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On the Significance of Dispersal Power for Populations of Carabid-Beetles (Coleoptera, Carabidae)

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Summary. By various observations on carabid populations the author attempts to give an impression of the quantitative occurrence of dispersal and of the relation between dispersal and the chance of founding populations (dispersal power). Pitfall-catches in the recently reclaimed "Zuiderzee"-polder E-Flevoland demonstrate that within seven years individuals of a number of monomorphic macropterous and dimorphic species had founded populations there. From the very high frequency of full-winged individuals within the latter populations it follows that full-winged carabid individuals generally must have a much greater power of dispersal than flightless ones. Therefore, winged individuals of dimorphic species were about equally able to reach E-Flevoland as were those of monomorphic macropterous ones, whereas individuals of monomorphic brachypterous species obviously are seriously hampered. The early appearance of individuals of riparian species on the shores of an artificial lake in the dune area "Meijendel" suggests that particularly populations living in unstable environments extensively "invest" in dispersal. It appears, however, that an important "investment" in dispersal apparently is not restricted to species from unstable environments; at least some sparse populations living in more stable environments also "sacrifice" relatively great numbers of individuals for dispersal (*Pterostichus strenuus*). The hypothesis is proposed, that populations facing a high risk of extinction generally will have a sufficient chance of founding populations (high "turnover") when "investing" extensively in dispersal. Not only macropterous but — at least in some populations — also brachypterous individuals participate in migration, although in the populations studied the dispersal power of flightless individuals is found to be very small (*Carabus problematicus*). Under certain conditions the dispersal of full-winged individuals from wing-dimorphic populations may ultimately lead to a decrease or even a loss of dispersal power by a decrease of the frequency of macropterous individuals. It is assumed, however, that under certain natural conditions also brachypterous individuals may contribute to the spreading of risk within and between populations. The dispersal power of monomorphic macropterous, dimorphic and monomorphic brachypterous populations in a cultivated countryside like Drenthe is discussed. The connection between the dispersal power of different kinds of carabid populations and the resulting chance of survival under different conditions is discussed. Some suggestions for nature preservation management are given.

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1. Introduction

From the unequal distribution of macropterous and brachypterous specimens within the geographic range of a wing-dimorphic carabid species Lindroth (1949, 1953) concludes that long- and short-winged individuals must have different powers of dispersal¹. At the periphery of a species range macropterous individuals — “the parachutists” — will outnumber the brachypterous ones, and this would indicate recent range extensions. On the other hand a preponderance of brachypterous specimens would characterize areas colonized long ago. Mainly directed by this hypothesis Lindroth (1949) was able to reconstruct the late Quarternary colonization history of 25 dimorphic carabid species in Fennoscandia.

The high percentage of brachypterous specimens in obviously old populations might indicate that under these conditions flightless individuals must have some selective advantage. Darlington (1936, 1943) supposed that brachypterous individuals might have an overall “higher viability”. Some preliminary experiments by Lindroth (1949, 1953) do not confirm this supposition. Hence, by lack of information the influence of possible differences between brachypterous and macropterous individuals on the chances to survive and to reproduce must be kept out of the present discussion. On the other hand Lindroth (1949) offers the very reasonable suggestion that for populations, which live in small areas surrounded by uninhabitable land or water, flying itself constitutes selection against macropterous individuals². This may be true more general, because the chances to return to the population will be smaller for individuals flying away than for those only running away. Only in large and overall densely populated areas individuals flying in from somewhere in the area may on the average counterbalance the local losses.

Leaving these things as they are, we may wonder whether it can be demonstrated that under natural conditions the dispersal power of the individuals of a wing-dimorphic population is indeed much greater in the macropterous than in the brachypterous individuals. Or, stated alternatively, is it justifiable to consider the macropterous specimens of a dimorphic species to represent the “dispersal morph” (diaspores)? In a more general sense we may wonder, to what extent the chance of founding a population and that of exchanging individuals between

1 Under dispersal power is understood the ability of a group of individuals to bridge relatively great distances. We are especially interested here in the extent to which dispersal power does increase the chance of founding populations.

2 The available information indicates that the wing-dimorphism in carabids is genetically determined, cf. Lindroth (1946, 1949), Palmén (1944). Compare also: Jackson (1928). In the carabid *Pterostichus anthracinus*, Illig. brachypterous wing is a dominant and the macropterous individuals, consequently, are homozygotes (Lindroth, 1946).

populations depends on the abundance of winged individuals, which refers to both wing-dimorphic and monomorphic macropterous populations. It may seem trivial to state these questions, because it looks evident that winged individuals will disperse better than unwinged ones. It must be noted, however, that observations on flying carabid beetles are scarce and in many species it appears to be difficult or even impossible to force winged individuals to fly (Lindroth, 1945, 1949, 1953). Moreover, Tietze (1963) shows that in many monomorphic macropterous and dimorphic carabid species a greater or smaller portion of the full-winged individuals have reduced flight muscles. It has still to be investigated whether, in these species, reduction of flight muscles occurs during the maturing of eggs as is shown to be the case in *Sitonia* by Jackson (1933) and in *Gerris*-species by Brinkhurst (1959). However this may be, macropterous individuals can be considered potential fliers only, since we can never be sure that a winged individual will ever fly.

On the other hand, we are not interested so much in the phenomenon of flying or running itself but more in its frequency of occurrence and particularly in its population dynamics effects, the latter not only in connection with the populating of new areas (section 2) but more generally in relation to the "turnover" of populations.

A great "investment" in dispersal — which does not necessarily imply a great dispersal power — may profoundly influence the density of the population from which the dispersing individuals are lost and therefore, we are interested in the relation between the chance of survival of populations and the chance to found populations ("turnover" of populations): section 3. The chance of survival of populations will be related a.o. to the degree of stability of the environment and thus, it may be expected that the dispersal power of populations will also be related to it (section 3). In this connection one would expect that the "turnover" of populations living in relatively stable environments (e.g. natural woods) will be rather small and therefore it may be important to gather information on the "investment" in dispersal of such populations. In sections 4 and 5 some relevant information will be discussed. Particularly the observations on the dimorphic species *Pterostichus strenuus* Panz. (section 4) which lives mainly in moist deciduous woods, and on the monomorphic brachypterous species *Carabus problematicus* Hbst. (section 5) which lives in dry woods, are conclusive in this respect.

In section 6 it will be tried to give an impression of the possible future of monomorphic macropterous, dimorphic and monomorphic brachypterous carabid populations in cultivated areas like The Netherlands.

1*

2. Invaders into the Polder E-Flevoland

The relatively high percentage of macropterous specimens at the limits of the range of a dimorphic species, as shown in some of the examples given by Lindroth (1949), is difficult to explain in another way than by a greater power of dispersal in macropterous than in brachypterous individuals. The same may be concluded from the fact that, among insects washed ashore in the Gulf of Finland, dimorphic carabid species are only represented by full-winged specimens (Palmén, 1944). The above hypothesis can be tested by creating a large virgin area within the range of a dimorphic species in order to compare the rate of immigration of macropterous and brachypterous individuals, and to follow the foundation of populations directly. Such an experiment, however impracticable it may seem, became a reality in the Netherlands through the reclamation of land from the former "Zuider Zee". In 1964 a group of "soil-ecologists" planned a sample experiment in different parts of the Netherlands, a.o. in the "Zuider Zee"-polder E-Flevoland (Fig. 1) which ran dry in 1957.

For the duration of one year (March 1964 — March 1965) we sampled weekly with ten formol-funnels surface anthropods from a poplar wood which was planted in 1958 in the then recently dried up sea-bottom. The sample site was situated near Kampen between "Ketelhaven" and "Roggebotsluis" (section N 60 of the polder), some 250 m from the dike which was closed in 1956. The distance to "the old land", across a freshwater lake of 700 m wide and 5 km long, is 1,000 m (Fig. 1: also the latest polders are indicated since investigations are running there).

