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Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference

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Abstract Local numbers of ground beetle species of heathland appeared to be significantly associated with size of total area, whereas such relationships were not found for the total number of ground beetle species and eurytopic ground beetle species. Presence of species with low chances of immigration was highly associated with area. This is in accordance with the "area per se" hypothesis for islands as far as extinction rates are concerned. The habitat diversity hypothesis and the random sampling hypothesis are of less importance for explaining this phenomenon. The importance of dispersal for presence and survival in fragmented habitats could be demonstrated. This result supports the founding hypothesis, under which founding of new populations is considered the main effect of dispersal. The frequency of heathland species with low powers of dispersal in habitats smaller than 10 ha was 76% lower on average than in areas larger than 100 ha. For heathland species with high powers of dispersal this frequency was only 22% lower on average. The period of isolation of the habitats studied, 26–113 years, appeared to be too long to persist for many populations of heathland species with low powers of dispersal.

Key words Ground beetles · Habitat fragmentation · Survival · Dispersal · Species-area relationship

Introduction

Many studies have demonstrated a decline of biological diversity in habitats after fragmentation, i.e. the subdivision of a continuous habitat into smaller pieces (Wilcove et al. 1986; Spellerberg 1991; Andrén 1994). The presence of ground beetle species is also expected to be highly affected by habitat fragmentation. Den Boer (1990) estimated the survival times of small populations of ground beetle species and predicted the loss of a high number of species in the province of Drenthe (The Netherlands). In one case the expected short survival times of populations of a ground beetle species, *Agonum ericeti*, in relation to habitat fragmentation could be documented (De Vries and Den Boer 1990). The decline of biological diversity after fragmentation is linked to the species-area relationship of island biogeography, in which the number of species of any taxonomic group is expected to decrease with decreasing area (Preston 1960, 1962; MacArthur and Wilson 1967; Connor and McCoy 1979).

Not only the size of the area is important in understanding presence and survival of species in habitat patches, but also species dispersal ability. Under the founding hypothesis of Den Boer (1971, 1977) the (re)founding of populations is supposed to be the main effect of dispersal. As extinction rates are often negatively related to area (MacArthur and Wilson 1967), it can be expected that the smaller an area, the more its species composition will be dominated by species with high dispersal abilities. Data on the species composition of large unfragmented areas are needed as a reference, because their species composition will merely be affected by local changes due to environmental variation and evolutionary processes. In this context it is useful to make a distinction between dispersal ability and dispersal opportunities. The first is connected with the species itself, whereas the dispersal opportunities are connected with the site of occurrence of a certain population in the landscape. Dispersal ability is connected with, for example, walking, flying, or ballooning behaviour, whereas dispersal opportunities are connected with, for example, habitat patch density, presence of corridors, or weather conditions. Knowledge of dispersal ability and of the preferred habitat of species, together with information on the spatial configuration of its habitat, enables the linking

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of presence of species to the occurrence of (re)colonizations and movements between habitats.

This study will address two questions. The first is: does the species composition of ground beetles differ between large and small areas? The second is: how can these differences be explained and what is the significance of dispersal? It is hypothesized that small areas will lack species with few opportunities for immigration. To test this hypothesis the presence of ground beetle species in fragmented heathlands in the Netherlands was investigated.

Materials and methods

Area of research

For centuries heathland has been the dominant kind of habitat in the north-east part of the Netherlands. This habitat is the result of old agricultural land use in which the land gradually entered a nutrient poor condition. This land use changed after the introduction of artificial fertilisers at about 1890. At that time large parts of the heathland were reclaimed and only very wet or very dry places were left. From the start of this century, and especially during the 1930s, very dry parts were changed into coniferous plantations and many wet parts were drained. Nowadays only very few large heathlands are left. To construct a data set with which the importance of dispersal power and habitat preference could be examined, the species composition of ground beetles of several isolated heathlands of different sizes was studied. Topographical maps (1:25,000) of the north-east part of the Netherlands were checked for the presence of heathlands (Fig. 1). The 6424 heathlands present, divided into eight size categories, are listed in Table 1. In a procedure in which degree of isolation and abundance of heath were checked, areas suitable for this study were selected. In 1990, out of these 6424 heathlands, 20 more or less isolated ones of different sizes were chosen. Most of the heathlands were 500 m or more away from other heathlands with a similar size or one size category (Table 1) smaller. In 1991 eight more areas were selected in a region where some of the heathland had been reclaimed early, about 100 years ago. As heath is less abundant in this older region, only a few isolated areas could be chosen there. In 1992 two more areas were investigated in a region where most of the heathland had been reclaimed only about 20 years ago. Two permanent study areas of the Biological Station were also used, making 32 areas being investigated in total.

Fig. 1 Part of the Netherlands (*box*) that was checked with the help of maps (1:25,000) for the presence of separate heathlands

Table 1 The frequency distribution of heathlands (Fig. 1) over eight size classes

Class	Ha	Total number
I	<0.4	3781
II	0.4–1.6	1744
III	1.6–6.3	593
IV	6.3–25	199
V	25–100	77
VI	100–400	21
VII	400–1600	6
VIII	>1600	3

Capture methods

Ground beetles were caught with plastic circular pitfall traps (cross-section and depth 10 cm). Near the rim of the pitfall a funnel was mounted to prevent the beetles caught from escaping again; each trap contained a few milliliters of 4% formalin. In all areas, except the two permanent study areas, five pitfalls were put into the soil, mostly four in the corners of a square with sides of about 15 m and one in the centre. The data for the two permanent study areas were taken from one square pitfall (with sides of 25 cm and a funnel leading towards a vessel with 4% formalin). In very small areas the places to put the pitfalls had to be adapted to local conditions. Otherwise they were placed in the centre of the area. In this way the sampling effort for each heathland was the same (or almost the same for the two permanent study areas) irrespective of total area. All pitfalls were used from mid-March to mid-July and from mid-August to December. Once every 2 weeks (once every week for the permanent study areas) they were replaced by pitfalls with fresh preservative and the beetles collected were taken to the laboratory for identification.

