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Flying as a survival strategy for wood ants in a fragmented landscape (Hymenoptera, Formicidae)

Abstract. The effects of habitat fragmentation on the survival chances of wood ant species with a different strategy was investigated in a region where negative human influences on the quality of habitat fragments could be neglected: an agricultural landscape in the Gorce Mts (southern Poland). Within this region, large forest fragments occur next to small, isolated woodlots. The study area (740 ha) includes two joining sectors, in which about half of the soil surface is cultivated. Four wood ant species occur there: *Formica polyctena* FOERST. (polygynous species, which disperse mainly by colony splitting) and *F. rufa* L., *F. pratensis* RETZ. and *F. truncorum* FABR. [mono-(oligo)gynous species, which disperse nearly exclusively by flying queens]; their distribution was analysed.

INTRODUCTION

European forests have become fragmented over extensive parts of their original distributional range, mainly due to agricultural intensification, urbanization and other human activities. Fragments of the original forest tend to decrease in size, whereas the distance between the fragments tends to increase. Consequently, populations of forest species have become dissected into smaller units (local populations), which will become more isolated from each other. This may have a negative effect on the survival chance of these species, as the extinction rate of local populations is inversely related to forest patch size and the (re)colonization rate of forest patches is inversely related to the distance between the patches (GOTTFRIED 1979, WEAVER, KELLMAN 1981, GEUSE et al. 1985, OPDAM et al. 1985, VAN DORP, OPDAM 1987, BLAKE, KARR 1987, VERBOOM et al. 1991, among others). However, the effect of habitat fragmentation on the extinction rate of local populations and the colonization rate of empty habitat patches is species-specific. The extinction rate depends on the susceptibility of the species to environmental fluctuations, while the colonization rate depends on the colonizing capacity of the species, i.e. its reproductive success, site fidelity, dispersal power and establishment capacity. Dispersal is not only important for the colonization of empty habitats, but also for lowering the extinction rate of local

populations by means of immigration ("rescue-effect", BROWN, KODRIC-BROWN 1977). Dispersal can be the key to survival for a species (BURKEY 1989, OPDAM 1990, DEN BOER 1990). Dispersal is affected by the permeability of the landscape, i.e. by the presence of barriers and corridors. These elements are particularly important for species which cannot fly (MADER 1984, MADER et al. 1990), although the significance of habitat patch connectivity for (meta) population survival has seldom been proved (FAHRIG, MERRIAM 1985, VERBOOM et al. 1991, SIMBERLOFF et al. 1992).

Most of the studies about the effect of habitat fragmentation on the survival chance of species deal with vertebrate species. The results of these studies cannot be extrapolated to invertebrate species, because the latter generally will have a larger population size, on the one hand, and a higher susceptibility to environmental fluctuations on the other. Only a few publications deal with the effect of habitat fragmentation on invertebrates: DEN BOER (1981, 1990; carabid beetles), WEBB, HOPKINS (1984; beetles, spiders and bugs), BRONMARK (1985; snails), PAJUNEN (1986; crustaceans), HARRISON et al. (1988; butterflies), BUREL (1989; carabid beetles), DE VRIES, DEN BOER (1990; carabid beetles) and TSCHARNTKE (1992; moths, midges, flies, aphids), among others.

More landscape ecological information about invertebrates is needed. Furthermore, ecologists also have to cope with a lack of information about the habitat requirements of many invertebrates and that many invertebrates are difficult to find if they occur in low densities. So we can never be sure whether a particular species is absent in a habitat patch or not. This problem does not apply to wood ants, because these social insects build nest mounds, which are relatively easy to find. Another advantage of wood ants as a study subject is that their habitat requirements are well known. Thus, ecologists are able to distinguish suitable patches for nest building, and this makes it possible to relate the presence (or absence) of colonies in these habitat patches to their area and degree of isolation. This may give an indication of the relative importance of these factors for the survival chance of the species. However, account should be taken to the facts that the extinction rate of colonies is relatively low (MABELIS 1986), and that (re)colonizations may also be a relatively rare event. This implies that there may be a time-lag between the distribution pattern of the colonies and the actual landscape structure. Thus it is clear that for a study on dynamic processes of wood ant (meta)populations, a long time scale is needed. Such studies are rare (e.g. ELTON in MABELIS 1986). Only a few publications deal with inventories of wood ant colonies which were repeated after several years (KLIMETZEK 1981, WUORENRINNE 1983, RONCHETTI et al. 1986). On the basis of these data, and impressions of foresters, it is concluded that wood ants are declining in many parts of their range (WELLS et al. 1983). In this article, the vulnerability of wood ants to habitat-fragmentation will be discussed.

Four wood ant species occur in the study area: *Formica polyctena* FOERST., *F. rufa* L., *F. pratensis* RETZ., and *F. truncorum* FABR. The species differ with respect to the number of queens in the nest. *F. polyctena* nests contain many queens (normally several hundreds), while nests of the other species contain one queen or a few queens. So *F. polyctena* is a polygynous species, while the others are monogynous or oligogynous. Consequently, *F. polyctena* can disperse not only by means of young flying queens but also by means of old, wingless queens that are transported by the workers

to a new nest site. The advantage of having many queens in a nest is that empty habitat patches within reach of the mother colony can be occupied relatively easily by budding. This is a relatively safe means of dispersal. The polygynous strategy also has the advantage of increasing the life expectancy of the colony, not only by increasing its potential for population growth but also by spreading spatially its risk of extinction by building daughter nests (ROSENGREN, PAMILO 1983, ROSENGREN 1985, MABELIS 1979a, 1986). Such a budding process results in a polydomous colony, i.e. a colony which consists of several nests, between which there is a regular exchange of workers and brood. However, budding is possible only in situations where enough space is available, i.e. within large habitat patches. A polydomous colony can survive in such patches for a very long time, i.e. more than 100 years, so the probability of extinction of a polydomous colony may be very low. If the colonization probability is also very low, then it may be expected that *F. polyctena* colonies will be found more often in relatively large habitat patches.

A monogynous society is more vulnerable than a polygynous one because it is dependent on a single queen. The queen may become very old, i.e. more than 20 years (GÖSSWALD 1989), but if the queen dies and the workers do not adopt a new queen, then the colony will become extinct in less than a few years. Adoption of queens is only possible in the period of nuptial flights, i.e. in spring. Such an adoption will be advantageous for monogynous ant societies because it will lower their probability of extinction; it may have a "rescue-effect" (BROWN, KODRIC-BROWN 1977). Nevertheless a colony of a "monogynous species", like *F. rufa*, only occasionally becomes a polygynous one, at least on the continent, as in England polydomous colonies of *F. rufa* are normal (COLLINGWOOD 1979). As long as the number of queens remains small then budding seldom occurs.

Monogynous and oligogynous species disperse almost exclusively by means of winged queens. However, leaving the colony is a very risky action. In the air wood ant queens run the risk of being captured by birds and on the ground of being killed by ants, mainly of their own species, and sometimes even of their own colony (MARIKOVSKY 1961, MABELIS 1986). There is still another risk: in order to colonize an empty habitat patch a queen needs to be adopted by workers of another ant species, i.e. a *Serviformica* FOR. species. These workers have to care for her brood, because a wood ant queen is not able to do it herself. However, the chance that those workers will kill the queen instead is very high (GÖSSWALD 1952).

So the establishment capacity of queens is important for the colonization rate of empty habitat patches. Besides that, the colonization rate is dependent on the sexual reproduction of existing nests and the dispersal power of the queens. Wood ant queens seem to be "clumsy flyers" (ROSENGREN, PAMILO 1983). If they disperse badly then the distance between the habitat patches may play a role in the chance of a patch becoming colonized. It is thus important to establish whether habitat patches are less often occupied the more they are isolated.

