Gene flow and population viscosity in *Myrmica* ants

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The amount of gene flow and population viscosity were studied in two red ant species, *Myrmica ruginodis* and *M. rubra*. Differentiation between populations at the local scale (within the dispersal distance of individuals) and between localities further apart was estimated using Wright's F -statistics. Population viscosity was described using spatial autocorrelation of allele frequencies of nests. The differentiation patterns in the two species are clearly distinct, F_{ST} values being an order of magnitude larger in *M. rubra* (*M. rubra*: F_{ST} = 0.205 between sites within localities and 0.199 between localities; *M. ruginodis*: F_{ST} = 0.027 and 0.014 between sites within localities, 0.009 between localities). Thus, assuming the island model, much less gene flow occurs between neighbouring *M. rubra* than *M. ruginodis* sites. Allele frequencies of nests close to each other are positively autocorrelated in both species. This suggests that new nests are commonly founded close to the mother nest, most probably by division of existing nests. *M. rubra* forms large multinest societies, which dominate substantial areas, whereas such multinest colonies are rare in *M. ruginodis*.

Keywords: dispersal, gene flow, *Myrmica* nest budding, social insects, sociogenetic organization.

Introduction

Mutation, genetic drift and locally differing selection pressures are evolutionary factors leading to major genetic differences, and ultimately to speciation of isolated populations. Apart from these factors genetic differences may arise because of the founder effect. If local populations are founded by a small number of individuals, through bottlenecks, they may differ from their source populations because of chance (e.g. Nei, 1987). On the other hand, dispersal of individuals prior to reproduction may lead to gene flow, which is a powerful factor opposing differentiation. Generally a very small number of migrants is enough to prevent substantial differentiation among populations (Slatkin, 1987). Gene flow can be restricted because of subdivision of populations, where individuals move mainly within physically or otherwise separated subpopulations, or because of isolation-by-distance in a continuous population.

Social insects live in family units, colonies, where individuals are usually more related to each other than to randomly chosen individuals of the population (e.g.

Hölldobler & Wilson, 1990). This adds another level to the studies of genetic differentiation in addition to the conventional geographical variation among separate populations or subpopulations. Genetic differentiation between colonies can be measured as genetic relatedness within colonies (genotypic correlation between colony members; Hamilton, 1972). Within-colony relatedness is a central element in the kin selection theory for the evolution of altruistic behaviour (Hamilton, 1964). Because of this most genetic studies of social insects have focused on intra-colony genetics instead of differentiation at higher levels of social organization or between geographical areas.

There is a strong association between the sociogenetic organization of the colonies and means of dispersal of ants. Monogynous species (species with a single queen in each colony) generally take part in mating flights and found new colonies independently or by temporarily parasitizing colonies of alien species whereas in polygynous species (many queens in a colony) females often mate within or close to the mother colony and colonies are frequently founded by division of existing ones (Rosengren & Pamilo, 1983; Keller, 1991). These differences in dispersal patterns

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lead to different expectations concerning the distribution of genetic variation. Monogyny associated with a mating flight should promote sufficient gene flow for a uniform distribution of allele frequencies over large areas. If polygynous colonies recruit their own daughters as new reproductives and polydomous (multi-nest) societies arise through budding, allele frequencies may cluster spatially, and the population become viscous. Budding and viscosity can, of course, be accompanied by long-distance dispersal of some sexuals, e.g. by males.

A pair of closely related red ant species, *Myrmica ruginodis* and *M. rubra*, provide a possibility to test whether the sociogenetic organization of populations is associated with gene flow (Pamilo & Rosengren, 1984). Ecological and genetic studies have previously shown that the colony types (number of queens per colony, affinity of nests) vary both within and between *Myrmica* species (Elmes, 1975, 1980; Seppä, 1992; Elmes & Keller, 1993; Pearson & Raybould, 1993). In this paper differentiation is studied at three levels: between nests within a site, between sites within the potential dispersal distance of sexuals and between localities covering a large geographical area. The study is based on allozyme markers, which are generally regarded as selectively neutral markers in the genome unless contradicting information is presented (Chakraborty & Leimar, 1987). No such information is available, and therefore selection is neglected as a force leading to genetic differences between populations and the results are interpreted merely to reflect the balance between gene flow and genetic drift.

