in many winged insects it is restricted to (a) short period(s) in the life cycle, the dispersal phase (Johnson, 1969). Outside this period, i.e. during the greater part of the life cycle—especially the reproductive period—when the chances of encountering 'adverse conditions' such as food shortages and overcrowding will be highest, most of these insects are actually unable to fly, because the wing muscles are reduced (Johnson, 1969). As far as carabids are

concerned we found only one common cause of flying during the dispersal phase: weather conditions that favour becoming airborne and being transported by the air, i.e. warm, sunny weather with thermal and light winds (Duffey, 1956; Van Huizen, 1979). This agrees with the observations of Palmén (1944), insofar that only if this kind of weather is interrupted by a thunderstorm will the dispersing insects get into the water and be washed ashore. The response to favourable weather can easily be tested by inducing dispersal artificially by simulating the right conditions (e.g. Van der Eijk, 1983). Not only winged arthropods react in this way to 'fine dispersal conditions'. Richter (1971) showed experimentally that spiders (*Pardosa* spp.) subjected to 'dispersal conditions' demonstrate 'tip-toe' behaviour, after which they excrete a silk thread and become airborne. Comparable phenomena were observed in spider mites (Sabelis & Laane, 1986), in the first-instar larvae of the spruce budworm *Choristoneura fumiferana* (Andrewartha & Birch, 1984), and in other arthropods. Larger wingless arthropods disperse by walking; for carabids see Den Boer (1970), Baars (1979a) and Rijnsdorp (1980).

The unexpectedly rapid colonization of new polders in The Netherlands by winged carabids (Den Boer, 1970; Haeck, 1971; Meijer, 1974) shows that aerial dispersal occurs each year and everywhere. The majority of species capable of flying seem to be involved, since the new colonizers of the Dutch polders were those species expected to occupy these environments (Haeck, 1971). If the biological significance of dispersal increases the chance of founding populations elsewhere one would expect that species with only sparse populations would have to 'invest' proportionally more in dispersal than species with generally dense populations. Den Boer (1971) showed that, as far as wing di(poly)morphic carabids are concerned, this expectation is confirmed: the numbers taking part in dispersal by flight are similar for both sparse and numerous species, so that the former have to 'invest' proportionally more in dispersal than the latter.

In accordance with this 'founding hypothesis of dispersal' (Den Boer, 1971, 1977), Aukema (1986) found that by generally suppressing the development of wings in genetically full-winged individuals of the wing dimorphic ground beetle *Calathus melanocephalus* L. the loss of reproductive potential by dispersal is restricted to periods with favourable conditions for larval development. Nelemans (1987a) discovered a similar 'strategy' in the permanently macropterous carabid *Nebria brevicollis* F., where wing muscles are only developed under favourable conditions. In both species (Aukema, 1987; Nelemans, 1987b), as well as in *Calathus erythroderus* Gemm. & Har. (Aukema, 1987), total egg production was much higher in dispersing females than in non-dispersing ones. Desender (1989) found similar phenomena in the carabid *Pogonus chalceus* Marsh., but in some other insects,

e.g. aphids, the reverse relationship is found (Harrison, 1980). A higher egg production and survival ability, i.e. a greater fitness, were found in dispersing, compared with non-dispersing, individuals of the western tent caterpillar *Malacosoma californicum pluviale* (Wellington *et al.*, 1975) and the snail *Cepaea nemoralis* (Oosterhoff, 1977). See also Udvardy (1969).

With the exception of *Cicindela* and some *Calosoma* and *Bembidion* species, carabids are weak flyers, their flight direction being highly influenced by wind. Because of this most carabids with functional hind wings are favourable objects for anemochorous or anemohydrochorous (Palmén, 1944) transport, which provides a good means for dispersal (Lindroth, 1949). Animals such as most birds, dragonflies, bumblebees, butterflies and, among carabids, *Cicindela* spp., which not only use their wings to disperse but also to collect food and to escape from predators, will less easily be drifted away by wind because they can actively direct their flight. This results in good flyers—especially if they are not ‘migratory’—showing a strong geographical conservatism more often than weak flyers, i.e. the first are more often subdivided into subspecies than the latter (Lindroth, 1957; Table 1), which leads to the paradox ‘*Weak flyers are better dispersers than good flyers*’.