Dispersal by means of flying queens has the advantage that habitat patches which are beyond the range of walking ants can be colonized. In a situation where the habitat is fragmented dispersal by flight might be a better option. If the higher extinction rate of a monogynous species is compensated for by a higher colonization rate, then it is possible to conclude that a monogynous species is better adapted to

habitat fragmentation than a polygynous species. By comparing the distribution pattern of the nests of a polygynous species, such as *F. polyctena*, with that of a mono(-oligo)gynous species, such as *F. rufa*, an indication of the difference in vulnerability of the species to habitat fragmentation may be obtained. If monogynous species are more successful in colonizing isolated habitat patches, it may be expected that small isolated habitat patches will be more often occupied by *F. rufa* than by *F. polyctena*.

The aim of the present study is to investigate whether monogynous wood ant species are better adapted to habitat fragmentation than polygynous wood ant species. The following hypotheses are tested:

1. Area. The number of *F. polyctena* nests that occur within a habitat patch will be positively related to the area of that patch. There will be a positive relationship between the area of a patch and the chance of *F. polyctena* being present. In the case of *F. rufa* there will not be such a relationship.

2. Isolation. Habitat patches are less often occupied by wood ants the more they are isolated.

3. Area + isolation. Small and isolated habitat patches will be more often occupied by *F. rufa* than by *F. polyctena*.

STUDY AREA

To study the effects of habitat fragmentation on the survival chances of wood ant species, it is necessary to exclude negative influences of agriculture on the quality of habitat fragments. Therefore, a region where such influences are negligible should be selected. For the present study, an agricultural area in southern Poland, the Gorce mountains, was chosen. Within this region, large forest fragments occur next to small, isolated fragments. The study area of 740 ha included two adjoining sectors, in which about half of the soil surface was cultivated (Figs 1, 2, 3). The area was chosen so that the probability of immigration of wood ant queens from nests outside the area will be as small as possible.

The mountains within the study area range from 600 m (the stream valleys) to about 1000 m above sea level on the west, north and east side (the lower mountain zone). The parent rock consists mainly of vertically situated beds of coarse-grained sandstone and conglomerates, separated by intercalations of shales and thin beds of fine-grained sandstone (SIKORA, ŻYTKO 1968). There are many natural outflows of underground water, forming watercourses, which feed the two main streams that intersect the study area: Jaszczce and Jamne. The soils most often found are sandy loams. The lower down the slope, the more clayish the soil usually becomes. Along streams, stony warp soils occur.

Until the mid-eighteenth century, the north west part of the study area was almost completely covered by more or less virgin forest, mainly *Fagetum carpaticum*, but following extensive felling of forest areas, especially in the lower parts of the original beech forest (Fig. 1), the landscape changed gradually into a mosaic of beech stands, secondary spruce stands, hayfields and nutrient-poor pastures with heath (*Calluno-*

Nardetum). Nowadays, about half of the forest in the western part of the study area (Jaszce valley) consists of spruce forest (Fig. 4). This forest type (mainly *Vaccinio-Piceion*) is even more common in the eastern part of the area (Jamne valley). The soils in the lower montane zone are mostly brown, although podzolic soils occur quite often, especially in the higher parts (ADAMCZYK, KOMORNICKI 1970). The higher parts of the area generally are poorer in nutrients than the lower parts. Above 1000 m the soil is either covered by spruce forest (*Piceum tatricum*) or by poor grassland (*Hieracio-Nardetum*). In recent times these grasslands were used as pastures for grazing sheep, but since grazing ceased, a dense grass carpet has developed, in which the grass *Nardus stricta* L. dominates.

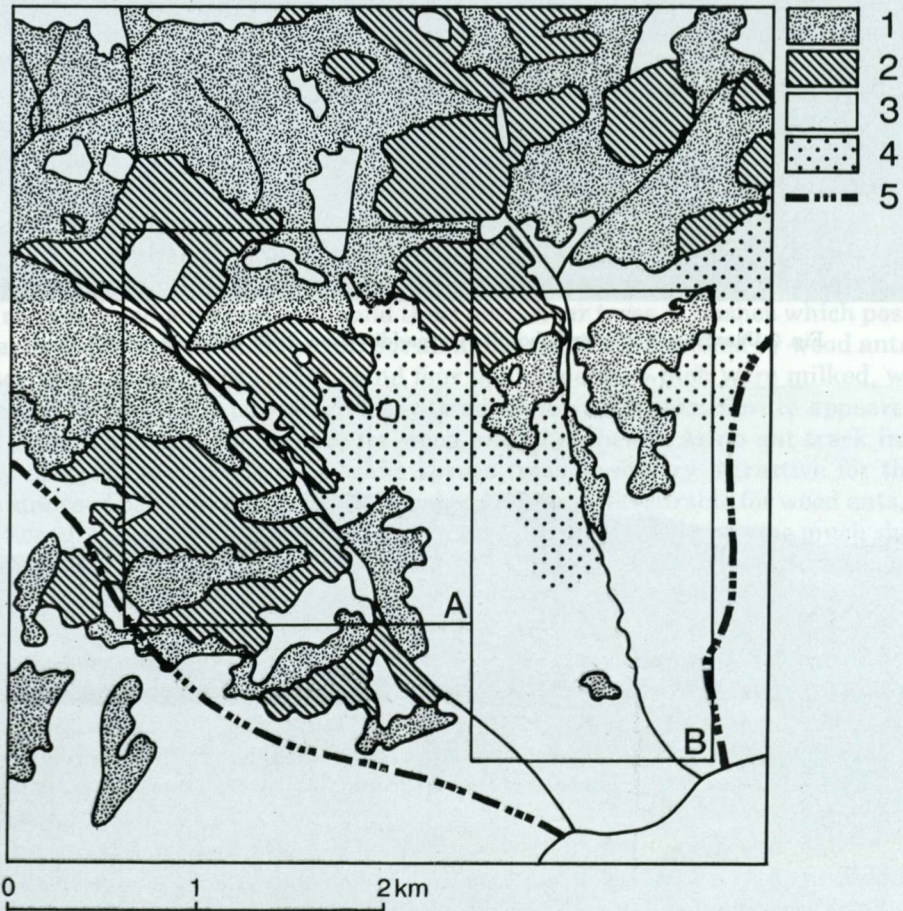


Fig. 1. Deforested areas in the valleys of the streams Jaszce and Jamne near Ochotnica Górna (Gorce National Park); the study area is outlined: 1 – unexploited forest, 2 – deforested from 1882 to 1932, 3 – deforested earlier, 4 – regeneration of spruce by self-seeding, 5 – boundary of drainage areas of Jaszce and Jamne (after JAROSZ 1935); A, B – sectors of the study area (see Figs 5, 6).

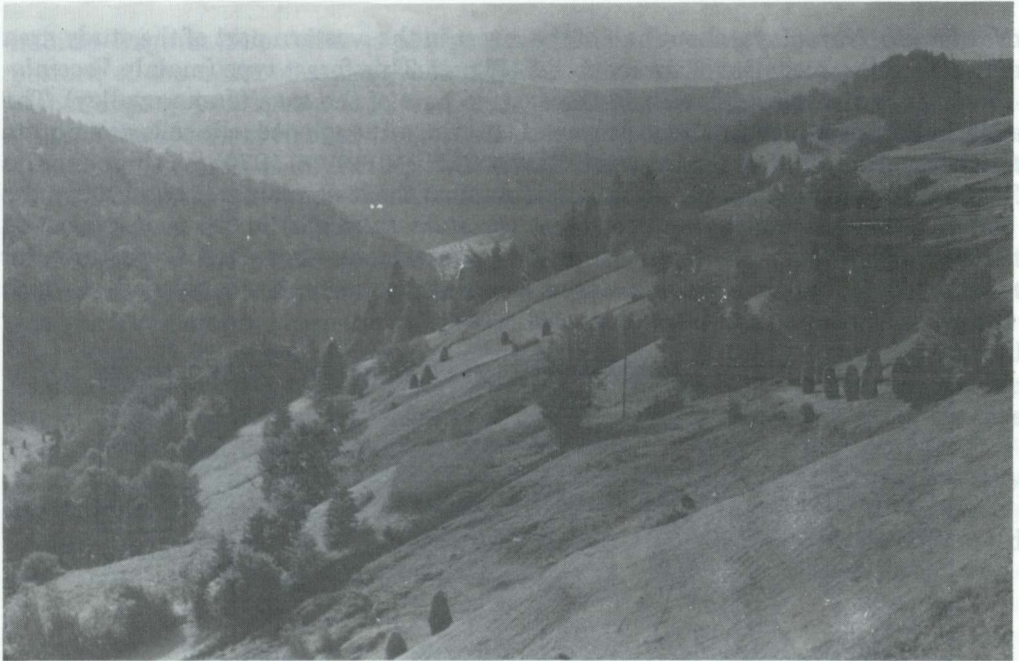


Fig. 2. Jaszcz valley near Ochotnica Górna (direction: NW). (Photo A. MABELIS).