Habitat preference

Some of the species caught may experience the heathland patches as islands, whereas others may not. A selection of species of both groups was made. Many species are known to occur in heathlands only, and an extensive data set of about 1.5 million pitfall catches from all kinds of habitat in the Netherlands was available to give a distinct definition of habitat preferences. Turin and others list the occurrence of ground beetles in 33 kinds of habitat (Turin et al. 1991). The species used in this study are related to heathland in two ways. They either only occur in heathland (heathland species) or they also occur in fertilized grassland or agricultural land (eurytopic species). For consideration as a "heathland species" only relatively very low (relative occurrences "1" at maximum, after Turin et al. 1991) numbers were caught outside the six oligotrophic habitats forming "heathland": peatmoor, heathland with *Molinia*, *Erica* heathland, *Calluna* heathland, heathland with *Deschampsia*, and Corynephoretum (fixed drift-sand). For one habitat the criterion was less stringent: occurrence in open coniferous plantations was allowed, because heathland often occurs in this kind of habitat. One species, *Miscodera arctica*, was added as a "heathland species", because recently it has been caught in much higher numbers than reported by Turin et al. (1991).

Dispersal ability

The dispersal abilities of ground beetles have been studied extensively. Several studies have shown that the distances they can walk are limited. For some of the largest species a distance of more than 1000 m is possible (Den Boer 1970), but for most species a distance of 500 m is very exceptional (Baars 1979; Klazenga and De Vries 1994). Longer distances of several kilometers or more are only possible for individuals able to fly. Hence, a rough estimator for the dispersal ability of ground beetles is its ability to fly. During a 20-year survey, Van Huizen (1980) and Van Huizen and Aukema (1992) used window traps to study the flight behaviour of ground beetles. By means of this survey together with some other observations with window traps there is much information about the dispersal abilities of ground beetles. Although this information does not completely exclude flight abilities of certain species, the relative dispersal ability of the ground beetle species in this study could be reliably estimated.

Data analysis

As in each area the samples were taken at a small site with the same sampling effort, they can be considered as samplings at one point. At each area several habitat variables were measured or estimated and related to species composition. The species collected were divided into several groups. Apart from total number of species (TS) four ecological groups were distinguished: (1) the number of species only occurring at heathland (heathland species: HS), (2) species which occur both in heathland and in land fertilised for agricultural use (eurytopic species: ES), (3) heathland species for which evidence of flight activity is available (heathland species with high powers of dispersal: HS-HPD), (4) heathland species without observations of flight activity (heathland species with low powers of dispersal: HS-LPD). The response of the number of species of each group to environmental variables was studied by stepwise multiple regression, using SPSS/PC+ Version 5.0.1. With this program a model was built using the explanatory variables with which the number of species was associated. During each step of selecting the next significant variable each already selected variable is tested again for its significance. The explanatory variables tested are shown in Table 2. Three categories of variables were used: habitat and isolation variables and area. For habitats four kinds were distinguished: PEATMOOR (presence of accumulated litter of *Sphagnum*), WET HEATHLAND (presence of *Erica*), DRY HEATHLAND (presence of *Calluna*) and CORYNEPHORETUM (presence of *Corynephorus*). Corynephoretum is a very dry drift sand area. Each habitat was included in the regression as being present or absent, except Corynephoretum which was only indirectly present in the analyses and was indicated by the absence of the other three habitats (method after Jongman et al. 1987). An indication of moisture (MOIST), using a score of one to four for Corynephoretum, dry heathland, wet heathland, and peatmoor respectively, was added as a second habitat variable and the abundance of *Molinia caerulea* (GRASS) as a third one. The size of each area (log-transformed: LOGAREA) and the degree of isolation, estimated as the total area of heathland being present within 0.5, 1 and 2 km from the edges of each area, were measured and estimated, respectively, from the most recent topographical map (1:25,000, 1984–1992) available (ISO500 M, ISO1000 M and ISO2000 M). The isolation period (ISOPER) was estimated as the period between now and the origin of the present area when it reached 200% or less of its present day size. Correlations between all tested explanatory variables were calculated. Special attention to this is only needed when correlated variables are selected in the same model. The presence of populations in relation to size and duration of isolation was further studied by comparing frequencies in different size or duration of isolation classes, respectively.

Results

Catches

From 32 areas 41,420 individuals of 116 species of ground beetles were identified. Using the criteria given in Materials and methods: data analysis, of these 116 species 19 were HS and 17 were ES (see Appendix). This means that a similar number of species caught consider the heathlands as islands (HS: 19) or as part of an inhabitable matrix (ES: 17). All the other species caught have associations with some of the other habitats mentioned by Turin et al. (1991) without clear associations with heathlands and fertilized grassland or agricultural land as well.

