

SURVIVAL OF POPULATIONS OF *AGONUM ERICETI* PANZ.  
(COL., CARABIDAE)  
IN RELATION TO FRAGMENTATION OF HABITATS

by

HENK H. DE VRIES & PIETER J. DEN BOER

(*Biological Station, Kampsweg 27, 9418 PD Wijster, The Netherlands*)

SUMMARY

The stenotopic carabid species *Agonum ericeti* Panz. of peat moor habitats is unable to fly, and therefore cannot bridge distances that exceed 200 meters between sites suitable for reproduction. At present in Drenthe (The Netherlands) suitable habitat conditions for this species are restricted to some remnants of large peat moors and a few moist heath areas (say >50 ha), on the one hand, and to a number of small and isolated peat bogs (in most cases <5 ha), on the other. By sampling 20 of these habitats in 1988 ('89), viz. 7 large habitats, 11 small ones and 2 intermediate sites, the presence of populations of *A. ericeti* could be established for all larger areas where the greater part of the surface consists of suitable habitat. Three of the habitats were also sampled in 1961 with the same result. However, after periods of between 24 and 66 years of complete isolation the species has become extinct in all but one small sites including two where it was still present between 1959 and 1962. From observations at Dwingelder Veld it could be concluded that in the larger habitats the species probably forms multipartite populations that to a certain extent are "protected" from extinction by spatial spreading of this risk over differently fluctuating subpopulations. In small habitats populations cannot be multipartite, and the survival time of such isolated populations is estimated at 7-44 years (mean 19 years) or less. This study gives a clear example where the "area-effect" of island biogeography, as far as it concerns rate of extinction, applies to habitat islands. A peaty upper layer of the soil seems to be a habitat condition that favours presence and survival of *A. ericeti*.

KEY WORDS: isolation, survival, fragmentation, population, carabid beetles.

INTRODUCTION

The Dutch landscape is man-made and was repeatedly modified over the centuries. Nowadays, only a few fragments of older, not—or no longer—utilized landscape elements are left, surrounded by cultivated areas. These remnants are generally regarded as valuable and are usually protected. However, success of protecting organisms in reserves depends on the suitability of the reserve for long-term survival of the species as well as on the degree to which negative influ-

ences can be kept out. In spite of protection several groups of plant and animal species show highly increased extinction rates. SOULÉ (1987) enumerates factors that have to be taken into account when trying to evaluate viability of populations: dynamics of numbers, variability of the environment, genetic composition and variation, frequency of catastrophes, metapopulation structure and degree of fragmentation. In our opinion, dispersal ability should be added to this list (DEN BOER, 1977, 1985, 1990), because it determines both the effectiveness of metapopulation structure and consequences of fragmentation. In the present study attention has been given to the effect of fragmentation, as indicated by area of the habitat fragment and its degree of isolation in space and time, for a species with low powers of dispersal.

The theory of island biogeography shows the importance of area for the survival of populations (e.g. MACARTHUR & WILSON, 1967; DIAMOND, 1972; SIMBERLOFF, 1976; CONNOR & MCCOY, 1979), but there is discussion about whether or not a suitable habitat should be continuous or could better be fragmented (e.g. SIMBERLOFF & ABELE, 1976a,b; QUINN & HARRISON, 1988). One of the effects of a larger area of the habitat is a larger population, which should have an increased chance of survival (e.g. DIAMOND, 1975; WILCOX & MURPHY, 1985). The opponents of this view argue that in a group of fragments of habitat of the same total size as a single unfragmented one more species will be observed (and are thus supposed to survive), because of a greater environmental heterogeneity, less interspecific competition, and a better spreading of the risk of catastrophes. This discussion evidently passes over the essential point, differences in dispersal power between species (see further DEN BOER, 1990).

Apart from this, DEN BOER (1981) showed that a larger population does not always have a better chance to survive than a smaller one, for, at least in carabid beetles, the fluctuation pattern of numbers generally is more crucial than mean population size. Besides mean numbers and local fluctuation patterns the structure of the entire population, viz. the subdivision into subpopulations (DEN BOER, 1977), appears to be decisive for the chance of survival of the population as a whole. A continuous population in which asynchronously fluctuating subpopulations can be distinguished (a multipartite population: ANDREWARTHA & BIRCH, 1984) in the long run has a far better chance to survive than a local population in a small isolated site, or a continuous population of synchronously fluctuating subpopulations (DEN BOER, 1981, 1986a). The movements of individuals between adjacent, but differently fluctuating, subpopulations will fill local lows in numbers and might rapidly compensate for local extinc-

tions by recolonization (“spreading of risk”: DEN BOER, 1968). On the other hand, violent fluctuations of numbers between years in a local population (a population that is too small to be subdivided into subpopulations), is expected to lead to rapid extinction (DEN BOER, 1981). Therefore, populations living in relatively small habitats are expected to show comparatively high extinction rates, not so much because of relatively low numbers, but because of not being subdivided into asynchronously fluctuating, and thus mutually compensating, subpopulations.

