Survival of the Black bog ant (*Formica transkaucasica* Nasanov) in relation to the fragmentation of its habitat

Abraham A. Mabelis[*] and J.P. Chardon
Alterra, Green World Research, Centre Landscape, P.O. Box 47, 6700 AA Wageningen, The Netherlands;
*Author for correspondence (e-mail: bram.mabelis@wur.nl; phone: +31 317 47 79 44)

Abstract

In the past, extensive areas in Drenthe (The Netherlands) were covered by peat bogs and wet heath lands, but nowadays only relatively small fragments are left. During the second half of the 20th century the quality of these fragments decreased, due to lowering of the water table and the input of nutrients. These factors will have a negative effect on the survival of species which are adapted to these stable type of biotopes, like the Black bog ant. The distribution pattern was analysed within a study area of 750 km^2, in order to find out if this species will survive in a landscape where its habitat is severely fragmented. Using multiple logistic regression analysis it appears that size and quality of the habitat patches, as well as openness of the environment, contribute significantly to patch-occupancy. No correlation was found between the probability of a patch being occupied and its distance to the nearest occupied patch. It appears that the spatial cohesion of local populations by means of flying queens is weak or absent on the scale of the study area. Only in parts of the area, where the distance between habitat patches is less than 3 km in open field, a habitat network may still exist. However, with ongoing habitat loss a threshold will be passed and the species will ultimately become extinct.

Introduction

Habitat fragmentation is a major cause of the loss of species in landscapes that have been modified by man. The creation of a network of natural elements within man-made landscapes will be crucial for a sustainable conservation of biodiversity. However, tools are needed for detecting effects of landscape change on the survival probability of species. Most publications about the effect of habitat fragmentation on the survival probability of animal species deal with vertebrates. The results of these studies cannot be extrapolated to invertebrate species, because the latter generally will have a larger population size and a higher susceptibility to environmental fluctuations. Studies about the effect of habitat fragmentation on invertebrates are relatively scarce, ants in particular (Mabelis 1992, 1994; Mabelis and Korczyńska 2001).

Species differ in their response to changes in landscape pattern, due to different habitat requirements and dispersal capacities. Species with a poor dispersal capacity are generally tied to a stable environment and will be more susceptible to habitat fragmentation then species which have a good dispersal capacity. Habitat fragmentation implies that the average size of habitat patches will

decrease as well as their connectivity. A decrease of patch areas may have consequences for the size of the local populations and hence for their extinction probability, while a decrease in patch connectivity may have consequences for the re-colonization chance of empty habitat patches. For species with a poor dispersal capacity, habitat patches may become so isolated that patch occupancy is only related to patch area and not to the position to other patches. In such a landscape the species will not have a metapopulation structure, i.e. a system of spatially separated local populations between which exchange of individuals takes place to some extent (Hanski 1994a; Verboom et al. 1991, 1993, among others). Such a situation was found for the stenotopic brachypterous carabid beetle *Agonum ericeti*, which lives in peat bogs and peaty heath lands (De Vries and Den Boer 1990; De Vries et al. 1996). Until the 17th century these biotopes covered extensive areas of the Dutch province of Drenthe, but nowadays only fragments are left, due to reclamation activities, mainly in the first half of the 20th century (Brouwer 1968). Consequently, habitat patches of this species have become so isolated from each other that re-colonization of a patch after extinction of its population is no longer possible.

The question arises if a stenotopic species with flight ability will have a much better chance to survive in a landscape where its habitat is fragmented. The Black bog ant (*Formica transkaucasica*) was chosen for this case study, because this species is restricted to the same habitat as *A. ericeti*, but is able to disperse by means of flying queens, in contrast to the brachypterous beetle, which cannot fly.

The Black bog ant is a boreal-alpine species, occurring in temperate and cold zones of Europe and Asia (Stitz 1939; Seifert 1996). The Netherlands is at the border of its distributional range, which may imply a lower reproductive rate and a poorer dispersal capacity than in the centre (Hengeveld 1990). Consequently it may be more vulnerable to habitat fragmentation than in the centre of its distributional range. Its distribution area in the southern part of the Netherlands seems to be shrinking (van Loon and Mabelis 1996). Nowadays the species is most common in the study area (Figure 1). In Germany and England the Black bog ant is assigned to the category 'Endangered' (Blab et al. 1984; Else and Spooner

1987) and in the IUCN Red List of Threatened Animals (1986) to the category 'Indeterminate', which means that the species is known to be 'Endangered', 'Vulnerable' or 'Rare', but that there is lack of information to say which of the three categories is appropriate.

Black bog ants are not so easy to find in the field, because a great deal of the food is found under the soil surface, namely fungi (Bönner 1915; Skwarra 1929) and excrements of root aphids (on *Erica, Molinia* and *Eriophorum*), although some worker ants forage also above ground on small invertebrates. Nest populations of the Black bog ant are generally small: Bönner (1915) often found only a few hundred workers in a nest, although sometimes more, up to 2000 workers (Bönner 1914; Skwarra 1929). A fair proportion of the nests may be monogynous (Pamilo 1982a), but some nest populations will adopt more queens, up to 6 (Bönner 1914; Skwarra 1929), 15 (Donisthorpe 1915) or 27 (Pamilo 1982b). In a Finnish peat bog the average number of queens per nest ($n = 35$) was 4.5 (Pamilo 1982b). It is assumed that there will be rarely more than 10 queens in a nest.

It is not known if all the queens in a nest take part in the reproduction. Functional monogyny, in which one queen suppresses the fertility of other queens, cannot be excluded, as functionally monogynous nests are found occasionally in facultative polygynous species (Heinze 1993). The advantage for the dominant queen will be that if she dies, a related queen can take over her task, increasing the life-time expectancy of the colony. Another advantage of adopting daughter queens in a nest is that it opens the possibility to disperse there own genes by means of budding, i.e. building daughter nests at some distance of the mother nest, forming a polydomous colony.

