Behav Ecol Sociobiol (2005) 57:339–349
DOI 10.1007/s00265-004-0864-8

ORIGINAL ARTICLE

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Seasonal polydomy and unicoloniality in a polygynous population of the red wood ant *Formica truncorum*

Received: 20 June 2004 / Revised: 8 October 2004 / Accepted: 12 October 2004 / Published online: 13 November 2004

Abstract Ant colonies may have a single or several reproductive queens (monogyny and polygyny, respectively). In polygynous colonies, colony reproduction may occur by budding, forming multinest, polydomous colonies. In most cases, budding leads to strong genetic structuring within populations, and positive relatedness among nestmates. However, in a few cases, polydomous populations may be unicolonial, with no structuring and intra-nest relatedness approaching zero. We investigated the spatial organisation and genetic structure of a polygynous, polydomous population of *Formica truncorum* in Finland. *F. truncorum* shifts nest sites between hibernation and the reproductive season, which raises the following question: are colonies maintained as genetic entities throughout the seasons, or is the population unicolonial throughout the season? Using nest-specific marking and five microsatellite loci, we found a high degree of mixing between individuals of the population, and no evidence for a biologically significant genetic structuring. The nestmate relatedness was also indistinguishable from zero. Taken together, the results show that the population is unicolonial. In addition, we found that the population has undergone a recent bottleneck, suggesting that the entire population may have been founded by a very limited number of females. The precise causes for unicoloniality in this species remain open, but we discuss the potential influence of intra-specific competition, disintegration of recognition cues and the particular hibernation habits of this species.

Keywords Ant · *Formica* · Unicoloniality · Seasonal polydomy · Genetic structure

Rainer Rosengren is deceased

Communicated by R.F.A. Moritz

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Introduction

Hamilton's (1964) theory of kin selection provides a framework to study helping behaviour and reproductive altruism. In social insects, colony members are typically highly related, and kin selection is considered the key force driving sociality (Bourke and Franks 1995; Crozier and Pamilo 1996), yet extensive variation in colony kin structure can be found even within species (Bourke and Franks 1995; Crozier and Pamilo 1996; Queller and Strassman 1998). Hence, colonies may have a single or several reproductively active queens (monogyny and polygyny, respectively). Nevertheless, in most cases, nestmates in polygynous colonies are related. Ecological factors have been invoked to explain the emergence of polygyny, in particular, high dispersal risks and low independent colony-founding success of individual queens (Nonacs 1988; Pamilo 1991; Keller 1995).

Polygyny is associated with new modes of colony reproduction. In addition to long-range nuptial flights, colony reproduction may also occur by budding, whereby mated females leave their natal nests with workers, and found a new nest nearby. The daughter nests may exchange workers, brood and food with their mother nest for several years. As a result multinest, polydomous colonies arise (Hölldobler and Wilson 1977, 1990; Pedersen and Boomsma 1999). Although polydomy per se has not been the subject of many theoretical studies (Nonacs 1993; Keller 1993a; Crozier and Pamilo 1996; see also for colony fission Macewicz 1979 and Bulmer 1983), it has been extensively described in terms of the genetic and social structure in many species (e.g. Seppä and Pamilo 1995; Banschbach and Herbers 1996a, 1996b; Chapuisat et al. 1997; Pedersen and Boomsma 1999; Van der Hammen et al. 2002). Colony reproduction by budding may give rise to populations with genetic structuring between groups of genealogically related nests, in addi-

tion to genetic structuring due to above-zero relatedness within nests. Such multicolonial populations comprise several colonies each with several nest units that exchange workers, as is the case, for example, in *Formica lugubris* (Gyllenstrand and Seppä 2003), *F. exsecta* (Liautard and Keller 2001) or *Plagiolepis pygmaea* (Trontti at al., unpublished work). Genetic structuring is often associated with variable levels of aggressiveness between nests of the same population, such that more distantly related nests behave more aggressively towards each other and thus are unlikely to exchange workers (Beye et al. 1997, 1998; Pirk et al. 2001; Debout et al. 2003).

However, in some extreme cases, populations are "unicolonial", with no clear colony boundaries. Consequently, little or no within-population structuring can be detected, and intra-nest relatedness within unicolonial populations is often statistically indistinguishable from zero. Such unicolonial populations often characterise tramp species, such as the Argentine ant *Linepithema humile* (Kaufmann et al. 1992; Passera 1994; Holway et al. 1998; Tsutsui and Case 2001; Giraud et al. 2002), the fire ant *Solenopsis invicta* (Ross et al. 1996), *Monomorium pharaonis* (Passera 1994), *Tetramorium bicarinatum* (Bolton 1980; Astruc et al. 2001) or *Lasius neglectus* (Boomsma et al. 1990). Multicoloniality and unicoloniality are, however, two extreme conditions along the same continuum (Bourke and Franks 1995), neither of them being permanent. Moreover, populations of a particular species may take different positions along this continuum, depending on the scale of the study. For instance, entire populations of *F. lugubris* can be considered multicolonial, but individual multi-nest colonies can be considered unicolonial (Gyllenstrand and Seppä 2003).

Unicoloniality has arisen repeatedly and confers undeniable ecological advantages, in terms of colonisation ability (Holway 1999; Tsutsui et al. 2000; Giraud et al. 2002), resource exploitation (Hölldobler and Lumsden 1980; Holway and Case 2001) and interspecific competition (Passera 1994; Human and Gordon 1996; Holway 1999). Complete worker sterility has been proposed to be a prerequisite for unicolonial societies to be evolutionarily stable (Passera 1994; Bourke and Franks 1995; Keller 1995). If intra-nest relatedness is low and workers are fertile, their incentive to lay male eggs increases dramatically (Wenseleers et al. 2004). This leads to reproductive conflicts (Keller 1995) and eventually to social disruption. Obligate worker sterility owing to lack of ovaries seems indeed to be the rule for most unicolonial species (Markin 1970; Oster and Wilson 1978; Bolton 1980; Keller 1988; Passera 1994; Ross 1993), with the exception of *Lasius neglectus*. Interestingly, *Lasius neglectus* is considered a newly emerged unicolonial, invasive species (Espadaler and Rey 2001). In ants of the subgenus *Formica* (or *Formica s. str.*), polygyny and polydomy are common, yet completely unicolonial populations seem to be absent (Pamilo 1983; Rosengren and Pamilo 1983; Rosengren et al. 1985; Beye et al. 1997, but see Chapuisat et al. 1997). Genetic data indicate that most *Formica* species, including our study species *F. truncorum*, have fertile workers, able to lay haploid male-destined eggs (Helanterä 2004). Hence, on grounds of worker fertility, unicoloniality would not be expected in *Formica* ants.

Here we investigate the spatial organisation and the genetic structure in the facultatively polygynous ant *F. truncorum* (Rosengren et al. 1985; Sundström 1993). Previous genetic studies on island populations have shown that monogynous populations of *F. truncorum* are unstructured, whereas polygynous ones tend to be structured at scales encompassing several neighbouring islands (Sundström 1989, 1993). The average nestmate relatedness varies among populations between zero and 0.75, with zero relatedness in some polygynous populations and above-zero relatedness in others (Sundström 1989, 1993; Seppä et al. 1995; Gyllenstrand 2002). The detailed genetic structure of polygynous *F. truncorum* populations with zero nestmate relatedness has not been studied, but behavioural data suggest that this species may have unicolonial populations (Rosengren et al. 1985, 1986). If so, this would be one of the first examples of a unicolonial non-invasive ant with fully fertile workers.

