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Carabid beetles in a changing environment

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Abstract

Between 1959 and 1989 the dynamics of carabid beetles have been studied at Kralo Heath in the National Park 'Dwingelder Veld', the Netherlands, by sampling all year round with standard sets of pitfalls. The sampling was not continued everywhere for all years, and during some years the catches from the standard sets were not completely identified. Therefore, a method for the estimation of the actual numbers in 10 interaction groups was developed.

Environmental conditions were not stationary during the study. In the 1960's the ground-water table gradually receded, and during the 1970's the effects of increasing air pollution became apparent: increasing acidification and fertilization of the upper layers of the soil and a gradual replacement of both *Calluna* and *Erica* by grasses; but also precipitation increased. During the 1980's a gradual repair of the original hydrology was observed. The grassy vegetation together with the polluted soil layer were cut and removed. Moreover, at the end of the 1980's the mean temperature increased.

A decline of numbers of many carabids stenotopic for heath areas and/or other sandy localities was apparent. Some species apparently disappeared completely, such as *Agonum krynickii* and *Carabus cancellatus* from 'Dwingelder Veld', and *C. cancellatus*, *C. nitens*, *Harpalus solitaris*, *Cicindela sylvatica*, *Amara infima*, *A. quenseli* and *A. praetermissa* from 'Hullen Zand', some of the latter possibly because of the small area of the isolated 'Hullen Zand' (4 ha). Other stenotopic species reached in the 1970's and/or 1980's critically low numbers. Eurytopic species were usually not significantly affected; some even increased in numbers. A number of stenotopic species reacted to sod cutting by increasing in numbers. Some of these species are also known to occur in heather-covered road-side verges. From a more general sampling at 38 sites of 'Dwingelder Veld' in 1991 it appeared that many endangered species are still present in other parts of the National Park. The ups and downs and the prospects of the separate species are discussed and explained as far as possible in the light of their ability to disperse in relation to changes in their environment.

Introduction

In 1959 at the Biological Station of Wijster an investigation into the dynamics of carabid populations was started at the Heath of Kralo, the south-eastern part of about 800 ha of the heath area (1600 ha) of the National Park 'Dwingelder Veld' (3500 ha), which also includes largely afforested areas of drift-sand, many pools, small peat moors, and some fields. This area is situated in the Northern part of the Netherlands, in the province of Drenthe (Fig. 1). This heath area was selected because it was thought to be both large enough and sufficiently stable to contain natural populations (Andrewartha & Birch, 1954: Ch. 13) of a number of carabid species.

The heath area developed on a plateau of boulder clay left by the ice-cap of the second to last glaciation (Saalien), and which is now covered by a layer of drift-sand of 0.5-2 metres (Bakker et al., 1986) with a well-developed podzol. For the greater part the heather vegetation originated from human activities from some centuries B.C. until the Middle Ages; and ever since has been kept in existence by grazing sheep and cattle, burning and sod cutting. As both the layer of boulder clay and the sand surface are undulated, there are shallow valleys with extensive growth of *Erica*, sometimes with an undergrowth of *Sphagnum*, and a number of shallow, oligotrophic pools. In the deepest part a peat moor (Holtveen) developed. The area drains into two small rivers, Wold Aa and Oude Vaart. Its water supply entirely depends on precipitation. Soil profiles suggest that during the greater part of its history both the hydrology and the vegetation of this area did not go through major changes.

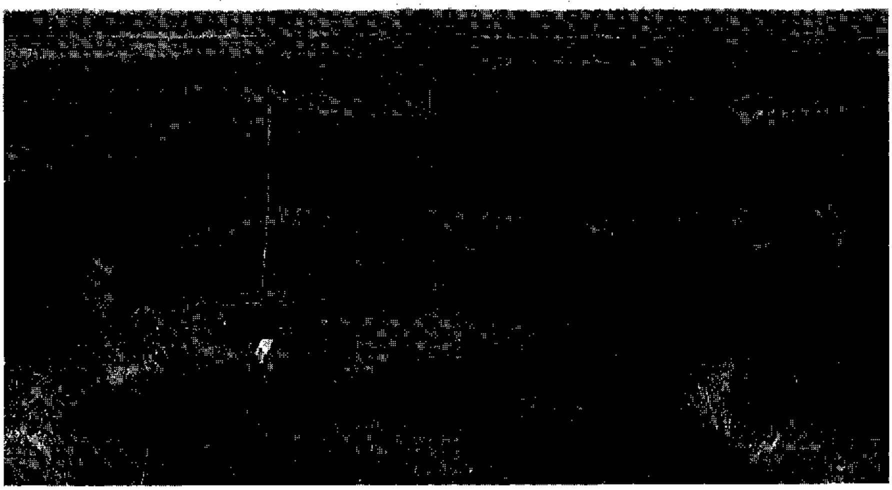
Therefore, it was expected to find old and stable carabid populations, the dynamics of which could show how natural populations persist during at least some centuries. After a few years of sampling it was realized that this expectation need not be correct, because several processes that might directionally change the environmental conditions in the area had recently started. First, since the end of the 19th century the drainage of the area was much 'improved' by a progressive canalization of the surrounding small rivers. Secondly, the introduction of the use of chemical fertilizer at about the same time greatly increased the reclamation of heathland. This both eliminated the old system of grazing of the heath and the use of natural dung. In the 1920's parts of the 'Dwingelder Veld' were reclaimed.

In the first decades of the twentieth century the old management of the heathlands -grazing, burning and sod cutting- had gradually ceased. So the new owners of the heath area (the private Foundation for the Preservation of Nature Reserves, 'Natuurmonumenten', who obtained the Heath of Dwingeloo in 1930, and the State Forest Service, 'Staatsbosbeheer', who obtained the Heath of Kralo in 1942: Brouwer, 1968) had to replace the old management in some way. They designed a careful burning plan and a large sheep herd, that is led daily over parts of the heath area, was established. Together these measures prevent the heather dying of old age and being gradually replaced by pines, birches and grasses.

In spite of the 'continued improvement' of the drainage of the heath area early in the 1960's the valleys were usually inundated for some weeks or months in winter, most probably because of a succession of years with more than normal precipitation. But in the 1970's the heath area became observably drier after the further obligatory improvement of the drainage of the fields and meadows in the 'Noordenveld', which was lead through the heath area, and the construction of a cycle path with efficient drainage along the 'Holtveen' (Fig. 1). However, most years continued to be wet, and the extensive wet areas of *Erica* heath survived. Also, the shallow pools did not run dry each summer, so that it could be expected that hygrophilous species could maintain themselves somewhere in the National Park. Also, the introduction of a burning plan generated a continued alternation of patches of old and young heather, and of open and dense vegetation. In fact, the changes introduced by the burning plan are periodic and do not differ fundamentally from the changes caused by the almost cyclic outbreaks of the heather beetle, *Lochmaea suturalis* (e.g. in 1962, 1967, 1973, 1979: Den Boer, 1986a: Fig. 2). Its larvae cause a patchy dying-off of *Calluna*, which is usually followed by a partial regeneration. Also *Erica* is sometimes severely damaged by the larvae of *Haltica ericetorum* Allard and *H. britteni* Sharp (Van Heijnsbergen, 1970). Thus, as periodic changes in structure, age and composition of the vegetation also occur naturally, it was not expected that -at least during the first decade of the investigation- any of the carabid species present was seriously endangered.

But in the 1970's, and especially in the 1980's, everything changed as a result of air pollution, which caused both acidification and fertilization of the poor soil. This resulted in an extension of grasses, mainly *Molinia caerulea* and *Deschampsia flexuosa*, replacing both *Calluna* and *Erica* (Heil, 1984; Berendse & Aerts, 1984; Heil & Bruggink, 1987; Aerts & Berendse, 1988; Aerts, 1989a, b). This air pollution mainly consists of ammonia, which originates from a rapid extension of intensive factory farming (chickens, pigs and boxed calves) and adds 20-40 kg of nitrogen per ha of heath per year. The fertilization of *Calluna* also leads to more severe infestations by larvae of the heather beetle and thus facilitates the replacement by grasses. Obviously, these changes were not generally recognized before the seventies, for Gimingham (1972) did not mention acidification or eutrophication of heathlands, replacement of heather by grasses, or an increase of infestations by heather beetles. The owners of the heath area reacted to this threat of the Nature Reserve by developing a machine for mechanical sod cutting. By cutting away the grasses together with the polluted humus layer down to the mineral soil the extra nitrogen could be removed. In most sites where this mechanical cutting had occurred, especially in the wet areas, *Erica* and *Calluna* rapidly reappeared. At the same time the unnecessary drainage of the heath area was gradually reduced by purchasing the fields and meadows in the 'Noordenveld' and blocking off the connected drainage systems.

In this way in the 1980's a slow recovery towards the situation of the 1950's and 1960's was started. As between 1959 and 1989 carabid populations were exten-



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Dwingelderveld, sample site AY in 1964 (photograph 1) and in 1983 (photograph 2). From 1970 and especially in the 1980's an extension of grasses mainly *Molinea caerulea* and *Deschampsia flexuosa* occurs, replacing both *Calluna* and *Erica*. As a consequence the structure and composition of the vegetation changed (compare photograph 1 and 2).

sively sampled in many sites of the Heath of Kralo these data could be used to investigate the possible influences of the above changes on the abundances of carabid species characteristic for heath areas. However, because of varying manpower not all sites were sampled continuously or completely, so that the overall changes of abundance over time had to be reconstructed from different sampling series.

Material and methods

Technique and frequency of sampling.

To be able to quantitatively compare the abundances of some carabid species at the same site in different years, and also at different sites in the same year, during the entire period 1959-1989, a number of sites in the heath area were sampled with standard sets of pitfalls. Such a standard set consisted of two square, 30 cm deep live traps and a single square funnel with an easily changeable container filled with 3% formaline. Each trap had a circumference of 100 cm and was dug into the soil with the upper rim level with the surface. The traps were constructed from durable, rust- proof, smoothly coated sheet iron. All traps had a drainage system and were freely suspended in a deeper outer container to avoid flooding and disturbance of the catch environment when taking out the pitfall. They were provided with a metal roof, and with wire netting suspended about 10 cm below the upper rim, to keep out predators. In the field the three traps of each set were placed 10 meters apart in a straight line in the centre of the site, the funnel in the middle. More details can be found in Den Boer (1977). The traps were emptied each week on Wednesday the whole year round.

The abundance of a certain carabid species during a certain year (designated a **'year-catch'**) was considered to be represented by the summed week-catches of that species in the standard set of pitfalls concerned during that year. A year was taken to run from the Wednesday nearest March 1 until the Wednesday nearest the following March 1. Baars (1979) and Den Boer (1979) showed that such year-catches give surprisingly accurate relative estimates of the abundance of the species around the set of pitfalls (see also Den Boer, 1986b,c). But the relationship of this year-catch to the actual mean density is different for each species and must be estimated with mark-recapture for each species separately. Depending on the species, between 0.1% and 5% of the individuals living in the subpopulation around the standard set of pitfalls (interaction group: Den Boer, 1977) appeared to be caught during a year (i.e. in a year-catch).