Adoption of young daughter queens seems to be the rule for species which are living exclusively in a stable but patchily distributed habitat, like *Formica uralensis*, which also inhabits peat bogs (Rosengren and Pamilo 1983; Rosengren 1985). A single nest population of *F. transkaucasica* can stand unfavourable conditions to some extent, but a group of interacting nest populations will be better off, as they can cooperate and eventually fuse as long as there is regular exchange of workers and brood between the nests. Such exchange will decrease the extinction risk of the nest
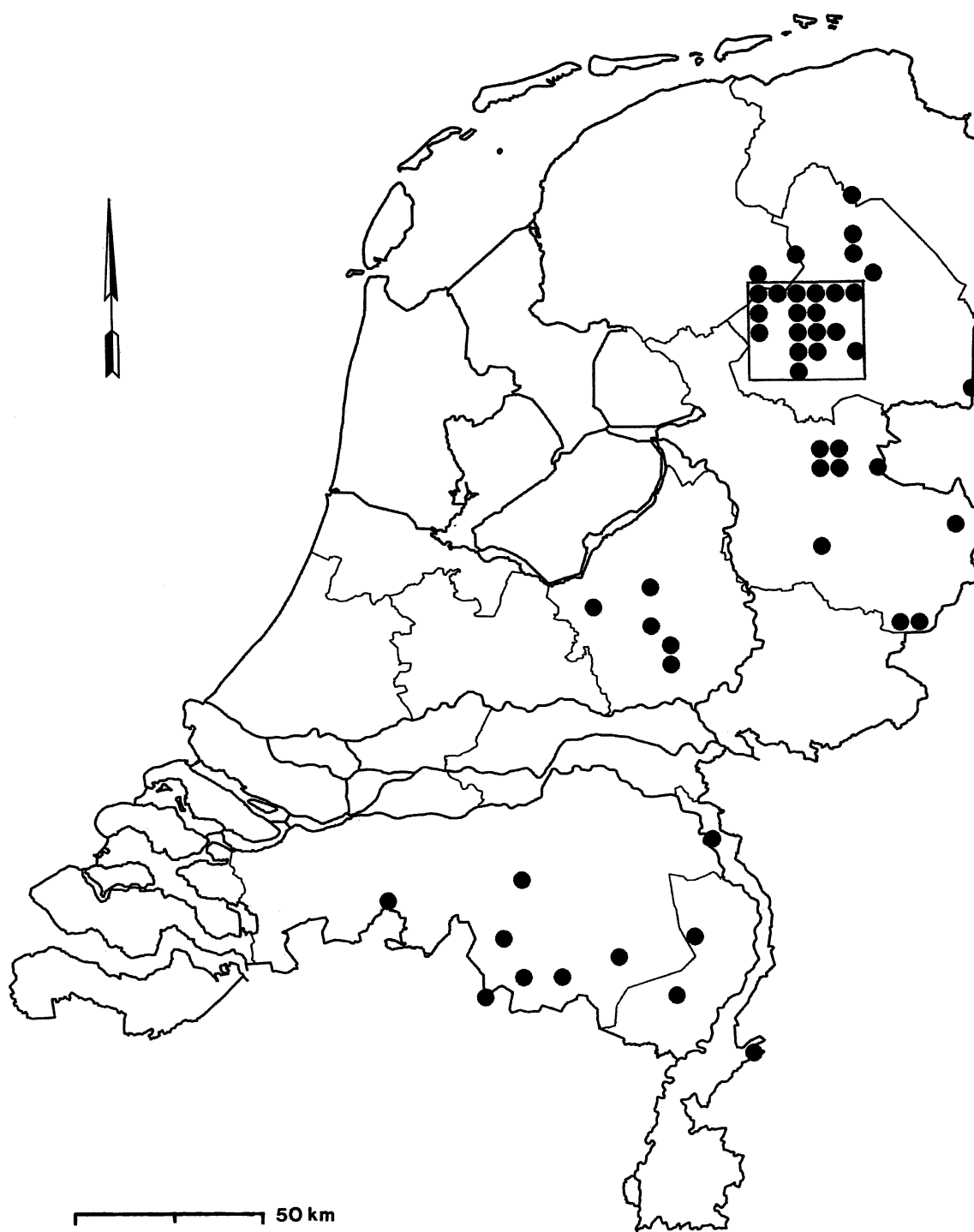
Figure 1. Distribution of the Black bog ant in The Netherlands (data collected after 1970); the study area is outlined.

populations. Risky dispersal and low probability of founding a new colony may be key factors for the development of polygyny (Wilson 1963; Holldobler and Wilson 1977; Rosengren et al. 1993; Herbers 1993). So, polygyny may be favoured by habitat fragmentation.

The aim of the investigation is to assess the regional persistence of the Black bog ant on the basis of the occupancy and connectivity of habitat patches. The hypothesis that patch occupancy will be positively correlated with patch area and patch quality and negatively with isolation of the patches was tested. Finally we discuss the implication of the findings for the conservation of the species.

Study area and methods

The study area covers 750 km^2 in the south-west part of the province of Drenthe (Figure 1). In the beginning of the last century this area was largely covered by peat bog and peaty heath, the habitat of the Black bog ant, but nowadays only relatively small and isolated areas with these biotopes are left (Figure 2). The largest one (Dwingeloo heath) is about 560 ha and has a National Park status. In the past the habitat of the Black bog ant used to be stable, but during the last part of the 20th century the quality became worse, due to lowering of the water table, increased nitrogen input and cutting sods more intensively in order to counteract domination of grasses.

