

**Changes in the Distribution of Carabid Beetles in The Netherlands Since 1880. II. Isolation of Habitats and Long-term Time Trends in the Occurrence of Carabid Species with Different Powers of Dispersal (Coleoptera, Carabidae)\***

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*ABSTRACT*

*The effects of habitat isolation on the occurrences of carabid species over a period of 110 years are studied, as part of a more general treatment of the changes in the fauna of carabid beetles of The Netherlands. According to the founding hypothesis of Den Boer (1977), poorly dispersing species are expected eventually to disappear from small and highly isolated habitat fragments. The time trends in the occurrences of well and of poorly dispersing species since about 1880 are compared by estimating the numbers per decade of occupied 10 × 10 km squares of the distribution maps. These figures are corrected for changes in collecting intensity. Poorly dispersing species generally show decreasing time trends, whereas the occurrences of well dispersing species appear to be more stable, or increasing. A test group of well dispersing species with a high tolerance for agricultural treatments, especially*

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*heavy fertilisation, show distinctly increasing time trends, as expected. The quantitative significance of habitat isolation, in comparison to habitat destruction, as an explanation of the gradual disappearance of species with low powers of dispersal, will be the subject of further studies.*

## INTRODUCTION

In a recent comparison of changes in the composition of the carabid faunas of Denmark, The Netherlands, Belgium and Luxemburg (Turin & Desender, in prep.), it appeared that nearly 35% of the carabid species are decreasing over the whole area of these countries. An unexpectedly high fraction of these species appeared to belong to the characteristic fauna of dry and rather poor habitats, such as heathlands and dry, unproductive grasslands (Nardo-Callunetea). Most of the decreasing species are stenotopic, and possibly intolerant of fertilisation. Hengeveld (1985), who in a multivariate analysis made use of about half of the data we use in our studies (compare 'Materials'), suggests that these recent decreases may be due to climatic changes. Eurytopic species, and especially those which are highly tolerant of fertilisation, appear to have increased, however (present paper). Although climatic changes will undoubtedly have significantly influenced the composition of our carabid fauna (Lindroth, 1972), this does not necessarily support the conclusion of Hengeveld (1985) that human influences seem to have only little effect, because the most radical human influences, such as habitat reduction and destruction, were not taken into account. We will try to fill this gap.

Next to habitat reduction and destruction, the isolation of natural, undisturbed habitat fragments is one of the principal concerns of nature conservation in northwestern Europe. Due to a wide variety of human activities, e.g. urbanisation, intensification of agriculture, and the cultivation of natural areas, our countryside has been drastically changed during the last century. It is generally understood that habitat reduction and destruction significantly impoverish the flora and fauna. But the isolation and fragmentation of the remaining areas seems also to have had important implications for certain species, thus additionally threatening their survival.

According to the founding hypothesis of Den Boer (1977) it may be expected that species with low powers of dispersal have suffered most from both the reduction of habitable area and the isolation of fragments of stable habitat (heathlands, moors and deciduous forests), by many local extinctions without refoundings. Consequently, such species can be expected to show a distinct decrease of occurrence in time. Well dispersing species of non-agricultural sites will also have suffered from reduction of the area of their generally preferred unstable habitats (by lowering of the water table,

canalisation of streams, reclamation of moors, etc.), but they will have been harmed much less by fragmentation and isolation of habitats, because their favoured habitats have always been rather small and more or less isolated. Such species are therefore expected either to have maintained their level of occurrence, or to show a smaller decrease in time than poorly dispersing species. This expectation is tested in the present paper by comparing the long-term trends in the occurrences of carabid species belonging to four groups with distinctly different powers of dispersal.

## MATERIALS

The basic material for our studies consists of data from collections and from literature, brought together for a more general Dutch carabid beetle fauna project (Turin & Peters, 1986). At present almost 85 000 records are available, covering a period of nearly 130 years, although early records (1850–1870) are sparse. From these distribution data a table was extracted, giving per species the presence/absence in each decade since 1870 in each of the  $10 \times 10$  km squares of the UTM grid system, covering the geographical area of The Netherlands (compare Fig. 1(a) and (b)).

Previously, i.e. without taking distribution data into account, four test groups (each consisting of 28 species) with (supposedly) distinctly different powers of dispersal were composed from the carabid species more commonly occurring in The Netherlands, *viz.* in Table 1, Tc-species: well dispersing, and highly tolerant of agricultural treatments, especially fertilisation; in Table 2, Wd-species: well dispersing species of non-agricultural sites; in Table 3, Im-species: non-agricultural species with unclear (intermediate?) powers of dispersal, but without, or with only very few, flight records; in Table 4, Pd-species: poorly dispersing species of non-agricultural sites.

Next, 20 species were taken from each group for further consideration on the following criteria:

(a) None of the species should occur only locally, and each should be represented by at least 75 records in the *Atlas of the Carabid beetles of The Netherlands* (Turin *et al.*, 1977), i.e. all species should have been frequently collected.

(b) As few as possible of the species should be within 500 km from the edge of their geographical ranges.

(c) Except those of the first group (Tc-species), none of the species should be very eurytopic and be favoured by intensive agriculture.

(d) The species of each test group should belong to as many genera as possible within the start group of 28 species.