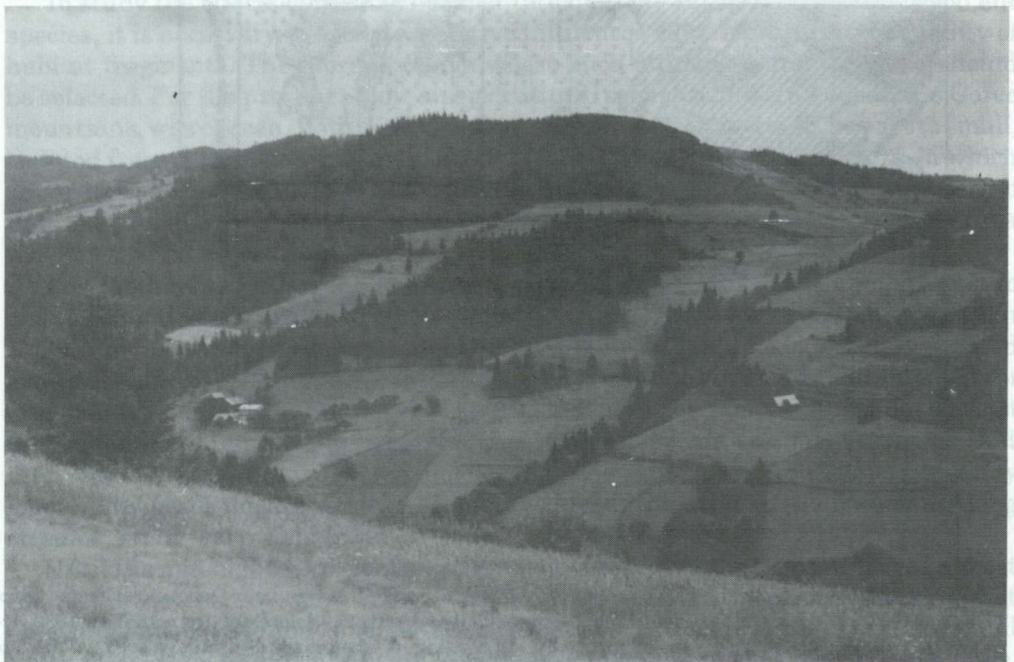


Fig. 3. Jamne valley near Ochotnica Górna (direction: NE). (Photo A. MABELIS).

Arable land is mainly found in the lowest part of the valleys. Even in this cultivated area, small forest patches remained on steep slopes, on rocky areas, along streams and road verges. Pesticides are not used and fertilizers only occasionally. Thus, land-use did not have a negative effect on the habitat quality of forest edge vegetations for wood ants.

HABITAT

Within the study area, suitable patches for wood ants were distinguished according to the availability of nesting places and food. Most of the wood ant nests were situated on a slope with a southern aspect affording much insolation: 75% of the nests received more than 112% relative insolation (measurements made by OBRĘBSKA-STARKŁOWA 1970). Therefore, a site was assumed to be suitable for nesting if it was exposed to sun, and if nesting materials, such as a tree trunk, small twigs or needles were available. All north-facing slopes were assumed to be unsuitable for nesting.

Food availability gives a less strict criterion for selecting habitat patches. Wood ants are polyphagous predators, so they can find prey everywhere, although areas with a dense herb vegetation are less suitable for hunting and may even be avoided. The most important food source for wood ants is honeydew, produced by aphids. For this reason, wood ants prefer to build their nests near trees or bushes which possess attractive aphid colonies. However, not all aphid species are milked by wood ants. In spruce trees, ZOEBELEIN (1956) found four aphid species which were milked, while in beech he found only one which was attractive for wood ants. Spruce appeared to be a more important food source for wood ants than beech, as no ant track in the study area led to a beech tree, while spruce trees were very attractive for them. Dominance of beech in a forest will make the biotope unfavourable for wood ants, not only because it provides less aphids for food but also because it gives too much shade. Nearly all nests occur within, or on the edge of, a spruce forest; no nests were found within a beech forest (Fig. 4). Therefore a beech forest was assumed to be unsuitable for nesting.

For colonizing an empty habitat patch, it is necessary that one of the *Serviformica* species be present, in order to help the wood ant queen to care for her first brood (GÖSSWALD 1989). However, it appeared that *Serviformica* species (i.e. *Formica fusca* L., *F. lemani* BONDR., *F. cunicularia* LATR.) were so common in the study area that their presence cannot be used as a criterion for estimating the suitability of habitat patches for colonization.

All wood ant species prefer to build their nests in sunny places. Moreover, they exploit the same food resources, and so are potential competitors. If the nest density is high in relation to the amount of food available, they will behave territorially, i.e. they will defend their foraging area against competing ant species (MABELIS 1979b, 1984). This implies that it will be impossible for a queen to colonize a small habitat patch which is already occupied by one of the other wood ant species. However, *F. rufa* and *F. polycytena* compete more often with each other than with *F. pratensis* and *F. truncorum*, because the latter, being more thermophilic, prefer a slightly different

habitat. Consequently, nests of *F. pratensis* and *F. truncorum* are found more often in open areas, while those of *F. rufa* and *F. polycytena* are normally situated within an open forest or on the edge of a forest. The different habitat preference of *F. pratensis* and *F. truncorum*, and the relative scarcity of their nests (Fig. 6), make it reasonable to assume that they will not have a significant impact on the distribution of the nests of *F. rufa* and *F. polycytena*.

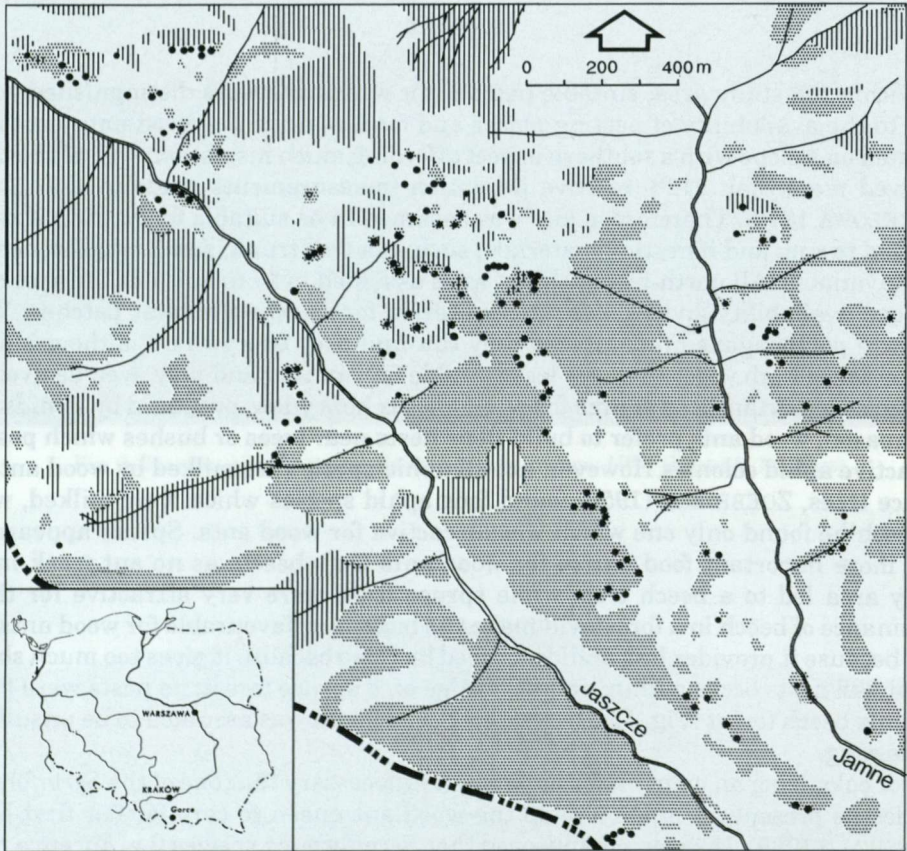


Fig. 4. Distribution of wood ant nests in a mountain area near Ochotnica Górna (Gorce National Park, sea inset), which is partly covered by two main forest types: dotted area – spruce forest (*Picetum tatricum*), hatched area – beech forest (*Fagetum carpaticum*), dots – wood ant nests, line of dashes and dots – watershed of Jaszczce.