DISPERSAL AND NATURAL SELECTION

Dispersal will be more subjected than migration to natural selection, because dispersers select themselves away from the parent population. Weak flyers will reach suitable sites only by chance and thus suffer a high mortality, so that the number of individuals leaving the parent population will usually be higher than that entering it from elsewhere, especially when the parent population is isolated. Natural selection will thus often favour the individuals which stay behind in the parent population, irrespective of whether or not this increases the chances of survival of the species. When this occurs genes connected with dispersal will only be maintained at the necessary frequencies if the production in newly founded populations is sufficiently high to compensate for the dispersal losses. This balance can shift (Southwood, 1962) (1) in favour of dispersal by flight, if new suitable habitats become available (e.g. in new polders, banks of new reservoirs, in clearings); or (2) in favour of remaining in the population, if suitable habitats become more isolated, and/or more stable.

A considerable decrease in dispersal power will result in a reduction in the frequency of new colonies being founded. This will bring about a further decrease in the production of dispersers when dispersal features are genetically determined, as in weevils and carabid beetles (Jackson, 1928; Lindroth, 1946; Stein, 1973; Aukema, 1986; Desender, 1989). This may bring

a species into a positive feedback situation, and when a point of no return is passed it will end in complete loss of flight ability. We assume that most carabid species of old, stable habitats, such as natural forest and peat moor, lost their wings in this way, and that as a consequence of habitat fragmentation many other carabid species are now in different stages of this positive feedback process (Den Boer *et al.*, 1980; Wilcox & Murphy, 1985).

Because a high 'investment' in dispersal also means an important loss of reproductive potential it will negatively influence the survival time of local groups (Den Boer, 1985; Fig. 4). For species of unstable habitats this need not be a disadvantage. A high turnover of local groups will prevent natural selection from significantly decreasing dispersal power in any of these groups. But as soon as the generally preferred type of habitat becomes more stable natural selection will reduce the powers of dispersal (see also Harrison, 1980), if the species does not disappear altogether (Van Dijk, 1986; Den Boer, 1990).

TURNOVER OF LOCAL (CARABID) POPULATIONS IN A CULTIVATED LANDSCAPE

If the biological significance of the dispersal of terrestrial arthropods is 'maintenance and/or extension of the presence of the species in space', just as reproduction is 'maintenance of the presence of the species in time', a drastic change of the infrastructure of the area, for example cultivation, would lead to a significant reduction of suitable habitat, particularly for species of the 'old landscape'. The cultivation of a natural area can be considered an experiment on the biological significance of the dispersal power of the species associated with it; it is a test of the 'founding hypothesis of dispersal' (Den Boer, 1977). The metapopulations of species with low powers of dispersal, which originally occupied extensive, stable habitats, will become split up into a number of isolated fragments. Small and highly isolated groups will become extinct in due time without possibility of replacement. If the 'cultivation experiment' is sufficiently long-term we may expect that many of the small, local populations will disappear. Most species which under natural conditions live in isolated and generally unstable habitats such as banks of rivers, lakes and pools, clearings in the forest caused by storm, fire, landslide, etc., and which will have high powers of dispersal, will scarcely be affected by the 'cultivation experiment' so long as the number of suitable sites is not drastically reduced.

To support the 'founding hypothesis' one will thus have to compare the (frequency) Distributions of Population Sizes (DPS) of species of stable habitats (with low powers of dispersal), *L-species* (Den Boer, 1987), with

those of species mainly occupying unstable habitats (with high powers of dispersal), *T*-species (Den Boer, 1987). With the help of reliable estimates of population sizes (Baars, 1979b; Den Boer, 1979a) of the 64 more abundant carabid species derived from many different sites and in many years, Den Boer (1977, 1979b) showed that in the case of complete turnover the general form of these distributions is lognormal. Deviations from this general form indicated that many small populations of L-species have disappeared from our cultivated landscapes (Den Boer, 1977, 1979b, 1987, 1990). For more information on L- and T-species see Table 1.

