

Survival of the trunk ant (*Formica truncorum* FABRICIUS, 1804; Hymenoptera: Formicidae) in a fragmented habitat

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Abstract

In The Netherlands the trunk ant (*Formica truncorum* FABRICIUS, 1804) occurs at the edge of its distributional range. It is present in a restricted area of 200 km², although more habitat is present in the whole eastern part of the country. Its scattered distribution pattern changes in time. The aim of the study was to assess the regional persistence of a metapopulation of this species on the basis of change in the occupancy of habitat patches over a period of seven years.

The perimeter and connectivity of a habitat patch are the best predictors for its occupancy. Occupancy of habitat patches is negatively correlated with their distance to all occupied patches, as well as to the core patch. However, the core patch is shrinking, due to succession of the vegetation. Habitat loss was also observed in many other habitat patches, which implies decreasing connectivity. The most effective way of increasing the regional survival probability of the trunk ant is by enlarging existing patches, improving their habitat quality and ensuring that they form part of a cohesive habitat network.

Key words: Formicidae, *Formica truncorum*, habitat fragmentation, habitat network, metapopulation persistence.

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Introduction

The maintenance 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 chance of animal species deal with vertebrates. The results of these studies cannot be extrapolated to invertebrate species, because the latter generally have a larger population size, and a greater susceptibility to environmental fluctuations. Studies about the effect of habitat fragmentation on insects deal mainly with butterflies (e.g., HARRISON & al. 1988, HANSKI & THOMAS 1994, HANSKI & al. 1995) and carabid beetles (e.g., DE VRIES & DEN BOER 1990, DEN BOER & VAN DIJK 1994). Similar studies on social insects, such as ants, are scarce (MABELIS 1992, 1994, SUAREZ & al. 1998, GOLDEN & CRIST 2000, MABELIS & KORCZYŃSKA 2001, MABELIS & CHARDON 2005). Social insects are bound to a nest and can only colonize other areas by means of flying fertilized females (queens).

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 is likely to have consequences for the re-colonization of empty habitat patches. For species with a poor dispersal capacity, habitat patches may become so isolated that patch occupancy then becomes related to patch area and not to the distance of a patch to the nearest occupied patch(es). 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 & GILPIN 1991, VERBOOM & al. 1991, 1993). A metapopulation of ants can be defined as a cluster of local populations between which exchange of genes is possible by means of flying sexuals. The regional survival probability of such a metapopulation depends upon the proportion between the extinction rate of local populations and the colonization rate of unoccupied habitat patches (LEVINS 1970). If the extinction rate exceeds the colonization rate over a long period of time, then the metapopulation will eventually become extinct.

The trunk ant (*Formica truncorum* FABRICIUS, 1804) has been chosen as an object to investigate the effect of habitat fragmentation on its regional survival because of its poor colonization ability, due to the fact that a queen depends on a *Serviformica* species (i.e., *Formica fusca* LINNEUS, 1758) for establishing a colony: the species is known as a temporary social parasite (GÖSSWALD 1989). It has a threatened status in parts of Europe (KVAMME & HAGVAR 1985, EHNSTRÖM & WALDÉN 1986, SEIFERT 1998) and a protected status in The Netherlands (MINISTRY OF LNV 2002). The Netherlands is at the edge of its distributional range, which may imply a lower reproductive rate and a poorer dispersal capacity than in the centre of its distributional range (HENGVELD 1990).

The trunk ant has a scattered distribution pattern (STITZ 1939, MABELIS 1987, 1994, SEIFERT 1996). In The Netherlands size and connectivity of the habitat patches are decreasing, due to succession of the vegetation and forestry practices. It means that habitat of the trunk ant becomes more fragmented, which affects its regional survival probability. In the study area the species has a metapopulation structure, because: (1) part of the habitat patches support local breeding populations, (2) no single population

is large enough to ensure long-term survival, (3) patches are not sufficiently isolated to prevent re-colonization and (4) local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely (HARRISON & QUINN 1989).

The aim of the investigation was to assess the regional persistence of a metapopulation of the trunk ant on the basis of the occupancy and configuration of habitat patches. The hypothesis tested was that patch occupancy will be correlated positively with the area, the connectivity and the habitat quality of the patches. The viability of local populations was estimated on the basis of extinction and colonization events over a period of seven years. Finally the regional persistence of the trunk ant is discussed in view of the configuration of its habitat network.

Material and methods

Distribution and study area

The distribution area of the trunk ant covers much of the Palaearctic region and extends into Siberia. The species is quite common in northern Europe, but is lacking in large parts of central Europe, where it occurs mainly in mountainous areas (STITZ 1939, SEIFERT 1996, MABELIS & KORCZYŃSKA 2001). The trunk ant is generally found in dry sandy areas, but has also been recorded in a Polish peat bog (A.A. Mabelis, unpubl.). The species prefers to build its nest in warm places. Consequently its distribution pattern is scattered. Its habitat can be characterized as a nutrient poor vegetation, generally of grass or ericaceous plants, in open woodland or on the southern edges of dense woodland. Trees and bushes are not only valuable for the ants to collect carbohydrate rich food from aphids and protein rich food from insects, but also to find enough nesting material. Nests are untidily built of pine needles, small twigs and pieces of dead grass, which are accumulated irregularly against the southern side of a tree trunk (Fig. 1). If no suitable trunks or logs are available, the ants have to find something else to support their nest, e.g., a tussock of grass or dwarf shrub. As herbs decay more quickly than trunks, the population will move sooner to another nesting place (MABELIS & KORCZYŃSKA 2001). Removals, during which queen(s), workers and brood are transported, find not only place to leave a decaying nest site, but also to avoid disturbance, increasing shade or competition.

