

Viability of ground beetle populations in fragmented heathlands

Henk de Vries

Promotoren: **Dr. L. Brussaard**
 Hoogleraar in de Bodembioogie

Dr. W. van Delden
Hoogleraar in de Populatiegenetica
Rijksuniversiteit Groningen

Co-promotor: **Dr. Th. S. van Dijk**
 Universitair docent Biologisch Station Wijster

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H. H. de Vries

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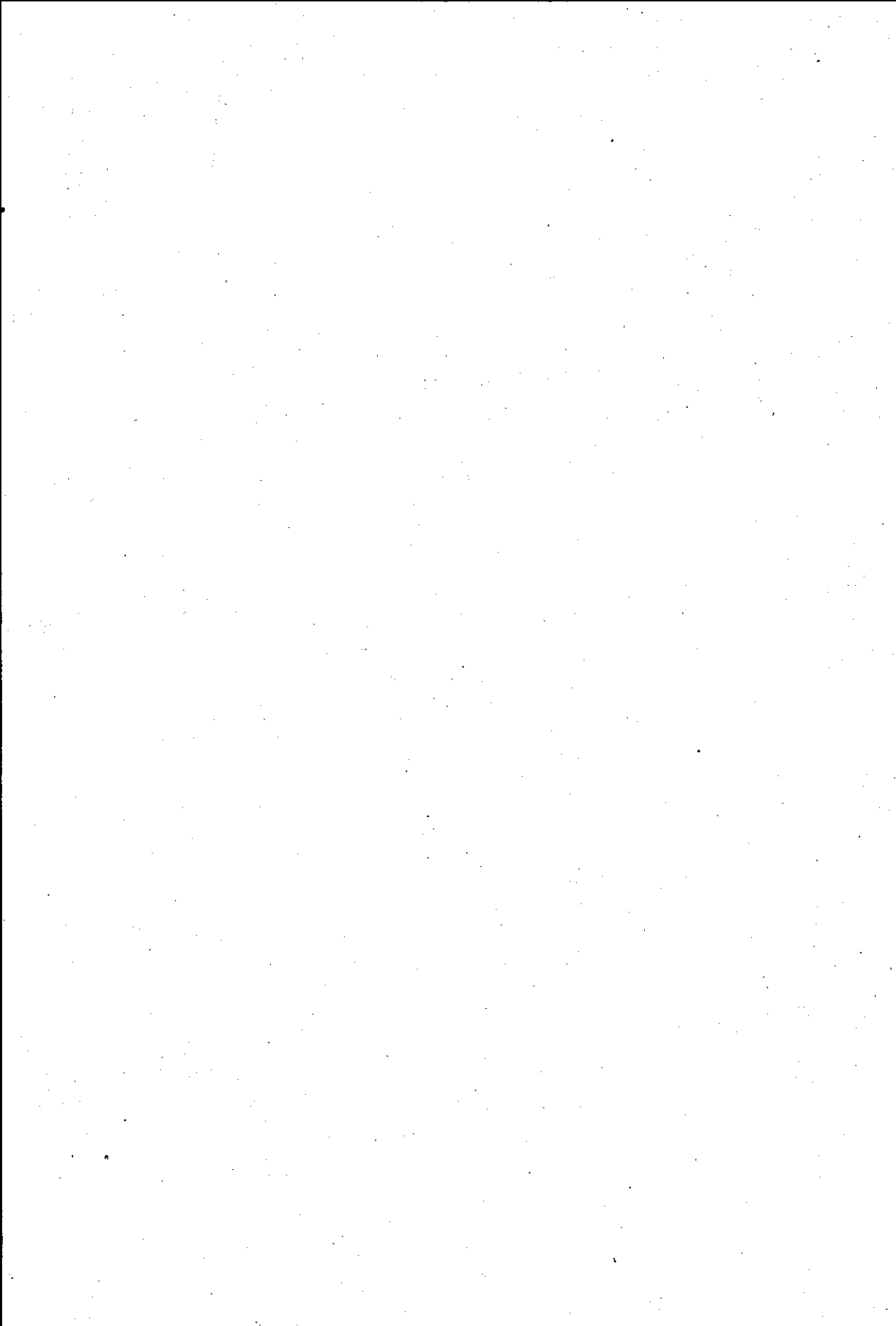
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Abstract

Numbers of ground beetle species that are characteristic for heathlands were negatively associated with area, whereas this relationship was not found for the total number of ground beetle species or for unspecialised ground beetle species. In particular the number of heathland species with low dispersal ability was strongly related to area. Transplant experiments showed that some heathland species with low dispersal ability experienced reduced habitat quality in small habitats, whereas for others at least part of the unoccupied areas were of sufficient quality for successful reproduction. From the presence of occupied as well as unoccupied habitats and from knowledge on its possibilities for dispersal, it is inferred that *Pterostichus lepidus* lives in metapopulations with continuously and discontinuously occupied patches. Using allozymes, high levels of genetic variation were found in *P. lepidus* and *Agonum ericeti* from large areas. In two small areas, however, populations of *P. lepidus* had relatively low levels of genetic variation and were genetically different from the other populations. As exchange of individuals of *P. lepidus* between the separate populations is possible, the divergent genetic composition of the two populations of *P. lepidus* probably results from founder events. Populations of *A. ericeti* from small patches were not genetically divergent from large areas. As exchange of individuals between populations in this species is not possible, it is concluded that dense populations in small areas have remained present since isolation. Genetic erosion could not be identified as an important process causing extinction of ground beetle populations. Environmental stochasticity is the most important threat for the survival of small and isolated ground beetle populations. The presence-absence data of ground beetles in heathlands of various sizes showed that specialized species need a habitat of more than 50 ha to provide a substantial chance to survive an isolation period between 25 and 100 year. For part of the endangered species two options are available to reduce extinction rates: enlargement of habitats and the formation of corridors between habitats.

Key words: allozymes, area, dispersal, genetic variation, ground beetles, habitat fragmentation, habitat preference, heathland, isolation, survival



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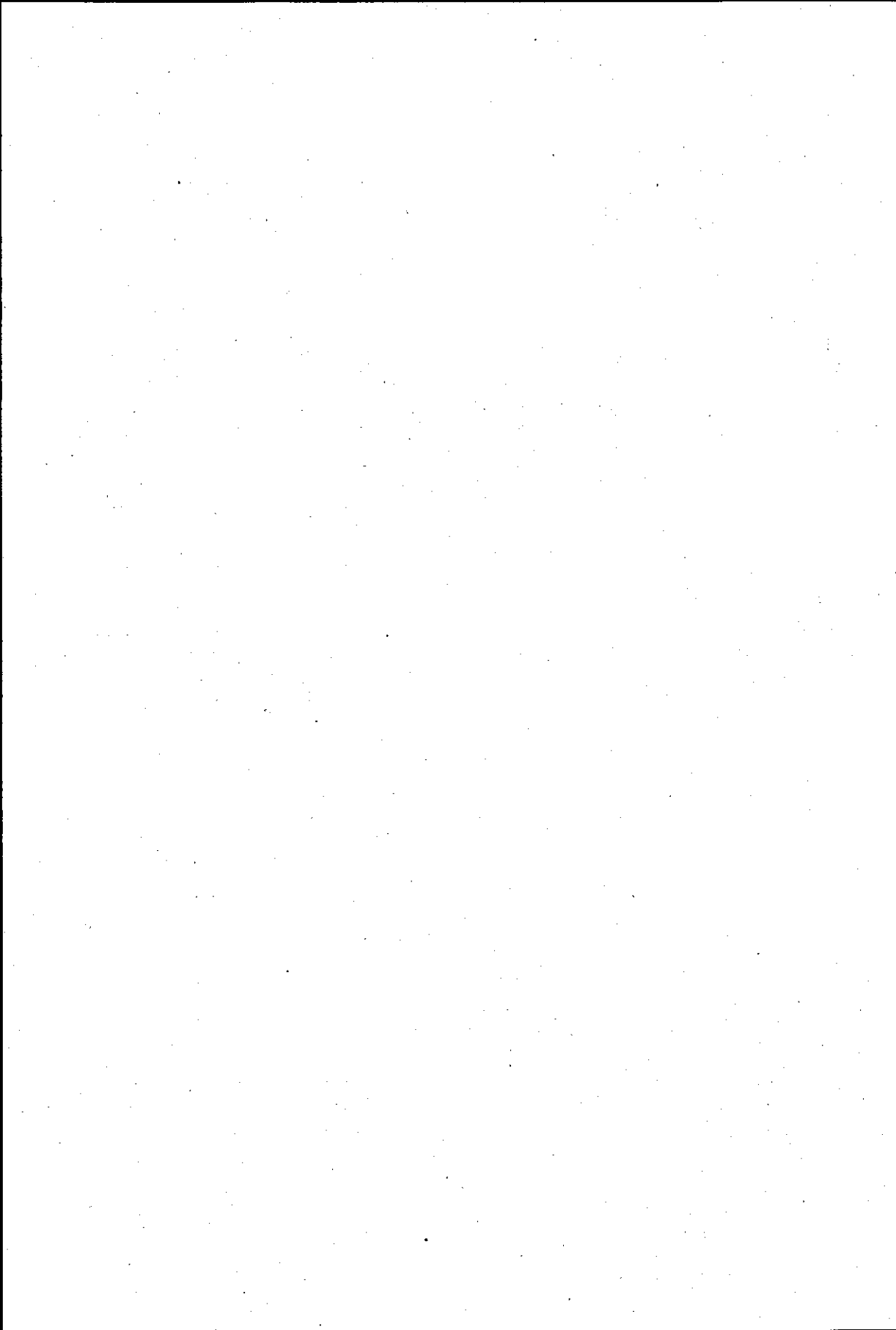
Behorende bij het proefschrift

'Viability of ground beetle populations in fragmented heathland'

1. Om populaties heideloopkevers gedurende enkele tientallen jaren effectief te kunnen beschermen is minimaal vijftig hectare heide nodig.
Dit proefschrift
2. Het vliegvermogen van sommige loopkeversoorten maakt het mogelijk dat deze soorten kunnen voortbestaan in kleine leefgebieden, het is echter geen garantie.
Dit proefschrift
3. Er zijn geen aanwijzingen dat genetische verarming een belangrijke rol speelt bij het uitsterven van loopkeverpopulaties.
Dit proefschrift
4. De levensverwachting van een geïsoleerde loopkeverpopulatie is korter dan die van de Nederlander.
5. Bij het gebruik van 'incidence-functies' binnen het natuurbeheer is het onjuist te veronderstellen dat vestigen en uitsterven van populaties even vaak plaatsvinden.
6. Ten onrechte worden goede verbreiders, zoals vogels, vaak als gidssoort gebruikt voor het functioneren van ecologische infrastructuur.
7. Technieken ontwikkeld binnen de moleculaire biologie en de toegepaste landbouwwetenschappen worden te weinig gebruikt ten behoeve van de natuurbescherming.
8. Het begrip 'democratie' dient te worden verruimd door Eerste Kamerleden nadrukkelijk de taak te geven het kabinetsbeleid te toetsen aan de belangen van toekomstige generaties.
9. Het bezit van spaarkaarten betekent voor de vaste klant van winkelbedrijven eerder een belasting dan een besparing.
10. Aangezien de meeste proefschriften ongelezen verdwijnen in de papierkringloop, kan men ze beter laten verschijnen op kringlooppapier.

Contents

	Voorwoord	9
<i>Chapter 1</i>	General introduction	11
<i>Chapter 2</i>	Survival of populations of <i>Agonum ericeti</i> in relation to fragmentation of habitats	27
<i>Chapter 3</i>	Ground beetle species in heathland fragments in relation to survival, dispersal, and habitat preference	43
<i>Chapter 4</i>	Metapopulation structure of <i>Pterostichus lepidus</i> and <i>Olisthopus rotundatus</i> on heathland in the Netherlands: results from transplant experiments	69
<i>Chapter 5</i>	Genetic variation in populations of two ground beetle species, <i>Agonum ericeti</i> and <i>Pterostichus lepidus</i> , in relation to fragmentation of habitats	85
<i>Chapter 6</i>	General discussion	105
	References	113
	Summary	123
	Samenvatting	127
	Curriculum vitae	131
	Appendix	133



Voorwoord

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Chapter 1

General introduction

In this thesis viability of ground beetle populations in fragmented habitats and the processes causing extinctions are studied. It is hypothesized that populations of species with low dispersal ability have a higher extinction rate than species with high dispersal ability. This was investigated for ground beetles of heathlands. In this chapter I will first review the current knowledge of extinction rates and relevant processes, including a brief overview of the work from the Biological Station relevant for this thesis. Next, I will give a description of this research, with an introduction of the landscape investigated and an outline of this thesis.

The loss of species

Estimates of the total number of living species on earth vary between five and one hundred million (Ehrlich, 1995). More than 1.8 million living plant and animal species have been described, among which approximately 1.2 million insect, 47 thousand vertebrate, and 240 thousand plant species (Smith et al., 1993). It is estimated from fossils that the currently living species comprise about 2 - 4% of all those that have ever lived (May et al., 1995). This means that extinction of species is a natural process. Fossil records indicate that the average species lifespan is about 5 - 10 million years (May et al., 1995). The rate of natural extinctions taking place during the past 600 million years, the so called 'background extinction', is roughly estimated as one species per year (Raup & Sepkoski, 1984). However, the current rate of species loss is much faster than expected from natural causes (Myers, 1986; Soulé, 1986; Wilson, 1988). The main reason for this is the elimination of large amounts of habitat by human activities, as e.g. tropical rain forest. More than half of the species occur in tropical rain forest, a habitat which covers about 7% of the earth and of which about 7 to 9 million hectares disappear

yearly (Myers, 1988). The loss of species due to deforestation is estimated at 10 to 25 thousand every year (May et al., 1995). This rate is in sharp contrast with the number of extinctions recorded by the World Conservation Monitoring Centre, which amounts to only 600 plant and 486 animal species (Smith et al., 1993). This illustrates the difficulty to record extinctions reliably.

Compared to vertebrates only a small percentage of insects is known to be currently threatened by extinction: approximately 5% of the vertebrates, whereas only approximately 0.09% of the insects (May et al., 1995). The reason for this difference is probably mainly the limited knowledge of insect diversity in large parts of the world. One of the best investigated countries with respect to insects is the Netherlands (17,521 species described, Koomen et al., 1995). By far the largest group of insects are beetles (world-wide about 290 thousand described species, Wagner & Liebherr, 1992). In the Netherlands about 4 thousand species have been recorded, of which 949 are Staphilinidae, 562 Curculionidae, and 388 Carabidae (ground beetles) (Koomen et al., 1995). Most knowledge about distribution and ecology of beetles concerns ground beetles, the object of study of this thesis. A comparison of datasets from before and after 1950 indicated a distinctive decrease in occurrence of sixty-two ground beetle species and the extinction of another twenty-eight species in the Netherlands (Turin, 1990).

Causes of extinction

The main causes of man induced extinctions (Caughly, 1994) are:

1. Habitat destruction and fragmentation most commonly by deforestation and/or turning natural into cultivated areas. Deterioration of habitats by pollution or excessive grazing by domestic animals also lead to large scale destruction. Often only fragments of the original habitat are left.
2. Introduction of species new for the area. In particular, species which live on islands without mammal predators are vulnerable to the introduction of predators.
3. Chains of extinction, associated with the extinction of particular species, on which other species depend.

4. Overkill, mostly by hunting of large mammals.

These four processes, which make populations sparse in the first place (which Simberloff (1986) calls the 'ultimate cause of extinction', and Caughley (1994) refers to as part of the 'declining population paradigm'), are often (e.g. Lawton, 1995) distinguished from processes finally causing the extinction, once populations are small (Simberloff's 'proximate causes', and Caughley's small population paradigm'). The latter causes include demographic and environmental stochasticity, catastrophes, and genetic deterioration (Shaffer, 1981, 1987). Often the creation of nature reserves will help to reduce the impact of these 'proximate' factors. Though practical experience with respect to these factors is limited, as far as invertebrates are concerned, theoretical knowledge is amply available (Caughley, 1994).

Size of habitat

The importance of habitat size for the survival of populations has been a subject of interest for many years, spurred by the theory of island biogeography of MacArthur and Wilson (1967). They described a relationship between the number of species present on an island and the colonization and extinction rates of species. According to this theory the colonization rate is negatively related to the number of species already present on a certain island. The more species already present, the lower the chance that an immigrating individual belongs to a new species. The distance to a source area, usually the mainland, is the second parameter of importance for immigration rates. The larger this distance the less individuals reach the island. The extinction rate is related to the number of species present on an island. The more species present, the more there are to become extinct. Secondly, extinction rate is supposedly related to the size of an island. Small islands have small populations which run a high risk of extinction. In a situation where the rate of colonization and extinction is about the same, the number of species is thought to be in dynamic equilibrium. According to Connor and McCoy (1979) three different explanations for the relationship between area and the number of species present can be given, which all three may be partly true. With an increase of area the diversity in habitats present (Williams, 1964) or the number of immigrating individuals (Connor & McCoy, 1979) are expected to increase, both resulting in

more species. The third explanation is that with increasing area extinction rates decrease (Preston, 1960, 1962; MacArthur & Wilson, 1967). Diamond (1972) showed that islands in the Pacific ocean, which previously had been connected to the mainland (continental islands), contain more species than similar sized islands which never had any contact to the mainland (oceanic islands). Continental islands are considered to be in the process of losing species on their way to a new equilibrium. This process is called relaxation (Diamond, 1972).

Nature reserves are often considered as islands in a 'sea' of cultivated land and are referred to as habitat islands. Sometimes a large habitat island can be substitute for the 'mainland' (e.g. Harrison, 1989), but in other cases all other reserves or only the nearby ones are donors of immigrating individuals. The fragmented heathlands in the Netherlands can be considered as habitat islands. Since the present landscape was formed, heathlands are expected to lose species until a new balance is reached between colonization and extinction. Whenever colonization rates are very low or zero, because of the hostile surrounding landscape, according to the theory of island biogeography, habitat islands lose species at a rate mostly depending, on the size of their populations.

Dispersal in the context of metapopulations

It is useful to make a conceptual distinction between the presence of species at different spatial scales (Hanski & Gilpin, 1991). The scale at which individuals move and interact with each other in the course of their routine feeding and breeding activities is often referred to as the local scale. The largest scale is the geographic scale, the scale of species' entire geographic range. Intermediate is the scale at which individuals infrequently move from one place (population) to another. The metapopulation concept refers to this scale. According to Hanski (1991) a metapopulation is defined as a set of populations which interact via individuals moving among populations. It refers to a situation in which different populations are at some distance of each other, because the habitat of the species in question is discontinuous in space (discontinuous habitats). Since Levins (1969) introduced the metapopulation model, many population structures have been

described showing features of a metapopulation (e.g. Harrison et al., 1988; Verboom et al., 1991; Ouborg, 1993; Hanski et al., 1994; Eber & Brandl, 1994).

Recently the distinction of several types of metapopulations have been proposed. Harrison (1991) and Harrison and Hastings (1996) describe four major types of metapopulations: (1) Mainland-island metapopulations. Local extinctions mainly occur among a subset of populations, the islands, and have little effect upon regional persistence since the extinction-resistant mainland is the major provider of colonists. (2) Patchy populations, which are distributed over a patchy and/or spatiotemporally variable habitat, but in which rates of dispersal effectively unite the patches into a single demographic entity. Discrete local populations rarely become extinct. (3) Non-equilibrium metapopulations, among which recolonization is either absent or insufficient to balance extinction. These metapopulations are regionally declining. (4) Classical metapopulations, sets of conspecific populations persisting in a dynamic regional balance between extinction and colonization, as represented by the standard metapopulation models.