This conclusion, however, was based on the assumption that the survival times of small local populations of L-species are shorter than the number of years since the most dramatic changes in the landscape. Although destruction of the forest started in prehistoric times and increased in the Middle Ages and during the Eighty Years' War, the fragmentation of the last large forests of Drenthe occurred some 200 years ago. The once extensive areas of heath, peat moor and blown sand almost completely disappeared between 1880 and 1950, i.e. between 100 and 40 years ago. Hence, a significant part of the smaller local populations of L-species to have already disappeared from isolated remnants of the 'old landscape' of Drenthe as a

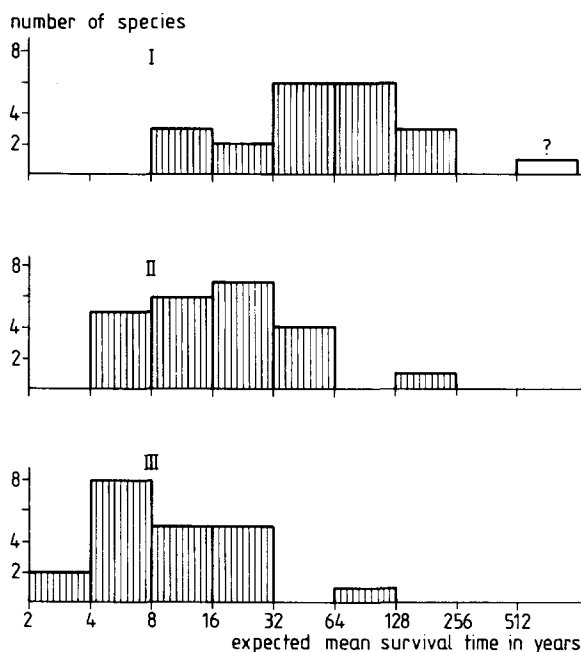


Fig. 1. Frequency distribution of estimates of mean survival time of local (interaction) groups (over \log_2 -classes) for the 64 more abundant carabid species of Drenthe I, 21 L-species; II, 20 intermediate species, whose powers of dispersal are uncertain; III, 23 T-species; see text.

TABLE 1
Some Properties of the 21 L- and 23 T-species, such as Preferred Habitats, Flight Abilities, Expected Mean Survival Time of Local Groups, Number of Positive Year-catches available from Pitfall Sampling (j), Total Number of Specimens Caught in Pitfalls (N)

Species ^a	Preferred habitat	j ^b	N ^a	DPS	Flight ability ^b	In window traps ^c	Survival time in years (mean) ^d
L-species							
<i>Abax parallelepipedus</i> P. & M.	Deciduous forest	56	969	0.6204	Unwinged	0	41- >109 (100)
<i>Bembidion nigricorne</i> Gyll.	Dry heath and sand	64	4457	0.6280	Unwinged	0	8- 11 (9)
<i>Pterostichus oblongopunctatus</i> F.	Forest	145	19511	0.6308	Small wings	4	13- 78? (20)
<i>Calathus erratus</i> Sahlb.	Dry heath and sand	137	15449	0.6457	0.2% winged	0	15- 103? (90)
<i>Cymindis macularis</i> Dej.	Dry heath	46	536	0.6484	Unwinged	0	19- >40 (30)
<i>Calathus melanocephalus</i> L.	Heath, some other open sites	207	35229	0.6491	0.2% winged	0	158- ? (200?)
<i>Pterostichus versicolor</i> Sturm	Heath and pastures	233	33902	0.6504	Small wings	10	25- 164? (114)
<i>Notiophilus rufipes</i> Curt.	Deciduous forest	81	2636	0.6536	Winged (?)	1	19- >123 (100)
<i>Pterostichus lepidus</i> Leske	Dry heath and sand	154	6339	0.6642	Unwinged	0	16- 118? (90)
<i>Notiophilus biguttatus</i> F.	Forest	118	4444	0.6708	79% winged	7	23- 61? (47)
<i>Notiophilus aquaticus</i> L.	Heath, some other open sites	174	11687	0.6727	1.2% winged	0	15- >137 (130)
<i>Amara brunnea</i> Gyll.	Light birch forest	47	2945	0.6841	Winged	2	12- >114 (100)
<i>Leistus rufomarginatus</i> Dfts.	Light deciduous forest	73	1345	0.6854	Winged ??	0	31- 46? (40)
<i>Calathus rotundicollis</i> Dej.	Borders of deciduous forest	85	1679	0.6862	93% winged (?)	1	34- >138 (120)
<i>Pterostichus diligens</i> Sturm	Wet, grassy heath and peat moor	202	7762	0.6889	3.7% winged	11	14- 121? (33)
<i>Amara lunicollis</i> Schiødt	All kinds of grassy vegetation	212	31664	0.6895	Winged	198	14- 147? (140?)
<i>Trichocellus placidus</i> Gyll.	Light deciduous forest	99	2533	0.7011	Winged	88	6- 51? (17)
<i>Dyschirius globosus</i> Hbst.	Heath, some other open sites	157	12166	0.7072	0.1% winged	0	7- 96? (11)
<i>Bradycellus ruficollis</i> Steph.	<i>Calluna</i> -heath	147	4123	0.7102	Winged	94	8- 89? (37)
<i>Amara infima</i> Dfts.	Dry heath and sand	64	1243	0.7111	1.3% winged	0	29- 44? (40)
<i>Brosicus cephalotes</i> L.	Dry heath and sand	58	658	0.7123	(Winged)	0	7- 38? (12)