In The Netherlands the trunk ant is found only within an area of 200 km², despite intensive searches in all parts of the country where potential habitat is available (PEETERS & al. 2004). Nearly all nests occur within a restricted area of 75 km², which belongs to the State Forestry of Ommen. This area was chosen as the study area. More habitat is available on dry sandy soils at distances of more than 3 km from the study area, but only three small local populations were found at distances of 3, 10 and 15 km from the nearest occupied patch in the study area. The first two local populations became extinct within a period of ten years. The trunk ant was not found in a cluster of 21 habitat patches which are situated at a distance of 2 - 6 km from the core area in a south-western direction, despite intensive searches of these patches and despite the fact that some habitat patches are large (> 20 ha). Although one nest was found 30 years ago in one of these patches, it can be assumed that they do not belong to the



Fig. 1: Nest of the trunk ant, *Formica truncorum*.

habitat network of the metapopulation. Therefore this area was omitted from the calculations.

The study area includes agricultural land, woodlands and small areas of grassland and heath. Habitat patches of the trunk ant are scattered throughout the area (Fig. 2). The southern slope of a low hill (32 m) is considered the core area of the species, as it has the largest local population (> 20 nests) and the highest nest density (c. 10 nests / ha). In the beginning of the twentieth century much of the site was planted with pine (*Pinus sylvestris* L.), but the vegetation became more open and more suitable for the trunk ant when heavy storms in 1972 and 1973 blew down most of the trees. Only a few old pine trees remained, as well as some oaks (*Quercus robur* L.) and beeches (*Fagus sylvatica* L.). In the open area established pine, birch (*Betula pendula* ROTH), rowan (*Sorbus aucuparia* L.), alder buckthorn (*Frangula alnus* MILLER) and some bushes of *Amelanchier lamarckii* SCHROED. The herb layer consists mainly of heather (*Calluna vulgaris* (L.)), whortleberry (*Vaccinium myrtillus* L.) and grasses (mainly *Deschampsia flexuosa* (L.)). In 1989 one hectare was ploughed and planted with young pine trees. This site was good habitat during the first few years, but later it became too shady for the trunk ant, due to tree growth.

Dispersal strategies of the trunk ant

Regional survival is only possible if extinctions of local populations of the trunk ant can be compensated by the colonization of unoccupied habitat patches by means of flying, fertilized queens. However, not all young queens will leave the nest flying; they either stay in the nest or disperse. Consequently, a nest may contain many queens, up to a few tens (polygyny), while others will contain a few queens (oligogyny) or just one queen (monogyny). Workers of a monogynous nestpopulation are less tolerant to accept young queens in their nest than workers of a polygynous nestpopulation (SUNDSTRÖM 1995, 1997). Leaving the nest will then be a better option for a young queen than staying. Most of the queens which leave the nest are still unfertilized, because generally queens are produced later than males in the study area, which implies that intranidal mating is impossible for most of the queens (MABELIS & KORCZYŃSKA 2001). In a polygynous nestpopulation part of the young queens stay in the nest. Later on they can be transported by the workers to new daughter nests, which are generally built within a

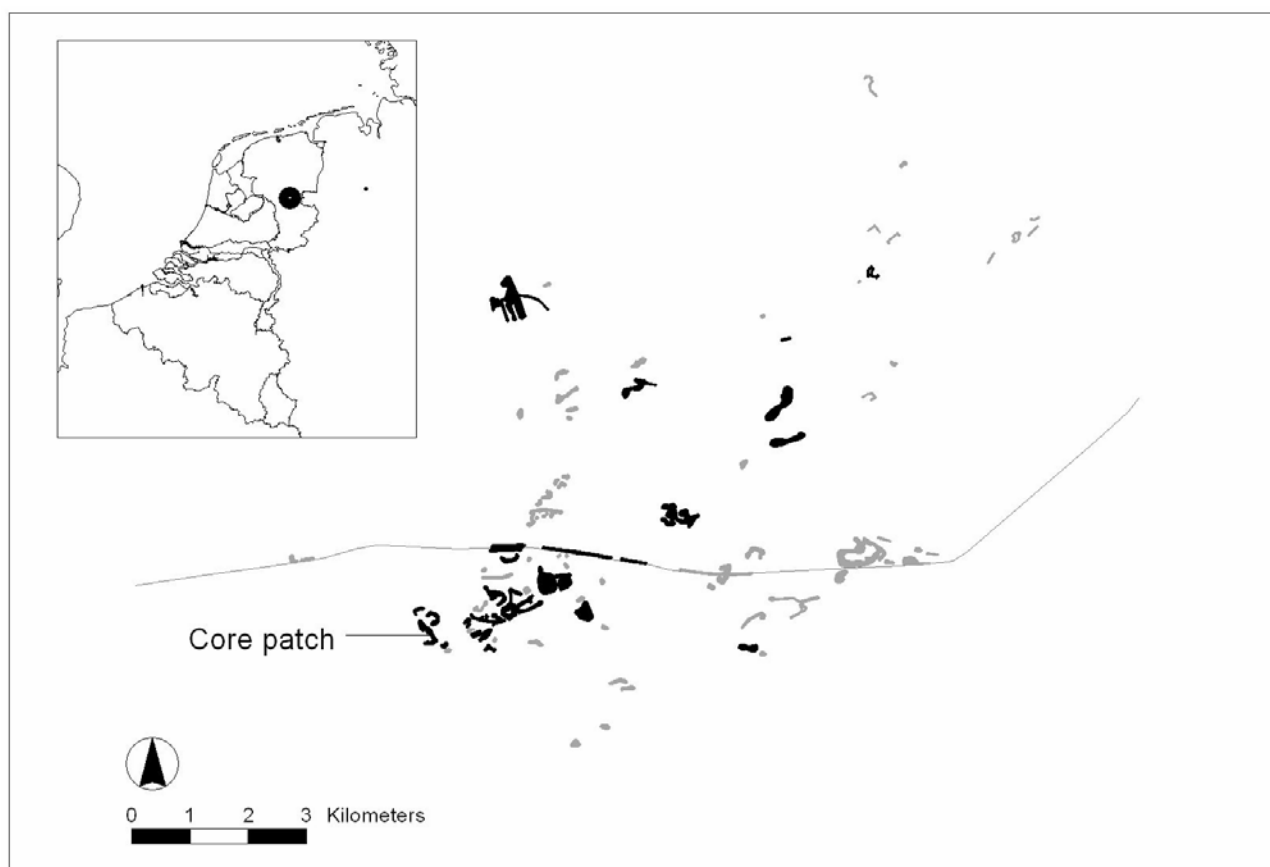


Fig. 2: Distribution of habitat patches of the trunk ant near Ommen (in 1995). Grey patches = not occupied habitats, black patches = occupied habitats, line = railway). Inset: Distribution of the trunk ant in The Netherlands.

few meters from the mother nest. In such a polydomous colony nestpopulations generally will exchange their workers. In this way much of the habitat patch can be monopolized by the inhabitants of one colony. A few times a daughter nest was built at a distance of more than 3 m from the mother nest. In these cases they were taken as two (monodamous) colonies, because exchange of workers will be very limited after some time or even absent (Fig. 3).