On the basis of the vegetation map of Drenthe (Dijkstra et al. 1992) 220 areas were selected where vegetation types with potential habitat occurred, i.e. peat bog and peaty heath land, dominated by *Erica tetralix* and/or *Molinia caerulea*.

The areas were visited in the period 1994–1995 and judged on its suitability for the Black bog ant on the basis of the vegetation, the availability of suitable nesting sites and the capacity of the soil to keep moisture. The following sites were judged as suitable: a relatively dry place in a thick *Sphagnum* cover, an old and peaty *Molinia* tussock, the peaty base of an old *Erica* plant or a naked site of peaty soil near a potential food source (root aphids), as long as the nest sites are not occupied by other ant species. The criteria to judge habitat suitability of areas are based on own experience in other peat bog areas in the Netherlands, as well as in other European countries. Habitat quality of suitable areas was classified as optimal, sub-optimal or marginal:
- Optimal: good soil capacity to keep moisture, many suitable nesting sites (> 50/h searching time), presence of characteristic plant species: for peat bogs (*S. magellanicum*, *S. papillosum*, *S. rubellum*, *Vaccinium oxycoccus*, *Andromeda*
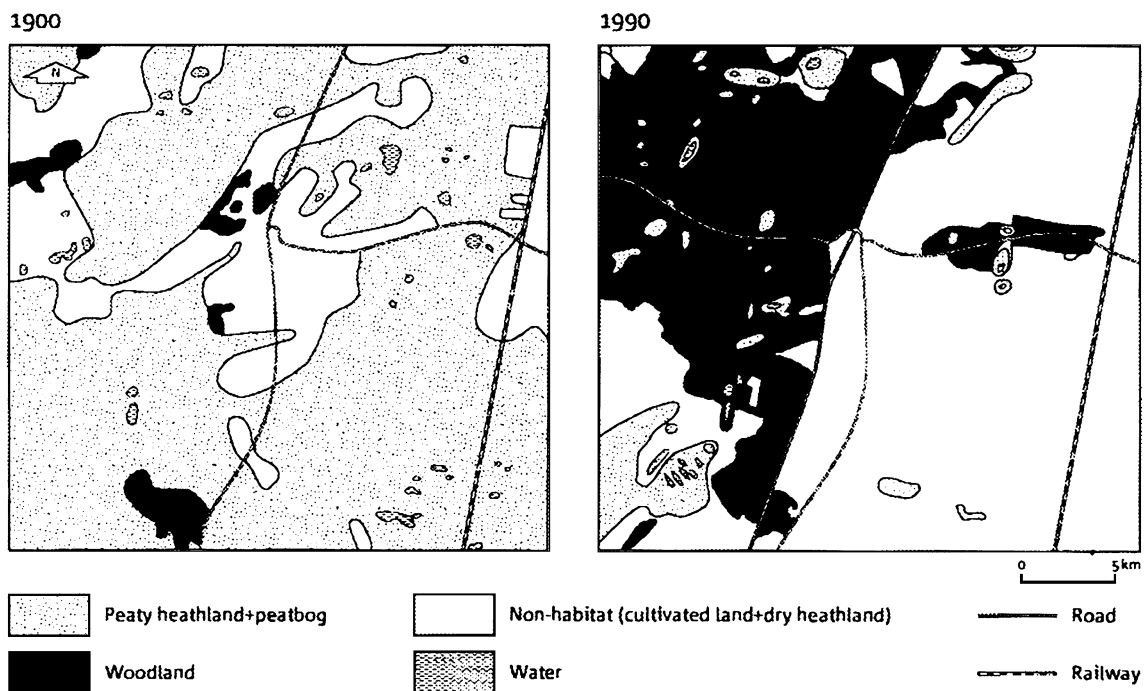

Figure 2. Fragmentation of Black bog ant habitat in part of the study area (period: 1900–1990). Source: Topographic Service The Netherlands.

polifolia, *Drosera* species, among others) and for wet heath lands (*S. compactum*, *S. tenellum*, *S. molle*, *Rhynchospora* species, *Drosera* species, *Juncus squarrossus*, among others).

- Sub-optimal: moderate soil capacity to keep moisture, less suitable nesting sites (10–50/h searching time), presence of plant species which are indicative for eutrophication or desiccation (respectively *Juncus effusus*, *Phragmites australis*, *Typha latifolia*, among others and *Rubus fruticosus*, *Deschampsia flexuosa*, young *Betula* and/ or *Pinus* trees, among others).

- Marginal: poor soil capacity to keep moisture, only a few suitable nesting sites (< 10/h searching time), clear indication of eutrophication and/ or desiccation.

All suitable patches were mapped with Auto-CAD into a geographic information system Arc-View (ESRI 1996). Neighbouring habitat patches within 100m, that were separated by a vegetation with a poor habitat quality, were considered one habitat patch and therefore clustered, assuming that contact between worker ants of the local populations was still possible in the recent past.

Next, all habitat patches were checked for the presence of the Black bog ant. A small stab-shovel appeared to be useful for checking the occupancy of nesting sites, as the workers are often not walking over the nest surface. Searching time was correlated with the size of the area, although relatively more time was spent in areas where no Black bog ants were found.

In order to find out what variables are most important for the present distribution of the Black bog ant, the presence/absence data were related to the area, habitat quality (3 levels) and isolation of the habitat patches (see Table 1). The following variables for isolation were used: the distance to the nearest habitat patch, the distance to the nearest occupied patch, the average distance to the three nearest patches, and the distance to the core area with the main source population. As a qualitative isolation variable the location of a patch with respect to woodland was used (3 levels: outside, at the border and inside woodland), because woodland is supposed to hinder dispersal of flying ant queens. Nest density was not taken into account as a variable, as it varied not only considerable between occupied habitat patches, but also within habitat patches.