In this way in the first 5 years 3-5 sites were sampled per year, 7 sites in 1964, 11 sites in 1965 and 1966, 7 sites each year until 1971, and from 1972 onwards 10-12 sites. From 1990 onwards not all sites were sampled in all years, except the sites N and Z, which will be sampled as long as possible. Most sampling sites are described (and some pictured) in Den Boer (1977: Appendix, Part II). The location of most sites is given in Figure 1. From 1971 (for some sites 1972) onwards the time-consuming identification of all carabid beetles caught had to be reduced. From then on in most sites that had already been sampled for many years (AY, AT, BH, BJ, BB, AG, M, BG) the beetles caught in the live traps were released again in the field

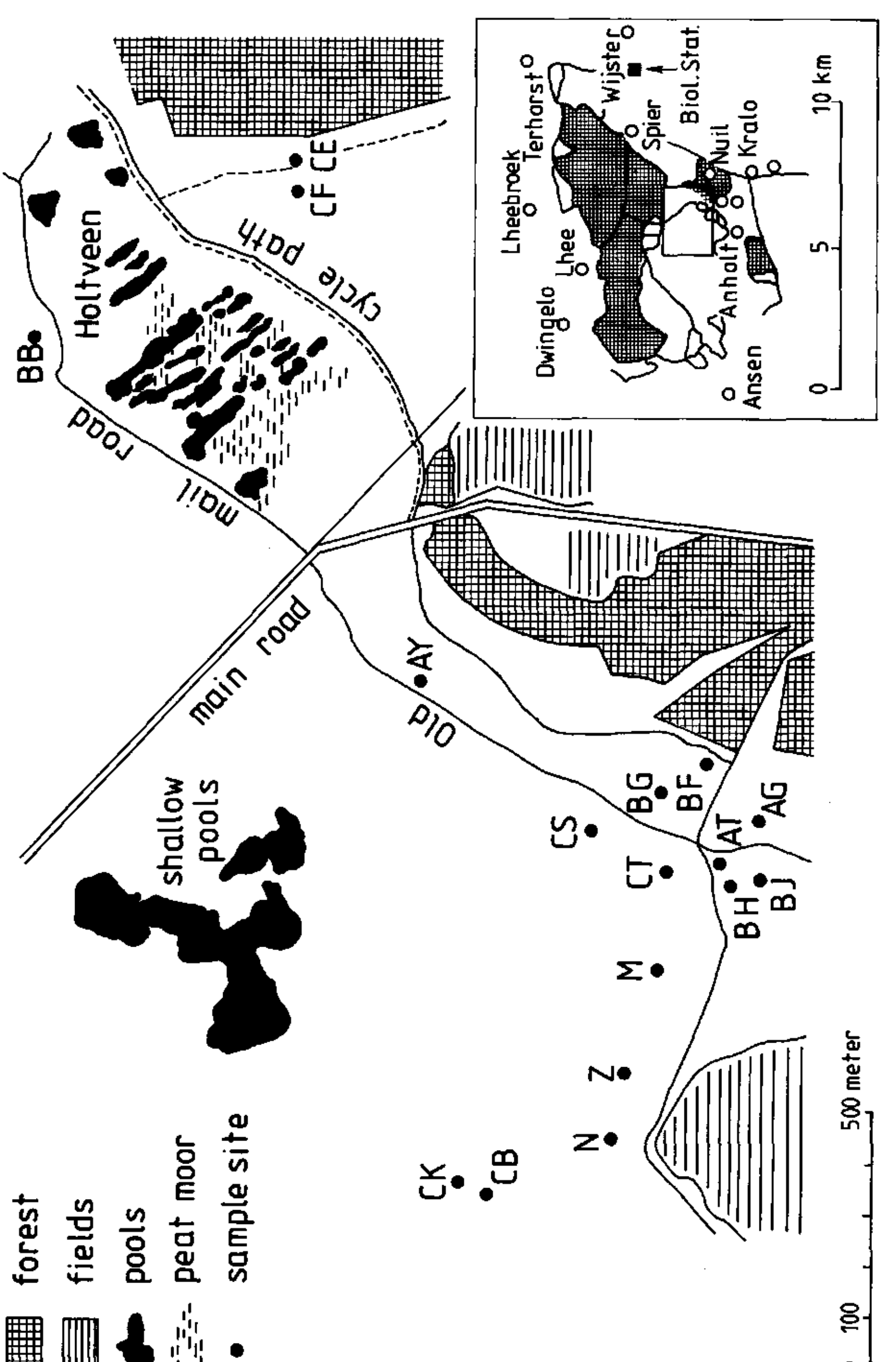
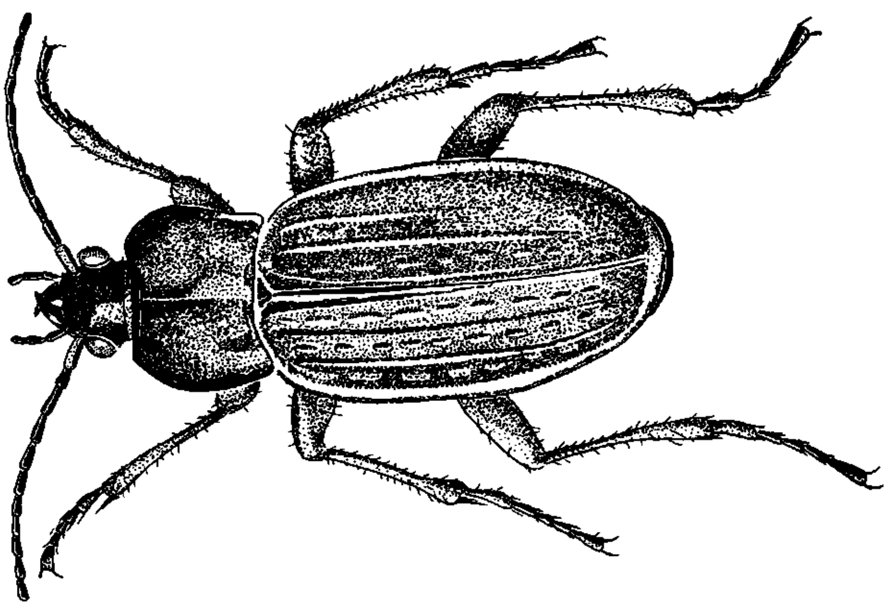


Fig. 1. Location of standard sets of pitfalls at Kralo Heath (indicated by capitals). At bottom right: 'Dwingelder Veld' with the investigation area at Kralo Heath framed.

after having noted the number of individuals caught of 7 key species *Pterostichus versicolor, P. diligens, P. lepidus, Calathus melanocephalus, C. erratus, Amara lunicollis, Harpalus latus*, and of some rare and easily recognized species, such as *Carabus cancellatus, C. nitens, Agonum ericeti, A. krynickii, Miscodera arctica, Cymindis vaporariorum*. The funnel-catches and all catches from some other sites in the heath area were taken to the laboratory and the beetles were carefully identified.

Estimation of relative abundances.

As the heath area is quite heterogeneous it was tried to sample a group of sites that represented the range of variation: moist to wet *Erica-Calluna* heath (N), moist *Calluna* heath (Z, CF), *Calluna-Empetrum* heath on drift-sand (AY, BB), wet *Molinia* (M), dryer *Festuca-Nardus* vegetation (AT, BH, BJ), moist mosaics of heather species and grasses (AG, BG, CB). See also Van Dijk & Den Boer (1992). But not all these sites were sampled in all years, so that for some years it was necessary in some way to estimate the totalled year-catch in 10 standard sets of pitfalls. The 10 sites N, M, Z, AG, AT, AY, BB, BG, BH, BJ were all sampled in both 1965, 1966 and again from 1972 until and including 1980, so that the summed catches in these 10 standard series of at least the 7 key species could be taken as a start. For those sites that were sampled in two succeeding years the common net rate of reproduction (R) was calculated and used to estimate the summed year-catches from 10 standard sets for the year in which not all 10 sites were sampled. From 1981 through 1985 for most species the sites AG and M, that were no longer



Carabus cancellatus unwinged 20-28 mm

sampled, were replaced by CB and CF. For the 7 key species the reliability of this method of estimation was tested by comparing the summed year-catches from the 10 standard sets in one of the years 1972-1980 with that obtained by calculating the common R-value from 7, 8 or 9 of the sets of pitfalls and estimating the sum for 10 sets. The differences were usually insignificant and only incidentally exceeded a few per cent. Therefore, for the 7 key species it was possible to reliably estimate the numbers during 31 years in the multipartite population (Andrewartha & Birch, 1984: 8.5; Van Dijk & Den Boer, 1992), consisting of 10 subpopulations (interaction groups) that covered about half of the Heath of Kralo, and all aspects of its heterogeneity. In Van Dijk & Den Boer (1992) all data are given and explained for *C. melanocephalus* and *P. versicolor*.

For most other species, however, the data are less complete, because, as mentioned, for some years and some sites only the funnel-catch was available, so that

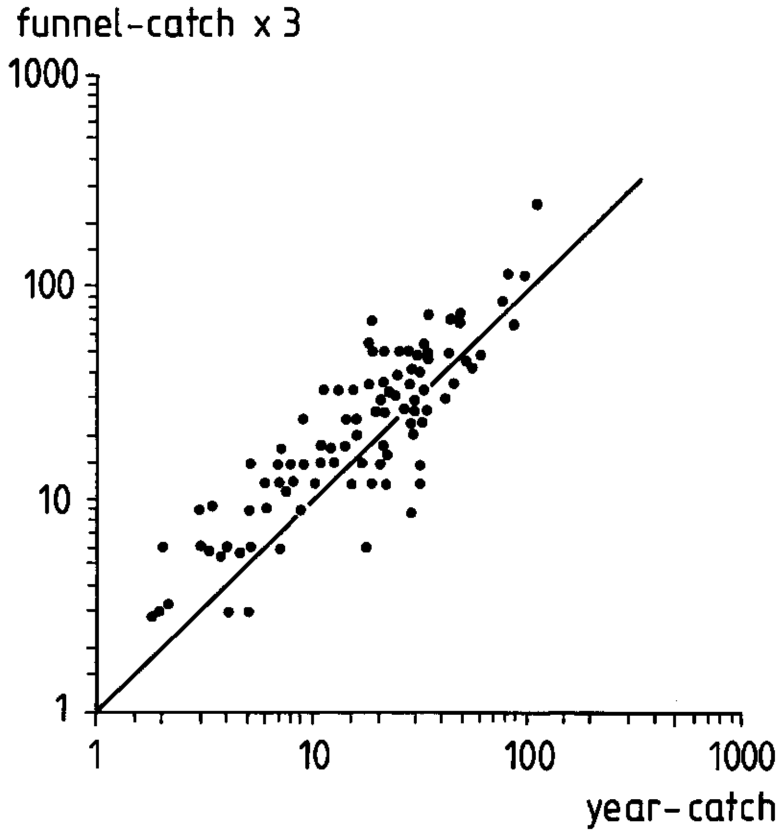


Fig. 2. The number of individuals of *Harpalus latus* in each of 96 year-catches at Kralo Heath plotted against the funnel-catch in each of these year-catches times three. The line represents exact equality of year-catch and 3 times funnel-catch.