Five of the heathland species had been caught in window traps in the past and therefore are able to fly (see Appendix). Still, it cannot be excluded that some

Table 2 List of explanatory variables used to analyze the species composition by stepwise multiple regression

Habitat variables
PEATMOOR: present/absent
WET HEATHLAND: present/absent
DRY HEATHLAND: present/absent
MOIST: analogous to the types above: peatmoor, wet heath, dry heath and Corynephoretum with 4, 3, 2, and 1 point respectively
GRASS: Coverage of amount of grass in percentages, an estimated mean in an area with a radius of 50 m

Size variable
LOGAREA: Logsize of total heathland area on most recent topographical map 1:25,000

Isolation variables
ISO500M: amount of heath present within 500 m of the border of the area
ISO1000M: amount of heath present within 1000 m of the border of the area
ISO2000M: amount of heath present within 2000 m of the border of the area
ISOPER: Isolation period, number of years between moment of sampling and the middle of the period between the dates of two available topographical maps in which the area had become about 200% or less of its present size

Table 3 Results of a stepwise multiple regression of five ecological groups on the variables of Table 2. Given are significant explanatory variables as part of a significant model

Group	Variable	Cumulative R^2_{Adj}
Total number of species, TS:	MOIST	0.16
Eurytopic species, ES:	DRY HEATHLAND	0.24
	PEATMOOR	0.34
Heath species, HS:	LOGAREA	0.47
Heath species with high powers of dispersal, HS-HPD:	LOGAREA	0.20
	MOIST	0.28
Heath species with low powers of dispersal, HS-LPD:	LOGAREA	0.40
	MOIST	0.55
	ISOPER	0.61

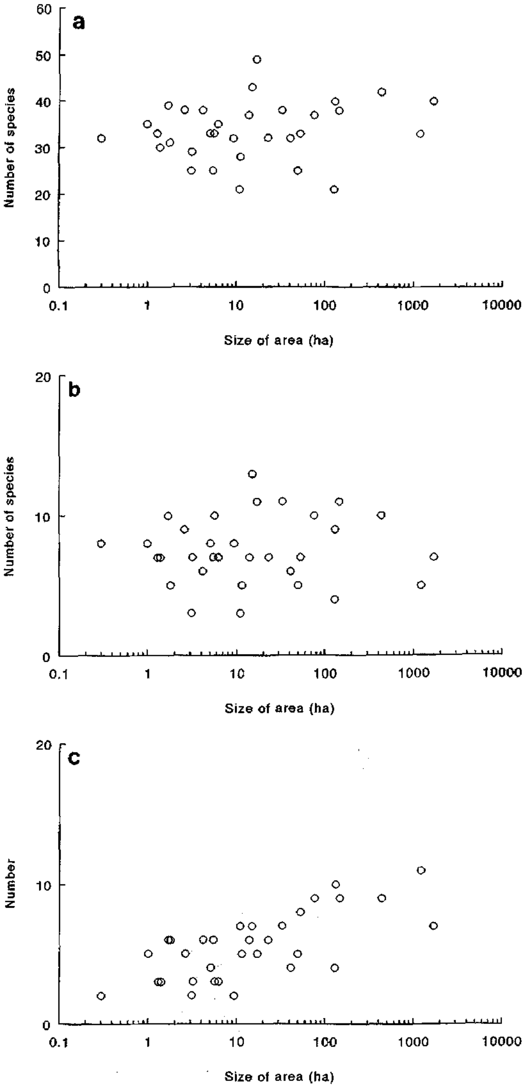
others, especially macropterous species, have this ability as well. However, the possibility of unrecorded flight in some species is not important for the distinction made by Van Huizen (1980) and Van Huizen and Aukema (1992) between species with high and those with low dispersal ability based on window trap catches. Even when a few species incidentally show flight, probably they do not fly as frequently as those caught more than once in window traps and consequently still have a lower chance of (re)colonizing any given area. The heathland species *Cymindis vaporariorum* was caught only once in a window trap and therefore could equally well be considered a species with high or low dispersal power. The next lowest number of catches of heathland species with high powers of dispersal in a window trap was for *Pterostichus diligens*, which had been caught considerably more often, 11 times in the course of 20 years.

Multiple regression

As no significant effect of capture method (in two areas only one large pitfall operated) was found in a stepwise multiple regression, in the following the 32 samples were treated as comparable units. Stepwise multiple regression applied to the five dependent variables, TS, ES, HS, HS-LPD and HS-HPD, gave the significant results shown in Table 3. Only five out of ten explanatory variables were selected during the stepwise regressions as explaining part of the variation in the dependent variable of the five groups ($P < 0.05$, Table 3). The only significant variable explaining some (16%) of the variation of TS was the habitat variable MOIST. Two habitat variables, DRY HEATHLAND and PEATMOOR, explained 24% and an additional 10% respectively of the variation found in the catches of ES. Dry heathland was positively and peatmoor negatively associated with ES. LOGAREA explained an important part of the variation of HS, HS-HDP, and HS-LDP: 47, 20, and 40% respectively, but was not significant for TS and ES (Table 3). Only species for which the areas can be considered as islands, i.e. species with a preference for heathland, showed a significantly positive relation with LOGAREA (Fig. 2c–e), whereas for TS and ES this relation was absent (Fig. 2a,b). As the number of species caught is not indicative of the number of species present in the whole area, but is based on similar sample sizes for each area irrespective of its size, Fig. 2a is not an example of the classical species-area relationship. However, for the ecologically defined groups, HS, HS-HPD, and HS-LPD, a relation with LOGAREA is evident (Table 3 and Fig. 2c–e). This relationship is based upon measuring the number of species per unit area. MOIST explained an additional 8 and 15% of the variation in HS-HDP and HS-LPD respectively, and another 6% of the variation in HS-LPD was explained by ISOPER. As MOIST was a significant factor for both HS-HPD and HS-LPD, the absence of MOIST in the multiple regression of HS is unexpected. This absence can be explained because there was a negative association between MOIST and HS-LPD and a positive association between MOIST and HS-HPD. The model calculated for the dependent variable HS-LPD is presented in Table 4. LOGAREA, MOIST and ISOPER together explained 61% of the total variation. The regression coefficients in this model are positive for LOGAREA and negative for MOIST and ISOPER. Therefore large dry heathlands which have become isolated only recently have the highest numbers of heathland species. The rather high value of 61% explained shows that the explanatory variables had a high predictive value for the presence of species with both a low dispersal ability and a preference for heathland, whereas, especially for TS, which is only based on a taxonomical criterion (ground beetle species), the predictive value of these is low.