Many authors stress the importance of dispersal for founding new populations in discontinuous habitats (Andrewartha & Birch, 1954; MacArthur & Wilson, 1967; Levins, 1970; Den Boer, 1970a, 1990a, 1990b; Opdam, 1990; Hanski, 1991). It can be inferred that differences in dispersal ability between species result in different patterns of occupancy of habitats that have become patchily distributed, giving basically three patterns in time of presence with respect to the populations in such habitats: temporary presence, continuous presence, and discontinuous presence. In the first case, once the population has gone extinct in the habitat patch, the species does not have any chance to recolonize a patch. This is the case when the population is effectively isolated and survival entirely depends on local reproduction and mortality. In the second case, a species will have a very low chance to go locally extinct due to ample dispersal between patches. Individuals so often move between habitat patches that no patch is unoccupied. According to the definition of Harrison (1991) such species live in 'patchy populations'. In the third case, species form metapopulations with frequent colonization and extinction of patchily distributed populations (Levins, 1970; Hanski & Gilpin, 1991). Not all suitable patches in the landscape are occupied at the same time. This results in a

discontinuous presence in a habitat patch. The species belonging to this group have limited walking or flight abilities. The temporary use of marginal habitats may enable them to disperse to some degree across largely unsuitable landscape. In this thesis examples will be presented of populations of all three groups, as well as examples of species in continuous habitats.

Population dynamics of ground beetles

The concept of 'population' refers to groups of individuals on very different scales, dependent on the problems being studied (Den Boer, 1977). Generally, it refers to a group in which each individual has more interaction with the other members of its group as compared to interactions with individuals outside the group. Den Boer (1977) states that the distances covered by individuals define the spatial dimensions of a particular kind of population, which he refers to as an interaction group, see fig. 1a. A population present in a continuous habitat several times larger than the distance covered by individuals is then referred to as a multipartite population (Andrewartha & Birch, 1984), see fig. 1b.

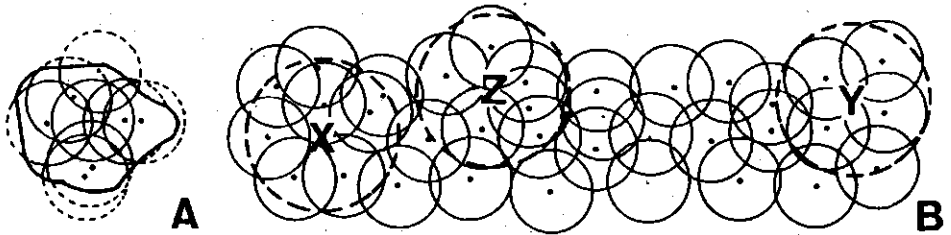


Fig. 1. Diagram of interaction groups (from Den Boer, 1977). Each dot represents a place where an individual is supposed to be born, and is the centre of a circle delimiting the maximum distances that can be covered by that individual in the normal patterns of activity, during its lifetime. Only a few individuals are pictured, of course.

A. An interaction group. A separate group at a more or less isolated site of about the right dimensions.

B. A multipartite population. Starting from each point an interaction group can be defined (dotted circles), e.g. starting from the point X, Y or Z.

For decades the fluctuations in density of individuals in interaction groups of ground beetles have been monitored in natural and semi-natural areas in the province of Drenthe (Den Boer & Van Dijk, 1994). From this work it became clear that densities in interaction groups of ground beetles fluctuate violently (Den Boer, 1977, 1981). As an example the dynamics of several interaction groups of *Pterostichus versicolor* are depicted in fig. 2. The different interaction groups are fluctuating asynchronously, indicating that favourable and unfavourable environmental conditions alternate in space and time. A combination of the dynamics of these interaction groups, representing the average density changes of the multipartite population, show considerably diminished fluctuations as compared to the separate interaction groups (see top of fig. 2). As a consequence the risk of extinction of the multipartite population is spread over all the different interaction groups ('spreading of risk', Den Boer, 1968, 1981). However, in another ground beetle, *Calathus melanocephalus*, a similar reduction in fluctuation of the multipartite population was not observed (fig. 3). The reason for this is that, contrary to *P. versicolor*, the interaction groups were fluctuating synchronously, due to overall winter conditions being similar at all sites (Van Dijk & Den Boer, 1992). Unlike *P. versicolor*, apparently *C. melanocephalus* experienced the conditions within this area as homogeneous. Most ground beetle species have, at least partly, asynchronously fluctuating interaction groups which as a consequence lowers the risk of extinction of the multipartite population (pers. comm. Den Boer).

Small patches of habitat are expected to be occupied by a small number of interaction groups, in extreme cases by only one. Extensive field research, in which the movements of a large number of ground beetles were individually monitored, showed that the area occupied by one interaction group is 2 ha for *C. melanocephalus* and 12 ha for *P. versicolor* (Baars & Van Dijk, 1984). Using two different methods, Den Boer calculated the survival times of species in patches too small for more than a single interaction group. Direct observations of the disappearance and establishment of species in a large number of sites gave an estimate of turnover rate, the rate at which species colonize and become extinct, and thus of average survival time (Den Boer, 1985). Another method (Den Boer,

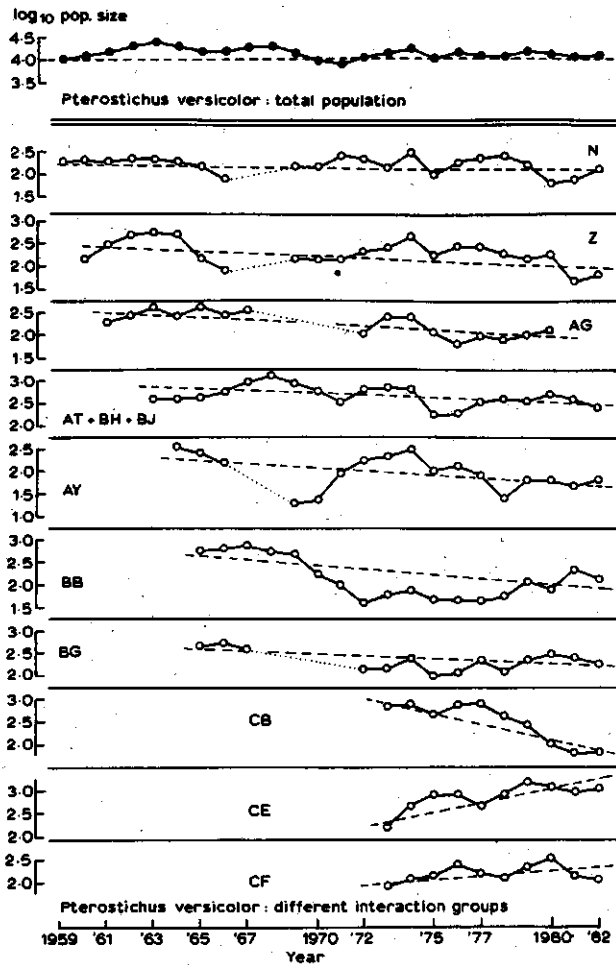


Fig. 2. Fluctuations and trends of mean densities in ten interaction groups (on about 12 ha) of *P. versicolor* Sturm at Dwingelder Veld (Drenthe), as compared with the fluctuation and trend in numbers in the multipartite population composed of these subpopulations (at the top). The different sample sites are indicated by capitals; the three sites AT, BH and BJ are taken together because they sample the same interaction group (mutual distances about 100 m). Open circles are relative estimates of subpopulation size (Den Boer 1981, 1985), so that the connecting solid lines give the changes of numbers from one year to the next. When the observations were interrupted for one or more years the line is stippled. The broken lines indicate the general trends of numbers during the entire observation period. (From Den Boer, 1986)

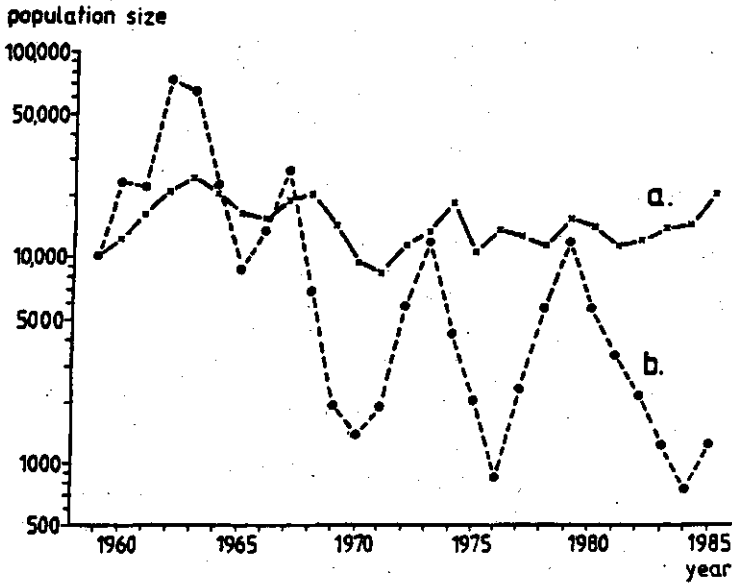


Fig. 3. Fluctuation of numbers in multipartite populations of two carabid species, *P. versicolor* (a) and *C. melanocephalus* (b) at Dwingelder veld (from Den Boer, 1986). Both populations are thought to be composed of subpopulations, plotted for *P. versicolor* in fig. 2. To facilitate comparison, population size was assumed to have been similar in both species in 1959 (an arbitrary value).

1986b) simulated random fluctuation patterns using a distribution of net reproductive values (R -values). A measure of density in year t divided by the measure of density in year $t-1$ yielded an R -value for an interaction group. With a large number of R -values from several sites a characteristic log-normal distribution of R -values was found to exist for almost every species. The average of a large number of simulations resulted in the expected mean survival time. The results from both methods indicated that most interaction groups, when isolated, should have survival times of less than 100 year. A mean turnover of 6% per year for 64 ground beetle species indicated that on the average isolated interaction groups run a risk of more than 50% to become extinct within 20 years (Den Boer, 1990a).

The spreading of risk, necessary for long-term survival, is only effective when there is an exchange of individuals between areas with high and low densities. Dispersive movements, here defined as undirected movements away from the habitat of origin, may result in the (re)founding and supplementing of areas with zero and low densities (Den Boer, 1990b). According to Den Boer this is the biological significance of dispersal ('founding hypothesis of dispersal', Den Boer, 1971, 1977, 1979b, 1990b). It has been shown that dispersal ability of ground beetle species is associated with habitat stability (Den Boer et al., 1980) and habitat quality (e.g. Aukema, 1995). The more stable the habitats occupied, the weaker natural selection forces that result in maintenance of flight ability. *Agonum ericeti* is an example of such a species as it occupies the stable peat moor habitat, and all its individuals have highly reduced wings unsuitable for flight (Den Boer et al., 1980). In some species, e.g. *Nebria brevicollis* (Nelemans, 1987b) and *C. melanocephalus* (Aukema, 1995) macropterous individuals do occur, but the dispersal potential is difficult to estimate, because it is under environmental control. For these species conditions must be highly favourable to lead to the production of macropterous individuals with wing muscles, which are able to fly.

Realizing the importance of dispersal for continuous presence of interaction groups in natural populations, the consequence of a large scale reduction of the availability of natural and semi-natural habitats for ground beetles in Drenthe became a matter of great interest (Den Boer, 1977, 1979b, 1990 a, b). Using frequency distributions of population sizes, Den Boer (1977) showed that species with low dispersal abilities were significantly more often sparse and/or absent from local habitats than species with high dispersal abilities. This means that species with low dispersal abilities do not compensate low or zero densities with immigration as efficiently as species with high dispersal abilities. Based upon this observation the hypothesis was formulated that in fragmented habitats species with low dispersal abilities are endangered by extinction.

Genetic variation

The presence of genetic variation within populations will in most cases contribute to the continuous presence of individuals which can meet, by relatively low

mortality and/or high recruitment, the demands from a changing environment. Though ample evidence is not available, lowering of the genetic variation over time is generally considered to lead to a reduction of fitness (Charlesworth & Charlesworth, 1987; Van Delden, 1992; Caughley, 1994). Populations which are small or have experienced a temporary decline in numbers at some time in the past, a so called bottleneck situation, will suffer loss of genetic variation, merely due to a stochastic process called genetic drift (Wright, 1931, Van Delden, 1992). As a result of drift homozygosity increases: loci become fixed for one particular allele, while other alleles get lost. Also inbreeding, the enhanced frequency of mating between genetically related individuals, may lower the fitness of individuals in the population (Charlesworth & Charlesworth, 1987; Van Delden, 1992; Caughley, 1994). Some detrimental alleles, normally only present at low frequencies will increase in frequency and may enhance mortality and reduce fitness when homozygous. This loss of fitness at the individual level may lead to an increased risk of extinction of the populations concerned. Hence, studying genetic variation in small populations, was considered vital in our study of viability of heathland ground beetle populations.

Generally, there is a considerable difference between actual population size and the so called effective population size. Effective population size (N_e) is defined as the number of breeding individuals in an idealized population that would show the same amount of genetic drift and inbreeding as the population under consideration (Crawford, 1984). The idealized population represents a population in which all individuals have an equal probability to contribute gametes to the next generation. The restrictive conditions of an idealized population can seldom be fulfilled in real populations (Falconer, 1989). Different numbers of males and females taking part in reproduction, non-random distribution of family sizes, unequal distribution of individuals in relation to birth and breeding sites, and overlapping generations are some of the factors affecting effective size (Falconer, 1989; Hartl, 1988). Furthermore effective population size is liable to great deviations when there are fluctuations in population sizes in the period of investigation or when a bottleneck occurs. Effective population size is then estimated over t years using the formula (Hartl, 1988): $1/N_e = 1/t * (1/N_1 + 1/N_2 + \dots + 1/N_t)$. The minimum effective

size necessary for maintaining genetic variation in populations has been much discussed (Franklin, 1980, Lacy, 1987; Land & Barrowclough, 1987; Boyce, 1992; Caughley, 1994). Franklin (1980) tentatively proposed that in order to prevent the disadvantageous effects of drift and inbreeding at least 50 individuals would be required and to ensure the maintenance of sufficient genetic variation for evolutionary change the minimum effective population size should be 500. The actual size of the population would have to be much higher, perhaps a factor 3 to 4 (Caughley, 1994) or sometimes even 25 (Crawford, 1984).

Loss of genetic variation will only occur in small populations which have a low immigration rate or no immigration at all. Sufficient immigrants are expected to prevent loss of genetic variability in small populations due to drift (Slatkin, 1985). Hence, both effective population size and dispersal determine loss of genetic variation in patchily distributed populations (Wade & McCaughley, 1988).

The research in this thesis

The aim of this thesis is measuring and explaining the viability of populations in fragmented habitats. For this purpose the presence of ground beetle species in fragmented heathland was investigated. Possible relationships of species composition with isolation period and area size were determined. The importance of dispersal ability and habitat preference of species for persistence of populations is evaluated. Often habitat size and habitat quality are correlated characteristics of areas, in particular in small areas. Therefore, special attention is paid to measuring the possible importance of habitat deterioration in small areas which still showed remainings of the vegetation of the former landscape. Some of the extant populations may be at risk to become extinct soon. Conservation genetic theory predicts that genetic variability is changing in small isolated populations. As extinctions of small populations are sometimes expected to be preceded by lowered levels of genetic variability, allozyme variability is studied. In several populations the genetic variability is estimated to obtain information about the importance to consider genetic processes for the protection of the remaining populations.

The landscape investigated

The province of Drenthe, situated in the North-Eastern part of the Netherlands, provides good opportunities for a study of viability of ground beetle populations in fragmented heathlands. The history is such that it can be compared with an experiment aiming at solving questions concerning effects of habitat fragmentation (Den Boer, 1977: 'experiment of cultivation'). Replicates of habitats within size classes ranging from less than 1 to more than 1000 ha are available.

In prehistoric times the province of Drenthe consisted of three types of habitat: peat moor, forest, and marshy habitats alongside small brooks. Settlement by man resulted in grasslands alongside the brooks, clearance of most of the forest, and the appearance of heathlands originating from a type of landuse that led to net offtake of nutrients (Heringa et al., 1985). As a result the landscape of Drenthe was dominated by heathland and peat moor for several centuries. After 1890 farming became increasingly based on the input of nutrients and large parts of the heathlands 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. Consequently oligotrophic species disappeared from large parts in the region (Van Zanden & Versteegen, 1993). An exemplary view of the change of the landscape in Drenthe is given in fig. 4. Much later, in the 1970s and 1980s, many of the heathlands left were changing into grassy areas, due to atmospheric nitrogen input (Heil & Bruggink, 1987; Aerts & Berendse, 1988) and consequently became less suitable habitats for many heathland species.

At the time the landscape was dominated by heathland and peat moor, a characteristic invertebrate fauna must have become established (e.g. Den Boer, 1977). A large part of the ground-dwelling invertebrates at heathlands consists out of ground beetles, which presents the opportunity to compare several closely related species. The ground beetles of this study were all studied in or close to the province of Drenthe in patchily distributed habitats, all of the oligotrophic type. Four kinds of open heathy habitats were distinguished: peat moor, wet heathland, dry heathland, and *Corynephorum*, the latter being dry sandy areas sparsely vegetated with *Corynephorus canescens* and heather species. The landscape

surrounding these areas consists of agricultural land or coniferous forest plantations, unsuitable for heathland ground beetles. However, some small linear parts of this landscape, in particular road-side verges (Vermeulen, 1993; 1994), but

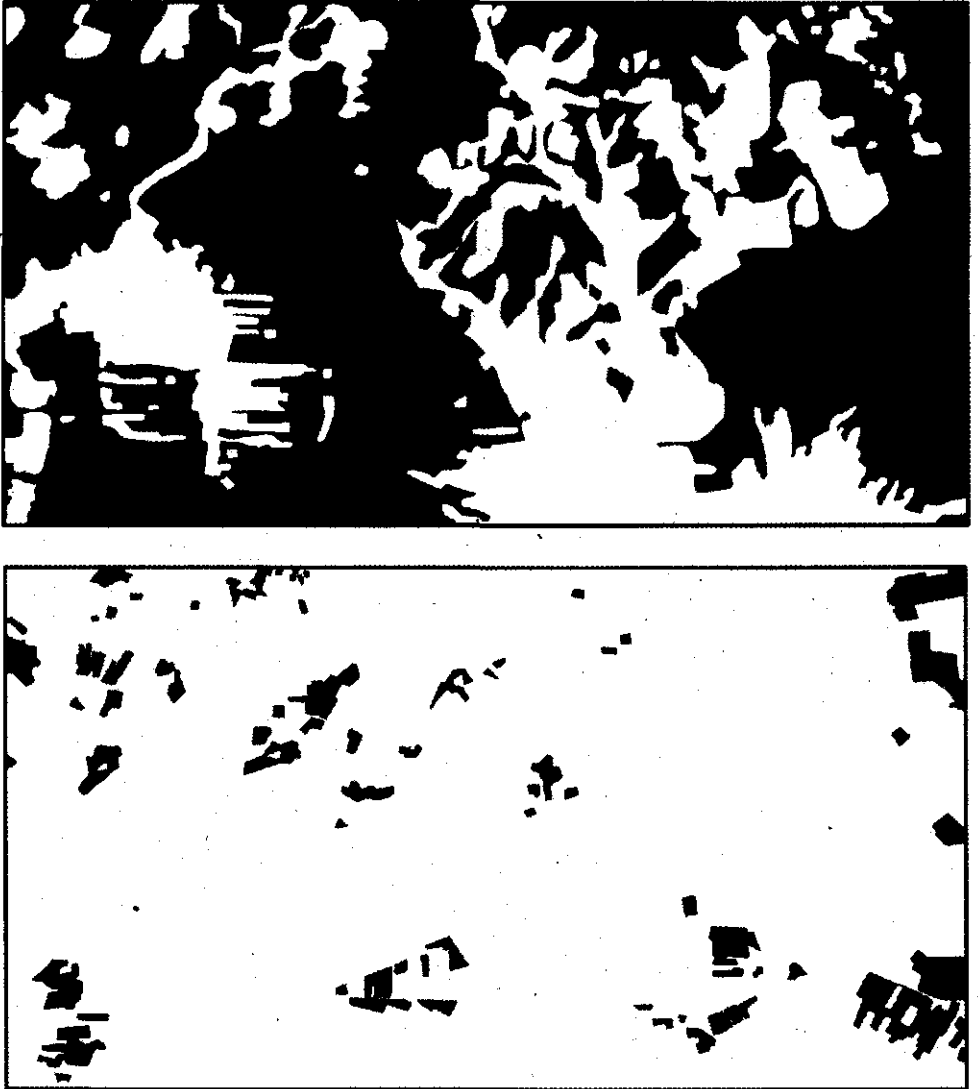


Fig. 4. The distribution of heathland (shaded areas) in the South-East (20 x 35 km) of the province of Drenthe, the Netherlands. The top box represents the situation in the year 1875 and the bottom box in 1971, approximately. (After Ormeling, 1971)

perhaps also ditch banks (Van Dorp, 1995) may constitute suitable habitats for some heathland ground beetles too.