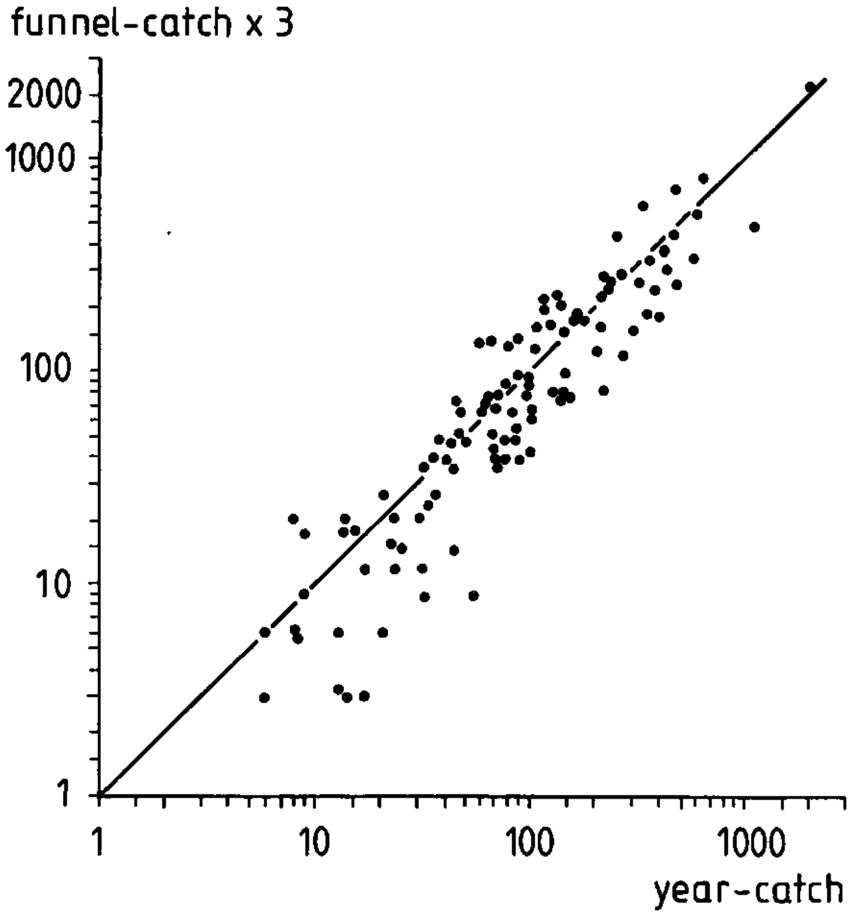


Fig. 3. The same as in Figure 2 for 105 year-catches of *Calathus melanocephalus*.

for these years and sites first the year-catches had to be estimated before being able to apply the above method. The funnel-catch is expected to be one third of the year-catch, but there can be considerable deviations from this expected value. First of all there is a distinct 'species-effect': small carabid beetles are usually caught in higher numbers in a funnel than in a live trap, and big carabid beetles usually in higher numbers in a live trap than in a funnel trap. Across 14 more abundant species the ratio year-catch/funnel-catch is significantly correlated with mean length of the beetles: r_s (Spearman's rank correlation)= +0.66 (P= 0.017, 2-sided).

To get an idea of the reliability of estimating year-catches from the funnel-catch only, for the 7 key species for many years and many sites the number of individuals in each year-catch was compared with 3 times the number caught in the funnel, and both the number of positive differences (year-catch higher than funnel-catch x3) and negative differences (year-catch lower than funnel-catch x3) was noted. The

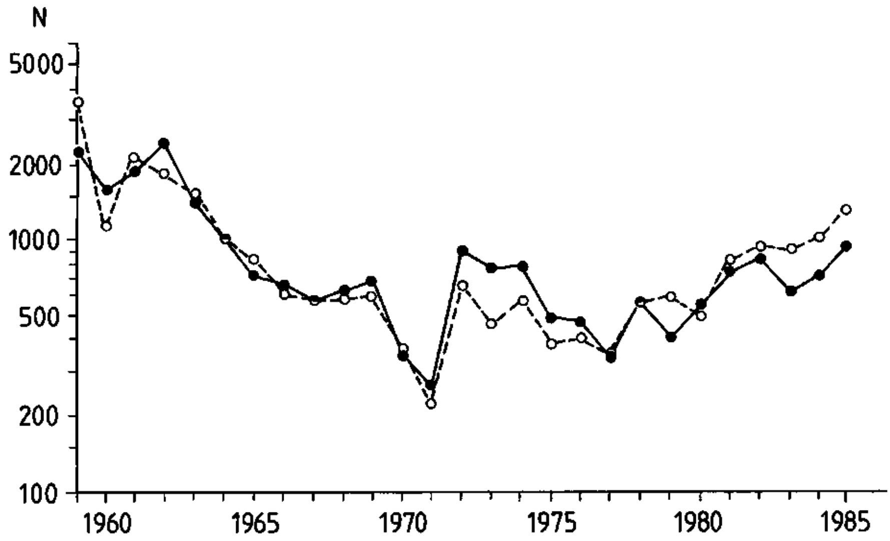


Fig. 4. The numbers of *Pterostichus diligens* from 1959 until 1985 as represented in each year by the sum of the year-catches from 10 interaction groups at Kralo Heath (filled circles and solid line) as well as by these sums as calculated from the funnel-catches times 2.50, as found in 1959-1971 (open circles and broken line).

results were: *H. latus*: 26+, 70– (Fig. 2); *A. lunicollis*: 46+, 71–; *P. diligens*: 50+, 63–; *P. versicolor*: 50+, 63–; *C. melanocephalus*: 64+, 41– (Fig. 3); *C. erratus*: 43+, 23–; *P. lepidus*: 62+, 24–; X^2 (Chi-square)= 56.69 (d.f.= 6), $P \ll 0.001$. For the 7 species together there is no significant 'year-effect' (1971-1985): X^2= 10.57 (d.f.= 13), $0.70 > P > 0.50$, but a significant 'site- effect' is apparent: X^2= 35.93 (d.f.= 10), $P < 0.001$. This 'site-effect' is almost completely caused by the sites AY (20+, 66–) and BH (46+, 27–); without these sites X^2= 6.78 (d.f.= 8), $0.70 > P > 0.50$.

Hence, the 'species-effect' is the most important cause for a deviation from the expected value. For the years 1959-1971 we could calculate a mean value for the year-catch/funnel-catch ratio for all species, because in these years all catches from all standard sets (live traps and funnels) were identified. Fig. 4 shows the year-catches estimated and summed for 10 standard sets as compared with these values estimated from the funnel-catch-x2.50 for *P. diligens* which is the smallest of the 7 species. In Fig. 5 similar data are given for *P. lepidus* (funnel-catch-x3.23) the biggest of the 7 species. Figures 4 and 5 show that the estimations from the funnel-catches are satisfactory as far as the general trend of numbers over time is concerned. The results for the other 5 key species were similar. Therefore, such estimations from the funnel-catches, which were necessary for part of the years in a number of non-key-species only, were expected to give a reliable impression of the relative numbers. For these non-key-species also a possible 'site-effect' was taken into account, which was not done for the 7 key species.

Between 1959 and 1989 for each of the carabid species that were abundant in the heath area in the 1960's, in this way the relative numbers were estimated as these

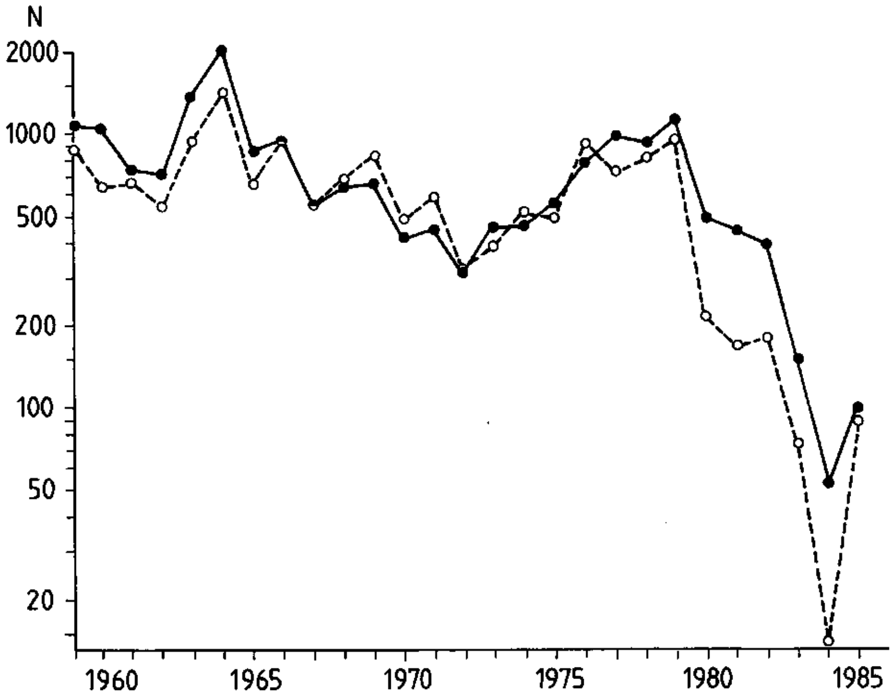


Fig. 5. The numbers of *Pterostichus lepidus* from 1959 until 1985 as represented in each year by the sum of the year-catches from 10 interaction groups at Kralo Heath (filled circles and solid line) as well as by these sums as calculated from the funnel-catches times 3.23, as found in 1959-1971 (open circles and broken line).

would have occurred in a multipartite population consisting of 10 interaction groups (subpopulations), i.e. in a heterogeneous area of about 50-500 ha of the Heath of Kralo. According to Turin et al. (1991) most of these species are quite characteristic for oligotrophic (poor in nutrients) sandy or peaty soils with a heath-like vegetation (A1- species: bottom of Table 1). In addition to these heath-species a few species occur on all kinds of sandy soils with a sparse vegetation (B1-species: bottom of Table 1) and some eurytopic species (i.e. occurring in many kinds of habitat) of sandy or peaty soils were abundant in the heath area.

Apart from the general trends of numbers over 31 years for a number of carabid species living in multipartite populations in a heterogeneous heath area, the effects of certain conservation managements, such as burning and sod cutting, on the trends, were studied by comparing the catches in sites where these were applied with those in other sites. The catches in a dry and hilly site in the heath area, AY, which was subjected to several managements, were also compared with those in an isolated dry and hilly heath area of less than 4 ha with a similar vegetation, the 'Hullen Zand', at about 10 km east of Dwingelder Veld, which was not managed in any way.

3

4

Hullenzand, sample site AU in 1967 (photograph 3) and in 1983 (photograph 2). A dry and hilly heath area of less than 4 ha which contrary to the Dwingelderveld did not change appreciably in composition and structure of the vegetation (compare photograph 3 and 4).