The aim of the present investigation is establishing the “area-effect” of island biogeography for habitat islands, as far as extinction rates are concerned. This means, we will estimate the survival times of carabid populations isolated in small fragments of habitat in relation to those occupying larger habitats. The latter have a better chance to be subdivided into asynchronously fluctuating subpopulations than the former, and thus should survive longer. To avoid confusion it must be noted that we prefer to discriminate between metapopulation, a group of distinctly recognizable—and therefore spatially separated—local populations between which exchange of individuals occurs to some extent (see LEVINS, 1968: VI), and multipartite population, a group of subpopulations (interaction groups according to DEN BOER, 1977), which in most places gradually merge into one another, so that boundaries between different subpopulations generally cannot be unambiguously defined (DEN BOER, 1977; ANDREWARTHA & BIRCH, 1984: 175, 184).

The Carabid species *Agonum ericeti* Panz. was chosen for this case study. Its habitat is narrowly defined by special conditions, i.e. the species is stenotopic. It only occupies moist sites with a peaty soil and a low vegetation. It is tyrphobiont, which means that it highly prefers peat moor areas. It has low powers of dispersal, because it is unable to fly (see DEN BOER *et al.*, 1980: fig. 1). Based on data of BAARS (1979a, 1982) for *Calathus melanocephalus* L., the individuals of which are of the same size as those of *A. ericeti*, we estimate 200 meters to be the maximal distance that might be bridged between areas suitable for reproduction (distances covered by walking depend on size of the individual: BAARS, 1982). In Drenthe (The Netherlands) both small local and larger multipartite populations of *A. ericeti* usually are miles away from each other, resulting in complete isolation, because at the relevant time scale passive transport between suitable habitats (by man or animals) can be excluded as development completely occurs in the soil. Therefore, this species can hardly be expected to survive for long in small fragments of habitat, because it will not form metapopulations *sensu stricto* in a fragmented countryside. This enables

us to study the survival of both small local and multipartite populations in habitat islands of different sizes without the need to take into account recolonization after extinction.

## MATERIALS AND METHODS

From sampling runs in the years 1959-1967 (and following years), taken from all kinds of habitat in Drenthe several areas were known to contain populations of *A. ericeti* (DEN BOER, 1977: 137). From these samples and from habitat descriptions by LINDROTH (1945), KROGERUS (1960), MOSSAKOWSKI (1970) and GROSSECAPPENBERG *et al.* (1978) a clear picture of the habitat of *A. ericeti* emerged. Three types of habitat could be distinguished (see also MOSSAKOWSKI, 1970): (1) peat moor areas, which are mainly covered by *Erica tetralix*, *Eriophorum vaginatum* and *E. angustifolium*, *Molinia caerulea*, *Rhynchospora alba* and *R. fusca*; (2) oligotrophic pools in which peat is developing under a floating vegetation of *Sphagnum*-species, *Eriophorum*, *Rhynchospora*, *Molinia*, *Andromeda polifolia* and *Vaccinium oxycoccus* (= *Oxycoccus palustris*); (3) wet heathland, especially *Erica*-heath. *A. ericeti* was never found by us outside of such areas. In 1988 twenty sites in Drenthe with obviously suitable habitat conditions for *A. ericeti*, including all sites that appeared to be occupied by the species between 1959 and 1962, were selected and sampled (table I). The size of these habitats varied between 0.65 and 1714 ha, most of them being isolated in cultivated land for more than 25 years. In most selected habitats at least the upper layers of the soil nearly completely consisted of peaty organic matter (table I), and generally *Erica tetralix*, *Sphagnum*-species or *Molinia caerulea* were abundant.

*A. ericeti* was sampled with the help of circular, plastic pitfalls with a diameter of 10 cm and about 10 cm deep, containing some peat to keep the beetles alive. Once each week or once each fortnight the beetles were taken from the pitfalls. As the reproductive period starts in April, peaks in May and ends during June, sampling was concentrated in May and June. During (reproductive) activities individual beetles move around in an area of about 2 ha or less, so that the chance is high that at least a few specimens will be caught in pitfalls from a population—even a sparse one—occupying an area of 5 ha (say) or less around the pitfalls. This means that the presence of an isolated population in a small site can easily be established, whereas the detection of a local group in a large area will depend on selecting the right site(s). We are confident that at most sites the catch effort was sufficient to show the presence or absence of a population of *A. ericeti* in an area of about 2-5 ha around the pitfalls. Table I enumerates the sampling sites, and the numbers of pitfalls in each.

