ON THE DISPERSAL POWER OF CARABID BEETLES AND ITS POSSIBLE SIGNIFICANCE

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Among other differences it looks like there is one important difference between the dispersal of most species of terrestrial animals and that of most terrestrial plant species. In the latter dispersal generally seems to coincide with reproduction. Without the forming of diaspores the plant would not reproduce (apart from vegetative propagation). Moreover, since plants generally are not able to move, the diaspores should be transported a certain distance to avoid overcrowding (especially in perennials where the individuals generally are forming diaspores repeatedly without making room). Hence, it seems not necessary to ask: Why do diaspores of plants disperse?

In many terrestrial animal species, however, dispersal does not coincide with reproduction: often full-grown individuals are dispersing. This means that each dispersing individual (with its reproductive potential) is lost from the population it started from. Therefore – by analogy – it seems to be obvious to suppose that in many animals dispersal is necessary to correct unfavourably high densities (e.g. densities resulting in shortage of food). This hypothesis which is adopted by many population ecologists seems to be confirmed mainly in a number of territorial vertebrates where dispersal must be considered a kind of 'overflow'.

Up till now, however, I have not succeeded in finding convincing indications that in populations of carabid beetles dispersal would be a kind of 'overflow' from too high densities. On the contrary, I have the impression that the flying away of full-winged individuals from wing-dimorphic carabid populations is quantitatively much more important in species which apparently live here in sparse populations (Table 1: *Agonum fuliginosum*, *Pterostichus strenuus*, *Olisthopus rotundatus*, *Notiophilus palustris* and *Cymindis vaporariorum*) than in species living here in more dense populations with a comparable or greater frequency of full-winged individuals (Table 1: *Calathus piceus*, *Notiophilus biguttatus*, *Bembidion lampros* and *Pterostichus diligens*).

This points to another hypothesis to understand dispersal, viz.: dispersal is necessary to increase the chance of founding (or refounding) populations (and probably to exchange between populations). For, it seems reasonable to suppose that in general sparse populations will have a greater chance to extinct than dense ones and, therefore, especially species represented by sparse populations will have to 'invest' highly in dispersal to reach a sufficient

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TABLE 1. Wing di(poly)morphic carabid species in Drenthe.

Mean number of individuals caught per year and per set of pitfalls (per set/year) (A) as compared with the number of obvious "stragglers' (C) among the full-winged individuals in part of these catches (B).

Species	Catches per set/year 1959–1967 all kinds of habitats		Frequency of full-winged individuals		Full-winged 'stragglers'	
	A mean number of individuals	number of set/year's	number of individuals examined	B % macro-pterous	C number caught	% 'stragglers' among macr. ind.
Agonum fuliginosum Panz.	4.0	71	119	28	7	21
Pterostichus strenuus Panz.	9.7	67	701	23	29	18[1]
Olisthopus rotundatus Payk.	9.6	58	305	21	11	17
Notiophilus palustris Dft.	5.1	49	143	7	2	20
Cymindis vaporariorum L.	3.3	45	87	5.8	1	20
Calathus piceus Mrsh.	22.6	56	235	93	–	–
Notiophilus biguttatus F.	54.3	74	415	79	2?	2.4?
Bembidion lampros Hbst.	14.0[2]	63	385	17	?	?
Pterostichus diligens Strm.	45.7	130	2210	3.7	6	7.4

[1] Compare DEN BOER (1970): 4.2, 4.3 and Fig. 3.
[2] Open agricultural fields where Bembidion lampros is very abundant were not sampled in that period.

'turnover' to be able to survive over large areas (DEN BOER, 1970). But even if the chance of extinction of sparse and of dense populations would be about the same, the 'investment' in dispersal of sparse populations will have to be relatively much greater than of dense ones to reach about the same 'turn-over'. Hence, at least in the case of carabid beetles it makes sense to ask: Why do (individuals of) animals disperse?

In my opinion carabids offer a suitable group of animals to test the 'overflow' hypothesis of dispersal against the alternative 'founding' hypothesis. Firstly, because density will often diverge widely in different species in the same year and within the same population in different years. Secondly, because in wing-di(poly)morphic populations some individuals have the disposal of both mechanisms of moving: running and flying, and others only of the mechanism running; under the 'overflow' hypothesis sensu stricto it may be expected to be immaterial how the surplus animals move away, but under the 'founding' hypothesis flying away generally may be superior to running away. Thirdly, because in carabids – with the exception of *Cicindela* species and of a number of species which have to change habitats during their life-cycle (e.g. riparian species) – flying apparently has no direct function in the life-cycle (think of dimorphic populations!); hence, it makes sense to ask: Why do carabid individuals fly? In the following I shall try to look at some of my observations in the light of these alternative hypotheses. It is not my intention to pose some unique truths or to prove anything; I only hope – by performing a kind of mental exercise – to contribute to a valuable discussion. In connection with our hypotheses we are a.o. interested in the relative frequencies of flying and of running away from a population and in the distances that may be covered.

1. At different places on the heath of Kralo individuals of the monomorphic brachypterous species *Carabus problematicus* HBST. are caught in pitfalls since 1959. These individuals were considered to be direct migrants from the surrounding woods – where the species is known to reproduce – because of the existence of a significant negative correlation between the mean number of adults caught per year at a sample-site and the distance from the site to the nearest woods (Fig. 1). This migration hypothesis is also supported by the fact that at sample-sites which are isolated from the woods by a dense growth of grasses (BJ, AT, BH, BG, M in Fig. 1) relatively too few individuals were caught. It must be noted, however, that matters are more complicated, because also larvae of all instars of *Carabus problematicus* are caught at nearly all sample-sites on the heath.