F. truncorum shares with its close relative, *F. yessensis* (Ito 1973; Ito and Imamura 1974; Higashi 1976), a unique way of hibernating, which involves a seasonal shift of nest site. Colonies of *F. truncorum* hibernate in forested areas (winter nests) and migrate at the onset of the reproductive season in May to summer nests in rocky outcrops located up to 100 m away (Rosengren at al. 1985). During the summer phase, workers have been observed to move extensively between nest units (Rosengren et al. 1985). We used nest-specific marking to study patterns of migration from winter nests towards summer nests, as well as movements between summer nests when the spring migration was completed. In addition, we used microsatellite markers to analyse whether individual colonies are maintained as genetic entities throughout the year or whether complete mixing occurs so that the population can be considered unicolonial.

Methods

Study population

Our polygynous, polydomous study population of *F. truncorum* is located in Haraholm, a 6-ha islet in the Inkoo archipelago, in the Gulf of Finland. The habitat consists mainly of sparsely pine-grown rock covered with lichen and mosses, with strips of denser pine forest in between. All suitable habitat on the island was inhabited by *F. truncorum* and, except for a few small peripheral areas, our sampling (performed on an area of approximately 3 ha) covered the inhabited area. Polygynous populations have a very high nest density compared to monogynous ones (around 18 nests/ha; Rosengren et al. 1985, 1986). During the summer 2001, the islet contained approximately 130 summer nests of *F. truncorum*, and no other *Formica* species. Our study area is representative of the whole population, and includes the main forest strip, containing most, if not all, winter nests present on the island (we did not find any winter nests outside this area), and three rocky areas with a high concentration of summer nests. Excluded summer nests were peripheral to the study area, and distributed evenly along the bor-

ders. Summer nests inside the study area that were established towards the end of the survey were not considered.

Study of migration patterns

In May 2001, the locations of all nests in the study area were mapped. Before the migration to summer nests had started, workers of 12 winter nests were mass marked with spray paints (Magix paints for white and light-blue, Maston paints for pink, silver, gold, copper, dark-blue, light-green, dark-green, grey and yellow). This method does not affect significantly the movements of the ants (Rosengren et al. 1985). At the end of the initial 2-week marking session, all winter nests were empty. Two days later we started to recapture workers in summer nests during two more weeks (six recapture events). In this way we were able to follow the entire process of migration. Recapture involved counting and removing all painted ants observed at the surface of each nest during 2 min. During this time approximately 700 marked workers were counted. This procedure enabled us to determine how many summer nests each winter nest was connected to, and whether each summer nest received workers from one or several winter nests. In addition, for each winter nest connected to more than two nests, the number of marked ants found in summer nests was regressed against the natural logarithm of the distance between the summer nests and the winter nest.

When the above colonisation and recapture phases were completed, workers of seven summer nests on the largest rocky area were mass marked with spray paint to survey movements between summer nests. Colours were carefully chosen to avoid confusion with workers painted in the winter nests. The recapture session started 2 days after marking was finished and was performed as described above. The entire recapture period lasted 3 weeks, and involved six recapture events. Approximately 1,700 marked ants were counted. From the recapture data, we calculated a drifting ratio, defined by Higashi (1978a) as, for each nest painted, the number of marked ants recaptured in a "wrong" nest divided by the sum of marked ants recaptured in their home nests and those recaptured in a "wrong" nest. To check whether pupae were moved between summer nests, worker pupae of 11 summer nests were marked with filter pen (500–2,500 pupae per nest, on average 1,235±743), and were recaptured 5 days later in their original summer nests, as well as in the surrounding ones (in total 38 nests).

In addition to the mark-recapture procedures, we collected 8 workers from 12 winter nests before colonisation (sample WW). Just after colonisation, 8 workers and 3 old queens were collected in each of 15 summer nests (samples WeS and QS, respectively). Finally, at the end of the breeding season, 8 workers and 8 worker pupae were sampled from each of 12 additional summer nests (samples WlS and PS, respectively). We refrained from collecting more than three queens per nest, as we did not want to jeopardise the survival of the nests and wanted to ensure a balanced sampling scheme. The very reasonable confidence intervals obtained also for the queens indicate that the statistical resolution even at these sample sizes was adequate. Eventually, the statistical power was considerably higher than indicated by the number of individuals sampled per collection event as the final analyses were performed on pooled samples (see Statistical analyses). The samples were stored in 99% ethanol for later analysis.

Genetic analyses

For the genetic characterisation of the population, we first performed a pre-selection for polymorphism at 11 microsatellite loci: Fl12, Fl20, Fl21, Fl29, Fl43 (Chapuisat 1996), Fe7, Fe13, Fe17, Fe19, Fe21 and Fe47 (Gyllenstrand et al. 2002). Six of these loci were discarded as five were monomorphic and one (Fl20) had null alleles. The statistical analyses were therefore performed using the five remaining polymorphic loci (Fl12, Fl21, Fe13, Fe17, Fe19). DNA was extracted from two legs of each individual in 200 μl 5% Chelex, and incubated for 2×15 min at 95°C (vortexed between the two incubation periods). PCR amplification was carried out in 10 μl reaction volume comprising 1.5 μl DNA template, 0.5 pmol primers, 1x Dynazyme PCR-buffer, 1.5 mM $MgCl_2$, 0.2 U enzyme (Dnazyme II, Finnzymes), 75 mM each dA/T/GTP and 6 mM dCTP nucleotides. The amplified fragments were internally labelled with α32P-dCTP (0.2 mCi/reaction). The PCR-profile comprised an initial denaturation step at 94°C for 5 min, 30 cycles of 1 min at 94°C, 30 s at the primer specific annealing temperature (55°C for Fl12, Fl21, Fe13, Fe19; 50°C for Fe17), and 30 s extension at 72°C, and then a final extension step of 5 min at 72°C. The PCR products were separated on 6% denaturing polyacrylamide sequencing gels (Sequagel, National Diagnostics) at 55 V/gel, and visualised by autoradiography.

Statistical analyses

Descriptive statistics [number of alleles, observed heterozygosity and gene diversity expressed as Nei's (1978) expected heterozygosity, He], as well as tests for Hardy-Weinberg proportions, tests for linkage disequilibria and Wright's *F*-statistics were computed with GENEPOP (Raymond and Rousset 1995) and GENETIX 4.02 (Belkhir et al. 2001). Significance of global and pair-wise Fst values were determined by 1,000 permutations of genotypes among nests (test for differentiation, Goudet et al. 1996). In addition, we estimated intra-nest relatedness with the program RELATEDNESS 4.2 (Queller and Goodnight 1989).

A test for bottleneck (reduction in population size) was performed using the method developed by Cornuet and Luikart (1996). After a bottleneck, populations experience a correlative reduction of the number of alleles and gene diversity (He in the sense of Nei 1978) at selectively neutral loci, but the number of alleles decreases faster than the gene diversity (Nei et al. 1975). Thus, in a population that has recently undergone a bottleneck, the observed gene diversity is higher than the gene diversity expected at mutation-drift equilibrium (Maruyama and Fuerst 1985) as computed from the observed number of alleles (Cornuet and Luikart 1996). To determine whether the study population had undergone a bottleneck, we applied the Wilcoxon sign-rank test implemented in the software BOTTLENECK 1.2 (Piry et al. 1999) on observed and expected gene diversities. We used a two-phase model (TPM) in which 90% of the mutations follow the strict stepwise mutation model and 10% produce multistep changes (variance: 30%). For all the above-mentioned analyses except the tests for bottleneck and linkage disequilibria, each nest was entered as one population. The five samples were analysed both separately, and after pooling the samples WeS and QS, and WlS and PS, respectively, which allowed us to increase the power of the tests. In both cases, workers and queens or workers and pupae were collected from the same nests at the same time, and the samples were genetically not differentiated (test for differentiation: P=0.368, and P=0.770, respectively, not assuming Hardy-Weinberg equilibrium).