2.1. Among the carabids caught in 1964 in E-Flevoland (N 60) was a sample of the dimorphic species *Trechus obtusus* Er. (cf. den Boer, 1965). In this case we are certain that the population sampled could not be older than seven years. Table 1 shows that the frequency of full-winged specimens in this sample was much higher than in any other sample available for comparison. The differences with any other sample are highly significant: χ^2 (L) between 56.388 and 201.174; one degree of freedom.

In most cases χ^2 was calculated with the l -test of Spitz (1965), a likelihood-ratio test described by Mood (1950). In some cases the exact probability according to Fisher (Siegel, 1956; de Jonge, 1963) was calculated. When χ^2 was calculated with the l -test the value of χ^2 (one degree of freedom) is generally indicated here by L . Level of significance ($P=0.05$): $L=3.841$ (one-sided) or $L=5.024$ (two-sided), like in χ^2 .

We may conclude from Table 1 that the *Trechus obtusus*-population in E-Flevoland was apparently completely started by macropterous individuals. Like in the case of *Pterostichus anthracinus* Illig: Lindroth (1946), these individuals may have been homozygous full-winged. The gene(s) "short-winged" may be brought in by accident (once?), e.g. by

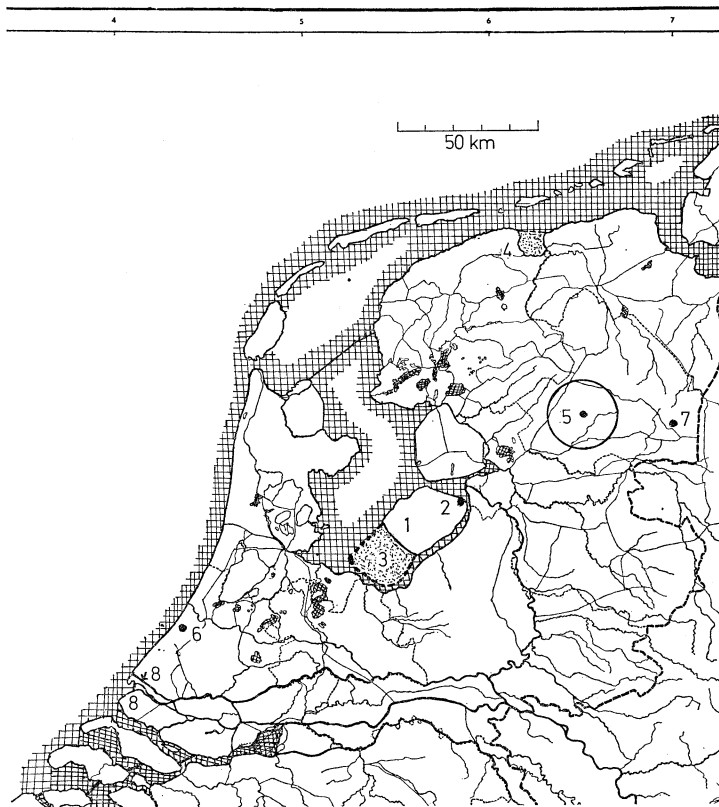


Fig. 1. Geographic situation of the different sample-sites. 1 Polder E-Flevoland; 2 sample site in section N 60 of E-Flevoland (●); 3 polder S-Flevoland; 4 polder "Lauwerszee", (3, 4 running dry in 1968—1969); 5 sample area around the Biological Station, Wijster (●); 6 dune area "Meijendel" (●) near the city of The Hague; 7 town Emmen (●); 8 islands of "Rozenburg" and "Voorne"

a macropterous female which was fertilized previously by a brachypterous male, or by transport of a brachypterous individual by man.

In spite of the rather short distance between the sample site and "the old land" active immigration "on foot" seems not plausible in the case of such a small animal (3—4 mm); presence of a population on the dike seems rather unlikely, since in the Netherlands *Trechus obtusus* is a species of shaded sites.

Therefore, at least in the case of the dimorphic carabid species *Trechus obtusus*, full-winged individuals appear to be of paramount importance for dispersal. On the other hand the frequency of macropterous individuals in relatively old populations obviously is rather low

(Table 1) and hence, in natural populations of *Trechus obtusus* brachypterous individuals appear to be often selectively favoured (compare: 4.4). Also of interest in this respect is the relatively high percentage of macropterous specimens in a sample from an evidently young population near Emmen (from a waste land created by a sand-pit in operation): Table 1.

Table 1. *Frequency of macropterous individuals of Trechus obtusus Er. in different areas*

Area sampled (cf. Fig. 1)	Total number of ind.	Macropterous	
		number	%
Drenthe, various sites, 1959—1966	44	1	2
Drenthe, Biol. Station, Wijster, 1966	85	3	4
Drenthe, Biol. Station, Wijster, 1967	160	4	3
The Hague, Meijendel, 1953	88	12	14
Drenthe, Emmen, waste land, 1960	29	7	24
E-Flevoland, polder, 1964	81	77	95
Netherlands: many sites ^a	282	52	18
W-Germany ^a	44	8	18
Iceland (collected by Lindroth)	120	0	0

^a See for map den Boer (1967, p. 53).

2.2. Five other dimorphic carabid species were sampled in 1964 in E-Flevoland in sufficiently high numbers to be taken into consideration here. The data on the frequency of macropterous and brachypterous specimens in these samples are compared with some data from Drenthe in Fig. 2.

The specimens from Drenthe were obtained with the same technique (pitfalls) as those from E-Flevoland and, where available, material from 1964 was drawn preferably into the comparison.

In spite of the fact that species of open habitats which a.o. live in waste lands (*Pterostichus vulgaris*, *Calathus melanocephalus* and *Dyschirius globosus*) could have settled already on the dike before the polder ran dry (the construction of stretches of dike on the seabottom started in 1950), in all species the percentage of macropterous specimens was much higher (statistically highly significant) in the samples from E-Flevoland than in those from Drenthe with the exception of *Notiophilus biguttatus* F³. If the many samples from Drenthe (in Fig. 2 only

³ The exception of the wood-species *Notiophilus biguttatus* (cf. Fig. 2: in fact the high frequency of full-winged individuals in Drenthe seems exceptional) is difficult of explanation, the more so because the distribution of wing-dimorphic forms of this species in Fennoscandia (Lindroth, 1949, p. 360 and 470) do support the hypothesis of a greater dispersal power of the full-winged individuals.