Both area of the habitat and the number of years during which a particular site has been isolated could be derived from archives of the organization for Forest Management and Nature Conservation of the government (Staatsbosbeheer), and from old maps of the Dutch Ordnance Survey. *A. ericeti* could successfully be bred in the laboratory with small maggots as food. Breeding methods for carabids, which also apply to *A. ericeti*, were developed by THIELE (1968), and further adjusted by Van Dijk; see e.g. NELEMANS (1987).

## RESULTS

Catches of *A. ericeti* in 1988 (1989), and in earlier years by workers of the Biological Station, are presented in table II. Among 20 areas investigated during this study *A. ericeti* was found in eight: in 5 peat

TABLE I

Characteristics of habitats that have been checked for the presence of *A. ericeti* in 1988. In each habitat pitfalls have been operating for several weeks at one or more sites that either were thought to be most suitable for the species, or had shown its presence in 1959-1962. Catch effort is expressed as "pitfall-days". Sites are arranged in order of decreasing area (see table II).

| Code  | local name of area | type of habitat             | upper layer of substratum:<br>floating Sphagnum | highly peaty | number of<br>pitfalls | catch effort        |
|-------|--------------------|-----------------------------|---|--------------|-----------------------|---------------------|
| XI    | Fochteloërveen     | peat moor                   | -   | +            | 5                     | 85                  |
| Dw    | Dwingelder Veld    | <i>Erica-Calluna</i> -heath | -   | +            | +                     | +                   |
| TB    | Bargerveen         | peat moor                   | +   | +            | 10                    | 260                 |
| AH    | Terhorster Zand    | sandy heath area            | +   | +            | 10                    | 250 <sup>2</sup>    |
| YA    | Hingssteveen       | peat moor                   | -   | +            | 6                     | 168                 |
| TD    | De Witten          | peat moor                   | -   | +            | 10-20                 | 320                 |
| XJ    | Gijsselterkoelen   | <i>Erica-Calluna</i> -heath | -   | +            | 10                    | 280                 |
| XF/XH | Karreveen          | moist heath and peat        | +   | +            | 20                    | 730 <sup>3</sup>    |
| YD    | Tweelingen         | degenerated peat moor       | +   | +            | 5                     | 140-70 <sup>4</sup> |
| AJ    | Lange veen         | pool: peat + moor-veg.      | +   | +            | 10-15                 | 830                 |
| XB    | Grote veen         | pool: peat + moor-veg.      | +   | -            | 10                    | 350                 |
| YC    | vak 61, Grolloo    | pool: peat + moor-veg.      | +   | -            | 7                     | 196                 |
| Q/R   | 2 pools, Kampsweg  | pool: peat + moor-veg.      | +   | -            | 20                    | 1260 <sup>3</sup>   |
| YE    | vak 115, Schoonloo | pool: peat + moor-veg.      | +   | +            | 5                     | 140                 |
| XG    | Droserven          | pool: peat + moor-veg.      | +   | +            | 10                    | 380                 |
| XC    | vak 63b, Dwingeloo | pool: peat + moor-veg.      | +   | -            | 10                    | 350                 |
| AB    | Poort II           | pool: peat + moor-veg.      | +   | +            | 10                    | 350                 |
| XA    | Benderse weg       | pool: peat + moor-veg.      | +   | -            | 10                    | 350                 |
| YB    | vak 116, Grolloo   | pool: peat + moor-veg.      | +   | +            | 5                     | 140                 |
| XD    | vak 63c, Dwingeloo | pool: peat + moor-veg.      | +   | -            | 10                    | 350                 |

<sup>1</sup> In that heath area the Biological Station, Wijster has a number of pitfall-series continuously in operation since 1959, so that also in 1988 the presence of *A. ericeti* could be checked.

<sup>2</sup> Only a few small sites at different distances in this heterogeneous area might be (have been) suitable for *A. ericeti*. Because of these uncertainties AH could not be included in the comparisons of table III.

<sup>3</sup> Suitable habitats that were less than 200 m from each other (as in this case) were considered to be parts of the same habitat.

<sup>4</sup> Although the pitfalls have been operating during four weeks, catching at the right spot occurred only two weeks.  
+ = availability of that substratum is restricted; + + = substratum is amply available.