METHOD

In order to compare the distribution patterns of the wood ant species, an inventory of nests was made in the study area. This work was done in the summer (two weeks

in June 1988 and two weeks in June 1989). Only for the two most common species in the area, *F. polyctena* and *F. rufa*, was it possible to relate their occurrence to the size of the habitat patch and its degree of isolation by using logistic regression analysis and associated deviance tests (JONGMAN et al. 1987). Two isolation parameters were used: firstly the distance of a habitat patch from the nearest occupied nest, and secondly all nests of a species within a distance of 100, 250 and 500 m from the edge of a habitat patch. Also, by using multiple regression analysis, the number of *F. polyctena* and *F. rufa* nests per habitat patch was related to the size of the patch and its degree of isolation. In the regression, the number of nests and the size of the patches were transformed to logarithms to obtain normal distributions of the data.

RESULTS

Nests of *F. polyctena* were the most common (107 nests). Many of these nests arose from budding, which explains why nests of *F. polyctena* had a clustered distribution, while nests of other wood ant species were more dispersed through the study area (Figs 5, 6). Nests of *F. polyctena* were assumed to belong to one colony if there was a regular exchange of workers between the nests, or if their foraging areas were not clearly separated by a "no man's land" (MABELIS 1979a). In this way, 17 colonies were distinguished. No time was available to carry out aggression tests in order to see whether workers of remote nests within a colony had become alienated. In that case the assumed number of 17 colonies will be too low. Mono- and oligogynous species normally do not split off daughter nests; most colonies remain monodomous. Consequently the number of their colonies normally equals the number of their nests (i.e. for the present study: *F. rufa* 26 colonies and 28 nests, *F. pratensis* 6 colonies and 7 nests and *F. truncorum* 20 colonies and 20 nests). Only two nest populations of *F. rufa* and one of *F. pratensis* split from a mother nest. These colonies certainly will have more than one queen. It appeared that 35% of the 57 habitat patches were not occupied by wood ants. It may be expected that patches which are smaller than 1 ha will be more often vacant than larger ones, because of a greater extinction chance of the local population, while the colonization chance will be less. According to this expectation it appeared that small patches were more often vacant than larger ones (41% and 9%, respectively; Fig. 7), but this difference was not significant (χ^2 test: $P > 0.05$).

Figure 7 shows a tendency for small habitat patches to be less often occupied by more than one species than large ones. This may be the result of competition, which will be more severe when there is a lack of space. In order to see whether habitat fragmentation may have a different effect on the survival chance of wood ant species with a different survival strategy, the occurrence of *F. polyctena* and *F. rufa* was related to the size of the habitat patches and their degree of isolation. It appeared that the presence of *F. rufa* as well as the number of its nests, was not correlated with patch area. So *F. rufa* built no more nests in large habitat patches than in small ones. However, in the case of *F. polyctena* there was a positive relationship ($P < 0.01$). This is in agreement with the expectation that a polygynous colony will thrive better in a

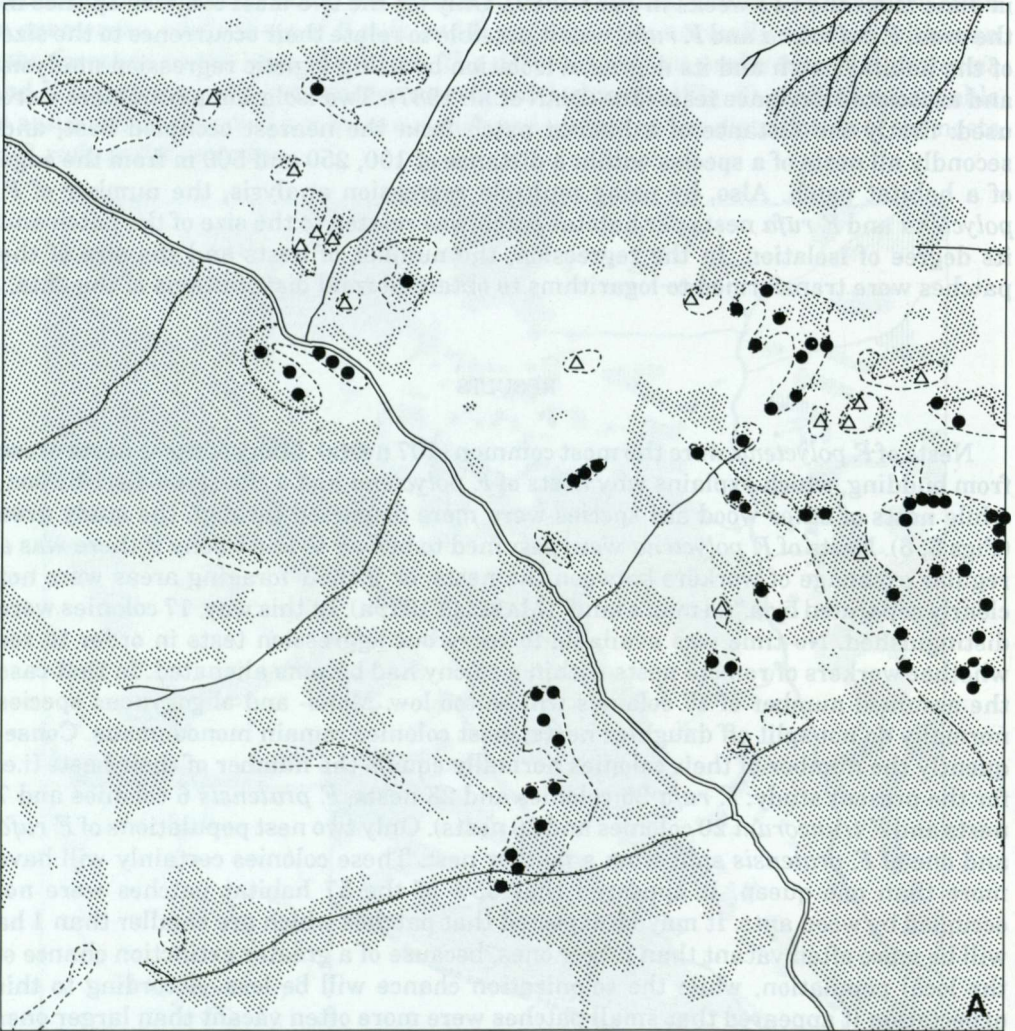


Fig. 5 A (for a caption: see next page).

large area of habitat, where it can spread its risk of extinction by budding, which a monogynous colony is not able to do.