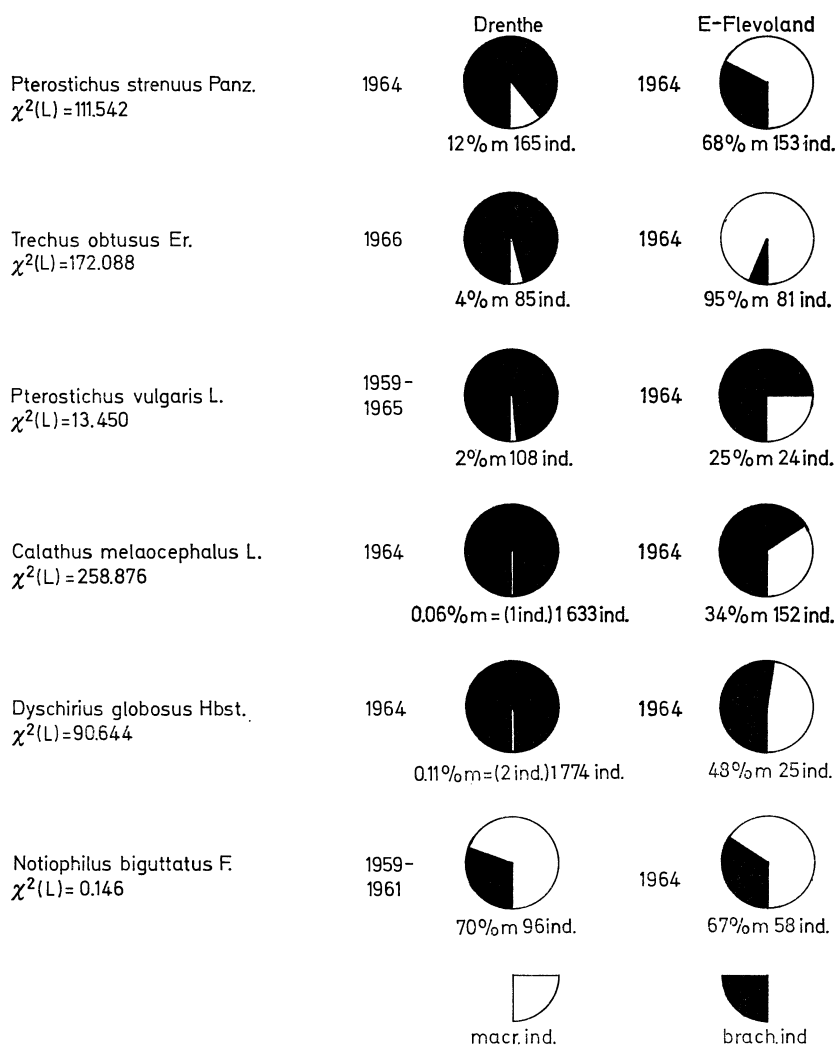


Fig. 2. Frequency of macropterous and brachypterous individuals in old and in newly founded populations (cf. Fig. 1) of some dimorphic carabid species

a few are shown) do not deviate importantly from the situation in “the old land” in general (the few available data do not contradict this assumption), we may conclude from Fig. 2 that in these dimorphic carabid species the full-winged individuals present in a population must have a much greater dispersal power than the flightless ones. This conclusion is also supported by the fact, that our data from Drenthe on the frequency of macropterous and brachypterous individuals in

populations of these dimorphic species agree with those from Fennoscandia as given by Lindroth (1949: p. 382, 396). In Fennoscandia also full-winged specimens of *Pterostichus vulgaris* L. and *Calathus melanocephalus* L. are very rare, while full-winged specimens of *Dyschirius globosus* Hbst. — a very abundant and wide-spread species in Fennoscandia — were even unknown to Lindroth (1945a, p. 439; 1945b, p. 179). For *Trechus obtusus* compare Table 1, and for *Pterostichus strenuus* Panz., cf. Fig. 3.

Hence, in many dimorphic carabid populations full-winged individuals are better able to found populations (greater dispersal power) than flightless ones.

Table 2. Frequency of dimorphic, macropterous and brachypterous carabid species in samples from E-Flevoland, Drenthe and Fennoscandia

Area sampled	Dimorphic species		Monomorphic macropterous species		Monomorphic brachypterous species	
	number	%	number	%	number	%
E-Flevoland, 1964	17	38	27	60	1 (one ind.)	(2)
Drenthe, 1964	34	33	55	53	14	14
Drenthe, 1959—1967	39	26	93	62	17	12
Fennoscandia ^a	50	13.8	263	72.6	49	13.6

^a Lindroth (1949, p. 579).

2.3. The total 1964-sample from E-Flevoland (N 60) consisted of 1,371 individuals of 45 carabid species. In Table 2 the distribution of these species over the categories "dimorphic", "monomorphic brachypterous" and "monomorphic macropterous" is given together with data of samples from Drenthe. It appears that the chances for reaching the sample-site in E-Flevoland within seven years were apparently not smaller in dimorphic species than in monomorphic macropterous ones (difference E-Flevoland and Drenthe, $L: 0.002$). Contrary to this, for monomorphic brachypterous species it seems almost impossible to reach this site within this space of time.

In this connection it is significant in my opinion that the only individual of a monomorphic brachypterous species caught in N 60 is a specimen of *Carabus monilis* F., a species especially known from river-dikes. It is hardly surprising that an individual of such a big carabid (24—28 mm) — which species was surely present in the adjacent "old land" with its many dikes — could reach the sample site (e.g. via founding of a population on the polder dike). Compare also 5.5.

Table 2 permits generalization of the conclusion reached in 2.2: not only in dimorphic populations, but in all carabids the power of dispersal must be much greater in full-winged individuals (as far as flight muscles are not reduced: see introduction) than in flightless ones.

3. Populations Living in Unstable Environments

We may now wonder whether the dispersal of full-winged individuals from carabid populations is just incidental or a frequently occurring, and thus quantitatively important, phenomenon.

3.1. The remarkably rapid expansion of the geographical range of e.g. *Amara majuscula* Chaud. (den Boer, 1962a, p. 92; Lindroth, 1949, p. 622 et seq.) suggests that in some monomorphic macropterous species flying away from the populations must be quantitatively important. The same conclusion can be drawn from the large numbers of winged specimens of some carabid species washed ashore in the Gulf of Finland: Palmén (1944). The surprisingly early appearance of riparian carabids at sites just emerged from the water shows that very large numbers of individuals must fly away from populations existing elsewhere. This is the more remarkable since most carabids — with only a few exceptions as *Cicindela* — are weak flyers, their flight-direction being highly influenced by wind (Lindroth, 1949, p. 579). This sudden appearance of riparian carabids has been noticed many times in Drenthe after the becoming wet again of pools which have been dried up. A particularly interesting case was observed in the dune area “Meijndel” near the city of The Hague (cf. Fig. 1).

After being used as a water reservoir for The Hague since 1874, Meijndel has steadily been drying up. From November 1955 onwards Meijndel has been locally flooded with freshwater to improve the water-supply situation of The Hague.

In May 1956 at least one riparian species was present already on the shores of the first artificial lake: *Bembidion varium* Oliv. In following years additional riparian species settled down (Table 3). With the exception of *Dyschirius arenosus* Steph. none of these species was observed in this dune area for many decades prior, although it was thoroughly searched. We are therefore, fairly sure that no suitable locality was left since the rigorous fall of the groundwater level and that the animals had to come from rather remote areas. In fact, to the best of our knowledge the nearest localities where these riparian species lived were 25—30 km to the Southwest (the islands of “Rozenburg” and “Voorne”: cf. Fig. 1). Hence, we must assume that individuals of these species were transported along the coast in a N.E.-direction by the prevailing S.W.-winds. One may guess how large a number of e.g. *Bembidion varium* must have been spread every spring over many km² of dune area to make it possible that immediately after the creation

Table 3. *Riparian carabid-species collected by hand on the shores of a newly inundated dune-valley (pan 26) in "Meijndel" (The Hague, Netherlands)*

		Number
1955 (November)	Inundation of the dune-valley with freshwater	
1956 (May)	<i>Bembidion varium</i> Oliv.	3
1957 (August)	<i>Bembidion varium</i> Oliv.	3
	<i>Bembidion bipunctatum</i> L.	2
	<i>Bembidion pallidipenne</i> Illig	3
	<i>Elaphrus riparius</i> L.	12
	<i>Dyschirius arenosus</i> Steph.	1
1958 (June)	<i>Bembidion pallidipenne</i> Illig	10
	<i>Elaphrus riparius</i> L.	25
	<i>Dyschirius arenosus</i> Steph.	8
	<i>Agonum marginatum</i> L.	3
	<i>Stenolophus teutonius</i> Schrk.	1

of the first lake a population can be founded along its shores! It must be noted, nevertheless, that the individuals may not have landed at random but (at short distance) may have been attracted by surfaces of water (Lindroth, pers. comm.). However it may be, the innumerable individuals lost each year will profoundly influence the size of the populations they started from.