Correlation coefficients

The correlation coefficients of the explanatory variables are given in Table 5. Significant correlations were found between the three isolation parameters ISO500 M, ISO1000 M, and ISO2000 M, between LOGAREA, ISO500 M, and GRASS and between MOIST, PEATMOOR, WET HEATHLAND and DRY HEATHLAND. Correlations with GRASS, WET HEATHLAND, DRY HEATHLAND were negative. This



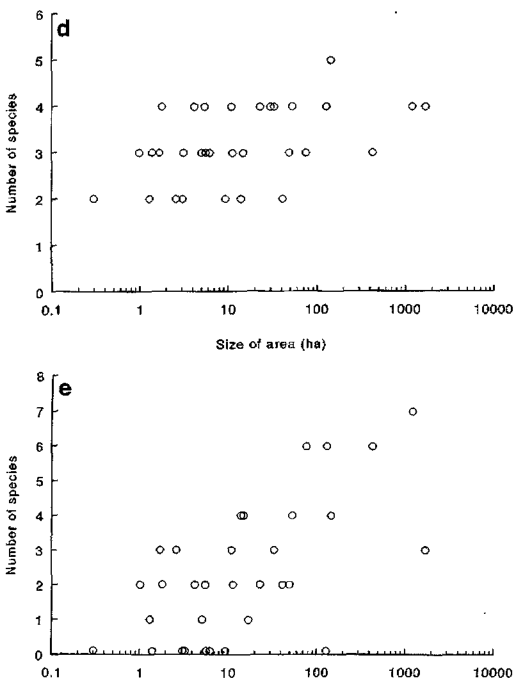


Fig. 2a–e Presence of species in relation to LOGAREA. Ordinate represents: **a** Total number of species caught (TS), **b** number of eurytopic species caught (ES), **c** total number of heathland species caught (HS), **d** number of heathland species caught with high powers of dispersal (HS-HPD), **e** Number of heathland species caught with low powers of dispersal (HS-LPD)

means that part of the variation explained by LOGAREA could also be explained by ISO500 M or GRASS. Also, the effects of the correlated habitat variables is difficult to separate, and in some cases can not realistically be separated, i.e. in MOIST and PEATMOOR. None of the correlated habitat variables are selected in the same model.

Presence and survival

In total the presence of HS-HPD in catches in areas larger than 100 ha was 23 out of 30 potential cases (76%) and in areas smaller than 10 ha it was 44 out of 75 potential cases (59%). The presence of HS-LPD in large areas was 26 out of 78 potential cases (33%), whereas in small areas the presence was 16 out of 195 potential cases (8%), see Table 6. Presence in small areas compared to large areas declined in HS-HPD with 22% and in HS-LPD with 76%. The ratio HS-LPD to HS-HPD differed significantly between small and large areas (Wilcoxon-Mann-Whitney test: $P < 0.025$).

Fourteen HS were present in one or more of 15 areas sampled that were smaller than 10 ha. *Amara equestris*, *Olisthopus rotundatus* and *Bembidion nigricorne*, all three species from HS-LPD, showed a significantly lower occurrence in areas smaller than 10 ha compared to those larger than 100 ha (Table 6: Fisher's exact test). The highest frequencies of occurrence in areas smaller than 10 ha were shown by three other species, all from HS-HPD: *Cicindela campestris*, *Bradycellus ruficollis* and *Pterostichus diligens* (Table 6). One species showed a result contrary to what was expected: *Bembidion humerale*. This species was only caught in three small areas, but the difference in occurrences with areas larger than 100 ha was not significant.

For each species which was present one time or more, the presence of populations in small areas in relation to isolation period is shown in Fig. 3. Three out of five HS-HPD, the same three species which showed highest frequency of occurrence in small areas, were present in two small areas which were isolated for a period longer than 100 years, whereas all 14 HS-LPD were absent. HS-LPD were only present in areas that had been isolated for less than 75 years. Among the HS-LPD, *Pterostichus lepidus* reached the highest frequency of occurrence in these small habitats: 4 out of 15 potential cases (Table 6 and Fig. 3), all in areas isolated for less than 60 years.