Although monogyny (and thus monodomy) can be maintained over considerable time, a monodamous colony sometimes switches to a polydomous one (ROSENGREN 1985, ROSENGREN & al. 1985, 1986, SUNDSTRÖM 1993, 1997, MABELIS & KORCZYŃSKA 2001). The opposite development is also possible: if workers from a polydomous colony stop to share their foraging area, two or more monodamous colonies come into being. Later on the populations of these nests may eventually fuse or move to another nesting site. Generally the distance between the old nest and the new nest is less than 10 m. Only once it was observed that a removal took place over a distance of 30 m. In measuring the number of nests of a local population yearly, we have to take into account that the number of inhabited nests will not only change as the result of mortality of nest populations and the establishment of new ones, but also because of moving, budding and fusion.

Sampling and data analysis

Potential habitat was mapped on the basis of its vegetation: an open nutrient poor herb vegetation (of heather, whortleberry and / or grasses) in open woodland of pine

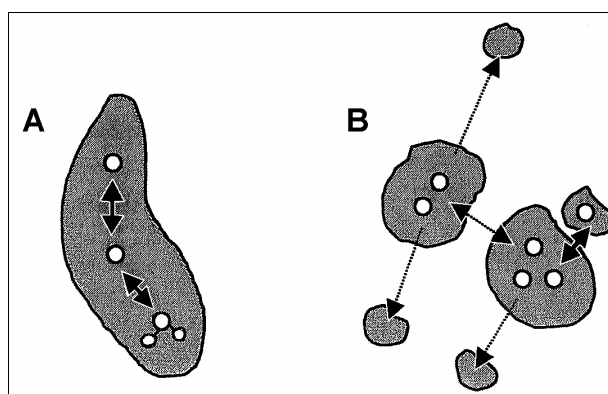


Fig. 3: Connectivity between populations of the trunk ant. (A) Habitat patch, occupied by one local population, consisting of three colonies, of which one is polydomous (in total: 5 nest populations). Exchange between colonies is possible by ant workers and sexuals (distance to nearest colony < 100 m). (B) Metapopulation, i.e., six habitat patches, partly occupied by a local population. Exchange between local populations only possible by sexuals (distance to nearest habitat patch < 2 km).

(occasionally mixed with birch and oak) and southern exposed edges of woodland, all on dry sandy soil. This work was mainly done in autumn and winter. All suitable patches were mapped with the programme AUTOCAD. An inventory of the trunk ant was made in all habitat patches

during the period of the year in which the ants are active. This time consuming work was done in 1989 and 1995 with help of volunteers. Habitat patches which are situated at a distance of less than 100 m from each other are considered as one habitat patch, assuming that contact between nest populations of both patches by means of walking individuals is still possible or was possible in the recent past, unless a barrier, such as an asphalt road or railway, makes contact impossible. In cases of such barriers two patches were recorded.

The presence-absence pattern of the trunk ant was related to the size of the habitat patches and their connectivity by means of logistic regression analysis (MCCULLAGH & NELDER 1989, JONGMAN & al. 1995). In this analysis the statistical package GENSTAT was used (GENSTAT 5 COMMITTEE 1993). The analysis was performed in two steps: at first area and habitat quality of the patches were taken into account and then their connectivity (VAN APeldoorn & al. 1992, VOS & CHARDON 1998). Not only the area of the habitat patches was taken as a variable, but also their edge length (perimeter), because the ants often build their nests along woodland edges, especially those in the south.

Habitat was selected on the basis of its vegetation, but differences in soil properties may also have an effect on patch occupancy, because for building a nest the ants have to dig an underground gallery system. The core area (with the highest nest density) consists of a podzolic soil with a low groundwater table. Soil type and soil humidity were therefore taken into account as variables of habitat quality. Using data from the Institute for Soil Mapping (VRIELINK & DIRKX 1986) two classes of soil type were distinguished within the habitat patches: podzolic soils and arenosolic soils (with less organic content in the A-horizon layer). For classifying the habitat patches on the basis of humidity, data relating to the groundwater table were used (VRIELINK & DIRKX 1986). Two classes were distinguished: low and very low.

In the core area also other factors which may affect habitat quality were ascertained, like grass cover, cover of trees and bushes and the nest density of potential competitors (i.e., *F. sanguinea* LATREILLE, 1798, *F. rufa* LINNAEUS, 1761, *F. exsecta* NYLANDER, 1846, and *F. pressilabris* NYLANDER, 1846), by mapping the vegetation and the nests of these species. This work was done in 1989, as well as in 1995. The nest density of *F. fusca*, which also affects the colonization chance of *F. truncorum*, was not measured because of its time consuming work (nests are often difficult to find).

The following variables were used for calculating the connectivity of the habitat patches (see Tab. 1): the average distance of a patch to the nearest three patches (1), the distance of a patch to the nearest occupied patch (2), the distance of a patch to the core area (3) and the incidence-function model (4), in which the contributions of all surrounding occupied patches within dispersal distance of flying queens are taken into account for their probability of colonization (VERBOOM & al. 1991, HANSKI 1994a, b):

$$CONNECTIVITY_i = \sum S_j * A_j * e^{-\alpha D_{ij}},$$

in which S_j equals one for the occupied patches and zero for the empty patches, A_j is the area of patch j , D_{ij} is the distance between the centre of patch i and that of

Tab. 1: Parameters used in the statistical analysis of patch occupancy.