3.2. It seems to me that, when the risk of extinction is high regardless the size of the populations, these populations may be expected to "sacrifice" a great number of individuals (3.1) to increase the chance of founding populations (otherwise the concerning species would have been exterminated for a long time). The result will be a high "turnover" of populations. Compare also: Wellington (1964). In most populations of riparian species, the risk of extinction is very high indeed: riparian habitats are generally quite unstable and will either be frequently flooded or become overgrown by dense vegetation. To be able to compensate largely for a high risk of extinction a considerable "investment" in dispersal may also be expected in carabid populations living in other unstable environments, such as agricultural fields, waste lands and other habitats whose structure is suddenly destroyed e.g. by burning, ploughing, harvesting, overrunning by sand, felling of trees, etc. Individuals of at least some of these species can be frequently observed flying, e.g. *Anisodactylus binotatus* F., *Amara apricaria* Payk., *Amara familiaris* Dfts.

Hence, in (carabid) populations living in unstable environments dispersal by full-winged individuals is expected to be a frequently occurring and quantitatively important phenomenon, similar to the dispersal by means of diaspores in plants. Obvious "stragglers" of

riparian species are caught in pitfalls occasionally, but the frequency of catches of such migrants is generally not higher than that of migrants of other macropterous or even dimorphic carabid species. This suggests that a high "investment" in dispersal need not be restricted to riparian species or to species from unstable environments in general.

3.3. In 3.1 and 3.2 some evidence was presented suggesting that in many monomorphic macropterous populations living in unstable environments dispersal is quantitatively important and may profoundly influence animal numbers. This does not imply that the same applies to all monomorphic full-winged carabid species and to dimorphic species.

Table 4. *Number of monomorphic macropterous and dimorphic carabid species originated from unstable resp. more stable environments sampled in 1964 in E-Flevoland (N 60) and Drenthe (many sites)*

"Specific habitat" ^a	E-Flevoland (1964)		Drenthe (1964)	
	monomorphic macropterous	dimorphic	monomorphic macropterous	dimorphic
Unstable (cf. 3.2)	15	3	24	7
More stable	12	14	31	27
Total	27	17	55	34

^a Derived from the data (comprising 176,316 individuals of 150 species) obtained by continuous pitfall-catching in 73 sites (sampled for a period of 1—8 years each) covering nearly all kinds of environments available in Drenthe; these data are replenished by a great number of "hand"-catches.

From Table 2 it can be concluded that the chance of reaching the sample-site in E-Flevoland within seven years was about the same for dimorphic as for monomorphic macropterous species (2.3), or in other words, no difference could be established between the dispersal power of populations of dimorphic and of monomorphic macropterous species. Table 4 shows that the relative frequencies of macropterous species originated from unstable (cf. 3.2) and more stable (or only gradually changing) environments, respectively, differ only slightly (not significantly) between the samples from E-Flevoland and from Drenthe (first and third column: $L = 1.032$). This also applies to the dimorphic species (second and fourth column: Fisher, exact $p > 0.537$, one-sided).

There seems, therefore, not to exist an important difference between the dispersal power of monomorphic full-winged populations and that of dimorphic ones, regardless of whether it concerns species from unstable or from more stable environments. Moreover, from 2.2 (Fig. 2) it was obvious that in dimorphic populations the dispersal power is generally much higher in full-winged individuals than in flightless ones

and 2.3 (Table 2) showed that the dispersal power of (some) monomorphic brachypterous species apparently is relatively low (cf. 5.5). We now arrive at the more general conclusion that the dispersal power of carabid populations depends mainly on the availability of full-winged individuals and is apparently not significantly influenced by the fact whether monomorphic macropterous or wing-dimorphic populations are concerned and whether populations from unstable or from more stable environments are involved. This does not mean, however, that in these populations the dispersal power would not show significant differences; important differences may exist, but then these differences are not clearly related to the above characteristics (cf. 4.3).

3.4. Table 4 (rows) shows another feature: in the sample from E-Flevoland as well as in that from Drenthe the frequency of monomorphic macropterous species as compared with that of dimorphic ones is significantly higher for species from unstable than for species from more stable environments (E-Flevoland: $L = 6.594$ and Drenthe: $L = 5.132$). This may mean that the population's chance to become wing-dimorphic is smaller in unstable than in more stable environments. It seems plausible to assume that in carabid species living in unstable environments the expectation of life of populations is much too low to allow some arisen gene (e.g. by mutation) "short-winged" to spread. Moreover, a drastic change of environment will leave the eventual occurring brachypterous specimens with their very small chances to reach another locality suitable for reproduction (cf. 5.5). This means that in unstable environments full-winged individuals will be highly favoured by selection. Compare: Lindroth (1949, p. 361 et seq.). In intensively cultured areas the selective disadvantage of flightless individuals in populations of species of agricultural fields may be less than that in riparian ones because of the relative ease with which individuals of the former populations can reach other suitable localities. This view agrees with the fact that only one strictly riparian species (out of 34:3%) from Drenthe (species from wet woods excluded) is dimorphic: *Carabus clathratus* L. On the other hand, five species from agricultural fields, waste lands, etc. (out of 26:19%) are dimorphic and two species are even monomorphic brachypterous (8%): *Calathus fuscipes* Goeze and *Patrobus atrofusus* Ström. (compare also Table 2).

4. Significance of Dispersal in Some Dimorphic Populations

After the discussions in section 3 we may wonder whether it can be demonstrated more directly that populations living in more stable environments may also extensively "invest" in dispersal. Particularly by studying some dimorphic populations in more detail relevant information may be expected.

4.1. When (part of) the full-winged individuals in dimorphic populations represent the "dispersal morph", it must be possible to find occasionally a single macropterous specimen in a locality where the species does not reproduce. During the nine years of pitfall-catching in Drenthe such obvious "stragglers" (migrants) were indeed caught from time to time, e.g. of: *Calathus melanocephalus* L., *Cymindis vaporariorum* L., *Olisthopus rotundatus* Payk., *Pterostichus diligens* Sturm, *Pterostichus strenuus* Panz., *Notiophilus palustris* Dfts., *Bembidion lampros* Hbst., *Agonum fuliginosum* Panz., *Trechus obtusus* Er. In particular the data on *Pterostichus strenuus* are convincing: Fig. 3. In Drenthe populations of this species are found mainly in moist deciduous woods. Many of them are highly isolated by fields with many ditches which will form unsurmountable barriers to the brachypterous individuals. Successful dispersal from such populations will occur exclusively by flying individuals which is illustrated by Fig. 3 (bottom row), in which all data from continuous sampling (pitfalls) in many different parts of Drenthe are brought together (until 1968).

4.2. Recently (1969) it was found, however, that populations of *Pterostichus strenuus* may also live in Drenthe in moist waste lands with a dense vegetation (e.g. farmyard: 16 macr. out of 34 ind.; neglected orchard: 8 macr. out of 53 ind.). Compare Heydemann (1964). Such generally short-lived populations (3.2: some neglected orchards possibly excepted) may be a source of great numbers of full-winged individuals and this situation may explain the surprisingly high number of full-winged migrants shown in the bottom row of Fig. 3. Moreover, one should not exclude the possibility that a fertilized macropterous female under exceptionally favourable conditions (e.g. a succession of wet years) may even reproduce on the heath and that in this way some brachypterous individuals are introduced indirectly. In this manner the catch of the only brachypterous specimen on the heath [AG (Fig. 4) at 200 m from the nearest deciduous wood] shown in the bottom row of Fig. 3 may be understood.