By comparing the relative numbers of old adults, callow adults, first, second and third instars caught on the heath of Kralo and in wood populations, it could be shown that *Carabus problematicus* produces normal amounts of young larvae on the heath of Kralo and that larval development through the three instars runs normally there, but that in the pupal stage something
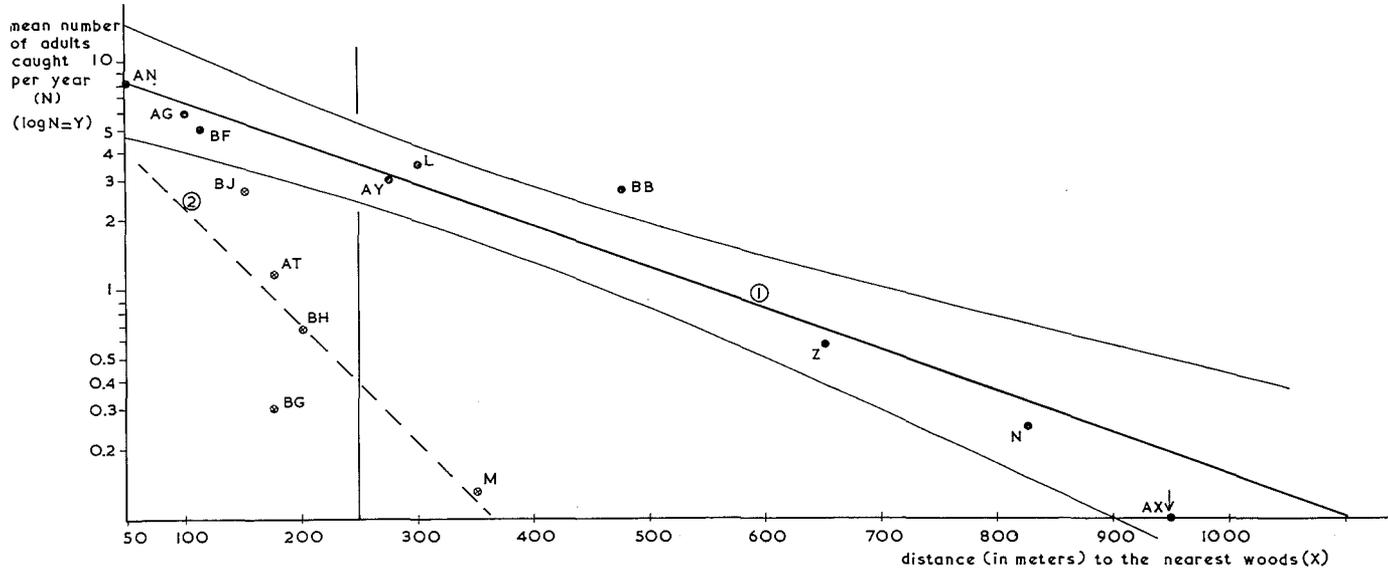
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Fig. 1. Mean number of adult individuals of *Carabus problematicus* caught per year at sample-sites on the heath of Kralo, which were situated at different distances from the nearest woods.
1. Sample-sites which may be reached without the necessity to overcome barriers. Regression: $y = -0.0018\,X + 1$ ($\log 0.1N = 0.0018\,X$); confidence interval figured. 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. Regression: $y = -0.00515\,X + 0.8669$.

is going wrong by which apparently no or only very few young adults are born on the heath (no callow adults). The concerning data are presented and discussed in DEN BOER (1970): section 5. Hence, the very sparse population of young adults on the heath is reinforced yearly by migrants from the neighbouring woods and 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. Therefore, the regression-line in Fig. 1 gives a somewhat too favourable impression of the distances that may be covered on the heath by individuals of *Carabus problematicus* leaving the woods. In spite of this, extrapolation of the regression-line above 1000 m (Fig. 3) learns us that it is very unlikely that an individual of *Carabus problematicus* would be able to cross the heath of Kralo and Dwingeloo (4000 m)[1] and, therefore, the dispersal power of *Carabus problematicus* is very small, in spite of its being the biggest carabid in Drenthe and also a 'good runner'.

Does this mean that the dispersal of *Carabus problematicus* onto the heath must merely be considered an 'overflow' from a too dense population? I don't think so, because the year-samples we draw with our standard-apparatus (pitfalls) in 1965 from the two concerning wood-populations belong to the smallest (mean: 23.5 ind.) we draw from *Carabus problematicus*-populations on the whole, not only in 1965 but also in most other years (35 standard-samples with a mean of 39.3 ind. could be compared). All the more remarkable it is that by extrapolating the regression line to distance 'zero' one gets the impression that about 30–60 % of the population would leave the woods (?). I will return to this point.

2. The data on *Carabus problematicus* suggest that the dispersal power of the concerning populations must be rather small and in other monomorphic brachypterous species can only be expected to be still smaller. We are in a position to test this expectation: during two years all individuals caught in a partly isolated subpopulation of *Calathus erratus* on the 'Hullenzand' were individually marked and released. Part of these marked individuals left the subpopulation and were recaptured in pitfalls in other parts of the 'Hullenzand' (Fig. 2). Since only one out of the 42 'wanderers' (1968 + 1969) was full-winged the recaptures of these 'wanderers' give some impression of the possibilities of running individuals of *Calathus erratus* SAHLB. to cover certain distances (Fig. 3). In Fig. 3 the regression-lines for *Calathus erratus* and *Carabus problematicus* are made comparable and although the data on *Calathus erratus* are only preliminary (more than two years recapturing is required) it will be obvious that the dispersal power of running individuals must be much smaller in *Calathus erratus* than in *Carabus problematicus* (*Calathus erratus*