Consequently, a polygynous species, like *F. polyclena*, has a much greater survival chance in a large habitat patch than a "monogynous" species, such as *F. rufa*, the more so because the former can exclude the latter from the patch by means of aggression; *F. polyclena* is a stronger competitor than *F. rufa* as a result of its greater worker force (MABELIS 1986). However, if *F. rufa* is present on a habitat patch which is not too large, it can prevent the establishment of *F. polyclena*. The smaller the

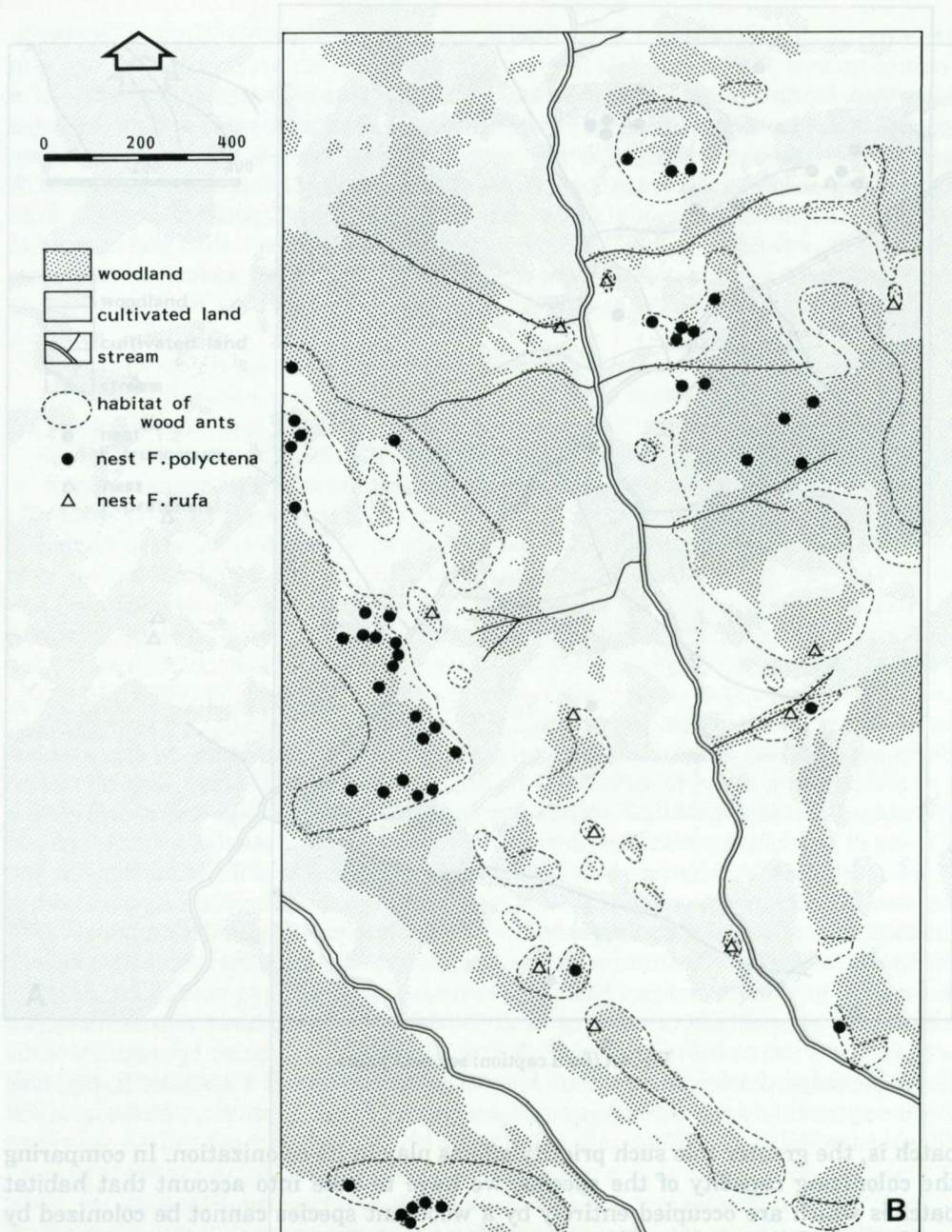


Fig. 5B. Distribution of nests of *Formica polyctena* and *F. rufa* in the sectors of the study area (A and B, respectively; see Fig. 1); habitat islands are encircled by a dashed line.



Fig. 6A (for a caption: see next page)

patch is, the greater role such priority effects play in its colonization. In comparing the colonizing capacity of the species, we have to take into account that habitat patches which are occupied entirely by a wood ant species cannot be colonized by another wood ant species. Therefore we excluded these patches from analysis as vacant habitat (13 for *F. rufa* and 22 for *F. polycтена*). Thus, 44 habitat patches were left for *F. rufa* and 35 for *F. polycтена*.

The analysis showed no significant correlation between the occurrence of a species in a habitat patch and the distance of that patch from the nearest occupied nest.

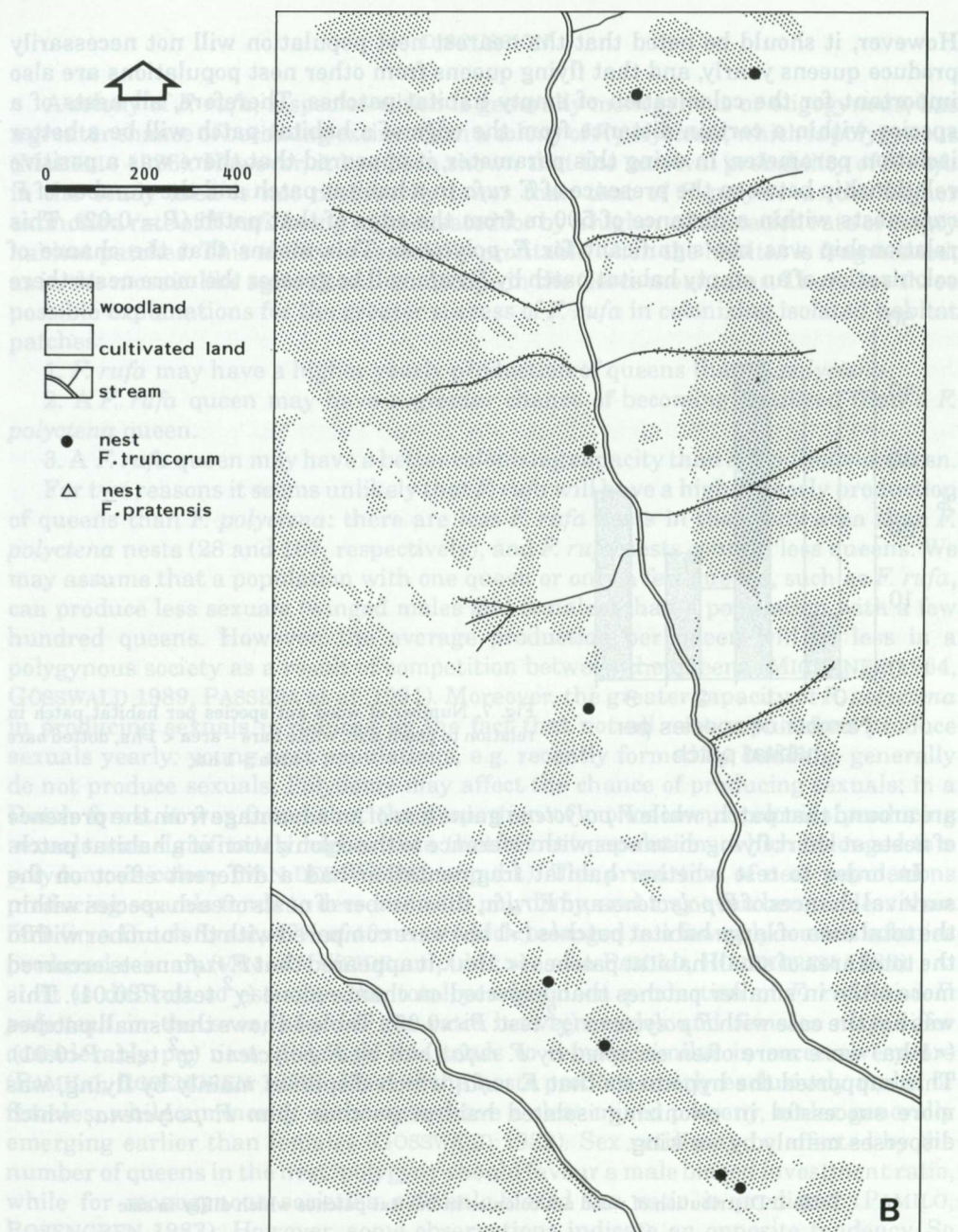


Fig. 6B. Distribution of nests of *Formica pratensis* and *F. truncorum* in the sectors of the study area (A and B, respectively; see Fig. 1).