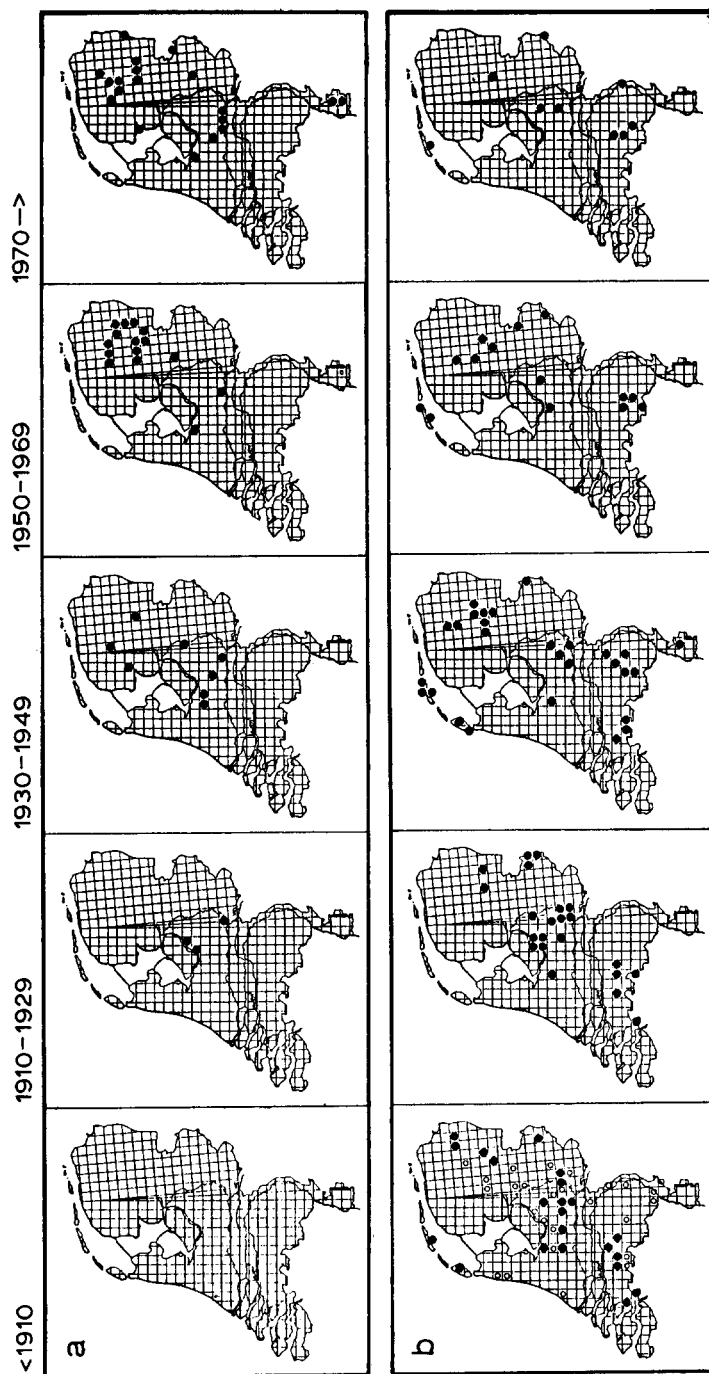


Fig. 1. Time trend of occurrences in The Netherlands (occupied  $10 \times 10$  km squares) of: (a) *Harpalus quadripunctatus* Dej., a constantly winged species (a few flight records are present: Van Huizen, 1980) of hedgerows, borders of deciduous forest, and other places shaded by deciduous trees, such as gardens and parks (the species may have been favoured by the attitude towards hedgerows, which has become much more positive during recent decades); and (b) *Carabus nitens* L., a constantly unwinged species of dry heathland and peat moor; both of these habitats are mainly represented at present by small and highly isolated fragments. The open circles in the first map concern undated records, which will have been made almost exclusively before 1900 (e.g. from lists published in the 19th century).

**TABLE 1**  
Tc-Species

	I	II	III	IV	V	VI	VII	VIII	IX
1. <i>Agonum dorsale</i> (Pont.)	+	m	m	PW	C	a.1	317	16912	558
<i>Agonum muelleri</i> (Herbst)	+	m	m	W	C	a.1	230	748	520
<i>Amara aenea</i> (DeGeer)	+		m	PW	C	a.2	515	4493	856
2. <i>Amara communis</i> (Panzer)	+		m	W	C	a.2	713	14375	519
<i>Amara familiaris</i> (Duft.)	+	m	m	PW	C	a.1	386	3618	684
3. <i>Amara plebeja</i> (Gyll.)	+	m	m	W	C	a.1	473	7638	774
4. <i>Anisodactylus binotatus</i> (F.)	+		m	W	C	a.3	241	6800	749
5. <i>Asaphidion flavipes</i> (L.)	+	m	m	W	C	a.1	146	898	479
6. <i>Bembidion lampros</i> (Herbst)	+	d	d	W	C	a.1	421	7570	811
<i>Bembidion quadrimaculatum</i> (L.)	+?		m	PW	C	a.2	96	1004	456
7. <i>Bembidion tetracolum</i> Say	+	d	d	W	C	a.1	296	19228	906
<i>Brosicus cephalotes</i> (L.)	+?	b	m		C	a.3	163	3531	508
<i>Calathus melanocephalus</i> (L.)*	+?		d		C?	a.1	(893)	(78 596)	(673)
8. <i>Calathus fuscipes</i> (Goeze)	-?	b	d		C	a.1	590	23 647	659
<i>Carabus granulatus</i> L.	-?	b	d		C	a.1	132	1 474	761
9. <i>Carabus nemoralis</i> O. F. Müller	-?	b	b		C	a.3	349	7 619	816
10. <i>Clivina fossor</i> (L.)	+	m	d	W	C	a.3	470	4 305	585
11. <i>Dyschirius globosus</i> (Herbst)	-?	b	d		C	a.2	445	38 822	704
12. <i>Harpalus affinis</i> (Schr.) = <i>aeneus</i>	+	m	m	W	C	a.1	360	4 270	1 275
13. <i>Harpalus rufipes</i> (DeGeer)	+	m	m	PW	C	a.1	549	7 409	625
14. <i>Loricera pilicornis</i> (F.)	+	m	m	PW	C	a.1	696	7 644	798
15. <i>Nebria brevicollis</i> (F.)	+?	m	m	W	C	a.1	681	31 101	890
<i>Pterostichus cupreus</i> (L.)	?	m			C	a.1	184	16 261	431
16. <i>Pterostichus melanarius</i> (Illiger)	?	d-	d		C	a.1	511	48 435	821
17. <i>Pterostichus niger</i> (Schaller)	-?	m	m		C	a.1	654	24 285	576
18. <i>Pterostichus strenuus</i> (Panzer)	+	d	d	W	C	a.1	642	33 144	577
19. <i>Synuchus vivalis</i> (Ill.) = <i>nivalis</i>	-?	d-	d		C	a.1	114	387	216
20. <i>Trechus quadristriatus</i> (Schränk)	+	m	m?	PW	C	a.1	452	9 618	542

Tc-species: This group consists of species which show a high tolerance of heavy fertilisation of cultivated land. These species are most abundant on arable land and intensively exploited meadows throughout a large area of northwestern Europe, and are part of a highly uniform carabid fauna (Basedow *et al.*, 1976; Thiele, 1977). Most of the species can be considered very eurytopic, and are found in many habitats. This group is used as a null group. Since the area of agricultural land increased greatly during the decades incorporated in this study, the species of this group will not have shown a decrease of occurrences, but are expected to have increased significantly. Most of them have high powers of dispersal. \* = This species is not used because the data appear to concern two good species i.e. *Calathus erythroderus* and *C. melanocephalus* (B. Aukema, pers. comm.).

