

Diversity and genetic structure of the wood ant *Formica lugubris* in unmanaged forests

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Wood ant species show differences in their social structure, especially in the level of polygyny (number of laying queens per nest) and polydomy (number of nest per colony), both within and between species. We demonstrate here for the first time that *Formica lugubris* displays two different social forms in close proximity in alpine unmanaged forests of the Swiss National Park. The genetic data (7 microsatellite loci) and field data indicate that one population is mostly monogynous to weakly polygynous ($r = 0.438$) and monodomous, the second one being polygynous ($r = 0.113$) and polydomous. Within this latter population new nests are founded by budding, leading to the observed high density of nests. These two different social structures, possibly being two expressions of a same continuum, could be explained by several ecological or environmental factors (e.g. habitat saturation, resource competition) and also historical effects.

Introduction

Ant colonies display large variation in their social organization, particularly in the number of laying queens per nest and the number of co-operating nests per colony, varying from monogynous (one laying queen) to polygynous (multiple laying queens) nests, and from monodomous (single nest) to polydomous (multinest) colonies (Pamilo & Rosengren 1984, Bourke & Franks 1995). The number of laying queens in a colony can be estimated by the relatedness value (r). Polygyny is commonly functional

and, assuming that queens share reproduction, the more queens are present the lower the mean relatedness among the workers (Hölldobler & Wilson 1990, Keller 1995). However, when queens share reproduction unequally (reproductive skew) relatedness declines less steeply with an increasing number of queens (Bourke & Franks 1995).

Sexuals of monogynous colonies generally mate after a nuptial flight and newly mated queens usually enter an established nest of the same species or found a new nest independently (i.e. without the help of workers), or through

interspecific temporary social parasitism (Gösswald 1952, 1989, Kutter 1969, Rosengren & Pamilo 1983, Rosengren *et al.* 1993). By contrast, sexuals of polygynous species can mate within the nest without taking part in a nuptial flight (Cherix *et al.* 1993). Moreover, new colonies are mostly founded by budding, a process in which queens leave the mother nest accompanied with workers and establish a new nest in the neighbourhood (Rosengren & Pamilo 1983). This latter strategy promotes genetic differentiation between geographically distant nests and may engender population viscosity (Hamilton 1972, Rosengren & Pamilo 1983, Chapuisat *et al.* 1997).

Polygyny commonly develops from monogyny through adoption of new queens under different ecological and physiological conditions (Rosengren & Pamilo 1983, Sundström 1995, Heinze & Keller 2000), whereas the direction of the evolutionary transition between monogynous and polygynous nesting strategies may have gone in both directions. The cost of independent colony founding is one of the main factors promoting polygyny (Keller 1995). When the costs are high (e.g. habitat saturation, nest site limitation), females should seek adoption in an established nest of the same species, rather than attempting solitary colony foundation (Nonacs 1988, Pamilo 1991) because the probability to found a new colony independently is low. Polygyny is thus expected to develop as a response to habitat saturation and nest-site limitation (Rosengren & Pamilo 1983, Rosengren *et al.* 1993), and has been observed to increase after the initial colonisation of disturbed habitat patches (Seppä *et al.* 1995).

Resource competition (food abundance vs. food shortage) can be an additional factor influencing the level of polygyny. According to this view, it is advantageous to disperse and to avoid resource competition when resources are scarce (Herbers 1993, Bourke & Heinze 1994, Pedersen & Boomsma 1999).

The *Formica rufa* group, so-called red wood ants, has been one of the most studied groups of ants in Europe during the last century (Cotti 1963, 1995, Gösswald 1989, 1990). This group includes several species of mound-building ants that inhabit, often sympatrically, woodlands

throughout Eurasia. *Formica* species show great differences in their social structure, and variation in the level of polygyny has been observed between related species as well as within a single species (Rosengren & Pamilo 1983, Pamilo & Rosengren 1984, Rosengren *et al.* 1993). *Formica lugubris* is a boreo-alpine species recorded at least in the French Pyrenees, Bulgaria, Finland, Norway, Sweden, Poland, Russia, United Kingdom and Ireland (Gösswald *et al.* 1965). In Switzerland it lives at an altitude of 800–2200 m in the Jura, the Prealps and the Alps (Kutter 1967, 1977, Collingwood 1979, Ronchetti 1980, Seifert 1996a, Maeder & Cherix 2001). *F. lugubris* has been described as monogynous (with occasional weakly polygynous nests) in Ireland (Breen 1976), Fennoscandia (Pamilo *et al.* 1994) and Switzerland (Maeder & Cherix 2001), whereas highly polygynous colonies have been observed in England (Gyllenstrand & Seppä 2003).