Outline of this thesis

The main objective of this thesis is to investigate survival and extinction of ground beetle populations in remnants of heathland and to relate the results to the characteristics of the investigated areas and to the characteristics of the absent and extant species. It was hypothesized that ground beetle species with low dispersal ability are threatened with extinction. Area size is expected to be positively, and isolation period negatively related to presence of these species. As regression techniques were used to analyze these relationships, other factors, if correlated with size of area or period of isolation, may have gone unnoticed in determining presence or absence of ground beetle species with low dispersal ability. For instance, after habitat fragmentation an increase of nutrient input like nitrogen and a lowering of the ground water table can be expected under Dutch conditions. Therefore, the hypothesis is tested that small and large habitats are of the same quality. During this research a few examples were found of extant populations of ground beetle species with low dispersal ability in small habitats. This gave the opportunity to estimate the genetic variation of these populations. It was hypothesized that they possessed a low genetic variability as compared to the populations in large habitats.

In chapter 2 the survival of one particular species, *Agonum ericeti*, is investigated. This species was selected because of its low dispersal ability and its specific preference for peat moor, a currently rare habitat. To be able to judge the generality of the conclusions drawn from the results of *A. ericeti* a similar kind of research was done for a greater number of species of heathland. The presence of species with different habitat preferences and different dispersal abilities in habitats of different sizes is compared. Conclusions are drawn about survival and extinction of populations after habitat fragmentation (chapter 3).

To test the suitability of small heathland patches for survival and reproduction a transplant experiment was conducted with two species: *Pterostichus lepidus* and *Olisthopus rotundatus*. Simultaneous transplant experiments were conducted at four

sites in two small patches and at two sites in a large area (chapter 4). Two species were selected for further genetic research. The genetic variability of eight populations of *A. ericeti* and seven populations of *P. lepidus* is estimated by means of electrophoresis (chapter 5). Finally, in chapter 6 the overall results are discussed.

Chapter 2

Survival of populations of *Agonum ericeti* in relation to fragmentation of habitats

with P. J. den Boer

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Summary

The stenotopic carabid species Agonum ericeti Panz. of peat moor habitats is unable to fly, and therefore cannot bridge distances that exceed 200 m 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 heathlands (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*.

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 influences 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, 1990b), 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 power 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, 1990b).

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 synchronously 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 extinctions 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 synchronously 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 synchronously 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), 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).

The ground beetle 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 tytrphobiont, 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). Based on data of Baars (1979b, 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). 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*-species, *Rhynchospora*, *Molinia caerulea*, *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 1). 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 1), 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 1 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 organisation 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 ground beetles, which also apply to *A. ericeti*, were developed by Thiele (1968), and further adjusted by Van Dijk; see e.g. Nelemans (1987a).

Table 1. 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 2).

Code ¹	type of habitat	upper layer of substratum:		number of pitfalls	catch effort
		floating <i>Sphagnum</i>	highly peaty		
XI	peat moor	—	++	5	85
Dw	<i>Erica-Calluna</i> heath	—	++	+	+ ²
TB	peat moor	++	++	10	260
AH	sandy heath area	+	+	10	250 ³
YA	peat moor	—	++	6	168
TD	peat moor	—	++	10-20	320
XJ	<i>Erica-Calluna</i> heath	—	+	10	280
XF/XH	moist heath and peat	++	+	20	730 ⁴
YD	degenerated peat moor	++	+	5	140-70 ⁵
AJ	pool: peat + moor-veg.	++	+	10-15	830
XB	pool: peat + moor-veg.	++	—	10	350
YC	pool: peat + moor-veg.	++	—	7	196
Q/R	pool: peat + moor-veg.	++	—	20	1260 ⁴
YE	pool: peat + moor-veg.	+	+	5	140
XG	pool: peat + moor-veg.	++	+	10	380
XC	pool: peat + moor-veg.	++	—	10	350
AB	pool: peat + moor-veg.	++	—	10	350
XA	pool: peat + moor-veg.	++	—	10	350
YB	pool: peat + moor-veg.	++	+	5	140
XD	pool: peat + moor-veg.	++	—	10	350

¹ XI = Fochteloeerveen; Dw = Dwingelder Veld; TB = Bargerveen; AH = Terhorster Zand; YA = Hingsteveen; TD = De Witten; XJ = Gijsselterkoelen; XF/XH = Karveen; YD = Tweelingen; AJ = Lange veen; XB = Grote veen; YC = vak 61, Grolloo; Q/R = 2 pools, Kampsweg; YE = vak 115, Schoonloo; XG = Droseraven; XC = vak 63b, Dwingeloo; AB = Poort II; XA = Benderse weg; YB = vak 116, Grolloo; XD = vak 63c, Dwingeloo.

² In that heathland 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.

³ 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 3.

⁴ Suitable habitats that were less than 200 m from each other (as in this case) were considered to be parts of the same habitat.

⁵ 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.

Results

Catches of *A. ericeti* in 1988 (1989), and in earlier years by workers of the Biological Station, are presented in table 2. Among 20 areas investigated during this study *A. ericeti* was found in eight: in 5 peat moors (tables 1, 2: XI, TB - only in 1989, YA, TD and YD), in one small peat site with pits that were filled again by *Sphagnum* (table 2: YE), and in two wet heathlands (tables 1, 2: Dw and XJ). Presence or absence of *A. ericeti* is related to area and duration of isolation (table 2). Isolation is considered absolute when separation from other suitable sites amounts to more than 200 m. Most study sites reach 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 fragmentation 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 2 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 1), 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 3), 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 1). In TB (Meerstalblok in Bargerveen) *A. ericeti* was found in 1961, but in 1988 it was not caught at that site, which had

Table 2. Total area of the habitats in which the sampling sites were situated, duration of isolation of 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 explanation of codes see table 1.

Code	Size of area (ha)	Isolated during years	Number of individuals of <i>A. ericeti</i> caught				
			1959	1960	1961	1962	1988
XI	1714	multipartite pop. ¹					16
Dw	1607	multipartite pop. ¹	7	57	142	111	18 ³
TB	290	multipartite pop. ¹			49		+ ⁴
AH	100	discontinuous area ²	—	—	1	—	— ²
YA	73	multipartite pop. ¹					14
TD	72	multipartite pop. ¹			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	1.00	46		—			—
YB	0.68	53					—
XD	0.65	59					—

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

¹ Suitable sites in these areas are sufficiently large and commonly present that isolation of subpopulations (interaction groups) may be excluded.

² See note 2 to table 1.

³ 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.

⁴ 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' (+).

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'.

Table 3. 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). For explanations of codes see table 1.

A		B		C		D	
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	4.1	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		

Populations in habitats smaller than 70 ha have been isolated in a 'sea' of unsuitable area for between 24 and 71 years (table 2). In site Q/R (3.6 ha), *A. ericeti* was present in 1959-1961 (table 2), but not in 1988. Apparently, 24 years of isolation is sufficient for small isolated populations to become extinct.

From the fluctuation patterns of three subpopulations at Dwingelder veld during 7 years and three 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 extinctions 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 2) thus fits with these estimates. This is less clear for site AJ, because isolation there lasted 59 years (table 2). This population was still present in 1961 and 1962 (table 2), 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

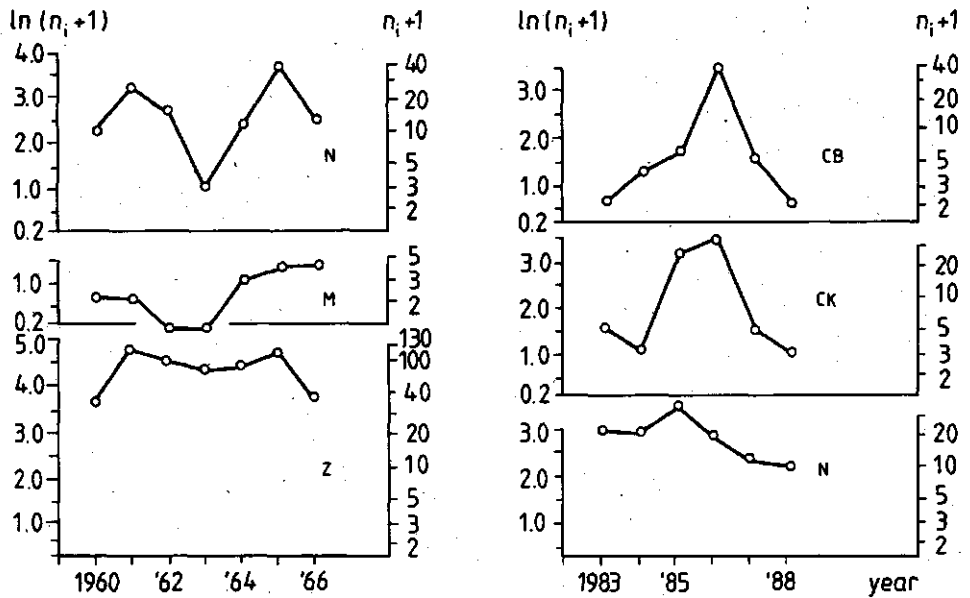


Fig. 1. Uninterrupted year-catches (n_i) of *A. ericeti* in standard series pitfalls (Den Boer, 1977) during a number (6 or 7) years from different subpopulations at Dwingelder Veld to show that usually numbers do not fluctuate synchronously: W (coefficient of concordance) = 0.59 for N, M, Z in 1960-1966, 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 sufficient 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.

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 1), and may contribute to the absence of *A. ericeti*. For, table 1 shows that there is 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 2), 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 ground beetle 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 island, but would still be present in large ones. Table 2 shows that this hypothesis cannot be rejected, and that it is confirmed with a high probability. However, in this conclusions 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 m.
- (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 15,000 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 2). 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 (Fochteloërveen) 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 (1979b) studied the walking patterns of two very different ground beetle 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 finds of Baars (1979b). Apparently, the walking patterns found by Baars are general for ground 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 1979a, 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, 1979a; 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 2), 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, 1990a).

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 2).

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 2) should be considered as one case among either 14 (YE + groups B + C of table 3) or 8 (YE + groups B + D of table 3), 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 1). 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.

Acknowledgements

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Chapter 3

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

with P. J. den Boer & Th. S. van Dijk
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Summary

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.

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 (1990a) 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 (chapter 2). 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 & Wilson, 1967; Connor & 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 & Wilson, 1967), it is 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 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.



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

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.

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

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

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 *Corynephorum* (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, 1979b; Klazenga & 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*). Corynephorum is a very dry drift sand area. Each habitat was included in the regression as being present or absent, except Corynephorum which was only indirectly present in the analyses and was indicated by the absence

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

Habitat variables

PEATMOOR: present/absent

WET HEATHLAND: present/absent

DRY HEATHLAND: present/absent

MOIST: analogous to the four types above: peatmoor, wet heath, dry heath and corynephorum 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 variables

LOGAREA: Logsize of total heath area on most recent topographical map 1:25,000.

Isolation variables

ISO500M: amount of heath present within 500 m from the border of the area.

ISO1000M: amount of heath present within 1000 m from the border of the area.

ISO2000M: amount of heath present within 2000 m from 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.

of the other three habitats (method after Jongman et al. 1987). An indication of moisture (MOIST), using a score of one to four for Corynephorum, 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 (ISO500M, ISO1000M and ISO2000M). 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 41420 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 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

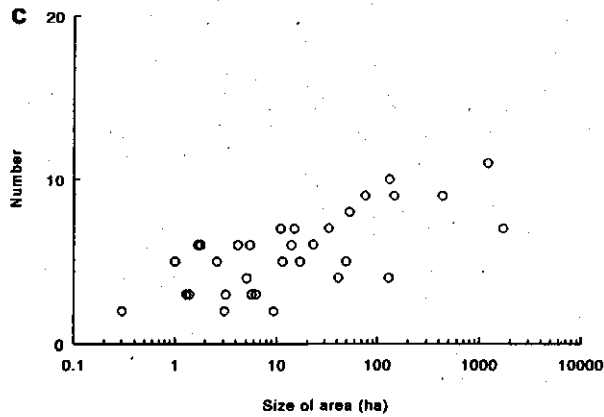
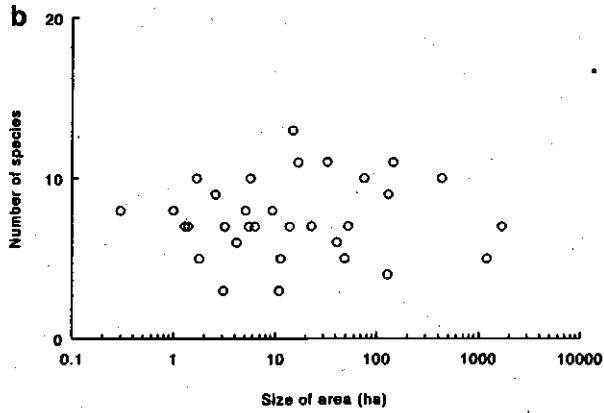
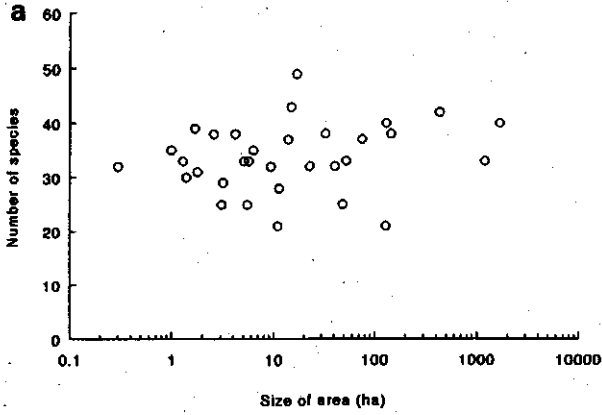
Table 3. Results of a stepwise multiple regression of five ecological groups on the variables of table 2. Given are significant explanatory variables as part of a significant model.

Group	Variable	$R^2_{Adj.}$ cumulative
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

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



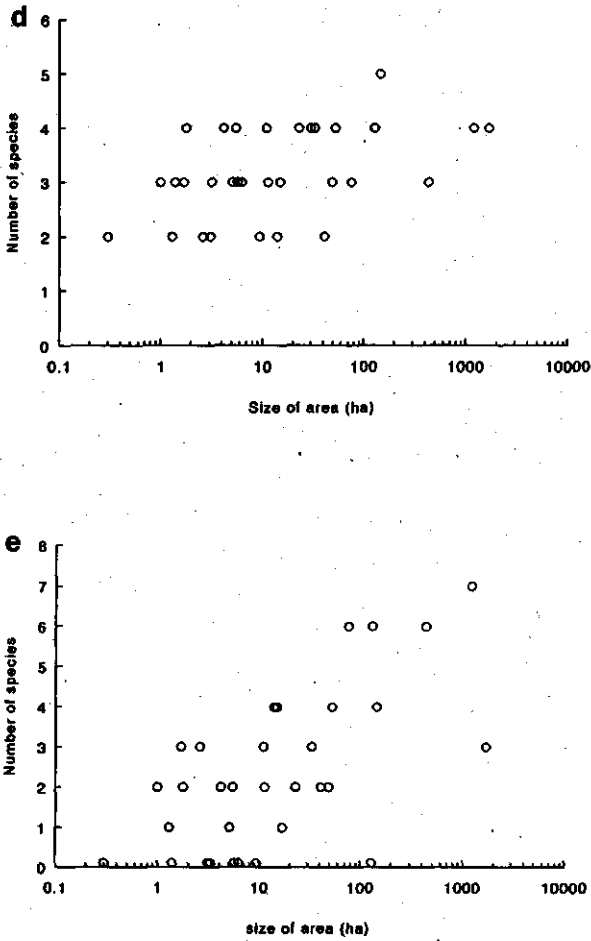


Fig. 2. Presence of species in relation to LOGAREA.

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).

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 additional 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-

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

Source	<i>df</i>	SS	MS			
Regression	3	80.09403	26.69801	$F = 17.33448$		
Residual	28	42.12472	1.54017	$P < 0.0001$		

Variable	<i>B</i>	SE <i>B</i>	Beta	<i>T</i>	Sig. <i>T</i>	R^2_{Adj} cumulative
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	

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

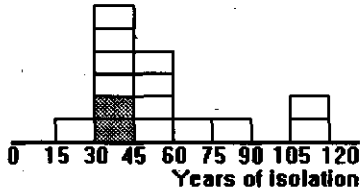
The correlation coefficients of the explanatory variables are given in table 5. Significant correlations were found between the three isolation parameters ISO500M, ISO1000M, and ISO2000M, between LOGAREA, ISO500M, and GRASS and between MOIST, PEATMOOR, WET HEATHLAND and DRY HEATHLAND. Correlations with GRASS, WET HEATHLAND, DRY HEATHLAND were negative. This means that part of the variation explained by LOGAREA could also be explained by ISO500M or GRASS. Also, the effects of

Table 5. Correlation matrix of the explanatory variables of table 2: A = LOGSIZE, B = ISOPER, C = ISO500M, D = ISO1000M, E = ISO2000M, F = GRASS, G = MOIST, H = PEATMOOR, I = WET HEATHLAND, J = DRY HEATHLAND.

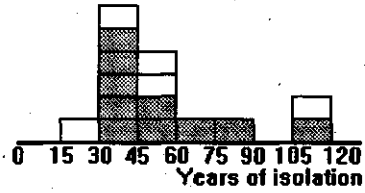
One-tailed significance: * = $P < 0.01$, ** = $P < 0.001$.