TABLE 2  
Wd-Species

	I	II	III	IV	V	VI	VII	VIII	IX
1. <i>Acupalpus parvulus</i> (Sturm)	+	m	m	PW	C	r	117	1766	380
2. <i>Agonum fuliginosum</i> (Panzer)	+	d—	d	W	5	f	171	698	380
3. <i>Agonum moestum</i> (Duft.)	+	d	m	W	C	f	112	1195	409
4. <i>Agonum sexpunctatum</i> (L.)	+	m—	m	W	C	r	160	1066	480
<i>Amara aulica</i> (Panzer)	+	m	m	PW	C	a—	60	318	262
5. <i>Amara famelica</i> Zimmermann	+	m—	m	W	5	r	170	2156	154
6. <i>Amara fulva</i> (Degeer)	+	m	m	W	C	s	151	792	439
7. <i>Amara lunicollis</i> Schiödte	?		m	W	C	h	571	53685	470
8. <i>Bembidion bruxellense</i> Wesmael	+	m	m	W	5	r	103	4516	487
9. <i>Bembidion varium</i> (Olivier)	+?	m	?	P	C	r	108	12454	532
10. <i>Bradycellus harpalinus</i> (Serville)	+	d	d	PW	C	h	390	3707	482
11. <i>Bradycellus ruficollis</i> (Stephens)	+	m	m	W	C	h	282	7121	204
<i>Chlaenius nigricornis</i> (F.)	?	m	m		C	r	41	461	371
<i>Cicindela campestris</i> L.	+?	m	m	W	C	h	82	181	804
<i>Cicindela maritima</i> Latr. & Dej.	+?		m		C	s	4	5	375
<i>Dromius spilotus</i> (Ill.) = <i>4-notatus</i>	+	m	m	W	C	f	10	15	360
<i>Dromius quadrimaculatus</i> (L.)	+?		m	PW	C	f	28	34	380
12. <i>Dicheirotrichus gustavi</i> Crotch	?		m		C	rh	140	62033	251
<i>Elaphrus riparius</i> (L.)	+	m	m	W	C	r	67	1957	735
13. <i>Harpalus rufipalpis</i> Sturm	+	m	m	W	5	h	112	1064	223
14. <i>Notiophilus biguttatus</i> (F.)	+	d—	d	W	C	f	455	7553	1069
15. <i>Pterostichus diligens</i> (Sturm)	?		d	W	C	rm	428	15975	566
16. <i>Pterostichus minor</i> (Gyll.)	+	d—	d	W	C	rm	123	979	569
17. <i>Pterostichus nigrita</i> (Paykull)	+	m	m	W	C	f	442	8076	827
18. <i>Pogonus chalceus</i> (Marsham)	+?		m		5	rh	98	8615	255
19. <i>Stenolophus mixtus</i> (Herbst)	+	m	m	PW	5	rm	124	35365	463
<i>Stenolophus teutonius</i> (Schrank)	+	m—	m	W	5	rm	2	2	329
20. <i>Trichocellus placidus</i> (Gyll.)	+	m—	m	W	C	f	260	5632	245

Wd-species: Well dispersing species. These species are not especially abundant on agricultural sites and show little tolerance of fertilisation. They inhabit different kinds of habitat, although most of them can be considered stenotopic. The species of this group are not expected to have shown increasing numbers or extension of their occurrences during the last century, at least not as distinctly as the Tc-species. They are expected to have maintained about the same number of occurrences through time or to have decreased slightly.

Criteria (a) and (b) were chosen because it is often assumed that climatic factors should have greater effects near the fringes of the geographical distribution of a species than in the centre (Haeck & Hengeveld, 1981). Most of the species which occur only locally in our country are also fringe species (compare: Den Boer, 1977), and most of these are excluded from the testing in order to minimise the possible influence of climatic changes on the time

TABLE 3  
Im-Species

	I	II	III	IV	V	VI	VII	VIII	IX
1. <i>Agonum marginatum</i> (L.)	?		m	W	C	r	140	1266	478
<i>Agonum viduum</i> (Panzer)	?		m	W	C	r	21	64	333
2. <i>Amara infima</i> (Duft.)	?		d		5	s	103	2850	127
3. <i>Amara spreta</i> Dejean	?		m		C	s	253	9998	673
4. <i>Bradycellus caucasicus</i> Chaudoir	?		d	W	C	h	286	1656	202
5. <i>Calathus ambiguus</i> (Paykull)	?	m	d		C	s	286	17776	216
6. <i>Calathus rotundicollis</i> Dejean	?	d	d	W	C	f	234	6559	352
<i>Carabus auratus</i> L.	+?		b		5	r,a—	58	2950	465
7. <i>Carabus coriaceus</i> L.	+?	b	b		5	f	55	703	227
8. <i>Carabus monilis</i> F.	+?		b		5	a.3?	81	1209	309
9. <i>Cicindela hybrida</i> L.	+	m	m	W	C	s	110	907	1036
<i>Cicindela sylvatica</i> L.	?	m	m		5	h	14	26	305
10. <i>Dyschirius thoracicus</i> (Rossi)	+?	m	m		C	r	131	23981	536
<i>Harpalus anxius</i> (Duft.)	?		m		C	s	44	158	229
11. <i>Harpalus quadripunctatus</i> Dejean	+?		m	W	5	f	88	1805	100
12. <i>Harpalus tardus</i> (Panzer)	?	m	m		C	s	178	1520	693
<i>Leistus spinibarbis</i> (F.)	?		m		5	fd	35	669	260
13. <i>Leistus terminatus</i> (Hellwig)	?	b	m?		5	fw	234	961	377
14. <i>Nebria salina</i> Fairm. & Lab.	?		m		5	open	121	1597	167
15. <i>Notiophilus aquaticus</i> (L.)	?	d	d		C	open	412	14916	519
16. <i>Notiophilus palustris</i> (Duft.)	?	d—	d		C	f	332	1459	555
17. <i>Notiophilus rufipes</i> Curtis	?	m—	d		5	f	208	4353	349
18. <i>Olisthopus rotundatus</i> (Paykull)	?		d		C	fw	114	884	179
<i>Oodes helopioides</i> (F.)	?		m		C	rm	30	251	269
<i>Panagaeus cruxmajor</i> (L.)	?		m		C	r	33	71	226
<i>Pterostichus anthracinus</i> (Illiger)	?		d		C	fw	27	388	255
19. <i>Pterostichus quadrioveolatus</i> Ltz.	?		m		5	fd	64	2939	190
20. <i>Trechus obtusus</i> Erichson	?	b	d	W	C	f	260	8010	214

Im-species: Intermediate group. The dispersal power of most of these species is not clear. Only a few occur incidentally in flight records. For most species which are noted here as dimorphic, the ability of flight is questionable, because either only very low numbers of fullwinged individuals occur, or the wings are relatively small. The greater part of the species will be committed to walking activities for dispersal. Because both the dispersal power and the ecological amplitude vary considerably among the species of this group, the trends with time are expected to be somewhere between those of the Wd- and Pd-species.

trends of occurrences (Hengeveld & Haeck, 1981, 1982; Hengeveld, 1985). For criterion (c) see the definition of the Tc-species, Table 1. Criterion (d) is considered necessary to avoid bias from a number of taxonomically related species within one or more of the test groups, for taxonomically related species tend also to be ecologically related (Den Boer, 1980). In order to identify 20 test species, criteria (b) and/or (d) were relaxed somewhat.

