Ann. Zool. Fennici 33: 77–84
Helsinki 14 June 1996

ISSN 0003-455X

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

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Received 7 September 1995, accepted 8 February 1996

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.

1. 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 (Turin & den Boer 1988, Desender & Turin 1989, De Vries & den Boer 1990, De Vries 1994). 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 (De Vries 1994). 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 (Schoener 1986, Harrison 1989). 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).

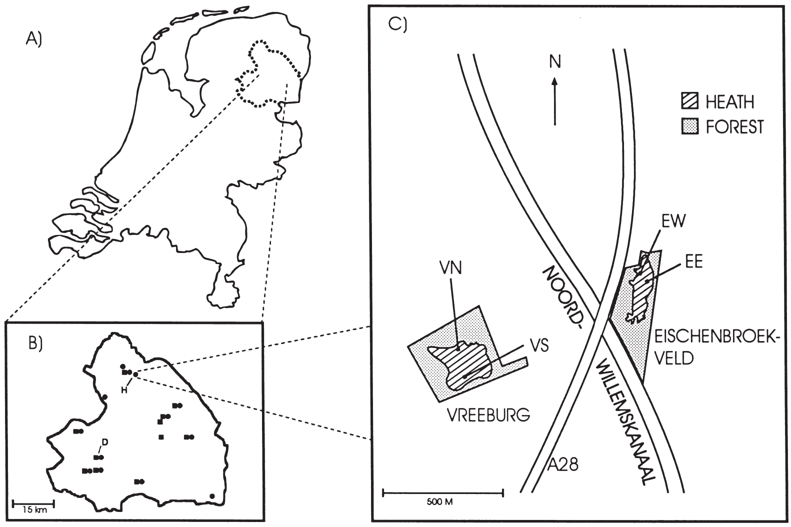

Fig. 1A–C. — A: The area within the dashed line represents the province of Drenthe in the Netherlands. — B: The locations of Heideheim (H), Dwingelderveld (D) and catches of *P. lepidus* (■) and *O. rotundatus* (●) in 1990, 1991 or 1992. — C: The location of the four enclosures (VN, VS, EW, and EE) in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

In this study the suitability of two heathland patches for two ground beetle species, *P. lepidus* and *O. 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 (De Vries 1994). 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.

2. Materials and methods

2.1. 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 (Den Boer & den Boer-Daanje 1990, Paarmann 1990). Tenerals 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).

O. rotundatus reproduces in autumn, mainly September and October and hibernates as larvae. Tenerals 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 pitfalls. *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.

2.2. 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 channel 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 1 600 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.

2.3. 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 m^2 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.

2.4. 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 25 cm 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*.

3. Results

3.1. 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.

3.2. 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 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.

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
		P. lepidus		
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
		O. rotundatus		
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

3.3. 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 100 m 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*.

3.4. 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

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	*P. lepidus*				*O. rotundatus*			
	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

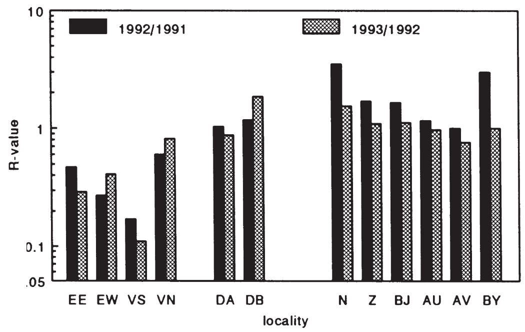

Fig. 2. The *R*-values $(N_t + 1)/(N_{t-1} + 1)$ in 1991–1992 and 1992–1993 of *P. lepidus* in six experimental enclosures, with the species being present beforehand in DA and DB, and at six permanent sampled sites (N, Z, BJ, AU, AV and BY).

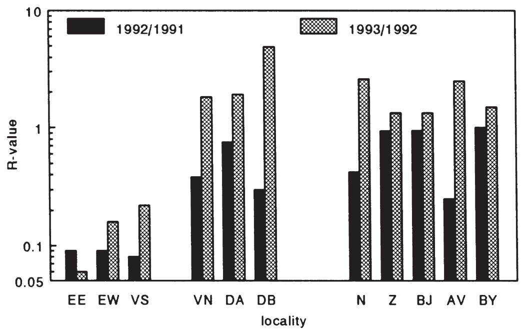

Fig. 3. The *R*-values $(N_t + 1)/(N_{t-1} + 1)$ in 1991–1992 and 1992–1993 of *O. rotundatus* in six experimental enclosures, with the species being present beforehand in DA, DB and VN, and at five permanent sampled sites (N, Z, BJ, AV and BY).

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.

4. Discussion

4.1. 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 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 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.

4.2. 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).

4.3. 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.

4.4. 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 1990). Using these intervals VS can be considered as an unsuitable location for both species, whereas EE and EW were unsuitable only for *O. rotundatus*.

4.5. 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*.

4.6. 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 (De Vries 1994). The smaller areas will probably have temporary occupancy of this species, whereas in larger areas extinction probabilities are much reduced (De Vries 1994). 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.

Acknowledgements. I am very grateful to the owners of the research areas, Stichting 'Het Drentse Landschap' and the state forestry department, for permitting me to place the enclosures. Theo van Dijk and Arnold Spee kindly let me use their sampling data and helped me with the erection of the enclosures. I also would like to thank Theo van Dijk, Piet den Boer, Lijbert Brussaard, and Jari Niemelä for improving the manuscript, and Martin Luff and Paul Stewart for improving the English. The Beijerinck-Popping Fonds partly financed my travel expenses.

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