The description of the social characteristics of *F. lugubris* in earlier literature should be taken with some caution as only recent studies (Rosengren & Cherix 1981, Cherix 1983, Pamilo *et al.* 1992, Rosengren *et al.* 1994) led to the description of *Formica paralugubris*, a morphologically very similar, but separate species (Seifert 1996b, *see also* Maeder *et al.* 2005). The latter species, as far as known, has highly polygynous and polydomous colonies (Chapuisat *et al.* 1997). *F. lugubris* and *F. paralugubris* are present in Switzerland in the Jura Mountains and in the Alps often in sympatry (Maeder & Cherix 2001). Whereas the social structure and reproductive strategies of *F. paralugubris* are well documented (Cherix *et al.* 1991, 1993, Fortelius *et al.* 1993, Chapuisat *et al.* 1997), that of *F. lugubris* is less well documented and the variation in the social structure of its colonies has been mainly considered geographical (*see above and* Rosengren *et al.* 1993, but *see* Maeder *et al.* 2005). During the long term monitoring of wood ants in unmanaged forest ecosystems of the Swiss National Park (D. Cherix unpubl. data) we recently discovered two populations (named 1 and 2) of *F. lugubris* presenting important social differences. Population 1 was located in a habitat where we observed a low nest density, indicating that the habitat was not saturated.

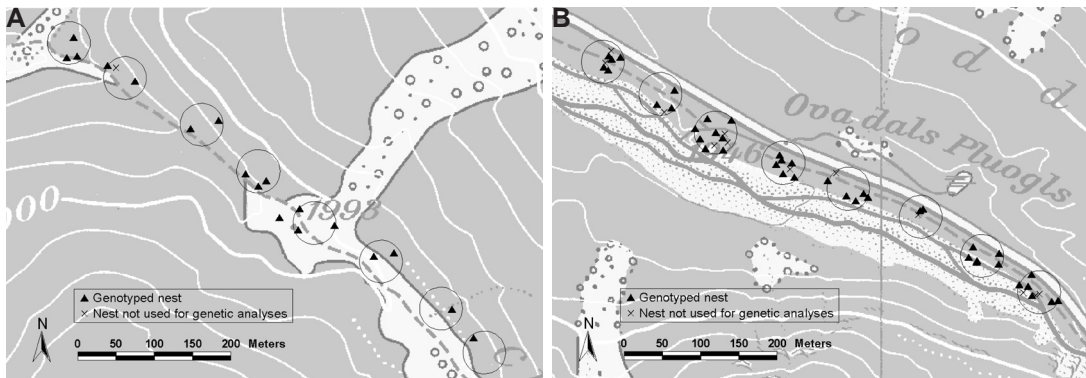


Fig. 1. Maps of the sampled nests of *Formica lugubris* within the two studied populations. The circles correspond to the sampling plots (60 m diameter). **(A)** Population 1: Polydomous populations of *F. aquilonia* (not indicated) are distributed in forest interiors (dark grey); nests of *F. (Coptoformica) exsecta* (not indicated) are distributed in the meadow (light grey). **(B)** Population 2: Numerous nests found outside the circles are not indicated. *F. lugubris* is the only mound building *Formica* species found in this site. Topographic layer: PK25©2004 swisstopo.

By contrast, population 2 had a high density of nests, habitat being most likely saturated. Based on these differences, one might expect that the two populations have also different genetic and social structures (Hannonen *et al.* 2004).

The aim of this study is to investigate the genetic and social structure of these two alpine populations of *F. lugubris* in order to demonstrate whether the apparent difference in the spatial distribution of nests in the two populations is accompanied by a difference in the social structure of the colonies. This would be an interesting example of the existence of two different social forms in a single wood ant species within a close geographical proximity.

Material and methods

In September 2001, two alpine populations of *Formica lugubris* separated by 7 km were sampled in the Swiss National Park (eastern Switzerland). Created in 1914, this strict nature reserve offers a unique opportunity to study the evolution of wood ant populations in unmanaged forests (for about 100 years). The main habitat in the area consists of typical alpine forest where *Pinus mugo* is the dominant species. *F. paralugubris* and *F. aquilonia* are the two other wood ants species commonly found in the park boundaries but they are known to display only highly polygynous and polydomous colonies.