[1] MOOK draw my attention to the fact that the data of Fig. 1 (1) do suggest a somewhat convex regression line instead of the straight one constructed, i.e. the data would show an only weak leptokurtosis. This may mean that the dispersal power of the concerning populations of *Carabus problematicus* is still smaller than suggested by Fig. 3 (DEN BOER, 1970: Table 9).
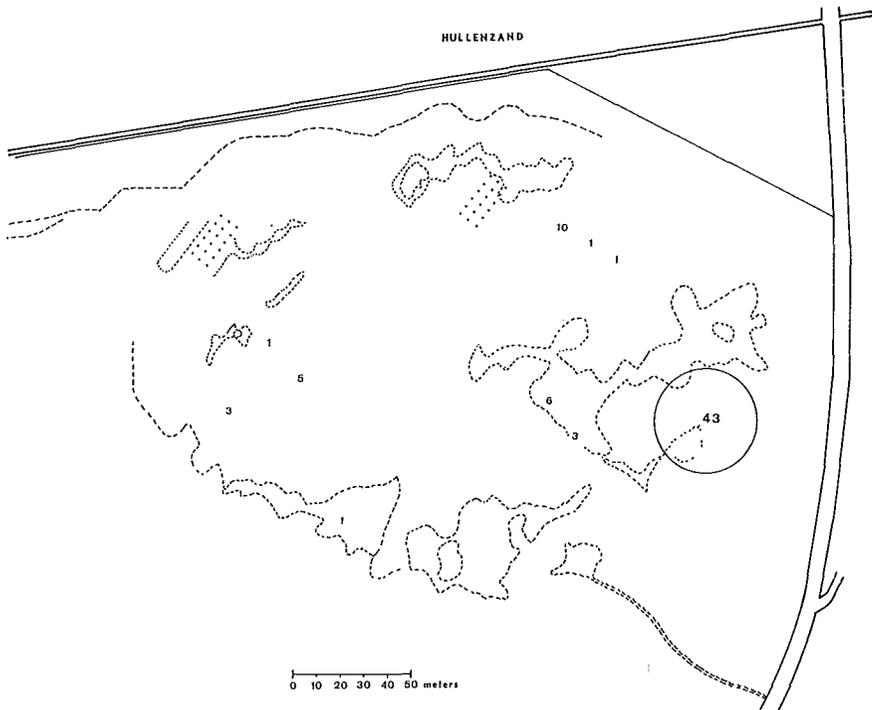
Fig. 2. Numbers of marked individuals of *Calathus erratus* recaptured in pitfalls outside the experimental area (small numerals) in 1968. The numeral within the circle gives the mean number of recaptures (per pitfall) within the experimental area. The experiment was continued in 1969.

measures 8–11 mm and *Carabus problematicus* 21–28 mm). After some years we hope to be able to relate the densities of *Calathus erratus* – calculated from our mark-release experiments – with the concerning numbers of 'wanderers' in the different years and thus to test more directly the 'overflow'-hypothesis of dispersal against the alternative 'founding'-hypothesis.

To conclude: for the moment I have the impression that the running activities of carabid beetles in general will hardly increase the chance to found populations except in the case where the uninhabitable area is interrupted at rather short distances by sites where at least some reproduction is possible. Otherwise the latter situation seems the more natural to me: many natural areas will consist of mosaics of more or less suitable sites and under these conditions even running individuals may have a good chance to reach another site suitable for reproduction (DEN BOER, 1970: section 6).

3. Before turning to the flying activities of carabid beetles we shall have a look at the activities at the borders of some populations of the dimorphic
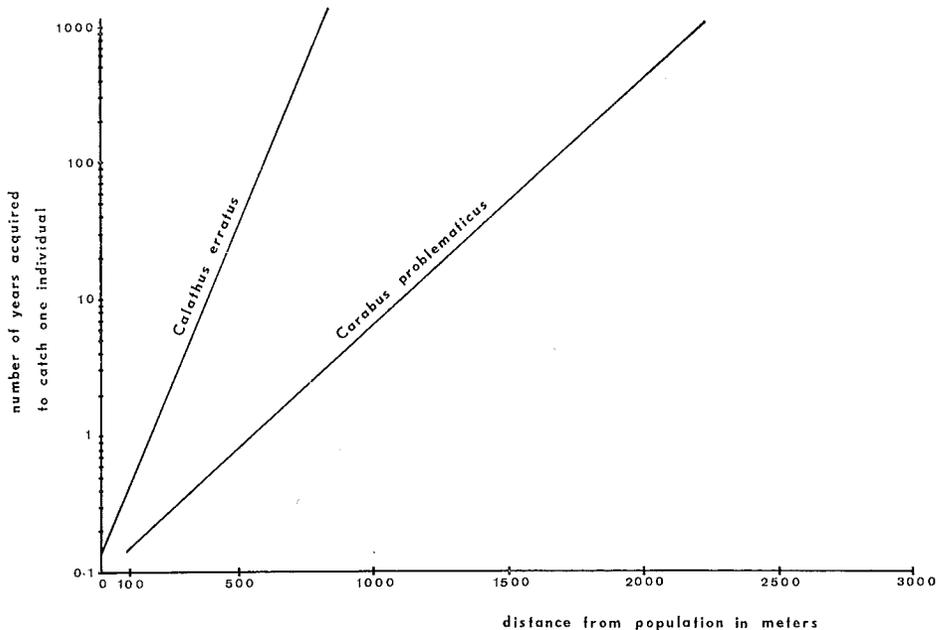
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Fig. 3. Number of years during which catching with one standard-set of pitfalls at a certain distance from the population should be continued to catch one individual. The line for *Carabus problematicus* is the regression-line 1 (with extrapolation) from Fig. 1, but with $1/N$ on the ordinate.