The genetic structure of the different samples, i.e. how individuals cluster together according to genetic criteria, was inferred from genotype data using the program STRUCTURE (Pritchard et al. 2000), based on a Bayesian approach. For each possible partition in K subpopulations, the program computes the probability of the observed genetic data X given K (Pr[X|K]). The posterior probability of each partition can then be calculated, as the ratio $Pr(X|K)/\Sigma Pr(X|K=i)$. Isolation by distance was tested by regressing genetic distances (Fst) on the logarithm of spatial distances, followed by a Mantel test (Mantel 1967) performed with the program GENETIX 4.02.

Results

Colonisation and migration patterns

During the migration from winter nests to summer nests, workers from the same winter nest colonised several

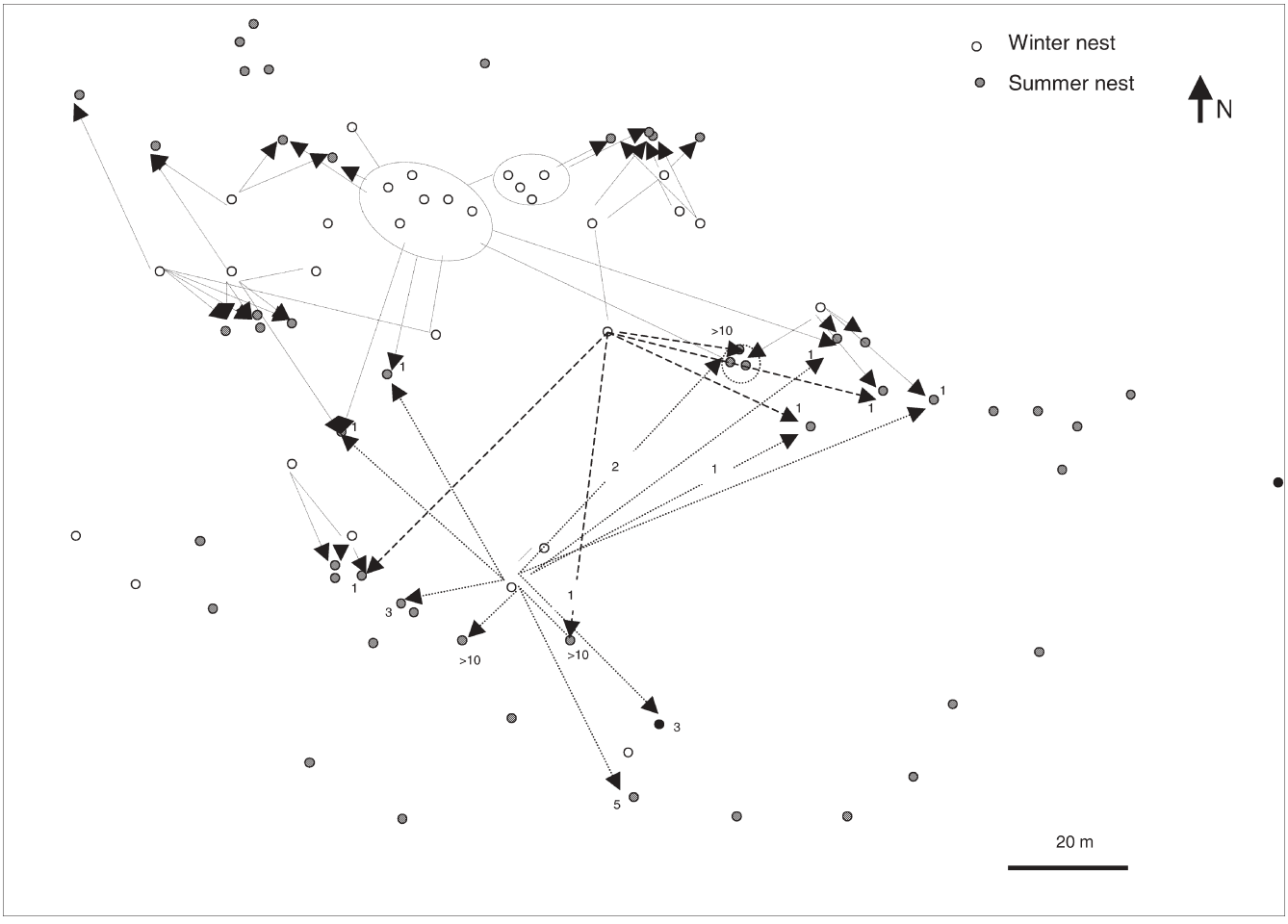

Fig. 1 Colonisation of summer nests from winter nests. The *arrows* indicate which summer nests are connected to the winter nests that were marked. For two winter nests (*underlined with special line patterns*) the number of marked ants recaptured in each of the connected summer nests (expressed as the largest number of marked ants observed during one recapture event) is shown. Movements between winter nests are also shown. *Ellipses* indicate intensive traffic between the nests.

summer nests, and eventually were found in areas up to 72 m from their original winter nest (Fig. 1). The number of marked workers recaptured in the summer nests decreased with distance to the source winter nest (correlation coefficient =–0.826±0.082, n=8, Fisher's combined probability: χ^2=46.13, df=16, P=0.012; 4 winter nests were connected to only 2 summer nests each, and could not be included in the analysis). Moreover, the same summer nest could be colonised by workers from different winter nests (Fig. 1). Because about 60% of the winter nests remained unpainted, the actual number of winter nests that were connected to the same summer nest is probably greater than this. Finally, we also found that ants moved between winter nests (Fig. 1).

After colonisation, movements between summer nests were extensive on all rocky areas, and sometimes occurred in both directions (Fig. 2). This probably reflects a stepwise and centrifugal colonisation process whereby the most distant summer nests are not colonised directly from the winter nests, but through a sequence of intermediate summer nests (Fig. 2). The maximum migration distance between two summer nests recorded during our survey was 95 m, although we found painted workers even further away several weeks later. The drifting ratio ranged from 0.38 to 0.80 (on average 0.655±0.173, n=7), showing that the majority of the ants do not stay in the nest they have first colonised. Pupae were found in only 13 of the 38 nests we checked. In these nests, on average 798±1,028 pupae per nest were collected. The recapture rate of painted pupae in their original nests was extremely low (1.50±2.00%, n=8), and even lower in the surrounding nests (0.12±0.27%, n=5). This was in part due to workers removing the pupal cocoon, and thus the mark. This occurs regularly in *F. truncorum* and also was observed in unmarked nests. Pupae were recaptured only in the nearest neighbours of the original nests. Moreover, while we frequently saw workers moving or being carried between nests, we saw pupae being carried only twice. These observations indicate that pupae were transported between summer nests to a much lesser extent than workers themselves moved or were carried between nests. We cannot entirely exclude that the procedure of marking caused the workers to move pupae.