T-species	149	2122	0.7542	Winged	5	5-88?	(11)
<i>Nebria brevicollis</i> F.	105	1764	0.7550	Winged	1046	4-71?	(10)
<i>Amara aenea</i> de Geer	103	1013	0.7630	23% winged	22	8-50?	(18)
<i>Pterostichus strenuus</i> Panz.	51	412	0.7750	Winged	0	3-8	(4)
<i>Nebria salina</i> Fairm.	74	285	0.7760	Unwinged	0	6-63	(9)
<i>Carabus nitens</i> L.	93	5094	0.7764	2% winged	0	4-106?	(7)
<i>Pterostichus melanarius</i> Illig.	148	2251	0.7772	Winged	22	4-20	(6)
<i>Harpalus rufipes</i> de Geer	63	210	0.7787	5.8% winged	1	5-44?	(30)
<i>Cymindis vaporariorum</i> L.	80	735	0.7787	Winged	32	3-63	(5)
<i>Amara famelica</i> Zimm.	210	1902	0.7814	Winged	12	11-126?	(100?)
<i>Pterostichus nigrita</i> F.	107	526	0.7823	7% winged	1	6-55?	(16)
<i>Notiophilus palustris</i> Dfts.	125	1565	0.7860	Unwinged	0	5-79?	(9)
<i>Carabus arvensis</i> Hbst.	200	1699	0.7866	Winged	127	6-134?	(31)
<i>Loricera pilicornis</i> F.	112	425	0.7872	Unwinged	0	4-67?	(7)
<i>Carabus cancellatus</i> L.	88	324	0.7879	Winged	251	5-60?	(8)
<i>Amara apricaria</i> Payk.	99	374	0.7903	Winged ?	0	2-5	(3)
<i>Leistus terminatus</i> Hell.	96	675	0.7932	Winged	958	4-65?	(16)
<i>Amara familiaris</i> Dfts.	64	864	0.7933	Winged	11	3-37	(5)
<i>Harpalus affinis</i> Schr.	100	338	0.7945	28% winged	3	4-300?	(6)
<i>Agonum fuliginosum</i> Panz.	129	502	0.7960	90% winged	59	7-90?	(21)
<i>Clivina fossor</i> L.	182	1934	0.7968	Winged	4133	8-120?	(30)
<i>Amara plebeja</i> Gyll.	85	276	0.8059	Winged	35	3-17	(5)
<i>Pterostichus vernalis</i> Panz.	116	697	0.8068	Winged	7	3-50?	(6)
<i>Agonum sexpunctatum</i> L.							

^a The species are ranked according to increasing DPS-values (see text), which correlates well with decreasing times of population survival ($r_s = -0.64$, $p = 0.00007$).

^b j and N summed over 1959 to 1981 inclusive, from which DPS was calculated (see Den Boer, 1977, 1987).

^c (?), Wings weak—rarely suitable for flying. ??, Wings both small and weak, probably unsuitable for flying.

^d Numbers of specimens caught in window traps (during the act of flying) in the years 1969 to 1988 inclusive.

^e ?, The upper limit of survival time could not be estimated because the mean correction for unobserved very low densities (mean pseudo-turnover) + its standard deviation > uncorrected turnover (for an explanation, see Den Boer, 1985).

result of the 'cultivation experiment' assumes a mean survival time of about 200 years in the case of forest species, and about 80–100 years for species of heath, peat moor or blown sand areas.

By simulating the fluctuation patterns of numbers of each species separately, and checking these against the field data, fluctuation patterns can be extrapolated to 'extinction' of the populations. Den Boer (1985, 1986b, 1990) was thus able to give reasonable estimates for the mean survival time of local populations of each of the 64 species in the present cultivated landscape of Drenthe (Fig. 1). This shows that the 'cultivation experiment' will have lasted sufficiently long to expect many of the smaller local groups of L-species to have disappeared. Compensation by (re)founding will evidently be insufficient, because walking individuals of these species will only exceptionally cover distances surpassing a few hundred meters through a hostile area, especially when they meet unsurmountable barriers such as roads and canals.