**TABLE 4**  
Pd-Species

	I	II	III	IV	V	VI	VII	VIII	IX
1. <i>Abax parallelepipedus</i> Piller & Mt.	—		b		C	f	493	24 343	415
<i>Abax parallelus</i> (Duft.)	—		b		F	f	46	1 916	177
<i>Agonum assimile</i> (Paykull)	—	m	m		C	f	120	3 994	645
<i>Agonum ericeti</i> (Panzer)	—		b		5	m	91	1 273	34
2. <i>Agonum obscurum</i> (Herbst)	—	d—	d		C	h	409	15 739	497
3. <i>Badister bullatus</i> (Schrank)	—?	m	m?		C	rm	228	688	450
<i>Badister sodalis</i> (Duft.)	—?	b			C	rm	37	151	225
4. <i>Bembidion nigricorne</i> Gyll.	—	d?	b		F	s	106	6 548	137
<i>Bembidion mannerheimi</i> C. R. Sahlb.	—		b		C	f	3	29	143
5. <i>Calathus erratus</i> (C. R. Sahlb.)	—	d—	d		C	s	629	55 232	798
6. <i>Calathus micropterus</i> (Duft.)	—	b	b		5	f	96	1 567	277
7. <i>Carabus arvensis</i> Herbst	—	b	b		C	h	169	1 879	260
8. <i>Carabus cancellatus</i> Illiger	—?	b	b		C	o	116	429	215
9. <i>Carabus nitens</i> L.	—	b	b		C	hm	75	286	273
10. <i>Carabus problematicus</i> Herbst	—?	b	b		C	fd	382	16 979	702
11. <i>Carabus violaceus</i> L. (var. <i>purp.</i> )	?	b	b		C	fd	139	2 098	351
12. <i>Cychrus caraboides</i> L.	—	b	b		C	f	93	347	273
<i>Demetrias monostigma</i> Samouelle	?	b			C	s	16	38	317
13. <i>Harpalus latus</i> (L.)	—?	m	m?	W	C	h	316	6 888	329
<i>Laemostenus terricola</i> (Herbst)	—	b	b		C	f	43	381	295
14. <i>Leistus ferrugineus</i> (L.)	?	b			C	fw	321	2 068	409
<i>Patrobus atrorufus</i> (Ström)	—	b	b		C	fw	48	988	234
15. <i>Pterostichus lepidus</i> (Leske)	—?	d—	b?		C	h	321	13 503	586
16. <i>Pterostichus madidus</i> (F.)	?				F	f	82	4 340	428
17. <i>Pterostichus oblongopunctatus</i> (F.)	—?	m—	m	W	C	fd	394	46 750	649
18. <i>Stomis pumicatus</i> (Panzer)	—	b	d?		C	a.2?	180	1 745	357
19. <i>Syntomus foveatus</i> (Fourcroy)	?	b	d	W	C	o/s	375	3 564	624
20. <i>Syntomus truncatellus</i> (L.)	?	d	d	W	C	o/s	312	3 754	339

Pd-species: Poorly dispersing species. They usually inhabit more or less stable or permanent habitats such as woods and moors. Most of these species are not found at intensively exploited agricultural sites. The majority of the species are constantly brachypterous and the few dimorphic ones only exceptionally show fullwinged individuals, and flight records are either absent or known from a single specimen only. The four macropterous species have relatively small wings and flight observations are very sparse or lacking. At the Biological Station Wijster (Den Boer *et al.*, 1980) either a few or no flight records of these four species are known during nearly twenty years! All species of the group are committed to walking activities. These species are expected to have shown a decreasing trend of occurrence with time.



## TABLES 1-4: Explanation

The numbered species were selected as test species

Column: I—'+' = Flight observations present

'-' = Species not capable of flight, no wings or no flight muscles

'?' = Flight ability not investigated, but no flight records available

II—Relative wing size in Fennoscandia (Lindroth, 1945, 1949) b = brachypterous;  
d = (wing)dimorphic; m = macropterous and '-' = no flight observations

III—Relative wing size in The Netherlands, mainly from Den Boer (1977) and Den Boer *et al.* (1980); see text

IV—Flight records available from Praha = P (Honěk & Pulpán, 1983) and from Wijster—Biological Station = W (Van Huizen, 1980)

V—Geographical area: C = The Netherlands in the centre of the geographical distribution of the species. 5 = fringe of the geographical distribution of the species less than 500 km from The Netherlands. F = The Netherlands at the fringe of the geographical distribution.

VI—Ecological group: a.1 = species extremely favoured by intensive fertilisation and agricultural exploitation

a.2 = same as a.1 but not extremely favoured

a.3 = resembling a.1 and a.2 in that the species is tolerant of these factors.

a - = agricultural sites but not tolerant of the a.1 factors  
e.g. in haylands and at ruderal places like gardens,  
parks, farmyards and roadside verges

d = species of dry sites (but not a)

f = species of forests and woodland

h = more or less confined to the sea shore

m = species of moors and bogs

o = species of open country (but not a)

r = riparian species, more or less hygrophilous

s = species of blowing sand/heath, dunes

w = species of wet or moist places (but not a)

VII—Number of year-samples from pitfalls (total = 1658 samples), in which the species has been recorded

VIII—Number of individuals caught in the number of pitfall year-samples mentioned under VII

IX—Number of records from collecting by hand as brought together in the present data bank. For the 80 test species, nearly 40 000 of such records are used to describe the time trends of occurrences in the present paper.

The criteria concerning dispersal power of the species are based on Den Boer (1977), Haeck (1971), Van Huizen (1980), and especially on the work of Lindroth (1945, 1949). Additional information about relative wing sizes has been derived from Bangsholt (1983), Den Boer *et al.* (1980), Jeannel (1941-42), and Lindroth (1974, 1985). It must be stressed that not only relative wing sizes or capability of flight could be used to rank the species according to dispersal power. Information on other biological aspects, e.g. hibernation, brood care, and preferred habitats, had also to be considered.

For instance, the species *Calathus fuscipes* and *Dyschirius globosus* (Tc-group), both being wing dimorphic with only a small fraction of winged individuals on average, and without flight records (Van Huizen, 1980; Honěk & Pulpán, 1983), are nevertheless found all over the country in ruderal places and on arable land. In particular the small, digging species *Dyschirius globosus* cannot be expected to cover significant distances by walking but it is a highly eurytopic species (Lindroth, 1945; Den Boer, 1977), by which it hardly meets ecological barriers. The same applies to the much bigger *Calathus fuscipes*, which, though much less eurytopic than *Dyschirius globosus* (Lindroth, 1945), will be able to cover appreciable distances by walking.

### TESTING METHODS AND RESULTS

The occurrence of a species in The Netherlands during a certain decade can be characterised by two estimates: (1) the number of occupied  $10 \times 10$  km