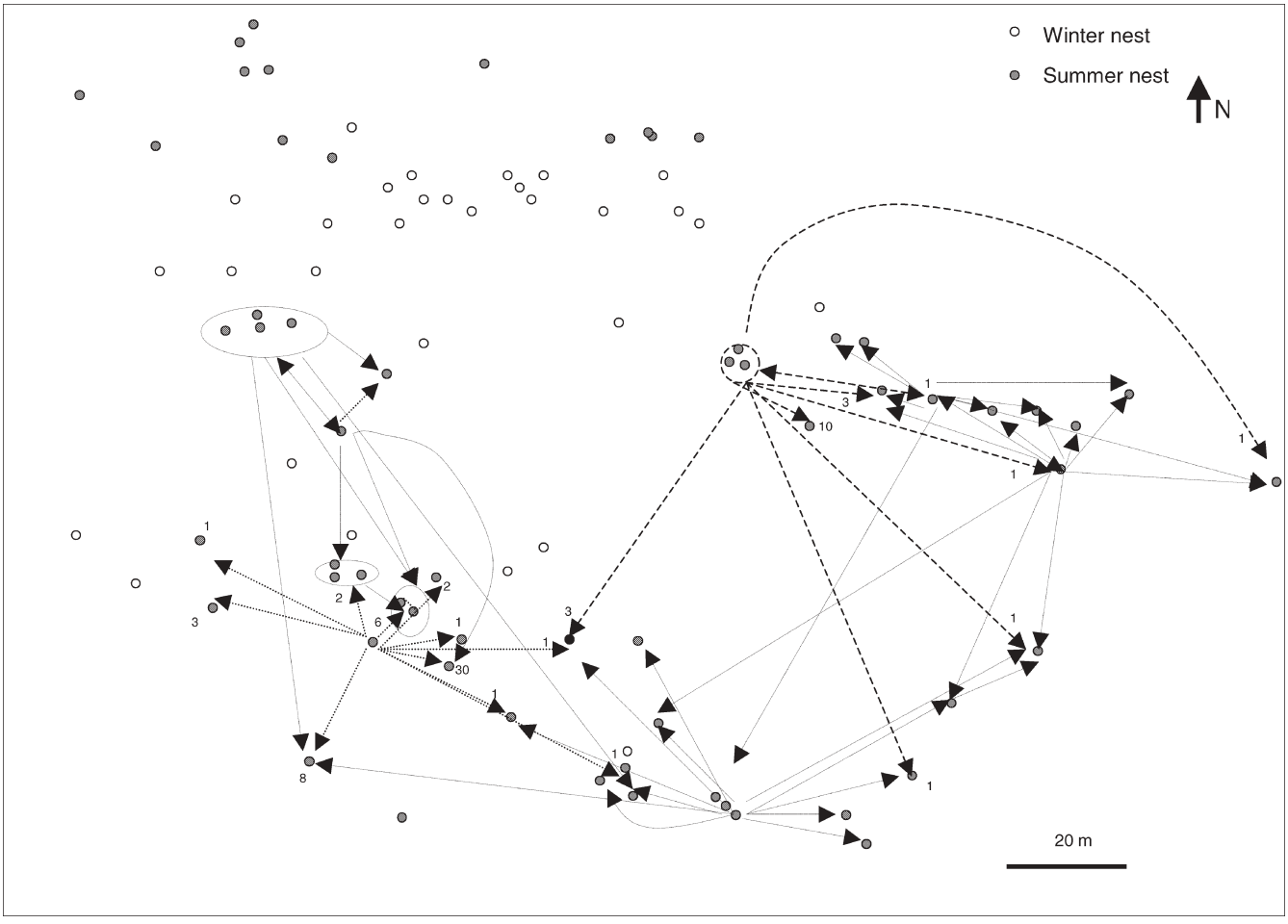

Fig. 2 Movements between summer nests of the main rocky area. The *arrows* indicate the direction of the movements. For two summer nests (*underlined with special line patterns*) the number of marked ants recaptured in each of the connected summer nests (expressed as the largest number of marked ants observed during one recapture event) is shown. *Ellipses* indicate intensive traffic between the nests.

Genetic analysis

Two loci (Fe19 and Fe13) showed significant linkage disequilibrium in the samples WW (P=0.032), and in the combined samples WeS+QS (P=0.008) and WlS+PS (P=0.0442). The correlation coefficients between alleles at these loci (Weir 1979) were r=0.207, r=0.128 and r=0.161, respectively. Given that these values were rather low, we decided to keep both loci for the analyses.

Despite the large sample size (in total, 453 individuals were screened), only little variation could be detected at the 5 microsatellite loci, the maximum being 3 alleles (Table 1). In each of the five samples, no heterozygote excess or deficit could be detected at any locus, indicating that none of the samples departed significantly from the Hardy-Weinberg equilibrium (Table 1). Furthermore, the observed gene diversity He was higher than gene diversity expected at mutation-drift equilibrium in all samples (Wilcoxon test: P=0.016 for samples WW, WlS, PS and combined sample WlS+PS; and P=0.032 for samples WeS, QS and combined sample WeS+QS), suggesting that the population has recently gone through a bottleneck. In none of the samples did the estimates of Fis and Fit depart significantly from zero (Table 2). The test for differentiation was positive for the samples WW and WeS, and for the combined sample WeS+QS (Table 2). However, in all three cases the Fst estimates were very low ($\leq$0.03, Table 2), and a closer examination of each case revealed that the significant outcome was due to only one pair of nests in the sample WW (pair-wise Fst: 0.103, P=0.032), two pairs of nests in the sample WeS (nests "SN49" and "SN16", pair-wise Fst: 0.1493, P=0.043 and nests "SN38" and "SN16", pairwise Fst: 0.172, P=0.036), and two pairs of nests for the combined sample WeS+QS (nests "SN49" and "SN16", pair-wise Fst: 0.090, P=0.031, and nests "SN49" and "SN42", pair-wise Fst: 0.070, P=0.045). None of the other pairs of nests (including all other pairs containing nests "SN49" and "SN16") differed significantly in their genotypic composition (mean of the non-significant pair-wise Fst: 0.028±0.043 for WW, 0.025±0.047 for WeS and 0.008±0.025 for WeQ). These results confirm that the population is close to Hardy-Weinberg equilibrium, and suggest that the population is genetically unstructured. In

Table 1 Genetic diversity at each microsatellite locus in the five samples of the study population (*n* number of alleles; *He* unbiased expected heterozygosity, Nei 1978; *Hobs* observed heterozygosity), and *P*-value of the test for departure from Hardy-Weinberg equilibrium. The number in parentheses after the name of each locus is the total number of alleles detected at the locus, over the samples

	Sample	WW	WeS	QS	WlS	PS
Loci	Number of nests	12	15	15	12	12
Fl12 (2)	*n*	2	2	2	2	2
	He	0.300	0.233	0.281	0.306	0.330
	Hobs	0.344	0.267	0.244	0.313	0.304
Fl21 (3)	*n*	3	3	3	2	2
	He	0.459	0.379	0.413	0.397	0.432
	Hobs	0.526	0.395	0.465	0.438	0.350
Fe13 (2)	*n*	2	2	2	2	2
	He	0.459	0.481	0.425	0.474	0.496
	Hobs	0.469	0.431	0.467	0.427	0.448
Fe17 (2)	*n*	2	2	2	2	2
	He	0.502	0.495	0.505	0.495	0.499
	Hobs	0.432	0.546	0.578	0.537	0.511
Fe19 (3)	*n*	3	3	3	3	3
	He	0.528	0.551	0.605	0.514	0.516
	Hobs	0.495	0.592	0.526	0.531	0.541
Average over	*n*	2.4	2.4	2.4	2.2	2.2
loci	He	0.449±0.089	0.428±0.126	0.446±0.129	0.437±0.086	0.455±0.077
	Hobs	0.453±0.070	0.446±0.129	0.456±0.127	0.449±0.092	0.431±0.070
Test for departure from HW (*P*-value)		0.631	0.202	0.579	0.294	0.509