Materials and methods

Species studied

The number of queens in *Myrmica* is a highly variable trait both within populations, between populations and between species. In this respect *M. rubra* and *M. ruginodis* represent the two ends of the spectrum: *M. rubra* usually has highly polygynous colonies whereas *M. ruginodis* is one of the most monogynous species of the genus. This distinction is, however, somewhat confused because of the coexistence of two social forms of *M. ruginodis*. The larger macrogyna form tends to have monogynous colonies, the smaller microgyna being on average more polygynous (Elmes, 1975, 1980; Elmes & Keller, 1993). The relative frequencies of the two forms cannot be estimated from the present data.

Mating flights in *Myrmica* are fairly local events and long-range dispersal is thought to be rare (Elmes & Clarke, 1981; Elmes, 1991). If gene flow is restricted,

genetic differentiation is expected between both *M. ruginodis* and *M. rubra* populations. *Myrmica* queens, including *M. ruginodis* and *M. rubra*, are typically adopted into existing colonies (Brian & Brian, 1949, 1955; Elmes, 1975, 1980; Mizutani, 1981; Kasugai *et al.*, 1983). Macrogyna queens of *M. ruginodis*, however, commonly found nests independently, either alone or in small groups (Brian & Brian, 1949). Therefore there are slightly different expectations concerning population viscosity in the two species: colonies of *M. rubra* should be more polydomous and their populations more viscous compared with *M. ruginodis*.

Samples

In *M. ruginodis* genetic viscosity within a population was studied in Savero, Anjalankoski, S.E. Finland, where 52 nests were found and sampled within a 20 × 20 m area. Differentiation of populations at a local scale was studied in two locations. Seven sites were sampled at Tvärminne zoological station, Hanko, S.W. Finland, and six in the vicinity of Hyytiälä forest research station, Juupajoki, Central Finland. The sample sites in Tvärminne were on different islands, separated by 250 m to 3 km within a 3 × 3 km area, which makes this population an ideal model of a subdivided population. The sites in Hyytiälä represent somewhat arbitrarily selected parts of a continuous population. The sites were located within a 6 × 6 km area and were separated by 500 m to 8 km. Genetic differentiation at a larger geographical scale was studied in an area covering most of the range of the species in Finland. Thirteen localities (including Savero, Tvärminne and Hyytiälä) were sampled (see Figs 1–3 and Table 1 for populations studied and sample sizes).

In *M. rubra* viscosity was studied within one site (TVP) at Tvärminne zoological station; 25 nests were found and sampled within a 10 × 20 m area. Five sites separated by 100 m to 1 km were sampled in Tvärminne. The sites were linearly located; three of them were on the mainland and two on different islands. Finally, even localities (including Tvärminne) were sampled (see Figs 1–3 and Table 1 for populations studied and sample sizes).

M. ruginodis is a very common red ant species in the Palearctic (Elmes & Clarke, 1981) and populations in boreal forests are often dense and continuous. Sampling covered large areas up to several square kilometers and, in Tvärminne, whole islands. Habitat requirements of *M. rubra* are more strict and populations are usually well-defined. Sampling was consequently carried out within smaller areas. From each population a considerable number of colonies was selected (see Table 1, for

Fig. 1 Location of the populations of *Myrmica* sampled in Finland.

sample sizes) and a small number of workers was sampled. The total number of colonies sampled was 824 in *M. ruginodis* and 227 in *M. rubra*; 6–20 workers from each colony in both species were analysed fresh or stored in -70°C up to several months before analysis. The number of workers analysed was generally equal per nest within a population, but varied between populations and species.