species *Pterostichus strenuus* PANZ. (compare DEN BOER, 1970: section 4). In some experiments pitfalls were placed at short distances from a deciduous wood where a population of *Pterostichus strenuus* was sampled with the same equipment. Table 2 shows that also in *Pterostichus strenuus* individuals may leave the population and apparently brachypterous and macropterous individuals to the same extent. Like in *Carabus problematicus* in these cases leaving the wood apparently is a quantitatively important phenomenon. Again we may wonder whether these data must be considered to support the 'over-flow'-hypothesis, especially because brachypterous and macropterous individuals seem to move away to the same extent. The samples we draw from the concerning wood populations (Table 2) were rather great in comparison with samples from other populations of *Pterostichus strenuus* (39 standard-samples with a mean of 14.8 ind. could be compared), but populations of *Pterostichus strenuus* seem to be anyhow sparse as compared with those of many other carabid species.[1] Hence, it may be that Table 2 illustrates that *Ptero-*

[1] The degree of reliability of such comparisons is investigated now in a number of species. For the moment is preliminary accepted that only great differences in the catches of different species (which show about the same kind of locomotory activities: running over the ground-surface) may be considered to point to differences in density. This is applied in the conclusions from the Tables 1 (column A), 3 and 4.

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TABLE 2. Frequency of brachypterous and macropterous individuals of *Pterostichus strenuus* caught inside and outside some small deciduous woods (without in-between barriers) on the grounds of the Biological Station, Wijster.

Within dec. wood		←⟶	Outside dec. wood		
number of brach. ind.	number of macr. ind.	distance between	number of brach. ind.	number of macr. ind.	significance of difference
1966: deciduous wood		20 meters	1966: coniferous wood		FISHER, exact P = 0.5385 (one-sided)
22	17		4	2	
1966: dec. wood (BO)		20 meters	1966: open site (BN)		$\chi^2 = 0.230$ P → 1.00
31	28		8	6	
1967: dec. wood (BO)		20 meters	1967: open site (BN)		$\chi^2 = 0.198$ P → 1.00
49	18		15	7	
1966: nearest dec. wood not sampled		40 meters	1966: veg. of Molinia (BM)		
			2	2	

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

stichus strenuus must be considered a candidat for the 'overflow'-hypothesis.

4. On the other hand, full-winged individuals of *Pterostichus strenuus* appear to have a good dispersal power (Fig. 4). In this figure the frequencies of macropterous and brachypterous individuals are diagrammed, respectively in samples from old deciduous woods (first row), in samples from young deciduous woods (second row) and in catches from all other sites at distances greater than 100 m (sometimes some km's) from deciduous wood (bottom row). From Fig. 4 we learn that a brachypterous individual of *Pterostichus strenuus* will have only a small chance to cover a distance greater than 100 m (only one out of 30 ind., in this case caught at 200 m from deciduous wood); it also confirms the statement by LINDROTH (1949) that old populations are characterized by a relative preponderance of brachypterous individuals. Moreover, HAECK told us already that the dispersal power of full-winged individuals of this species apparently is such that a population could be founded in O-Flevoland (see DEN BOER, 1970: section 2) and, therefore, *Pterostichus strenuus* seems also to be a candidat for the 'founding'-hypothesis. This is the more likely, because many populations of this species in Drenthe obviously are so sparse that in my opinion their chance of extinction may be relatively high, which implies the 'desirability' of an accordingly high chance of founding (or refounding) populations. If we suppose that the tendency to migrate in this species is not at all linked to the development of the wings, it is no longer surprising that brachypterous and macropterous individuals leave the woods to the same extent (see: postscript). As long as it is possible and favourable to found populations natural selection will not prevent such a waste of individuals. This reasoning does not mean, however, that the 'overflow'-hypothesis must be rejected in this case.
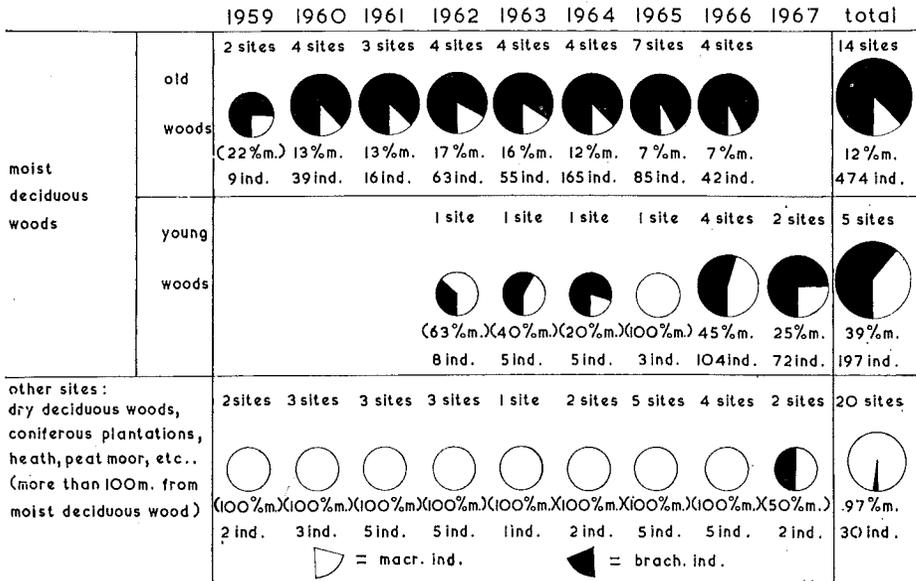
		1959	1960	1961	1962	1963	1964	1965	1966	1967	total
moist deciduous woods	old woods	2 sites	4 sites	3 sites	4 sites	4 sites	4 sites	7 sites	4 sites		14 sites
		(22%m.)	13%m.	13%m.	17%m.	16%m.	12%m.	7%m.	7%m.		12%m.
		9 ind.	39 ind.	16 ind.	63 ind.	55 ind.	165 ind.	85 ind.	42 ind.		474 ind.
	young woods				1 site	1 site	1 site	1 site	4 sites	2 sites	5 sites
					(63%m.)	(40%m.)	(20%m.)	(100%m.)	45%m.	25%m.	39%m.
					8 ind.	5 ind.	5 ind.	3 ind.	104 ind.	72 ind.	197 ind.
other sites: dry deciduous woods, coniferous plantations, heath, peat moor, etc.. (more than 100m. from moist deciduous wood)		2 sites	3 sites	3 sites	3 sites	1 site	2 sites	5 sites	4 sites	2 sites	20 sites
		(100%m.)	(100%m.)	(100%m.)	(100%m.)	(100%m.)	(100%m.)	(100%m.)	(100%m.)	(50%m.)	.97%m.
		2 ind.	3 ind.	5 ind.	5 ind.	1 ind.	2 ind.	5 ind.	5 ind.	2 ind.	30 ind.