Table 2 *F*-statistics (Weir and Cockerham 1984) and standard errors obtained by jackknifing over loci, and *P*-value determined by permutations of genotypes among nests (test for differentiation, Goudet et al. 1996)

Sample	Fis±SE	Fit±SE	Fst±SE	*P*
WW	−0.037±0.065	−0.007±0.056	0.029±0.010	0.007
WeS	−0.075±0.045	−0.042±0.044	0.030±0.015	0.001
QS	−0.039±0.059	−0.022±0.070	0.016±0.025	0.558
WeS+QS	−0.047±0.030	−0.036±0.032	0.010±0.006	0.028
WlS	−0.037±0.028	−0.027±0.039	0.010±0.014	0.122
PS	0.050±0.063	0.053±0.044	0.007±0.021	0.095
WlS+PS	0.004±0.031	0.010±0.032	0.006±0.002	0.278

Table 3 Mantel tests (Mantel 1967) of correlation between pair-wise Fst and natural logarithm of spatial distances between nests: number of nests in each sample (*N*), Pearson's correlation coefficient (*r*), *Z*-statistics and its associated *P*-value

Sample	*N*	Pearson's *r*	*Z*	*P*
WW	12	0.154	15.64	0.194
WeS	15	0.138	29.60	0.106
QS	15	0.060	3.33	0.505
WeS+QS	15	0.102	10.19	0.170
WlS	12	0.110	5.40	0.146
PS	12	−0.079	3.77	0.708
WlS+PS	12	0.167	3.13	0.081

agreement with this, the most likely genetic structure inferred from the genotype data was for each sample (and for the combined samples) only one cluster containing all the individuals (K=1), the posterior probabilities of K=1 being 0.999 for WW, 0.887 for WeS, 0.887 for QS, 0.975 for WeS+QS, 0.820 for WlS, 0.940 for PS and 0.942 for WlS and PS. The posterior probabilities of other partitions were all smaller than 0.05. Similarly, no correlation was detected between the genetic distance (pair-wise Fst), and the logarithm of spatial distance (Table 3), which is also consistent with absence of structure and absence of isolation by distance.

Genetic relatedness among nestmate workers, nestmate queens and nestmate pupae did not differ significantly from zero, after a Bonferroni correction for multiple independent tests (Table 4). Similarly, workers sampled early in the summer nests were not related to the queens

Table 4 Relatedness (*r*) between nestmate individuals (*W* workers, *Q* queens, *P* pupae) in the different samples of the study population, and 95% confidence intervals (CI-95) obtained from jackknifing over nests and loci. None of the estimates retained significance after a Bonferroni correction for multiple comparisons (five independent samples, threshold *P*-value=0.01)

Samples		WN	WeS and QS				WlS and PS			
Relatedness between:		W-W	W-W	Q-Q	W-Q	Q-W	W-W	P-P	W-P	P-W
r		0.044	0.094	0.025	−0.030	0.012	0.032	−0.008	−0.021	0.024
CI-95 (nests)	upper	0.124	0.172	0.164	0.064	0.071	0.099	0.059	0.038	0.059
	lower	−0.036	0.016	−0.114	−0.124	−0.047	−0.035	−0.075	−0.080	−0.011
CI-95 (loci)	upper	0.064	0.161	0.052	0.084	0.130	0.095	0.098	0.024	0.061
	lower	0.005	0.027	−0.002	−0.144	−0.106	−0.031	−0.114	−0.066	−0.013

collected from the same nests, and queens found in the same nests were not related to each other (Table 4). Workers sampled from the summer nests late in the season were neither related to each other, nor to the pupae collected at the same time in the same summer nests (Table 4). Similarly, pupae collected from the same nest were unrelated (Table 4).

Discussion

Our genetic analyses and field observations both suggest an absence of genetic structuring in the study population. In each of the samples, virtually all the nests were genetically undifferentiated, and the most likely structure was always one cluster containing all the nests. Similarly, in none of the samples studied could isolation by distance be detected. The detection power in STRUCTURE is admittedly low given that only five loci with rather few alleles were available. However, all the available genetic evidence consistently suggests the same pattern. Furthermore, in agreement with the genetic data, field observations showed movements between winter nests at the onset of spring migration, extensive and diffuse colonisation patterns from winter nests to summer nests, as well as extensive movements between the summer nests, with many of the ants leaving the nest they had colonised first. For some of the colours we used, we noticed that some workers tended to lose their marks, but this would only underestimate the actual movements from these particular nests. Hence, individuals were neither aggregated according to genetic lineages in the winter nests, nor did they migrate according to any genetic lineages. This indicates that the population is unicolonial, a rare feature in a species with fertile workers. The fact that pupae collected in the same nest are unrelated is, however, probably due to the large number of reproductive queens, rather than extensive movement of the pupae.

In the study population, the allelic diversity was low, compared to that found at the same loci in a monogynous population of *F. truncorum* located 100 km west from our study population. At loci Fl12, Fl21, Fe17 and Fe19, Sundström (unpublished data) and Gyllenstrand (2002) detected 6, 6, 2 and 6 alleles, respectively. In the present study, the low allelic diversity was associated with a relatively high gene diversity (He), suggesting the occurrence of a bottleneck, attributable to a founder effect. This is also consistent with the results from earlier allozyme studies that show considerable genetic differentiation between the study population and those of adjacent islands, which are inhabited by this species (Sundström 1993). In another polygynous population of this species, Gyllenstrand (2002) also detected a lower allelic diversity than in the neighbouring monogynous population mentioned above. The author noticed the presence of fewer microsatellite private alleles than expected if the population was at mutation-drift equilibrium, which also indicates the occurrence of a bottleneck. In contrast, we found no evidence for bottleneck in this monogynous population (Wilcoxon test: P=0.234, data from Gyllenstrand 2002).

The colonisation patterns and inter-nest movements observed here confirm earlier observations on migration patterns in the same species, but conducted on another island of the same archipelago (Rosengren et al. 1985). Here we have shown that these movements are associated with an absence of genetic structuring. In agreement with these observations, studies on two additional island populations also show intra-nest relatedness values close to zero (Sundström 1993; Gyllenstrand 2002). Nevertheless, not all populations that have been studied show a complete lack of genetic structuring. Several Finnish mainland and island populations of *F. truncorum* have polygynous colonies, yet show positive relatedness values and sub-structuring indicating multicoloniality (Sundström 1993; Seppä et al. 1995). This suggests that unicoloniality is not a universal feature of polygynous populations of this species, but that also polygynous populations may differ with respect to genetic structure.