Electrophoresis

Worker samples were analysed using standard horizontal electrophoretic systems described in more detail by Seppä (1992) and Pamilo (1993). The loci studied in *M. ruginodis* were α -glycerophosphate dehydrogenase-1 (α *Gpdh-1*, E.C. number: 1.1.1.8), phosphoglycerate kinase (*Pgk*, 2.7.2.3) and esterase-2 (*Est-2*, 3.1.1.1, substrate: 4-methylumbelliferyl acetate). In the Savero population peptidase (*Pep*, 3.4.*., substrate: glycyl-L-leucine) was also studied. For *M. rubra* *Est-2*, *Pgk*, *Pep* and glutamate-oxaloacetate transaminase-1 (*Got-1*, 2.6.1.1) were examined.

Estimation of genetic differentiation

Genetic differentiation within subdivided populations is commonly described using Wright's F -statistics, where the standardized allele frequency variance among populations, F_{ST} , describes the amount of genetic differentiation between subpopulations (Wright, 1951). F_{ST} was estimated using the method of Cockerham (1969, 1973), which corrects for unequal sample sizes. Standard errors of the estimates were obtained by jackknifing over populations and loci and deviation from zero was determined using these values. The F_{ST} calculations were performed using B. Weir's DIPLOID.FOR computer program (Weir, 1990).

The island model of migration assumes that gene flow happens from any subpopulation to any subpopulation with the same probability and at an equilibrium of gene flow and genetic drift, F_{ST} is a function of the effective population size (N_e) and migration rate (m): $F_{ST} = 1/(1 + 4N_em)$ (Wright, 1943). F_{ST} can be estimated from genetic data and the number of migrating individuals (N_em) can be obtained. If $F_{ST} > 0.2$, there is said to be significant genetic differentiation between populations (Wright, 1943; Endler, 1977; Slatkin, 1987).

Population viscosity within the sites studied was characterized with a spatial autocorrelation method. The spatial autocorrelation coefficient of the variable, Moran's I , is obtained by correlating the values of the variable (e.g. allele frequencies) in the contiguous pairs of nests (Sokal & Oden, 1978). A pair of nests is contiguous if the nests are, for instance, connected with a Gabriel network. Two nests, A and B, are Gabriel-connected if all other nests are outside the circle whose diameter is the line A–B (Gabriel & Sokal, 1969). Another way to calculate the autocorrelation coefficient is to use a distance-connected correlogram, where correlation is calculated separately for all the pairs of nests belonging to a given distance class (Sokal & Wartenberg, 1983). Values of the variables are positively autocorrelated if the coefficient I is larger than the random expectation, which is slightly negative (Sokal & Oden, 1978).

In this work Moran's autocorrelation coefficient I was calculated for both Gabriel-connected and distance-connected nests. In order to study the extent of the viscosity several distance units were used in the distance-connected correlogram: 2, 3, 4, 5, 7 and 10 m (calculated in a cumulative way, the larger distance units including the smaller ones). The autocorrelation coefficient was calculated for all the alleles in the datasets as well as for the factor scores of the nests associated with the principal components of the complete set of alleles (Crozier *et al.*, 1984).

Fig. 2 Location of the *Myrmica* sampling sites at the Tvärminne Zoological Station (*).

Results

All the loci studied, except *a Gpdh-1* in *M. ruginodis*, were biallelic systems. In populations 1.1–1.7 and 2–7 (Table 2) up to three alleles were detected in *a Gpdh-1*, two slow ones (91 and 81) besides the common one (100). Later a fourth allele (fast, *F*) could be separated from the common one. Because *F* was most probably missed in the first populations and combined with 100, the alleles were joined also in the rest of the populations before the analyses. Furthermore, because 81 was always very rare, it was combined with 91. Allele frequencies were calculated weighting colonies equally irrespective of the number of individuals studied (Table 2).