Area of habitat patches
Area
Perimeter
Habitat quality
Soil type
Soil humidity
Connectivity
Average distance of a patch to the three nearest patches (1)
Distance of a patch to the nearest occupied patch (2)
Distance of a patch to the core area (3)
Incidence function model (4)

patch j , while α is a species specific constant, setting the survival rate of dispersing queens over distance D_{ij} . Distances between patches were calculated with the programme ARCINFO. Data of perimeter and distances were logarithmically transformed to approximate normality.

The turnover rate of local populations was assessed annually (from 1989 - 1995) and involved 35 habitat patches in the central part of the study area for extinctions and (re-) colonizations. The turnover rate was calculated by dividing the sum of the number of local populations which became extinct and the number of local populations which established by the sum of the number of local populations in 1989 and 1995 (see DEN BOER 1990). The turnover rate of colonies in the core area was calculated in a similar way. In this area the number of colonies was assessed yearly from 1989 - 1999 and at last in 2004. In order to find new nests the area was searched thoroughly. Inhabited nests were mapped and judged (by observing workers) if they have contact with neighbouring nest populations, i.e., if they belong to a polydomous colony. The production of sexuals was checked yearly (in July and August) by lifting a thin wooden plate, which was put on the southern slope of the nests. The size of foraging areas was measured by observing foraging workers and by laying out baits at territory borders (see: MABELIS & KORCZYŃSKA 2001).

Results

Habitat area

Within the study area 127 habitat patches were identified, of which 32 were occupied (25 %). The total habitat area amounted to 256 ha, which is 3.4 % of the study area. The average size of an occupied habitat patch was 3.2 ha, the minimum size 0.15 ha and the maximum size 14.3 ha. The foraging area of a colony was small: on average 213 m² ($n = 20$). The habitat patches contained one nest (7.6 %), 2-5 nests (12.7 %) or 6-10 nests (4.2 %). One patch, the core area (3.7 ha), contained more than 20 nests. It appeared that patch area was not positively correlated with the size of the local populations, i.e., the number of colonies. The probability of a patch being occupied is positively correlated with patch area and the edge length, i.e., perimeter of the patches. The perimeter gives the best fit and

Tab. 2: Most important parameters of the incidence function model of the trunk ant. Degrees of freedom (df), significance (sign.), deviance, and level of significance (P) given for the last parameter.

Parameter	df	sign.	deviance	P
ln perimeter	1	+	16.38	< 0.001
ln perimeter + ln connectivity (4)	1	+	39.24	< 0.001
Residual deviance	115		78.18	
Total deviance	117		133.80	

was therefore used in the incidence-function model (Tab. 2, Fig. 4).

Habitat connectivity

In the second step of the regression analysis the four connectivity variables were added separately to analyse their contribution to the model. The first three variables (Tab. 1) showed a significant, negative correlation with patch occupancy. The negative sign is in accordance with the expectation: the further the distance of a neighbouring patch, the lower the colonization probability. However, the fourth variable contributed more significantly to patch occupancy and was therefore chosen in the final regression model (Tab. 2). The positive sign is also in accordance with the expectation: the higher the connectivity of a patch, the higher the probability of occurrence (Fig. 4).

The value of α for this connectivity variable was found by examining the best fit. The highest significance was found with $\alpha = 3$. Figure 5 shows that populations which are situated within a distance of 2 km from a habitat patch may contribute to its colonization.

Habitat quality

Habitat patches were mainly located in open pine forest (75 %) with the other patches being situated on woodland edges. Most nests (c. 70 %) are built against the southern side of a tree trunk or a fallen tree, while the others are built against the southern side of a tussock of grass or heather. Nearly all nests are situated within a distance of 10 m from the nearest stable food source: a tree or bush with aphids, which are milked by the ants.

Most of the patches were on arenosolic soils (75 %), the rest on podzolic soils. The soil humidity was very low in 86 % of the patches and low in 14 % of the patches. When soil type and soil humidity are included in the incidence-function model their estimates did not significantly differ from zero. Therefore, these variables were not included in the model.

It appeared that the habitat quality of many patches is decreasing. This is due to the development of a dense grass cover and to succession of the vegetation in which trees and bushes become older and as such give more shade. This results in a decreasing carrying capacity of patches. Consequently the extinction probability of many colonies is increasing. Succession of the vegetation affects also the nest density of *F. fusca* negatively, which implies a lower chance for young trunk ant queens to establish a colony.

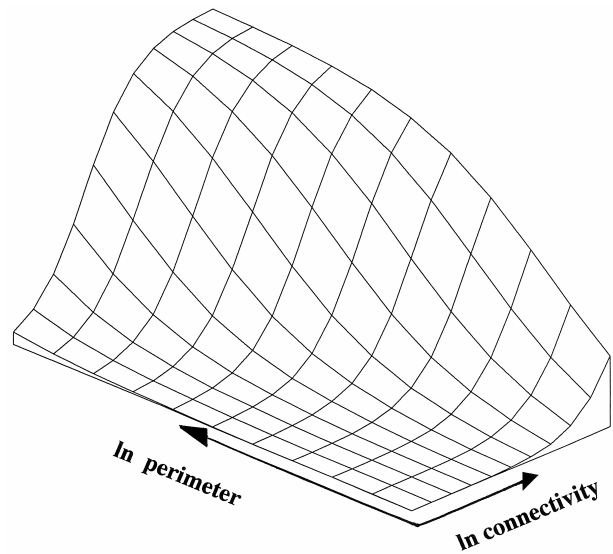


Fig. 4: The probability of occurrence of the trunk ant in a habitat patch is positively related to the natural logarithm of the perimeter and the natural logarithm of the connectivity of the patch.