Table 4 Results of a stepwise multiple regression of heathland species with low powers of dispersal on the variables of Table 2

Source	*df*	SS	MS			
Regression	3	80.09403	26.69801	F = 17.33448		
Residual	28	42.12472	1.54017	P < 0.0001		
Variable	B	SE B	Beta	T	Sig T	Cumulative R^2_{Adj}
LOGAREA	1.51527	0.24931	0.68156	6.078	<0.0001	0.39667
MOIST	−0.97060	0.27139	−0.40039	−3.576	0.0013	0.54794
ISOPER	−0.01987	0.00823	−0.27047	−2.415	0.0225	0.61252
Constant	4.59609	0.97656		4.706	0.0001	

Table 5 Correlation matrix of the explanatory variables of Table 2

	LOGSIZE	ISOPER	ISO500M	ISO1000M	ISO2000M	GRASS	MOIST	PEATMOOR	WET HEATH
ISOPER	0.058								
ISO500M	0.704**	−0.299							
ISO1000M	0.519*	−0.361	0.762**						
ISO2000M	0.301	−0.359	0.545**	0.739**					
GRASS	−0.530**	0.141	−0.458*	−0.295	−0.238				
MOIST	0.052	0.008	0.125	0.151	0.246	0.247			
PEATMOOR	0.144	−0.128	0.224	0.174	0.316	0.042	0.736**		
WET HEATH	−0.099	0.231	−0.125	−0.044	−0.217	0.231	0.041	−0.615**	
DRY HEATH	−0.129	−0.157	−0.180	−0.164	0.016	−0.236	−0.515*	−0.249	−0.458*'

*P < 0.01, **P < 0.001, one-tailed

Table 6 The presence of 18 heath species at sites in small heathland areas (<10 ha), large heathland areas (>100 ha) and one continuous heathland area (Dwingelderveld: Van Essen 1993). The survival of heath species, calculated (Den Boer 1990) and observed, in small areas. The difference in presence in small, large or continuous areas was tested with Fisher's exact test. Non-significance (P > 0.05) is indicated by presence of the same letter, *a* or *b*, at the frequencies compared

Species	Presence			Survival	
	<10 ha^{c}	>100 ha^{d}	Dw^{e}	C^{f}	O^{g}
	Heath species with high power of dispersal, HS-HPD				
Bradycellus ruficollis	14/15^{a}	6/6^{a}	20/21^{a}	37 (8–89)	116
Trichocellus cognatus	3/15^{a}	4/6^{a}	16/21^{a}	14 (9–87)	60
Cicindela campestris	11/15^{a}	6/6^{a}	15/21^{a}	–	114
Pterostichus diligens	15/15^{a}	6/6^{a}	19/21^{a}	33 (14–121)	116
Cymindis vaporariorum	1/15^{a}	1/6^{a}	2/21^{a}	30 (5–44)	36
	Heath species with low power of dispersal, HS-LPD				
Bembidion humerale	3/15^{a}	0/6^{a}	0/21^{a}	–	60
Miscodera arctica	1/15^{a}	1/6^{a}	0/21^{a}	–	36
Harpalus solitaris	1/15^{a}	1/6^{ab}	9/21^{b}	–	54
Amara equestris	2/15^{a}	4/6^{b}	14/21^{b}	22 (7–62)	37
Anisodactylus nemorivagus	1/15^{a}	0/6^{a}	2/21^{a}	–	26
Amara infima	0/15^{a}	1/6^{a}	4/21^{a}	40 (29–44)	< 26
Olisthopus rotundatus	2/15^{a}	5/6^{b}	14/21^{b}	24 (8–61)	37
Carabus arvensis	1/15^{a}	3/6^{ab}	19/21^{b}	9 (5–79)	36
Carabus nitens	0/15^{a}	1/6^{a}	20/21^{b}	9 (6–63)	< 26
Pterostichus lepidus	4/15^{a}	4/6^{ab}	19/21^{b}	90 (16–118)	51
Cymindis macularis	0/15^{a}	2/6^{ab}	6/21^{b}	30 (19–>40)	< 26
Agonum ericeti	1/15^{a}	1/6^{a}	6/21^{a}	19 (7–44)	60
Bembidion nigricorne	0/15^{a}	3/6^{b}	12/21^{b}	9 (8–11)	< 26

[c] The presence of the species in the fifteen areas surveyed smaller than 10 ha

[d] The presence of the species in the six areas surveyed larger than 100 ha

[e] Dw = Dwingelderveld = data of Van Essen (1993): the catches from 21 series placed in one large heath area of 1210 ha, using the same catch effort per series as in this study, five pitfalls with a diameter of 10 cm

[f] C = calculations Den Boer (1990): the calculated survival time in years of one interaction group (Den Boer, 1977) without re-colonization

[g] O = observed survival time = the longest observed survival time in years of populations in areas smaller than 10 ha, see also Fig. 3