= macr. ind.　　= brach. ind.

Fig. 4. *Pterostichus strenuus:* 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).

5. There is another point that deserves our attention. If full-winged carabids fly away to increase the chance of founding populations, one would expect young fertilized females to be the most effective kind of 'diaspore'. As in 1968 HAECK had already shown that window-traps are suitable to sample flying carabids, it was obvious to place some window-traps on the grounds of the Biological Station in order to test this suppostition (Fig. 5). Between the beginning of May and half October in two window-traps 152 carabid individuals were caught belonging to 23 species. By the way it must be noted that this number of individuals suggests that carabids (comparing it with the data of HAECK) are not preferably flying into virgin areas. Among these 152 individuals were 91 females of which 89 were dissected. The results are given in Table 3 (left part): half of the females were young with undeveloped ovaries (but not fertilized) and half of them were 'spent' (partly hibernated old females and partly females that had apparently just finished the depositing of eggs). Only two females carried some normal eggs, but they seemed not to have copulated. Hence, carabid females seem to fly preferably before and after the reproductive season, when they are not the most effective 'diaspores'. Does this mean, that flying carabids must merely be considered an 'overflow' from too high densities? This seems not very probable, in my opinion, because individuals can only react on density by the frequency of interactions between individuals, which can be measured by

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Fig. 5. Window-trap on the grounds of the Biological Station to sample flying carabids.

the numbers of individuals caught in pitfalls (amount of activity, i.e. chance to interact directly or indirectly) and exactly very young females and 'spent' females are many times less active (caught in pitfalls in much smaller numbers) than reproducing females. In fact, in most species very young females and 'spent' females show so little running activity that it can hardly be expected that they will anyhow interact with other individuals in this way. Perhaps this relatively inefficient dispersal is unescapable, e.g. because females with many eggs are too heavy to fly, or because during the reproductive

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season the wing muscles are reduced or the females are in some other way (e.g. physiologically) unable to fly, etc. (see: postscript). On the other hand, it is obvious from the papers read at this symposium that flying carabids sometimes are able to found populations and probably the 'need' to found (or refound) populations is so predominate for the overall survival of the species that natural selection will not counteract this inefficient dispersal in spite of the resulting loss of innumerable individuals in most cases. Because not every year polders are reclamed or islands arise from the sea within the geographical range of most species, in the same time this reasoning would mean that the chance of extinction of many carabid populations would be relatively high. This is certainly the case for species living in unstable environments, e.g. riparian species and species from agricultural fields, since populations of such species will vanish with the disappearance of the suitable habitat. I must recall in this connection that I have the impression that the flying away of full-winged individuals from wing-dimorphic populations is quantitatively much more important in species apparently living here in relatively sparse populations than in species – with a comparable or greater frequency of full-winged individuals – which live here in more dense ones (Table 1). It was supposed that this difference may be related to the relative greater chance of extinction of sparse populations as compard with dense ones. It must be noted, however, that the species mentioned in Table 1 (with the exception of *Bembidion lampros*) are not living (or only exceptionally) in temporary habitats (compare: TISCHLER 1965, for agricultural species).

6. When comparing the left and the right part of Table 3 one gets the impression that the species predominating in the catches in the window-traps are generally not living here in very dense populations. This is clearly illustrated by *Amara lunicollis* (Table 4), a species with fully developed wings, of which flying could be demonstrated (LINDROTH, 1945: 148; 1949: 847) and which is caught in Drenthe in very large numbers (pitfalls) in every grassy locality including the sites where the window-traps were erected; not a single individual of this species was caught in the window-traps in 1969.[1] The contrast with species like e.g. *Bradycellus harpalinus, Amara plebeja, familiaris, bifrons* and *apricaria* (relatively high numbers in the window-traps as compared with pitfall-catches) is so striking (Table 3), that in the life-cycle of the latter species dispersal must play a relatively important role. It may even be supposed that the small numbers of individuals caught in pitfalls result from a very great 'investment' in dispersal by flight. The concept 'population' will be difficult to operate in such species, because they apparently inhabit large areas in the form of a yearly changing mosaic of many relatively sparse local

[1] In the spring of 1970, however, some specimens of *Amara lunicollis* were caught in the window-traps, but this does not alter the contrast with many other species as discussed in the following.

TABLE 3. Sample of flying carabids caught in window-traps on the grounds of the Biological Station (with notes on the development of ovaries) as compared with frequencies in pitfall-catches.