However, it should be noted that the nearest nest population will not necessarily produce queens yearly, and that flying queens from other nest populations are also important for the colonization of empty habitat patches. Therefore, all nests of a species within a certain distance from the edge of a habitat patch will be a better isolation parameter. In using this parameter, it appeared that there was a positive relationship between the presence of *F. rufa* in a habitat patch and the number of *F. rufa* nests within a distance of 500 m from the edge of that patch ($P = 0.02$). This relationship was not significant for *F. polyctena*. This means that the chance of colonization of an empty habitat patch by *F. rufa* will be greater the more nests there

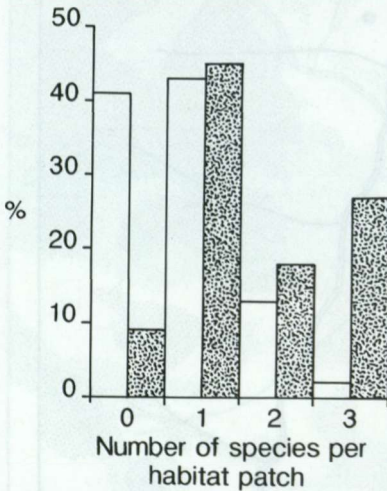


Fig. 7. Number of wood ant species per habitat patch in relation to patch size; white bars – area < 1 ha, dotted bars – area > 1 ha.

are around that patch, while *F. polyctena* gains less of an advantage from the presence of nests at short flying distances with reference to the colonization of a habitat patch.

In order to test whether habitat fragmentation had a different effect on the survival chances of *F. polyctena* and *F. rufa*, the number of nests of each species within the total area of large habitat patches (>1 ha) were compared with the number within the total area of small habitat patches (<1 ha). It appeared that *F. rufa* nests occurred more often in smaller patches than expected on chance alone (χ^2 test: $P < 0.01$). This was not the case with *F. polyctena* (χ^2 test: $P > 0.05$). Table 1 shows that small patches (<1 ha) were more often occupied by *F. rufa* than by *F. polyctena* (χ^2 test: $P < 0.01$). This supported the hypothesis that *F. rufa*, which disperses mainly by flying, was more successful in colonizing isolated habitat patches than *F. polyctena*, which disperses mainly by walking.

Table 1. Distribution of wood ant colonies in habitat patches which differ in size

Species present	Area		
	< 1ha	> 1ha	Total
<i>F. rufa</i>	19	2	21
<i>F. polyctena</i>	6	7	13
<i>F. rufa</i> + <i>F. polyctena</i>	1	3	4
Total	26	12	38

DISCUSSION

A colony of *F. rufa*, a species which is generally monogynous or oligogynous, has a greater chance of becoming extinct than a colony of *F. polyclena*, which is polygynous (MABELIS 1986). However, it has been shown that the survival probability of *F. rufa* in the study area is not necessarily lower than that of *F. polyclena*: the higher extinction rate of *F. rufa* being compensated for by a higher colonization rate of empty habitat patches. This ability is especially profitable when the habitat is fragmented, as in the mosaic-like agricultural landscape in the Gorce mountains. There are three possible explanations for the greater success of *F. rufa* in colonizing isolated habitat patches:

1. *F. rufa* may have a higher yearly production of queens than *F. polyclena*.

2. A *F. rufa* queen may have a greater chance of becoming fertilized than a *F. polyclena* queen.

3. A *F. rufa* queen may have a better colonizing capacity than a *F. polyclena* queen.

For two reasons it seems unlikely that *F. rufa* will have a higher yearly production of queens than *F. polyclena*: there are less *F. rufa* nests in the study area than *F. polyclena* nests (28 and 107, respectively), and *F. rufa* nests contain less queens. We may assume that a population with one queen or only a few queens, such as *F. rufa*, can produce less sexuals (winged males and females) than a population with a few hundred queens. However, the average production per queen will be less in a polygynous society as a result of competition between the queens (MICHENER 1964, GÖSSWALD 1989, PASSERA et al. 1991). Moreover, the greater capacity of *F. polyclena* in producing sexuals is reduced by the fact that not all nest populations produce sexuals yearly: young nest populations, e.g. recently formed by budding, generally do not produce sexuals. Polydomy may affect the chance of producing sexuals: in a Dutch forest it was found that the proportion of monodomous colonies producing sexuals was significantly higher than that of nest populations which belonged to a polydomous colony (VAN DER WEIDE, unpubl.). The proportion of nest populations producing sexuals tends to decrease with polydomy, and may even become less than 50% (in a Dutch forest, 47% of 40 nests which belonged to a few polydomous colonies produced sexuals (VAN DER WEIDE, unpubl.; see also PAMILO, ROSENGREN 1983).

It is difficult to estimate the total yearly queen production of *F. rufa* and *F. polyclena* in the area, because the ratio between males and females may differ considerably per nest, although this tends to remain similar in successive years (PAMILO, ROSENGREN 1983). Most of the nests produce nearly exclusively males or females, while a minority of the nests have a clear mixed progeny, males generally emerging earlier than females (GÖSSWALD 1989). Sex ratio may be affected by the number of queens in the nest: polygyny should favour a male biased investment ratio, while for monogynous societies a female-biased sex ratio is predicted (PAMILO, ROSENGREN 1983). However, some observations indicate an opposite tendency. So more factors may play a role in the sex ratio produced, e.g. the proportion of old and unseminated queens, as such queens can only produce males (EHRHARDT 1970, SCHMIDT 1972). Also, microclimate can affect sex-ratio: at low temperatures only males are produced (GÖSSWALD, BIER 1957). So shady conditions may favour a male-biased sex ratio. When the nest density is high, as in a polydomous colony, some

of the daughter nests may be established in a shady place. Such is the case in the study area: more nests of *F. polyctena* are situated on a shady place than nests of *F. rufa* (χ^2 test: $P < 0.05$). Thus, a relatively small proportion of the nests of a polydomous colony will produce sexuals, and only a relatively small proportion of the sexuals will be queens. Nevertheless, observations do not give enough support to the hypothesis that a nest population of *F. polyctena* will produce less queens on average than a nest population of *F. rufa*. Moreover, it is necessary to take into account that there are nearly four times more *F. polyctena* nests in the study area than *F. rufa* nests (107 and 28, respectively). Suppose that only half of the *F. polyctena* nests produce sexuals yearly and that 20% of these nests have a mixed progeny, 30% will produce queens and 50% males, then the number of *F. polyctena* nests that produce queens equals that of the number of *F. rufa* nests that occur in the area. Therefore, it is not likely that *F. rufa* will have a higher total yearly production of queens than *F. polyctena*.

The next step is to establish whether a *F. rufa* queen has a greater chance of becoming fertilized than a *F. polyctena* queen. In order to found a colony, a queen must leave the nest and find a male to fertilize her. However, not all queens in a polygynous society leave the nest. If males and queens are both present in the nest, it is very likely that the queens will be fertilized by their male nestmates and will stay in the nest. Observing a polygynous society of *F. lugubris* ZETT. in the Jura mountains during four successive days, it was noticed that all queens which left the nest interior were fertilized by males from the same nest as soon as they appeared on the nest surface (MABELIS, pers. observ.). Only males left the nest. The queens reentered the nest once they had been fertilized. Thus, not all the queens produced in any one nest, will take part in dispersal. However, the simultaneous occurrence of males and females in a nest population is rather exceptional and may have a negligible influence on the total number of dispersing females of *F. polyctena* in the study area.