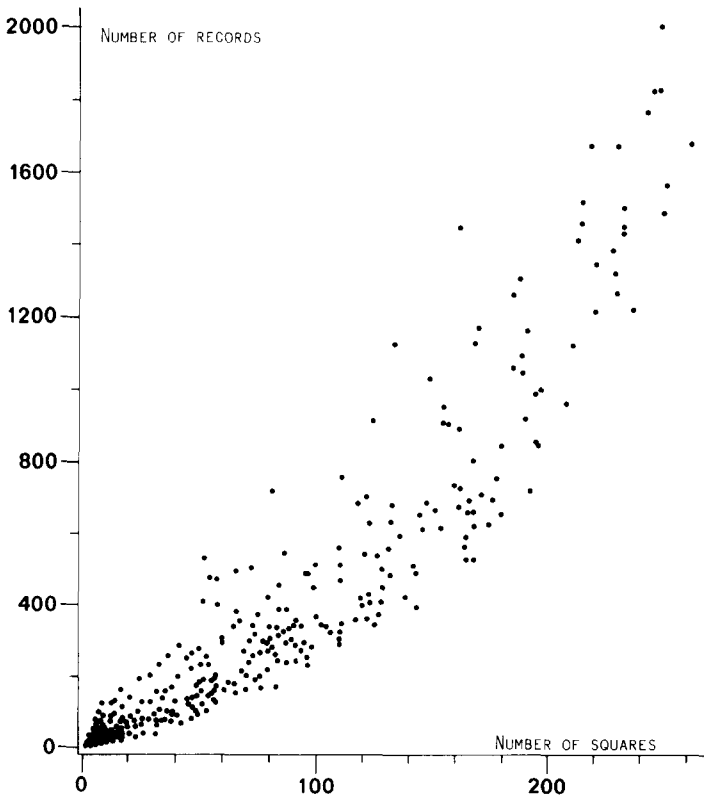
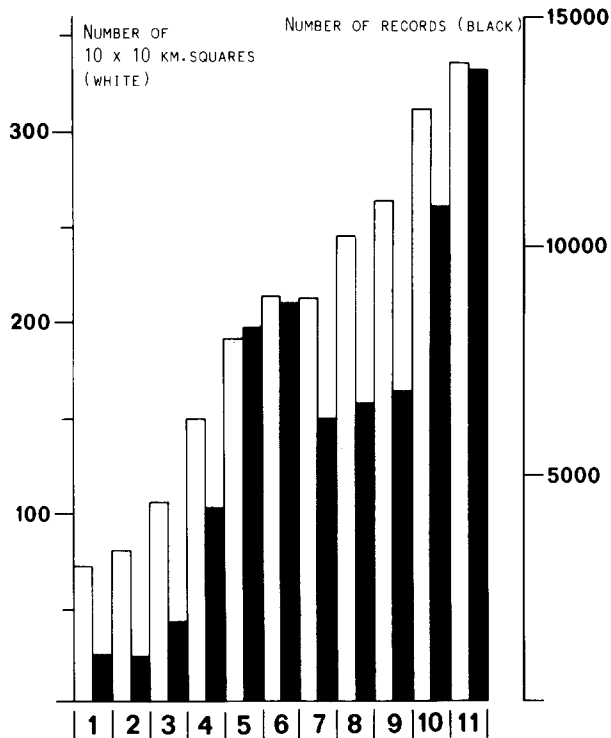


Fig. 2. Scattergram showing per species the number of  $10 \times 10$  km squares in which the given number of records occurred.

squares per decade; (2) the number of records per decade. Both can also be used to quantify the degree of change in the occurrences of the species in the course of time. In Fig. 2 these estimates are plotted against each other for each of the nearly 380 species known from The Netherlands. Note that the relationship between these estimates is fairly rectilinear on the left but then increases in favour of the number of records. This results from the number of squares being restricted in The Netherlands, with a maximum of 448, whereas the number of records can increase unlimitedly. Figure 3 gives the number of squares and the number of records per decade for all species together. It is evident that the increase in the number of records is much more irregular than that of the number of squares occupied per decade. Therefore, we suppose that the number of occupied squares will be a better indicator for the occurrence of a species (in The Netherlands) than the number of records, since the number of squares is far less affected by variation in collecting intensity (= variation in the number of records).

In order to test the differences in trends of occurrence over time between the groups of species, it is necessary to quantify the time trends in some way.



**Fig. 3.** Total number of  $10 \times 10$  km squares from which carabid beetles were recorded, and the total number of records per decade in these squares; (1) = period 1870-1879, (2) = 1880-1889, (3) = 1890-1899, etc.

As an estimate for this the Spearman rank correlation (Sokal & Rohlf, 1969) between the number of occupied  $10 \times 10$  km squares and the decade rank (compare Fig. 3) can be used. However, as the earlier decades are highly 'undersampled', the correlations of nearly all test species would be positively correlated with the decade rank. To get a more realistic picture the time trends of occurrences need to be corrected for variation in collection intensity. The total numbers of squares occupied by all species, as given in Fig. 3 and Table 5, show an almost rectilinear increase in time. Therefore, the best fitting regression line of number of squares on decade rank was calculated, and in Table 5 the expected numbers of squares occupied according to this relationship are given for each decade. As there is no special reason to assume a linear relationship between decade and number of squares for individual species, we preferred an even simpler correction factor, i.e. the total number of squares (448) divided by the number of squares occupied by all species in that decade, as given in Table 5. However, the two correction factors, by one of which the number of squares occupied by separate species has to be multiplied, did not appear to be very different (Table 5). The corrected numbers (correction factor 2) of squares per decade for each of the 80 test species are given in Table 6 (A + B).

TABLE 5

Frequency of Occupied  $10 \times 10$  km Squares per Decade (Total of Squares in The Netherlands = 448) and the Factors used for the Correction of the Time Trends According to Collecting Intensity

<i>No. = Decade</i> (i)	<i>Number of squares occupied</i>	<i>Expected number of squares<sup>a</sup></i>	<i>Correction factor 1<sup>b</sup></i>	<i>Correction factor 2<sup>c</sup></i>
1. 1870-1879	72	65.95	5.03	6.22
2. 1880-1889	81	92.54	3.59	5.53
3. 1890-1899	108	119.13	2.79	4.15
4. 1900-1909	150	145.72	2.28	3.03
5. 1910-1919	192	172.32	1.93	2.35
6. 1920-1929	214	198.91	1.67	2.10
7. 1930-1939	213	225.50	1.47	2.10
8. 1940-1949	246	252.10	1.32	1.82
9. 1950-1959	264	278.68	1.19	1.70
10. 1960-1969	312	305.27	1.09	1.44
11. 1970-1979	336	331.86	0	1.33

<sup>a</sup> Expected number of squares according to least squares line (see text).

<sup>b</sup> Correction factor calculated from the previous column (correction factor =  $N$  (squares in decade 11) (= 336)/ $N$  (squares in decade i)).

<sup>c</sup> Correction factor calculated from the total number of squares over all decades (factor =  $448/N$  (squares in decade i)).

**TABLE 6**  
 The Corrected Number of Squares Occupied During 11 Decades by the Four Test Groups of 20 Species Each: Corrections According to Correction Factor 2 (Table 5)

A. Well dispersing species ( <i>Tc-</i> and <i>Wd</i> -species)																							
<i>Tc</i> species	Decades																						
	1	2	3	4	5	6	7	8	9	10	11												
<i>Wd</i> species	Decades																						
	1	2	3	4	5	6	7	8	9	10	11												
1.	25	28	8	42	42	29	38	38	61	66	72	1.	12	11	0	24	40	42	32	44	27	50	59
2.	19	17	37	42	61	65	46	53	49	56	80	2.	12	0	21	15	42	42	23	29	32	56	73
3.	31	44	21	52	78	76	84	84	71	88	100	3.	37	33	37	33	66	55	29	46	36	35	51
4.	31	33	0	48	49	29	34	33	49	56	70	4.	12	17	25	24	75	53	44	71	44	63	36
5.	25	33	21	61	73	86	63	49	61	76	102	5.	6	11	25	9	28	25	17	13	22	23	28
6.	25	39	21	48	94	74	86	67	56	102	116	6.	37	22	37	55	61	65	29	46	49	60	48
7.	62	56	25	48	75	57	53	69	65	78	94	7.	6	6	33	45	68	67	42	51	46	45	67
8.	50	44	21	82	85	74	82	53	65	53	81	8.	31	22	12	24	59	67	34	38	31	86	67
9.	19	22	58	79	80	80	55	56	54	72	89	9.	31	17	29	24	49	57	44	36	32	42	84
10.	19	44	8	42	71	59	59	47	41	73	97	10.	25	11	17	52	54	57	44	31	51	62	52
11.	25	44	41	48	71	84	78	46	44	75	85	11.	12	11	21	21	38	29	29	29	15	32	27
12.	44	77	54	64	115	128	103	93	77	78	102	12.	25	0	17	15	14	17	27	9	17	14	37
13.	44	44	21	55	78	84	71	46	58	45	88	13.	0	0	12	6	31	61	29	24	17	30	15
14.	25	28	21	48	99	80	74	55	82	86	106	14.	25	50	46	52	101	126	111	87	85	96	120
15.	44	28	29	48	80	76	82	55	85	79	126	15.	19	11	25	30	66	50	57	33	37	76	93
16.	31	50	29	82	106	90	65	73	66	75	96	16.	12	11	33	42	42	67	48	18	32	60	89
17.	37	28	33	39	73	38	57	51	70	68	96	17.	62	44	37	79	108	103	69	53	53	73	93
18.	25	22	41	48	78	59	48	44	63	84	126	18.	25	6	17	18	5	23	19	16	12	14	48
19.	19	28	21	45	35	34	25	27	19	19	21	19.	12	22	17	27	35	44	48	38	41	46	73
20.	25	50	12	45	75	61	84	25	51	53	59	20.	6	6	17	18	12	21	11	24	17	39	49