Differentiation between sites and localities

In both species F_{ST} was estimated separately at two levels, between sites within Tvärminne and Hyytiälä areas and between localities. The estimates for individual loci and means over loci are presented in Table 3. Differentiation among *M. rubra* sites in Tvärminne is strong and significantly different from zero ($F_{ST} = 0.205 \pm 0.039$, $t_4 = 5.26$, $0.01 > P > 0.001$) and the estimate among localities is of the same magnitude ($F_{ST} = 0.199 \pm 0.062$, $t_7 = 3.21$, $0.05 > P > 0.01$).

In *M. ruginodis*, there is less differentiation among sites ($F_{ST} = 0.027 \pm 0.014$ in Tvärminne and 0.014 ± 0.007 in Hyytiälä). These values are not significantly different from zero ($t_6 = 1.93$, $t_{12} = 2.0$, respectively). Differentiation among *M. ruginodis* localities is

Fig. 3 Location of the *Myrmica* sampling sites in the vicinity of Hyytiälä Forest Research Station (*).

significant, although the F_{ST} estimate is even smaller ($F_{ST} = 0.009 \pm 0.000$). Assuming the island model, the estimates of the number of migrating individuals between sites, $N_e m$, are generally an order of magnitude larger in *M. ruginodis* than in *M. rubra* (Table 3).

Viscosity of populations

Moran's autocorrelation coefficients I are shown in Table 4 for individual alleles and factor scores of principal components (PCA). Because one of the aims of this work was to study the extent of viscosity within populations, only coefficients of the shortest distances are given (Table 4).

In *M. ruginodis* the first two factors of principal components explain 42 per cent and 21 per cent of the total variation. However, there is very little covariance among loci in this dataset and the first two factors describe mainly variation in two *aGpdh* alleles, 100 and *F*, respectively. Hence *PCA1* and *PCA2* give a similar result concerning autocorrelation as these alleles. The most polymorphic alleles contain most information, therefore the allele 100 of *aGpdh-1* and *PCA1* give the most reliable information about population viscosity. According to them both Gabriel-connected nests and nests up to 4 m from each other are positively autocorrelated. *PCA2* and the rest of the alleles show similar patterns, although the extent of the positive autocorrelation coefficients varies.

Table 1 Populations of *Myrmica* studied and sample sizes (N) as the number of colonies

Locality	N	Locality	N
<i>M. ruginodis</i>		<i>M. rubra</i>	
1 Tvärminne	217	1 Tvärminne	97
2 Oitti	35	9 Pusula	25
3 Verla	33	14 Hailuto	8
4 Jaala	41	15 Täktbukten	19
5 Lammi	24	16 Letto	23
6 Virrat	36	17 Tenkkula	27
7 Helsinki	13	18 Gallträsk	28
8 Oulanka	26		
9 Pusula	9		
10 Täktom	113		
11 Seitsemien	65		
12 Savero	52		
13 Hyytiälä	160		
Sites in the Tvärminne area			
1.1 Tvärminne Ö	36	1.A Niitty	21
1.2 Kvarnskär	17	1.B Pelto	26
1.3 Halsholmen	38	1.C Kasvimaa	12
1.4 Brännskär	25	1.D Porsgrundet	19
1.5 Skomakarskär	33	1.E Halsholmen	19
1.6 Kalvholmen	25		
1.7 Mellanskär	43		
Sites in the Hyytiälä area			
13.1 Ahvenkangas N	20		
13.2 Ahvenkangas S	26		
13.3 Kulo	22		
13.4 Susimäki	34		
13.5 Hyytiälä	29		
13.6 Naurisvuori	29		

There were two exceptions from the general pattern in *M. ruginodis*. Firstly, the autocorrelation coefficient of the Gabriel-connected nests in *Pep* was slightly smaller than the expected. However, the coefficient was larger than the expected in the distance class 0–2 m. This discrepancy probably arises because in some cases Gabriel-connected nests are further apart than 2 m. A more serious problem is that *Est* shows highly significant negative spatial autocorrelation consistently throughout the analysis. In other genetic analyses of *Est* (F_{ST} -analysis in this work and relatedness calculations elsewhere; Seppä, 1992, 1994 and unpublished data), the *Est* locus gives results similar to other loci and there has been no reason to suspect that *Est* is not a selectively neutral marker locus. The reason for the deviating result for *Est* remains unknown.