Factors that drive the evolution of polygyny and unicoloniality have been extensively discussed (Nonacs 1988, 1993; Pamilo 1991; Keller 1993b; Banschbach and Herbers 1996a, 1996b; Seppä and Walin 1996; Liautard and Keller 2001; see Keller 1995 for a review), and studied (Rosengren and Pamilo 1983; Herbers 1986; Keller 1993b; Bourke and Heinze 1994; Seppä et al. 1995; Ross and Keller 1998; Tsutsui et al. 2000; Giraud et al. 2002). Chapman and Bourke (2001) proposed four mutually non-exclusive mechanisms that may play a role in a transition from structured societies to unicoloniality following invasion events: (1) introduction to a new environment entails release of ecological constraints and a rapid saturation of the habitat; (2) introduction to a new environment entails loss of genetic variation due to founder effect, with inbreeding and the production of diploid males as a consequence, which is likely to reduce the success of solitary colony foundation; (3) a "green beard" allele evolves following invasion, with workers carrying this allele tolerating multiple queens, provided that these carry the same allele; (4) founder effects and the associated loss of genetic variation entails loss of nestmate recognition, thus erasing colony boundaries.

Our and Gyllenstrand's (2002) results show that polygyny in *F. truncorum* probably is associated with founder effects. Although new alleles can be introduced through immigrant males, this may occur at too low a frequency to compensate for founder effects (Gyllenstrand 2002). Loss of allelic diversity at the sex determination locus may result in the production of diploid males. Our study population is known to produce diploid males, but also pure monogynous populations have reasonable levels of diploid male production (Pamilo et al. 1994). Assuming that workers of mono- and polygynous colonies do not differ in their propensity to eliminate diploid male eggs, costs of colony foundation due to diploid males seem an unlikely cause of unicoloniality. The presence of specific green beard alleles such as those in the fire ant (Keller and Ross 1998; Ross and Keller

1998) remains so far unexplored in *F. truncorum*. Reduced kin recognition abilities owing to impoverishment of genetically determined recognition cues or receptors following a bottleneck may have contributed to the emergence of unicoloniality in our study population. Cuticular hydrocarbons are known to be involved in recognition (Clément et al. 1987; Breed et al. 1995), but increased cuticular hydrocarbon diversity may not directly translate into enhanced discrimination abilities. Although previous studies suggested a higher diversity of cuticular hydrocarbons in the polygynous, than in the monogynous population (Nielsen et al. 1999; Boomsma et al. 2003), recent data suggest otherwise (C. Johnson, personal communication).

Perhaps the most plausible explanation is that the competitive exclusion of monogynous colonies may have led to a shift from monogyny to polygyny. New populations of this species are necessarily founded by single dispersing queens, and therefore initially comprise monogynous colonies (Collingwood 1979). Such colonies may become polygynous by adopting their own daughter queens, which become breeders in the colony. Assuming that polygyny confers an increased rate of colony growth owing to the presence of several egg-layers, such colonies may quickly spread by budding and so outcompete surrounding monogynous colonies. Thus, if only one colony turns polygynous, it may be the only one to monopolise the habitat, whereas if several colonies within a short time turn polygynous, intraspecific competition is stronger and may prevent monopolisation of the habitat. In the former case, a unicolonial population type could emerge, whereas in the latter case, a structured polygynous population could emerge.

This begs the question of which factors lead to the occasional formation of unicolonial populations in *F. truncorum*, while the highly polygynous populations of *F. polyctena* or *F. lugubris* remain genetically structured (Pamilo 1982; Sundström 1993; Seppä et al. 1995; Beye et al. 1997; Gyllenstrand and Seppä 2003). The unique diffuse hibernation habits of *F. truncorum* may, in fact, predispose this species to unicoloniality given suitable conditions. The migration between winter and summer nests can create a situation where workers from different colonies accidentally mingle and become imprinted on the collective gestalt odour instead of a colony-specific odour. This may lead to a chance erasure of colony boundaries in areas of high nest density, where colony territories regularly overlap, as is the case in polygynous populations. Once polygyny has arisen and competitive exclusion has commenced, it may become a self-reinforcing process. Seasonal migration and polydomy also occurs in other ant species such as *Plagiolepis pygmaea* (Passera et al. 2001) and *Myrmica punctiventris* (Snyder and Herbers 1991), and yet these are not unicolonial (Trontti et al., unpublished work; Banschbach and Herbers 1996a; DeHeer et al. 2001). This is inconsistent with our argument above. However, migration in these species occurs over much shorter distances (a few metres), and the winter nests are spaced over distances greater than the average yearly migration distance (Snyder and Herbers 1991; Passera et al. 2001; Trontti et al., unpublished work). A better test case is *F. yessensis*, which also has long-range seasonal migrations similar to *F. truncorum*. Studies on migration behaviour indeed strongly suggest unicoloniality in this species also (Higashi 1976, 1978a, 1978b).

Unicoloniality provides ecological advantages in terms of colonisation ability, resource exploitation and interspecific competition (e.g. *Linepithema humile*; Human and Gordon 1996; Tsutsui et al. 2000), and such ants frequently become pest species. Polydomous populations *F. truncorum* tend to exclude competing ant species (Rosengren 1986), and may reach extremely high densities (Rosengren et al. 1985). Indeed, our study area was entirely dominated by *F. truncorum*, which may indicate that the transition to unicoloniality was precipitated by a release of ecological pressure. Alternatively, the absence of other species is a consequence, rather than a cause, of unicoloniality in *F. truncorum*. *F. truncorum* may not be a large-scale invasive species, because it requires specific xerothermic habitats, which are only patchily distributed in southern Finland. These areas are mostly located on rocky islands in the archipelago, or are ephemeral and arise following forest fires or forest felling. In both cases, populations are isolated and dispersal success is likely to be limited.

Although unicoloniality can be dramatically advantageous in the short term, it is likely to be unstable for ecological and social reasons in the long term. In particular, unicoloniality can be detrimental because the higher nest density and the greater potential for interactions among individuals from different nests may facilitate the spread of pathogens (Schmid-Hempel 1998). Such a phenomenon might have caused the mysterious collapse of the polygynous population surveyed by Rosengren et al. (1985, 1986) in 1996. Furthermore, unicoloniality is often associated with low genetic variability, which may be responsible for a high diploid male load. As mentioned previously, diploid males are produced in the study population, but without any apparent effect on colony survival (Pamilo et al. 1994). However, diploid males mainly pose a cost to the colony at the founding stage, not to mature colonies, so this may not be a major factor driving the population to extinction. Unicoloniality, but not multicolonial polydomy, may also be subject to social instability, because workers display altruistic behaviour towards unrelated individuals. Hence, worker traits can no longer evolve adaptively (Queller and Strassman 1998; Tsutsui et al. 2003). In addition, selfish mutant queens that lay only sexual brood, thus parasitising the worker force produced by other queens, can quickly spread in the population (Crozier 1979; Bourke and Franks 1995). The same holds for workers in *F. truncorum*, which are potentially able to lay male-destined eggs (Helanterä 2004). The view that unicoloniality is evolutionarily unstable is also supported by the scattered distribution of unicolonial species across the ant phylogeny (Hölldobler and Wilson 1990; Queller and Strassman 1998). Hence, unicoloniality

may arise relatively frequently in *F. truncorum*, but such populations may only have a limited life span compared to genetically structured populations.