TABLE II

Total area of the habitats in which the sampling sites were situated, duration of isolation of the area in 1988, and catches of *A. ericeti* from sampling sites in 1988 (and in a single case in 1989) as well as in 1959-1962. For explanations of codes see table I.

| Code  | Size of area<br>(ha) | Isolated during<br>.... years   | Number of individuals of <i>A. ericeti</i> caught |      |      |      |                 |
|-------|----------------------|---------------------------------|---|------|------|------|-----------------|
|       |                      |                                 | 1959  | 1960 | 1961 | 1962 | 1988            |
| XI    | 1714                 | multipartite pop. <sup>1</sup>  |   |      |      |      | 16              |
| Dw    | 1607                 | multipartite pop. <sup>1</sup>  | 7   | 57   | 142  | 111  | 18 <sup>3</sup> |
| TB    | 290                  | multipartite pop. <sup>1</sup>  |   |      | 49   |      | + <sup>4</sup>  |
| AH    | 100                  | discontinuous area <sup>2</sup> | -   | -    | 1    | -    | - <sup>2</sup>  |
| YA    | 73                   | multipartite pop. <sup>1</sup>  |   |      |      |      | 14              |
| TD    | 72                   | multipartite pop. <sup>1</sup>  |   |      | 23   | 14   | 50              |
| XJ    | 55                   | 26                              |   |      |      |      | 1               |
| XF/XH | 13.6/56              | 54                              |   |      |      |      | -               |
| YD    | 22.2                 | 55                              |   |      |      |      | 4               |
| AJ    | 4.15                 | 59                              |   |      | 16   | 6    | -               |
| XB    | 4.15                 | 66                              |   |      |      |      | -               |
| YC    | 4.10                 | 52                              |   |      |      |      | -               |
| Q/R   | 3.56                 | 24                              | 46  | 40   | 2    |      | -               |
| YE    | 1.69                 | 54                              |   |      |      |      | 8               |
| XG    | 1.30                 | 62                              |   |      |      |      | -               |
| XC    | 1.15                 | 64                              |   |      |      |      | -               |
| AB    | 1.10                 | 71                              |   | -    |      |      | -               |
| XA    | 1.0                  | 46                              |   |      |      |      | -               |
| YB    | 0.68                 | 53                              |   |      |      |      | -               |
| XD    | 0.65                 | 59                              |   |      |      |      | -               |

-: sampling occurred, but no catches of *A. ericeti*.

<sup>1</sup> Suitable sites in these areas are sufficiently large and commonly present that isolation of sub-populations (interaction groups) may be excluded.

<sup>2</sup> See note 2 to table I.

<sup>3</sup> Between 1962 and 1988 *A. ericeti* was also caught at Dwingelder Veld in different (5-12) sampling sites; total numbers in these years were successively: 81, 124, 159, 67, 17, 5, 58, 20, 42, 53, 14, 10, 5, 2, 3, 1, 0, 2, 1, 10, 24, 26, 65, 91, 15 and 18. In 1988 students, who sampled some other—not yet investigated—sites at Dwingelder Veld with a well-developed peaty upperlayer of the soil, caught 199 individuals of *A. ericeti*, mainly young (callow) individuals.

<sup>4</sup> In 1989 B. Takman (Staatsbosbeheer) sampled some other sites in this heterogeneous area and caught *A. ericeti*, so that the species appeared still to be present in "Bargerveen" (+).

moors (tables I, II: XI, TB – only in 1989, YA, TD, and YD), in one small peat site with pits that were filled again by *Sphagnum* (table II: YE), and in two wet heathlands (tables I, II: Dw and XJ). Presence or absence of *A. ericeti* is related to area and duration of isolation (table II). Isolation is considered absolute when separation from other suitable sites amounts to more than 200 m. Most study sites reached their present size in the period 1930-1940, when unemployed workmen were brought to Drenthe to reclaim poor sandy heathland and peat moors. Usually only small pieces of the original landscape were left behind. It is impossible to estimate exact periods of isolation for the larger areas (>70 ha), because the reduction and fragmenta-

TABLE III

Relationship between area of habitat and presence/absence of *A. ericeti*. The study sites are divided into four groups, *A*: *A. ericeti* was caught there in 1988 (1989); *B*: *A. ericeti* was caught there in the past, but not in 1988 (1989); *C*: all sites where *A. ericeti* was not caught in 1988 (1989); *D*: the same as *C*, but sampling sites in blown sand areas excluded. Given are "Code" and "Area" of habitat (ha).