LOCAL POPULATIONS AND METAPOPOPULATIONS

Baars & Van Dijk (1984) estimated that 90% of the individuals of the ground beetle *Pterostichus versicolor* (size 9–12 mm) caught in a standard set of pitfalls were living within 200 m from the pitfalls, i.e. they were moving around in an area of about 12.5 ha. With a mean density of 0.5 individuals/m² such an interaction group (Den Boer, 1977, 1981) would consist of about 60 000 beetles, from which about 400 individuals will be caught during a year in the pitfalls (Baars, 1979b). In *Calathus melanocephalus* (6–9 mm) an interaction group will live in an area of about 2 ha, and with a mean density of 2 individuals/m² it will consist of about 40 000 individuals, from which a year's pitfall catch will be about 150 beetles (Baars, 1979b). In general, the area occupied by a single interaction group will depend on the size of the individuals, so that for small carabids it will only be a fraction of a hectare and for big carabids, such as *Carabus problematicus* with individuals of 18–30 mm, the area will cover some km² (Den Boer, 1970; Rijnsdorp, 1980). This means that the majority of remnants of the 'old landscape' in our area (only a few hectares or even less) will contain a single interaction group of middle-sized (6–12 mm) carabid beetles (68% of our species), and since the distances between such remnants usually exceed a few hundred meters such local groups of walking beetles are effectively isolated. This will be true for nearly all L-species, but may also apply to 11 of the 20 intermediate species (Fig. 1), so that half of the 64 more numerous carabid species of our area are endangered in the isolated and small habitat fragments where they were left by the 'cultivation experiment'. This applies not only to Drenthe: Turin & Den Boer (1988) showed that throughout The Netherlands, and

Desender & Turin (1989) that throughout Western Europe, the numbers of places where species with low dispersal powers and/or other stenotopic species of the old landscape (L-species; Table 1) can be collected are decreasing.

The above species are adapted to large areas where suitable habitats generally were within reach by walking. This means that they were living in *metapopulations*, that is in groups of local populations that are interconnected by dispersing individuals. With the help of simulation experiments, Van der Eijk (1987) showed that an exchange of only a few percent of individuals between local populations suffices to decrease the fluctuations in numbers by spreading the risk of extinction over local groups (Den Boer, 1968; Reddingius & Den Boer, 1970). Moreover, under favourable conditions dispersal of that magnitude will also contribute to sufficient refoundings of local groups, i.e. it will increase the chance of complete turnover, the more so because the need for refoundings is reduced by the same amount of dispersal.

The Dwingelder Veld (1607 ha) is one of the very few remnants of the 'old landscape' of our area still large enough to hold metapopulations of many species, including all kinds of carabid beetles with low dispersal powers (L-species). Therefore, soon after the start of our investigations we concentrated many of our standard sampling series in that area to learn more about the possibilities of survival of a group of subpopulations. Figure 2 shows the fluctuations of numbers in different interaction groups (indicated by capitals) of *P. versicolor* in this heath area. Since most sampling sites (except AG, AT + BH + BJ and CE, CF) are more than a few hundred meters apart, the fluctuations in numbers may be considered independent of each other. As the heath area is nearly everywhere occupied by *P. versicolor*, different interaction groups merge into each other. This means that there will be a considerable exchange of individuals between neighbouring groups, so that the risk of extinction is spread over all groups (Den Boer, 1968). We prefer to use the term '*multipartite population*' rather than 'metapopulation' to describe subpopulations which are not spatially separated but gradually merge into one another, as in the present case, following Andrewartha & Birch (1984). If we consider the 10 interaction groups illustrated in Fig. 2 to be the different units of a multipartite population inhabiting an area of not more than 150–200 ha, the top graph represents the expected fluctuations of total numbers (Den Boer, 1981, 1986a). Simulation and extrapolation of the patterns in Fig. 2 indicate that an average interaction group of *P. versicolor* at Dwingelder Veld might be expected to survive for 100–200 years, whereas the multipartite population will survive for very much longer. Note that isolated interaction groups of this species, e.g. in a remote remnant of heath of about 10 ha, would probably survive less than 100 years, because the