The 'Hullen Zand' was sampled with standard sets of pitfalls at two sites (AU and AV) during the years 1963-1970 and 1986-1989. The composition and structure of the vegetation of this small area did not change appreciably during these 25 years; photographs made in 1967 (photos 22 and 23 in Den Boer, 1977) could even directly be compared with photos made in 1983 from the same positions. This stability is curious because 'Hullen Zand' will also have had its share of air pollution. But, just as AY, the heather vegetation will not have been influenced by overall lowering of the ground-water level, because both areas were already situated many meters above the ground-water when the samplings were started .

AY is a broad, blown-sand ridge originating from sand set in motion by the passages over several centuries of the stage-coach from Zwolle to Groningen along the 'Oude Postweg', an old sand road through the Dwingelder Veld. AY has changed considerably since 1964 when sampling was started there. First of all, in 1968 a big fire completely burned the vegetation of AY. Secondly, during the 1970's grasses gradually replaced the greater part of the regenerating vegetation. And in 1988 the vegetation was mechanically cut. In 1964, however, the composition and structure of the vegetation of AY were about similar to those of 'Hullen Zand'. Therefore, concerning possible effects of changes in composition and structure of vegetation 'Hullen Zand' can be considered the null case for AY.

In the following our data often are compared with those from other surveys. To avoid irritating interruptions of the text these sources are indicated by capitals, **L** for Lindroth (1945), **B** for Den Boer (1977), **V** for Vermeulen (1993), **E** for Van Essen (1993), **H** for Van Huizen (1980), **DT** for Desender & Turin (1989).

Results

The numbers between 1959 and 1989 of the more abundant carabid species at Kralo Heath, estimated according to the procedures described above, are shown in Table 1. The most apparent feature of this table is the disappearance or near disappearance of both some A1- and some B1-species from the catches.

The partial drying of the area at the end of the 1960's and in the 1970's may have been one of the causes, because the most hygrophilous species *Agonum ericeti* and *Pterostichus diligens*, and possibly also the more eurytopic *Amara lunicollis*, did decrease in the 1970's. This conclusion seems to be supported by the disappearance from the catches of *Agonum krynickii*, a very hygrophilous species (**L**) that was only incidentally caught in the valleys of the area during the 1960's. The same applies to *Agonum marginatum*, a stenotopic species (only occurring in a few kinds of habitat) of moist, bare shores. However, a few specimens of this species reappeared in CK after the vegetation had been cut in 1982/'83. A similar reaction to cutting of the vegetation, but without disappearance in the 1970's, was found in the less stenotopic shore species *Agonum sexpunctatum*, not only reappearing in CK (Table 2), but also in some other cut areas. Therefore, this species became more abundant in the 1980's than it had been since 1959 (Table 1). An unfavourable effect of drought is also suggested by decrease of the numbers of both *A. ericeti* and *P. diligens* after the dry summers of 1959 and 1978 (Table 1).

Table 1. Estimates of the annual numbers of some characteristic carabid species at the Heath of Kralo of "Dwingelder Veld" (The Netherlands). All values are recalculated in such a way that they represent the summarized year-catches from 10 interaction groups.

species	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
A1-species															
Carabus cancellatus	18	10	12	14	13	25	23	11	12	4	3	2	.	1	2
Carabus nitens	24	20	6	8	15	12	17	12	14	.	2	2	.	.	.
Harpalus solitaris	.	.	35	26	30	34	32	89	43	12	8	.	.	18	.
Amara infima	.	.	10	30	22	58	42	65	32	14	18	193	143	72	33
Cymindis vaporariorum	24	32	34	18	16	12	9	21	23	13	15	10	38	15	27
Agonum sexpunctatum	5	7	3	3	4	12	8	6	10	8	4	7	2	4	6
Amara equestris	239	225	169	247	185	270	115	284	337	176	207	173	247	140	114
Agonum ericeti	93	51	148	117	86	96	158	64	85	77	55	20	45	84	56
Olisthopus rotundatus	12	30	72	79	35	48	59	42	.	.	3	7	11	15	59
Bradycellus ruficollis	415	1140	548	373	268	343	246	585	428	.	56	159	394	335	132
Trichocellus cognatus	267	426	199	262	297	604	179	173	313	27	88	418	491	1176	493
Carabus arvensis	112	123	43	50	66	92	66	143	164	59	29	14	5	3	.
Pterostichus lepidus	1073	1066	755	713	1393	2064	877	970	552	645	670	411	453	308	461
Harpalus latus	235	576	946	1060	958	1014	441	517	437	298	360	238	148	191	296
Pterostichus diligens	2322	1599	1905	2484	1443	1003	728	667	571	620	691	365	266	914	776
B1-species															
Notiophilus germinyi	15	14	30	20	28	9	25	26	42	6	3	5	4	2	25
Bembidion nigricorne	80	75	105	370	110	68	60	96	30	10	8	54	115	361	321
Cymindis macularis	.	.	.	.	10	9	21	14	65	38	21	12	9	2	9
Eurytopic species															
Syntomus foveatus	12	17	21	52	22	29	51	76	168	6	12	31	42	46	234
Calathus erratus	3075	1650	768	1245	2001	3412	1346	1754	1162	1216	483	427	925	995	1505
C. melanocephalus	2607	6056	5788	17630	15691	5492	2142	3302	6599	2375	660	479	651	1368	2626
P. versicolor	1525	1859	2453	3179	3649	3154	2484	2368	2887	3043	2019	1432	1269	1556	1810
Amara lunicollis	4152	284	3388	6728	3370	6408	799	2637	8242	6943	5148	892	1327	1001	1238

species	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
A1-species																
Carabus cancellatus	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Carabus nitens	.	.	.	.	.	.	.	.	1	1	1	1	.	.	8	34
Harpalus solitaris	2	4	2		.	.	.	.	.	.	.	2	2	.	.	.
Amara infima	32	91	114	43	15	22	17	6	3	.	.	3	.	.	.	.
Cymindis vaporariorum	15	22	38	30	22	7	2	4	2	12	6	5	7	2	8	1
Agonum sexpunctatum	6	5	.	2	.	3	2	3	.	.	21	33	80	30	57	38
Amara equestris	105	211	334	403	181	87	28	43	17	14	3	16	21	44	71	9
Agonum ericeti	42	28	15	14	8	.	6	3	14	29	35	68	186	29	25	36
Olisthopus rotundatus	61	35	17	19	8	13	13	2	.	1	5	11	6	10	94	22
Bradycellus ruficollis	151	117	179	169	118	92	94	84	79	94	98	82	156	5	30	155
Trichocellus cognatus	318	138	182	134	89	93	34	27	45	37	57	33	51	12	46	149
Carabus arvensis	.	.	4	18	12	12	480	335	156	143	95	97	52	70	102	199
Pterostichus lepidus	462	554	791	993	920	1128	495	449	400	153	53	101	146	119	147	244
Harpalus latus	238	100	81	100	83	86	75	96	75	96	108	174	276	163	132	161
Pterostichus diligens	783	491	470	338	573	413	553	751	855	623	720	951	766	453	471	378
B1-species																
Notiophilus germinyi	23	13	10	.	.	3	3	.	.	.	.	3	.	1	3	2
Bembidion nigricorne	272	59	14	6	29	.	2	.	2	1	14	3	4	.	1	34
Cymindis macularis	9	2	2	.	.	.	.	.		6	.	.	2	5	6	18
Eurytopic species																
Syntomus foveatus	67	70	13	6	9	2	3	.	1	8	10	52	10	33	102	66
Calathus erratus	1057	635	317	397	510	459	137	74	78	147	74	43	273	536	653	727
C. melanocephalus	1107	506	167	645	1529	3700	2011	1198	600	320	184	269	1289	1589	1333	978
P. versicolor	2382	838	1034	1324	988	1178	1356	1063	964	1115	1072	967	900	827	528	419
Amara lunicollis	1118	984	806	1051	1537	1847	1162	1050	2431	1955	1996	1682	2452	1060	1482	1884

A1-species are species of peaty soils and/or oligotrophic sandy soils
B1-species are species of non-oligotrophic sandy soils with sparse vegetation (*Corynephoretum*, and poor grassland)
The eurytopic species prefer peaty and/or sandy soils
These categories are described in Turin et al. (1991): Tables 2, 3 and 8.
In years with '.' not a single specimen of that species was caught in any of the sampling series.
7-Key-species in italics.

A. lunicollis only reacted in that way -but violently- to the extremely dry summer of 1959.

Table 2. Numerical responses of some carabid species to removal of the vegetation overgrown by grasses by mechanical cutting. All catches in CK are complete year-catches, but those in BJ only from 1986 onwards, so that the other year-catches in BJ had to be estimated from funnel-catches.

	1983	1984	1985	1986	1987	1988	1989
Site CK (cut in 1982/'83)							
A1-species							
Carabus nitens	.	.	.	.	.	1	4
Amara equestris	2	.	4	1	.	1	.
Olisthopus rotundatus	.	1	3	2	.	1	.
Agonum sexpunctatum	.	3	11	22	1	.	1
Bradycellus ruficollis	1	1	3	2	.	7	25
Trichocellus cognatus	.	1	2	10	2	15	36
Agonum ericeti	4	2	23	35	4	2	2
Harpalus latus	2	20	41	99	64	31	41
Carabus arvensis	29	14	8	15	20	13	65
Pterostichus lepidus	27	29	75	102	14	4	4
B1-species							
Bembidion nigricorne	1	12	1	.	.	1	.
Eurytopic species							
Syntomus foveatus	8	6	2	1	2	.	.
Calathus erratus	31	7	8	3	7	5	9
Bembidion lampros	31	88	46	24	10	28	4
Notiophilus aquaticus	182	339	182	211	118	36	12
Site BJ (cut in 1985/'86)							
A1-species			cut				
Amara equestris	.	.	.	3	8	10	8
Carabus arvensis	12	.	.	1	2	1	.
Pterostichus lepidus	39	20	18	25	68	120	258
B1-species							
Cymindis macularis	.	.	.	.	3	3	4
B2-species							
Nebria salina	.	.	.	191	289	820	1008
G4-species							
Amara famelica	.	.	.	.	.	14	227
Eurytopic species							
Syntomus foveatus	.	.	.	.	1	4	10
Bembidion lampros	.	.	.	1	7	9	17
Calathus erratus	.	.	.	113	295	402	330

For definitions of A1-, B1-, B2-, G4-, and Eurytopic species see tables 1 and 3 (footnotes).
Species that are absent from this table but were present in the tables 1 and/or 3 were not caught or in low numbers only. Key-species in italics.

The above conclusions -and other conclusions to follow- are complicated by certain trends in the climate of Western Europe from 1940 onwards: an increase of mean temperature and a decrease of precipitation (Kalina et al., 1985; Landmann, 1992). Also the climate of Drenthe changed in that period, but in a different direction: as compared to the mean precipitation per year of 741 mm (1928-1949) in Wijster (6 km NE of Kralo), in the period between 1958 and 1972, 12 years had a higher and only 3 years a lower than average amount of precipitation (X^2= 5.4, P= 0.02). Also between 1973 and 1992 annual precipitation in Eelde (40 km North of Kralo) deviated significantly from the average amount in the period 1921-1950 (713 mm): in 14 years higher, in only 6 years lower (X^2= 3.2; 0.10 >P >0.05). Combining these results (Siegel, 1956) gives P= 0.015 (Fig. 6). Especially winters were much wetter than in the period 1928-1949: between 1958 and 1991 26 winters had a higher and only 7 years a lower than average precipitation: X^2= 10.97 (combined, d.f.= 2), P< 0.01. Only in the last years mean year temperature increased: in the Netherlands 1989, 1990 and 1992 were the warmest years of this century (Fig. 6), which accords with the global trend since 1985 (Jones & Wigley, 1990). Be this as it may, it does not seem obvious that hygrophilous species would be harmed by an increase of precipitation. Nevertheless, the output of water from the 'Dwingelder Veld' by an improved drainage seems to have had more effect than the increased input.