	A	B	C	D	E	F	G	H	I
B	0.058								
C	0.704**	-.299							
D	0.519*	-.361	0.762**						
E	0.301	-.359	0.545**	0.739**					
F	-.530**	0.141	-.458*	-.295	-.238				
G	0.052	0.008	0.125	0.151	0.246	0.247			
H	0.144	-.128	0.224	0.174	0.316	0.042	0.736**		
I	-.099	0.231	-.125	-.044	-.217	0.231	0.041	-.615**	
J	-.129	-.157	-.180	-.164	0.016	-.236	-.515*	-.249	-.458*

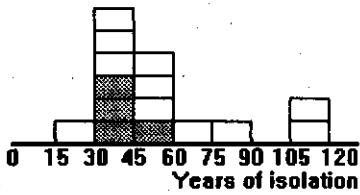
Ollisthopus rotundatus



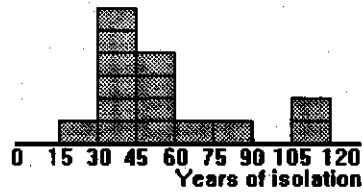
Cicindela campestris *



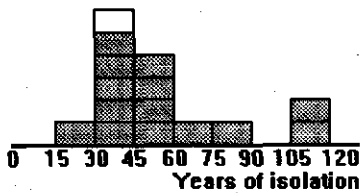
Pterostichus lepidus



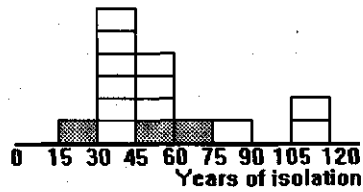
Pterostichus diligens *



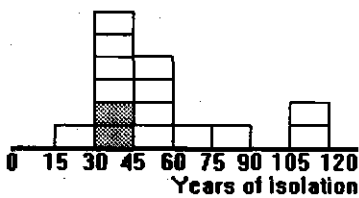
Bradycellus ruficollis *



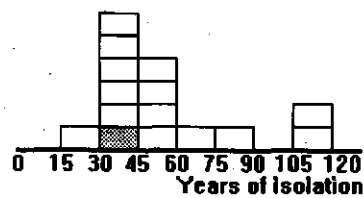
Trichocellus cognatus *



Amara equestris



Carabus arvensis



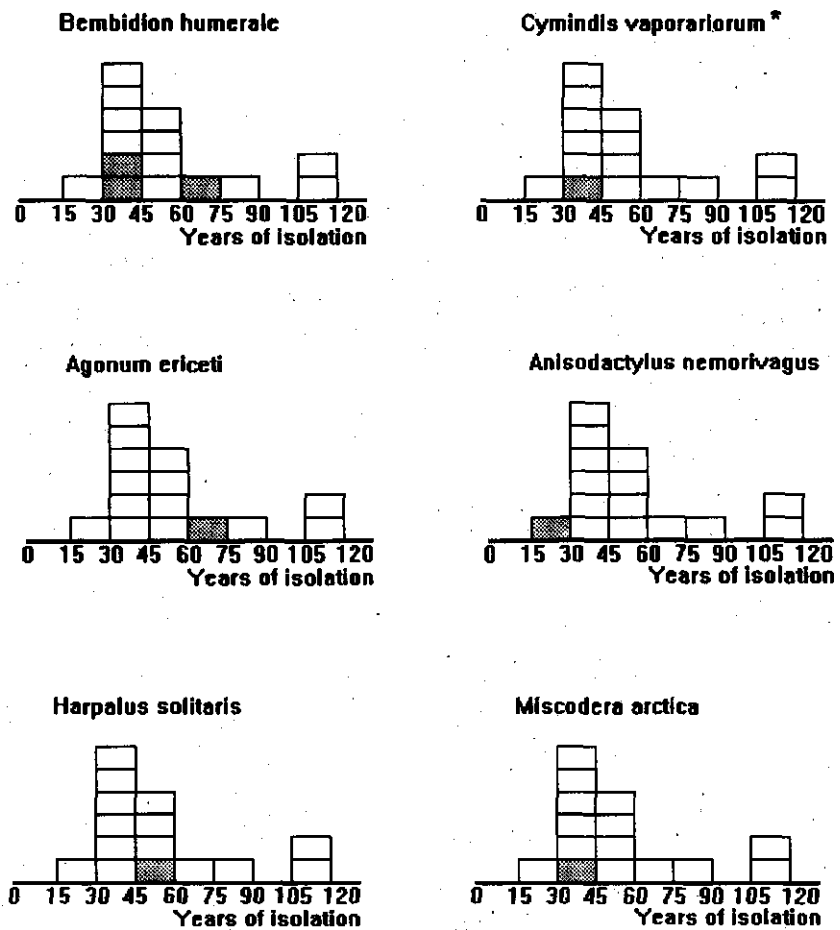


Fig. 3. The presences (dark blocks) of catches of HS-HPD and HS-LPD in 15 sampled areas ordered on the abscissa by their period of isolation as compared to potential presences (open blocks). Species that have been caught in window traps are marked with *.

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

- 1 The presence of the species in the fifteen areas surveyed smaller than 10 ha.
- 2 The presence of the species in the six areas surveyed larger than 100 ha.
- 3 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.
- 4 C = calculations Den Boer (1990): the calculated survival time in years of one interaction group (Den Boer, 1977) without re-colonization.
- 5 O = observed survivaltime = the longest observed survivaltime in years of populations in areas smaller than 10 ha, see also fig. 3.

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.

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 & 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 & 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

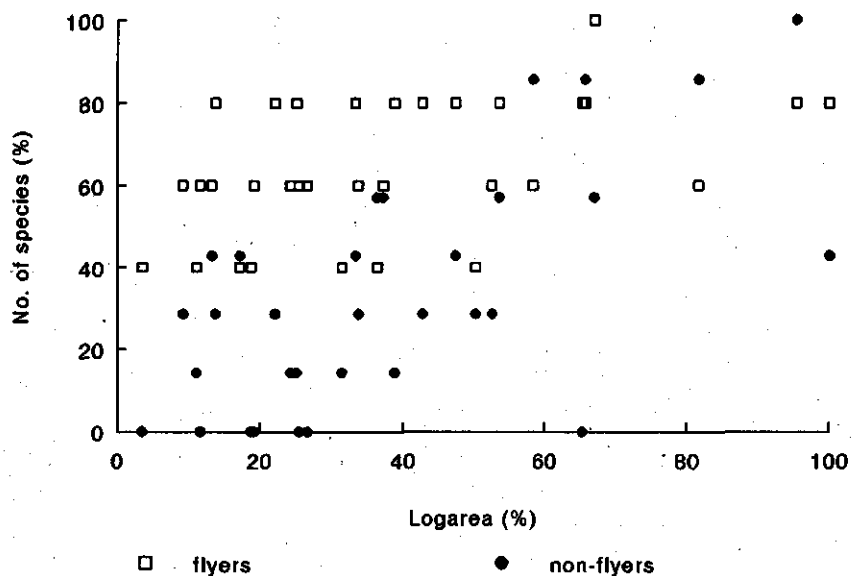


Fig. 4. The presence of heathland species with high (HS-HPD: squares) and low (HS-LPD: dots) powers of dispersal in relation to LOGAREA. The largest numbers caught of each group (HS-HPD: 5, HS-LPD: 7) and the largest area investigated (1700 ha) was set at 100%.

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 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 & 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, 1979b; Klazenga & 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, 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 & 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 (chapter 2). 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 (1990a) 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 (1990a). 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 (1990a). 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 as 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 *Molinia 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 & 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 in chapter 2, 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 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.

Acknowledgements

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Chapter 4

Metapopulation structure of *Pterostichus lepidus* and *Olisthopus rotundatus* on heathland in the Netherlands: results from transplant experiments

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Summary

A 3-year field experiment tested the suitability of isolated habitat patches for two ground beetle species in the Netherlands. Both species have low dispersal ability and occur at low frequencies in small isolated heathland patches. The results gave no evidence for the presence of unoccupied habitat patches for Olisthopus rotundatus. Successful reproduction of artificially introduced Pterostichus lepidus, however, proved the existence of unoccupied habitat patches for this species. It is concluded that extinction of P. lepidus in isolated habitat patches is only partially balanced by colonization. Hence, P. lepidus occurs in metapopulations with both continuously and discontinuously occupied habitat patches.

Introduction

The study of ground beetles in Europe has revealed a large change in species composition since 1950 (Desender & Turin, 1989). The reduction, fragmentation and deterioration of habitats are expected to be the main causal factors (chapter 2, 3; Turin & Den Boer, 1988; Desender & Turin, 1989). Some species are much more vulnerable to this change than others. Ground beetles which are not able to fly are more often sparse in, or absent from, local habitats than are good dispersers (Den Boer, 1977). Heathland species which are able to fly persist far better in

small isolated habitats than heathland species which are not able to fly (chapter 3). These small isolated patches, which are expected to be suitable for colonization, are frequently found unoccupied by species with low dispersal ability. The suitability of unoccupied patches is often implicitly assumed, because the suitability of empty habitat patches for successful colonization is difficult to prove. Few investigations into the suitability of patches for invertebrates within a metapopulation structure have been published (Harrison, 1989; Schoener, 1986). Introduction experiments with invertebrates for purposes other than testing the metapopulation structure have been done more frequently (e.g. Holdren & Ehrlich, 1981; Loreau, 1990; Oates & Warren, 1990; Elmes & Thomas, 1992). Most of these experiments fail, but often it is difficult to identify the factors causing the poor results. To eliminate the effect of emigration the use of enclosures seems to have great advantages (Loreau, 1990; Van Dijk, 1994).

In this study the suitability of two heathland patches for two ground beetle species, *Pterostichus lepidus* and *Olisthopus rotundatus*, was examined by means of enclosures. Both species show a clear preference for heathy habitats (Turin et al., 1991). Dry as well as wet heathland may offer suitable habitats in the Netherlands. Earlier investigations showed that some areas considered to be suitable appeared not to be occupied (chapter 3). The isolated situation of these areas must be the cause of the absence of these two species, if patch suitability is assumed to be sufficient. To test the suitability of the unoccupied patches for colonization, both species were artificially introduced into such patches. Survival and reproduction of the introduced beetles would be indicative of the suitability of the patches. Success of these introductions would give more information about the metapopulation structure of these two species.

Materials and methods

Beetles

The species used for the experiments, *P. lepidus* and *O. rotundatus*, are stenotopic according to Turin et al. (1991). This means that their habitats are narrowly

defined by special conditions. In this case they are both restricted to heathlands and are common in several heathlands in Drenthe (fig. 1). Both species have low dispersal power. *P. lepidus* is a spring breeder, mainly laying eggs in June and July, and with larval development in summer. Some individuals probably do not complete development before the end of the summer and will hibernate as larvae (Paarmann, 1990, Den Boer & Den Boer-Daanje, 1990). Teneral occur in July. In the Netherlands *P. lepidus* is brachypterous (Den Boer, 1977) and unable to fly. During a test in heathland with *P. lepidus* and *P. versicolor*, both species showed a comparable ability to bridge distances by walking (Klazenga & De Vries, 1994). Extensive research showed a largest distance covered by *P. versicolor* of about 900 m (Baars, 1982).

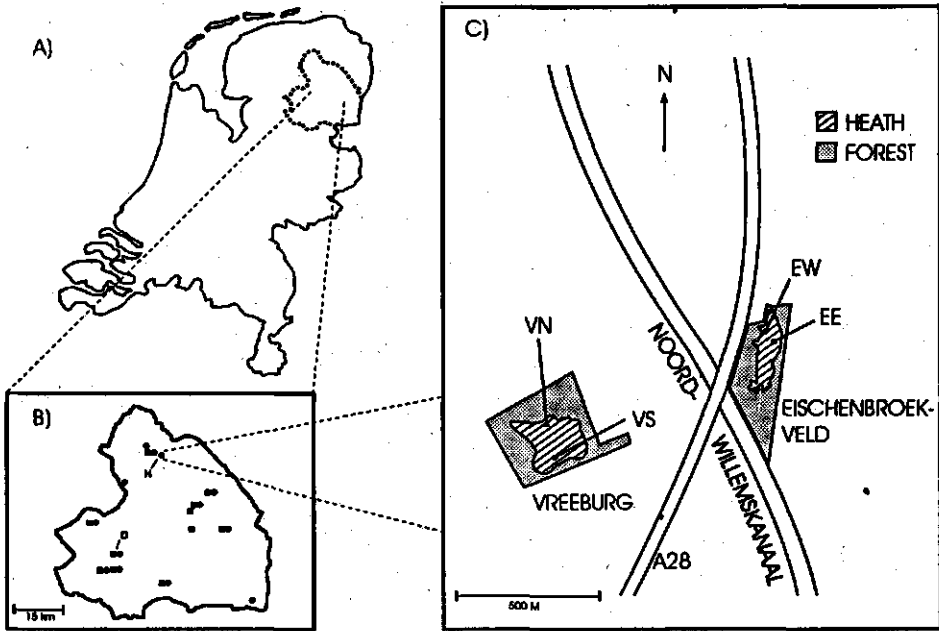


Fig. 1. - a. The area within the dashed line represents the province of Drenthe in the Netherlands. - b. The locations of Heideheim (H), Dwingelderveld (D) and catches of *P. lepidus* (■) and *O. rotundatus* (●) in 1990, 1991 or 1992. - c. The location of the four enclosures (VN, VS, EW, and EE) in both small heathlands at Heideheim. Both areas are separated by a highway (A28) and a canal (Noord-Willemskanaal).

O. rotundatus reproduces in autumn, mainly September and October and hibernates as larvae. Teneral adults occur in June and July. The dispersal ability of this species is unknown. There are no data on walking behaviour, but based on its smaller size it can be expected to walk shorter distances than *P. lepidus*. About 20% of the individuals are macropterous (Den Boer, 1977), but during a 20-year survey with window traps no flight was observed (Van Huizen, 1980; Van Huizen & Aukema, 1992). Therefore, it is unlikely that this species has high abilities to colonize isolated habitat patches.

The individuals of both species used for the experiments were caught with pit-falls. *O. rotundatus* was collected during 1991 and 1992, at Dwingelderveld (fig. 1). Individuals of *P. lepidus* were collected from two other areas in the province of Drenthe.

Experimental sites

Three localities were selected for this study (see fig. 1b and c). Two of them are small heathland patches in which neither of the species had been found during a survey in 1990. The patches are about 600 m apart from each other, separated by a highway and a wide canal. They are the remaining parts of a once largely continuous heathland in the province of Drenthe. The reclamation of this heathland started before 1800. About 1935 the landscape had reached its present form. In 1860 a canal was dug that separated the two small heathland patches. In 1970, the construction of a highway further isolated these small heathland fragments from neighbouring patches. Also the growth of trees at the borders of these areas made them smaller and may have restricted immigration from other heathland habitats.

One of the two patches, Heideheim Vreeburg, is about 3.2 ha, and several kilometres removed from all other heathlands, except for the other patch. It consists of a wet heathland vegetation with grasses, mainly surrounded by birches. The site was unmanaged until 1982, when the encroaching birches were removed, the vegetation was burned, and nowadays a well developed heather vegetation occurs there. It is grazed by sheep and some yearlings.

The second patch, Heideheim Eischenbroekveld, is a 1.3 ha wet heathland patch, which is somewhat dehydrated. It also has a very isolated position. Initially,

the heathland was largely unmanaged and slowly overgrown by birches and grasses. After removal of the birches the area has mainly been managed by grazing with Highland cattle.

The third area, the heathland of Dwingelderveld, is used as a control area. It is a very large continuous wet heathland of 1600 ha where both beetle species are abundant (Den Boer, 1977; Den Boer & Van Dijk, 1994). The distance between the two small patches and Dwingelderveld is about 35 km. Apart from a very abundant growth of grasses little has changed in this area during the last decades. Encroachment of trees is very limited. At present a large part of the heathland is in relatively good condition as a result of local sod-cutting and sheep grazing.

Experimental design and procedures

To test the possibilities of survival and reproduction for both species, marked individuals were introduced in the areas. Because of the difficulty of estimating the success of the introduction of a limited number of free moving ground beetles, plastic fences were erected, about 10 cm deep into the ground and 20 cm above it. In each of the three areas two circular fences, enclosing an area of about 150 m² each, were placed. At Dwingelderveld two enclosures, DA and DB, were placed in an area where sod-cutting had occurred in 1985 and 1983 respectively. At Heideheim Vreeburg the two enclosures were placed at the north side, VN, and south side, VS, of the terrain respectively. The enclosure VS was at about the same place as the 1990 survey. At Heideheim Eischenbroekveld the enclosures were placed at the east and west side, EE and EW respectively. The survey in 1990 was at about the same location as where EW was erected. The coverage of *Molinea caerulea* differed among the heathlands. Both enclosures at Dwingelderveld had coverage of *M. caerulea* of less than 12,5%, whereas enclosures at Heideheim showed abundances between 12.5 and 75%. To prevent the beetles from climbing out of the enclosures by means of grasses and small shrubs, the vegetation along the fences was cut regularly. None of the ground beetles present beforehand were removed, including possible naturally occurring *P. lepidus* and *O. rotundatus* in some of the enclosures. By doing the same experiments in the control area

Dwingelderveld, a check was obtained about the suitability of the method for survival and reproduction of these species within a limited area for a year or more.

During spring 1991, a mixture of one or more years old individuals of *P. lepidus* (15 ♂♂ and 14 ♀♀), brandmarked on the left elytra, were released at several dates in the enclosures, and during autumn the same was done with individuals of *O. rotundatus* (7-9 ♂♂ and 12-13 ♀♀). To estimate the numbers of marked and non-marked individuals present during the next two years, inside each enclosure a limited number of five pitfalls were dug into the soil against the plastic fence. A great number of pitfalls would have limited too much the normal behaviour of the introduced beetles. To check possible presence of the species at Vreeburg and Eischenbroekveld, five pitfalls were placed against the outside of these enclosures as well. In order to minimize disturbance of the normal reproductive behaviour during 1992, the pitfalls were only used for a relatively short period. In 1992, they were open during 8 weeks: 10 - 17 June, 1 - 8 July, 6 (7 for Dwingelderveld) - 20 (24 for Dwingelderveld) August and 24 September - 23 October. Unmarked as well as marked individuals which were caught were brandmarked on the right elytra and placed back into the enclosure. The first catches in 1992 gave insight into the reproductive success of 1991. Based on these first results, more beetles, brandmarked on the right elytra, were added in some enclosures. For *P. lepidus* these were 7 ♂♂ and 7 ♀♀ in EE, EW, VS and VN. For *O. rotundatus*, 7 ♂♂, 9 ♀♀, 8 ♂♂, 9 ♀♀, 3 ♂♂, 4 ♀♀, 3 ♂♂, 4 ♀♀, 2 ♂♂, 3 ♀♀, 2 ♂♂ and 3 ♀♀ in EE, EW, VS, VN, DA and DB respectively. Also during 1993 the total number of beetles of these two species present in the enclosures was estimated with pitfall catches. In 1993 the pitfalls were open during 18 weeks: 10 June - 20 October. As the experiment was stopped in the autumn of 1993 the beetles caught during 1993 were not returned into the enclosures.

Reproductive values

In each enclosure the reproductive values (*R*-values), $N_{t+1}/N_{t-1}+1$, were calculated, using the numbers introduced in 1991 and the total number of individuals caught in 1992 for N_{t-1} and N_t respectively. For 1992-1993, the

numbers introduced in 1992 were added to the numbers caught in 1992 for N_{t-1} , and the numbers caught in 1993 were used for N_t .

The R -values of populations of both species were also estimated every year in several areas by means of a standard set of pitfalls, each coded by one or two characters. These sets consist of three metal pitfalls, each 25cm square, placed in a row, with only the middle one containing formalin as a fixative (for details see Den Boer, 1977). With this method R -values, based on the total sum of reproduction, mortality, immigration and emigration were estimated. During 1991-1993 *P. lepidus* was caught in six sets. Three were at the wet heathland area of Dwingelderveld, N, Z, and BJ, two at the very dry drift-sand area of Hullenzand, AU and AV, and one at a small wet heathland, BJ. All these sets except one, AU, also gave R -values for *O. rotundatus*.

Results

Survival

Survival of *P. lepidus* and *O. rotundatus* was estimated by counting the numbers of marked individuals recaptured (table 1). In 1992 the catches of marked *P. lepidus* were highest at VN and DB with 10 and 13 individuals, respectively. In the other four enclosures the catch was 4 individuals or less. In 1993 the catches of marked individuals were highest at DA, DB and VN with 8, 14 and 8 individuals respectively. The catches in the other three enclosures were 1 or zero individuals.

The survival of *O. rotundatus* was very low in all six enclosures. Marked individuals were only found occasionally.

Reproduction

Reproduction was estimated by counting the numbers of unmarked individuals sampled from each enclosure (table 1). In *P. lepidus* the highest numbers of unmarked individuals were sampled at Dwingelderveld in both years (18 - 50 per enclosure). From the remaining enclosures lower numbers of unmarked individuals

Table 1. Catches of marked and unmarked individuals of *P. lepidus* and *O. rotundatus* during 1992 and 1993 in six enclosures. The catches of 1992 were collected during 8 weeks and those of 1993 during 18 weeks. Enclosures: DA and DB were at Dwingelderveld, EE and EW were at Eischenbroekveld, VN and VS were at Vreeburg. M = marked, U = unmarked.

Enclosure	M 1992	U 1992	M 1993	U 1993
<i>P. lepidus</i>				
DA	4	26	8	18
DB	13	21	14	50
EE	2	11	0	7
EW	3	4	1	7
VS	4	0	1	0
VN	10	7	8	17
<i>O. rotundatus</i>				
DA	0	14	1	36
DB	1	4	0	53
EE	0	1	0	0
EW	0	1	1	1
VS	1	0	1	0
VN	1	7	0	28

were caught, while in VS not a single unmarked individual was found. In DA, DB and VN during both years 4 to 53 unmarked individuals of *O. rotundatus* were caught. Unmarked individuals were only caught incidentally in EE and EW, and no unmarked individuals were caught in enclosure VS.