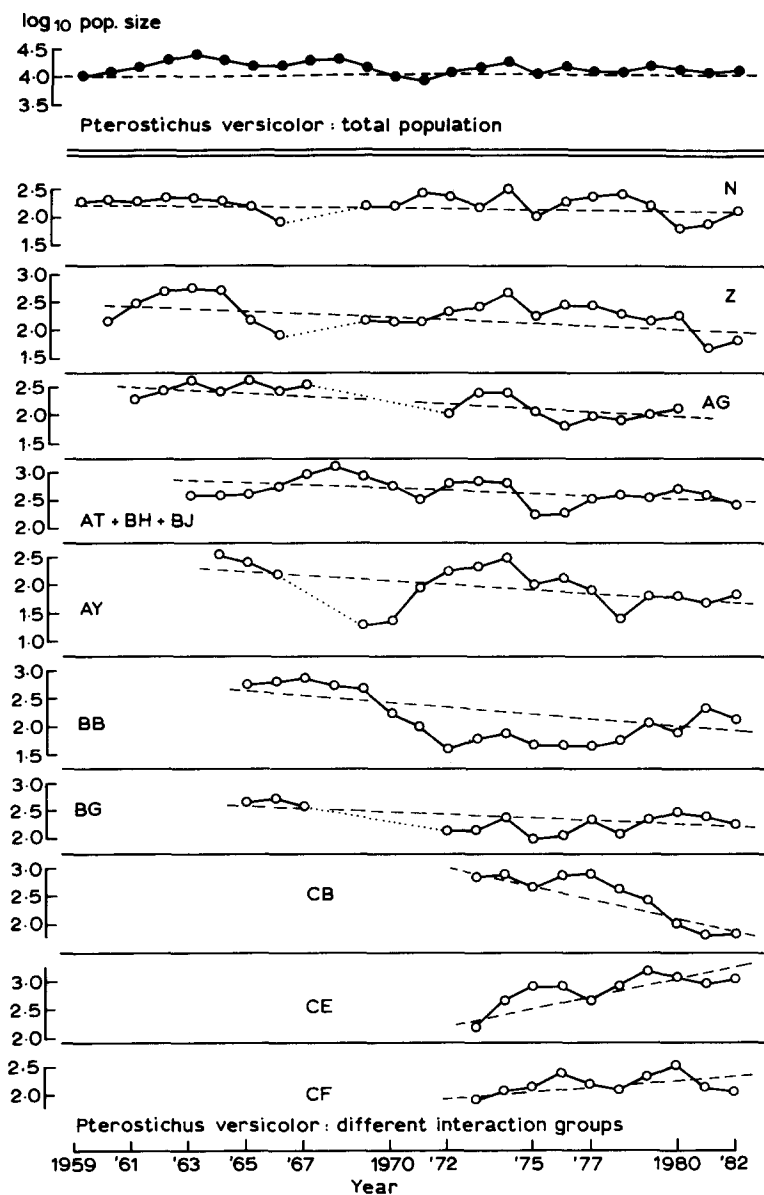


Fig. 2. Fluctuations and trends of mean densities in ten interaction groups (local groups—in about 12.5 ha—around a standard set of pitfalls) of *Pterostichus versicolor* Sturm at Dwingelder Veld (Drenthe), as compared with the fluctuation and trend in numbers in the metapopulation composed of these subpopulations (at the top). The different sample sites are indicated by capitals; the three sites AT, BH and BJ are taken together because they sample the same interaction group (mutual distances about 100 m). Open circles are relative estimates of subpopulation size (Den Boer, 1981, 1985, 1986a), so that the connecting solid lines give the changes of numbers from one year to the next. When the observations were interrupted for one or more years the line is stippled. The broken lines indicate the general trends of numbers during the entire observation period.

fluctuation pattern of numbers would not be buffered by an exchange of individuals with neighbouring groups. It is expected, although not certain because of low catches in most years, that many other species at the Dwingelder Veld are favoured, in a way comparable to *P. versicolor*. But this does not apply to *C. melanocephalus*. See further Den Boer (1981, 1986a).

Effective environmental heterogeneity will be a function of distance, i.e. it will decrease with reduction of the areas available for metapopulations. Under natural conditions many species with low dispersal powers will occupy extensive areas in which effective environmental heterogeneity will always occur. Because of the resulting spreading of the risk of extinction these species can survive in such areas for many thousands of years.