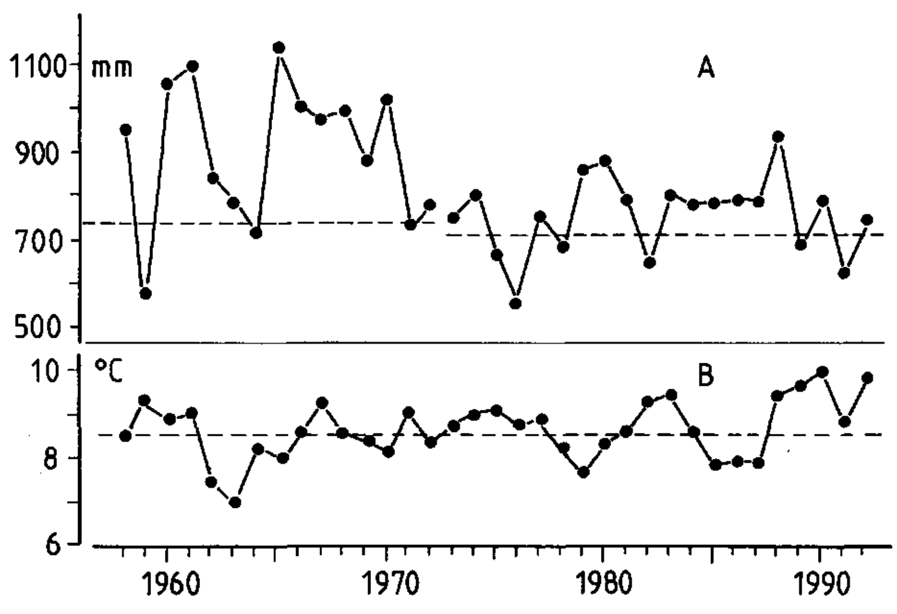
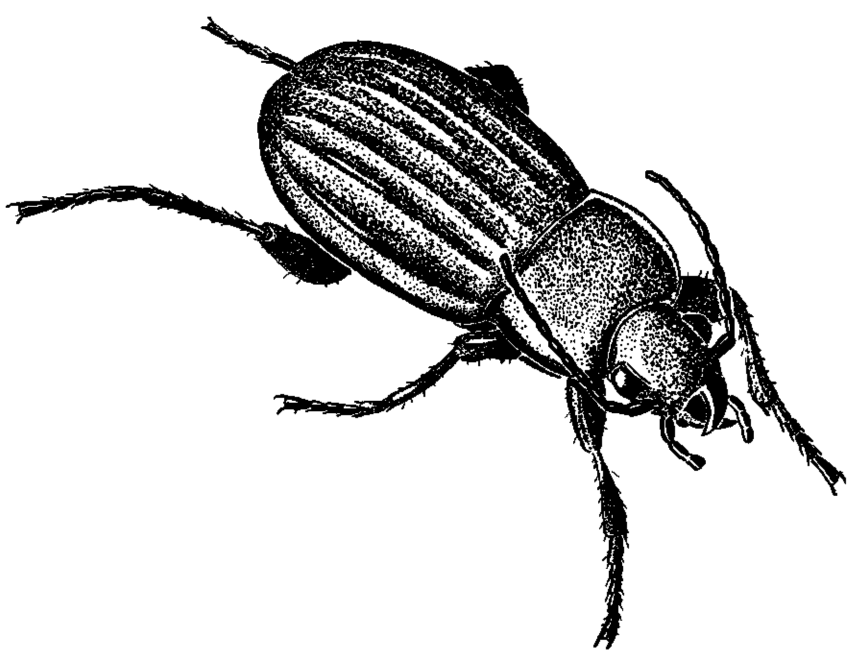


Fig. 6. A. Annual precipitation (in mm) at Wijster (1958-1972) and at Eelde (1973-1992) respectively. Broken horizontal: average precipitation per year for the period 1928-1949 (Wijster) and 1921-1950 (Eelde) respectively.
B. Mean air temperature (in °C.) per year at Eelde. Broken horizontal: average mean year temperature in the period 1921-1950 (Eelde).

A. ericeti not only reacted negatively to dry years, but also seems to react positively to the new conservation measure of sod cutting (Table 1). A stenotopic species of peat moor (De Vries & Den Boer 1990), at 'Dwingelder Veld' it is almost restricted to the *Erica*-vegetations in the valleys. Therefore, it does not appear everywhere after sod cutting; not in BJ (Table 2) where it has never been caught, and hardly in Z (Table 3) where it was found in high numbers only in the 1960's (De Vries & Den Boer 1990: Fig. 1). The species also reacted positively to the maintenance burning of N (Table 3), but the *Erica-Calluna* vegetation of N always has been a favourable habitat for *A. ericeti* (De Vries & Den Boer 1990: Fig. 1).

This positive reaction of these hygrophilous and day-active species to sod cutting is also connected with their preference for open vegetation where solar radiation can easily warm the soil. Therefore, *P. diligens* and *A. lunicollis*, which prefer dense and moist to wet grass vegetation (**B**) did not increase in numbers in the 1980's as compared to the 1960's (Table 1).

But also some non-hygrophilous A1- and B1-species almost disappeared or greatly decreased during the 1970's, e.g. *Carabus cancellatus*, *C. nitens*, *Harpalus solitaris*, *Notiophilus germinyi* (Table 1). In fact, most stenotopic species, both A1- and B1-species, and even some of the eurytopic species, decreased during the 1970's. Only a few species, such as *Amara infima*, *Cymindis vaporariorum*, *A. equestris*, *Trichocellus cognatus*, *Syntomus foveatus*, did not follow this trend, the



Carabus nitens unwinged 13-18 mm

Table 3. Numerical responses of some carabid species to removal of the vegetation, either by mechanically cutting the vegetation overgrown by grasses, or by burning an old heather vegetation. Until 1985 the year-catches in Z had to be estimated from funnel-catches, in N only for the year 1979.

	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
Site Z (cut in 1985/'86)												
A1-species							cut					
Carabus nitens	.	.	.	.	.	.	.	.	.	7	23	36
Amara equestris	12	4	.	3	.	.	.	2	2	2	3	15
Agonum ericeti	.	.	.	.	.	28	9	3	.	3	1	3
Olisthopus rotundatus	3	.	.	.	.	.	.	.	.	10	10	40
Bradycellus ruficollis	26	20	36	22	18	26	23	.	1	14	31	10
Trichocellus cognatus	12	9	.	28	8	12	.	3	.	6	23	35
Carabus arvensis	13	9	26	34	19	36	30	1	8	2	26	19
Harpalus latus	.	.	.	2	1	2	3	15	15	4	9	41
Pterostichus lepidus	126	42	5	5	1	.	1	19	25	28	48	43
B1-species												
Bembidion nigricorne	.	.	.	.	.	.	.	.	.	.	33	16
Cymindis macularis	.	.	.	.	.	.	.	.	4	8	4	3
B2-species												
Nebria salina	.	.	.	.	.	.	.	9	30	69	83	78
G4-species												
Amara famelica	.	.	.	.	.	.	.	.	.	179	371	31
Eurytopic species												
Syntomus foveatus	.	.	.	.	.	.	16	4	23	99	48	119
Calathus erratus	1	1	2	1	2	3	.	22	95	159	253	619
Bembidion lampros	.	28	8	6	.	4	30	3	49	110	38	135
Notiophilus aquaticus	26	9	.	4	.	18	14	2	11	49	116	386
Site N (burned in 1979/'80)												
A1-species		burned										
Carabus nitens	.	.	.	1	1	.	1	.	.	.	.	9
Amara equestris	24	3	.	2	4	1	1	8	1	.	.	.
Agonum ericeti	.	2	1	10	19	18	34	18	10	9	4	4
Olisthopus rotundatus	.	1	.	.	1	4	8	4	1	3	4	4
Bradycellus ruficollis	26	18	3	1	8	25	10	76	1	2	4	13
Trichocellus cognatus	.	3	.	.	10	9	1	4	.	.	12	2
Carabus arvensis	.	478	299	85	53	29	4	21	30	67	65	52
Harpalus latus	.	1	1	2	2	8	10	22	8	9	14	65
Pterostichus lepidus	67	42	18	21	18	4	11	11	13	10	6	11
G4-species												
Amara famelica	.	.	12	36	5	10	.	.	.	1	1	.
Eurytopic species												
Calathus erratus	.	9	23	52	107	55	3	2	2	1	1	4
Bembidion lampros	2	3	11	9	16	33	57	28	15	15	14	43
Notiophilus aquaticus	28	5	47	104	89	87	75	56	72	37	38	65

For definitions of A1-, B1-, and Eurytopic species see Table 1
B2-species are species of sandy arable land and coniferous plantations
G4-species are species of marshes and wet meadows
See Turin et al. (1991: Tables 2, 3, 6, 8)
Key-species in italics.

first three merely to react later, i.e. decreasing in the 1980's (Table 1). Apparantly, during the 1970's some general 'factor' in the environment had become increasingly unfavourable for most species. This may have been either acidification/fertilization of the soil by air pollution, or the most apparent effect of it, the extension of grasses at the expense of heather species (see Introduction). It may also have been an effect of the climatic trends mentioned above. The first hypothesis is supported by the fact that in the course of the 1980's, when the sod cutting machine became increasingly active, especially a number of heath (A1) species recovered (for instance, *C. nitens*, *A. sexpunctatum*, *A. ericeti*, *Olisthopus rotundatus*, *Carabus arvensis*, and possibly also *Bembidion nigricorne* and *Cymindis macularis*).

Possibly, we come closer to a hypothesis about a cause-effect relationship when also considering Tables 2 and 3. It then appears that at some sites most of the above species reacted positively to sod cutting, though often with a delay of some years. For some other species, for which it was not evident from the general trend in Table 1, and for those which were not in that table because they occurred too locally, such a reaction was often more convincing at specific sites (e.g. for *Nebria salina* at BJ, Z, *Pterostichus lepidus* at CK, BJ, Z, *A. equestris* at BJ, Z, *Calathus erratus* at BJ, Z, *Notiophilus aquaticus* at CK, Z, *Amara famelica* at Z and *S. foveatus* at BJ, Z), whereas these species did not react at sites that were not managed.