The effects of these variables were analysed using logistic regression (Jongman et al. 1995), with the statistical programme Genstat (Genstat 5 Committee 1993). In order to test if isolation variables contribute significantly to the regression model in addition to habitat area and quality a two-step regression method was used (Fahrig et al. 1995; Vos and Stumpel 1996; Vos and Chardon 1998). Differences between the habitat patches in area and quality were accounted for by entering these variables in the model first (step 1). To investigate if isolation could explain part of the occupancy of the Black bog ant, the regression model was extended with one isolation variable

Table 1. Summary of the variables used in the regression analysis; mean and standard deviation (SD) are given for quantitative variables.

Variables	Occupied patches	Unoccupied patches
Area		
Mean area habitat patch (ha)[a]	5.63 ± 6.4	1.47 ± 2.0
Habitat quality (qualitative: 3 levels):		
– # optimal patches	14 (30%)	33 (70%)
– # suboptimal patches	5 (9%)	50 (91%)
– # marginal patches	2 (4%)	45 (96%)
Isolation		
Location with respect to woodland (qualitative: 3 levels):		
– # patches outside woodland	12 (22%)	43 (78%)
– # patches bordering woodland	4 (19%)	17 (81%)
– # patches inside woodland	5 (7%)	68 (93%)
Mean distance to source population (m)[a]	8960 ± 4392	10555 ± 5304
Mean distance to nearest habitat patch (m)[a]	652 ± 557	517 ± 474
Mean distance to nearest occupied habitat patch (m)[a]	2350 ± 1689	1974 ± 1895
Mean distance to the 3 nearest habitat patches (m)[a]	967 ± 686	862 ± 627

[a]Because of skewed distribution logtransformation was used

each time (step 2). In addition, the effect of the occurence of a potential competitor, i.e. *F. sanguinea*, on the presence of *F. transkaucasica was* tested in the same way.

Results

Out of 220 wet heath lands and peat bogs that were visited, 149 were judged as suitable for the Black bog ant. These habitat patches were classified as optimal (47), sub-optimal (55) and marginal (47). The Black bog ant was present in 33% of the optimal patches, 7% of the sub-optimal patches, and 4% of the marginal patches, occurring in a total of 22 (15%) sites.

Patch size in the study area ranges from 0.1 to 26.5 ha (average: 20.5 ha). Results from regression analysis showed that there was an increasing probability of Black bog ants occurrence with increasing patch area (Table 2, Figure 3). Addition of the habitat quality variable resulted in a significant increase of the explained deviance ($p < 0.001$, χ^2-test). Both variables indicate that size and quality of the patch are relevant for the presence of the Black bog ant.

Nest density varied considerably, due to habitat heterogeneity. It was lowest in desiccated areas where litter accumulated and in areas where micro-relief was lacking. In an *Erica–Molinia* vegetation
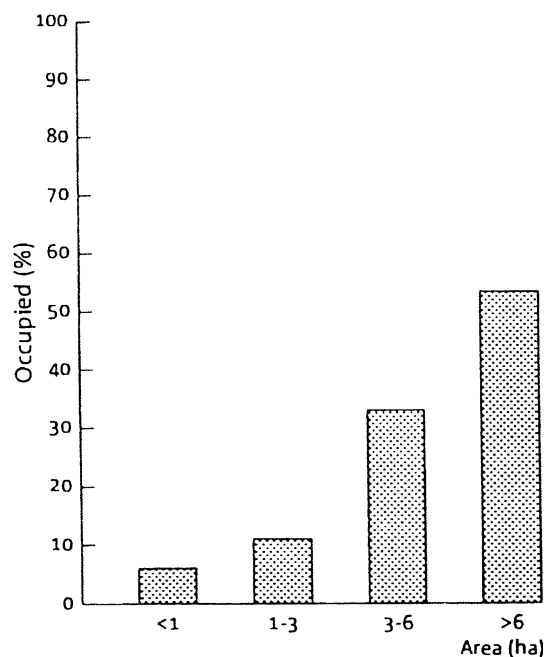

Figure 3. Percentage occupancy of different-sized habitat patches by the Black bog ant.

(on Dwingeloo heath) nest density varied from 1 to 30 nests per 100 m. The mean nest density of 500 small random plots (a circle with 1 m radius) was 7 nests per 100 m. Nearly half of the nests within this vegetation type were built on a *Molinia*

Table 2. Results of the logistic regression on Black bog ant presence–absence data.