Acknowledgements We are grateful to Katja Bargum, Christine Johnson, Soile Kupiainen, Kristian Lindqvist, Petro Pynnönen, Elina Ranta, Ayman Abu Saleh and Jaime de Vizcaya for their help in the field and in the laboratory, and to Cathy Liautard, Marie-Hélène Muller, Jes Pedersen, and especially Pekka Pamilo, for fruitful discussions and comments on early versions of this paper. We also thank Niclas Gyllenstrand, Pekka Pamilo and Perttu Seppä for allowing us to perform a bottleneck analysis on their data set, Marita Rosengren for "logistic" support and three anonymous referees, whose comments greatly improved the quality of this paper. This work was funded by the Center for International Mobility of Finland (CIMO), and by the Academy of Finland (grants 42725, 173227 and 206505). Marianne Elias acknowledges the financial support provided through the European Community's Improving Human Potential Programme under contract HPRN-CT-2000-00052, INSECTS network, and under contract HPMF-CT-2002-01781 (Marie Curie individual fellowship). The experiments carried out in this study comply with the current laws of Finland.

References

Astruc C, Malosse C, Errard C (2001) Lack of intraspecific aggression in the ant *Tetramorium bicarinatum*: a chemical hypothesis. J Chem Ecol 27:1229–1248

Banschbach VS, Herbers JM (1996a) Complex colony structure in social insects. I. Ecological determinants and genetic consequences. Evolution 50:285–297

Banschbach VS, Herbers JM (1996b) Complex colony structure in social insects. II. Reproduction, queen-worker conflict, and levels of selection. Evolution 50:298–307

Belkhir K, Borsa P, Chikhi L, Raufaste N, Bonhomme F (2001) GENETIX 4.02, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome Populations et Intéractions, Université Montpellier II, France

Beye M, Neumann P, Moritz RFA (1997) Nestmate recognition and the genetic gestalt in the mound-building ant *Formica polyctena*. Insectes Soc 44:49–58

Beye M, Neumann P, Chapuisat M, Pamilo P, Moritz RFA (1998) Nestmate recognition and the genetic relatedness of nests in the ant *Formica pratensis*. Behav Ecol Sociobiol 43:67–72

Bolton B (1980) The ant tribe Tetramoriini. The genus *Tetramorium* Mayr in the oriental and Indo-Australian regions, and in Australia. Bull Br Mus Nat Hist 40:192–384

Boomsma JJ, Brouwer AH, Van Loon AJ (1990) A new polygynou *Lasius* species (Hymenoptera: Formicidae) from Central Europe. II. Allozymatic confirmation of specific status and social structure. Insectes Soc 37:363–375

Boomsma JJ, Nielsen J, Sundström L, Oldham NJ, Tentschert J, Petersen HC, Morgan ED (2003) Informational constraint on optimal sex allocation in ants. Proc Natl Acad Sci USA 100:8799–8804

Bourke AFG, Franks NR (1995) Social evolution in ants. Princeton University Press, Princeton

Bourke AFG, Heinze J (1994) The ecology of communal breeding: the case of multiple-queen leptothoracine ants. Philos Trans R Soc Lond Ser B 345:359–372

Breed MD, Garry MF, Pearce AN, Hibbard BE, Bjostad LB, Page RE Jr (1995) The role of wax comb in honey bee nestmate recognition. Anim Behav 50:489–496

Bulmer MG (1983) Sex ratio theory in social insects with swarming. J Theor Biol 100:329–339

Chapman RE, Bourke AFG (2001) The influence of sociality on the conservation biology of social insects. Ecol Lett 4:650–662

Chapuisat M (1996) Characterization of microsatellite loci in *Formica lugubris* B and their variability in other ant species. Mol Ecol 5:599–601

Chapuisat M, Goudet J, Keller L (1997) Microsatellite reveal high population viscosity and limited dispersal in the ant *Formica paralugubris*. Evolution 51:475–482

Clément JL, Bonavita-Courgourdan AB, Lange C (1987) Nestmate recognition and cuticular hydrocarbons in *Camponotus vagus* Scop.In: Eder J, Rembold H (eds) Chemistry and biology of social insects. Perperny, Munich, pp 473–474

Collingwood CA (1979) The Formicidae (Hymenoptera) of Fennoscandia and Denmark. Scandinavian Science, Klampenborg

Cornuet JM, Luikart G (1996) Description and power analysis of two test for detecting recent population bottlenecks from allele frequency data. Genetics 144:2001–2014

Crozier RH (1979) Genetics of sociality. In: Hermann HR (ed) Social insects, vol I. Academic, New York, pp 223–286

Crozier RH, Pamilo P (1996) Evolution of social insects colonies: sex allocation and kin selection. Oxford University Press, Oxford

Debout G, Provost E, Renucci M, Tirard A, Schatz B, McKey D (2003) Colony structure in a plant-ant: behavioural, chemical and genetic study of polydomy in *Cataulacus mckeyi* (Myrmicinae). Oecologia 137:195–204

DeHeer CJ, Backus VL, Herbers JM (2001) Sociogenetic responses to ecological variation in the ant *Myrmica punctiventris* are context dependent. Behav Ecol Sociobiol 49:375–386

Espadaler X, Rey S (2001) Biological constraints and colony founding in the polygynous invasive ant *Lasius neglectus* (Hymenoptera, Formicidae). Insectes Soc 48:159–164

Giraud T, Pedersen JS, Keller L (2002) Evolution of supercolonies: the Argentine ants of southern Europe. Proc Natl Acad Sci USA 99:6075–6079

Goudet J, Raymond M, De Meeüs T, Rousset F (1996) Testing differentiation in diploid populations. Genetics 144:1933–1940

Gyllenstrand N (2002) Effects of social organization on spatial genetic structures in Formica ants. PhD Thesis, Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology

Gyllenstrand N, Gertsch PJ, Pamilo P (2002) Polymorphic microsatellite DNA markers in the ant *Formica exsecta.* Mol Ecol Notes 2:67–69

Gyllenstrand P, Seppä P (2003) Conservation genetics of the wood ant, *Formica lugubris*, in a fragmented landscape. Mol Ecol 12:2931–2940

Hamilton WD (1964) The genetical evolution of social behaviour. J Theor Biol 7:1–52

Helanterä H (2004) Kinship and conflicts over male production in Formica ants. PhD Thesis, University of Helsinki (in press)

Herbers JM (1986) Nest site limitation and facultative polygyny in the ant *Leptothorax longispinosus*. Behav Ecol Sociobiol 19:115–122

Higashi S (1976) Nest proliferation by budding and nest growth pattern in *Formica* (*Formica*) *yessensis* in Ishikari Shore. J Fac Sci Hokkaido Univ Ser VI Zool 20:359–389

Higashi S (1978a) Analysis of of internest drifting in a super colonial ant *Formica* (*Formica*) *yessensis* by individually marked workers. Kontyû 46:176–191

Higashi S (1978b) Task and areal conservatism and internest drifting in a red wood ant *Formica* (*Formica*) *yessensis* Forel. Jpn J Ecol 28:257–264

Hölldobler B, Lumsden CJ (1980) Territorial strategies in ants. Science 210:732–739

Hölldobler B, Wilson EO (1977) The number of queens: an important trait in evolution. Naturwissenschaften 64:8–15

Hölldobler B, Wilson EO (1990) The ants. Harvard University Press, Cambridge, Mass

Holway DA (1999) Competitive mechanism underlying the displacement of native ants by the invasive Argentine ant. Ecology 80:238–251

Holway DA, Case JT (2001) Effect of colony-level variation on competitive ability in the invasive Argentine ant. Anim Behav 61:1181–1192

Holway DA, Suarez AV, Case JT (1998) Loss of intraspecific aggression in the success of a widespread invasive social insect. Science 282:949–952

Human KG, Gordon DM (1996) Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. Oecologia 105:405–412