C. arvensis sometimes increases in response to burning (Table 3: N). In only a few species burning had a positive effect similar to sod cutting (e.g. in *A. famelica*, *C. erratus*, *N. aquaticus*, and possibly in *A. ericeti*: Table 3, N). Burning does not take away the effects of air pollution. Thus most species did not increase in numbers after burning. These observations were confirmed by other samplings after burning and/or sod cutting. The reaction of *N. salina* to sod cutting is especially remarkable. This opportunistic species was caught only incidentally during the 1960's (mainly in N and Z, **B**: 161), became still scarcer during the 1970's, and then reappeared in high to very high numbers only immediately after sod cutting (e.g. also in CS (Fig. 1), cut in 1987: in '88: 1017 exx., in '89: 1636 exx.). Although this species is always fully winged, only one beetle of 752 specimens from Kralo Heath caught in the 1980's had functional wing muscles. Flight was observed once (compare *N. brevicollis*: Nelemans 1987). Therefore, the outbreaks of this species must have been caused by extraordinary reproductive success of the few individuals that happened to reach the newly cut heath areas.

But what actually causes the recovery of a number of stenotopic (mainly A1) carabids after sod cutting? The removal of the dense grassy vegetation or the taking away of the acidified/eutrophicated litter? Or a combination of both, whether or not stimulated by climatic changes? Table 3 shows that, at least for a number of these species the removal of the polluted layer of litter must have been more important than the disappearance of the vegetation. Only a few species that reacted positively to sod cutting in Z did the same after burning, and then their response was usually weaker (e.g. in *A. famelica*, *C. erratus*, *N. aquaticus* in N).

Possibly, we can get a step further in this causal analysis by also taking into account the changes in time at 'Hullen Zand', where the vegetation did not visibly change, and compare with AY, where it changed very much.

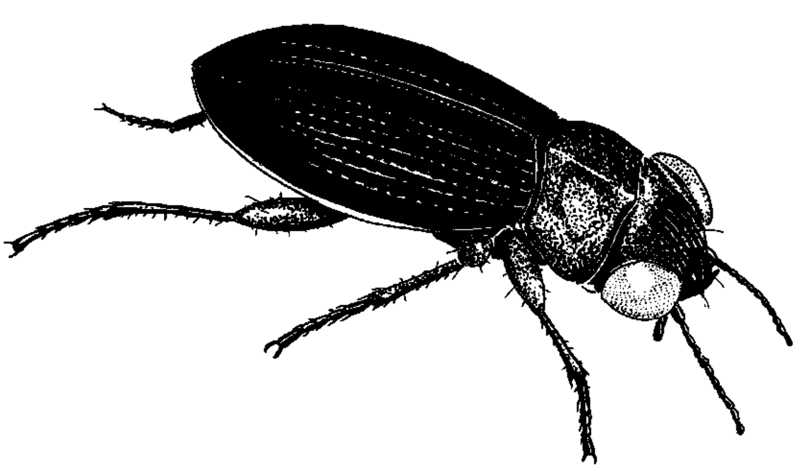
Table 4. Summed (complete) year-catches in two standard series of pitfalls (AU, AV) at **'Hullen Zand'**, a dry and hilly heath area with blown sand.

	1963	1964	1965	1966	1967	1968	1969	1970	1986	1987	1988	1989
A1-species												
Carabus cancellatus	26	17	1	19	20	12	16	1	.	.	.	.
Carabus nitens	2	9	6	6	8	2	2	1	.	.	.	.
Harpalus solitaris	1	1	3	3	.	.	.	.	.	.	.	.
Amara infima	32	33	22	24	97	5	29	59	.	.	.	.
Olisthopus rotundatus	25	8	17	9	8	5	4	3	.	1	.	1
Trichocellus cognatus	32	65	9	19	94	1	30	43	.	.	1	.
Bradycellus ruficollis	44	20	15	20	44	.	5	19	6	1	6	9
Agonum sexpunctatum	2	1	10	10	4	1	4	2	6	1	5	2
Amara equestris	.	.	.	.	.	.	.	3	10	23	80	30
Harpalus latus		3	1	1	.	.	.	.	1	2	.	2
Pterostichus diligens	8	5	4	.	3	10	9	1	16	13	38	81
Pterostichus lepidus	101	70	70	72	62	41	106	59	88	101	117	254
B1-species												
Cicindela sylvatica	1	.	.	1	.	2	5	.	.	.	.	.
Cicindela hybrida	.	2	18	4	2	3	10	6	1	3	1	.
Masoreus wetterhalii	.	1	2	3	4	1	1	1	1	2	1	5
Notiophilus germinyi	69	69	109	49	93	.	11	42	.	.	1	3
Bembidion nigricorne	157	134	439	368	830	.	95	170	1	1	.	.
Cymindis macularis	22	24	24	24	47	36	42	35	13	13	34	28
B2-species												
Broscus cephalotes	55	61	27	44	51	23	19	17	.	.	.	1
Harpalus anxius	4	3	3	.	3	.	1	.	24	13	18	18
Harpalus rufitarsis	.	1	1	2	1	1	.	.	47	47	61	69
other species of sandy areas												
Amara quenseli (C1)	7	9	1	4	1	.	.	.	.	.	.	.
Amara fulva (C1)	2	1	2	.	3	4	2	1	.	.	.	2
Amara praetermissa (D3)	3	3	3	.	1	.	.	.	.	.	.	.
Amara famelica (G4)	1	1	2	3	4	1	.	1	.	.	1	.
Eurytopic species												
Bradycellus harpalinus	23	9	5	25	32	2	16	29	1	1	10	11
Notiophilus aquaticus	295	58	491	407	189	1	18	54	1	21	45	49
Syntomus foveatus	65	55	68	65	177	.	57	26	1	4	10	57
Leistus terminatus	20	.	7	.	1	1	.	.	14	7	2	9
Dyschirius globosus	6	8	1	10	5	.	7	.	.	15	1	1
Bembidion lampros	3	3	1	4	5	2	21	1	4	.	.	3
Amara plebeja	1	4	3	2	13	20	15	13	22	6	7	12
Amara aenea	1	.	1	.	1	3	3	1	3	3	22	11
Amara lunicollis	2	5	2	2	10	6	15	.	90	27	397	145
Calathus fuscipes	.	.	.	.	.	.	.	.	9	2	1	7
Calathus erratus	1055	1119	639	792	1485	981	832	416	659	486	461	725
Calathus melanocephalus	198	119	91	89	131	67	99	80	1330	535	570	646
Harpalus rufipes	2	.	1	2	1	.	.	2	1	27	12	24
Pterostichus niger	17	4	7	2	.	1	.	.	10	31	43	21
Pterostichus versicolor	5	13	7	7	9	12	39	15	60	66	221	201

For A1-, B1-, B2-, G4-and Eurytopic species see Tables 1 and 3 at the bottom.
C1-species are species from open sites that differ from those of the B-species
D3-species are species from shaded and somewhat ruderal sites
Key-species in italics.

Table 4 shows that most of the stenotopic species that disappeared or strongly decreased in numbers in the 1970's and/or 1980's at Kralo Heath (Table 1) reacted similarly at 'Hullen Zand' (e.g. *C. cancellatus*, *C. nitens*, *H. solitaris*, *A. infima*, *N. germinyi* were not or hardly caught there in the 1980's). Therefore, the cause may have been the same – eutrophication and/or acidification of the soil. But only *C. nitens* recovered after sod cutting (Tables 2 and 3), so we cannot be sure that only air pollution was the cause. Climatic changes may have played a part too, for *C. nitens* seems to be a thermophilous species (Thiele, pers. comm.). Acidification/fertilization as a cause is better supported in other stenotopic species that strongly decreased at 'Hullen Zand', either reacting positively to sod cutting (*O. rotundatus*, *B. nigricorne*, *A. famelica*), or not clearly decreasing at all at Kralo Heath (*Trichocellus cognatus*, *Bradycellus ruficollis*): Tables 1, 2, 3, 4. In AY (Table 5) all these species reacted as at 'Hullen Zand', though in 1969, 1970 and 1971, i.e. just after burning of the vegetation, numbers did not clearly decrease in *A. infima*, *T. cognatus*, *B. nigricorne* and *A. famelica*, but air pollution did not yet play a significant part in these years (compare Table 1). A negative effect of the increase of precipitation (Fig. 6) cannot be excluded either.

But there were more stenotopic species that disappeared or strongly decreased in numbers at 'Hullen Zand': *Cicindela sylvatica*, *C. hybrida* (?), *Broscus cephalotes*, *Amara quenseli*, *A. fulva* and *A. praetermissa*. As the suitable habitat at 'Hullen Zand' is very small (less than 4 ha) these, and others among the above mentioned species, may have disappeared because the area is too small to maintain viable populations (**B**; De Vries & Den Boer 1990). Also in these species higher precipitation may have been disadvantageous. On the other hand, there were some species which were decreasing in AY, which did not decrease or even increased at 'Hullen Zand': the A1-species *A. equestris* and *P. lepidus*, the B1-species *Cymindis macularis*, and



Notiophilus germinyi wing-dimorphic 4.5-5.5 mm

Table 5. Year-catches in series **AY**, a dry, sandy ridge with a mosaic vegetation.

	1964	1965	1966	1969	1970	1971	1985	1986	1987	1988	1989
A1-species			burned							cut	
Carabus cancellatus	1	3	.	1	.	.	.	.	.	.	.
Carabus nitens	1	1	.	.	.	.	.	.	.	1	.
Harpalus solitaris	3	1	2	.	.	.	.	.	.	.	.
Miscodera arctica	5	.	2	.	1	.	.	.	.	.	.
Olisthopus rotundatus	9	9	4	1	2	2	.	.	.	.	.
Amara infima	41	32	51	14	179	127	2	.	.	.	.
Bradycellus ruficollis	59	85	251	4	13	41	.	.	.	.	.
Trichocellus cognatus	35	71	74	15	291	311	18	31	8	2	.
Amara equestris	17	10	14	2	12	50	3	2	3	2	1
Harpalus latus	6	5	4	6	8	**11**	**27**	**27**	**29**	**13**	4
Pterostichus diligens	29	24	28	11	3	**3**	**23**	**34**	**26**	**28**	19
Pterostichus lepidus	247	145	149	93	61	**105**	**19**	**30**	**20**	**9**	9
B1-species											
Bembidion nigricorne	24	44	76	2	46	52	.	.	.	.	.
Cymindis macularis	3	9	5	2	6	6	.	.	.	.	.
Notiophilus germinyi	1	4	4	.	3	.	.	1	.	.	.
B2-species											
Broscus cephalotes	6	.	1	1	.	.	.	.	2	.	.
Harpalus rufitarsis	.	.	.	9	11	2	.	1	3	2	.
Nebria salina	1	.	.	17	2	8	.	.	.	2	104
other species of sandy sites											
Amara famelica (G4)	.	3	.	.	36	21	.	.	.	.	.
Eurytopic species											
Syntomus foveatus	14	13	7	4	17	12	1	.	.	.	.
Bembidion lampros	.	1	.	3	.	2	2	.	.	.	.
Amara aenea	.	.	.	.	9	3	2	.	.	2	4
Amara plebeja	.	1	1	4	1	2	8	6	2	.	1
Bradycellus harpalinus	29	14	25	4	14	35	35	58	2	.	1
Agonum obscurum	15	32	31	1	.	.	9	23	8	.	.
Notiophilus aquaticus	137	167	117	7	52	24	4	6	23	19	7
Dyschirius globosus	62	30	111	4	1	2	5	3	5	7	4
Amara lunicollis	44	59	67	52	147	**128**	**44**	**75**	**165**	**76**	28
Calathus fuscipes	1	.	.	.	.	.	1	12	.	.	.
Calathus erratus	17	106	98	146	148	**234**	**5**	**8**	**18**	**6**	51
Calathus melanocephalus	13	518	509	48	41	**43**	**97**	**418**	**402**	**202**	59
Harpalus rufipes	1	.	1	.	20	24	.	.	8	.	2
Pterostichus niger	15	4	1	1	.	.	9	13	18	2	2
Pterostichus versicolor	367	264	163	22	24	**90**	**117**	**107**	**126**	**45**	10

For definitions of different groups of species see Tables 1 and 3.
In the years 1971 until and including 1988 only of the 7 italicized species (with bold type numbers for these years) complete year-catches were available; for all other species the year-catches for these years had to be estimated from the funnel-catches according to the procedure explained in Methods (catches of 1972 through 1984 are omitted). In 1968 AY was burned, and in 1988 the vegetation was mechanically cut.

the eurytopic species *S. foveatus* and *C. erratus* (Tables 4 and 5). Possibly, these species are less sensitive to the consequences of air pollution and/or increase of precipitation.