| <i>A</i> |      | <i>B</i> |     | <i>C</i> |         | <i>D</i> |         |
|----------|------|----------|-----|----------|---------|----------|---------|
| TB       | 290  | AJ       | 4.2 | XF/XH    | 13.5/56 | XF/XH    | 13.5/56 |
| TD       | 72   | Q/R      | 3.6 | AJ       | 4.4     | AJ       | 4.4     |
| XI       | 1714 |          |     | XB       | 4.2     | YC       | 4.1     |
| Dw       | 1670 |          |     | YC       | 4.12    | Q/R      | 3.6     |
| YA       | 73   |          |     | Q/R      | 3.6     | AB       | 1.1     |
| XJ       | 55   |          |     | XG       | 1.3     |          |         |
| YD       | 22   |          |     | XC       | 1.2     |          |         |
| YE       | 1.7  |          |     | AB       | 1.1     |          |         |
|          |      |          |     | XA       | 1.0     |          |         |
|          |      |          |     | YB       | 0.7     |          |         |
|          |      |          |     | XD       | 0.7     |          |         |

For explanation of codes see table I.

tion of the natural peat moor areas from which they originated was a continuously progressing process. For the present study this is not considered a serious disadvantage, because in large habitats the majority of the subpopulations sampled were living far from the borders and thus are not isolated at all.

Table II clearly shows the presence of *A. ericeti* in the larger habitats, and its almost complete absence in the smaller ones. Some of the smaller sample sites concern peat that was formed in depressions in blown sand areas (XB, XG, XC, XA, YB and XD: table I), and we cannot exclude that these small peat bogs always have been isolated, viz. farther than 200 meters away from other sites suitable for *A. ericeti*. When we remove these sites from our comparison (table III) the remaining sites where *A. ericeti* was not found in 1988 (or 1989), group D, were still highly significantly smaller than those where it appeared to be present, group A (Mann-Whitney,  $P = 0.015$ , one-sided). The same is true, of course, if we compare groups A and C ( $P = 0.001$ , one-sided): SOKAL & ROHLF (1981).

YE was the only small and isolated site where *A. ericeti* was found to be present. It is one of the few smaller habitats where an appreciable layer of the surface soil is highly peatlike (see table I). In TB (Meerstablok in Bargerveen) *A. ericeti* was found in 1961, but in 1988 it was not caught at that side, which had become much drier since

about 1965. It must be noted that in such a large and heterogeneous area (290 ha) the right spot to put the pitfalls can easily be missed. Therefore, B. Takman of "Staatsbosbeheer" placed some pitfalls at another spot in the same reserve in 1989, and found that *A. ericeti* is still present in "Bargerveen".

Populations in habitats smaller than 70 ha have been isolated in a "sea" of unsuitable area for between 24 and 71 years (table II). In site Q/R (3.6 ha), *A. ericeti* was present in 1959-1961 (table II), but not in 1988. Apparently, 24 years of isolation is sufficient for small isolated populations to become extinct.

From the fluctuation patterns of 3 subpopulations at Dwingelder Veld during 7 years and 3 others during 6 years (fig. 1) we estimated the degrees of similarity of the sequences of catch-numbers (ranks),  $W$  (coefficient of concordance: KENDALL, 1962) to be 0.59 and 0.65 respectively ( $P \approx 0.10$ ), which is not essentially different from  $W = 0.54$  for *Pterostichus versicolor* for 4 subpopulations during 10 years at Dwingelder Veld (DEN BOER, 1982). For, if in *P. versicolor* we calculate  $W$  for subpopulations at the same sites and during the same years as we did in *A. ericeti* we get the value 0.64 and even 0.95 respectively. This suggests that in larger habitats *A. ericeti* will be protected from extinction by spreading of risk in space to a not lower extent than *P. versicolor* (compare DEN BOER, 1981, 1982, 1986a). Therefore, we can sufficiently support the supposition that *A. ericeti* can survive in larger habitats, because it forms there multipartite populations that are comparable with those of *P. versicolor* at Dwingelder Veld (e.g. DEN BOER, 1986a).

From the same fluctuations in numbers at Dwingelder Veld (above) we could estimate survival times of 8 separate subpopulations of *A. ericeti*, according to the method developed by DEN BOER (1985, 1986b), to be 7-44 years, with a mean value of 19 years. The disappearance of the small and isolated population in site Q/R after 24 years of isolation (table II) thus fits with these estimates. This is less clear for site AJ, because isolation there lasted 59 years (table II). This population was still present in 1961 and 1962 (table II), i.e. after 32 (33) years of isolation, but had disappeared after 27 (26) more years of isolation.