Discussion

Relations with log area

Not all species of the five ecological groups show clear relationships with area; these were especially distinct among heathland species and heathland species with low powers of dispersal. The results from this study, gathered with point samples, cannot be compared directly with studies of species-area relationships. In the latter studies it is supposed that all species present have been recorded, or at least nearly all. In this study, however, the pitfalls used only take a sample of the ground beetles present in a local site. Therefore, the catches especially in the large areas do not represent the species present in the entire area. Connor and McCoy (1979) give three hypotheses which are supposed to explain why species-area relationships are found: the habitat diversity hypothesis, the random sampling hypothesis, and the area-per se hypothesis. With the present results it is not possible to give a species-area relationship as discussed by Connor and McCoy. Nevertheless, one or more of these three hypotheses might explain the effects of area on species composition. The habitat diversity hypothesis (Williams 1964) states that the number of habitats sampled increases with area. In this study, however, in all areas only a small site was sampled and therefore the number of habitats sampled could hardly be expected to increase with area. The random sampling hypothesis (Connor and McCoy 1979) emphasizes the effects of area on the chance of immigration. Larger areas are expected to "sample" a larger portion of the potential immigrants. However, our results clearly show a more distinct relationship with area when immigration is expected to be less important, as for heathland species with low powers of dispersal (Fig. 4). Eurytopic species and heathland species with high powers of dispersal are expected to have a good chance of immigration, but they show no or a much weaker relation with area than do the heathland species with low powers of dispersal (Fig. 2b and 4). This means that the random sampling hypothesis does not explain the relationships with area found. The third hypothesis, termed the area-per se hypothesis (Preston 1960, 1962; MacArthur and Wilson 1967) emphasizes the effects of area on extinction rates. Extinction rates are expected to be inversely proportional to mean population size and are therefore assumed to be also inversely related to area. Not only can small areas be expected to contain small populations, but the chance to accommodate asynchronously fluctuating subpopulations is also reduced (Den Boer 1968, 1981). Only this hypothesis can explain the relationships found

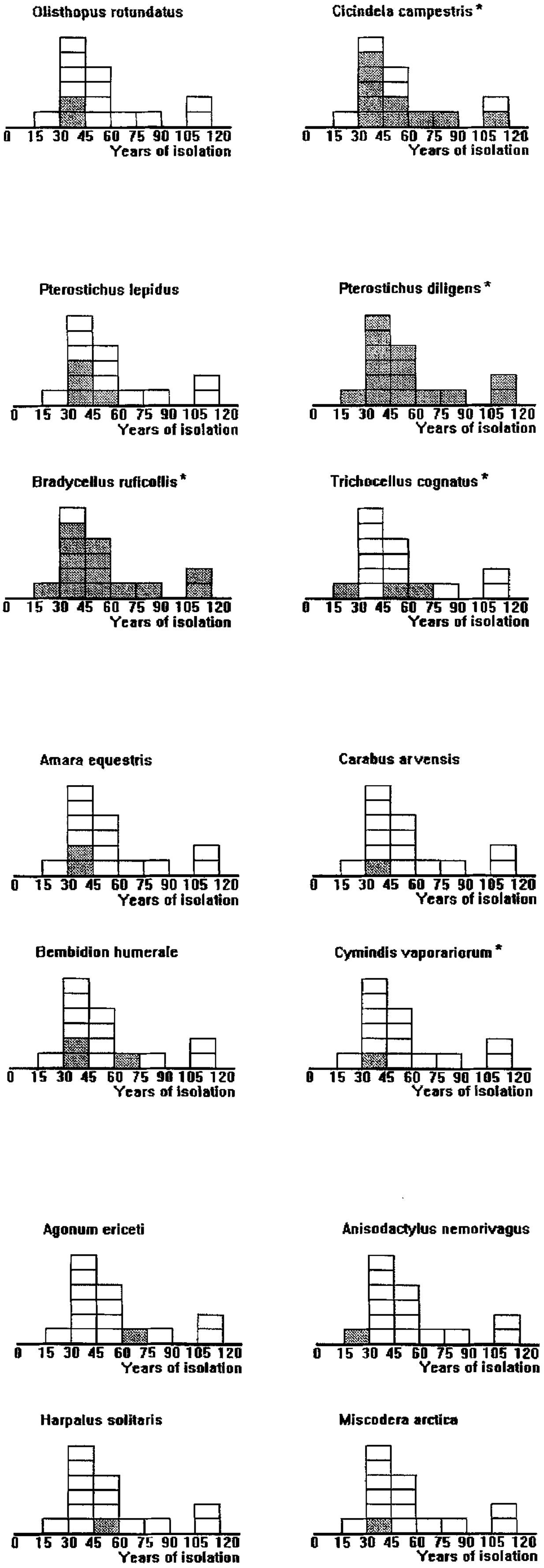


Fig. 3 The presence (*dark blocks*) of catches of heathland species (HS) in 15 sampled areas ordered on the abscissa by their period of isolation as compared to potential presence (*open blocks*). Species that have been caught in window traps (HS-HPD) are marked with *

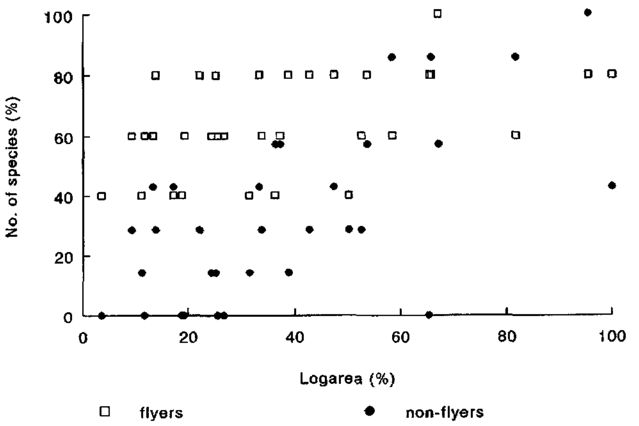


Fig. 4 The presence of heathland species with high (HS-HPD: squares) and low (HS-LPD: dots) powers of dispersal in relation to LOGAREA. The largest numbers caught of each group (HS-HPD: 5, HS-LPD: 7) and the largest area investigated (1700 ha) were set at 100%

between area and the presence of some groups of ground beetles. Moreover, there is an analogy between the immigration rates of species with differences in dispersal power colonizing areas at the same distance to the source region and the immigration rates depending on the distance towards the main land of species with the same powers of dispersal. This latter relation was used by MacArthur and Wilson (1967) to explain the number of species present on an island.