Species (between brackets: % macropterous in di(poly)morphic species)	Number of ind. in window-traps 1969			Ovaries of females			Catches in pitfalls per set/year (1959–'67) all kinds of habitats		Mean number of ind. per set of pitfalls on the grounds of the Biol. Station (1966+1967)
	♂	♀	total	without eggs young	'spent'	with eggs	mean number of ind.	number of set/year's	
Bradycellus harpalinus Serv. (78%)	29	35	64	4	31	–	10.6	83	10
Amara plebeja Gyll.	12	15	27	11	3	1	3.2	112	7
Amara familiaris Dft.	7	8	15	5	2	1	2.5	48	1
Amara bifrons Gyll.	2	8	10	7	1	–	1.8	5	0.3
Amara apricaria Payk.	1	7	8	2	5	–	3.6	49	0.6
Trichocellus placidus Gyll.	2	3	5	2	1	–	36.2	66	11
Amara aenea Deg.	1	2	3	2	–	–	1.5	27	1
Amara communis Panz.	–	2	2	2	–	–	8.8	62	0.3
Pterostichus strenuus Panz. (23%)	2	–	2	–	–	–	9.7	67	1
Bradycellus similis Dej.	1	1	2	–	1	–	31.3	103	10
Trichocellus cognatus Gyll.	–	2	2	1	1	–	24.7	84	3
Acupalpus flavicollis Strm.	–	1	1	not dissected			1	2	–
Agonum dorsale Pont.	1	–	1	–	–	–	1.6	27	0.3
Agonum mülleri Hbst.	1	–	1	–	–	–	1.5	27	–
Amara brunnea Gyll.	–	1	1	1	–	–	69.7	42	13
Amara fulva Deg.	–	1	1	1	–	–	2.8	23	0.3
Amara similata Gyll.	–	1	1	1	–	–	1.2	13	–
Anisodactylus binotatus F.	–	1	1	–	1	–	2.2	22	2
Bembidion lampros Hbst. (17%)	1	–	1	–	–	–	14.0	63	91
Bembidion 4-maculatum L.	–	1	1	not dissected			1.8	5	2
Clivina fossor L. (?)	1	–	1	–	–	–	3.2	65	0.6
Pterostichus minor Gyll. (?)	–	1	1	1	–	–	6.9	40	0.3
Trechus 4-striatus Schrk.	–	1	1	1	–	–	1.3	3	–
total in window-traps	61	91	152	42	47	2	175 set/year's in total (9 years)		3 sets of pittfals

TABLE 4. Full-winged or di(poly)morphic species (frequency of macr. ind. more than 1%) caught in more than one specimen per set/year on the grounds of the Biological Station, of which no specimens were caught in the window-traps (1969).

Species (between brackets: % macropterous in di(poly)morphic species)	Catches in pitfalls per set/year (1959–'67) all kinds of habitats		Mean number of individuals per set of pitfalls and per year on the grounds of the Biological Station (1966+1967)
	mean number of individuals	number of set/year's	
Amara lunicollis Schdte.	143.7	116	117
Pterostichus angustatus Dft.	85.9	13	35
Notiophilus biguttatus F. (79%)	54.3	74	62
Pterostichus diligens Strm. (3.7%)	45.7	130	118
Agonum 6-punctatum L.	4.2	66	35
Pterostichus niger Schall.	15.7	164	16
Nebria brevicollis F.	12.3	74	11
Bembidion ustulatum L. (?)	6.2	20	14
Trechus obtusus Er. (2.8%)	16.6	20	12
Bradycellus collaris Payk. (15%)	11.4	76	7
Leistus rufescens F.	4.2	79	6
Loricera pilicornis F.	7.8	134	4
Notiophilus palustris Dft. (7%)	5.1	49	3
Harpalus pubescens Müll.	5.3[1]	72	3
Pterostichus vernalis Panz. (?)	2.6	56	2
Acupalpus dorsalis F.	4.8	12	1.3
Agonum fuliginosum Panz. (28%)	4.0	71	1.3
Harpalus latus L.	42.9	85	1.3
Leistus rufomarginatus Dft.	22.7	49	1.3
Pterostichus nigrita F.	10.8	166	1.3

(7 species were caught in less than one specimen per set/year) on the grounds of the Biological Station).

Agonum assimile, Pterostichus coerulescens and P. oblongopunctatus are not taken up in this table, since they are not supposed – although generally considered macropterous – to be able to fly.

[1] Open agricultural fields where Harpalus pubescens is very abundant were not sampled in that period.

groups with a high rate of dispersal and exchange. In other words such species would live more or less 'nomadic'.

It will be obvious that this way of life is 'adaptive' in species living in temporary habitats. In Table 5 I have tried to divide the carabid species mentioned in Tables 3 and 4 according to their principal habitat(s) in Drenthe. I must admit that this is a rather subjective procedure, since no species is restricted to only one type of habitat and the variation in the fitting to types of habitat (fluctuation of numbers caught) may be considerable. However, as long as the results of the multi-variate analysis of our pitfall-catches (which is running at Wageningen) are not available, we have to get on with 'experience'. With this restriction in mind we may conclude from

Table 5 that the principal habitat of many species of which individuals were caught in the window-traps is indeed temporary[1]. But in my opinion this is not the whole story and on this point I disagree with SOUTHWOOD & GREENSLADE (1962). Among the species represented in the window-traps also species from heath and deciduous wood are found. In fact, the distribution of the numbers of species over temporary and stable habitats in Table 5 does not differ very strikingly for species of which no specimens were caught as compared with species of which one or more specimens were caught in the window-traps. This means that for the carabid populations on the grounds of the Biological Station the chance of individuals to fly away, on the average seems not to differ very importantly between species principally living in temporary habitats and species principally living in more stable habitats. (This preliminary conclusion is not statistically tested here, because in 1970 the carabids living on the grounds of the Biological Station will be sampled both with window-traps and with pitfalls, by which a more direct comparison becomes possible). After combining this with the apparent preference of individuals from relatively sparse populations to disperse by flight (compare Tables 3 and 4 and see also Table 1) I should like to venture a speculation: I have the impression that many so-called 'rare' species – with the exception of highly localized ones – are living more or less 'nomadic'. This means that this way of life may have survival value also in more stable environments. This survival value may consist of the high degree of spatial spreading of the risk of extinction that is reached in this way (DEN BOER, 1968): the larger the area over which the members of a population[2] are spread, the greater will be the variation in environmental conditions to which the different individuals are exposed and the smaller the chance that all individuals will be exposed to adverse conditions at the same time. Hence, within the population as a whole the effects of too unfavourable and too favourable conditions will be levelled out to an important degree, i.e. animal numbers will be relatively stabilized.