Population 1 is located near the plateau of Champlönch at an altitude of around 1970 m. It is located at the forest edge, surrounded by the forest in the north and by a small river and a meadow in the south (Fig. 1A). Nest density varies from one to three nests per sampled area (circle of 60 m diameter) and, during field work, *Formica aquilonia* and *F. (Coptoformica) exsecta* were found in the same area in syntopy with *Formica lugubris*. Population 2 is located near Buffalora (“God dal Bass”) at an altitude of about 1950 m. Nests are distributed in an open forest limited northward by the Ofenpass road and southward by a river (Ova dal Fuorn) (Fig. 1B). Nest density varies from three to eleven nests per sampled area and the lowest density corresponds to the maximum density observed in population 1. *Formica lugubris* was the only mound building *Formica* species observed within this location.

In both populations, the same sampling scheme was applied. Eight circles of 60 m diameter and located along a transect of about 760 meters were first established; every nest found within each area was then sampled (Fig. 1). We collected workers from 18 nests in population 1 and 41 nests in population 2. In each nest, about 30 workers were collected, stored in absolute ethanol and deposited in the Museum of Zoology of Lausanne (Switzerland) as voucher specimens. The species was identified according to Seifert (1996a, 1996b). Altitude, size and exposure of

each nest were recorded. Using Geographical Positioning System (GPS), the coordinates of each nest were taken in order to determine the metric inter-nest distances.

Genomic DNA was isolated from workers using QIAamp DNA Mini Kit (Qiagen). The entire body of ants was used for DNA extraction. Eight workers from each nest were genotyped using seven microsatellite loci (FL12, FL21, FL29 by Chapuisat 1996, and FE13, FE19, FE21 and FE38 by Gyllenstrand *et al.* 2002). PCR conditions were as described by Chapuisat (1996) and Gyllenstrand *et al.* (2002). Amplification conditions were also optimised according to Mäki-Petäys *et al.* (2005). Primers were labelled with HEX, NED and FAM fluorescent dyes and the amplification products were analyzed on an ABI Prism 377 XL DNA sequencer (Applied Biosystems, Foster City, CA). Alleles were scored by length and genotyping was carried out using the computer programs Genotyper ver. 2.5 and Genescan ver. 3.02 (Perkin Elmer ABI).

Relatedness (r) among worker nest mates was estimated with the computer program Relatedness 5.0.5 (Queller & Goodnight 1989). Nests were weighted equally and the estimates were jack-knifed over loci to obtain standard errors. The estimates are inflated by spatial genetic differentiation and inbreeding (Pamilo 1985) so we used Pamilo's inbreeding adjustment (Pamilo 1985) in order to remove that component from the relatedness estimate. The number of matrilineal within a nest was also estimated manually by identifying the putative sib ships. The genetic structure of both populations was characterised by Wright's fixation indices (Wright 1943, Weir

& Cockerham 1984). Calculations were carried out using the program FSTAT ver. 2.9.2 (Goudet 1995). Standard errors of F -statistics were obtained by jack-knifing over nests and confidence intervals were obtained by permutation tests over loci (5000 permutations) (Goudet 1995). Population viscosity was investigated by calculating pairwise F_{ST} values of colonies and plotting $F_{ST}/(1 - F_{ST})$ against the geographical distance ($\ln(\text{distance})$) (Rousset 1997). Significance of the regression was determined with the Mantel test (Mantel 1967, Manly 1997) (2000 permutations). These calculations were performed with FSTAT ver. 2.9.2 (Goudet 1995).

To identify potential genetic units within the populations a hierarchical analysis of variance was performed by using the software Arlequin (ver. 2000) (Schneider *et al.* 2000). In our hierarchical design, three levels were chosen: the nests, the groups of nests (according to sampling, nests within the same circle belong to the same group) and the whole population.

Results

Population 1

Eighteen nests of *F. lugubris* from population 1 were selected for molecular analysis and a total of 144 workers were genotyped. The number of alleles ranged from four at FE21 and FE38 to eight at FE19 (total 40, Table 1). The inbreeding coefficient was slightly but significantly greater than zero when estimated over all the seven loci ($F_{IT} = 0.084$, $p < 0.05$, 95% CI = 0.05–0.12; Table 1) indicating a certain amount of inbreeding within

Table 1. Number of alleles (n_A), relatedness (r) and F -statistics calculated over all loci and over all 18 nests of the population 1. Nests treated as subpopulations. Deviations from zero*: $p < 0.05$;***: $p < 0.001$ (permutation test).