The conclusion that for many species the effects of air pollution may have been a more important cause of the changes in numbers at 'Hullen Zand' than changes in the structure and composition of the vegetation, seems to be supported by the fact that the somewhat ruderal B2-species *Harpalus anxius* and *H. rufitarsis* (= *rufipalpis* Sturm), together with a number of eurytopic species (*A. lunicollis*, *Calathus fuscipes*, *C. melanocephalus*, *Pterostichus niger* and *P. versicolor*) increased in numbers in the 1980's (Table 4). The numbers of other eurytopic species at 'Hullen Zand' did not significantly change. Nor did any eurytopic species in AY, with the exception of *S. foveatus*, which decreased in numbers (Table 5).

The question remains: By what process does air pollution harm so many stenotopic carabids? In fact, we don't know. Probably, the larvae of these species do not tolerate a further acidification of the poor and already acid soil (at Kralo Heath in the 1960's pH was about 3.0). This hypothesis seems to be supported by the fact that one of the most stenotopic as well as oligotrophic species *Agonum ericeti* was harmed comparatively least. Krogerus (1960) found that the larvae of this species thrive well at the very acid conditions often occuring in *Sphagnum*-moors. On the other hand, it can hardly be expected that the larvae of many eurytopic species are better able to tolerate highly acid conditions than those of oligotrophic species.

Discussion

By studying the fluctuation patterns of carabid beetles and by simulating these patterns with the computer Den Boer (1981, 1985, 1990a) could estimate expected survival times. These simulations were based on the assumption that the environment is stationary. This means that in the future environmental conditions would vary about the same as was found during the field observations from which the simulations were derived. However, this study demonstrates that the environment was not stationary. For most species, especially stenotopic ones, conditions became less favourable as the ground-water level fell, air pollution increased, and climate changed. These changes were not restricted to Kralo Heath, but occur all over Western Europe. Therefore, Den Boer's estimates of survival times are too optimistic for stenotopic species of heath and/or other open sandy sites. These changes will have affected the net reproduction (R) values estimated in the field in the 1970's and 1980's, but the more favourable R-values, estimated in the 1960's, will have contributed equally to the frequency distributions of R-values that formed the input of the simulation experiments.

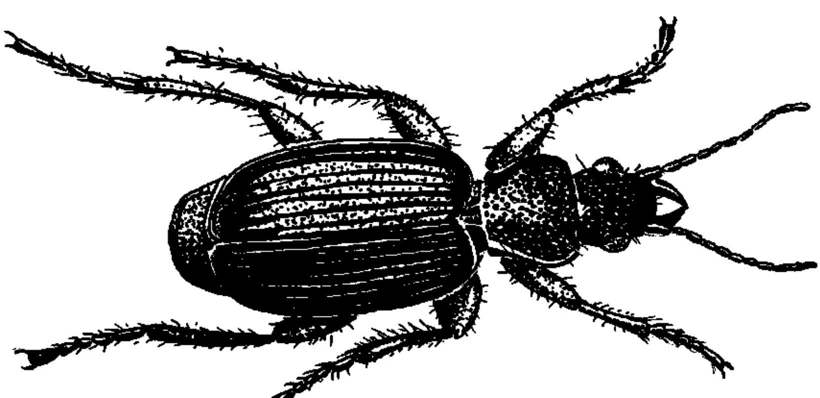
As the expected survival times of interaction groups of many species were already low (e.g. in *Agonum ericeti*, De Vries & Den Boer, 1990; see further Den Boer, 1990a: Table 4, Fig. 5, and 1990b: Table 1), many species are seriously threatened, especially oligotrophic species with low powers of dispersal. It may be that in large areas, such as the heath area of 'Dwingelder Veld', which is occupied by many interaction groups, the chance to survive this unfavourable period will be high -in any case higher than in smaller areas. This is probably right as far as the negative effects of a lowered ground-water level are concerned, because in the 'Dwingelder Veld' many moist and even wet sites are left, and precipitation increased. Moreover, the conservation authorities try to repair the past hydrological situation, as far as possible, by closing several drainage systems. But the deleterious effects of air pollution are more general. We don't know how many years this situation will be continued in spite of growing protests. It is true that sod cutting seems to take away part of the deleterious effects of air pollution. However, there are increasing objections against the use by plant growers of the cut materials, because these appeared to contain too high levels of heavy metals. Without any possibility of recycling these materials sod cutting will soon be stopped. And this in spite of the often spectacularly favourable effects, both for the recovery of heather vegetation and for the survival of many stenotopic carabids.

As long as larger heath areas persist, eurytopic carabids of heath areas are not endangered. On the contrary, they seem to be favoured by the present level of air pollution, as long as all the heather is not replaced by grasses. For, even in the 1960's a dense *Molinia*-vegetation at Kralo Heath (M) was only populated by a few eurytopic species (*Agonum obscurum*, *Amara lunicollis*, *Calathus melanocephalus*, *Dyschirius globosus*, *Pterostichus versicolor* and *P. niger*) and two A1-species (*Pterostichus diligens* and *Harpalus latus*). At the same time heath areas were populated by higher numbers of 20-30 carabid species, most of which were stenotopic.

Therefore, we have to consider which of the stenotopic carabids of the heath can be expected to survive the recent changes of the environment, especially in connection with their abilities to disperse.

Unwinged (brachypterous species)

Small brachypterous species (3-6 mm), such as *Bembidion nigricorne* and *Masoreus wetterhalli*, can easily become completely isolated in small habitat frag-



Cymindis vaporariorum wing-dimorphic 7.5-9.6 mm ments (e.g. 'Hullen Zand': Table 4), where they are unlikely to survive for several centuries.

B. nigricorne is a winter reproducer (Den Boer et al. 1990) that shows heavy fluctuations of numbers. In the 1960's it was caught in some years at 'Hullen Zand' in very high numbers, but it had almost disappeared there in the 1980's (Table 4). Fortunately, at Kralo Heath, where it occurred at several sites (**B**: 145), it reacted positively to sod cutting (Table 3).

Masoreus wetterhalli, on the other hand, was never found at Kralo Heath. It is still present at 'Hullen Zand', but it is seriously endangered in this small area. 'Hullen Zand' is planned to be connected to 'Balinger en Mantinger Zand', 'Lentsche Veen' and 'Martensplek' by purchase of the intervening agricultural fields and changing them back into areas of heath and drift-sand. The species is still present in some other drift-sand areas in the Netherlands (also in Drenthe) and in some heather-covered road-side verges (**V**).

Bigger brachypterous heath species (7-10 mm), such as *Agonum ericeti* and *Cymindis macularis* can cover larger distances between suitable habitats, but may become completely isolated when habitat fragments are more than (say) 200 meters apart. *A. ericeti* is still present in several moist to wet sites of 'Dwingelder Veld', and can be expected to survive there as long as the extensive *Erica*-vegetation in the valleys can be maintained (see further: De Vries & Den Boer 1990; **B**: 137).

C. macularis was caught in low numbers in a few sites of 'Dwingelder Veld' (**B**: 153), though it seems to react positively to sod cutting (Tables 1, 2, 3). It is still abundant at 'Hullen Zand' (Table 4), and might possibly be saved by the planned extension of the area (plan 'Goudplevier').

Another carabid, the supposedly brachypterous and very rare *Cicindela germanica*, a single specimen of which was caught in 1960 at Kralo Heath, must be considered to have become extinct at 'Dwingelder Veld'.

In the 1970's *Carabus nitens* (13-18 mm) was supposed to have become extinct at Kralo Heath (Table 1), but in the 1980's it reappeared at sites where the vegetation had been cut (Table 3: Z), not only in Drenthe, but also in other heath areas in the Netherlands. During a sampling program at 38 sites spread over the entire National Park of 'Dwingelder Veld' *C. nitens* was caught again in 25 series (**E**: 308 exx.). Possibly it also reacted to the recent, general increase of temperature.

Carabus cancellatus (20-27 mm) seems to have become extinct during the 1980's, both from the 'Dwingelder Veld' (Table 1) and from 'Hullen Zand' (Table 4). The area of distribution of both *C. cancellatus* and *C. nitens* since 1950 decreased significantly in the three West European countries of where reliable data are available, the Netherlands, Belgium (including Luxembourg) and Denmark (**DT**). It also severely decreased in Slovakia (Kleinert, 1987).

The future of *Carabus arvensis* is unclear. At Kralo Heath it decreased in the 1970's, but in the 1980's it surpassed the abundance level of the 1960's (Table 1). It is considered an endangered species by Desender & Turin (1989). It is the only heath species with a gradually shifting habitat preference, from *Calluna*-heath to coniferous plantations and forests from West to East across Europe (**L**; Szyszko 1990).

Only a single brachypterous species of heath areas, *Pterostichus lepidus* (11-15 mm), seems not to be endangered, both at 'Dwingelder Veld' (Tables 1, 2, 3, 5; **B**: 166; **E**), at 'Hullen Zand' (Table 4), and in other sandy areas (**V**). This is the more remarkable since the distribution area of this species was observed to have decreased significantly since 1950, both in the Netherlands (Turin & Peters 1986: Fig's 3, 4; Turin & Den Boer 1988: Table 6, Pd 15) and in other West-European countries (**DT**: Table 3). Figure 5 shows that in the 1980's *P. lepidus* also decreased at Kralo Heath.

Wing-dimorphic species

Stenotopic heath species with poor powers of dispersal, either because winged specimens are sporadic, or because flight has never or only very incidentally been observed, are seriously threatened by the recent environmental changes.