To summarize: apparently dispersal by flight is not only 'adaptive' in species living in temporary habitats, but more generally in species living in temporary (sub)populations.

After this exposition it will be clear that I consider dispersal to be a phenomenon which contributes to the survival of the population[2] and/or the species as a whole more or less independent of other demographic characteristics of the population. In most carabid species the ability to disperse even seems to be the only function of the wings. This does not mean, however, that in some cases – even in carabid beetles – dispersal could not originate

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[1] It must be noted, however, that not for all species agricultural fields and waste lands do represent temporary habitats. Especially some waste lands are rather permanent (farmyards, ruderal roadside verges, neglected orchards etc.).

[2] By population is understood here the 'difficult concept' mentioned above: a yearly changing mosaic of many local groups in a large area.

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TABLE 5. Principal habitat(s) in Drenthe of the carabid species mentioned in Tables 3 and 4 (derived from pitfall-catching in 175 set/year's between 1959 and 1967).

Temporary habitats			Stable habitats	
banks of pools, wet peat moor and other temporarily wet places	agricultural fields and waste lands	other temporary habitats (e.g. fire places, drifting sand)	deciduous woods and permanent gardens, parks, etc.	old heaths and permanent (natural) grassy vegetations
	(Bradycellus harpalinus)			Bradycellus harpalinus
	(Amara plebeja)		Amara plebeja	Amara plebeja
	(Amara communis)			Amara communis
	Amara familiaris	(Amara bifrons)	Trichocellus placidus	Bradycellus similis
	Amara apricaria			Trichocellus cognatus
	Amara aenea			
	(Pterostichus strenuus)		Pterostichus strenuus	
Acupalpus flavicollis[1]	Agonum dorsale	(Amara fulva)	Amara brunnea	Amara fulva
	(Agonum mülleri)			Clivina fossor
	Amara similata[1]			
Anisodactylus binotatus	Anisodactylus binotatus			
Bembidion lampros	Bembidion lampros			
Bembidion 4-maculatum	Bembidion 4-maculatum			
Pterostichus minor	Trechus 4-striatus			
	(Amara lunicollis)	Pterostichus angustatus	Notiophilus biguttatus	Amara lunicollis
Pterostichus diligens				Pterostichus diligens
Agonum 6-punctatum	Agonum 6-punctatum			
Pterostichus niger	Pterostichus niger		Pterostichus niger	Pterostichus niger
	Nebria brevicollis		Nebria brevicollis	
Bembidion ustulatum	Bembidion ustulatum		Trechus obtusus	Bradycellus collaris
	(Leistus rufescens)		Leistus rufescens	Leistus rufescens
(Loricera pilicornis)	(Loricera pilicornis)		Loricera pilicornis	Loricera pilicornis
Pterostichus vernalis	Harpalus pubescens		Notiophilus palustris	Harpalus latus
Acupalpus dorsalis			Agonum fuliginosum	
Pterostichus nigrita			Leistus rufomarginatus	

Between brackets: from our data and/or partly from literature it is not at all obvious that (one of) the principal habitat(s) of this species is temporary.
[1] Not known from the grounds of the Biological Station.

incidentally from an 'overflow' from too high densities. In fact in each separate case we can only guess what really is the significance of dispersal. In this connection there is a great need to study the dynamics of sparse populations and to gather reliable data on the frequency of the extinction and the re-founding of populations. Not only to satisfy our curiosity, but also to learn how to preserve part of the diversity of nature in the long run.
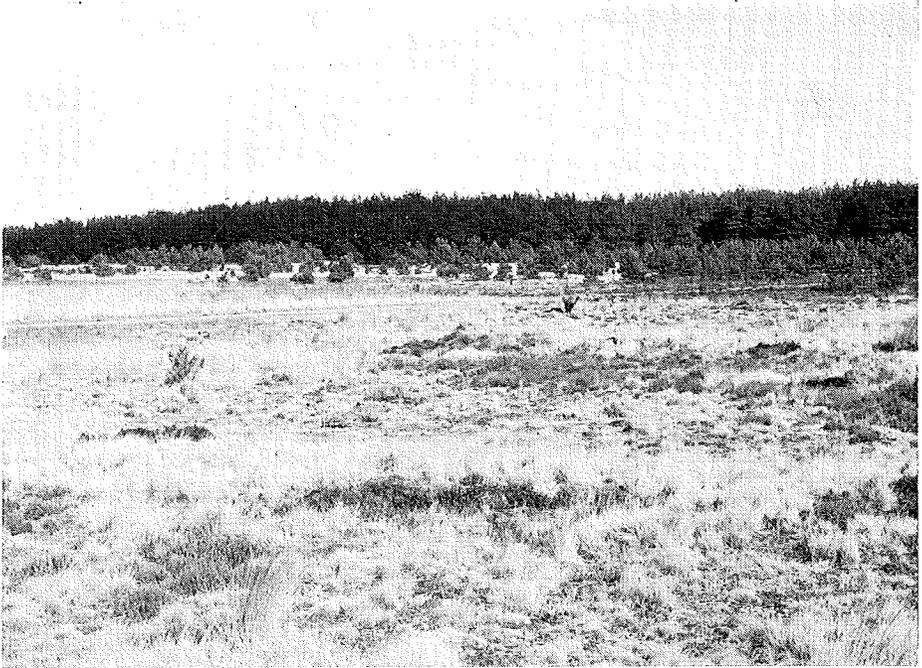

Fig. 6. Heath of Kralo seen from the sample site AG (in the foreground) and in the direction of the woods from which individuals of *Carabus problematicus* are dispersing each year onto the heath.