Locus	n_A	F_{IT}	r	F_{ST}
FL12	6	0.050 ± 0.070	0.476 ± 0.080	0.250 ± 0.044
FL21	6	0.103 ± 0.092	0.568 ± 0.077	0.313 ± 0.056
FL29	6	0.024 ± 0.103	0.465 ± 0.083	0.238 ± 0.055
FE13	6	0.086 ± 0.133	0.395 ± 0.171	0.214 ± 0.106
FE19	8	0.055 ± 0.093	0.512 ± 0.063	0.270 ± 0.050
FE21	4	0.177 ± 0.172	0.453 ± 0.076	0.266 ± 0.078
FE38	4	0.136 ± 0.098	0.559 ± 0.081	0.317 ± 0.062
All loci	40	0.084 ± 0.017*	0.495 ± 0.024***	0.269 ± 0.015***

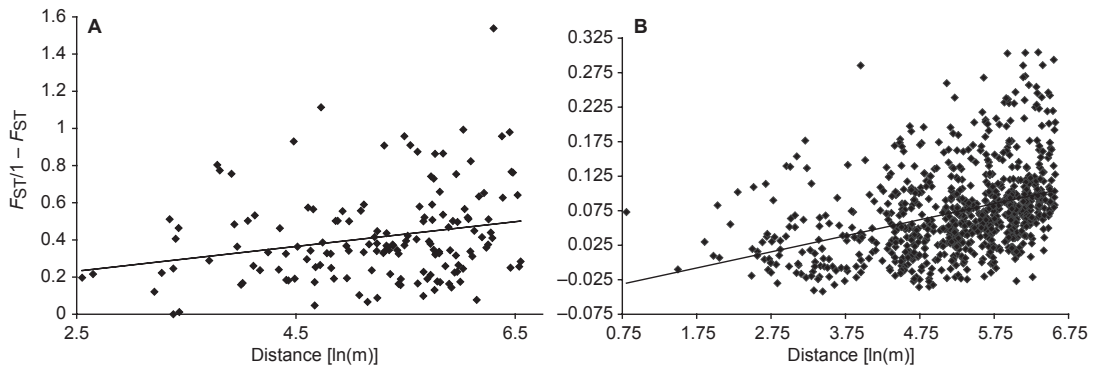


Fig. 2. Relationship between genetic differentiation (F_{ST} for pairs of nests) and geographic distance (A) within population 1 and (B) within population 2.

the population. Mean genetic relatedness among worker nest mates within population 1 estimated over all loci was significantly greater than zero ($r = 0.495 \pm 0.024$ (mean \pm S.D.), $p < 0.001$; Table 1). Removing the small effect of inbreeding changed this estimate to $r_c = 0.438$. As seen from the small standard error of the relatedness estimate, the loci gave very consistent information. The relatedness values for the individual loci (Table 1) varied between 0.39 ± 0.17 (mean \pm S.D.) for FE13 and 0.56 ± 0.08 (mean \pm S.D.) for FE38. Relatedness values calculated for single nests ranged from 0.14 ± 0.07 to 0.84 ± 0.07 (mean \pm S.D.), indicating that the degree of polygyny varied considerably within this population.

The relatedness estimates agree with an average of one to two queens per nest depending on the level of polyandry (*see* Seppä 1994 for details). Genotypes in four nests could be explained by one laying queen; ten nests could be considered weakly polygynous (2–3 laying queens) and four nests had more than three laying queens. F_{ST} is closely related to the relatedness estimate (r) and was significantly greater than zero ($F_{ST} = 0.269 \pm 0.015$ (mean \pm S.D.), $p < 0.001$; Table 1). Genetic differences between pairs of nests were measured as pairwise F_{ST} values and they were significantly correlated with the geographical distance (Mantel test: $p < 0.01$; Fig. 2A), indicating that two nearby nests were genetically more similar than two distant ones, even though isolation by distance was small ($R^2 = 0.06$). F_{ST} values between pairs of nests were high even at short distances showing that the nests did not form local genetic group-

ings. Only two pairs of nests have very low pairwise F_{ST} values (0.0002 and 0.01).