Catches outside the enclosures

The numbers of marked individuals caught outside the enclosures were low, 0 - 3 (table 2). A few unmarked *P. lepidus* were also caught outside the enclosures (table 2). Outside VN many unmarked individuals of *O. rotundatus* were caught, whereas outside VS, which is about 100m distant from VN, only one individual was caught (table 2). After the start of these catches of unmarked *O. rotundatus* outside VN, additional pitfalls were put into the soil more than hundred metres from the enclosures at the east end of the terrain. These catches at the east side showed an abundance of *O. rotundatus*.

Table 2. Captures of *P. lepidus* and *O. rotundatus* along the fences outside four enclosures (EE, EW, VS, VN) during 1992 and 1993. M = marked, U = unmarked.

Enclosure	<i>P. lepidus</i>				<i>O. rotundatus</i>			
	1992		1993		1992		1993	
	M	U	M	U	M	U	M	U
EE	0	0	0	0	1	0	0	0
EW	0	2	0	1	1	0	0	1
VS	0	0	0	0	0	1	0	0
VN	3	0	0	0	0	6	0	4

Reproductive values

For *P. lepidus* in both years the R -values of the six enclosures and of the six standard series are plotted on a log-scale in fig. 2. There are no large differences between the years on each locality. DA and DB and the six standard series show very similar R -values. VS shows the lowest R -value, EE and EW show intermediate values, whereas VN shows values comparable to or slightly lower than the values at the standard sets.

The same has been plotted for *O. rotundatus* in fig. 3. In this case the R -values show large differences between the years. During 1992-1993 reproduction was much higher than during 1991-1992. The enclosures DA, DB, VN, and the standard series show very similar R -values: in 1992-1993 all were above 1, whereas in 1991-1992 all were 1 or lower. The enclosures EE, EW, and VS during both years had values of 0.22 or lower.

Discussion

Barrier efficiency and presence beforehand

The catch of some marked beetles outside the enclosures indicates that the fences were not complete barriers. Hence, a quantitative comparison of the data may be biased by possible emigration from and/or immigration into the enclosures. From

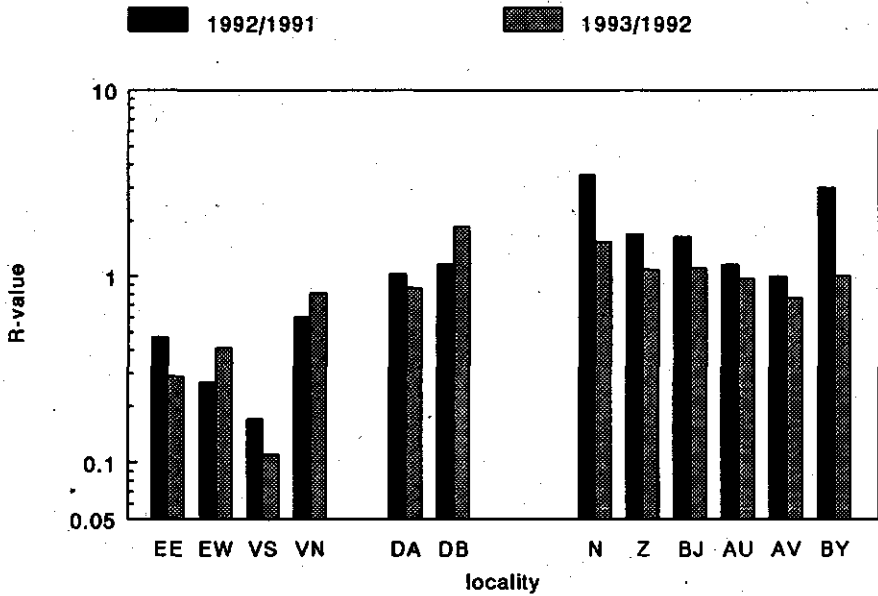


Fig. 2. The R -values $(N_t+1)/(N_{t-1}+1)$ in 1991-1992 and 1992-1993 of *P. lepidus* in six experimental enclosures, with the species being present beforehand in DA and DB, and at six permanent sampled sites (N, Z, BJ, AU, AV and BY).

the enclosures within the areas where the species were absent beforehand there could be only emigration. Therefore, the reproduction estimates in these areas may have been underestimates. Immigration into the enclosures may only occur in the areas in which the trial species were already present beforehand. There the numbers of unmarked beetles caught may have caused overestimates of the reproduction of the beetles introduced, at least for 1991-1992. Together, this means that the comparison of reproduction between the occupied and the unoccupied areas leads to conservative conclusions concerning the suitability of unoccupied habitats.

Only the experiments in DA and DB were meant to have both species present beforehand. However, the catches of some unmarked beetles outside some of the other enclosures hamper a clear distinction between experiments made in areas where the species were present beforehand and those made in areas where the species were absent. The catches of *O. rotundatus* outside VN in such high

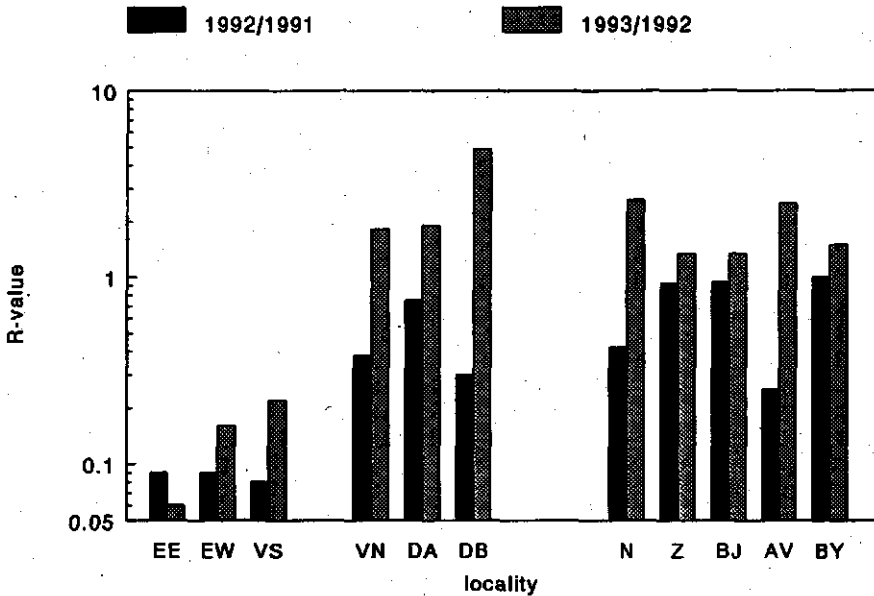


Fig. 3. The R -values $(N_t+1)/(N_{t-1}+1)$ in 1991-1992 and 1992-1993 of *O. rotundatus* in six experimental enclosures, with the species being present beforehand in DA, DB and VN, and at five permanent sampled sites (N, Z, BJ, AV and BY).

numbers indicates that most likely the species was present there beforehand. This was confirmed by the catches of this species at the east side of the terrain. The catches of unmarked *P. lepidus* outside EW and the catch of an unmarked *O. rotundatus* outside EW can almost certainly be interpreted as escaped beetles from the enclosures or offspring from escaped beetles. However, the possibility of presence of the species beforehand can not totally be excluded.

Survival of individuals

During the first year all research areas show survival of *P. lepidus*, and apart from EE also during both years. The age of the introduced individuals was not known, but most of the introduced individuals will have been one or two years old. Based on experiments by Van Dijk (1979) with *Calathus melanocephalus* and with *P. versicolor*, which is closely related to *P. lepidus*, it may be supposed that about

60% of the introduced individuals were reproducing for the first time. Using data of survival of different age classes (calculated with data of Van Dijk, 1979) it can be concluded that during 1991-1992 four enclosures (all, except DA and DB) and during 1992-1993 three (EE, EW and VS) gave a lower survival than expected.

There was almost no survival of marked individuals of *O. rotundatus* in all six enclosures. The most probable conclusion is that there is only a very limited survival of adult *O. rotundatus* between reproduction periods. This means that at least in these areas this species will be largely semelparous (one reproduction period per individual).

Reproduction of individuals

The high numbers of unmarked *P. lepidus* which were caught at Dwingelderveld during both years show that both enclosures were suitable for reproduction in an area where *P. lepidus* was already present. Therefore, the available space in the enclosures did not seriously limit reproduction. Quantification of the reproduction at Dwingelderveld is only possible for 1993, because in 1992 the number of unmarked beetles was partly due to beetles being present before the start of the experiment. At Heideheim considerable numbers of unmarked *P. lepidus* were caught in all enclosures except VS. Though the reproduction in VN, EE, and EW is lower than at DA and DB, all three showed suitability for *P. lepidus* to complete its lifecycle.

In both years relatively high numbers of unmarked individuals of *O. rotundatus* were caught in the enclosures DA, DB and VN. As in the other three enclosures only one or even no unmarked beetles were caught, three out of six enclosures were put into unsuitable localities. However, as was shown above, the most positive result for *O. rotundatus*, the successful reproduction in VN, cannot be considered an experiment in an unoccupied habitat. Apparently the absence of *O. rotundatus* during 1990, at about the same location as VS, was not representative of the whole area. Hence, in VN the reproduction of 1992 was also biased by the presence of beetles before the start of the experiment, just as in DA and DB. In 1993 the reproduction in DA, DB and VN was 36, 53 and 28 individuals

respectively, demonstrating a very large difference between reproduction in suitable and in unsuitable enclosures.

Reproductive values

Survival of adults and reproductive success are both parameters of lifetime reproductive success and can fluctuate enormously. The fluctuations of population size depend on both together and have been studied thoroughly for ground beetles (Den Boer, 1977; Den Boer & Van Dijk, 1994). To be able to interpret the results from the enclosures presented here, it is useful to compare the fluctuation patterns with those at nearby areas. In particular, the enclosure DA and a permanently used standard set of three pitfalls of the Biological Station (code Z) were only about 50 m removed from each other.

The results show that the *R*-values in the enclosures where the species were present beforehand, DA, DB and for *O. rotundatus* also VN, were very similar to the *R*-values of some standard sets at the same region. Hence, both methods, the standard sets and the enclosures in occupied areas give comparable results. As is shown in the section 'barrier efficiency' a comparison between enclosure experiments in occupied and unoccupied areas leads to conservative conclusions.

Compared to the standard sets and the enclosures in the occupied areas, the *R*-values for *P. lepidus* in EE and EW are somewhat lower. Considerable lower are the *R*-values for both species in VS and for *O. rotundatus* in EE and EW as well. These lower values indicate, at least for these years, less suitable conditions for reproduction or survival. A 95% confidence interval based on a large number of *R*-values at several areas for 23 years in the province of Drenthe was available for both species: 0,2 - 5 (after Den Boer, 1990a). Using these intervals VS can be considered as an unsuitable location for both species, whereas EE and EW were unsuitable only for *O. rotundatus*.

Factors influencing the success of colonization

A surprisingly large difference in suitability for reproduction of both species appeared to exist between VS and VN. The vegetation present does not give any indication that VS would be unsuitable as a habitat. Therefore, it appears difficult

to know beforehand what factors determine the suitability of a heathland area for reproduction. A factor which might have made VS less suitable than VN may have been the presence of forest at the south side of the enclosure VS at a distance of about 15 m. As a result VS had less exposure to sunlight. The presence and reproduction of both species at moist sites such as the enclosures DA and DB, and their presence in dry areas such as fixed drift-sand (De Vries, 1994) shows that moisture is less important than exposure to sunlight.

To some extent the results could be dependent on number of propagules as found by Crowell (1973). Therefore, it is possible that in the area Heideheim Eischenbroekveld an experiment with *O. rotundatus* using more beetles would be more successful. Interspecific competition between introduced and already present ground beetles, if any, did not seem to prevent successful reproduction in *P. lepidus*.

Metapopulations and dispersal

The results with *O. rotundatus* show that it is difficult to ascertain whether or not a population of a ground beetle species is present in a certain area. A similar difficulty was experienced by Harrison (1989) during her introduction experiments with the butterfly *Euphydryas editha bayensis*.

As the reproduction of *O. rotundatus* at Heideheim Eischenbroekveld was unsuccessful no evidence was found for the existence of unoccupied habitat patches for this species. For two reasons the colonization ability of *O. rotundatus* may be considerably higher than expected from the absence of flight observations. First, some of the individuals have macropterous wings making it possible that this species occasionally flies. Second, studies by Vermeulen (1993) showed that *O. rotundatus* occurs in roadside verges and it is able to disperse along these. Therefore, it could well be that *O. rotundatus* merely forms metapopulations in which the habitat patches are continuously occupied or only unoccupied for a short period. Metapopulations are defined here as a set of local populations which interact via individuals moving among populations (Hanski & Gilpin, 1991; Harrison 1991).

The experiments with *P. lepidus* demonstrate the presence of unoccupied habitat patches in the landscape of Drenthe. The results show that during 1991-1993 such patches were suitable for reproduction. Because of its inability to fly, its capability to disperse over long distances is low and consequently the chances to recolonize fragments in the present landscape of Drenthe will be small. The catches of this species in road-side verges (Vermeulen, 1993) indicates some possibilities to disperse outside patches. It is highly likely that, apart from the areas investigated here, several more areas at which *P. lepidus* was not found are suitable for reproduction. The survey of 1990 showed that *P. lepidus* was present in all suitable areas (all heathlands except peatmoors) larger than 10 ha and isolated since the first half of this century (chapter 3). The smaller areas will probably have temporary occupancy of this species, whereas in larger areas extinction probabilities are much reduced (chapter 3). The possibilities for dispersal and colonization of *P. lepidus*, combined with the absence of this species from some habitat patches indicates that this species forms metapopulations in which discontinuously occupied habitat patches are present. As continuously and discontinuously occupied patches are present in Drenthe, there is a resemblance to mainland-island or sink-source situations (Harrison, 1991), though the habitat islands do not necessarily get their colonists from the larger patches.

As the existence of unoccupied habitat patches for *P. lepidus* was successfully demonstrated, the inability of this species to balance extinctions by colonizations is caused by the isolated position of the habitat patches. The extinctions are probably due to environmental stochasticity. The poor dispersal capacity of this species together with the fragmented habitat result in the absence of this species from several small isolated habitat patches.

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Chapter 5

Genetic variation in populations of two ground beetle species, *Agonum ericeti* and *Pterostichus lepidus*, in relation to fragmentation of habitats

with A. Kamping, I. C. Knevel, Th. S. van Dijk & W. van Delden
submitted to *Oecologia*

Summary

*In the Netherlands some stenotopic ground beetle species with low dispersal ability occur in remnants of peat moor and wet heathland. This presents the opportunity to investigate the influence of habitat fragmentation on genetic variability and differentiation in populations of two ground beetle species, *Agonum ericeti* and *Pterostichus lepidus*, by means of allozyme electrophoresis. For all populations of *A. ericeti*, heterozygosity, mean number of alleles per locus, and percentage polymorphic alleles were about the same. The mean F_{st} -value was 0.038, indicating that the genetic divergence between these populations was still small after about 60 years of habitat fragmentation. In *P. lepidus* however, two populations in relatively small patches showed fewer alleles per locus and a relatively large genetic distance to the other populations studied. The mean F_{st} -value was 0.090, indicating moderate genetic divergence after 40 years of habitat fragmentation. Though many of the populations of *A. ericeti* in small and isolated habitats have already become extinct, it is concluded to be unlikely that extinctions will be caused by genetic erosion in the near future. Unlike *A. ericeti*, *P. lepidus* is expected sometimes to be able to recolonize empty habitat patches in the Netherlands. Hence, the genetic variation of populations of *P. lepidus* in some small patches is probably showing a founder effect. The results show that it is difficult to estimate gene flow between populations in a fragmented landscape without additional data on dispersal.*

Introduction

Populations of many ground beetle species in the Netherlands have become small and isolated after fragmentation of their habitats. In consequence many populations became extinct (Turin & Den Boer, 1988; Desender & Turin, 1989; chapter 2 and 3). In chapter 3 it was shown that the extinction of ground beetle populations in heathlands is related to habitat preference, size of habitat, dispersal ability and dispersal opportunities. A period of between 25 and 116 years of isolation appeared to lead to the extinction of many populations of heathland species in small isolated patches. In particular for heathland species with low dispersal ability, only a limited number of populations was still present in small patches. Den Boer (1981) showed the stabilizing effect of a large habitat size on the fluctuations of number of individuals in the population. However, the processes taking place between the moment of fragmentation and the eventual extinction are not sufficiently known. Conservation theory often recognizes four factors affecting small and isolated populations (Shaffer, 1981; Gilpin & Soulé, 1986; Caughly, 1994). Firstly, demographic stochasticity (random variation in birth and mortality rates and gender among individuals) can cause the loss of populations, e.g. when the last generation only consists of individuals of one sex. This factor is only of importance in populations with very small numbers of individuals. Secondly, stochastic fluctuations of animal numbers due to environmental factors can result in a succession of low reproduction values, which eventually may end up in the disappearance of the population. Thirdly, events which are categorized as catastrophes, e.g. fires, are expected to be an important cause of the loss of isolated populations. Fourthly, when due to isolation immigration is absent or nearly absent, small populations or populations which experienced a bottleneck in population size may be confronted with the effects of genetic drift and inbreeding. Due to genetic drift, allele frequencies will fluctuate in the course of generations. As a consequence alleles, and in particular alleles at low frequencies, will get lost. Finally, drift will lead to fixation of one particular allele. Genetic drift will thus lead to a decrease of genetic variation in small and isolated populations and increase levels of homozygosity. Another process manifest in small populations is

inbreeding: the enhanced frequency of mating between genetically related individuals. Inbreeding leads to reduction of heterozygosity. Inbreeding depression, that is a reduction in fitness in inbred individuals compared to outbred ones, often accompanies inbreeding.

Conservation genetic theory warns of decreasing levels of genetic variation in small and isolated populations as a consequence of genetic drift and inbreeding (Berry, 1971; Brakefield, 1991; Van Delden, 1992; Caughly, 1994). The fitness of individuals may be reduced considerably in small and isolated populations (Vrijenhoek, 1985; Frankel, 1983; Charlesworth & Charlesworth, 1987, Van Delden, 1992). Data from various studies suggest strongly that more heterozygous individuals are often fitter than individuals of the same cohort with less heterozygosity (Mitton & Grant, 1984; Mitton, 1993; Van Delden, 1992; Caughly, 1994). So far, cases of loss of genetic variation in fragmented populations mostly concern vertebrates and higher plants (Schaal & Smith, 1980; Schwaegerle & Schaal, 1979; Van Treuren et al., 1991; Avise & Hamrick, 1996). Insects normally show high levels of genetic variability (Nevo, 1978; Rank, 1992; Baughman et al., 1990; Cronau-Roy, 1989; Liebherr, 1986, King, 1987) and are therefore suitable objects for estimating loss of genetic variability, if any, in small populations. Many small ground beetle populations still present in the province of Drenthe, the Netherlands, are in great danger of becoming extinct and several already are extinct (chapter 3). In particular the small size of some of the habitat patches and the isolated position of the populations involved decreases the probability of long-term survival. This situation provides ample opportunities to test whether reduction of genetic variability has occurred in these populations. Such a reduction would indicate a potential additional threat for the viability of these populations and insight into the processes leading to extinction.

In this study ground beetles of two species, *Agonum ericeti* and *Pterostichus lepidus* were used for an analysis of the level of genetic variation. In an earlier study both species were selected as heathland species (chapter 3). They have a low dispersal ability, because they are not able to fly and the distances covered by walking are limited. Earlier research (chapter 2 and 3) revealed the extinction of many populations of the two species in small habitat patches isolated for many

years. Nevertheless, a few populations were still present in such patches. Individuals were sampled in populations in isolated heathland areas (including peat moors) of different sizes and genetic variability was estimated to detect a possible reduction of genetic variation. General patterns of fluctuation in numbers of both species are known from some areas (Den Boer, 1985; Den Boer, 1990a; chapter 2) and a rough estimate of population sizes in the recent past of most populations of *P. lepidus* could be made to relate these to the level of genetic variation.