In all other cases brachypterous individuals of *Pterostichus strenuus* are only caught at a few meters from deciduous woods. These cases are given in Table 5 and because of the very short distances from deciduous woods and the apparent unsuitability of the places these catches can hardly be interpreted as resulting from reproduction outside the woods. Hence, Table 5 shows — in the light of the available information on this species from Drenthe — that the chances for leaving the populations were the same for brachypterous and macropterous individuals. Note, that leaving the wood apparently is not just incidental (Table 5), but will influence the density of the populations from which the migrants start (compare 5.4). Comparing Table 5 with

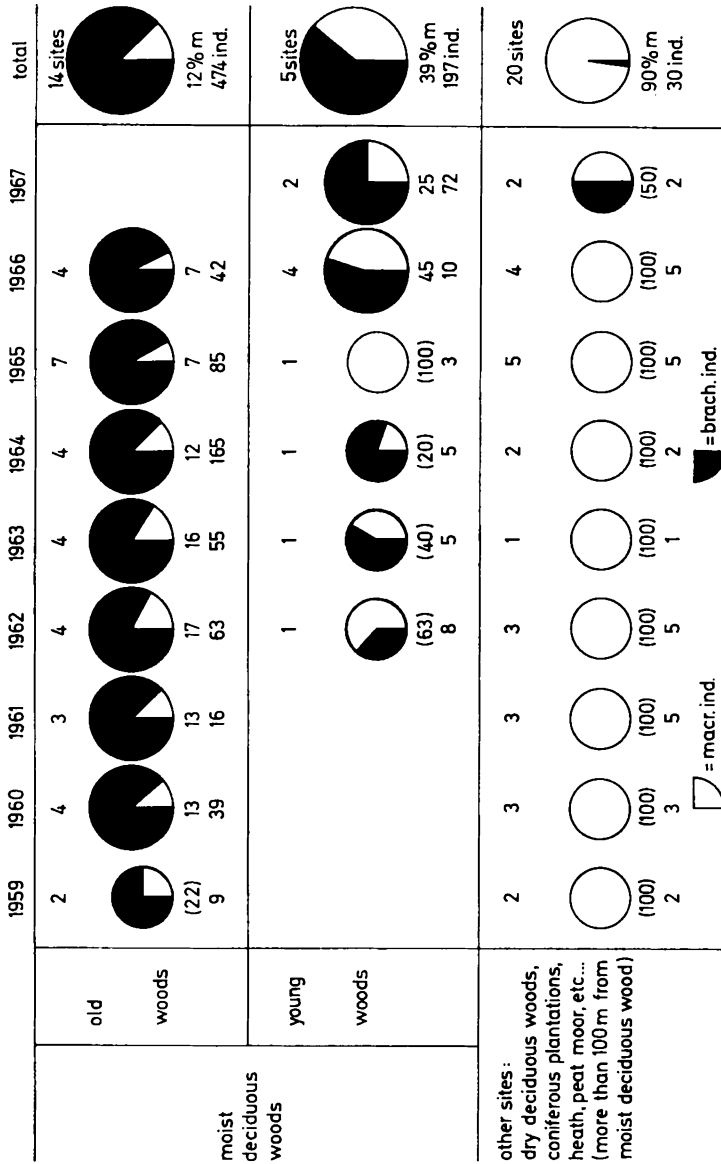


Fig. 3. *Pterostichus strenuus* Panz.: Frequency of macropterous and brachypterous individuals in old and in young woods and in sites where the species does not reproduce; between brackets: unreliable frequencies (very small samples)

Fig. 3 (bottom row) it is obvious that brachypterous individuals leaving the population will have only a very small chance to cover a distance of more than hundred meters (cf. 5.5).

Table 5. Frequency of brachypterous and macropterous individuals of *Pterostichus strenuus* Panz. caught inside and outside some small deciduous woods (without in-between barriers) on the grounds of the Biological Station, Wijster

Within dec. wood		Distance between	Outside dec. wood		Significance of difference
number of brach. ind.	number of macr. ind.		number of brach. ind.	number of macr. ind.	
1966: deciduous wood		20 m	1966: coniferous wood		Fisher, exact
22	17		4	2	$P = 0.5385$ (one-sided)
1966: dec. wood (BO)		20 m	1966: open site (BN)		$L = 0.230$
31	28		8	6	$P \rightarrow 1.00$
1967: dec. wood (BO)		20 m	1967: open site (BN)		$L = 0.198$
49	18		15	7	$P \rightarrow 1.00$
1966: nearest dec. wood not sampled		40 m	1966: veg. of <i>Molinia</i> (BM)		
			2	2	

(In the series that are compared the number and line-up of pitfalls was exactly the same.)

4.3. The example of *Pterostichus strenuus* (Fig. 3) nicely illustrates the conclusion reached more indirectly in 3.3: the dispersal power of carabid populations depends mainly on the occurrence of full-winged individuals, regardless of whether monomorphic macropterous or wing-dimorphic populations are concerned and whether populations from unstable or from more stable environments are involved.

In fact, macropterous individuals in this species must truly be considered to represent the "dispersal morph" (diaspores) of the populations.

These data do not indicate that in *Pterostichus strenuus* dispersal by full-winged individuals is more important quantitatively than it may be in other dimorphic species. In the former species conditions for getting unambiguous results (Fig. 3: bottom row) are just very favourable. But apart from the distinctness of the data (Fig. 3) the high number of obvious "stragglers" of *Pterostichus strenuus* caught (4.3% of the total catches of this species: Fig. 3) is very surprising, since in general populations of *Pterostichus strenuus* are sparse. At best a few dozen specimens are caught annually at a "specific" site. However, the same remarkable relation between sparse populations and high numbers of full-winged "stragglers" (1–6% of the total catches) is found in the dimorphic species: *Agonum fuliginosum*, *Olisthopus rotundatus*, *Notiophilus*

palustris and probably in *Cymindis vaporariorum*. There is a striking contrast between the above species and species as: *Bembidion lampros*, *Pterostichus diligens*, *Notiophilus biguttatus* and *Calathus piceus* with a comparable or greater frequency of full-winged specimens (den Boer, 1962b) but with more dense populations and from which only a few full-winged "stragglers" (less than 0.3% of the total catches per species) or none at all (*Calathus piceus*, *Bembidion lampros*) are caught. Although these data are not conclusive and more detailed information is lacking at the moment, it is tempting to propose the following hypothesis: not only populations living in an unstable environment but also many sparse populations living in more stable environments will face a high risk of extinction, and these species will only be able to survive when "investing" extensively in dispersal. Table 5 actually suggests that a large part of the population participates in migration and, rather unexpectedly, brachypterous and macropterous individuals to the same extent.

4.4. Fig. 3 illustrates that the frequency of full-winged individuals is much lower (significantly) in populations living in small remnants of natural forest than in young ones to be found in woods not older than a few decades (e.g. on the grounds of the Biological Station): $L = 55.974$ (only for 1966: $L = 22.826$). This confirms the statement by Lindroth (1949) that old populations are characterized by a preponderance of brachypterous individuals (cf. 1); compare also: 2.1 (Table 1) and 2.2 (Fig. 2). The underlying process may result, however, in a dangerous situation: a decrease in the frequency of individuals which are able to fly will mean a decrease in dispersal power. As a consequence the possibility to produce full-winged individuals (in newly founded populations) will also decrease. If no other factors intervene the species may ultimately enter a process of positive feed-back which may end in monomorphic brachypterousness. Obviously *Pterostichus strenuus* has not yet reached this dangerous situation, probably because the supply of macropterous individuals is continually replenished by the short-lived populations in waste land (4.2). However, in dimorphic species as *Calathus melanocephalus*, *Calathus erratus*, *Dyschirius globosus* the frequency of macropterous specimens in Drenthe is already less than one percent (Fig. 2 and den Boer, 1962b). On the other hand these are also the species that are very abundant in many localities and hence, they may, nevertheless, be able to produce an appreciable number of "diaspores" with which to found populations (cf. Fig. 2, 2.2). Species such as *Pterostichus lepidus* Leske, *Agonum ericeti* Panz., *Agonum obscurum* Hbst. *Bembidion nigricornis* Gyll., which are dimorphic in other parts of their range (Lindroth, 1945a, 1949) in Drenthe apparently have reached the monomorphic brachypterous state (den Boer, 1962b).

5. Dispersal in Monomorphic Brachypterous Species

To complete the picture of the dispersal power of carabid populations the available information on the rate of dispersal in monomorphic brachypterous populations must also be drawn into the discussion; populations of most monomorphic brachypterous species are living in relatively stable environments (natural forests; compare: 4.4).