Ito M (1973) Seasonal population trends and nest structure in a polydomous ant, *Formica* (*Formica*) *yessensis* Forel. J Fac Sci Hokkaido Univ Ser VI Zool 19:270–293

Ito M, Imamura S (1974) Observations on the nuptial flight and internidal relationship in a polydomous ant, *Formica* (*Formica*) *yessensis* Forel. J Fac Sci Hokkaido Univ Ser VI Zool 19:681–694

Kaufmann B, Boomsma JJ, Passera L, Petersen KN (1992) Relatedness and inbreeding in a French population of the unicolonial ant *Iridomyrmex humilis* (Mayr). Insectes Soc 39:195–213

Keller L (1988) Evolutionary implications of polygyny in the Argentine ant, *Iridomyrmex humilis* (Mayr) (Hymenoptera: Formicidae): an experimental study. Anim Behav 36:159–165

Keller L (1993a) The assessment of reproductive success of queens in ants and social insects. Oikos 67:177–180

Keller L (1993b) Queen number and sociality in insects. Oxford University Press, Oxford

Keller L (1995) Social life: the paradox of multiple-queen colonies. Trends Ecol Evol 10:353–360

Keller L, Ross KG (1998) Selfish genes: a green beard in the red fire ant. Nature 394:573–575

Liautard C, Keller L (2001) Restricted effective queen dispersal at a microgeographic scale in polygynous populations of the ant *Formica exsecta.* Evolution 55:2484–2492

Macewicz S (1979) Some consequences of Fisher's sex ratio principle for social Hymenoptera that reproduce by colony fission. Am Nat 113:363–371

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–220

Markin GP (1970) The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis*, in southern California. Ann Entomol Soc Am 63:1238–1242

Maruyama T, Fuerst PA (1985) Population bottlenecks and nonequilibrium models in population genetics. II. Number of alleles in a small population that was formed by a recent bottleneck. Genetics 111:675–689

Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590

Nei M, Maruyama T, Chakraborty R (1975) The bottleneck effect and genetic variability in populations. Evolution 29:1–10

Nielsen J, Boomsma JJ, Oldham NJ, Petersen HC, Morgan ED (1999) Colony-level and season-specific variation in cuticular hydrocarbon profiles of individual workers in the ant *Formica truncorum.* Insectes Soc 46:58–65

Nonacs P (1988) Queen number in colonies of social Hymenoptera as a kin-selected adaptation. Evolution 42:566–580

Nonacs P (1993) The effects of polygyny and colony life history on optimal sex investissment. In Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 110–131

Oster GF, Wilson EO (1978) Caste and ecology in the social insects. Princeton University Press, Princeton

Pamilo P (1982) Genetic population structure in polygynous *Formica* ants. Heredity 48:95–106

Pamilo P (1983) Genetic differentiation within subdivided population of *Formica* ants. Evolution 37:1010–1022

Pamilo P (1991) Evolution of colony characteristics in social insects. II. Number of reproductive individuals. Am Nat 138:412–433

Pamilo P, Sundström L, Fortelius W, Rosengren R (1994) Diploid males and colony-level selection in *Formica* ants. Ethol Ecol Evol 6:221–235

Passera L (1994) Characteristics of tramp species. In: Williams DF (ed) Exotic ants: biology, impact, and control of introduced species. Westview, Boulder, Colo, pp 23–43

Passera L, Gilbert M, Aron S (2001) Social parasitism in ants: effect of the inquiline parasite *Plagiolepis xene* St. on queen distribution and worker production of its host *plagiolepis pygmaea* Latr. Insectes Soc 48:1–82

Pedersen JS, Boomsma JJ (1999) Genetic analysis of colony structure in polydmous and polygynous ant populations. Biol J Linn Soc 66:115–144

Pirk CWW, Neumann P, Moritz RFA, Pamilo P (2001) Intranest relatedness and nestmate recognition in the meadow ant *Formica pratensis* (R.). Behav Ecol Sociobiol 49:366–374

Piry S, Luikart G, Cornuet JM (1999) Bottleneck: a computer program for detecting recent reductions in effective population size from allele frequency data. J Hered 90:502–503

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. Evolution 242:258–275

Queller DC, Strassman JE (1998) Kin selection and social insects. Bioscience 48:165–175

Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J Hered 86:248–249

Rosengren R (1986) Competition and coexistence in an insular ant community—a manipulation experiment (Hymenoptera: Formicidae). Ann Zool Fenn 23:297–302

Rosengren R, Pamilo P (1983) The evolution and polygyny and polydomy in mound building *Formica* ants. Acta Entomol Fenn 42:65–77

Rosengren R, Cherix D, Pamilo P (1985) Insular ecology of the red wood ant *Formica truncorum* Fabr. I. Polydomous nesting, population size and foraging. Mitt Schweiz Entomol Ges 58:147–175

Rosengren R, Cherix D, Pamilo P (1986) Insular ecology of the red wood ant *Formica truncorum* Fabr. I. Distribution, reproductive strategy and competition. Mitt Schweiz Entomol Ges 59:63–94

Ross KG (1993) The breeding system of the fire ant *Solenopsis invicta*: effects of colony genetic structure. Am Nat 141:554–576

Ross KG, Keller L (1998) Genetic control of social organization in an ant. Proc Natl Acad Sci USA 95:14232–14237

Ross KG, Vargo EL, Keller L (1996) Social evolution in a new environment: the case of introduced fire ants. Proc Natl Acad Sci USA 93:3021–3025

Schmid-Hempel P (1998) Parasites in social insects. Princeton University Press, Princeton

Seppä P, Pamilo P (1995) Gene flow and population viscosity in *Myrmica* ants. Heredity 74:200–209

Seppä P, Walin L (1996) Sociogenetic organization of the red ant *Myrmica rubra.* Behav Ecol Sociobiol 38:207–217

Seppä P, Sundström L, Punttila P (1995) Facultative polygyny and habitat succession in boreal ants. Biol J Linn Soc 56:533–551

Snyder LE, Herbers JM (1991) Polydomy and sexual allocation ratios in the ant *Myrmica punctiventris*. Behav Ecol Sociobiol 28:409–415

Sundström L (1989) Genetic relatedness and population structure in *Formica truncorum* Fabr. (Hymenoptera: Formicidae). Actes Coll Insectes Soc 5:93–100

Sundström L (1993) Genetic population structure and sociogenetic organization in *Formica truncorum*. Behav Ecol Sociobiol 33:345–354

Tsutsui ND, Case TJ (2001) Population genetics and colony structure of the Argentine ant (*Linepithema humile*) in its native and introduced ranges. Evolution 55:976–985

Tsutsui ND, Suarez AV, Holway DA, Case TJ (2000) Reduced genetic variation and the success of invasive species. Proc Natl Acad Sci USA 97:5948–5953

Tsutsui ND, Suarez AV, Grosberg-RK (2003) Genetic diversity, asymmetrical aggression, and recognition in a widespread invasive species. Proc Natl Acad Sci USA 100:1078–1083

Van der Hammen T, Pedersen JS, Boomsma JJ (2002) Convergent development of low-relatedness supercolonies in *Myrmica* ants. Heredity 89:83–89

Weir BS (1979) Inferences about linkage disequilibrium. Biometrics 35:235–254

Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38:1358–1370

Wenseleers T, Helanterä H, Hart AG, Ratnieks FLW (2004) Worker reproduction and policing in insect societies. An ESS analysis. J Evol Biol 17:1035–1047