Materials and methods

The species and its habitat

The species used in this study are *Agonum ericeti* and *Pterostichus lepidus*. Earlier investigations of *A. ericeti* showed its endangered status in the province of Drenthe, the Netherlands (chapter 2 and 3). A map of the distribution of populations currently known is given in fig. 1a. It depicts almost all populations of this species in Drenthe. *A. ericeti* is a species which only occurs in peat moors and very wet heathlands (chapter 2). All other kinds of habitat are unsuitable for this species. It prefers a thick layer of organic matter as substrate. It has a low dispersal ability: flying individuals have never been caught in the Netherlands (Van Huizen, 1980; Van Huizen & Aukema, 1992). It is brachypterous and in spite of wing measurements of many individuals of *A. ericeti*, no individuals with wings large enough for flight have been found (Den Boer, 1977, De Vries & Den Bak, unpublished data). Based on earlier work (Baars, 1982; Klazenga & de Vries, 1994; Vermeulen, 1994), maximum displacement distance can be estimated to be about 300 m per year in suitable habitats. Annual changes of local population density of ground beetles can be quite large (Den Boer, 1985). Between successive years in 42 year-catches of *A. ericeti* (1959 - 1993) maximum differences in population density differed by a factor of 10.

The distribution of currently known populations of *P. lepidus* in Drenthe, given in fig 1b, most likely represents only a small part of the populations present. *P. lepidus* occurs in heathland, both wet and dry, but not in peat moor, and sometimes

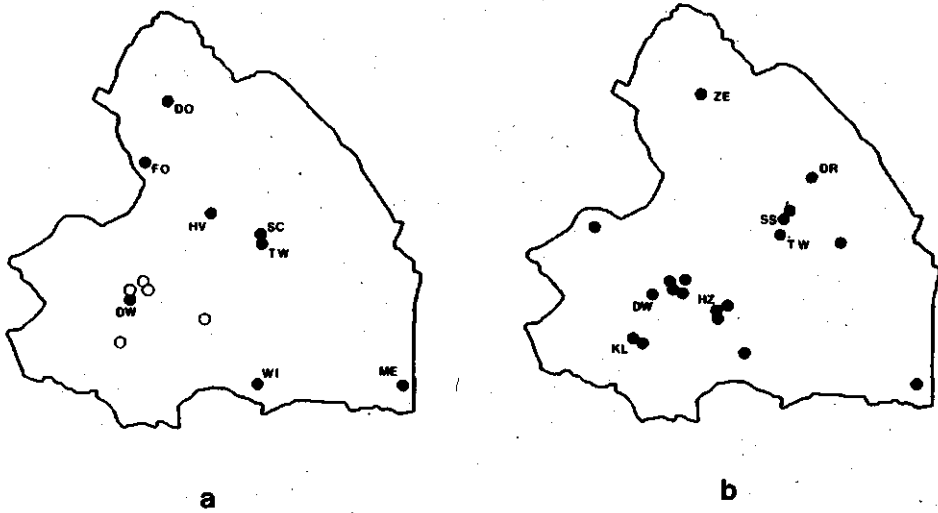


Fig 1. Map of Drenthe with marked populations of *A. ericeti* (a) or *P. lepidus* (b). Empty circles indicate extinct populations.

in open young coniferous plantations (Turin et al., 1991; chapter 3 and 4). In Drenthe its occurrence is restricted to sandy oligotrophic areas and is largely independent of moisture. This species also has a low dispersal ability, flying individuals have never been caught in the Netherlands (Van Huizen, 1980; Van Huizen & Aukema, 1992). In the Netherlands *P. lepidus* is brachypterous with only small rudimentary wings (Den Boer, 1977). Maximum displacement distances in suitable habitats can be estimated to be about 800 m per year (Baars, 1982; Klazenga & de Vries, 1994; Vermeulen, 1994). In 105 year samples of *P. lepidus* (1959-1993) a 24-fold maximum difference in population density was found between successive years.

The investigated populations

For several centuries the landscape of the province of Drenthe was dominated by ample presence of heathland and peat moors. Even at the beginning of this century large parts were still covered with these habitats (Wieberdink, 1990). Because both

Table 1. The areas sampled, the codes used, and some of their characteristics.

Areas	Code	Habitat	Habitat size ¹	Isolation period ²
<i>A. ericeti</i>				
Fochteloërveen	FO	peatmoor	1700	-
Dwingelderveld	DW	wet heathland/ peatmoor	1000	-
Meerstalblok	ME	peatmoor	< 1700 ³	-
Hingsteveen	HV	peatmoor	77	-
De Witten	WI	peatmoor	53	36
Tweelingen	TW	peatmoor	7	59
Doktersveen	DO	peatmoor	4.2	62
Schoonloërveenputjes	SC	peatmoor	1.3	58
<i>P. lepidus</i>				
Dwingelderveld	DW	wet heathland	1000	-
Drouwenezand	DR	Corynephorum	131	-
Hunnenkloosterberg	KL	dry heathland	15	37
Tweelingen	TW	dry heathland	14	61
Hullenzand	HZ	Corynephorum	14	36
Schoonloërstrubben	SS	dry heathland	1.7	49
Zeyerlaar	ZE	wet heathland	0.3	35

¹ Estimated size of habitat (ha).

² Estimated isolation period (in years).

³ Difficult to estimate, probably more than 50 ha.

species, *A. ericeti* and *P. lepidus*, have a strong association with open heathy habitats, it can be inferred that they were common at that time. After large scale reclamation only less than five percent of these habitats remained and as a consequence the presence of both species diminished. The investigated populations are located in patchily distributed remnants of these habitats (chapter 3). The surrounding landscape of these isolated habitats is largely agricultural, with crops, grasses, and mature coniferous forest plantations and is therefore largely unsuitable for both species.

Eight populations (fig 1a) of *A. ericeti* were sampled by means of pitfall trapping; some additional specimens were caught by hand. All eight areas except one, DW, are peat moors. The sizes of the habitats were estimated by measuring the size of the total heathy area on the most recent topographical map and subtracting the estimated amount of dry sandy areas in it. Sizes ranged from 1.3 to 1700 ha (table 1). All populations were completely isolated from each other, due to

a large distance between the different populations (one or more km), a strong preference of this species for its currently rare habitat, and its low dispersal ability (chapter 2). In order to estimate the period at which potential effects of fragmentation had been realized, the isolation periods of the populations in the four smallest areas were estimated by using old topographic maps (method chapter 3), see table 1. For genetic analysis an amount of 30 or more individuals was preferred, but not available from each area. In particular the numbers caught at the large area ME were far less and even at DW, where in other years at some sites *A. ericeti* had been caught in high numbers, in 1992 the catches were low. Because *A. ericeti* is a rare species in the Netherlands, a limited mark-recapture experiment was done to ensure that in small areas after the removal of the individuals for the genetic analysis more than 85% of the individuals still remained.

In Drenthe populations of *P. lepidus* are more numerous as compared to those of *A. ericeti*, mainly because its habitat, all kinds of heathland except peat moor (Turin et al., 1991), is much more available. For this study *P. lepidus* was caught at seven areas, see fig. 1b. The sizes of the areas were estimated as for *A. ericeti*, and ranged from 0.3 to 1210 (table 1). The isolation periods of the populations in the five smallest areas were estimated (table 1). As the habitat of *P. lepidus* is sometimes also available in road-side verges, it is possible for this species, despite its low dispersal power, to show limited dispersal through the landscape (Vermeulen, 1993, 1994). From each population forty specimens were used.

Population size

Population sizes are expected to be crucial for predicting changes of genetic variability due to genetic drift. Unfortunately no extensive mark-recapture experiments were done for both species. Only an estimated rank in population size (*A. ericeti*) or a rough estimate of population size (*P. lepidus*) could be derived. Both estimates are calculated using the total size of habitat and the number of individuals caught during one year at a site in it. It has been demonstrated that there is a linear relationship between the year-catch (the individuals caught by means of one standard set of pitfalls during one year: Den Boer, 1977) and population density (Baars, 1979a). This means that year-catches at different sites or

Table 2. Catches of *A. ericeti* and *P. lepidus* for one to three years, if available. Estimated rank of population size of *A. ericeti* (year-catch from one site times estimated habitat size in ha) and estimated population size of *P. lepidus* $(\{\text{year-catch} + 1\} / 783)$ is individuals per square meter (Baars, 1979) times estimated habitat size in square meters).

<i>A. ericeti</i>				<i>P. lepidus</i>			
Code	Year	Catch	Rank of population size	Code	Year	Catch	Estimated population size
FO	1990	134	227800	DW	1990	23	306513
DW	1990	4	4000		1991	54	702427
	1991	3	3000		1992	101	1302681
	1992	1	1000	DR	1990	150	252631
ME	1990	-		KL	1990	821	157471
HV	1990	-		TW	1990	-	
WI	1990	265	14045	HZ	1990	138	24853
	1991	95	5035		1991	178	32005
	1992	23	1219		1992	187	33614
TW	1990	-		SS	1990	62	1368
DO	1990	208	874	ZE	1990	36	142
	1991	170	714		1991	165	636
	1992	72	302		1992	201	774
SC	1990	-					

at the same site in different years reflect the differences or fluctuations in local population densities. For *A. ericeti* and *P. lepidus* year-catches were available in some habitats from one site during one to three years (table 2). Multiplying year-catches with habitat size, a relative estimate of population size became available for *A. ericeti*, which is referred to as 'rank of population size', see table 2. For only two species the regression lines are known (Baars, 1979a), and for one of them, *P. versicolor*, it is known that walking behaviour is very similar to *P. lepidus* (Baars, 1982; Klazenga & De Vries, 1994). This means that, by using the regression line of *P. versicolor* (Baars, 1979a): individuals per square meter is $(\text{year-catch} + 1) / 783$, a rough estimate of numbers of *P. lepidus* per square meter became available for some sites. Multiplying density of *P. lepidus* at one site and habitat size resulted in an 'estimated population size' in individuals, see table 2. Because only densities at one site were used to estimate average density of the whole habitat, deviations of actual population size and actual rank of population size can be expected to increase with size of habitat.

Table 3. List of loci used for the estimation of genetic diversity together with enzyme structure, number of observed alleles, the buffersystem used (see text). References for the staining procedure used are Ho = Hofman (1988), Mu = Murphy et al. (1990), Ei = Eisses et al. (1979), Ha = Harris & Hopkinson (1976).

Locus	EC no.	Staining	Buffer system	Structure	No. of alleles
<i>A. ericeti</i>					
<i>Est</i>	EC 3.1.1.-	Ha	3	monomeric	5
<i>αGpdh</i>	EC 1.1.1.8	Ei	1	?	1
<i>Gpi</i>	EC 5.3.1.9	Ha	3	dimeric	5
<i>Hbdh</i>	EC 1.1.1.30	Mu	2	dimeric	3
<i>ldh-1</i>	EC 1.1.1.42	Ha	1	?	1
<i>ldh-2</i>	EC 1.1.1.42	Ha	1	dimeric	5
<i>Mdh</i>	EC 1.1.1.37	Ho	4	dimeric	2
<i>Pgm-1</i>	EC 5.4.2.2	Ho	1	monomeric	10
<i>Pgm-2</i>	EC 5.4.2.2	Ho	1	monomeric	3
<i>Sod</i>	EC 1.15.1.1	Ho	1	?	1
<i>P. lepidus</i>					
<i>Hadh</i>	EC 1.1.99.6	Mu	2	dimeric	3
<i>Gpi</i>	EC 5.3.1.9	Ha	3	dimeric	8
<i>ldh</i>	EC 1.1.1.42	Ha	3/2	dimeric	4
<i>Tpi</i>	EC 5.3.1.1	Mu	2	dimeric	2
<i>6Pgdh</i>	EC 1.1.1.44	Mu	1	?	1
<i>Hk</i>	EC 2.7.1.1	Mu	2	?	1

Allozyme electrophoresis

The individuals caught were numbered and kept alive in the laboratory until they were starved for a few hours and frozen at -80°C . Individuals were prepared for electrophoresis by removing the elytra, wing remnants (if present), the last part of the abdomen, and, in the case of *P. lepidus*, the head. Thereafter they were homogenized with a drop of grinding buffer (100 μl 0.1 M Tris-citrate pH 8) in a ceramic tray on ice. Electrophoresis was carried out on horizontal starch gels (12% starch). Four buffer systems were used (see table 3). System 1 was a Tris-citrate pH 7.0 system (Hofman, 1988), system 2 was a LiOH-borate pH 8.3 system (Hofman, 1988), system 3 was a Trismaleaat pH 6.0 system (0.05 M maleinezuuranhydride adjusted with Tris to pH 6.0, gel: 36 g starch in 20 ml buffer added to 280 ml aquadest), system 4 was a Triscitrate buffer pH 7.5 (buffer: 0.15 M Tris and 0.005 M EDTA adjusted to pH 7.5 with citrate, gel: 36 g starch in 20 ml buffer added to 280ml aquadest). Initially 20 and 21 enzyme systems were

tested in *A. ericeti* and *P. lepidus*, respectively. The references for the staining methods are given in table 3.

Data processing

The genetic basis of allozyme variation was ascertained by breeding experiments and the subsequent analyses of banding patterns. The collected data on locus polymorphism and allele frequency were used for a calculation of variability of separate populations and a calculation of the standardized variance of allele frequencies, F_{st} (Wright 1978; Nei 1977, 1978), by using the BIOSYS program of Swofort and Selander (1981). Deviations from Hardy-Weinberg frequencies were tested with a Chi-square test, using, where possible, pooled allele frequencies of all alleles except the most dominant one. Significance of gene frequency differences among populations was tested for each locus with a Chi-square test (King, 1987). Correlations between genetic parameters of populations and habitat size, population

Table 4. The mean sample size per locus (n), percentage polymorphic loci (P), using a criterion of less than 99% for the most common allele, mean number of alleles per locus (A), and mean observed heterozygosity (H) of each population.

Area	n	P	A	H
<i>A. ericeti</i>				
FO	29.1	40	2.4	0.184
DW	20.4	40	2.1	0.204
ME	10.9	50	2.2	0.242
HV	22.6	50	2.3	0.202
WI	51.1	60	2.8	0.217
TW	37.0	60	2.8	0.220
DO	30.1	50	2.4	0.212
SC	26.7	40	2.2	0.197
<i>P. lepidus</i>				
DW	38.8	68	2.7	0.277
DR	39.3	68	2.8	0.252
KL	39.2	50	2.3	0.274
TW	38.5	68	2.7	0.258
HZ	39.0	68	2.7	0.234
SS	39.3	50	2.7	0.284
ZE	38.7	68	1.8	0.251

size in 1990, and sample size were calculated using Kendall's coefficient of rank correlation (Sokal & Rohlf, 1981). Genetic distances between populations were estimated and their association with geographic distances was tested using a Mantel test (Sokal & Rohlf, 1995).

Results

Genetic variability

After using criteria as consistent banding patterns and satisfactory genetic interpretation, ten and six loci could be used for genetic analysis in *A. ericeti* and in *P. lepidus*, respectively (table 3). The breeding experiments were supportive to our genetic interpretations, but, due to multiple paternity in our experiments, could not provide final evidence in all cases. In *A. ericeti* three loci proved to be monomorphic and seven others were polymorphic (table 2). In *P. lepidus* two loci were monomorphic and four polymorphic. Polymorphic loci possessed two to ten alleles in *A. ericeti* and two to eight alleles in *P. lepidus*. For both species no loci were observed to be fixed for alternative alleles in different populations. *A. ericeti* was polymorphic at 70% of the loci scored, and the percentage polymorphic loci in the populations varied between 40 - 60% (table 4). *P. lepidus* was polymorphic at 68% of the loci scored, the individual populations were polymorphic for 50 - 68% of the loci (table 4). The mean number of alleles per locus ranged from 2.1 to 2.8 in *A. ericeti* and from 1.8 to 2.8 in *P. lepidus*, respectively (table 4). The lowest numbers of alleles were found in populations of *A. ericeti* at DW, ME, and SC and in populations of *P. lepidus* at ZE and KL. Observed heterozygosity in *A. ericeti* was on average 0.210, ranging from 0.184 to 0.242 and in *P. lepidus* 0.261, ranging from 0.234 to 0.284. As *A. ericeti* was collected in some populations at different sites, deviations from Hardy-Weinberg equilibrium could have been present due to substructuring by the Wahlund effect. However, in *A. ericeti* only one significant deviation (a deficiency of heterozygotes: $P < 0.05$) was found in 34 cases (*Gpi* in SC). In *P. lepidus* deviations from Hardy-Weinberg equilibrium

Table 5. F_{st} -values of the populations and their significance for each polymorphic locus.

Locus	F_{st}	Chi ² -value	d.f.
<i>A. ericeti</i>			
<i>Est</i>	0.034	72.4***	28
<i>Gpi</i>	0.041	87.3***	28
<i>Hbdh</i>	0.045	42.7***	14
<i>Idh</i>	0.020	42.6*	28
<i>Mdh</i>	0.016	5.7	7
<i>Pgm-1</i>	0.036	171.1***	63
<i>Pgm-2</i>	0.012	10.8	14
Mean	0.038	432.6***	182
<i>P. lepidus</i>			
<i>Hadh</i>	0.064	71.7 ***	12
<i>Gpi</i>	0.108	376.5***	42
<i>Idh</i>	0.081	130.3***	18
<i>Tpi</i>	0.124	69.4 ***	6
Mean	0.090	647.9***	78

* = $P < 0.05$, *** = $P < 0.001$

were significant in two out of 26 cases (*Hadh* in DR and *Idh* in ZE, both deficiencies of heterozygotes).

F-statistics were calculated, see table 5. The mean F_{st} values of 0.038 and 0.090 for *A. ericeti* and *P. lepidus* respectively, indicated that significant genetic differentiation existed among populations of both species (table 5). In *A. ericeti* the differentiation of allele frequencies was significant for *Est*, *Hbdh*, *Gpi*, and *Pgm-1*. The other three polymorphic loci of *A. ericeti* showed lower and insignificant F_{st} values and had one dominantly present allele and other very rare alleles. In *P. lepidus* all four polymorphic loci showed significant differentiation.

Genetic distance

The values of unbiased genetic distances for the different populations of both species using the method of Nei (1978) ranged from 0.000 to 0.019 in *A. ericeti* and 0.000 to 0.132 in *P. lepidus* (table 6 and 7). In *A. ericeti* maximum genetic distance between large populations was 0.012, which is only slightly different from the maximum value (0.019) found for the populations in the two smallest patches.

Table 6. Values of unbiased genetic distances between eight populations of *A. ericeti*.

Population	FO	DW	ME	HV	WI	TW	DO	SC
FO	****	.010	.003	.001	.008	.004	.009	.016
DW		****	.012	.003	.002	.011	.004	.004
ME			****	.000	.008	.005	.014	.014
HV				****	.000	.002	.010	.006
WI					****	.002	.014	.000
TW						****	.018	.003
DO							****	.019
SC								****

Table 7. Values of unbiased genetic distances between seven populations of *P. lepidus*.

Population	DW	DR	KL	TW	HZ	SS	ZE
DW	****	.002	.024	.002	.009	.000	.097
DR		****	.033	.003	.008	.002	.107
KL			****	.050	.064	.037	.123
TW				****	.000	.000	.112
HZ					****	.005	.132
SS						****	.096
ZE							****

For *P. lepidus* one population, ZE, showed the largest deviation from the other populations. For this population the genetic distance from the other six populations ranged from 0.096 to 0.132. Another population, KL, showed an intermediate genetic distance to the remaining five populations, with differences ranging from 0.024 to 0.064. The genetic distances among the other five populations were much lower and did not exceed 0.009. The genetic distance data were used to obtain an UPGMA dendrogram (Sneath & Sokal, 1973), see fig. 2. The cluster of eight populations of *A. ericeti* was genetically very similar compared to the genetic distance among the populations of *P. lepidus*.

Comparisons of genetic variation with population size and geographic distance

The correlations of observed heterozygosity, mean number of alleles per locus, and percentage polymorphic loci, with rank of population size of *A. ericeti* and estimated population sizes of *P. lepidus* were calculated. Correlations between

habitat size and these three parameters for genetic diversity of both species were not significant ($P > 0.05$). Rank of population size for *A. ericeti* (table 2) gave no significant correlation with the three genetic parameters ($P > 0.05$). The estimate for *P. lepidus* population size (table 2) gave also no significant correlation with the three genetic parameters. When relating the three genetic parameters to sample size, these only gave significant results in *A. ericeti* for the mean number of alleles per locus ($n = 8$, $\tau = 0.605$, one-tailed, $P < 0.05$).