|	df	Sign	Deviance	p-value χ^2-test	R^2_{adj} of the total model (%)
Patch area	1	+	23.23	< 0.001	19
Addition of Habitat quality	2	+	13.91	< 0.001	31
marginal (reference model)					
suboptimal (param. estimate = +0.50)					
optimal (param. estimate = +2.35)					
Residual deviance	145		84.05		
Total deviance	148		121.19		
Addition of :					
Presence of F. sanguinea	1	−		0.064 (ns)	
Addition of isolation variables					
Location with respect to woodland:	2	−		0.061 (ns)	
outside (reference model)					
bordering (param. estimate = −0.74)					
inside (param. estimate = −1.57)					
Mean distance to source population	1	−		0.54 (ns)	
Mean distance to nearest habitat patch	1	+		0.40 (ns)	
Mean distance to nearest occupied habitat p.	1	+		0.09 (ns)	
Mean distance to 3 nearest habitat patches	1	+		0.63 (ns)	
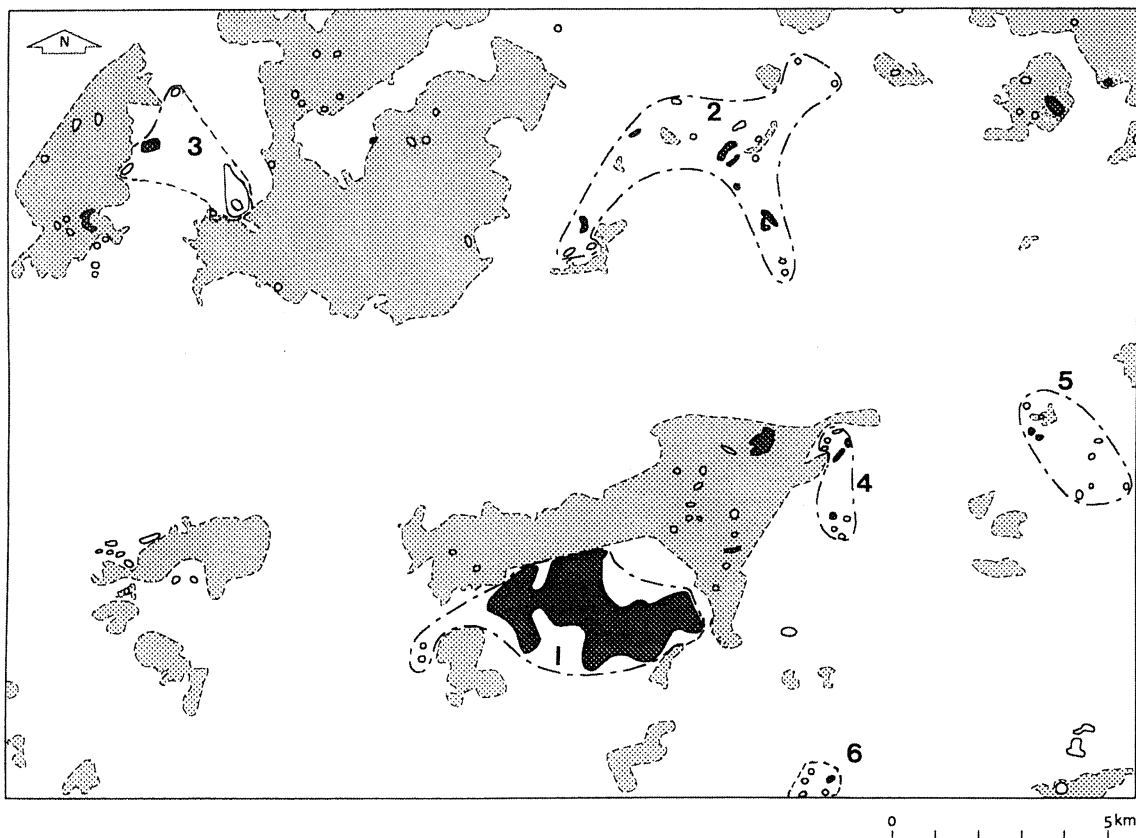
Figure 4. Occupancy of habitat patches by the Black bog ant in part of the investigated area. The largest habitat area (in the middle, below the centre) is inhabited by several local populations. Habitat networks of which at least one of the patches are occupied by the Black bog ant are numbered and encircled by a dashed line. Black habitat patch: occupied, white habitat patch: not occupied, grey: woodland, matrix (white): non habitat.

tussock (45%) and nearly half of them in the peaty soil beneath an old *Erica* plant (44%). In peatbogs all nests were built on the *Sphagnum* cover. As building material small pieces of *Molinia*, *Erica* or *Sphagnum* were used.

Figure 4 shows the occupancy of habitat patches within part of the study area. The biggest cluster of habitat patches (Dwingeloo heath) may function as a source of young ant queens for habitat patches in its surroundings. Most of the habitat patches situated within a distance of 3 km from the core area are surrounded by woodland and only one of them is occupied by the Black bog ant (Figure 4). Overall, about half of the habitat patches ($n = 73$) are surrounded by woodland, and hardly 7% ($n = 5$) of these patches are occupied by the Black bog ant, compared with 22% of patches in open field ($n = 12$). It seems that the probability of occupancy of a habitat patch which is surrounded by woodland is less than of a habitat patch in open field.

Adding each of the isolation variables separately as third term to the model did not result in further significant explanation of the total model deviance, although the variable 'location with respect to woodland' comes close with a *p*-value of 0.061 (Table 2). The negative sign of this variable is in accordance with the increasing unsuitability of the levels.

Competition for nesting sites with other ant species may hamper the establishment of new colonies. The minimum habitat size in the study area (0.1 ha) is large enough for establishing colonies, but competitive exclusion of *F. transkaucasica* by a territorial ant species is imaginable in such small areas (e.g. see: Vepsäläinen and Pisarski 1982; Boomsma et al. 1987; Savolainen and Vepsäläinen 1988). This is most likely in small habitat patches

where *F. sanguinea* is occurring. This slave-making species, which rob pupae from nests of *F. transkaucasica* and *F. fusca*, was found in a quarter of the habitat patches of the Black bog ant, but always in a very low density: one or a few nests per habitat patch, while at least tens of nests of *F. transkaucasica* were found in occupied patches. *F. sanguinea* occurred only two times together with *F. transkaucasica* in the same area. It concerned in both cases a mixed nest population *F. sanguinea – F. transkaucasica*. Mixed nest populations of *F. sanguinea–F. fusca* were found more often (12×), as both species prefer dryer places than *F. transkaucasica*. Addition of the presence of *F. sanguinea* as a variable to the regression model did not contribute significantly to the explanation of the variance (Table 2). In other words: *F. sanguinea* does not play a significant role in the occupation of habitat patches by *F. transkaucasica*. The negative sign is in accordance with the finding that the habitat of the species overlaps only for a small part: *F. sanguinea* occurs more often in dryer places, which are less suitable for *F. transkaucasica*.