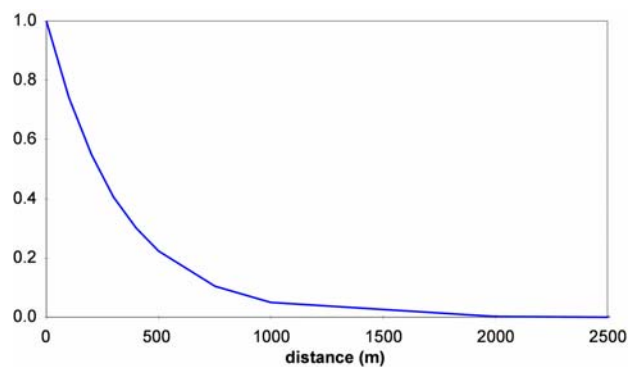


Fig. 5: Estimated dispersal curve of trunk ant queens ($\alpha = 3$). Y-axis: fraction of flying queens.

A decrease of habitat quality will gradually reduce the size of the habitat patch and this may intensify the competition with ant species with overlapping habitat requirements. In the core area four potential competitors occur. The nest density of all these species decreased in time, just like the trunk ant. In seven years: *F. sanguinea* (from 70 to 40

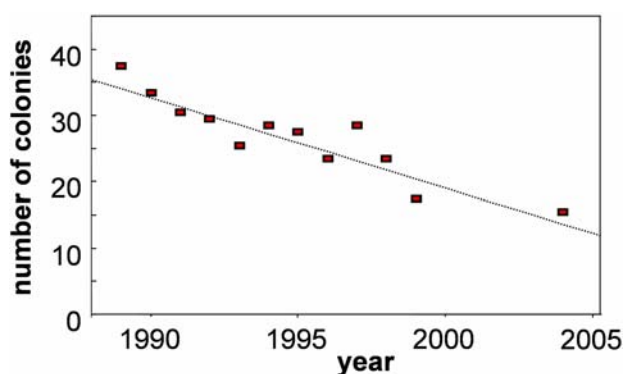


Fig. 6: Decrease of the number of trunk ant colonies in the core patch (1989 - 2004).

nests), *F. exsecta* (from 42 to 29 nests, *F. pressilabris* (from 27 to 10 nests) and *F. rufa* (from 7 to 2 nests).

Survival probability

The probability of a patch being occupied was positively correlated with patch area. However, the area of many patches has become gradually smaller, due to succession of the vegetation. Without any management the number of inhabited nests of these patches will decrease over time. For example: the core area has decreased in size from 5.0 ha (in 1989) to 3.7 ha (in 1995). Consequently the number of colonies has decreased: in that period from 37 to 27 (Fig. 6). By continuing the annual inventory of the core area another four years and at last in 2004, it was found that 30 colonies had disappeared in the period 1989 - 2004, while 8 colonies were counted as new.

The average time left of a colony (since 1989) to become extinct was estimated as follows:

Extinction probability in 16 years: $e_{16} = 30/37 = 0.81$

Survival probability in 16 years: $s_{16} = (1 - e_{16}) = 0.19$
per year, $s_1 = (1 - e_1) = \sqrt[16]{0.19} = 0.90$

Extinction probability per year: $e_1 = 1 - s_1 = 0.10$

Average time left of a colony to become extinct:

$L = 1/e_1 = 1/0.10 = 10$ years

However, at least two of the abandoned nests are most likely the result of the removal of a nest population to a new nest site, because a new nest was found in the same period that the old nest appeared to be abandoned. It means that the number of "extinctions" will be at least two less (i.e., 28). So, the average time left of a colony to become extinct will be 11 years. The average life-span of a colony will be longer, may be 15 years, although it is not known how long the 37 colonies were present before 1989 (six of them were detected four years earlier).

To estimate the time left of the local population of the core area new established colonies should be taken into account: eight colonies were counted as new. Two are most likely the result of a removal, two others may be the result of the establishment of a queen, because the new nests found were mixed (*F. truncorum* - *F. fusca*), while four may be the result of budding, during which a new nest was built at a few meters from the mother nest (both nests inhabited).

The time left of the local population of the core area (37 colonies) was calculated as follows:

The probability of the local population to become extinct in 16 years: $e_{16} = (-30 + 8) / 37 = 0.59$

Survival probability (in 16 years): $s_{16} = 1 - e_{16} = 0.41$;
i.e., per year: $s_1 = (1 - e_1) = \sqrt[16]{0.41} = 0.95$

Extinction probability per year: $e_1 = 1 - s_1 = 0.05$

Estimated time left of the local population:

$L = 1/e_1 = 20$ years (after 1989).

So, the local population of the core area will become extinct about 2009, if disadvantage factors continue operating.

The turnover rate of colonies in the core area = $(N_e + N_c) / (N_1 + N_{16}) = (30 + 8) / (37 + 15) = 0.73$ in sixteen years, i.e., c. 4.6 % per year. (N_e = number of colonies which became extinct, N_c = number of new colonies, $N_{1,16}$ = number of colonies in year 1 and year 16, respectively).

The turnover rate of local populations was assessed by checking 35 habitat patches in the central part of the study yearly (over a period of seven years) to find out about extinction and colonization events. Most of these patches (63 %) were occupied by the trunk ant. Establishing colonization events is problematic, because it is not certain if newly discovered nests have been overlooked in the past. Colonization is only likely in cases that a mixed nest *F. truncorum* - *F. fusca* was found, although it cannot be excluded that trunk ant workers had robbed pupae from a *F. fusca* nest. Colonization of vacant patches occurred probably only twice, while only two times a local population became extinct in a period of seven years. These populations consisted of only one (monodamous) colony. So, the turnover rate of local populations was low: $(N_e + N_m) / (N_1 + N_7) = 2 + 2 / 22 + 22 = 0.09$ in seven years (i.e., 1.3 % / year), in which N_e = number of extinct local populations and N_c = number of new local populations. It appears that colonization and extinction events are too rare to make predictions about the survival of the metapopulation of the trunk ant in the study area.