The three types of habitat that were considered suitable for *A. ericeti*, and that were investigated in this study, viz. peat moor areas, oligotrophic pools with a growing layer of peat, and wet heathlands, all have a peaty upper layer of the soil. Only oligotrophic pools where the peat has been cut during the last half century, have hardly yet accumulated peat under the floating *Sphagnum*-vegetation. This more or less applies to sites XB, YC, Q/R, XC, AB, XA and XD (table I), and may contribute to the absence of *A. ericeti*. For, table I shows that



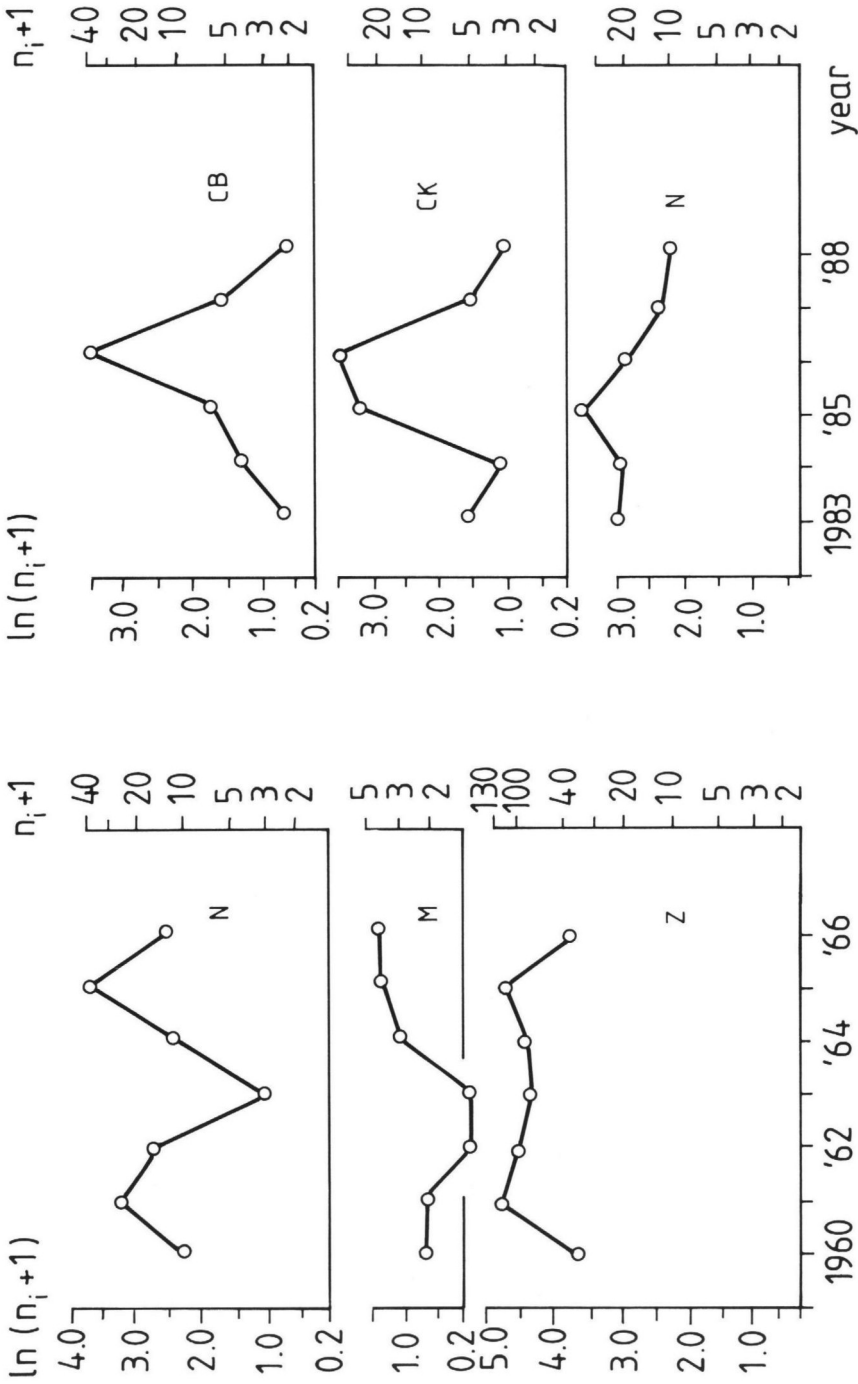


Fig. 1. Uninterrupted year-catches ( $n_i$ ) of *A. ericeti* in standard series of pitfalls (Den Boer, 1977) during a number (6 or 7) years from different subpopulations at Dwingelder Veld to show that usually numbers do not fluctuate synchronously: W (coefficient of concordance) = 0.59 for N, M, Z in 1960-1966, and W = 0.65 for CB, CK, N in 1983-1988 respectively. The degree of concordance (59-65%) is not significant ( $P \approx 0.10$ ), so that the degree of discordance (35-41%) seems to be sufficiently effective. We added unity to  $n_i$  to avoid the necessity to picture the natural logarithm ( $\ln$ ) of zero, which otherwise had to occur for M in 1962 and 1963.