(continued)

TABLE 6—contd.

<i>Im</i> species	<i>Decades</i>											<i>Pd</i> species											
	1	2	3	4	5	6	7	8	9	10	11												
1.	44	28	25	33	59	69	36	35	46	59	55	1.	12	22	12	39	47	53	17	31	26	39	32
2.	12	17	0	18	35	27	6	11	10	16	16	2.	12	17	33	30	56	42	44	29	27	73	81
3.	62	44	37	55	92	95	57	67	78	71	84	3.	37	39	62	30	31	36	44	36	36	42	51
4.	25	22	29	18	31	25	15	24	26	27	27	4.	6	6	21	12	33	19	17	9	7	13	11
5.	37	11	17	36	42	42	21	22	20	24	19	5.	50	33	37	58	92	92	20	71	70	72	69
6.	25	33	21	36	38	53	40	11	24	36	59	6.	12	11	17	21	40	34	27	22	24	43	25
7.	12	28	25	21	35	17	8	9	20	13	9	7.	12	6	25	27	31	38	11	24	19	17	13
8.	25	44	29	30	26	21	13	16	15	19	20	8.	0	28	33	30	26	29	17	27	12	7	11
9.	37	44	100	103	125	101	88	111	90	81	59	9.	6	0	37	24	35	21	27	33	15	16	9
10.	50	39	21	45	54	57	57	29	41	55	77	10.	12	33	37	52	68	67	61	64	56	68	67
11.	6?	0	0	0	2	4	4	11	15	20	17	11.	25	50	21	36	47	44	21	29	22	26	23
12.	50	44	46	42	78	97	76	73	71	40	55	12.	12	17	17	24	33	17	13	24	29	36	27
13.	19	17	58	15	40	44	17	22	44	60	61	13.	37	33	41	30	73	40	36	31	37	60	43
14.	12	11	4	9	21	25	25	11	15	23	27	14.	44	44	46	39	96	69	50	49	44	45	43
15.	44	28	46	42	75	69	38	42	51	73	63	15.	25	33	25	45	40	34	25	22	19	20	12
16.	12	33	37	36	78	71	50	58	65	66	73	16.	25	22	41	30	75	61	40	40	43	65	77
17.	19	6	17	27	56	46	34	42	51	30	38	17.	44	22	17	24	45	23	32	25	37	45	52
18.	6	17	17	15	31	32	23	13	19	26	17	18.	50	28	33	30	80	78	88	47	48	40	68
19.	6	11	12	27	38	29	21	16	12	19	25	19.	19	11	17	24	38	29	38	40	22	50	55
20.	6	28	8	24	19	21	15	7	10	40	39	20.	25	17	25	45	33	36	38	44	46	42	33

TABLE 7

Spearman Rank Correlation Coefficients Between the Corrected Number of Squares Occupied During each of the Eleven Decades and the Decade Rank, for the Twenty Species of Each Test Group. Between Brackets the Coefficients for the Last Eight Decades (20th Century) Only

NR:	<i>Tc-species</i>	<i>Wd-species</i>	<i>Im-species</i>	<i>Pd-species</i>
1.	+0.83** (+0.63*)	+0.85** (+0.69*)	+0.51 (+0.18)	+0.40 (-0.40)
2.	+0.76* (+0.40)	+0.84** (+0.64*)	-0.10 (-0.48)	+0.64* (+0.33)
3.	+0.87** (+0.73*)	+0.14 (-0.02)	+0.55 (+0.14)	+0.15 (+0.81**)
4.	+0.70* (+0.60†)	+0.59† (-0.04)	+0.20 (+0.35)	+0.11 (-0.52)
5.	+0.72* (+0.33)	+0.50 (+0.32)	-0.08 (-0.74*)	+0.43 (-0.08)
6.	+0.80* (+0.55)	+0.38 (-0.36)	+0.31 (+0.05)	+0.67* (+0.17)
7.	+0.66* (+0.71*)	+0.61† (-0.02)	-0.49 (-0.55)	+0.03 (-0.67*)
8.	+0.35 (-0.59†)	+0.71* (+0.49)	-0.73* (-0.55)	-0.38 (-0.86**)
9.	+0.45 (-0.08)	+0.65* (+0.26)	+0.10 (-0.76*)	+0.02 (-0.69*)
10.	+0.67* (+0.42)	+0.58† (-0.03)	+0.46 (+0.26)	+0.72* (+0.27)
11.	+0.66* (+0.21)	+0.52 (-0.10)	+0.79* (+0.97**)	-0.28 (-0.62†)
12.	+0.51 (-0.14)	+0.20 (+0.27)	+0.15 (-0.43)	+0.65† (+0.36)
13.	+0.58† (-0.02)	+0.54 (-0.17)	+0.60† (+0.78**)	+0.30 (+0.31)
14.	+0.80* (+0.55)	+0.68* (+0.19)	+0.63* (+0.25)	+0.02 (-0.31)
15.	+0.83** (+0.62*)	+0.83** (+0.57†)	+0.41 (+0.10)	-0.67* (-0.98**)
16.	+0.52 (-0.19)	+0.63* (+0.30)	+0.71* (+0.26)	+0.71* (+0.49)
17.	+0.80* (+0.55)	+0.31 (-0.36)	+0.57 (-0.05)	+0.56 (+0.64†)
18.	+0.82** (+0.54)	+0.06 (+0.17)	+0.35 (-0.17)	+0.30 (-0.10)
19.	-0.27 (-0.89**)	+0.89** (+0.74*)	+0.36 (-0.62†)	+0.82** (+0.60†)
20.	+0.44 (-0.12)	+0.77* (+0.62†)	+0.39 (+0.19)	+0.59† (-0.04)

†  $p \sim 0.05$ , \*  $p < 0.05$ , \*\*  $p < 0.01$ .