Hierarchical analyses of variance indicate that the genetic differentiation between nests explains 25.7% of the observed genetic variation while the genetic differentiation between groups of nests explains only 2% of the total variation. This suggests that there are no groups of related nests within this population. The remaining genetic variation is due to variation between individuals and this could be explained by the low level of polygyny.

Population 2

We selected 41 nests for molecular analysis and a total of 328 workers were genotyped. The number of alleles varied from three at FE21 to nine at FE13 (total 45, Table 2). F_{IT} estimated over all loci, although low, was significantly greater than zero ($F_{IT} = 0.044$, $p < 0.05$, 95% CI = 0.003–0.09; Table 2) indicating a certain amount of inbreeding within the population. The mean genetic relatedness among workers within the nests in population 2 over all loci was $r = 0.123 \pm 0.011$ (mean \pm S.D.) ($p < 0.001$, Table 2). All seven loci used for the analysis gave fairly similar estimates and the relatedness values for the individual loci vary between 0.08 ± 0.03 (mean \pm S.D.) for FE19 and 0.18 ± 0.06 (mean \pm S.D.) for FE21. Removal of the small effect of the positive inbreeding coefficient resulted in only a slight reduction of the relatedness estimate ($r_c = 0.113$). Relatedness values calculated for

single nests ranged from -0.03 ± 0.05 to 0.39 ± 0.12 (mean \pm S.D.). These estimates were lower than those in population 1, and indicate that the nests in population 2 were mostly polygynous. The relatedness estimate agrees with an average of 7–8 laying queens per nest, depending on the level of polyandry (*see* Seppä 1994 for details).

F_{ST} among the nests, estimated over all loci, was low but significantly greater than zero ($F_{ST} = 0.064 \pm 0.007$ (mean \pm S.D.), $p < 0.001$; Table 2) suggesting that even though the nests were polygynous, they were genetically differentiated. Pairwise genetic differentiation was significantly correlated with geographical distance (Mantel test: $p < 0.01$; Fig. 2B). Isolation by distance ($R^2 = 0.14$) was somewhat more pronounced than in population 1. Hierarchical analyses of variance indicate that the genetic differentiation between groups of nests (5%) explains more of the total variance than the variation between nests within the groups (1.6%), indicating the presence of genetic units within population 2. Genetic differentiation between the two populations, $F_{ST} = 0.156 \pm 0.013$ (mean \pm S.D.) ($p < 0.01$), indicates that gene flow between population 1 and population 2 is also very restricted.

Discussion

The first main result of our study is that within alpine forests of the Swiss National Park two populations of the wood ant *Formica lugubris* differed in their genetic structure with a significant difference of worker relatedness ($t_{57} = 23.2$, $p < 0.001$). Population 1 was characterized by high relatedness between workers, which

corresponds to an average of one to two laying queens. Population 2 was characterized by low worker relatedness, corresponding to an average of seven to eight laying queens per nest, depending on the level of polyandry (*see* Seppä 1994 for details). Even though the relatedness in population 2 was low, the estimate was significantly greater than zero, indicating that individual nests, or small groups of nests, were genetically separate entities. The relatedness observed within population 1 could also agree with a higher level of polygyny, if queens share reproduction unequally (Heinze & Keller 2000). Indeed, a direct count of reproductively active queens (C. Bernasconi & A. Maeder unpubl. data) gave a median of 4 queens (2–7) in population 1 and 36 (17 to 85) queens in population 2 ($n = 5$ in both cases). These numbers are greater than those indicated by our relatedness estimates, suggesting some degree of reproductive skew in both populations.

The second main result is that within population 2 we observed significant genetic structuring and isolation by distance, indicating limited gene flow between distant parts of the study area. Isolation by distance can be due to foundation of new nests by budding (step-by-step dispersal) and/or to intra-nidal mating. The high density of nests and the observed exchange of workers between neighbouring nests (A. Maeder unpubl. data) indicate that budding is common, and agrees well with our genetic results. A social structure similar to that observed in population 2 has earlier been described in *F. paralugubris* in the Swiss Jura Mountains, with the exception that the level of polygyny in this latter species is higher (Chapuisat *et al.* 1997, Chapuisat &

Table 2. Number of alleles (n_A), relatedness (r) and F -statistics calculated over all loci and over all 41 nests of the population 2. Nests treated as subpopulations. Deviations from zero: * $p < 0.05$; *** $p < 0.001$ (permutation test).