there is a correlation between the presence of a peaty layer at the surface of the soil and the presence of *A. ericeti*: G-test,  $0.010 < P < 0.025$  (SOKAL & ROHLF, 1981). In this respect habitat conditions in site YE, the only small site where *A. ericeti* was still present after more than 40 years of isolation (table II), must be very favourable, because a firm peat-soil is combined there with thick layers of peat moor vegetation in pits.

#### DISCUSSION

This study aimed to test the extinction rate of populations isolated in habitat islands, i.e. to test the "area-effect" of island biogeography. The stenotopic carabid species *A. ericeti* with low powers of dispersal (unable to fly) was chosen as a test species. We predicted that *A. ericeti* would have disappeared from small habitat islands, but would still be present in large ones. Table II shows that this hypothesis cannot be rejected, and that it is confirmed with a high probability. However, in this conclusion some implicit assumptions are taken for granted:

- (1) All sample sites are situated in suitable habitats that were not isolated before large-scale reclamations occurred in Drenthe.
- (2) In the past all suitable sites contained populations of *A. ericeti*.
- (3) Since the time of evident isolation the habitat conditions in the sites studied remained suitable for *A. ericeti*.
- (4) All sites considered suitable are actually suitable for *A. ericeti*.
- (5) Individuals of *A. ericeti* are not able to bridge distances between suitable sites that greatly exceed 200 meters.
- (6) In all areas where a viable population of *A. ericeti* was present the chance is high that at least a single specimen will be caught.

These assumptions are reasonable, but they should be discussed below to ascertain their correctness.

- (1) Until the 17th century Drenthe was an island of heathland—with extensive areas of wet *Erica*-heath—amidst huge peat moors. The reclamation of the peat moors advanced slowly so that even after the Second World War about 15000 ha of peat moor was still left in the SE-corner of Drenthe. Reclamation of the heathlands started in the second part of the 19th century, but even in 1928, when the Society for the Preservation of Nature Reserves in The Netherlands (Natuurmonumenten) planned to save at least one of the vast heathland areas of Drenthe, Beijerinck (the founder of the Biological Station, Wijster) and Brouwer (BROUWER, 1968) had the possibility to choose among twelve such areas. In short, assumption 1 is correct, with the exception of small, natural peat bogs formed in depressions of blown sand areas. In this study these areas were considered separately.

(2) This cannot be proved. But all authors (see: Material and Methods) agree that the species is highly characteristic for peat moor areas, and may be expected to occur in all undisturbed areas of that kind. Given the history of the landscape of Drenthe—see (1)—*A. ericeti* must have been a very common species, so that especially in the remnants of this landscape selected by us (compare Ordnance Survey maps of the 19th century) populations of *A. ericeti* could be expected.

In the still growing peat moors of larger area, e.g. TD, it is indeed found everywhere (unpublished data from 1961, 1962, 1988, 1990).

(3) We choose *A. ericeti* for this case study because its habitat—apart from the majority of the small peat bogs formed in pools—is amongst the most stable in our areas. We can only give some information concerning the continuous presence of *A. ericeti* for Dwingelder Veld (see table II). Unfortunately, such detailed information is lacking for other habitats, so that for the time being assumption 3 is not necessarily correct.

(4) This assumption also cannot be strictly proved, but the finding of the species in all larger areas that we considered suitable, including those that were not sampled in the past, such as XI (Fochteloeërveen) and YA (Hingsteveen), gives us some confidence. The fact that in the past *A. ericeti* was found in two (Q/R, AJ) of three (also AB) small peat bogs in pools suggests that also there habitat conditions were suitable, at least in the period 1959-1961. Of course, small sites are more susceptible than large ones to negative influences from the outside, but apart from site Q (as a part of Q/R), which has been eutrophicated and partly grown with birches and pines, there are no indications that this played a significant role in our results.