The Spearman correlation coefficients between these corrected data and the decade rank (Table 7) should give a fair impression of the relative changes of the species occurrences in the course of time. Pictures of the corrected time trends of occurrences of some interesting species are given in Fig. 4(a)–(h), which indeed show that the trends are not always a simple increase or decrease. For testing the differences between each pair of groups of correlation coefficients (Table 7), the non-parametric test of Mann-Whitney (Siegel, 1956, Sokal & Rohlf, 1969) was used. The results are given in Table 8A. It appears that the groups of Im- and Pd-species on the one hand, and the Wd- and Tc-species on the other, differ significantly from each other in all combinations. No difference was found, however, between the Im- and Pd-species, nor between the Wd- and Tc-species. As could be expected, the well dispersing species that are not favoured by agriculture (Wd-species: Table 2) differ less from the poorly dispersing species (Im- and Pd-species) than the species of agricultural fields (Tc-species: Table 1). But

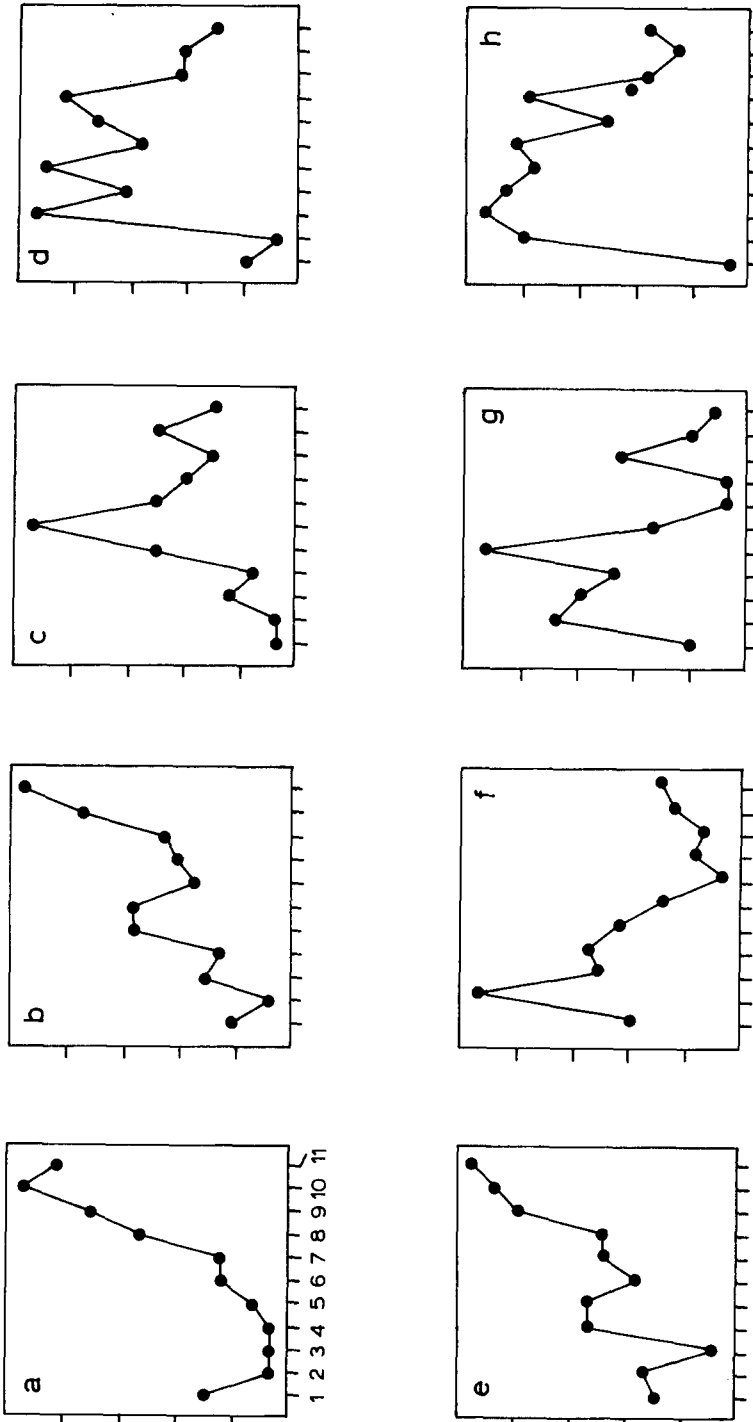


Fig. 4. Plots of the corrected time trends of occurrences of eight species; decades: (1) = 1870-1879, (2) = 1880-1889, (3) = 1890-1899, etc. The scales of the plots are adapted to the lowest and highest scores, respectively, and are thus not similar in all cases. (a) *Harpalus quadripunctatus* Dej. (Table 3: Im. 11, Fig. 1); (b) *Agonum fuliginosum* (Panz.) (Table 2: Wd. 2); (c) *Harpalus rufipalpis* Sturm (Table 2: Wd. 13); (d) *Carabus nitens* L. (Table 4: Pd. 9, Fig. 1); (e) *Agonum dorsale* (Pont.) (Table 1: Tc. 1); (f) *Carabus montis* F. (Table 3: Im. 8); (g) *Carabus coriaceus* L. (Table 3: Im. 7); (h) *Carabus cancellatus* Illig. (Table 4: Pd. 8).



TABLE 8

The Results of Mann-Whitney Tests Applied to the Spearman Rank Correlation Coefficients of Table 7. The Framed Figures show which Groups Differ Significantly from Each Other ( $p < 0.05$ ). A: For all Eleven Decades; B: for the Last Eight Decades (20th century) Only

A	Tc	Wd	Im	Pd
Tc	—			
Wd	0.38	—		
Im	0.0005	0.012	—	
Pd	0.0024	0.03	0.99	—
B	Tc	Wd	Im	Pd
Tc	—			
Wd	0.31	—		
Im	0.027	0.04	—	
Pd	0.076	0.063	0.46	—

the difference between the relatively poorly dispersing species (Im- and Pd-group) and the well dispersing ones (Wd- and Tc-group) seems to be greater for the Im- than for the Pd-species. It may be supposed that the powers of dispersal of most Im-species are not intermediate but are as poor as among Pd-species; Den Boer (1977) suggested the same concerning most of his C-(mainly Im-) species as compared with his A-(mainly Pd-) species. Together with the fact that there are more eurytopic species among the Pd-species than among the Im-species, this possibly explains the above difference.