Discussion

Landscape change

The hypothesis that patch occupancy is correlated positively with patch area and connectivity of the patches is supported by the results of the logistic regression analysis. A positive relation with patch area is often attributed to the fact that a larger habitat patch generally will have a greater carrying capacity. This gives a given species the possibility to develop a larger population, leading to a lower possibility of extinction. However, patch area was not positively correlated with the size of the local populations, i.e., the number of colonies. The number of trunk ant colonies per patch is generally low, with the exception of the core area. Dispersion of the trunk ant over the area of a habitat patch is often hindered by competing ant species. On the other hand a larger patch offers the species more possibilities to establish and later to move to nesting sites with a higher habitat quality.

The fact that patch occupancy is better correlated with the perimeter of the patches than with their area is understandable, because patches with a protracted shape, such as southern exposed forest borders, are often occupied. This supports the finding of GOLDEN & CRIST (2000) that habitat generalists, like ants, respond to experimental habitat fragmentation in a manner that is more consistent with the amount of habitat edge rather than habitat area.

The area of most habitat patches has become gradually smaller (between 1989 and 2004). This is mainly due to

succession of the vegetation in which trees and bushes become older and as such give more shade. Moreover, the habitat quality of many patches is decreasing, due to the development of a dense grass cover, caused by a high atmospheric deposition of nitrogen (RIVM 2003). By ploughing the soil and planting young pine trees in parts of the area new habitat became available, but only for a few years, because the open space between the trees became too shady rather soon. A similar development was observed in several other parts of the study area.

Colony survival

The average lifespan of a colony of *F. truncorum* was estimated at 15 years, which is much lower than that of the polygynous *F. polycтена* (MABELIS & KORCZYŃSKA 2001). The maximum longevity of a red wood ant queen may be 20 years (STITZ 1939, GÖSSWALD 1951), but will generally be much shorter (HORSTMANN 1983). So, monogynous colonies cannot live longer than 20 years, unless they accept a daughter queen when the old queen dies. Accepting more queens in a nest will make the nest population less vulnerable, because if one of the queens dies a related queen can take over her egg-laying task. Moreover, a nest population with many queens can disperse their genes by means of building daughter nests at walking distance, spreading their extinction risk in space (ROSENGREN & al. 1993). Consequently, polygynous (polydomous) colonies can live longer than monogynous (monodamous) colonies (ROSENGREN & PAMILO 1983, MABELIS 1986). However, it is questionable if polydomy will foster the life expectancy of *F. truncorum* colonies in the study area very much, because a polydomous situation will not last very long. Not one colony (out of 72) stayed polydomous during the observation period of seven years. Most monodamous colonies (61 %) switched now and then to polydomy for a short period of time. It implies that one or more small daughter nests were built in the surroundings of the mother nest, but most of these untidily built nests were abandoned before winter or the next year. A few times it was observed that during the budding process several (unwinged) queens were transported to the new nest site. Mother and daughter nest(s) produced offspring the following year, indicating that both nests had at least one queen. Yearly surveys showed that most *F. truncorum* nests are monodamous (over a period of seven years on average 85 % : 82 - 92 %), but only 39 % of the colonies (n = 72) stayed monodamous during the whole observation period. These nests may contain only one queen. This presumption is supported by the observation of P.M. Zaaijer (pers. comm.) in an artificial nest: two groups of 300 workers did not accept more than one winged queen of their own colony; the other queens were killed (i.e., 9 in both groups). WASMANN (1909), LANGE (1958), and BETREM (1960) found exclusively single nests and concluded that *F. truncorum* is a monogynous species, but later polydomous colonies were found in Switzerland (KUTTER 1963), Germany (PREUSS 1979), and Finland (ROSENGREN & al. 1985, 1986), which implies polygyny. In Finland, where the species occurs quite common on islands near the coast, the number of queens varied between 1 and 15 per nest (c. 6 queens on average). It was found that mortality and natality of nest populations was very high in this area (21 %

and 13 %, respectively). This is mainly due to the abandonment of many nests in autumn, and the repopulation of most of them the following spring (ROSENGREN & al. 1985). On these rocky islands nesting is decentralized: nests are often connected with nesting material along stone crevices, in contrast to the situation in the Dutch study area where most nests are separate and situated far apart from each other (see MABELIS & KORCZYŃSKA 2001). Consequently, the turnover rate of inhabited nests on the rocky islands in Finland is much higher than the turnover rate of colonies in our study area (17 % and 4.6 % per year, respectively), but if we take all daughter nests into account, then the turnover rate of inhabited nests is similar (i.e., 18 % per year). The daughter nests will stay inhabited as long as the environment (nest, microclimate) is suitable for hibernation and reproduction.

Colony survival can be affected by habitat fragmentation. According to SUNDSTRÖM (1995) increasing habitat fragmentation may result in a switch to polygyny. She argued that habitat fragmentation implies that the average size of habitat patches will decrease and this may lead to increasing competition between existing colonies if resources are limited. As patch resources are important for female growth and physiological condition, young queens with less fat and glycogen will loose their wings without flying: they stay in the nest. So, monogynous colonies may be more prone to switch to polygyny if the habitat patch becomes poorer (SUNDSTRÖM 1995). This proximate factor may favour the development of polygyny, but ultimately a queen could disperse her genes better if her daughters will eventually leave the nest rather than to stay in an environment which may become progressively poorer (HÖLDOBLER & WILSON 1977, ROSENGREN & PAMILO 1983, ROSENGREN & al. 1986, 1993). However, if a colony becomes so isolated from other colonies that the distance between them exceeds the flying distance of most of the queens, then staying in the nest may be a better option for young queens than leaving the nest flying (MABELIS 1994). Risky dispersal and low probability of founding a new colony may be the ultimate factors for the development of polygyny (WILSON 1963, ROSENGREN & PAMILO 1983, ROSENGREN & al. 1985, 1993, SUNDSTRÖM 1995). So, polygyny, and consequently polydomy, may be favoured by isolation, which may be the result of habitat fragmentation. In a period of seven years the habitat of the trunk ant became more fragmented in the study area. Habitat patches became smaller and more isolated, due to succession of the vegetation and forestry measures, like ploughing and planting trees. In that period the proportion of polydomous colonies increased slightly, but not significantly (from 22 to 33 %).