For both species no significant associations were found between genetic distance, employing the distance values from tables 6 and 7, and a geographic distance matrix when using a Mantel test (Sokal & Rohlf, 1995): $P = 0.16$ and 0.09 in *A. ericeti* and *P. lepidus*, respectively.

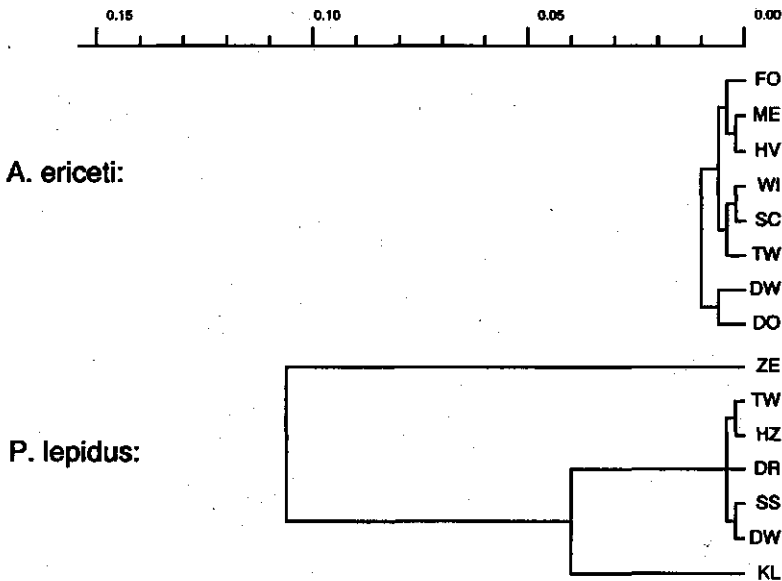


Fig. 2. The results from a cluster analysis of *A. ericeti* and *P. lepidus* using Nei's (1978) unbiased genetic distance.

Discussion

A. ericeti

Considering that 70% of the loci scored were polymorphic and that the average heterozygosity was 0.210, it can be concluded that *A. ericeti* is a species with a high level of genetic variation. The results showed slight, but significant genetic differentiation of allozymes between populations of *A. ericeti*, but provided no indication of a lower genetic variation in small isolated patches as compared with larger ones. Two parameters determine genetic differentiation: the effective number of locally breeding adults and the rate and pattern of gene flow among the populations in the array of local breeding populations (Wade & McCaughley, 1988). As mentioned before, in the case of *A. ericeti* dispersal between populations is absent. Therefore, the most likely reason why genetic variability of *A. ericeti* is still high, even in the smallest populations, is that though some of the populations are the smallest known in this region, the effective population size (N_e) was not or has not been sufficiently small to cause loss of genetic variation. Slatkin (1985, 1987) gives a rule stating that, if the average time in generations to extinction of local populations is less than or equal to the effective number of locally breeding adults, then, even in the absence of migration, extinction and recolonization will prohibit the genetic differentiation of local populations due to drift.

The results of a very limited mark-recapture experiment at Schoonloërveenputjes (most probably the smallest population) and the catch in Doktersveen in 1990 of more than 200 individuals indicate the presence of populations of at least several hundreds of individuals. Based on Slatkin's rule, it can be expected that after 60 years of isolation the effects of drift on genetic variation will probably still be low. As for most of the other populations of this species in small and isolated patches time to extinction is less than 60 years (chapter 2 and 3), many populations probably disappear before substantial loss of genetic variation has occurred. Nevertheless, bottleneck situations could well have occurred in the past, but the high level of genetic variation in all populations does not prove this. Also an other factor could have reduced the rate at which loss of genetic variability was taking place: the possible occurrence of overlapping

generations in this species. Most ground beetle species are known to have overlapping generations (Den Boer, 1979a; Van Dijk, 1979), but as exceptions occur (Nelemans et al., 1989), it is unknown whether or not overlapping generations occur in *A. ericeti*.

The two smallest populations show the largest genetic distance observed between the investigated populations, indicating the effects of decreasing population size. The F_{st} values (mean value: 0.038) indicate that slight genetic differentiation between separate populations occurs. A comparison with other studies of genetic variation in spatially subdivided insect populations indicates that the F_{st} values of *A. ericeti* are relatively low. In an endemic beetle species (Melyridae) (King, 1987) F_{st} was 0.192; in a troglobitic beetle species (Cronau-Roy, 1989) F_{st} was 0.112; in six cave cricket species (Caccone & Sbordoni, 1987) F_{st} was 0.240-0.720; in five ground beetle species (Liebherr, 1988) F_{st} varied between 0.003 and 0.270. In most studies, however, the period in which these populations had been in their present configuration was a geological one. So far, studies of insect populations fragmented by recent large-scale anthropogenic changes of the landscape have given only few examples of a significant decline in genetic variation (Brakefield, 1991; Usher, 1994). A study of the ground beetle *Carabus auronitens* (Terlutter, 1991; Niehues et al., 1996) is perhaps an example of this. In most cases the genetic patterns merely still reflect the gene flow in habitats that were continuous in the past (e.g. Baughman et al., 1990; Gerber, 1996). For *A. ericeti* this seems also to be the most reasonable interpretation of our data.

P. lepidus

The percentage of polymorphic alleles (68%) and the average heterozygosity of 0.261 both indicate that *P. lepidus* is also a species with high variability. The mean F_{st} -value of 0.090 indicates a moderate genetic divergence between populations of *P. lepidus*. Two populations of *P. lepidus* in particular, at Zeyerlaar and Hunnenkloosterberg, show a large genetic distance and a lower mean number of alleles per locus as compared to the other five investigated populations, indicating much more genetic divergence between populations as compared to *A. ericeti*. At the same time it is shown that populations of both species in large patches are

genetically largely identical. Therefore, it may be expected that small populations of *P. lepidus* more frequently experience low levels of genetic variation than those of *A. ericeti*. This is a remarkable result, because the populations of *A. ericeti* are expected to be totally isolated without any immigration (chapter 2), whereas for *P. lepidus* infrequent immigration is a real possibility (Vermeulen, 1993, 1994; chapter 4). Furthermore, surveys show that only eight populations of *A. ericeti* seem to have survived in Drenthe, whereas a much higher number of populations of *P. lepidus* are left, resulting in much shorter distances between separate populations for the latter. The isolation period of the populations of *P. lepidus* of the two genetically most distant populations is short compared to several populations of *A. ericeti*. Moreover, it is known that *P. lepidus* shows overlapping generations (chapter 4); even three year old individuals have been found (De Vries, unpublished data).

Assuming that dispersal between populations of *A. ericeti* is much more limited than between populations of *P. lepidus*, two explanations are possible for the results of *A. ericeti* differing from those of *P. lepidus*. Either *P. lepidus* populations experience more frequent bottleneck situations or they show effects from founder events (Holgate, 1966; Neel & Thompson, 1978). Also the estimated number of *P. lepidus* at Zeyerlaar of 142 (census size) in 1990 and the higher numbers during 1991 and 1992 may indicate that in 1994 this population was recovering from a bottleneck situation or founder event. It is difficult to comment on the first explanation. The longest period known for populations of *P. lepidus* to survive in small patches (< 10 ha) is 51 years (chapter 3), whereas this is 60 years for *A. ericeti* (chapter 2). This may indicate that in small patches both species have comparably viable populations. Still, unknown ecological features of *P. lepidus* could give this species a better ability to recover from bottleneck situations. The second explanation seems to be a very likely one. Though in the present landscape of Drenthe founder events are not expected to occur for *A. ericeti*, they are much more likely for *P. lepidus*. This species has some opportunities to recolonize habitat patches which have become empty (Vermeulen, 1993, 1994; chapter 4). As *P. lepidus* is a non-flying species, it will most likely colonize according to the propagule model (Wade, 1978): colonizers will come from one or perhaps two

nearby populations. This is expected to give a higher chance of genetic differentiation between populations, as compared with a situation in which colonists can arrive from several populations from different parts of the region (Wade & McCauley, 1988), as is possible for ground beetle species with flight ability. Moreover, founder events could have been induced by the management of the areas of the two genetically most different populations of *P. lepidus*. Both these areas have been managed by sod-cutting after having become overgrown by an abundant vegetation of grasses. After sod-cutting succession starts soon, in particular with heather, and the area becomes highly suitable for *P. lepidus*. This dynamic situation differs highly from that in the most important habitat of *A. ericeti*, peatmoor areas, which can be considered as relatively stable.

Conclusions

As both species show an average time to extinction which is less than the effective number of locally breeding adults, Slatkin's rule would predict not much genetic differentiation between populations. The results from the populations of *A. ericeti* confirm this rule. They indicate that loss of genetic variation is not an important threat for the viability of the smallest populations of this species currently known in Drenthe. For species which have no chance of recolonization and experience a short time to extinction, demographic or environmental factors might be more causative in bringing about extinction of populations than genetic factors. The fact that we have estimated relatively low levels of genetic variation in the smallest population of *P. lepidus* is less confirmative towards Slatkin's rule. Though it can not be excluded that the genetic differentiation in *P. lepidus* is related to bottleneck situations, it is more likely that it is caused by a founder events. This means that we have found no evidence for genetic erosion in fragmented ground beetle populations. Recent fragmented ground beetle populations often still have high numbers of individuals and therefore probably do not meet the conditions of Wright's infinite island model (Wright, 1931, 1969). They have a gene diversity which largely reflects the situation before fragmentation took place. The possible occurrence of founder effects in transient populations of some species makes it

difficult to draw the right conclusions about gene flow between separate populations without having an independent estimate of dispersal.

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Chapter 6

General discussion

The decline of biological diversity in habitats after fragmentation has been demonstrated by many studies (Wilcove et al., 1986; Spellerberg, 1991; Andrén, 1994). Habitat fragmentation results in reduction of the size of areas occupied by populations, reduction of population size and decreasing dispersal rates between populations. As a result many of the remaining populations are threatened with extinction. Several processes are considered to be responsible for extinction of populations in fragmented habitats. As the protection of the species in these habitats is an important task of nature conservationists, questions about which processes predominate and under what conditions are often put forward. Also insect populations are expected to be highly affected by habitat fragmentation. An analysis of the fluctuation patterns of ground beetle populations in the province of Drenthe led to the hypothesis that in fragmented habitats in particular species with low powers of dispersal are endangered with extinction (Den Boer, 1977; 1990b). Hence, dispersal is expected to play a key-role in the survival of populations, in particular in fragmented populations (Den Boer, 1977; 1990b; Opdam, 1990). Low dispersal rates are not only affecting population dynamics, but can have consequences for the genetic variation of a population as well. One of the processes often feared by managers of small populations is the possible loss of genetic variation, which is occurring when immigration rates are low. So far no proof has been found that loss of genetic variation has led to accelerating extinction rates of insect populations.

Habitat fragmentation

Presence in relation to area

Effects of fragmentation of heathland were not found for the total number of ground beetle species caught at local sites, but only for species characteristic for

heathlands (chapter 2 and 3). In small isolated areas the presence of heathland species was significantly less than in large areas. This is exactly the same result as Hopkins and Webb (1984) found for spiders. Though the whole group of heathland ground beetles showed negative effects of fragmentation, heathland ground beetles with low dispersal ability were much more affected than species with high dispersal ability (chapter 3), which is in accordance with the predictions of Den Boer (1977, 1990b). As there was a significant negative relation between isolation period and the number of heathland species with low dispersal ability present and because of the absence of such a relation for heathland species with high dispersal ability (chapter 3), presence of the latter species was probably due to either the 'rescue effect' (Brown & Kodric-Brown, 1977) or to recolonizations. Also for vertebrates it has been found that distribution of non-flying species is more affected by insularization as compared to flying species (Lomolino, 1984). These findings are in accordance with the founding hypothesis (Den Boer 1971, 1977, 1979b, 1990b), which states that founding new populations is the biological significance of dispersal. It implies that survival of small populations is limited when immigration is not taking place. The relation between presence of heathland species with low dispersal ability and area was explained by area-dependent extinction rates (chapter 3) as described in the 'area per se' hypothesis of Connor and McCoy (1979).

Presence of populations and metapopulations

Some of the investigated species, e.g. *Cicindela campestris* and to a certain extent also *Trichocellus cognatus*, have a high dispersal ability and still show absence from part of the habitat patches. Extinction as well as colonization of these species can be expected to happen frequently in some of the patches, where their presence will alternate in space and time. They show distinct features of a metapopulation as defined by Hanski (1991): a set of populations which interact via individuals moving among populations. But for many heathland ground beetle species extinction processes seem to dominate in the smaller habitats (< 10 ha), despite presence of larger patches in the region. This means that the large occupied patches do not provide the necessary colonists for the small patches. Hence, a population approach is necessary in addition to the metapopulation approach.

Populations in fragmented habitats can be divided into three types with respect to their presence in time: temporarily, continuously, and discontinuously present populations (chapter 1). Analogous to metapopulations the types are based on extinction rates, which are correlated with habitat sizes, and immigration rates, which are related to dispersal abilities and opportunities. In Drenthe populations of heathland ground beetle species occupy habitats of sizes ranging from less than 1 to 1700 ha. It has been shown in chapters 2 and 3 that persistence of isolated populations of heathland ground beetle species is far better in large areas (> 100 ha) than in small areas (< 10 ha). Two heathland species, *Pterostichus diligens* and *Bradycellus ruficollis*, were present in almost every heathland patch (chapter 3) and therefore can be considered to have only continuously present populations. Three heathland species, *Trichocellus cognatus*, *Cicindela campestris* (chapter 3), and *P. lepidus* (chapter 3 and 4) can be considered to occur in part in continuously present populations, viz. the ones occupying large habitats, and in part in discontinuously present populations, viz. the ones occupying small habitats. Many of the other 14 heathland ground beetle species (chapter 3) can be considered in part to exist of continuously and in part of temporarily present populations, e.g. *Carabus arvensis* (chapter 3) and *A. ericeti* (chapter 2 and 3). Once *C. arvensis* and *A. ericeti* have gone extinct in small and isolated patches, both species do not have any chance to recolonize a patch. In a situation not investigated in the present study, where habitat patches are close to one another, say within a distance of 200 m, these species will probably also be present in discontinuously occupied patches. Of course, no population persists for ever, so the above typology must be limited to a timescale of a hundred years or so (see chapter 3), assuming that habitat quality is not severely affected by catastrophes or human impact in that period.

Survival times

Den Boer calculated average survival times for small and isolated populations (each consisting of one interaction group) for several heathland species. He expected almost no survival after 100 years of isolation (Den Boer, 1990a) and for 64 ground beetle species found an average turnover of 6% per year for small populations. The data presented in chapters 2 and 3 confirmed that almost all small

populations of species with low dispersal abilities went extinct within 50 years. Consequently, average turnover rate has a lower limit of 2% per year, possibly for some species 4% per year. For example, *Cymindis macularis* and *Bembidion nigricorne* were not found in habitats smaller than 10 ha, which were all isolated for 26 or more years (chapter 3). It is difficult to compare these data with those of other investigations. Schoener (1983) showed that in several studies of arthropod populations turnover rates are found in the range of 10 to 100% per year in areas of 11 to 8600 m². The difference between these data and the data of chapter 2 and 3 may be caused by the larger size of almost all areas investigated in the present study. Another factor which Schoener (1983) showed to be negatively correlated with turnover is the generation time of species. Unlike many other arthropods, ground beetles can often become more than a year old, which could also explain the difference.

Habitat quality

One of the most important threats for the heathlands and their inhabitants is expected to be the disappearance of the heather due to atmospheric deposition of nitrogen and as a consequence the abundant growth of grasses in the heathlands (Aerts & Berendse, 1988; Heil & Bruggink, 1987, Den Boer & Van Dijk, 1994). The added nitrogen leads to large scale changes in the vegetation and to a decrease in available habitat for heathland species. Removal of nutrients by sod-cutting is commonly used to restore heathland for at least some time. In particular for small areas the management is often less intensive and the availability of suitable patches for specialized species may be restricted. The difference in presence in small patches of heathland species with high dispersal ability and heathland species with low dispersal ability indicates that habitat quality is not the predominant factor causing frequent absence of the latter (chapter 3). However, the results of the transplant experiments (chapter 4) show that *O. rotundatus* was not or almost not able to reproduce in an uninhabited patch, which beforehand was assumed to be suitable. This means that *O. rotundatus* may be dealing with marginal habitats as a result of habitat fragmentation. For the presence of *P. lepidus* in the two patches

habitat quality was not the limiting factor, but this was the lack of opportunities to immigrate into the area, as hypothesized.

The different results obtained for the two species, *O. rotundatus* and *P. lepidus* indicate that the distribution of presence-absence data over habitat patches, as used in incidence functions (Gilpin & Diamond, 1981; Hanski, 1991; 1994), is not always related exclusively to area and isolation, but can be influenced by habitat quality as well. Similar experiments done with spiders on true islands (Schoener, 1986) and butterflies on habitat islands (Harrison, 1989) indicate the existence of empty habitats for invertebrates and thus show that at least in some patches habitat quality is sufficient for reproduction. However, an observation of at least one individual of a new generation following an introduction, as done by Harrison (1989), may not be enough for a conclusion about the suitability of the patch. A comparison of fluctuation in numbers in experimental and natural populations, as was done for the two ground beetle species in chapter 4, is to be preferred for a prediction of long-term persistence of a population.

Genetic variability

After habitat fragmentation the extinction of populations in small patches is determined by four processes: Genetic, demographic, and environmental stochasticity and catastrophes (Shaffer, 1981, 1987). In this thesis the first process has been investigated for two ground beetle species: *A. ericeti* and *P. lepidus*. Due to stochastic processes the genetic variation of subdivided populations may be differentiating. Apart from genetic differences present beforehand, after habitat fragmentation two factors determine the rate and the extent of genetic differentiation among populations: the effective number of locally breeding adults and rate and pattern of gene flow among the separated populations (Wade & McCaughley, 1988). High genetic differentiation between fragmented and small populations and low differentiation between large populations indicates low rates of gene flow between the populations and/or small population size, at least temporarily. The results from chapter 5 show low genetic differentiation between large populations of two ground beetle species with low dispersal ability. Despite their isolated position for about 60 years in small patches, none of the populations

of *A. ericeti* show consistent genetic differentiation. As for this species isolation between populations was absolute (chapter 2), the absence of genetic erosion must probably be due to the continuous presence of a large number of individuals, even in populations in the smallest patches. The genetic variation is probably still showing much of the situation as it was before fragmentation took place. Similar results for insects were found by Baughman et al. (1990) for the checkerspot butterfly. For *P. lepidus* lower genetic variability and considerable population differentiation was found for two populations, one in a very small patch, the other in a patch of intermediate size. As isolation is less stringent for this species (chapter 4), it is difficult to determine whether bottlenecks or founder events are responsible for this result. The ecological information available is limited, but gives no indications that bottleneck situations should be more often expected in *P. lepidus* as compared to *A. ericeti*. Earlier research of presence of both species in the landscape (chapter 2, 3, 4, Vermeulen, 1993) indicates that the most probable explanation for this differentiation is the occurrence, albeit rare, of founder events. Though the effects of founder events are often mentioned (Slatkin, 1977; Maruyama & Kimura, 1980; Wade & McCaughley, 1988; Harrison & Hastings, 1996), not many, well documented, cases for insect populations are known.

Threats for ground beetles

For two heathland ground beetle species genetic erosion could not be considered an immediate threat for the remaining populations in small and isolated patches (chapter 5). When considering the four factors Shaffer (1987) mentions, also demographic stochasticity can be left out. Demographic processes can be expected to be unimportant in relatively large populations (100 individuals or more: Shaffer, 1987; Lande, 1988) and as most ground beetle populations will be larger (e.g. chapter 5), this factor probably is relatively unimportant. A third factor, catastrophes, was not investigated in this thesis, but is often considered as a special case of a fourth factor: environmental stochasticity. Therefore, environmental stochasticity, including catastrophes, can be expected to be the dominant factor

causing extinctions in fragmented habitats. The influence of environmental stochasticity on population dynamics of ground beetle species has been studied for decades by Den Boer (e.g. Den Boer, 1970; 1977; 1981; 1985; 1991; Den Boer & Van Dijk, 1994). This preceding research showed high fluctuations in numbers between successive years in ground beetle populations in small patches, which consequently point to a high risk of extinction (chapter 1).