5.1. With the exception of some *Carabus*-individuals, obvious migrants (stragglers) of monomorphic brachypterous species are caught only sporadically (for a period of nine years only the catch of one ind. of *Abax ater* Villers on the heath of Kralo in 1960 was noticed). On the whole, populations of monomorphic brachypterous species — apart from some *Carabus*-species — are highly localized, e.g. of: *Cychrus caraboides* L., *Bembidion unicolor* Chaud., *Trechus secalis* Payk., *Stomis pumicatus* Panz., *Abax ater* Villers. This confirms the conclusion reached in foregoing sections that the dispersal power must be much smaller in flightless individuals than in full-winged ones. In *Carabus*-species this is apparently compensated to a certain extent by the size of the animals

5.2. From the pitfall-catches of the monomorphic brachypterous species *Carabus problematicus* Hbst. (21—28 mm) some quantitative information on dispersal is available. At first, *Carabus problematicus* was thought to represent in Drenthe — just as in Central Europe — a species of relatively dry (coniferous and deciduous) woods (Dahl, 1928). Specimens caught on the heath of Kralo were considered to be migrants from the surrounding woods. This seemed to be confirmed by the significant negative correlation between mean number of adults caught per year at a sample-site and the distance from the site to the nearest woods (Figs. 4 and 5, Table 6). Apparently, the chance of an individual to cover a straight-line distance of 825 m on the heath is such, that only two specimens were caught at sample-site N during eight years. This compares with 41 specimens caught during seven years at sample-site AG at a distance of 100 m from the nearest woods (Fig. 4). When it was found, however, that larvae of all instars also occur on the heath of Kralo, it was realized that in this case matters are more complicated.

5.3. It seems rather improbable that the vulnerable carabid-larvae would be able to cover large distances, in this case to migrate — also in the first instar — from the woods to sample-sites N and Z (Fig. 4). Hence, we must assume that *Carabus problematicus* is capable of reproducing on the heath of Kralo; this is in accordance with data from Fennoscandia where the species is even confined to open heath (Lindroth, 1945a, p. 368). It is also confirmed by Table 6: the correlation between mean numbers of adults and distance to woods is much improved

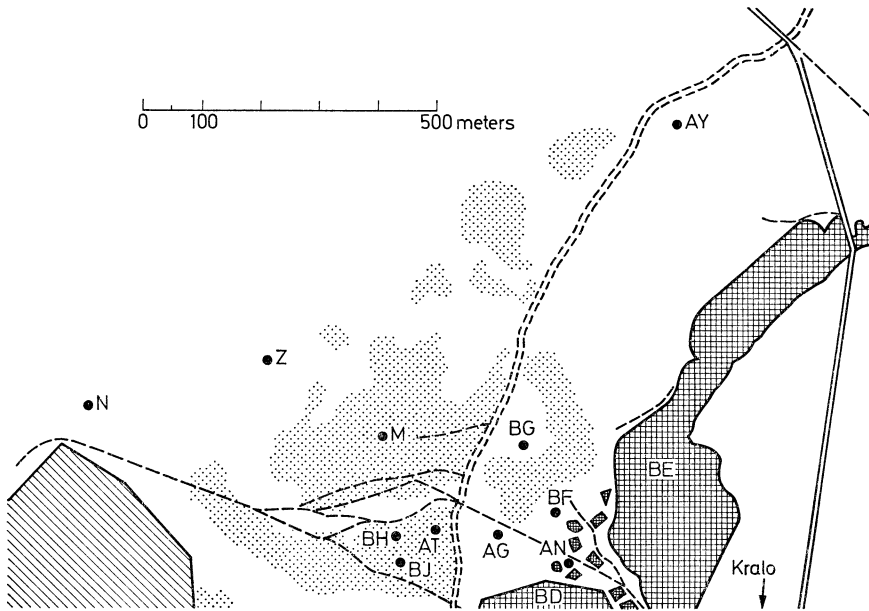


Fig. 4. Sample-sites in the S.E.-part of the heath of Kralo. ● sample-site
 ▨ wood (*Pinus*), ▩ agricultural fields, ▤ dense growth of grasses (especially *Molinia*), - - - sand-roads and tracks. Note: The sample-sites L, BB and AX are situated in the N.E.-part of the heath of Kralo and are not in the picture: they are not isolated by a dense growth of grasses

by separately ranking sample-sites isolated by a dense growth of grasses and the remaining ones (Figs. 4 and 5). This is not the case, however, when treating the larvae in the same way. Obviously, migrating adults are hampered by dense grass, whereas the larvae are only indirectly influenced because they do not migrate, but are born at the site from migrating adults. On the heath of Kralo mortality during the course of larval development through the three instars does not appear to be significantly different from that in dry woods (the “specific habitat” in Drenthe): Table 7. Even the relative number of young larvae that have been born from the adults does not show a significant difference between the heath of Kralo (AG) and dry wood (AE): Table 8, left part. But the number of adults relative to that of the old larvae from which they have been born appears to be about six times greater in dry wood (AE) than on the heath of Kralo (AG): Table 8, right part. The survival of adults from old larvae on the heath must be even substantially smaller than suggested by the data in Table 8, because a large number of the adults in AG will be direct migrants from the woods in the vicinity.

Table 6. Correlations^a of mean number of adults, resp. mean number of larvae, or adults minus larvae (and adults/larvae) of *Carabus problematicus* Hbst. caught per year with distance of sample-sites on the heath of Kralo from the nearest woods

	Adults	Larvae	Adults-larvae	Adults/larvae
All sample-sites in one ranking (n = 14)	$\tau = -0.619$ $P = 0.00252$	$\tau = -0.371$ $P = 0.0688$	$\tau = -0.385$ $P = 0.0628$	$\tau = -0.341$ $P = 0.1010$
Sample-sites 1: Fig. 5 (n = 9)	$\tau = -0.944$ $P = 0.00005$	$\tau = -0.395$ $P = 0.180$	$\tau = -0.723$ $P = 0.0058$	$\tau = -0.610$ $P = 0.024$
Sample-sites 2: Fig. 5 (n = 5)	$\tau = -0.800$ $P = 0.0854$	$\tau = -0.152$ $P = 0.816$	$\tau = -0.400$ $P = 0.484$	$\tau = -0.400$ $P = 0.484$
Average of rankings 1 and 2 ^b	$\bar{\tau} = -0.872$ $P = 0.00036$	$\bar{\tau} = -0.274$ $P = 0.2628$	$\bar{\tau} = -0.562$ $P = 0.0214$	$\bar{\tau} = -0.505$ $P = 0.0884$
Sample-sites 3: Fig. 5 (n = 7)	$\tau = -0.905$ $P = 0.0028$	$\tau = -0.350$ $P = 0.3472$	$\tau = -0.905$ $P = 0.0028$	$\tau = -0.715$ $P = 0.030$
Sample-sites 4: Fig. 5 (n = 7)	$\tau = -0.619$ $P = 0.070$	$\tau = 0.000$ $P \rightarrow 1.00$	$\tau = -0.524$ $P = 0.056$	$\tau = -0.333$ $P = 0.382$
Average of rankings 3 and 4 ^b	$\bar{\tau} = -0.762$ $P = 0.00068$	$\bar{\tau} = -0.175$ $P = 0.4354$	$\bar{\tau} = -0.715$ $P = 0.00148$	$\bar{\tau} = -0.574$ $P = 0.01046$

^a Rank correlations: Kendall (1962).

^b den Boer (1961: 1.7.5).

Table 7. Numbers of first, second and third instar larvae of *Carabus problematicus* Hbst. caught at sample-sites in dry woods and on the heath of Kralo

Year	On the heath of Kralo			In dry woods		
	1st larvae	2nd larvae	3rd larvae	1st larvae	2nd larvae	3rd larvae
1961	3	1	1	4	7	13
1962	2	2	3	7	3	10
1963	5	2	4	8	6	2
1964	8	3	2	5	8	6
1965	4	3	2	7	8	4
1966	5	9	3	9	13	2
Total	27	20	15	40	45	37

L of totals = 2.088 (two degrees of freedom); $P > 0.60$.