M. rubra shows a similar absence of covariance among loci and the first principal component factor

Table 2 Allele frequencies of the populations. In *Myrmica ruginodis* populations 1.1–1.7 and 2–7 allele *F* of *aGpdh-1* could not be separated from allele 100 and their frequencies are pooled into 100

<i>M. ruginodis</i>								
	<i>aGpdh-1</i>				<i>Pgk</i>		<i>Est-2</i>	
	100	<i>F</i>	91	81	100	<i>F</i>	100	<i>S</i>
1.1	0.737	—	0.220	0.044	0.886	0.114	0.644	0.356
1.2	0.759	—	0.241	—	0.826	0.174	0.885	0.115
1.3	0.786	—	0.214	—	0.895	0.105	0.811	0.189
1.4	0.644	—	0.329	0.027	0.876	0.124	0.842	0.158
1.5	0.766	—	0.210	0.023	0.966	0.034	0.647	0.353
1.6	0.740	—	0.245	0.015	0.957	0.043	0.762	0.238
1.7	0.743	—	0.213	0.044	0.791	0.209	0.647	0.353
2	0.673	—	0.325	0.003	0.857	0.143	0.696	0.304
3	0.744	—	0.250	0.006	0.805	0.195	0.695	0.305
4	0.678	—	0.297	0.025	0.836	0.164	0.624	0.376
5	0.743	—	0.244	0.013	0.813	0.187	0.777	0.223
6	0.667	—	0.320	0.013	0.753	0.247	0.743	0.257
7	0.477	—	0.523	—	0.785	0.215	0.801	0.199
8	0.494	0.146	0.360	—	0.794	0.206	0.702	0.298
9	0.474	0.226	0.300	—	0.662	0.338	0.646	0.354
10	0.557	0.161	0.272	0.009	0.800	0.200	0.690	0.310
11	0.510	0.154	0.300	0.034	0.743	0.267	0.691	0.309
12	0.493	0.200	0.286	0.021	0.833	0.167	0.740	0.260
13.1	0.610	0.122	0.255	0.013	0.782	0.218	0.493	0.507
13.2	0.600	0.082	0.318	—	0.790	0.210	0.669	0.331
13.3	0.609	0.088	0.253	0.049	0.855	0.145	0.669	0.331
13.4	0.543	0.106	0.327	0.024	0.874	0.126	0.666	0.334
13.5	0.497	0.108	0.365	0.030	0.771	0.229	0.751	0.249
13.6	0.502	0.140	0.335	0.022	0.793	0.207	0.657	0.343

<i>M. rubra</i>								
	<i>Est-2</i>		<i>Pgk</i>		<i>Pep</i>		<i>Got-1</i>	
	100	<i>F</i>	100	<i>S</i>	100	<i>F</i>	100	<i>F</i>
1.A	0.618	0.382	0.843	0.157	0.863	0.137	0.671	0.329
1.B	0.986	0.014	0.827	0.173	0.470	0.530	0.991	0.009
1.C	0.457	0.543	1	—	0.920	0.080	0.983	0.017
1.D	0.993	0.007	1	—	0.802	0.198	0.987	0.013
1.E	0.629	0.371	0.989	0.011	0.632	0.368	0.981	0.019
9	0.422	0.578	1	—	0.897	0.103	0.862	0.138
19	0.247	0.753	1	—	0.671	0.329	0.914	0.086
20	0.801	0.199	0.947	0.053	0.782	0.218	0.914	0.086
21	0.732	0.268	0.972	0.028	0.822	0.178	0.767	0.233
22	0.605	0.395	0.809	0.191	1	—	0.864	0.136
23	0.882	0.118	1	—	0.998	0.002	0.998	0.002

explains 67 per cent of the total variation, which almost exclusively arises from variation in *Pep*. *PCAl* and *Pep* show highly positive spatial autocorrelation both between Gabriel-connected nests and between nests up to 7 m from each other. The other variable locus, *Pgk*, gives a similar result.