Discussion

The regional survival probability of a species depends on the ratio between the extinction rate of local populations and the colonization rate of empty habitat patches. The extinction rate of local populations depends mainly on habitat size and quality, while the colonization rate depends for a great deal on habitat connectivity, i.e. the configuration of empty habitat patches in relation to occupied ones. These factors will be discussed successively.

Habitat size

The hypothesis that patch occupancy of *F. transkaucasica* will be positively correlated with patch area is supported by the result of the regression analysis (Table 2). Generally the size of a local population (number of nests) increases with the size of a habitat patch. Consequently, the extinction probability of a local population of *F. transkaucasica* will be smaller the larger the habitat patch will be.

An area of 100 m optimal habitat appears to be sufficient for a nest population of the Black bog ant. However, its survival chance will be greater if more habitat is available at walking distance, as it will increase the possibility to adapt to changes in the environment by moving the whole nest population to a better site and it will give the possibility to build daughter nests by means of budding (Figure 5a). Such a polydomous colony can be considered a multipartite population, i.e. an interacting group of subpopulations (i.e. nest populations), which can gradually merge into one another (Den Boer 1977; Andrewartha and Birch 1954). Due to environmental heterogeneity, such subpopulations may fluctuate asynchronously, which gives the local population a better chance to survive (Den Boer 1981). Consequently, the extinction chance of a group of interacting nest populations (as in a polydomous colony) will be lower than that of an isolated nest population, as was found in red wood ants (Mabelis 1986; Mabelis and Korczyńska 2001).

So, interacting nest populations will reduce the probability to become extinct. However, contact between mother and daughter populations will become less as workers of one of the nests will move the whole nest population to a more remote nesting place. Removals in autumn by means of transport by nestmates to hibernation sites, as was observed in *F. uralensis* (Rosengren and Pamilo 1983), are not known from *F. transkaucasica*, but we observed that Black bog ants remove rather quickly after disturbance (see also Bönner 1915). A decrease of contact between nest populations may lead to alienation of colony odour and hence to a switch from cooperative to competitive behaviour, as was found in the polygynous *Formica polyctena* (Mabelis 1979). However, this was not observed in the Black bog ant.

A polydomous colony of the Black bog ant needs at a rough estimate at least 0.5 ha optimal habitat. However, in the field, where optimal habitat is generally mixed with marginal habitat, the minimum habitat size for such a local population will be at least two times greater. The survival chance of the species will be highest within the core area (Dwingeloo heath), where extensive peaty heath lands occur, due to a retaining soil layer of boulder clay, which is covered by a 0.2–1 m thick layer of sand. The
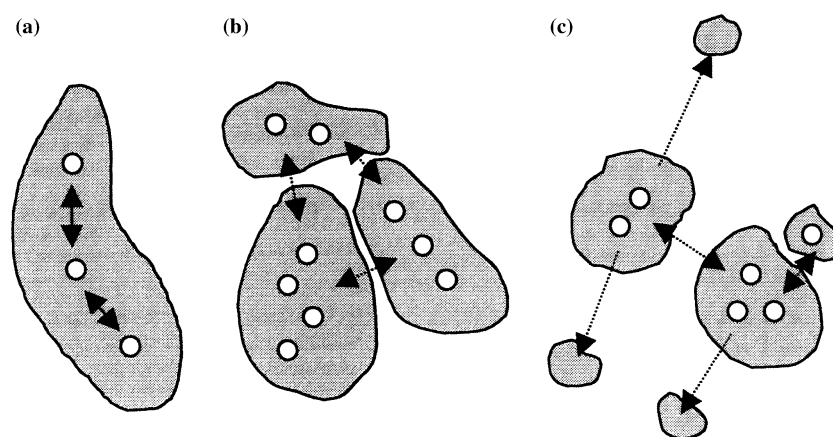
Figure 5. Connectivity between populations (a) Multipartite population, i.e. one habitat patch, occupied by one local population, consisting of three nest populations. Exchange between nest populations by ant workers and sexuals (distance to nearest nest: < 100 m). (b) Patchy population, i.e. three habitat patches, all occupied by a local population. Exchange between local populations only by sexuals (distance to nearest habitat patch: < 500 m). (c) Metapopulation, i.e. six habitat patches, partly occupied by a local population Exchange between local populations only by sexuals (distance to nearest habitat patch: < 3 km).

species was found to be distributed over the whole area, although it did not occur on dryer places, where *Calluna vulgaris*, *Empetrum nigrum* and *Deschampsia flexuosa* were dominating.

Habitat quality

The hypothesis that patch occupancy of *F. transkaucasica* will be positively correlated with patch quality is supported with the results of the logistic regression analysis (Table 2).

Deterioration of habitat quality will result in a decrease of nest density. However, it will take some years before an effect on the nest density of this species can be measured, because there is a time lag between cause and effect, i.e. between a decrease of habitat quality and the extinction of nest populations. It was found that the density dropped from 14 to 4 nests per 100 m in a plot with an *Erica–Molinia* vegetation within a period of 5 years (1977–1982). At first deterioration will result in a decrease of population size and the production of sexuals and workers, but this can only be measured by excavating nests.

Deterioration of habitat quality is most clear in small habitat patches, which are surrounded by agricultural fields. Generally it implies lowering of the ground water level within the habitat patch and a high input of nutrients. Desiccation will make areas more suitable for potential competitors

of *F. transkaucasica*, like *F. sanguina* and its congener *F. fusca*. The presence of these species may hamper the establishment of Black bog ant queens, but it is unlikely that they can exclude the species from optimal habitat patches.