Many species atypical of heathlands were caught during this study. Often such species can also survive in some other habitats than heathland and therefore do not show a relationship with area. Because of the absence of a relationship between area and total number of species, a simple diversity index based on total number of ground beetle species caught at one or a few sites should not be used as a criterion supporting conservation strategies. When investigating a certain area containing one or a limited number of biotopes, conclusions about species richness for reasons of conservation should be restricted to species with a strong relationship with the biotopes in question. On the basis of results with heathland spiders, Hopkins and Webb (1984) came to the same conclusion.

Habitat variables

The only factor shown to be significant for total number of species was moisture. The importance of moisture as a decisive factor for the presence of most ground beetle species, as also shown in the models for heathland species with high and low powers of dispersal, is well known (Luff et al. 1989; Turin et al. 1991; Van Dijk and Den Boer 1992). The sign of the associations with moisture depends very much on the relation with moist of the separate species. As heathland species with low powers of dispersal are negatively associated with moisture and heathland species with high powers of dispersal positively, this could mean that flight ability is more important in moist habitats compared to dry habitats.

The variables dry heathland and peatmoor were significantly positively and negatively associated with the presence of eurytopic species, respectively. This can be explained by the fact that most selected eurytopic species, 14 species, occur in both agricultural land and dry heathland, whereas only four species occur in both agricultural land and peatmoors. Apparently, for many species agricultural land is most similar to dry heathland when given the choice between different kinds of heathland. This can be explained by the history of these habitats. Dry heathlands, particularly, have been extended during centuries of land use with low nutrient input, whereas peatmoor mostly is not related to human activities.

Isolation

To establish the survival of populations in small habitats data from highly isolated patches, where there was only a small chance of re-colonization, were required. This means that habitat islands were selected which were more than 500 m from the nearest relevant heathland. A distance of 500 m from another habitat is expected to be unbridgeable for most non-flying ground beetles (Baars 1979; Klazenga and De Vries 1994). Hence, only if non-isolated areas had also been sampled in this study, could isolation related to distance have been demonstrated to be a significant explanatory variable for heathland species with low powers of dispersal. Although the extra variation explained by duration of isolation was only 6%, it was significant, and therefore indicates a detectable effect. The absence of most populations of heathland species with low powers of dispersal from 15 small heathlands indicates that for many species the duration of isolation was already too long. All these 15 areas studied had been isolated for more than 25 years. On the other hand, the absence of heathland species with low powers of dispersal in areas which have been isolated for more than 100 years is contrasted by the presence of three heathland species with high powers of dispersal there, *Trichocellus cognatus*, *Pterostichus diligens*, and *Bradycellus ruficollis*. The latter two of these species were found in almost all areas, which indicates that these species show sufficient dispersal to compensate for extinction in very small and isolated areas.

Presence

The presence of species at certain sites gives relevant information for this study, but the absence of species can only be interpreted by statistical analyses. The frequency of occurrence of species in samples from large areas as compared with that in samples from small areas gave statistical information about the presence of certain species in relation to size of area. The results indicate that flight ability significantly contributes to the survival of heathland species in small isolated habitats. As adequate data from one large continuous area collected with the same sampling effort per locality are available (Van Essen 1993), a comparison with these data (from 1991) could be made (Table 6). Again, the difference between presence of heathland species with low powers of dispersal in large areas and in small areas was significant for the same three species which in the present study showed a significant difference between presence in areas larger and smaller than 100 or 10 ha respectively (Table 6): *Amara equestris*, *Olisthopus rotundatus*, and *Bembidion nigricorne*. Moreover, five more species appeared to be significantly less present in small fragmented areas. For instance *Carabus nitens* was caught by Van Essen in the continuous area in 20 of 21 sampling sites, but it was absent from all other areas sampled by us. Even the difference between its presence in this one continuous area (20 out of 21 sites), and its presence in six large areas (1 out of 6 areas, of which one is this continuous area), was significant. This species is unwinged and some 10 years ago was thought to have become extinct in the large continuous area, but in 1982 it was caught again and now it is a very common beetle in this area. Therefore, it must have survived in one or more unmonitored sites in this large area. Apparently, the species increased in numbers after a change in management of the area. In conclusion, it has now been shown that eight ground beetle species with low powers of dispersal are present significantly less in smaller areas than in large or continuous areas, without having to take into account effects expected by the sampling hypothesis or the habitat diversity hypothesis.

Survival

One of the questions left is whether the presence of populations in small habitats resulted from continued survival since the onset of isolation, due to the "rescue effect" (Brown and Kodric-Brown 1971), or from turnover, i.e. from successful recolonizations after extinction. For most areas it is not possible to discriminate between these possibilities with certainty. Generally, recolonization is expected to be infrequent in isolated areas. Some heathland species with low powers of dispersal incidentally may show flight activities, though they were never caught in window traps. For example the species *Bembidion humerale* is macropterous, so that its absence from samples with window traps may only be due to its rareness. Another possibility is that supposedly unsuitable areas might be more suitable for reproduction than expected. Also, some species may be able to cross distances of 1 km or more. At least for *Agonum ericeti* a continued presence in some areas is most likely because of its very specific habitat demands (De Vries and Den Boer 1990). The selection of isolation period as an explanatory variable for heathland species with low powers of dispersal in the stepwise regression process, rather than one of the other isolation variables, is probably due to the careful choice of highly isolated areas. This might indicate that at least some populations of heathland species with low powers of dispersal, which were recorded as present, have been there continuously.