Discussion

Gene flow and geographical differentiation

M. ruginodis and *M. rubra* are clearly distinctive in their patterns of gene flow. *M. rubra* populations show extremely strong differentiation. The estimate of F_{ST}

Table 3 F_{ST} estimates ($\pm$ SE) for individual loci, mean of loci and the consequent estimates of the number of migrating *Myrmica* individuals (N_{em}) assuming the equilibrium of the island model

Locus	Tvärminne	Hyytiälä	Whole data
<i>M. ruginodis</i>			
α Gpdh-1	0.007 $\pm$ 0.009	0.004 $\pm$ 0.004	0.009 $\pm$ 0.004
Pgk	0.035 $\pm$ 0.020	0.013 $\pm$ 0.008	0.010 $\pm$ 0.005
Est	0.043 $\pm$ 0.012	0.024 $\pm$ 0.022	0.010 $\pm$ 0.007
Mean	0.027 $\pm$ 0.014	0.014 $\pm$ 0.007	0.009 $\pm$ 0.000
N_{em}	9.0	17.6	
<i>M. rubra</i>			
Est-2	0.259 $\pm$ 0.138		0.244 $\pm$ 0.105
Pgk	0.111 $\pm$ 0.047		0.137 $\pm$ 0.099
Pep	0.158 $\pm$ 0.078		0.139 $\pm$ 0.067
Got-1	0.263 $\pm$ 0.218		0.073 $\pm$ 0.059
Mean	0.205 $\pm$ 0.039		0.199 $\pm$ 0.062
N_{em}	1.0		

was 0.2 both among sites and localities, a figure which has been interpreted to indicate significant differentiation between populations (Wright, 1943; Endler, 1977; Slatkin, 1987). This differentiation can be interpreted in terms of migration among the sites in the Tvärminne population, and the estimate of migrants, N_{em} , is one per generation. Hence the populations were rather isolated from each other, although they were separated by only 1 km at most.

The amount of differentiation between *M. ruginodis* populations was much smaller and the estimates of N_{em} were generally more than an order of magnitude larger. In contrast to *M. rubra*, dispersal of *M. ruginodis* sexuals apparently leads to gene flow between separate subpopulations. The higher F_{ST} value in Tvärminne compared with the continuous Hyytiälä population suggests that distances between the islands in Tvärminne form a dispersal barrier of some kind.

Elmes & Clarke (1981) failed to find any substantial morphological differentiation in *M. ruginodis* workers between nests or between higher levels of isolation. This study shows a similar pattern at the genetic level and supports the conclusion of genetic homogeneity within the species. Elmes & Clarke (1981) further suggested that the recent expansion of the species to its present range has caused the lack of variation. Alternatively, homogeneity can be maintained by continuous gene flow between populations.

Population viscosity and colony founding

Based on autocorrelation coefficients, populations are viscous in both species suggesting limited dispersal of females. A fraction of *Myrmica* females apparently do not disperse but stay in the mother colony and found new nests through budding. This is supported by the fact that coexisting queens are usually related in *Myrmica* (Pearson & Raybould, 1993; Seppä, 1994 and unpublished data), which in practice means that colonies do recruit their own daughters as new queens. Limited dispersal is probably mostly associated with the establishment of polydomous colonies by the splitting of existing polygynous colonies, but females could also found new nests independently in the vicinity of the parental nest. Whether the groups of nests are interconnected (polycalic) was not studied.