Nest populations which belong to the same colony can later fuse. In this way a nest population can be rescued (BROWN & KODRIC-BROWN 1977). This may be even possible between single neighbouring colonies, as aggressive encounters between their workers could hardly be provoked (MABELIS & KORCZYŃSKA 2001), in contrast to what is observed in *F. polycтена* (MABELIS 1979). So declining nest populations can be rescued by workers from other nest populations in the vicinity, while declining local populations can be rescued by queens from other local populations at flying distance.

Habitat connectivity

Occupancy of habitat patches is negatively correlated with the distance of a patch to the core area, suggesting that the local population of the core area could function as a source for colonizing patches in its environment. It appears that only patches which are situated north-east from the core area are occupied, while more habitat is present in south-western direction at a distance of 2 - 6 km from the core area. It seems that dispersing queens may profit from the prevailing south-western wind to fly in north-eastern direction. However, they prefer to start flying on nearly windless days. Consequently, no correlation between wind and flight direction was found (MABELIS & KORCZYŃSKA 2001).

Little is known about the flight capacity of young queens. The maximum distance which a queen of the trunk ant can fly may be 10 km in open field, on the basis of what was found for a *Formica rufa*-queen (HAESLER 1982), but a queen probably will achieve such a distance only occasionally (MABELIS 1994, MABELIS & KORCZYŃSKA 2001). Evidence for limited dispersal of queens (< 1 km) was found in *F. paralugubris* SEIFERT, 1996 (CHAPUISAT & al. 1997) and in *F. exsecta* (LIAUTARD & KELLER 2001, SUNDSTRÖM & al. 2003) on the basis of genetic relatedness of the ants. If it is assumed that 95 % of dispersing trunk ant queens will not fly further than 2 km, then the colonization probability of the patches which are situated south-west of the core area will be very small. Only habitat patches which are situated at a distance of < 2 km from the nearest occupied patch are considered to belong to the habitat network. It appears that about 75 % of the patches which belong to the habitat network are still unoccupied.

For calculating connectivity the shortest distance between habitat patches was measured, but it would make more biological sense to incorporate landscape elements into the connectivity parameter (CHARDON & al. 2003), i.e., to correct distance variables for distances that queens have to fly over dense woodland, which is a dispersal barrier. However, this will not be reliable, as it is not known how dispersing queens behave exactly in respect to woodland: queens avoid woodland after leaving their nest flying (MABELIS & KORCZYŃSKA 2001), but they may be attracted by woodland when flying over open field in order to find a nesting place.

Regional survival

If habitat is fragmented in such a way that the distance between the patches does not exceed dispersal distance of the queens, it may have some positive effect on the survival probability of the metapopulation by spreading the extinction risk of the local populations in space (DEN BOER 1981, QUINN & HASTINGS 1987). However, the trunk ant can only survive in a fragmented habitat if extinctions of local populations can be compensated by the colonization of unoccupied habitat patches by means of flying fertilized queens. It was not possible to assess this, because the observation period (i.e., seven years) was too short in comparison to the lifespan of a local population. Anyway, reproduction and dispersal of sexuals will be crucial for the survival of the species in a relatively dynamic environment where its habitat is patchily distributed. It appears

that 70 - 85 % of the nests of the core area produced sexuals yearly (MABELIS & KORCZYŃSKA 2001), which is higher than in the mono-oligogynous *F. rufa* (68 %, n = 22) and the polygynous *F. polyctena* (47 %, n = 40). In Finland a much lower percentage of the *F. truncorum* nests produced sexuals: 33 % on average over a period of four years (numbers of nests varied between 49 and 63) (ROSENGREN & al. 1985). The proportion of nests which produced sexuals was 20 - 25 % in *F. opaciventris* EMERY, 1893 (SCHERBA 1961) and even less in *F. yessensis* WHEELER, 1913, a species which lives in Japan and is very similar to *F. truncorum* (JAPANESE ANT DATABASE GROUP 2003): only 6.4 % of 178 nests contained sexual pupae. If newly formed daughter nests are omitted, assuming that they don't produce sexuals, then 13.7 % contained sexual pupae (ITO & AMAMURA 1974). Nests of all these examples belong to an extensive polydomous colony, which makes it possible to leave the reproduction function to the most suitable nests of the colony (SCHERBA 1961, ROSENGREN & al. 1985), while most of the nests in the present study area are single. A greater proportion of them will produce sexuals, but the number of sexuals that left the nests flying appeared to be rather low (MABELIS & KORCZYŃSKA 2001). The colonization probability will increase if more habitat becomes available. The larger the number of patches within colonizing distance of one another, the better.

Some existing habitat patches have become smaller and may at last disappear if the vegetation becomes too dense and shady. On the other hand new habitat patches may occasionally become available by felling trees. However, new trees are usually planted in these areas, which implies that they will be only suitable for the trunk ant for a couple of years after planting. These habitat patches can be colonized only if the distance to the nearest occupied patch is not too great for flying queens, if the host ant *F. fusca* is present and if the density of potential competitors is not too high.

Colonies of *F. truncorum* are much smaller than those of *F. rufa* and *F. polyctena*. Consequently, the extinction rate of *F. truncorum* colonies is greater than the extinction rate of *F. rufa* and *F. polyctena* colonies (MABELIS & KORCZYŃSKA 2001), but if this will be compensated by a higher colonization rate is still unclear. It can be assumed that the colonization probability of unoccupied patches will be very low, due to the low chance of a queen to find a mate, her low dispersal capacity and her low chance to establish a colony. So, inter-patch dispersal will be probably too weak for all habitat patches to be reached and colonized to counteract local extinctions. Nevertheless, it may be that a *F. truncorum* queen has a higher chance to become adopted by *F. fusca* than a queen of *F. rufa* and a much higher chance than a queen of *F. polyctena* (GÖSSWALD 1952, 1989). If so, then the species is better adapted to a dynamic environment than the other red wood ant species: i.e., an environment where its habitat is fragmented and where the quality of nesting sites will change rather quickly in time (SEIFERT 1996, MABELIS & KORCZYŃSKA 2001).