(5) Since most distances between suitable habitats for *A. ericeti* are much larger than 200 m, this assumption is not very critical. Baars (1979a) studied the walking patterns of two very different carabid species: *Calathus melanocephalus* with individuals of 6-8 mm, and *Pterostichus versicolor* with individuals of 10-12 mm. In spite of many ecological differences the walking patterns were similar, only the distances covered were greater in *P. versicolor* than in the smaller *C. melanocephalus* (see BAARS, 1982). Less detailed studies in other species, e.g. in *Carabus problematicus* with individuals of 21-27 mm (RIJNSDORP, 1980) confirmed the findings of BAARS (1979a). Apparently, the walking patterns found by Baars are general for carabid beetles, and the distances covered are related to the size of the beetles. Therefore, we can safely assume the distances covered by *A. ericeti*, with individuals of the same size as in *C. melanocephalus*, to be similar to that of *C. melanocephalus*. In a standard set of pitfalls (DEN BOER, 1977) 90% of the adults of *C. melanocephalus* caught originated from distances within

80 m from the pitfalls (BAARS & VAN DIJK, 1984). The maximal distance covered by walking individuals of *C. melanocephalus* is about 200 meters, so that we suppose the same for the monomorphic brachypterous *A. ericeti*.

(6) In subpopulations, for instance in the centre of Dwingelder Veld, in a standard set of pitfalls (with about the "catchability" of 9-10 plastic pitfalls as used in this study: BAARS, 1979b, 1982) we catch up to a few percent of the local group of some middle-sized carabid species (6-12 mm). In small, isolated populations, however, the catch may amount to about 10% of population size (compare DEN BOER, 1979; NELEMANS *et al.*, 1989). Therefore, in large areas a sparse population of *A. ericeti* may remain unobserved. However, since the presence of the species could be shown for all larger habitats sampled (table II), we need not worry about this possibility. On the other hand, in habitats smaller than about 5 ha catchability has been sufficiently high to be sure that no population above the level of "underpopulation" (ANDREWARTHA & BIRCH, 1954) will have escaped our attention. More information on the relationship between year-catches in pitfalls and population size can be found in DEN BOER (1977, 1986a, 1990).

The assumptions implicit in our prediction are sufficiently close to reality to enable us to conclude that *A. ericeti* can only survive in the long run in suitable habitats that are large enough (say >50-70 ha) to contain a number of different subpopulations. This explains why isolation of local populations of *A. ericeti* in small habitats, in all cases except one (YE), resulted in extinction in less than 24-66 years (table II).

Small and separated local populations (or subpopulations) of *A. ericeti* are expected to survive 7-44 years with a mean value of 19 years. Such groups are living in habitats of about 2-5 ha. Since this survival range was fixed at values between one and two standard deviations from the mean we could expect that on the average one among ten of such isolated populations will survive longer than 44 years. The presence of a population in YE (1.7 ha) after 54 years of isolation (table II) should be considered as one case among either 14 (YE + groups B + C of table III) or 8 (YE + groups B + D of table III), depending on whether one incorporates small peat bogs in blown sand areas or not. This nicely fits with our expectations, *i.e.* one of 11 sites on average. That it was exactly YE among the small sites where this expected small population of *A. ericeti* was found, shows that also highly favourable habitat conditions can prolong survival in a small site (table I). As we cannot exclude that the fluctuation patterns of separate subpopulations at Dwingelder Veld were significantly levelled by movements of individuals between subpopulations, our

estimates of survival times might even have been too high. If so, the presence of a population of *A. ericeti* in YE after 54 years of isolation is still more remarkable.

Our study is a clear example where the "area effect" of island biogeography, as far as it rests on the extinction rate of populations, also applies to habitat islands, in spite of criticisms (*e.g.* GILBERT, 1980). It shows especially that when the expected survival time of a population in a small isolated site (a local population) is lower than the period of isolation of that "island"—as in the case of *A. ericeti*—habitat islands should be sufficiently large. This means, large enough to contain a multipartite population (ANDREWARTHA & BIRCH, 1984). In other words, such a habitat island should contain sufficient effective environmental heterogeneity to give the turnover of local groups enough degrees of freedom to minimize significantly the chance that all groups would die out at the same time: spreading of the risk of extinction (DEN BOER, 1968). Discussions among biogeographers, such as those about the most desirable design of nature reserves which occurred under the acronym SLOSS (a Single Large Or Several Small reserves), see WILCOX & MURPHY (1985), must take into account differences in dispersal power between species. This means that, if nature conservation policy would result in preserving many small sites instead of a few large ones of the same combined size, one would protect species with high powers of dispersal at the expense of species with low powers of dispersal. On the other hand, if it is decided to preserve a few large habitats species with both low and high powers of dispersal may have a chance to survive.

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