The mainly monogynous macrogyna form of *M. ruginodis* has previously been considered also as monodomous with independent colony founding (Brian & Brian, 1949, 1955). In contrast, the more polygynous microgyna form is known to be polydomous and to found new colonies by division of existing ones (Brian & Brian, 1949, 1955; Kasugai *et al.*, 1983). The population studied in our work (Savero) is a mixture of the two forms and there are several polydomous colonies of both forms (P. Seppä, unpublished data).

In order to maintain substantial genetic differences, as observed between *M. rubra* sites, gene flow must be very restricted. It is possible that sexuals do not disperse from one site to another, but it is more probable that they do disperse but are actively prevented from joining the gene pool of an alien colony. This should restrict the gene flow by females, but some gene flow would be expected to be carried by males. Restricted gene flow is expected to be associated with matings between members of the same colony.

We have interpreted the F_{ST} estimates as reflecting the numbers of migrating individuals. However, it is not at all certain that the study population of *M. rubra* fulfils the underlying assumptions (island model, equilibrium between gene flow and drift) and the pattern of genetic differentiation can largely reflect the founding history of the subpopulations. Differences between sites agree with the interpretation that the populations are founded by very few individuals. After a successful colonization *M. rubra* colonies become polygynous and polydomous and seem to be able to dominate large areas just as some mound-building *Formica* ants do (the 'rare patch dominators', Rosengren & Pamilo, 1983). Genetic differences between nearby *M. rubra* subpopulations are in fact as large as differences between colonies in the more monodomous *M. ruginodis*.

Table 4 Autocorrelation (*I*) for the independent alleles and factor scores of principal components (*PCA*)

	<i>α Gpdh-1</i>				<i>P_{gk}</i>	<i>Est</i>	<i>Pep</i>	<i>PCAI</i>	<i>PCA2</i>
	<i>100</i>	<i>F</i>	<i>91</i>	<i>81</i>					
<i>M. ruginodis</i>									
Allele frequency	0.493	0.200	0.286	0.021	0.833	0.740	0.794		
Gabriel-connected, <i>n</i> = 88	0.109***	0.192***	0.033***	0.418***	-0.033NS	-0.271***	-0.043**	0.119***	0.070***
Distance-connected correlogram									
0-2 m, <i>n</i> = 46	0.181***	0.391***	0.080***	0.217***	0.101***	-0.278***	0.038**	0.229***	0.187***
0-3 m, <i>n</i> = 107	0.075***	0.166***	-0.026NS	0.318***	0.110***	-0.119***	0.086***	0.125***	0.017***
0-4 m, <i>n</i> = 181	0.014***	0.162***	-0.018NS	0.310***	0.008***	-0.096***	0.022***	0.047***	0.091***
0-5 m, <i>n</i> = 267	-0.041***	0.096***	-0.054***	0.232***	0.033***	-0.116***	0.028***	-0.023NS	0.055***
0-7 m, <i>n</i> = 479	-0.051***	0.094***	-0.027***	0.120***	0.039***	-0.026***	0.006***	-0.041***	0.071***
0-10 m, <i>n</i> = 845	-0.029***	0.050***	-0.012***	0.014***	-0.007***	-0.029***	-0.050***	-0.040***	0.048***
<i>M. rubra</i>									
Allele frequency					0.827		0.530		
Gabriel-connected, <i>n</i> = 33					0.047**		0.276***	0.170***	
Distance-connected correlogram									
0-2 m, <i>n</i> = 31					-0.028NS		0.227***	0.116***	
0-3 m, <i>n</i> = 54					-0.021NS		0.150***	0.099***	
0-5 m, <i>n</i> = 113					0.007***		0.012***	0.021***	
0-7 m, <i>n</i> = 188					0.012***		-0.025***	-0.035*	
0-10 m, <i>n</i> = 255					-0.028***		-0.046***	-0.046***	

Gabriel-connected and distance-connected correlograms are shown; *n* is the number of observations in each case. Deviation from the expected value (*t*-test): NS *P* > 0.05; *0.01 ≤ *P* < 0.05; **0.001 < *P* ≤ 0.01; ****P* ≤ 0.001. Values significantly smaller than the expected (*M. ruginodis* - 0.020; *M. rubra* - 0.042) are in bold.