Unfertilized queens produce only males. Thus, in order to colonize a habitat patch, a queen must meet a male. The chance of a meeting between males and females seems to be highest in a situation with a high nest density, as in a polydomous colony. For young queens of monodomous colonies, which are scattered through the area, it will be more difficult to find males from another nest, except when there are prominent local swarming sites nearby, such as a hilltop or a tree crown, where alates of both sexes gather. Such a gathering point for *F. rufa* was observed in W. Siberia (MARIKOVSKY 1961) and in Poland (WOYCIECHOWSKI 1990). Occasionally "ground swarms" of *F. rufa* were observed (MARIKOVSKY 1961). Swarming will increase the fertilization chance of a queen considerably. However, this phenomenon is rarely observed in *Formica* L. ants (e.g. CHAPMAN 1954, 1957, TALBOT, 1959, 1972), so we have no reason to assume that *F. rufa* queens have a higher chance of becoming fertilized than *F. polyctena* queens.

Finally, it is necessary to discuss whether the species have different colonizing capacities. A *F. rufa* queen will have a greater colonizing capacity than a *F. polyctena* queen if it has a greater dispersal power and/or a better establishment capacity. There is no information in the literature about dispersal distances of wood ant queens. Generally they are characterized as poor dispersers because of their clumsy flight behaviour (GÖSSWALD 1957, PAMILO et al. 1978, MIKKOLA 1986). Many young queens

which leave the nest flying will land a relatively short distance from the nest: on a calm sunny day in the Jura mountains (Switzerland) over 20% of the queens landed within a distance of 50 m from the nest ($n = 60$), and it is likely that most queens land within a distance of 500 m from the nest (MABELIS, FORTELIUS, unpubl.). However, with the help of a breeze they may cover longer distances. On several occasions wood ant queens were found at a distance of a few km from the nearest nest (MABELIS, pers. observ.), but longer flight distances are also observed: e.g. a *F. rufa* queen was found on a lightship at a distance of more than 6 km from the coast (HAESELER 1982). A *F. rufa* queen has a more convex thorax (mesonotum) than a *F. polyctena* queen (GÖSSWALD 1989), but there is no information in the literature about the possibility that a *F. rufa* queen has a better developed flight musculature, and consequently a better dispersal capacity, than a *F. polyctena* queen.

GÖSSWALD (1952) gives some data about differences in the chance of establishment of wood ant queens. It appears that a *F. rufa* queen has a greater chance of becoming adopted by a *F. fusca* population (with one queen) than a *F. polyctena* queen (χ^2 test: $0.025 < P < 0.05$). It may be that a *F. rufa* queen is more attractive to *F. fusca* workers than a *F. polyctena* queen (GÖSSWALD 1989). This suggests that *F. rufa* has a better establishment capacity than *F. polyctena*, and hence a greater success in colonizing habitat patches by means of (flying) queens.

Only occasionally has a *F. polyctena* queen succeeded in colonizing an isolated habitat patch, such as those in the south-east and north-west corners of the study area. However, there is also the possibility that those colonies are remnants of larger ones from a period in which a greater part of the area was covered by forest.

The chance that a queen from a nest will land on a habitat patch which is situated nearby will be greater than on a more remote habitat patch. However, the distribution pattern of the nests give no support to the idea that empty habitat patches which are situated at a greater distance from the nearest nest have a lower chance of becoming colonized by flying queens. It appears that the distance between empty patches and the nearest nest is not an important factor for their chance of becoming colonized. This result is not surprising, for two reasons. Firstly, the measured distances should be corrected for incline (flying uphill or downhill) and prevailing wind direction (flying upwind or downwind). Secondly, the nearest nest population will not necessarily produce queens yearly, and flying queens from other nest populations are also important for the colonization of empty habitat patches. Therefore, the distance of a habitat patch to all nests in the neighbourhood will be a better isolation parameter than a simple nearest-neighbour distance. The colonization chance of an empty habitat patch will generally be greater the more nests there are within a distance of 500 m of that patch. However, the relationship between the presence in a habitat patch and the number of nests within a distance of 500 m from the edge of that patch, was not significant for *F. polyctena*. It is obvious that this species was less able to benefit from nests at short flying distances from suitable patches than *F. rufa*. This is understandable, because walking is the most common means for *F. polyctena* to disperse. If the fact that some nest populations of the bigger polydomous colonies only occasionally have contact is taken into account, it is possible to divide these colonies into sub-colonies, i.e. interacting groups of nest populations. In doing so it appears that the distance of an occupied patch to the nearest *F. polyctena* nest is less than the

distance of an empty patch to the nearest nest (Wilcoxon test: $P < 0.01$). Thus, the distance between inhabited sites and empty patches is important for the chance of colonizing them by walking. The maximum distance which can be covered by this "step-by-step-dispersal" is about 100 m in one year (ROSENGREN, PAMILO 1983, MABELIS, unpubl.), but in general ants do not build daughter nests at such large



Fig. 8. Connectedness of the landscape near the Gorce National Park; the narrow wooded strip in the centre acts as habitat and a corridor for wood ants (see Fig. 9). (Photo A. MABELIS).

distances from their own nest, and certainly will not do so yearly. So the dispersal speed by means of budding is much less than 100 m per year. The connectivity of the landscape for walking individuals is crucial for the dispersal of polygynous species. It is high in the study area (Figs 8, 9): narrow wooded and stony strips amidst inhabitable land are sometimes used by wood ants as a corridor in order to enlarge their foraging area or to avoid potentially fatal intraspecific encounters (MABELIS 1979a, b). If the wooded strip is of good habitat quality, it may be used as a habitat in itself (Figs 8, 9), in contrast to intensively-used agricultural areas, where such landscape elements are subject to disturbances. The resistance of heterogeneous hayfields for wood ant workers is also much lower than that of highly productive meadows, which have a dense and homogenous grass cover. Several times it was observed that wood ants were crossing a hayfield over a distance of 40–50 m in order to colonize a habitat patch, while in the Netherlands it was established that wood ants do not walk further than a few meters from the forest edge into highly productive grassland (MABELIS, pers. observ.). Sunken roads and streams are barriers for walking individuals. Only occasionally are wood ants able to cross such a barrier, e.g.

they can use a tree which has fallen over a stream as a bridge. On two locations it was observed that wood ants had built a daughter nest on the other side of a stream, using a tree stem as a bridge. After the bridges collapsed, the daughter populations became isolated from the rest of the colony and died the next year.

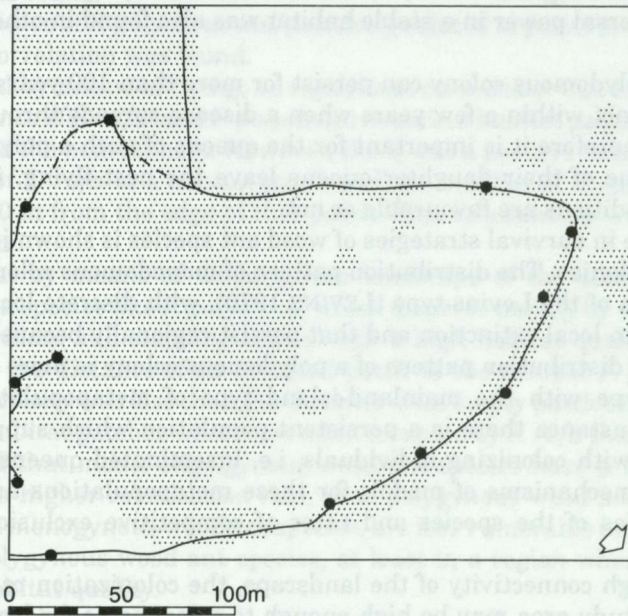


Fig. 9. Connectivity function of a wooded strip for wood ants; dotted area – woodland, white area – hayfield, dots – nests of *Formica polyctena*, lines – wood ant tracks (see Fig. 8).