Especially at distances less than 250 m from the nearest woods the number of migrating adults caught does significantly influence the total catches of adults: the number of adults minus larvae is the greater the smaller the distance from the woods (Table 6).

2*

Table 8. *Relative survival of Carabus problematicus Hbst. on the heath of Kralo (sample-site AG) and in dry birch-wood (sample-site AE)*

Year	AE		AG		Year	AE		AG	
	catches of adults (summer)	catches of larvae in autumn	catches of adults (summer)	catches of larvae in autumn		catches of larvae in spring	catches of adults (summer)	catches of larvae in spring	catches of adults (summer)
1961	17	8	4	2	1962	8	58	4	6
1962	58	5	6	—	1963	8	61	3	15
1963	61	2	15	4	1964	2	71	6	4
1964	71	6	4	—	1965	1	52	3	5
1965	52	3	5	2	1966	5	75	—	5
1966	75	14	5	—					
Total	334	38	39	8	Total	24	317	16	35

$L = 1.796$ ($P = 0.40$): survival of young larvae from adults about the same in AE and AG.
 $L = 21.260$ ($P < 0.001$): survival of adults from old larvae about six times better in AE than in AG.

5.4. A very rough estimate from the data in 5.3 suggests that at least one third of the total number of adults caught at sample-sites on the heath of Kralo may be considered direct migrants from the woods (i.e. the number of adults that need to be subtracted from the catches to nullify the correlations given in Table 6, first row). To give some idea of the importance of this migration: in 1965 the mean number of adults caught in the woods BD + BE (Fig. 4) amounted to 23.5 and at the two nearest sample-sites on the heath AG + BF (100 resp. 112.5 m from the woods) to 6.0. From Fig. 5 one may even speculate — by extrapolating the regression line — that at distance “zero” 10 ind. (7—15 ind.) would have been caught per year, i.e. 30—60% of the population would leave the woods! Hence, we arrive at the remarkable conclusion that even in populations of some monomorphic brachypterous species the “investment” in dispersal may be substantial (compare: 4.3), although generally such dispersal can hardly be expected to increase the chance to found populations and thus the dispersal power is relatively very small.

The information on the occurrence of *Carabus problematicus* on the heath of Kralo may be summarized as follows: During each summer relatively large numbers of adults leave the woods and “diffuse” into the heath. These adults are capable of reproducing on the heath and the larvae seem to develop normally (Table 7). Apparently during the pupal stage something goes wrong (Table 8), which causes only relatively few adults to be born. This agrees with the fact that in dry woods about 10% of the adults caught is callow (young), whereas among 112 adults caught during nine years on the heath of Kralo not a single callow individual was noticed.

The latter fact conflicts with the alternative hypothesis to “explain” the regression given in Fig. 5: “the reproductive success (number of adults born) of *Carabus problematicus* on the heath of Kralo decreases with increase of the distance from the nearest woods”. Everywhere on the heath the survival of pupae apparently is very low, however (no callow adults).

The very sparse population on the heath is reinforced yearly by migrants from the neighbouring woods; this reinforcement is of such a quantitative importance that a high correlation is kept up between the mean number of adults caught and the distance from the nearest woods (Fig. 5, Table 6). It does not appear very likely that without migration the population of *Carabus problematicus* on the heath of Kralo would be able to survive.

5.5. One may speculate on the mean number of adults that might be expected to be caught per year at distances greater than 950 m (AX) from the woods by extrapolating from the regression-line I given in Fig. 5. These extrapolations can also be expressed as the number of

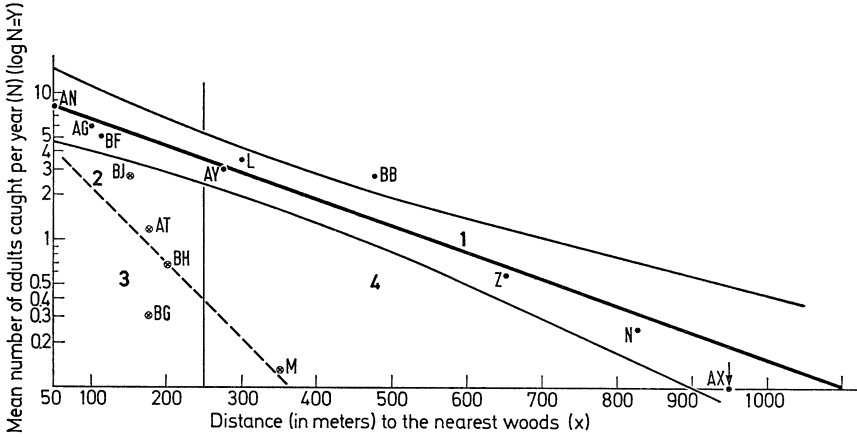


Fig. 5. Mean number of adult individuals of *Carabus problematicus* Hbst. caught per year at sample-sites on the heath of Kralo, which were situated at different distances from the nearest woods; see Fig. 4: the presence of populations of *Carabus problematicus* in these woods has been demonstrated (sample-sites: BD and BE; cf. 5.4). 1 Sample-sites which may be reached without the necessity to overcome barriers (Fig. 4). Regression: $y = -0.0018x + 1$ ($\log 0.1N = 0.0018x$). AX is not included in this regression-analysis as no adults were caught there. 2 Sample-sites situated within or isolated by (BG) a dense growth of grasses (Fig. 4). Regression: $y = -0.00515x + 0.8669$. 3 Sample-sites situated at 250 m or less from the nearest woods. 4 Sample-sites situated at more than 250 m from the nearest woods

years during which catching should be continued to obtain only one individual of *Carabus problematicus*. The results are given in Table 9.

The chance of an individual to be caught during a year in one of our sample-units (three catch-boxes (-funnels) separated by approximately 10 m) unfortunately is unknown for *Carabus problematicus*, but may tentatively be estimated at 0.01 for a surface of 100×100 m or greater.

Apart from the speculative nature of quantitative extrapolations it will at least be obvious from Table 9 that the chance for crossing the heath of Kralo and Dwingelo (4,000 m) must be negligibly small, the more so since it is not very probable that all adults caught on the heath are migrants (cf. 5.3). Under the same hypothesis the probability, that the sparse population on the heath would form a "bridge" by which genes may be exchanged between wood-populations at opposite sides ($2 \times 2,000$ m) will be negligible too. These data illustrate clearly that the dispersal power of monomorphic brachypterous species will be rather small, the more so since *Carabus problematicus* is the biggest carabid in Drenthe and also appears to be a "good runner" and hence, for populations of other monomorphic brachypterous species dispersal power can only be expected to be smaller (cf. 5.1). Dispersal from very large and

Table 9. Values of N — with confidence interval — calculated from $y (= \log N) = -0.0018x + 1$ (cf. Fig. 5) with different values of x

Distance from woods in meters (x)	Mean number of adults to be caught per year (N)	Confidence interval (95%) for N	Number of years acquired to catch one individual ($1/N$)	Confidence interval (95%) for $1/N$
500	1.26	1.06—1.5	0.8	0.7—1
1,000	0.16	0.08—0.3	6	3—13
1,500	0.02	0.005—0.08	50	13—190
2,000	0.003	0.0 ³ 4—0.02	400	60—2,600
4,000	0.0 ⁶ 6	0.0 ⁶ 9—0.0 ⁴ 4	10 ⁶	2×10^4 — 10^8

Note: repeated zeros are indicated by powers, e.g. 0.0⁶6 stands for 0.0000066.

dense populations perhaps may bridge greater distances than *Carabus problematicus* on the heath of Kralo, strictly as a result of the number of participating individuals, but it will never reach a large scale. Therefore, it can be expected that many monomorphic brachypterous carabid-species will show a great geographic isolation and thus variation. This is indeed a well-known fact for many *Carabus*-species, see e.g. Rensch (1943, 1947), Lindroth (1968). Monomorphic brachypterous populations that are more or less synanthropous may show an increased dispersal power (e.g. *Carabus nemoralis* Müll., *Patrobus atrorufus* Ström., *Pristonychus terricola* Hbst.) through passive transport by human activities. A survey of the possibilities of passive transport is given by Lindroth (1957).