Gene flow, population viscosity and sociogenetic organization

The results from *M. ruginodis* and *M. rubra* generally agree with and strengthen the pattern arising from similar studies. *Formica truncorum* has two population types. One resembles *M. ruginodis* and has only monogynous colonies the other has polygynous colonies and resembles *M. rubra* (Sundström, 1993). As in *M. ruginodis* and *M. rubra*, the amount of gene flow between local populations is strikingly different in these two types ($F_{ST}=0.030$ and 0.190 , respectively; Sundström, 1993). There are no other good comparisons available, but our results can also be compared with some single species studies. Differentiation within a subdivided population is less in *M. ruginodis* ($F_{ST}=0.027$) than in *F. exsecta* and *F. fusca* on the same islands ($F_{ST}=0.090$ and 0.074 , respectively; Pamilo, 1983). Differentiation is also less between sampling sites within a continuous population in *M. ruginodis* ($F_{ST}=0.014$) than in smaller continuous areas in *F. transcaucasica* and *F. sanguinea* ($F_{ST}=0.072$ and 0.046 , respectively; Pamilo, 1983). Differentiation has not been studied in highly polygynous and polydomous ants, but our unpublished results in *F. aquilonia* show patterns similar to *M. rubra* and the polygynous *F. truncorum*. These results suggest that polydomous colonies in general can have little gene flow.

Population viscosity, or genetic similarity of closely located nests within a population, most probably results from nest budding and polydomy. Viscosity is shown by positive autocorrelation of closely located nests in *M. ruginodis* and *M. rubra*. Similar positive values of autocorrelation over short distances have been found in *F. sanguinea* (Pamilo, 1983) and *Rhytidoponera* sp. 12 (Crozier *et al.*, 1984). Viscosity has also been found in polydomous populations of *F. exsecta* (Pamilo & Rosengren, 1984) and in *Lasius neglectus* (Boomsma *et al.*, 1990), although detected with other methods. On the contrary, no short-distance autocorrelation was found in weakly polygynous *F. fusca* and *F. transcaucasica*. Their colonies are probably monodomous, although allele frequency differences among subpopulations and different parts of a continuous population suggested restricted dispersal (Pamilo, 1983).

Finally, based on RFLP polymorphism of mitochondrial DNA, *Leptothorax acervorum* nests having a common origin have been shown to be clustered. If the nests share the same genotype (haplotype), there is no doubt about the common maternal ancestor, because dispersing males cannot dilute the genetic composition of the maternally inherited mtDNA in daughter nests. This shows that dispersal of queens is restricted in *L.*

acervorum and nest founding is most probably dependent on budding (Stille & Stille, 1993).

In conclusion, *M. ruginodis* and *M. rubra* fulfil rather well the expectations of gene flow based on dispersal, sociogenetic organization and mode of nest founding outlined above. Both species are facultatively polygynous with limited dispersal during mating flights. This results in significant genetic differentiation between populations in *M. rubra* and in slight differentiation in *M. ruginodis*. New nests of the highly polygynous *M. rubra* are commonly started by budding from existing ones and colonies develop into large polydomous entities in suitable habitats. Once a polydomous colony has been established, gene flow at least by females is restricted and alien sexuals do not breed in the colonies. *M. ruginodis* employs a mixed strategy of dispersal and nest founding. Most of the colonies are monodomous, but a few polydomous ones can be found. The former colonies must have been founded independently by dispersing queens whereas the latter group also reproduces by budding.

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