So a polygynous species, like *F. polyctena*, can only disperse effectively in large, continuous habitats and in a situation where habitat patches are connected by corridors. In such situations, *F. polyctena* can exclude gradually all monogynous and oligogynous colonies of *F. rufa*, because of its superior competitive ability. However, *F. rufa* is more effective in colonizing isolated habitat patches. So there is a trade-off between competitive and dispersal abilities: *F. rufa* is a better colonizer, while *F. polyctena* is a better exploiter of its habitat (compare *Daphnia* species in rockpools: HANSKI, RANTA 1983, BENGTTSSON 1991). Patchiness of their habitat in the study area allows the coexistence of these competitors, which would not coexist for such a long time in a homogeneous environment (cf. LEVIN 1974). Coexistence of the two competitors can also be ascribed to the difference between the local and the regional time-scales of their population dynamics: *F. rufa* occupies a higher fraction of the habitat patches in the study area than *F. polyctena* (44% and 23%, respectively), while the average local population size of *F. rufa* is smaller, and hence the extinction rate higher (cf HANSKI 1983).

Leaving the colony is very risky for young queens: most of them succumb to predators, such as worker ants and birds. So in large and stable habitats it will be more profitable for queens to remain in the population, i.e. either to stay in the mother nest, or to be transported by worker ants to new nest sites. In other words: budding and reduced nuptial flight are more or less correlated (ITO, IMAMURA 1974). Such a reduction of dispersal power in a stable habitat was also found in other insects (e.g. DEN BOER 1990).

Although a polydomous colony can persist for more than 100 years in an area, it may become extinct within a few years when a disease spreads through the colony (ELTON 1977). Therefore it is important for the queens of such a polygynous colony that at least some of their daughter queens leave the nest flying, irrespective of whether nest conditions are favourable or not.

The difference in survival strategies of wood ant species is shown in the distribution pattern of colonies. The distribution pattern of monodomous colonies resembles a metapopulation of the Levins type (LEVINS 1970), with discrete local populations that are subject to local extinction and that persist regionally because of (re)colonization, while the distribution pattern of a polydomous colony is more a combination of the Levins type with the mainland-island type of metapopulation structure, because in this instance there is a persistent population which supplies marginal habitat patches with colonizing individuals, i.e. inseminated queens (cf HARRISON 1991). The key mechanisms of models for these metapopulations are the relative colonizing abilities of the species and rates of competitive exclusion (cf HANSKI, GILPIN 1991).

Due to the high connectivity of the landscape, the colonization rate of wood ant colonies in the study area may be high enough to compensate for local extinctions. This may be true for mono(-oligo)gynous species which disperse by means of flying queens, as well as for polygynous species, which disperse mainly by means of walking individuals. However, a good habitat quality is crucial for maintaining a high connectivity of the landscape. Intensification of agriculture in the study area will not only increase the extinction rate of local populations, but also decrease the colonization rate of empty habitat patches, and thus threaten the survival of wood ant species in the area.

RECAPITULATION

1. Most of the wood ant nests are situated on a slope with a southern aspect affording much insolation.
2. Nearly all nests occur within, or the edge of, a spruce forest; no nests were found within a beech forest (Fig. 4).
3. In the study area four wood ant species occur (Figs 5, 6): *Formica polyctena* (107 nests), *F. rufa* (28 nests), *F. pratensis* (7 nests) and *F. truncorum* (20 nests).
4. The chance that small habitat islands will be occupied by wood ants is not significantly less than that for larger islands (Table 1).

5. Large habitat islands are more often occupied by more than one species than small islands (Fig. 7).

6. The number of *F. polyclena* nests per habitat patch (as a measure of local population size) was positively correlated with patch area. In the case of *F. rufa*, no correlation was found.

7. The presence of *F. polyclena* was positively related to patch area, but in the case of *F. rufa* no correlation was found.

8. Dispersal by means of flying: no significant correlation was found between the presence/absence of *F. rufa* (and *F. polyclena*) nests in a habitat patch and the distance of that patch to the nearest nest. However, there was a positive relationship between the presence of *F. rufa* in a habitat patch and the number of *F. rufa* nests within a distance of 500 m from the edge of that patch. This relationship was not significant for *F. polyclena*.

9. Dispersal by means of walking: the landscape of the study area is highly permeable for a species like *F. polyclena*, which disperse mainly by walking, i.e. there are many corridors and stepping stones with a high habitat quality (Figs 2, 3, 9). Consequently, the distance of an occupied patch to the nearest *F. polyclena* nest of another (sub-)colony was less than the distance of an empty patch to the nearest nest.

10. Small habitat patches were more often occupied by *F. rufa* than by *F. polyclena*. It is concluded that mono-(oligo)gynous wood ant species have a higher extinction rate, but also a higher colonization rate, than polygynous wood ant species. Hence, it appears that monogynous wood ant species, are less vulnerable to habitat fragmentation than polygynous wood ant species, at least in a region where the fragments have a high habitat quality.

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STRESZCZENIE

Loty jako wyraz strategii życiowej rudych mrówek leśnych (*Hymenoptera, Formicidae*) w krajobrazie mozaikowym

Badano rozsiadanie populacji rudych mrówek leśnych w rolniczo-leśnym krajobrazie Gorców (Karpaty Wsch.) w dolinach potoków Jaszczce i Jamne. Stwierdzono tam występowanie czterech gatunków: *Formica polyctena* FOERST. (107 gniazd), *F. rufa* L. (28 gniazd), *F. pratensis* RETZ. (7 gniazd) i *F. truncorum* FABR. (20 gniazd) (Figs 5, 6). Gniazda w większości zlokalizowane były na stokach o wystawie południowej, zapewniających mrówkom odpowiednie nasłonecznienie. Niemal wszystkie gniazda były położone w obrębie lub na brzegach lasów świerkowych; w buczynach nie znaleziono ani jednego mrowiska (Fig. 4). Możliwość zasiedlenia przez rude mrówki leśne małych "wysp" środowiskowych nie była istotnie mniejsza niż "wysp" dużych (Tab. 1). Duże wyspy środowiskowe były natomiast częściej niż małe zasiedlone przez więcej niż jeden gatunek (Fig. 7). Zagęszczenie gniazd *F. polyctena* na danym skrawku odpowiedniego środowiska (jako miara wielkości lokalnej populacji) było pozytywnie skorelowane z wielkością obszaru. W przypadku *F. rufa* takiego związku nie stwierdzono. Także obecność *F. polyctena* była, a *F. rufa* nie była, związana z rozmiarem środowiska. Rozprzestrzenianiu się *F. rufa* służą loty godowe; nie stwierdzono istotnego związku między obecnością lub brakiem *F. rufa* (i *F. polyctena*) na danej wyspie środowiskowej a odlegością tej wyspy od najbliższego gniazda. Tym niemniej znaleziono pozytywną korelację między obecnością *F. rufa* na wyspie środowiskowej a liczbą gniazd tego gatunku w promieniu 500 m od brzegu tej wyspy. Taka zależność nie występowała w przypadku *F. polyctena*. *F. polyctena* rozprzestrzenia się głównie poprzez podziały społeczeństw, a więc drogą naziemną, czemu sprzyja ukształtowanie krajobrazu na badanym obszarze (korytarze ekologiczne i oderwane skrawki optymalnego środowiska, układające się w ciągi "stacji przejściowych") (Figs 2, 3, 9). W związku z tym odległość zajętej wyspy środowiskowej od najbliższego gniazda innego społeczeństwa *F. polyctena* była mniejsza niż odległość między wolną wyspą a najbliższym mrowiskiem. Małe wyspy środowiskowe były częściej zajęte przez *F. rufa* niż *F. polyctena*. Stwierdzono, że mono(-oligo)geniczne gatunki rudych mrówek leśnych odznaczają się wyższym wskaźnikiem wymierania, ale zarazem większą efektywnością kolonizowania nowych obszarów. Tym samym mrówki monogeniczne są mniej niż poligeniczne wrażliwe na fragmentację środowiska, przynajmniej tam, gdzie zachowane skrawki środowiska zachowują charakter korzystny dla rudych mrówek.