Conservation of threatened insects

The formation of nature reserves does not only preserve popular and well known plants and animals, but also gives cryptobiotic species with special habitat demands a chance to survive. With the present study it has been shown that nature reserves in the North-East of the Netherlands still contain several highly specialised ground beetle species. At the same time it was shown that several populations of these species in small and isolated habitats are threatened with extinction, mainly due to environmental stochasticity. Global or regional factors, such as atmospheric nitrogen deposition and management of ground water tables, are probably the most important factors which contribute to the extinction of threatened insect populations in the Netherlands (Desender & Turin, 1989), but an analysis of the effect of these factors was largely beyond the scope of this thesis. The results of this thesis, but also the findings about the survival of many threatened species in the 1210 ha large area Dwingelderveld (Van Essen, 1993; Den Boer & Van Dijk, 1994), show that large areas have the best chance to protect threatened species, in particular when overall conditions are temporarily adverse. So expanding present reserves or suitable habitats within present reserves is very valuable for ground beetles. How large isolated ground beetle populations must be, to be safe from extinction is difficult to estimate. According to Boyce (1992) effective population sizes of insects must probably be much larger than the sizes estimated for viable populations of the investigated higher taxa, e.g. birds. It can be inferred from a comparison between species with high and low dispersal ability (chapter 3) that in Drenthe more than 50 ha was necessary for preserving most of the characteristic

ground beetle species for a period of up to 100 years. It is interesting to note that a population of *P. lepidus* with an estimated average field density of 0.06 individuals per square meter (as calculated with data of Van Essen, 1993, using the formula of Baars, 1979a, see chapter 5) at 50 ha comprises perhaps more than 30 thousand individuals, though the effective population size will of course be lower. This indicates that rules like the one that a minimum viable population should have an effective population size of at least 50 or 500 individuals (Franklin 1980) can not be applied to ground beetles. Considering the high fluctuation patterns of many ground beetle species (Den Boer, 1970b; Den Boer, 1991, chapter 2 and 5), it seems to be more reasonable to express minimum viable ground beetle populations in hectares rather than individuals.

Another option for dealing with management of too small and too isolated ground beetle populations is the formation of corridors (Vermeulen, 1995). Corridors, showing features similar to the areas they are connecting, are expected to enhance survival of the connected populations by increasing the immigration rates and providing occasional spots that are suitable for reproduction. The creation of corridors will reduce isolation between separate populations and result in the formation of metapopulations. Populations with high extinction rates, e.g. populations in small patches, can only persist when colonization rates are balancing the extinctions. According to Vermeulen and Opdam (1995) corridors can only be effective for ground beetle populations occurring at distances of less than 1 to 2 km. The results of Vermeulen (1994, 1995) together with results in chapter 5 indicate that for *P. lepidus* corridors are already functional in the landscape. For some species, however, it is almost impossible to create new habitat, e.g. peatmoor for *A. ericeti*. This means that corridors or enlargements of areas can almost never be realized for species like *A. ericeti*. Therefore, remaining populations of these species can best be protected by removal of possible threats to the extant habitats.

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Summary

During the last 100 years the landscape of Drenthe has changed from a continuous heathland into an intensely cultivated landscape with only few remnants of heathland. About 95% of the remaining patches have a limited size of less than 6 ha, but a number of areas exceeding 100 ha are still present (chapter 3). The animal and plant species present in these patchily distributed heathlands are more or less isolated from neighbouring populations. Extinction rates of the inhabiting species of such patches are expected to be inversely related to patch size and immigration rates. In this thesis it was investigated how viable ground beetle populations in these heathland patches are and which processes determine extinction rates of populations.

An example of a ground beetle species which became completely isolated after habitat fragmentation took place is *Agonum ericeti*. This species is, contrary to some ground beetle species, not able to fly and it prefers peat-moor, a nowadays rare habitat. Twenty areas of different sizes were sampled for the presence of *A. ericeti* (chapter 2). An analysis of the data showed that this species was absent from a large number of apparently suitable small patches (in most cases < 5 ha), whereas it was present in all large habitats of about 50 ha or more. An estimated period of between 24 and 66 years of complete isolation had resulted in extinction of almost all small populations. Presently, only two populations of *A. ericeti* are known to occupy small patches, both with an isolation period of about 60 years (chapter 5).

In a large number of heathlands surveys at local sites resulted in the catch of 116 ground beetle species in total (chapter 3). The total number of species present showed no relationship with the total size of the investigated areas. Eurytopic species, i.e. species which occur in both heathland and cultivated areas, did not show a relationship with size of area either. Heathland species, i.e. species with a high preference for heathland, however, showed a positive relationship with area. Their presence ranged from 2 to 11 species per site. A comparison between the presence of heathland species with high and with low dispersal ability showed that a reduction of habitat size mostly affected the latter group. The frequency of

heathland species with low dispersal ability in habitats smaller than 10 ha was 76% lower on average than in areas larger than 100 ha. For heathland species with high dispersal ability this frequency was only 22% lower on average. It was shown that both habitat size and, to a much lesser extent, isolation period determine the presence of heathland species with low dispersal ability. These results indicate that in habitat islands in particular specialised species with a low dispersal ability show a strong species-area relationship, which is mainly explained by area-dependent extinction rates. Other explanations, such as 'a larger area has higher immigration rates' and 'a larger area comprises more habitat diversity' were of less importance in the present study.

Transplant experiments with two heathland species with low dispersal ability, *P. lepidus* and *O. rotundatus*, showed that small and isolated heathland patches can provide suitable localities for reproduction of both species (chapter 4). For *P. lepidus* it was demonstrated that some unoccupied patches were suitable for persistence of populations at least for some time, whereas for *O. rotundatus* this could not be shown. Earlier investigations showed that *P. lepidus* has some opportunities to recolonize habitat patches. Therefore, it is concluded that *P. lepidus* occurs in metapopulations with both continuously (the large ones) and discontinuously (the small and isolated ones) occupied patches.

Two main factors are considered to be the potential determinants of extinction rates in small and isolated populations of ground beetles: environmental and genetic stochasticity. Populations are either expected to become extinct due to a succession of years with unfavourable conditions or genetic variation can be lowered due to random processes affecting gene frequencies in populations. The latter process may be accompanied, among others, by inbreeding depression. The potential occurrence of loss of genetic variation was investigated in fragmented populations of two species by means of allozyme electrophoresis (chapter 5). A study of the genetic variation of populations of *A. ericeti* did not show any lowering of levels of genetic variation due to habitat fragmentation. Apparently the genetic variation has not been much influenced by habitat fragmentation. This is probably due to a continuous presence of at least several hundreds of individuals, even in small habitat patches which have been isolated for about 60 years. A study of *P. lepidus*,

however, did reveal that two populations in small habitat patches had less alleles and were genetically different from the other populations. Occurrence of bottlenecks and founder events can both explain the different level of genetic variation in these two populations. Because *P. lepidus* is able to disperse between habitat patches at low frequencies and *A. ericeti* is not able to do so, it is concluded that founder events are the most likely explanation for the results in the two differing populations of *P. lepidus*.

It is concluded that environmental stochasticity is the most important threat for the survival of small and isolated ground beetle populations (chapter 5 and 6). In small patches population density is fluctuating violently and a succession of unfavourable years can lead to extinction of the populations. To protect populations from this environmental stochasticity the best option is to enlarge habitats where possible (chapter 6). Large areas provide a better chance of heterogeneous habitat conditions, which will diminish the fluctuations of population density. The presence of heathland ground beetles in patches of various sizes showed that specialized species need a habitat of more than 50 ha to have a substantial chance to survive an isolation period of between 25 and 100 year.

A second option to lower the extinction rates of small populations is to reduce the degree of isolation (chapter 6). Corridors, i.e. linear structures of habitat, enhance immigration rates and the formation of metapopulations. Metapopulations have a far better chance of long-term survival than isolated populations, but can only be realized for species whose habitat can be restored or created.

Samenvatting

De afgelopen honderd jaar is het landschap in Drenthe veranderd van een groot aaneengesloten heidelandschap in een intensief bewerkt cultuurlandschap. In dit cultuurlandschap zijn nog maar enkele snippers heide aanwezig. Vaak zijn deze restanten klein, 95 procent is kleiner dan 6 ha (hoofdstuk 3), maar er zijn nog enkele gebieden van meer dan 100 ha aanwezig. De planten- en diersoorten in deze heideterreinen zijn in toenemende mate geïsoleerd geraakt ten opzichte van naburige populaties. Ook zijn de gebieden die zij bewonen sterk verkleind. Op grond van de conclusies uit een groot aantal eerdere onderzoeken mag worden verondersteld dat veel populaties verdwijnen als gevolg van isolatie en verkleining van leefgebieden. Ook kan worden verwacht dat de uitsterfsnelheid van de versnipperde populaties groter zal zijn naarmate er minder immigratie plaatsvindt en de oppervlakte van een bewoond leefgebied kleiner is. Gedurende dit onderzoek werd de levensvatbaarheid van loopkeverpopulaties in heiderestanten bepaald en werden de mogelijke verklaringen voor de waargenomen uitsterfsnelheden onderzocht.

De loopkever *Agonum ericeti* is een goed voorbeeld van een soort waarvan de beschikbaarheid van het leefmilieu, hoogveen, sterk is afgenomen in Drenthe. Omdat *A. ericeti* niet kan vliegen en lopend slechts geringe afstanden kan overbruggen, ontstonden gedurende de eerste helft van deze eeuw versnipperde populaties die van elkaar geïsoleerd waren. Twintig gebieden die geschikt leken als leefgebied werden onderzocht op de aanwezigheid van deze soort (hoofdstuk 2). *A. ericeti* bleek afwezig in bijna alle onderzochte terreinen die kleiner waren dan 5 ha, terwijl de soort aanwezig was in alle gebieden die groter dan 50 ha waren. Het bleek dat bijna alle populaties van kleine gebieden verdwenen waren binnen een periode van tussen 24 en 66 jaar. Momenteel zijn nog slechts twee populaties van *A. ericeti* in kleine gebieden over. Beide hebben een periode van ongeveer 60 jaar isolatie overleefd.

Vervolgens werden de effecten van habitat fragmentatie op veel meer soorten onderzocht. In 32 heideterreinen werden de loopkevers van een beperkt oppervlak geïnventariseerd met behulp van telkens vijf bodemvallen. In totaal werden er 116

soorten gevangen (hoofdstuk 3). Het aantal gevangen soorten per lokatie vertoonde geen verband met het oppervlak van het gehele gebied. Ook voor eurytope soorten, die niet alleen in heideterreinen maar ook in akkers of weilanden voorkomen, kon een dergelijk verband niet worden aangetoond. Soorten met een meer specifieke voorkeur voor heideterreinen, heidesoorten, vertoonden wel een positief verband met het oppervlak van het gehele gebied. Hun aanwezigheid varieerde van 2 tot 11 soorten per lokatie. Het bleek dat zich slecht verbreidende soorten een veel sterker verband vertoonden met het totale oppervlak van een gebied dan zich goed verbreidende soorten. Zich slecht verbreidende heidesoorten bleken in kleine terreinen (< 10 ha) met gemiddeld 76 procent te zijn afgenomen ten opzichte van grote terreinen (> 100 ha). Voor zich goed verbreidende heidesoorten bleek deze afname gemiddeld slechts 22 procent. Er kon worden aangetoond dat zowel het oppervlak als, zij het in mindere mate, de duur van isolatie de aanwezigheid van zich slecht verbreidende heidesoorten bepalen. Hieruit blijkt dat in een versnipperd landschap het voorkomen van met name gespecialiseerde soorten met een slecht verbreidingsvermogen gerelateerd is aan oppervlak van leefgebied. De verklaring voor dit verschijnsel is dat de uitsterfsnelheid van soorten vooral afhankelijk is van het bewoonde oppervlak. Andere mogelijke verklaringen zoals 'een groter oppervlak heeft een grotere kans op immigranten' en 'een groter oppervlak bestaat uit een grotere verscheidenheid aan leefmilieus' bleken in dit onderzoek minder van belang.

Met twee loopkeversoorten zijn transplantatie experimenten uitgevoerd, namelijk *Pterostichus lepidus* and *Olisthopus rotundatus* (hoofdstuk 4). Beide zijn heidesoorten met een gering verbreidingsvermogen. Met behulp van deze experimenten kon worden aangetoond dat kleine en geïsoleerde heideterreinen geschikte voortplantingsgebieden kunnen vormen voor beide soorten. Ook werd aangetoond dat ondanks de eerdere afwezigheid van *P. lepidus* van sommige van deze heideterreintjes, deze soort wel in staat is om zich daar enkele jaren te handhaven. Eerder onderzoek toonde al aan dat er voor *P. lepidus* beperkte mogelijkheden zijn om op natuurlijke wijze gebieden te herkoloniseren. Hierdoor kan worden geconcludeerd dat *P. lepidus* in Drenthe voorkomt in een complex van ruimtelijk gescheiden populaties die onderling individuen uitwisselen: een

zogenaamde metapopulatie. Deze metapopulatie bestaat deels uit populaties die hun gebieden permanent bewonen, de grote populaties, en deels uit populaties die afwisselend uitsterven en herkoloniseren, de kleine populaties. De metapopulatie structuur van *O. rotundatus* kon niet worden aangetoond.

Twee processen komen in aanmerking als belangrijkste veroorzakers van het uitsterven van loopkevers in kleine geïsoleerde terreintjes: omgevings- en genetische stochasticiteit. Omgevingsstochasticiteit is het op grond van toeval ontstaan van gunstige of ongunstige omstandigheden voor overleving en voortplanting van individuen. Bij genetische stochasticiteit zijn er toevallige fluctuaties in de genetische samenstelling van een populatie. Deze fluctuaties nemen toe naarmate een populatie kleiner wordt, wat kan resulteren in een afname van de genetische variatie. De mogelijke bijdrage van deze laatste factor aan het uitsterven van kleine populaties is onderzocht voor twee soorten: *A. ericeti* en *P. lepidus* (hoofdstuk 5). Van beide soorten werden bepaalde eiwitten van een aantal populaties onderzocht op genetische varianten. Bij *A. ericeti* bleken de populaties van grote en kleine terreinen grotendeels dezelfde genetische samenstelling te vertonen. Waarschijnlijk hebben zelfs de populaties van de kleinere terreinen permanent bestaan uit minstens enkele honderden individuen gedurende de periode na het ontstaan van de isolatie, ongeveer 60 jaar geleden. Bij *P. lepidus* bleek dat twee populaties van kleine terreinen minder variatie vertoonden en genetisch verschilden van de andere onderzochte populaties. Twee processen kunnen dit verschijnsel verklaren: (1) de populatie heeft in het verleden enige tijd uit een klein aantal individuen bestaan of (2) de populatie is gevestigd door een klein aantal individuen. In ieder geval toont dit verschijnsel aan dat immigratie van individuen niet frequent plaats vindt. Een belangrijk verschil tussen *A. ericeti* en *P. lepidus* is dat in Drenthe alleen de laatste de mogelijkheid heeft om gebieden te herkoloniseren, maar ook dit gebeurt zelden. Om deze reden wordt het opnieuw vestigen van populaties door een gering aantal individuen van *P. lepidus* beschouwd als de meest waarschijnlijke verklaring voor de gevonden verschillen in omvang en structuur van de genetische variatie tussen beide soorten.

Uit dit onderzoek kan worden geconcludeerd dat omgevingsstochasticiteit de belangrijkste bedreiging vormt voor het langdurig voortbestaan van versnipperde

loopkeverpopulaties (hoofdstuk 5 en 6). De populatiegrootte van loopkevers fluctueert sterk in kleine leefgebieden. Dit betekent dat een reeks van ongunstige jaren al snel kan leiden tot het uitsterven van de betreffende populatie. Populaties kunnen het beste worden beschermd tegen deze bedreiging door een vergroting van het beschikbare leefgebied (hoofdstuk 6). Grote leefgebieden zijn vaak heterogeen. Hierdoor zullen gunstige en ongunstige omstandigheden elkaar niet alleen afwisselen in de tijd, maar ook in de ruimte. Dit verkleint het risico van uitsterven. De aan- en afwezigheid van soorten heideloopkevers in terreinen van verschillende grootte toonden aan dat een populatie minstens 50 ha nodig heeft om een aanzienlijke kans te hebben een periode van isolatie van 25 - 100 jaar te overleven.

Een andere mogelijkheid om uitsterfsnelheden van kleine populaties te verlagen is het stimuleren van immigratie (hoofdstuk 6). Dit kan met behulp van corridors, lineaire stroken leefgebied die twee gebieden met elkaar verbinden. Wegbermen zouden zo'n functie kunnen vervullen. Door het aanleggen van corridors worden populaties met elkaar verbonden, wat resulteert in een metapopulatie. Metapopulaties hebben een veel lagere uitsterfsnelheid dan geïsoleerde populaties. Deze mogelijkheid is echter alleen aanwezig voor die soorten waarvoor het mogelijk is om het leefmilieu te herstellen of nieuwe leefmilieus te creëren.

Curriculum vitae

Henk de Vries werd op 2 februari 1963 geboren op een boerderij in Winsum (Gr.). Hij behaalde in 1982 zijn v.w.o.-diploma aan het Zernike College te Groningen, waarna hij in Wageningen biologie ging studeren aan de Landbouwniversiteit. Daar specialiseerde hij zich in Natuurbeheer en deed tijdens zijn doctoraalfase afstudeervakken in de richtingen Aquatische ecologie, Dieroecologie en Toxicologie. Bij het bureau Ontgrondingen van het Provinciehuis Noord-Brabant heeft hij als stageopdracht een studie verricht naar de mogelijkheden voor natuurontwikkeling bij zandwinplassen. In 1989 ontving hij zijn bul en startte zijn werk aan loopkevers bij het Biologisch Station te Wijster. De eerste jaren werkte hij voor de vervulling van zijn vervangende dienstplicht, daarna als AIO van de vakgroep Natuurbeheer en vanaf 1994 als gastmedewerker. Dit proefschrift is het resultaat van deze werkzaamheden. Vanaf 1995 zet hij zich in, als part-time vrijwilliger bij de Milieufederatie Flevoland, voor de realisering van een afdeling Landschapsbeheer. In februari 1994 kregen hij en zijn vriendin Simone de Jong een dochter, Lana, en in april 1996 een zoon, Wiebe.

Appendix

Ground beetle species of two ecological groups collected in this study: eurytopic species and heathland species. Heathland species with high powers of dispersal are indicated by *.

Eurytopic species	Heathland species
<i>Harpalus latus</i>	<i>Bradycellus ruficollis</i> *
<i>Notiophilus substriatus</i>	<i>Trichocellus cognatus</i> *
<i>Broscus cephalotus</i>	<i>Cicindela campestris</i> *
<i>Harpalus anxius</i>	<i>Pterostichus diligens</i> *
<i>Carabus granulatus</i>	<i>Cymindis vaporariorum</i> *
<i>Pterostichus versicolor</i>	<i>Bembidion humerale</i>
<i>Calathus erratus</i>	<i>Miscodera arctica</i>
<i>Amara apricaria</i>	<i>Harpalus solitarius</i>
<i>Syntomus foveatus</i>	<i>Amara equestris</i>
<i>Bembidion lampros</i>	<i>Anisodactylus nemorivagus</i>
<i>Agonum obscurum</i>	<i>Amara infima</i>
<i>Pterostichus vernalis</i>	<i>Olisthopus rotundatus</i>
<i>Calathus melanocephalus</i>	<i>Carabus arvensis</i>
<i>Calathus fuscipes</i>	<i>Carabus nitens</i>
<i>Harpalus rufipes</i>	<i>Pterostichus lepidus</i>
<i>Amara communis</i>	<i>Cymindis humeralis</i>
<i>Nebria brevicollis</i>	<i>Cymindis macularis</i>
	<i>Agonum ericeti</i>
	<i>Bembidion nigricorne</i>