Locus	n_A	F_{IT}	r	F_{ST}
FL12	5	0.004 ± 0.042	0.090 ± 0.032	0.045 ± 0.016
FL21	8	0.092 ± 0.028	0.142 ± 0.025	0.077 ± 0.014
FE38	5	0.012 ± 0.043	0.134 ± 0.042	0.067 ± 0.023
FE19	8	-0.012 ± 0.036	0.080 ± 0.026	0.039 ± 0.013
FE13	9	0.156 ± 0.045	0.126 ± 0.032	0.072 ± 0.02
FE21	3	0.032 ± 0.053	0.184 ± 0.056	0.095 ± 0.031
FL29	7	0.006 ± 0.066	0.126 ± 0.068	0.062 ± 0.036
Overall	45	$0.044 \pm 0.025^*$	$0.123 \pm 0.011^{***}$	$0.064 \pm 0.007^{***}$

Keller 1999, Cherix *et al.* 2004). Isolation by distance has also been observed in several other *Formica* ants (Seppä & Pamilo 1995, Chapuisat *et al.* 1997, Liautard & Keller 2001, Hannonen *et al.* 2004, Sundström *et al.* 2005, but *see* DeHeer & Herbers 2004).

In contrast to population 2, the high relatedness and weak isolation by distance in population 1 may indicate that the nests in this population are inhabited by distinct genetic families and that budding is less common. In fact, we found only two cases where nearby nests had similar genotypes and may have arisen through local budding. Field observations (A. Maeder unpubl. data) confirm these results as almost no connections and no worker exchange has been observed between nests. The two pairs of nests with low F_{ST} were the only ones connected by trails allowing a genetic homogenisation through worker exchange. Below we discuss different scenarios that might explain the difference between population 1 and 2.

The differences between the two populations may be due to divergent dispersal strategies. Population 2 had a high density of nests (polydomy) with main and secondary nests connected by permanent trails (polycaly, *see* Rosengren & Pamilo 1983). This pattern may be due to habitat saturation because a river and a road spatially limit population expansion by independent founding. However, a reproductive strategy exclusively based on budding is probably evolutionary unstable as it prevents or slows down colonisation of new areas (Cherix *et al.* 1991, Seifert 1991, Bourke & Heinze 1994). Hence, evolutionary models predict dispersal also under high dispersal risks (Hamilton & May 1977). Indeed, we observed nuptial flights in population 2 as well as young females on mating places (A. Maeder unpubl. data). In population 1, the density of nests was very low as compared with that in population 2, so constraints on independent founding are likely to be lower. Recent studies have also discussed the mixed dispersal strategy of other *Formica* queens within polygynous colonies (Rosengren *et al.* 1993, Sundström 1995, Chapuisat *et al.* 1997). Thus, relatively high dispersal coupled with relatively low gene flow (*see* DeHeer *et al.* 1999) could also be found in the polygynous *F. lugubris* populations.

In agreement with the proposed divergent dispersal strategies we found that females from population 1 need a nuptial flight before mating and are physiologically adapted for dispersal, whereas the majority of females from population 2 will mate without a nuptial flight and are not physiologically adapted for long dispersal (Cherix *et al.* 2004, A. Maeder unpubl. data). Hence, our findings agree with the expectation that polygynous colonies produce sexuals that often mate within the nest without a nuptial flight and form new nests by budding (Rosengren & Pamilo 1983, Rosengren *et al.* 1993, Chapuisat *et al.* 1997). Physiological plasticity could be influenced by environmental factors such as the amount of resources that queens received during their development, or by intrinsic genetic differences between monogynous and polygynous colonies (Sundström 1995, Bargum *et al.* 2004).

Snyder and Herbers (1991) pointed out that resource competition could influence the social structure of a colony. Within the area of population 1, two additional mound-building *Formica* species were present (*F. aquilonia* in forest interiors and *F. (Coptoformica) exsecta* in meadows), whereas *F. lugubris* was the only mound-building *Formica* species in population 2 (forest interiors). These territorial species (Vepsäläinen & Pisarski 1982) are known to exclude each other (Savolainen *et al.* 1989, Punttila *et al.* 1991). Thus, within population 1 the monodomous *F. lugubris* could be restricted by the polydomous and highly polygynous *F. aquilonia* to less favourable sites (i.e. forest edges) (Laine & Niemela 1989). Interestingly, the nests of population 1 are rather regularly spaced, which may indicate competitive interactions. This intraspecific pattern is indeed expected for monogynous nests (Bennett 1987). It is, however, difficult to infer the causal relationships between the social structure of *F. lugubris* and the presence/absence of its competitors (Punttila *et al.* 1991).