A good example of such an endangered species is *Amara infima*, a small beetle (4-5 mm) that reproduces in winter at bare or sparsely covered, moist sandy sites. Although it is wing-dimorphic, winged specimens are rare (**B**: Table 3) and flight has never been observed (**L**; **H**). At Kralo Heath it was only caught in a few localities (**B**: 142), and almost disappeared in the 1980's (Table 1, but see also **E**). In the sixties it was abundant at 'Hullen Zand', but had disappeared late in the 1980's (Table 4). The future of this species therefore seems to be as precarious as that of *B. nigricorne* -or even worse (compare **DT**; **V**). Such winter-reproducing species have the extra disadvantage that conditions for reproduction are highly variable, some winters being continually very unfavourable (too wet or continuous frost): Den Boer et al. (1990).

The prospects of another wing-dimorphic species, *Notiophilus germinyi* (4-6 mm) (**B**: Table 3) are not much better. It reproduces late in summer in open sandy sites and has to pass winter in the larval stage. In the 1960's it was caught at several sites of Kralo Heath (**B**: 162), but almost disappeared in the 1970's and 1980's (Table 1; **E**); the same occurred at 'Hullen Zand' (Table 4). But there is still some hope, the decline seems not to be general (**DT**: Table 3), and the species is also present in heather-covered road-side verges (**V**).

Olisthopus rotundatus (6-7 mm) has winter larvae (Den Boer et al., 1990), and is able to survive at road-side verges (**V**). Although winged individuals are not rare (**B**: Table 3) we never observed flight (**H**, but see also **L**). In the 1960's the species occurred at several sites of Kralo Heath (**B**: 164) and at 'Hullen Zand' (Table 4), sometimes it reacted positively to sod cutting (Table 3), and as a result of these reactions in the 1980's it restored its abundance (Table 1). Therefore, we have reasons to believe that in the long run *O. rotundatus* will be able to maintain itself, at least at Dwingelder Veld (**E**).

The boreo-montane *Cymindis vaporariorum* (8-9 mm) (**L**) seems to be a much more endangered species (**B**: Table 3). At Kralo Heath it is sparsely distributed over localities with a moist heath-like vegetation (**B**: 154), and it decreased in numbers in the 1980's (Table 1, **E**). This decline seems to be more general in Western Europe (**DT**). Fully winged individuals sometimes take flight (**L**): only a single specimen was caught in flight in 1970 in a window trap at Kralo Heath. However, the prospects of this species seem to be bad, because outside 'Dwingelder Veld' it is hardly ever found in heath or peat moor areas. On the other hand, the area of 'Dwingelder Veld' is sufficiently large to give it a chance of survival, if conditions improve soon.

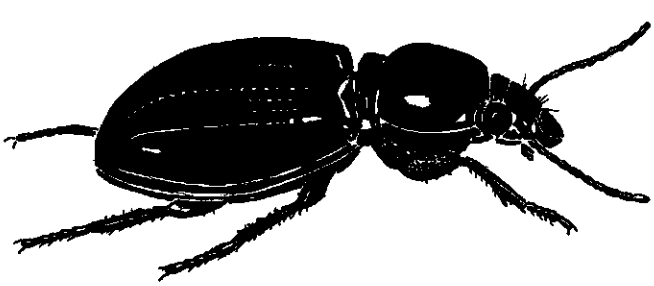
The only wing-dimorphic heath species that seems to thrive well is *Pterostichus diligens* (5-6 mm), though the numbers were higher in the 1960's than in the 1970's and 1980's (Table 1, Fig. 4). Although it prefers dense and moist grass vegetations (**B**: 165), and both grasses and moisture increased in the 1970's and 1980's, perhaps it does not favour the connected acidification and/or fertilization. The relative success of this species will depend only slightly on flight, because the frequency of fully winged specimens is low (**B**: Table 3), and flight does not occur very often, even when it is abundant. In 20 years of window trap catches we only caught 11 specimens in flight (see also **L**).

Fully winged (macropterous) species

Among the constantly macropterous, stenotopic species there are also some that are seriously endangered, mainly because the wings are not or only exceptionally used. Such a species is *Harpalus solitaris* (=*fuliginosus* Dfts.), which in the 1960's was abundant in some mosaic vegetations (AG, BG, BF) at Kralo Heath (**B**: 155), but sharply decreased in numbers in the 1970's and almost disappeared in the 1980's (Table 1). It also disappeared from 'Hullen Zand' (Table 4). The wings are large enough to be used (Den Boer et al. 1980: Table 2), but it has never been observed in flight (**L**; **H**). It is still present at 'Dwingelder Veld' (**E**), and it occurs also at some heather-covered road-side verges (**V**).

The only -but very sparse- population of *Agonum krynickii* west of the river Elbe that in the 1960's occupied the valleys of Kralo Heath almost certainly has become extinct. The wings of this species are fully developed, but we never saw a specimen with functional flight muscles (see also **L**).

It is not clear whether the almost boreo-alpine *Miscodera arctica* is still present at 'Dwingelder Veld'. Single specimens were caught in several sites of Kralo Heath between 1964 and 1972 (see e.g. Table 5), but during the last 20 years it was not seen again (see also **E**), though it was caught at several heather-covered road-



Miscodera arctica fully winged 6.5-8 mm

side verges (**V**). The species is fully winged, but flight has never been observed so far (**L**; **H**).

For a long time *Amara quenseli* was only caught at 'Hullen Zand' (**B**: 144), but was disappeared in 1968 (Table 4). Something similar happened to *Amara praetermissa* and *Cicindela sylvatica* (Table 4). In 1989, however, *A. quenseli* appeared at Kralo Heath. As the two *Amara* species do not or only rarely fly (**L**; **H**), one is inclined to suppose that these species became extinct because the populations in this area of only 4 ha were too small. *C. sylvatica*, however, is an active flyer, it even hunts by flight. In the 1940's it still was a common species along sand roads in coniferous plantations in the central and eastern parts of the Netherlands. But since 1950 its area of distribution has sharply decreased (Turin & Peters 1986: Fig's 1, 2); the causes are unknown, but may be connected with climatic changes. We fear that these three species, which were quite characteristic for 'Hullen Zand', and were not or only incidentally caught in other sampling series in Drenthe, will never return to 'Hullen Zand', and will have to be reintroduced after the planned extension of the area.

Amara fulva, which was only incidentally caught at Kralo Heath, also almost disappeared from 'Hullen Zand' (Table 4). It is a characteristic species of almost bare drift-sand localities. It is able to fly, but was only caught in window traps three times during 20 years (see also **L**) It is still present in other drift-sand areas. In 1991 it was caught at 'Dwingelder Veld' (**E**).

Other macropterous, stenotopic species seem not especially threatened. The winter reproducers (Den Boer et al., 1990) *Bradycellus ruficollis* and *Trichocellus cognatus* decreased in numbers in the 1980's, but recovered after sod cutting (Table 1). Both species are regular flyers. We caught 94 specimens and 83 specimens respectively in flight in the course of 20 years (see also **L**). Both species occur at heather-covered road-side verges (**V**).

Amara equestris is a more special case. It was common at many sites of Kralo Heath, especially in mosaic vegetations (AG, BG, BF, BB; **B**: 140). It decreased in numbers during the 1980's (Table 1), but exactly at that time increased at 'Hullen Zand'. Has it been favoured by climatic changes or by the effects of air pollution? It is also a common species at heather-covered road-side verges (**V**). Although it is winged, the wings are small (Den Boer et al., 1980: Table 1), and possibly unsuitable for flight. In this respect *A. equestris* might be comparable to *Harpalus latus*, which also has small wings (Den Boer et al., 1980: Table 2), but is caught in window traps (12 specimens in 20 years).

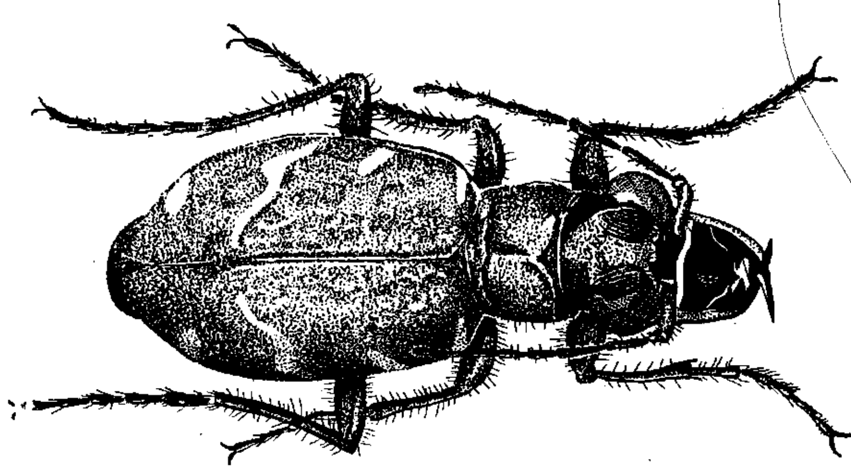
Amara famelica, a very stenotopic species of moist and open sites with only short vegetation, often appears soon after a disturbance, such as inundation (**B**: 141, e.g. P), fire, or sod cutting (Tables 2, 3, 5). It is a regular flyer: we caught 32 specimens in window traps in the course of 20 years. Because of its high powers of dispersal it is unlikely to be seriously endangered by the recent changes of the environment as long as suitable habitats remain available.

Agonum sexpunctatum is less stenotopic than *A. famelica*, but otherwise shows a similar way of life, and therefore the two species are often found together (**B**: 138). Also *A. sexpunctatum* flies regularly. We caught 7 specimens in window traps.

Summarizing, in the 1970's and 1980's air pollution, dehydration, and possibly climatic changes caused unfavourable changes in the environment of most stenotopic carabids of heath areas and other open sandy sites. Some of these species have already disappeared from Kralo Heath and/or 'Hullen Zand', others recovered after vegetation overgrown by grasses was mechanically cut. In many sites, however, such as 'Hullen Zand', they are gradually being replaced by eurytopic species. An alternative hypothesis, stating that these replacements resulted from direct competition, probably is incorrect, because competition can hardly be expected to play a prominent role among these inefficient and highly polyphagous predators (Den Boer, 1986a; Van Dijk & Den Boer, 1992). Many oligotrophic heath species were still present at other sites of 'Dwingelder Veld' in 1991 (**E**), and a number of these species are also able to survive at heather-covered road-side verges (**V**).

It is remarkable that many of the stenotopic species of heath and other open sandy sites occur at heather-covered road-side verges and are favoured by sod cutting. The only common feature of these two kinds of habitat is that the soil surface only recently became exposed. The entire soil of the road-side verges was brought up only some decades ago at most. The soil surface of the cut areas was recently stripped of its litter that probably collected most of the acidifying/fertilizing agents. This does not mean that air pollution should not be decreased or stopped as soon as possible, in order to prevent a return after some years or decades, to the situation of the 1970's. And more road-side verges should be made suitable for the development of a heather vegetation.

It remains uncertain whether, and if so to what extent, also climatic changes played a part in the phenomena discussed in this paper. The increase of precipitation may have unfavourably influenced some species of dry, sandy areas (Desender & Turin, 1989). The most intensive application of mechanical sod cutting at Kralo Heath (about 1989) coincided with an increase of temperature (Fig. 6).



Cicindela sylvatica fully winged 14-20 mm

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