Implications for conservation

The question has been posed whether the survival probability of the species will be influenced by constructing a golf course in one of the habitat patches where *F. trun-*

corum occurs. Such a question cannot be answered if it is not possible to make a prediction about the survival probability of the metapopulation. It can be assumed that as long as this patch (13 ha) is part of the habitat network it may play a role in the sustainability of the metapopulation. This will not only be the case when *F. truncorum* is present, but also when the species does not occur, because such a patch still has the chance to become re-colonized. Colonization probability will be proportional to the number of occupied patches at dispersal distance. It is argued that the fraction of occupied patches is a useful predictor of metapopulation viability (HANSKI 1994a, b, VOS & al. 2001). An occupation of 50 % is taken by some authors as threshold below which regional survival of a species is threatened (VOS & al. 2001). If we may accept this for the trunk ant, then it can be judged as threatened in The Netherlands, because only 25 % of the habitat patches within its distribution area is occupied. Moreover, it should be realized that there will be a time lag between deterioration of habitat and the extinction of local populations. So patch occupancy can give an impression of the status of the species which is too optimistic. We tried to make predictions about the survival probability of a metapopulation of *F. truncorum*, but did not succeed, due to a lack of data about extinction and colonization events of local populations within the relative short observation period of seven years. Therefore we focussed on extinction of colonies. On the basis of a high extinction rate and a low colonization rate of colonies we judge the trunk ant as endangered in The Netherlands. It means that its survival in this country is unlikely if causal factors continue operating.

The regional survival probability of the trunk 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 increasing the carrying capacity of the patches, namely by enlarging the opportunities for nesting, i.e., by felling some trees and removing some bushes. The enlargement of southern exposed edges of bushes can be an effective measure to increase habitat area for the trunk ant, as well as for other thermophilic species: many ant nests were found along such linear elements as wide forest tracks, road verges and a railway verge (see Fig. 2). The improvement of the habitat quality of existing patches which are part of a network with the greatest spatial cohesion will be most effective. The cohesion can be judged on the basis of average carrying capacity and average connectivity of the patches (VOS & al. 2001, OPDAM & al. 2003). The carrying capacity of a patch ($K_i = \text{area}_i / \text{CAR}$, in which CAR is the colony area requirement), gives an impression of the maximum size of the local population, although in reality this size is limited by competing ant species. Judging the habitat cohesion on the basis of the size and the average connectivity of the patches it appears that the spatial cohesion is greatest in the forestry of Ommen, in which 45 habitat patches are situated, including the core patch. The core patch may function as a source for the colonization of habitat patches in its environment, but as long as the size of the core area is decreasing it cannot be assessed as a key-patch, which contains a key-population, i.e., a population with an extinction probability of < 5 % in 100 years, given an immigration rate of one im-

migrant per generation (VERBOOM & al. 2001, OPDAM & al. 2003). Missing a key patch in the network implies that more habitat is needed for the survival of the species. The trunk ant can be judged as a species which belongs to the category of species with a high fragmentation sensitivity on the basis of its high extinction risk and low colonizing ability (VOS & al. 2001). Opportunities for colonization can be improved not only by enlarging opportunities for nesting within habitat patches, but also by increasing the number of patches within the habitat network. As long as the majority of the patches within the habitat network is occupied, the trunk ant may have a great chance to survive a period of 100 years, but with ongoing habitat loss a threshold will be passed and the species ultimately become extinct in The Netherlands.

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Zusammenfassung

Die Strunkameise (*Formica truncorum* FABRICIUS, 1804) erreicht in den Niederlanden den Rand ihres Verbreitungsgebiets. Sie besiedelt hier ein Gebiet von nur 200 km², obwohl die prinzipiell geeigneten Lebensräume im gesamten Osten des Landes eine wesentlich größere Fläche ausmachen. Das zerstreute Verbreitungsmuster ändert sich im Lauf der Zeit, infolge forstwirtschaftlicher Maßnahmen und natürlicher Sukzession. Regional ist das Überleben der Strunkameise nur möglich, wenn die Besiedlung unbesetzter Habitatinseln durch den Anflug befruchteter Königinnen dem Aussterben lokaler Populationen die Waage hält.

Ziel der Untersuchung war, den regionalen Zustand einer Metapopulation der Strunkameise auf der Basis der Veränderungen in der Besiedlung von Habitatinseln über einen Zeitraum von sieben Jahren zu erheben.

Umfang der Habitatinseln und Verbindung der besiedelten Habitat-Inseln miteinander ermöglichen die beste Vorhersage der Besiedlung einer Habitatinsel. Die Besiedlung von Habitatinseln ist negativ korreliert mit ihrem Abstand zu den anderen besiedelten Habitatinseln in der Nähe, sowie mit ihrem Abstand zur zentralen Habitatinsel mit der höchsten Dichte von Nestern und somit der größten lokalen Population.

Viele Habitatinseln schrumpfen in Folge der natürlichen Vegetation. Dadurch nimmt die Überlebenschance vieler lokaler Populationen ab. Die Überlebenszeit einer lokalen Population wird – im Fall, dass Pflegemaßnahmen

zur Verbesserung der Lebensraumqualität ausbleiben – auf 20 Jahre geschätzt. Lebensraumverlust bedeutet auch eine verringerte Verbindung zwischen den Habitatsinseln und eine dadurch verringerte Chance einer Wiederbesiedlung, was die regionale Überlebenschance insgesamt verringert.

Die regionale Überlebenschance der Strunkameise kann durch Verbesserung der Lebensraumqualität der einzelnen Habitatsinseln, durch die Vermehrung der Zahl der Habitatsinseln, sowie durch eine Verbesserung des Vernetzungsgrads des Lebensraumverbundes erzielt werden.

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