Another factor influencing the social structure is the age of the population, old populations having higher number of laying queens (Sundström 1993, Seppä *et al.* 1995, Hannonen *et al.* 2004) and establishing new colonies mainly by budding (Punttila *et al.* 1991, Punttila 1996). Thus our two populations of *Formica lugubris* could be of different age, population 2 being

older than population 1. Unfortunately there are no data available to assess when *Formica lugubris* may have arrived on these two sites. Nevertheless, the site harbouring population 2 has been massively exploited (clear cutting) between 1850 and 1862 (Parolini 1995), which would have led to the extinction of the colonies within 1–2 years (Punntila et al. 1991). After that, a mature forest (> 100 years) has probably developed naturally with almost no human influence (Swiss National Park = strict nature reserve protected and managed mainly for science, IUCN category), allowing wood ants to re-colonize the area (Punntila et al. 1991, Seppä et al. 1995). By contrast, no clear cutting is reported for the site harbouring population 1 (the forest is thus assumed to be old and mature), but the presence of sheep until the creation of the Swiss National Park in 1914 (Parolini 1995) and alpine ungulates might have a negative influence (Paraschivescu 1982). Within population 1, the local budding and the presence of weakly polygynous nests could indicate the very beginning of a shift to a polygynous and polydomous stage but this would imply a rather recent colonization. It is also possible that colonization occurred a long time ago but due to several ecological factors the system has remained at the monogynous and monodomous stage. Thus, population age is in this case unlikely to account for the difference in social structure between the two populations.

In the Swiss Jura Mountains, where *F. paralugubris* reaches high densities, *F. lugubris* seems to display principally the monogynous (to weakly polygynous) and monodomous form (P. Persico, A. Maeder, A. Freitag, A. Guisan & D. Cherix unpubl. data). By contrast, within the Swiss National Park, *F. lugubris* clearly displays social flexibility. The main habitat in the Swiss Jura Mountains encompasses wooded pastures, where spruce (*Picea abies*) is the dominant tree species. Ecological variables such as altitude, slope and exposition are similar over large surfaces and therefore the ecological and climatic conditions are quite constant over big areas. The habitat can be thus considered rather homogenous (i.e. with low habitat patchiness). By contrast, the Swiss National Park is characterised by variation in altitude, slope and exposition, which fragments the woodland system into small uni-

form patches. A coarse-grained habitat pattern may favour mixed dispersal strategies (Mabelis 1994, Höfener et al. 1996, Mathias et al. 2001), as was indeed found here.

In conclusion, our study shows that *Formica lugubris* displays social plasticity at a local scale in the Alps. Different social organization of *Formica lugubris* has earlier been detected in separate geographical areas (Breen 1976, Pamilo et al. 1994, Gyllenstrand & Seppä 2003, Mäki-Petäys et al. 2005) and this suggests that the variation can be induced by historical factors. Nevertheless, our study demonstrates for the first time that the two social forms of this *Formica sensu stricto* species can also occur in close proximity as is also the case in *F. truncorum*, *F. (Serviformica) cinerea* and *F. (Coptoformica) exsecta* (Sundström 1993, Zhu et al. 2002, Seppä et al. 2004). This social plasticity may be associated with differences in ecological and environmental factors and further studies are required to clarify the causal links. As discussed by Seppä et al. (2004) the two social forms resemble those of source (monogynous) and sink (polygynous) populations, respectively. In the unmanaged and stable habitats of the Swiss National Park the development of polygynous long-lived nests could have emerged locally from monogynous colonies by the monopolization of the habitat and as a result of ecological constraints (risky dispersal and progressive habitat saturation) (Hölldobler & Wilson 1977, Rosengren et al. 1993, Bourke & Franks 1995, Chapuisat et al. 1997, Chapuisat & Keller 1999). Finally, colonisation history is probably another key factor that should be tested at different scales for better understanding of the formation and the maintenance of this social flexibility.

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