With this study it is shown that, for survival in fragmented areas, dispersal is very significant. On average, the presence of heathland species with low powers of dispersal in habitats smaller than 10 ha is reduced by a factor of four compared to that in areas larger than 100 ha. The average survival time of populations of heathland species in small habitats (habitats which are occupied by a single interaction group only according to the definition of Den Boer 1977) was estimated by Den Boer (1990) to be 9–40 years, except for *P. lepidus* (90 years). All values of heathland species with low powers of dispersal found by us are within or close to that range (Table 6). This means that almost all populations became extinct within the survival time as estimated for one interaction group by Den Boer (1990). Only three heathland species, all three with high powers of dispersal, showed a high survival time of more than 100 years in our studies (Table 6 and Fig. 3) and therefore differ from the estimations of Den Boer (1990). Two explanations are possible for this difference. More than one interaction group might be present in an area of only slightly less than 10 ha. As prolonged survival would then have been expected for some heathland species with low powers of dispersal as well, this is not a very likely explanation. More probable is the occurrence of successful immigration by flight.

Cymindis vaporariorum might be characterized as a species with low rates of immigration. Two factors could be responsible for this: either flight occurs too infrequently or the species is very rare. The latter is indicated by its absence in most large and continuous heathlands. Despite flight activity, populations of *Trichocellus cognatus* were not able to survive in a lot of small areas. Either the extinction rates were high compared to other species or colonization rates were low. High extinction rates could depend on high sensitivity to some kind of habitat degradation correlated with patch size, e.g. the growing dominance of grasses. Lower colonization rates could be due to a higher number of individuals needed to realize successful colonization.

Importance of habitat preference and dispersal opportunities

The results of the multiple regression demonstrate that the species-area relationships in this study depend highly on habitat preference of the species. Because point samples were taken, sampling effects can largely be excluded. Only the presence of heathland species could be linked to size of area, whereas for eurytopic species or total number of species such a relationship was not found. Some influence of degradation of the heathland or of the absence of nearby heathland on populations in small patches, indicated by correlations between area with presence of heathland within 0.5 km and with the abundance of *Molinea caerulea* respectively, cannot be excluded.

The difference in occurrence of heathland species with high powers of dispersal as compared to heathland species with low powers of dispersal in relation to degree of habitat fragmentation clearly demonstrates the importance of dispersal for the persistence in this fragmented landscape, and therefore supports the founding hypothesis of Den Boer (1971, 1977). However, apart from (re)founding new populations, another aspect of dispersal, gene flow resulting in the maintenance of genetic variability (Lidicker and Stenseth 1992), could have enhanced survival of heathland species with high powers of dispersal as well. Without data on extinctions followed by colonizations it is difficult to discriminate between these two effects of dispersal.

Compared to heathland species, eurytopic species were found much more often in small areas and showed no relationship with size of area (Fig. 2b versus 2c–e). This illustrates the greater importance of dispersal opportunities rather than of dispersal ability for survival. Together with eurytopic species, three heathland species with high powers of dispersal seem to be not much affected by fragmentation and more than 100 years of isolation. Many heathland species with low powers of dispersal, however, will not have had opportunities to recolonize isolated habitats after having become extinct. Clearly, the absence of *A. ericeti* in small isolated areas, as shown by De Vries and Den Boer (1990), is just one case out of many.

It can be inferred that the fragmentation of the landscape has resulted in the disappearance of many populations of species with low dispersal opportunities. Relationships between environmental conditions and species composition are widely in use for management purposes, e.g. higher plant species are used as indicators of nitrogen, moisture, or pH conditions of the soil (Ellenberg numbers: Ellenberg 1991). Similarly, an indicator of the dispersal ability can be used in questions relating to nature conservation. In nature reserves species with high powers of dispersal, if characteristic of a certain habitat, are indicative of the suitability of a patch at the moment of observation, whereas characteristic species with low powers of dispersal are indicative of long-term survival. The absence of both groups would indicate unsuitable conditions within the area, whereas absence of species with low powers of dispersal only would indicate that part of the species group which potentially could have been present has had too few possibilities of recolonization.

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Appendix

Eurytopic species (ES)	Heathland species (HS-HPD are indicated by *, others are HS-LPD)
Harpalus latus	*Bradycellus ruficollis**
Notiophilus substriatus	*Trichocellus cognatus**
Broscus cephalotus	*Cicindela campestris**
Harpalus anxius	*Pterostichus diligens**
Carabus granulatus	*Cymindis vaporariorum**
Pterostichus versicolor	*Bembidion humerale*
Calathus erratus	*Miscodera arctica*
Amara apricaria	*Harpalus solitaris*
Syntomus foveatus	*Amara equestris*
Bembidion lampros	*Anisodactylus nemorivagus*
Agonum obscurum	*Amara infima*
Pterostichus vernalis	*Olisthopus rotundatus*
Calathus melanocephalus	*Carabus arvensis*
Calathus fuscipes	*Carabus nitens*
Harpalus rufipes	*Pterostichus lepidus*
Amara communis	*Cymindis humeralis*
Nebria brevicollis	*Cymindis macularis*
	Agonum ericeti
	Bembidion nigricorne

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