The average nest density in areas with good habitat quality (on Dwingeloo heath) was 7 nests per 100 m, which is more than was found by Bönner (1914) in a Danish peatbog (ca. 1 nest per 100 m^2), but less than was found by Pamilo (1982b) in a Finnish peat bog (ca. 9 nests per 100 m^2). Sometimes a cluster of nests was found (5–10 nests per 4 m^2). Such a nest concentration may be either due to a strong habitat selection by nest-founding queens, or to nest budding, i.e. the formation of daughter nests nearby the mother nest.

It appears that one third of potential habitat patches already have become unsuitable and it is expected that the habitat quality of suitable patches will decrease if causal factors continue operating. Consequently, more of the small isolated populations will become extinct in the near future, while the habitat patches will not any more become re-colonized.

Habitat connectivity

The hypothesis that patch occupancy will be negatively correlated with the distance to nearest occupied patches is not supported by the results of the logistic regression analysis. It seems that the

distance between habitat patches is generally too great for (re)colonization. In other words: habitat connectivity seems to be too low.

Habitat connectivity of ants should be judged on two scales: for walking individuals and for flying individuals. The existence of barriers for walking ants will reduce the positive effect of spreading the risk of extinction of a population. Due to isolation, nest populations may stay longer in low quality sites and at the same time optimal patches may remain empty. Local populations may become isolated by digging ditches, and by constructing roads or dry tracks, which function as a barrier for Black bog ant workers. Within the core area (Dwingeloo heath) several such barriers exist. It implies that several local populations can be distinguished (i.e. 14). Genetic exchange between them can only occur by means of flying sexuals. Every local population inhabits a habitat patch. So in fact Dwingeloo heath includes 14 habitat patches, instead of one as used in the logistic regression analysis. Some of the patches are large enough to contain a key population, i.e. a population with an extinction chance of $< 5\%$ in 100 years, given an immigration rate of one immigrant per generation (Verboom et al. 2001). Although such populations are large, they still depend on other local populations for their persistence. Thus the habitat patches must be part of a network for the maintenance of the Black bog ant. On the Dwingeloo heath, where the distance between habitat patches is smaller than a few hundred metres, we may expect that migration of fertilized queens will take place regularly. Consequently the extinction chance of the total (patchy) population will be very low, due to this rescue effect (Brown and Kodric-Brown 1977). So declining nest populations may be rescued by workers from other nest populations in the vicinity and declining local populations may be rescued by queens from other local populations at flying distance (Figure 5b). Nevertheless it may happen that a local population will disappear due to deterioration of habitat quality. An estimated number of 10 habitat patches (> 1 ha), within flying distance of the queens, are necessary for a persistent population. As generally a great deal of a peat bog or heath land area will be unsuitable for the Black bog ant (too dry or too wet) the whole area which should be protected to guarantee long lasting persistence may be 10-times greater, e.g. 10×10 ha =

100 ha. For comparison: the area of Dwingeloo heath is 560 ha and contains 14 habitat patches, which varies in size from 1–150 ha (on average: 40 ha). All these habitat patches are occupied. So, the Black bog ant population of Dwingeloo heath will be persistent. Such a persistent population may function as a source area for the (re)colonization of small habitat patches in its surroundings. However, evidence for such a source-sink relationship, as mentioned by Pulliam (1988), is lacking.

In the study area patch-occupancy of the Black bog ant is not correlated with the distance to the core area (Dwingeloo heath), nor with the distance to the nearest occupied patch. The immigration rate of flying queens seems to be very low in patches which are situated > 1 km from an occupied patch. The immigration rate depends on the number and flight capacity of dispersing queens in relation to the configuration of habitat patches. These factors will be discussed successively.

Young queens will leave the nest in summer (July–August). However, no data are available about the number of queens which will disperse from a nest. We assume that the number will be low, because nest populations are generally small and the number of queens produced per nest is rather low, 15 queens per nest at most, according to Bönner (1915). We assume that only a few young daughter queens will leave the nest, as we caught them only occasionally in traps and we never observed flying queens (see also Pamilo 1982a; Kaschek and Königschulte 1982). For the Black bog ant, reproduction by budding is likely to be the main mode of formation of new nests.

Little is known about the flight capacity of young queens. The maximum distance which a queen of the Black bog ant can fly may be 10 km in open field, on the basis of what was found for a *Formica rufa*-queen (Haeseler 1982), but a queen probably achieve such a distance only occasionally (Mabelis 1994; Mabelis and Korczyńska 2001). Evidence for limited dispersal of queens (< 1 km) was found in *F. paralugubris* (Chapuisat et al. 1997) and in *F. exsecta* (Liautard and Keller 2001; Sundström et al. 2003) on the basis of genetic relatedness of the ants. If we assume that 95% of dispersing queens will not fly further than 3 km, then the distance of most habitat patches to their nearest occupied patch will be too great to be bridged by most of the queens.

In the study area many local populations have not only become isolated from other local populations by distance, but also by woodland. Woodland may be avoided by flying queens, as was found in *Formica truncorum* (Mabelis and Korczyńska 2001). However, in the case of the Black bog ant it will not be reliable to incorporate distances that queens have to fly over woodland in the distance variables (Chardon et al. 2003), as it is not known how dispersing queens behave: they may fly over woodland when leaving an isolated patch which is surrounded by woodland, while they may avoid woodland when leaving a patch in open field, but there are no observations to confirm this.

In case of ongoing habitat loss, the distance between the remaining patches will increase and consequently a patchy population will turn into a set of local populations in a habitat network, which shows temporary absences in habitat patches, due to local extinction and (re)colonization events (Figure 5c).