6. Discussion

In the present paper the information on dispersal power of carabid populations available to the author has been arranged in such a way that some insight into the significance of dispersal power may be obtained. An attempt will now be made to unify the conclusions and suggestions discussed in the different sections and to arrive at a working hypothesis on the chance of survival of carabid populations in cultivated areas (as found in large parts of the Netherlands).

6.1. In spite of the fact that full-winged carabid individuals can be considered potential fliers only (cf. 1), all our information leads to the inevitable conclusion that the dispersal power is generally much greater in full-winged carabids than in flightless ones. Particularly the observations on *Pterostichus strenuus* can be considered an actual proof of this statement (section 4), whereas the observations on *Carabus problematicus* (section 5) illustrate this in a negative way. The "experiments" of the

reclamation of the polder E-Flevoland and the flooding of the dry dunes in Meijndel (sections 2 and 3) demonstrate the significance of the dispersal power of flying carabids.

To summarize: As long as it is possible and favourable to found populations — i.e. in an environment in which the rate of extinction of populations is relatively high and/or in which new suitable areas are added to old ones — full-winged individuals will highly increase the chance of survival of the species as a whole and may be considered its “dispersal morph”. In addition, macropterous individuals may play a significant role in the exchange of genes between populations.

6.2. One expects that in particular the dispersal power of populations living in unstable environments would be very great (cf. 3.1 and 3.2), because it may be expected to compensate for a high risk of extinction of populations. Table 4 (3.3) shows, however, that this expectation is not supported at the present time and in 4.3 the hypothesis is proposed that also many sparse populations living in more stable environments may face a high risk of extinction and will be expected to compensate by “investing” extensively in dispersal. Rather unexpectedly, it appears that also brachypterous individuals may participate in dispersal to a great extent (cf. 4.2, Table 5), even in monomorphic brachypterous populations (cf. 5.4 and 5.5, Fig. 5). Hence, the “investment” in dispersal need not always be related to the chance of founding populations or to that of exchanging between populations, at least in the open countryside in which these populations were studied.

6.3. The paradox offered in 6.2 may become acceptable if we imagine species as *Pterostichus strenuus* and *Carabus problematicus* living in a vast natural area consisting of more or less suitable localities which merge gradually into one another. Under these conditions dispersing individuals will generally have a fairly good chance to reach another more or less suitable locality. A high “investment” in dispersal will then mean an important spatial spreading of the risk of extinction of the population as a whole: den Boer (1968), Reddingius and den Boer (in press). Even brachypterous individuals may contribute to this spreading of the risk, especially on a small spatial scale. Under such circumstances being a sparse population with a high “investment” in dispersal need not be unfavourable and the chance of survival of the population as a whole may even be better than in the case of a very dense but much more localized population (cf. 4.3). The fact that so many populations are sparse may even be the result of a very high “investment” in dispersal! The condition for survival of this kind of “rare” species seems thus to be the availability of a vast area where suitable sites are within travelling distances for migrating individuals, or are interrupted by “stepping stones” in the form of less suitable sites in which sufficient

reproduction is possible to bridge the distances indirectly. In natural areas the number of species represented by sparse populations (rare species) is relatively high (Williams, 1964), but as a consequence of the above condition for survival this number may be expected to be relatively smaller per unit-area the smaller the total area available (den Boer, 1968). As a result of comparing the numbers of species of many kinds of animals and plants sampled from islands with different areas, several authors have drawn attention to this phenomenon: e.g. Darlington (1943, 1957), Preston (1962). Perhaps the relatively high number of sparse populations of "rare" carabid species on the heath of Kralo and Dwingelo (1,200 ha) as compared to smaller heaths in Drenthe can be explained in this manner.

6.4. Returning to the results of our investigations in Drenthe we can see that — with the exception of species of agricultural fields — the situation is quite different from the "vast natural area" described in 6.3 (for arthropods the heath of Kralo and Dwingelo may approximate such an area): "natural" areas generally are small to very small, few in number, sharply bounded and usually widely separated (especially remnants of natural forest). The chance of survival of many carabid species of natural habitats must be greatly influenced by this artificial situation. Populations of monomorphic brachypterous species will generally be small and highly isolated, since they are unable to bridge even moderate distances (cf. 5.5). Deprived of the opportunity to spread the risk between populations (den Boer, 1968) such populations may be expected to become extinct in the long run, one after another without a chance of founding new ones⁴. Many populations of dimorphic species living in isolated natural localities will nowadays be subject to an increased selection against flying individuals — the loss of individuals flying away no longer being compensated by those flying in —, particularly populations from more stable environments, e.g. the few remnants of natural forest. This increased selection may be the major cause for the low frequency of full-winged individuals in relatively old populations of dimorphic species (cf. 4.4)⁵. Hence, the chances of many dimorphic populations to enter the process of positive feed-back as mentioned in 4.4 may be highly increased in our cultivated countryside. As a result

4 Since the beginning of the 20th century *Carabus coriaceus* L. and *intricatus* L. disappeared from many localities where entomologists used to collect them. In many of these cases the conditions apparently had not changed importantly. Although detailed information is lacking there are indications that the same holds true for many other monomorphic brachypterous species of natural forest.

5 It must be noted that most of the natural forest in Drenthe disappeared already some centuries ago; the number and distribution of the few small remnants did not change importantly for the last century.

of the reduced chances for founding populations in the long run dispersal may fail more and more to compensate for the risk of extinction (cf. 6.3).

This may culminate in contraction and/or breaking up of the geographical range and ultimately in the extinction of the species. Total extinction may be prevented, when in parts of the range spreading of the risk between populations (cf. den Boer, 1968) is still high enough. Although the fate of many monomorphic macropterous species of natural localities may be less definite, reduction and breaking up of the inhabitable area may leave a number of such species with an ultimately insufficient power of dispersal. On the other hand, when the chances for founding populations are greatly increased, as for species of agricultural fields, waste lands, gardens, etc. (cf. 3.4), in the long run dispersal may overcompensate the risk of extinction of populations. The number of populations will increase and therefore the number of dispersing individuals. If there are no other intervening factors this may also lead to a process of positive feed-back, which culminates in a rapid expansion of the geographical range as observed a.o. in *Amara majuscula* and *Amara ingenua* Dfts. (cf. 3.1). Such an extension of range will cease when areas are reached where ultimately other factors are so unfavourable as to compensate to some extent the steady flow of migrating animals (cf. Andrewartha and Birch, 1954). Many agricultural "pests" may have originated as well from such a positive feed-back.

6.5. To conclude, in our cultivated countryside the dispersal power of many carabid species living in "natural" localities may be insufficient and in the long run this may lead to an irrecoverable impoverishment of the carabid fauna. We may be sure that about the same holds true for other groups of animals and for many plants. Nature preservation management should therefore primarily be directed towards the conservation and even creation of large and heterogeneous ("natural") areas, but also to establishing as many "stepping-stones" as possible in our cultivated areas.

In this connection special attention should be paid to hedgerows and roadside verges (cf. Elton, 1958). A dense network of such seminatural strips covering great distances can highly facilitate dispersal of many species from one natural locality to another. At the same time we should not hesitate to establish a positive floral and faunal "falsification" (by introducing highly localized species into new suitable localities) as a counterpart to the negative "falsification" consisting of the reclamation of large natural areas for cultivation. If we want to preserve part of the diversity of nature we shall have to obstruct as far as possible the positive feed-back which may lead from a reduced dispersal power to extinction.

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