In fact, metapopulations of species with high dispersal powers do not differ fundamentally in the processes described from those of species with low dispersal powers. Suitable sites should be within reach of flying individuals, which means that the distances between them may be large. Dispersal losses will depend on the magnitude of the distances that have to be covered. The dispersal of arable land species as well as that of *Amara plebeja* (Van Huizen, 1977), so far the only migratory species among our carabids (Table 1), will not be affected by distances. T-species occupying more 'natural' sites in our cultivated landscape will be able to maintain sufficient exchange of individuals between local groups for longer than L-species (Table 1). Nevertheless, there are indications that in spite of considerable flight activities, some T-species have already lost many smaller populations without replacement, and thus have acquired the characteristics of L-species, for instance *Amara lunicollis*, and possibly *Trichocellus placidus* and *Bradycellus ruficollis* (Table 1). Other T-species, and especially the majority of the intermediate species, are likely to follow.

CONCLUSIONS

Each year individuals of terrestrial arthropods disperse from localities where their lives are not threatened, and often with only a low chance of survival. If this paradoxical behaviour did not occur the species would not persist very long. In terrestrial animals dispersal appears to be as universal as in sessile marine (and freshwater) animals and in plants, but it is not directly related to reproduction, so that the maintenance of the species in space is disconnected from that in time. This gives natural selection two points of action: (1) increasing the chance of successful colonization by increasing the fitness of dispersing individuals; (2) decreasing dispersal from the parent population when it lives in a fairly stable habitat.

Carabid beetles are especially valuable in these studies because of the

frequent occurrence of wing di(poly)morphic populations, providing the opportunity to study separately the features of dispersers and of non-dispersers (e.g. Lindroth, 1949; Aukema, 1986, 1987). Non-sexual wing di(poly)morphism is widely spread among beetles, e.g. in weevils (Jackson, 1928; Stein, 1968, 1973), staphylinids and chrysomelids, as well as among Hemiptera and Orthoptera (e.g. Brinkhurst, 1959; Vepsäläinen, 1974; Denno & Grissell, 1979; Harrison, 1979, 1980).

Differences in dispersal power *between* species can be found in each group of terrestrial animals. However, in many groups these differences are difficult to quantify. In particular this is a handicap in island biogeography where the turnover of bird populations on islands is a central item of interest (Diamond, 1969). Recently, Karr (1982) progressed significantly in this respect by comparing the bird species that disappeared from Barro Colorado Island (BCI) since 1910–14, when it was separated from nearby forests by the creation of the Panama Canal, with the species that still occur in these forests on the mainland. There appeared to be clear relations with dispersal tendencies: ground-dwelling birds fly only infrequently and will not cross the 500 m of water that separates BCI from the mainland, whereas birds of the canopy group fly frequently, and water of this width is not an obstacle. Many of the former species died out on BCI within 70 years, just as we predict to occur in infrequently flying carabid beetles (L-species) left behind by the 'cultivation experiment' in small 'habitat islands'.

This paper, I hope, has shown that the SLOSS discussion in Wilcox & Murphy (1985) on the design of nature reserves as proposed by Diamond (1975) passes over the essential point: the differences in dispersal power between species. Most participants in this discussion have assumed that individuals of all species can always reach all suitable sites, which is unrealistic, as we show in this paper. Neither is it generally realized that the survival time of a local population depends not so much on the mean number of individuals in the population (as long as the level of 'underpopulation' (Andrewartha & Birch, 1954) is not approached or even passed) but more on the fluctuation pattern of numbers in time. This at least applies to arthropods, because their numbers usually fluctuate more widely than those of vertebrates. Den Boer (1981) showed that, given the quite different fluctuation patterns in numbers of two carabid species, in both species mean population size would have to be increased 100–1000 times merely to double survival time. Hence, in order to increase survival times considerably the fluctuation patterns of numbers have to be levelled. This occurs by interconnecting differently fluctuating interaction groups, because in this situation the risk of extinction becomes effectively spread over them. Therefore, comparing only number of species with size of area, which is the basis of much work on the biogeography of islands, is insufficient; it does not

solve the problems concerned with the most desirable infrastructure design of a cultivated landscape. For that, we must investigate the dynamics of the population units concerned, in order to estimate the most probable survival times. To assess the survival value of different configurations of population units we will have to judge the effectiveness of the interconnections between them. That is, we must know the potential for dispersal of the species concerned.

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