Isolation of local populations means that there will be no rescue effect by means of immigrating queens and extinction of local populations will not be compensated by the colonization of empty patches. So, the species don't have a metapopulation structure, at least not on the scale of the study area, as the spatial cohesion of the local populations is absent or very weak. Only in parts of the area, where the distance between habitat patches is less than 3 km in open field, a habitat network still exists. If part of the patches of such a network are occupied by the Black bog ant, the species may have locally a metapopulation structure (Verboom et al. 1991; Verboom et al. 1993). However, with ongoing habitat loss a threshold will be passed and the species will ultimately become regionally extinct.

Implications for conservation

The regional survival probability of the Black bog ant can be increased by minimizing the extinction probability of local populations and by maximizing the opportunities for colonization. The extinction probability of local populations can be decreased by enlarging the size of habitat patches and by improving their quality in order to optimise the growth rate of nest populations and to increase the carrying capacity of the habitat patches. Opportunities for colonization can be improved by increasing the number of habitat patches at flying distance of the queens. It is likely that this flying distance will be rather short (< 1 km) for most of the queens. As peat bogs and wet heath lands cannot be created, the situation can only be improved by restoration measures. So habitat patches can be enlarged and stepping stones between them can be made by improving the habitat quality of existing peat bogs and wet heath lands.

Habitat quality of peat bog and heath deteriorated during the last decades, at least in the Netherlands. This is mainly the result of a high atmospheric deposition of nitrogen, which promotes the dominance of grasses at the expense of heather species (Berendse et al. 1993; Diemont 1996). Habitat quality can be improved by sod-cutting: the removal of organic matter. Although efforts are made to decrease atmospheric N-deposition in the Netherlands, this deposition is still very high (RIVM 2003). So sod cutting often will be repeated after a relatively short period of time (e.g. < 20 years). A few years after sod cutting a *Molinia* vegetation, *Erica* may already become dominant, but it will take many more years before the area becomes suitable again for the Black bog ant. On Dwingeloo heath it was found that 30 years after sod cutting there was hardly enough accumulation of humus to cut sods again (Diemont et al. 1982). So the managed area was probably not yet suitable for the Black bog ant for nesting. As soon as such an area becomes suitable it can be re-colonized from neighbouring occupied patches, but we have to keep in mind that measures of management should be taken on such a scale of space and time that re-colonizations can still keep up with extinctions of local populations. A decrease of habitat quality is not only due to the great nutrient supply, but also to desiccation. The species can overcome desiccation to some extent as long as nest populations can move to more suitable sites, but a long-lasting trend, due to lowering of the groundwater table (ample 1 m), will lead to the extinction of local populations. Desiccation may have resulted in a quicker mineralization of organic matter and consequently in a higher nutrient availability. This process will promote *Molinia* at the expense of *Erica* (Diemont 1996). The grass cover may become so dense that it will become unsuitable for the Black bog ant.

Table 3. Sustainability of six habitat networks (Figure 4) on the basis of the following criteria: Number of patches, number and % of occupied patches, size of the biggest habitat patch, number of occupied patches > 10 ha (which may contain a key population), average patch size (as an indicator of average patch carrying capacity), average connectivity of the patches.
Connectivity for patch $i = \Sigma\, A_j \cdot e^{-\alpha \cdot D_{ij}}$, where A_j is the area of habitat patch j, D_{ij} is the distance between centre point of patch i and patch j, $\alpha\; =\; 1.67$, based on the dispersal capacity of the Black bog ant (see Hanski 1994a; Verboom et al. 2001; Vos et al. 2001).

Network-number	Total # of patches	Number and % of occupied patches	Biggest habitat patch (ha)	Number of key populations	Average patch area (ha)	Average patch connectivity
1	16	14 (88%)	150	8	35.26	–
2	16	7 (35%)	10	1	3.25	5.12
3	5	1 (20%)	12	1	6.09	3.28
4	9	3 (33%)	2	0	0.73	2.03
5	8	2 (25%)	1,7	0	0.73	1.20
6	5	1 (20%)	1,3	0	0.47	0.93

Measures taken in the field to oppose nutrient enrichment will be most effective in areas where habitat networks can be restored. Networks where at least one of the patches is occupied by a key population will have a good chance for developing a persistent metapopulation (Verboom et al. 2001). The fraction of occupied patches within the network should also be taken into account, as it is suggested that the fraction of occupied patches is a useful predictor of meta population viability (Hanski 1994a, 1994b; Vos et al. 2001). The probability of chance extinctions generally will increase as the number of occupied patches decreases (Vos et al. 2001).

Some authors take an occupation of habitat patches of 50% as a threshold below which regional survival of a species is threatened (Vos et al. 2001), while only 15% of the habitat patches within the study area are occupied by the Black bog ant. For the interpretation of occupancy data we have to keep in mind that the turnover rate of nest populations is low and that there will be a time-lag between deterioration of the habitat and the extinction of local populations. Thus an interpretation of patch occupancy may be too optimistic.

The improvement of the quality of habitat patches which are part of a network with the greatest cohesion (judged on the basis of average patch carrying capacity and average connectivity of the patches) will be most effective (Vos et al. 2001; Opdam et al. 2003). In the study area six occupied habitat networks are distinguished (Table 3). Habitat networks of which only a small number of patches is occupied will not be viable, unless at least one of the patches contains a key population.

Source directed measures, like increasing the groundwater level and decreasing the input of nutrients, are most important to improve habitat quality. The proposed measures will not only increase the survival chance of the Black bog ant, but of all species which are dependent of peat bogs and wet heath.

Acknowledgements

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