SUMMARY

Some observations on dispersal in carabids are discussed in the light of two alternative hypotheses: the 'overflow'-hypothesis and the 'founding'-hypothesis. Although the incidental occurrence of dispersal resulting from an 'overflow' of too high densities can not be excluded, most observations seem to favour the 'founding'-hypothesis of dispersal. It is suggested that dispersal by flight may not only occur in populations of species living in temporary habitats, but more generally in species living in temporary (sub)populations (which may also occur in more stable habitats), i.e. dispersal by flight would be quantitatively related with the degree of 'turnover' of populations.

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POSTSCRIPT: After the symposium I had the opportunity to study the new book of JOHNSON, C. G.: Migration & dispersal of insects by flight (METHUEN, London, 1969). In consequence of this it seems useful to add some notes to my paper.

a. In general at the beginning of migration the ovaries are almost always either quite undeveloped or only partly mature (compare Table 3). The females of many species stop migrating when the ovaries become mature. The length of the pre-oviposition period generally controls the duration of migration; in many species this period is extended to cover the period of winter diapause and there may be a hiatus in the development of the ovaries, often with partial development and subsequent resorption of eggs. It is likely that migration is affected, if not controlled by an endocrine balance that involves also the hormones controlling the development of the ovaries. In that case it is not surprising that brachypterous and macropterous individuals may take part in migration to the same extent (compare 4).

b. According to JOHNSON migratory behaviour has evolved particularly in those species whose habitats periodically become adverse for breeding or disappear altogether (compare 6). But he also notes that many newly emerged insects migrate from sites that seem to be still suitable for breeding; moreover the instability of the habitat may take many forms and the responses of populations, even to the same factors, may also vary at different times and places. In his opinion the view that in general a species need to migrate in order to relieve the pressure of population in the habitat (the 'overflow'-hypothesis) must be revised.

DISCUSSION: DEN BOER, LINDROTH, VAN DER AART, VLIJM.

LINDROTH again poses the very important question on the meaning of dispersal. He does not believe that it is correct to look at dispersal as having survival value for the species. He prefers to look at the advantage of dispersal for the individual. Some examples are given:

a. *Cicindela*-individuals use their wings to catch prey.

b. In other species, individuals (and not species) have to leave when

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the habitat becomes unsuitable, e.g. *Oödes* in autumn and many other riparian species. A species can only be riparian if the individuals are able to 'solve' the problem of temporary unsuitability of the habitat.

DEN BOER agrees with LINDROTH: he also prefers to look at the individuals, but he has encountered the contradiction that also individuals of species of which it is not known (and not very probable) that they would show habitat-change are caught in the window-traps. The conclusion that dispersal may not be restricted to species reproducing in temporary habitats is confirmed by other data. It can hardly be favourable to an individual 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. That is why he considered the alternative hypothesis: 'overflow from too high densities', but this did not solve the problem. In his opinion dispersal can only be understood if we suppose that the chance to found or refound populations ultimately is more important than the 'sacrifice' of so many individuals, i.e. that the chance of extinction is not only relatively high in populations living in unstable habitats. But in the latter case it can hardly be expected that individuals are externally stimulated to fly away... hence, there must be an internal impulse (physiological condition?) or even some genetic (phenotypic) determination (?). Although natural selection can only be selection of individuals the result of dispersal may be: survival of the species, i.e. the very few individuals that arrive in another suitable locality may increase the chance of survival of the species as a whole.

VAN DER AART concludes that not the macropterous but the brachypterous form is a problem: he imagines that originally all species will have been constantly macropterous and that brachypterous individuals will have originated from loss-mutations. Such mutations are known to arise in all kinds of characters and in all kinds of organism.

DEN BOER wholly agrees with him and mentions that his explanations are founded on the same premise: if such a loss-mutation increases the chance that its progeny contributes positively to the numbers of the population it will spread through the population. But in the same time the increase of the proportion of brachypterous individuals will decrease the dispersal power of the population (DEN BOER, 1970). As already mentioned in the discussion with LINDROTH (above) natural selection is selection of individuals and hence, selection within the population has another 'direction' than the selective forces to which dispersing macropterous individuals are exposed.

VLIJM arguments that observations on density of activity are not measurements of population-density.

DEN BOER answers that he had hoped that this critisism would not have been expressed at this moment, because the quantitative relation between density and activity is indeed a difficult one (and what is the best population

characteristic?). At the moment a number of models on this relation is tested with the help of the computer at Wageningen, but the results are not yet available. On the other hand there are arguments to assume that the total number of individuals caught during the reproductive season from a carabid population (continuous pitfall trapping) gives a reasonable relative measure of population density. One of these arguments is borrowed from mark-recapture experiments in a population of *Agonum assimile*: by a very fortunate line-up of the pitfalls 40–60 % recaptures could be reached and population density during the reproductive season could be calculated for each week separately within narrow confidence intervals. It appeared that the ratio between the densities (at the climax of the reproductive season) in two successive years was the same as the ratio between the numbers of individuals caught for the first time (in our pitfalls) during the reproductive season in the same successive years. Hence, the one (total of pitfall catches) apparently can be used as a reasonable measure of the other (density), or at least, we may use it as a reliable working hypothesis. Within a few years we hope to be able to prove this working hypothesis.