If the poorly dispersing species have actually declined, we would have expected more negative correlations among the Im- and Pd-species than in Table 7. In spite of having corrected the numbers of squares, this may still be an artefact of the low collecting intensity in the 19th century. At that time collecting occurred highly traditionally; in particular a number of more localised species were only collected from a few sites, or even from a single one. To learn what may be the effect of this possible bias we recalculated the correlation coefficients for the last eight decades (20th century) only (Table 7, between brackets). Nearly all coefficients decreased (on the average by 0.35, so that many more coefficients became negative, e.g. 9 among Im- and 11 among Pd-species). The coefficients of some more localised species indeed decreased most, e.g. of *Abax parallelepipedus* (Pd. 1), *Bembidion nigricorne* (Pd. 4), *Carabus nitens* (Pd. 9, Figs 2 and 5(d)), *Calathus ambiguus* (Im. 5), *Harpalus tardus* (Im. 12), *Olisthopus rotundatus* (Im. 18), *Agonum sexpunctatus* (Wd. 4), *Amara fulva* (Wd. 6), *Bradycellus ruficollis* (Wd. 11); Tables 1-4, 6 and 7. Hence, collecting intensity during the 19th century was

not only low, but seems also to have been somewhat deviating (Table 6, A + B). Applying Mann–Whitney tests to these coefficients for the eight 20th century decades does not change our conclusions: Table 8B. As we cannot be sure of such a 19th-century effect for all species, and because some Tc-species also show negative correlations if only the 20th century is considered (Table 7, between brackets), only taking into account 20th century data does not provide indisputable conclusions. When looking at the Figs 9a and 9b (also 10b) of Hengeveld (1985) one gets the impression that the main climatic change during the present century concerns warmer and somewhat drier springs/summers in the decades 1930–40 and 1940–50. Before and after that period climatic conditions were, on average, apparently about similar so that we can largely exclude the effects of climatic changes by comparing the occurrences before 1930–50, *viz.* in the period 1900–30, with those after it, *viz.* in the period 1950–80. This can best be done by Wilcoxon's signed ranks test (Sokal & Rohlf, 1969). It then appears that the occurrences of the Tc-species significantly increased in 1950–80 when compared with 1900–30 ( $T_s = 57$ ,  $p = 0.04$ ); those of the Wd-species also increased, though not yet significantly so ( $T_s = 68$ ,  $p = 0.09$ ). However, the occurrences of both the Im- and the Pd-species decreased ( $T_s = 74.5$ ,  $p = 0.135$ , and  $T_s = 67$ ,  $p = 0.08$ , respectively). This difference in trend between Tc- and Wd-species on the one hand, and Im- and Pd-species on the other, is significant:  $\chi^2 = 4.27$  ( $p < 0.05$ ,  $df = 1$ ). It is interesting to learn from Table 6 (A and B) that species whose occurrences relatively decreased between 1930 and 1950 (decades 7 and 8) recovered again after 1950 if they were Tc- or Wd-species, but often did not if they were Im- or Pd-species, e.g. not in *Amara infima* (Im. 2), *Calathus ambiguus* (Im. 5), *Carabus monilis* (Im. 8), *Carabus arvensis* (Pd. 7), *Carabus violaceus* (Pd. 11), *Pterostichus lepidus* (Pd. 15), and others. This corroborates our impression that, although climatic changes clearly affect the occurrences of carabid species, in many poorly dispersing species losses during periods, which are, for example, climatically relatively unfavourable cannot or can only insufficiently be compensated for by (re)foundings when conditions improve again, most probably as a result of isolation by fragmentation of habitats (Den Boer, 1977).

## DISCUSSION

The theory of island biogeography describes a number of processes in animal populations when they are isolated (MacArthur & Wilson, 1963, 1967). Under certain assumptions predictions can be made on the probabilities of immigration and/or extinction of species on islands with different areas, and/or at different distances from the mainland, which again

leads to different expected numbers of species on these islands. The founding hypothesis of Den Boer (1977) has a broader scope. Whereas the theory of island biogeography hardly takes into account differences in the probability of immigration and/or extinction between species, the founding hypothesis explicitly discriminates between well and poorly dispersing species. The species with low powers of dispersal must be considered as slow immigrants, but at the same time (especially in an (habitat) island situation) relatively good survivors. The species with high dispersal powers are good immigrants, but this same mobility, particularly in species that colonise easily, may cause relatively rapid extinction of local populations (Den Boer, 1985). Therefore, most of the predictions from the island theory of MacArthur & Wilson, such as area-effects, distance-effects, and especially turnover rates, should in the first place be attributed to species with high powers of dispersal. Den Boer (1977) expected that, in a landscape with a high degree of habitat fragmentation, the poorly dispersing species would suffer from habitat isolation by local extinction without re-founding. With relatively short distances between the fragments recolonisation may still be possible, though it will be difficult in comparison with that of well dispersing species. In small and highly isolated fragments, however, all species with low powers of dispersal are expected in due course to disappear. In large parts of The Netherlands the majority of woods and heathlands indeed are highly reduced, fragmented and isolated.

Since the end of the 19th century the extensive heathlands of The Netherlands were either brought into cultivation or afforested, and thus highly reduced. Around 1835 in The Netherlands dry heathlands covered approximately 800 000 ha, but by 1900 this area was reduced, mainly by cultivation, to 100 000 ha. Afforestation, which mainly occurred between 1880 and 1930, further reduced the area to about 60 000 ha in 1950 and to 40 000 in 1980. Moreover, a substantial part, at least 25% of the present fragments, is occupied by grasses (*Molinia* and *Deschampsia*). The extensive peat moors have almost completely disappeared. The total area of woodland, the major reduction of which already started in the Middle Ages, might superficially be considered to have increased again during the last century, but the majority (about 80%) of the afforestations is of conifers.

The supposition that these coniferous forests must be considered unsuitable or, at best, marginal habitats for most carabid species of deciduous forest (Den Boer, 1963, 1968), was not confirmed by recent comparisons of both kinds of forest at 45 sites in different parts of The Netherlands (Heijerman & Turin, in prep.). The results of these studies were in agreement with those of Den Boer (1968) in that the most abundant deciduous forest species only occur in comparatively low numbers in coniferous forests.

The most important prediction from the founding hypothesis, *viz.* that in the course of time, in cultivated countrysides, significant differences in the time trends of occurrences will develop between species with low powers of dispersal and those with high powers of dispersal, is convincingly corroborated by the present study. The striking difference in time trend of occurrences between Wd-species on the one hand, and Im- and Pd-species on the other, suggests that, apart from an evidently negative effect on all species of habitat reduction, which will not appear from collection data (collectors know where to find the desired species), isolation has had a great additional influence on the occurrences of Im- and Pd-species. However, we are not sure that such an overall conclusion can yet be drawn. It was hoped that data from many old collections would enable us to discriminate better between these possibilities. Although carabid beetles were amongst the earliest insect groups studied, major changes in collecting intensity, together with the highly unequal exploration of different parts of the country, have introduced too many uncertainties to attain this purpose. Nevertheless, we expect that a more detailed study, in different parts of the country, of the trends of occurrences in time of particular species, whose history is well documented, will enable us better to separate the effects of isolation from those of habitat reduction. The many data available from pitfall trapping will give us a clear picture of habitat preferences of many species. This will enable us to understand the trends of occurrences in certain critical ecological groups; for instance, in the stenotopic forest species, especially in those parts of the country where the most drastic changes have taken place. The increasing or decreasing trends of occurrences of all species known from The Netherlands will be compared with the trends in adjacent countries (Turin & Desender, in prep.). The latter study will possibly also enable us, for the different species, to discriminate better between positive and negative climatic influences (Hengeveld, 1985), and to investigate the influence of habitat destruction and isolation as opposed to habitat extension for 'ruderal' species. Some of the earlier pitfall samplings in small and isolated woods and dry heathlands (originally undertaken some 25 years ago) will be repeated at regular time intervals, so that eventually some direct data on survival in habitat islands will become available.

## CONCLUSION

In accordance with Den Boer (1977, 1985) this study showed that, in a rapidly changing landscape, species with low powers of dispersal are progressively endangered, whereas many species with high powers of dispersal, especially those thriving in man-made sites, are favoured as long as suitable habitats are amply available.

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