GENETIC RELATEDNESS AND POPULATION STRUCTURE IN *Formica truncorum* Fabr. (HYMENOPTERA, FORMICIDAE)

L. SUNDSTRÖM

Department of Zoology, Univ. of Helsinhi, P. Rautatiekatu 13, SF 00100 Helsinki, Finlande

RESUME

Formica truncorum Fabr., qui fait partie des fourmis de bois crée des colonies monodomes et polydomes contenant une ou plusieurs reines. On a étudié avec des méthodes génétiques l'influence de la structure des colonies sur la dynamique des populations de l'espece et sur la structure des nids dans les populations de cinq îles différentes. Les colonies monodomes se montrent essentiellement monogynes et les colonies polydomes plutôt polygynes. De plus, les populations etudiées se sont averées appartenir principalément a l'un ou l'autre type de colonies. En laboratoire on a remarqué que les reines s'accouplent en moyenne 1.3 fois. Le degré de parenté est alors en moyenne de 0.63 dans les colonies mono-domes et de 0.27 dans les colonies polydomes. La différen-ciation des sous-populations, estimee grâce à l'examen des frèquences d'alleles, est plus importante dans les popula-tions polydomes que dans les populations monodomes, ce qui indique une similarité génétique plus grande à l'intérieur des sous-populations dans les colonies polydomes que dans les colonies monodomes. Il s'agit d'une petite différence ÄFst = 0.08 (monodomes) et Fst = 0.13 (polydomes) en moyen-neA, mais si l'on prend en considération la proportion de la population qui se reproduit, il résulte comme produit de la grandeur de la population et du degré de la migration (N*m): 25 pour les monodomes et 2 pour les polydomes, ce qui veut dire qu'on peut voir une différenciation entre les sous-populations polydomes mais pas entre les sous-populations monodomes.

Mots clés: Formica, monodomie et polydomie, génétique des populations, degré de parenté, allozymes.

SUMMARY

5 island populations of mono- and polydomous colonies of Formica truncorum Fabr. were studied. The colonies within each population were predominantly of a single type, mono- or polydomous, colony type correlating with the number of

queens, so that monodomous colonies were monogynous and polydomous were polygynous. At least 20% of the queens had mated twice. The colony types differed also in the population structure, the polydomous colonies showing greater population viscosity within the subpopulations than the monodomous ones.

INTRODUCTION

Polydomy and polygyny are common features in red wood ants of the genus Formica (Buschinger 1974). The present study concerns _Formica_ _truncorum_ Fabr., which occurs on rocky islets in the Finnish archipelago, and whose ecology has been described in more detail by Rosengren et al (1985,1986). _Formica_ _truncorum_, forms both mono- and polydomous colonies, having one or multiple queens. These differences in colony patterns are not necessarily due to different stages in colony growth, as the production of reproductives is not correlated to type of colony.

The central issue in the present work is to study the intracolony structure, such as the degree of relatedness among workers, queen numbers and numbers of matings, and the association of colony structure with population-level differentiation in physically subdivided populations.

These problems can be studied genetically on two levels: 1) The population structure and gene flow can be studied by analyzing allele frequency variations at different allozyme marker loci. 2) The intracolony structure can be studied by analyzing the genotype distributions in these same allozyme marker loci.

MATERIAL AND METHODS

5 separate island populations were studied (table 1), defining each island as one subpopulation. The existence of internest communication was used when defining a nest as mono- or polydomous. All nests were sampled in the monodomous populations. In the polydomous populations 5-6 nests as far away from each other as possible were sampled. Horisontal starch gel electrophoresis was performed and 4 separate enzymes were stained using 10 workers per nest for each run. One of the enzyme loci segregated for three alleles the others for two. The progeny of old queens in 20 laboratory cultures were also analysed to check for multiple matings (see Pamilo 1982).

The statistical procedures are based on Wrights F-statistics and the relatedness estimates described in Pamilo (1984).

Genealogical relationships reflecting the probability to
share identical genes in common can be estimated as correla
tion coefficients. This coefficient of relatedness (Wright
1922) can be defined as follows:

Gametic correlation: estimates genetic differentiation and
population structure separately, and is based on differences
in allele frequencies between separate subpopulations.

Genotypic correlation: estimates genetic identity within
groups including the effects of the population breeding
structure, such as inbreeding.

The "effective" sample size in terms of the number of non-
related haploid genomes per nest can be calculated from the
estimated relatednesses. For example a nest with one, singly
mated queen has 3 such genoms.

RESULTS

Each population studied tended to be either mono- or polydo-
mous. The Sibbo population was an exception, not forming a
clearly defined entity, but consisting of islands from a
large area. Each island, however, tended to harbour either
mono- or polydomous colonies. Monogynous nests can be, ten-
tatively at least, identified by the genotype distribution
in the nest. The distribution of mono- and polygyny accor-
ding to colony type is presented in table 1.

The observed genotype distributions in the offspring of the
laboratory cultures, show that at least 20% of the queens
had mated twice. The coefficient of relatedness in these
laboratory progenies was 0.63, indicating that the average
number of matings per female is 1.32 (table 2).

	monodomous		polydomous		nr of	total
	mono-	poly-	mono-	poly-	islands	nr of
	gynous	gynous	gynous	gynous		nests
Hitis I	4	2	–	–	6	6
Hitis II	–	–	1	10	2	11
Tv.minne	16	4	–	–	4	20
Inkoo	–	–	–	20	6	20
Sibbo	6	2	–	14	5	22

Table 1. Mono- and polygyny in mono- and polydomous nests.
The monodomous nests tend to monogynous and the polydomous
ones to be polygynous $X^2 = 51.3$, $p < 0.001$.
Tableau 1. Mono- et polygynie dans les nids mono- et poly-
domes. Les nids monodomes sont essentiellement monogynes
tandis que les nids polydomes sont essentiellement poly-
gynes. $X^2 = 51.3$, $p < 0.001$

A more accurate description of colony structures can be
based on the coefficient of relatedness estimated in rela-
tion to a reference population (Pamilo 1984); this also
allows a hierarchical analysis (table 2). Correcting the
estimate of relatedness for multiple matings, allows a com-
parison of the number of nonrelated queens per nest (table 2
calculations according to Pamilo (1983)).

The relatedness estimates in monodomous nests corresponds
well with that observed in the laboratory cultures. Thus
monogyny with multiple matings could well account for the
lower relatedness estimates in the monodomous populations,
but not for the genotype distribution in the polydomous
nests, their observed value of relatedness being much lower
than expected from polyandry alone (table 2).

	Rcs	Rct	Rst	nr of queens
Monodomous				
Tvminne	0.57	0.67 ± 0.06	0.23 ± 0.07	1
Sibbo	0.51	0.61 ± 0.23	0.20 ± 0.01	1
Hitis I	–	0.61 ± 0.15	–	1
Polydomous				
Inkoo	0.06	0.21 ± 0.07	0.16 ± 0.04	>10
Sibbo	0.14	0.21 ± 0.14	0.08 ± 0.03	>4.5
Hitis II	0.03	0.40 ± 0.09	0.38 ± 0.01	>21
Culture		0.63 ± 0.23	–	1

Table 2. Coefficients of relatedness for mono- and polydo-
mous nests separately. Mean relatedness: within nests with
reference to the same subpopulation (Rcs), within nests with
reference to the total population (Rct), within subpopu-
lations (Rst), and for the cultures. (R=relatedness, c=nest,
s=subpopulation, t=population).
Tableau 2. Degrés de parenté estimés séparément pour les
nids mono- et polydomes. Parenté moyenne à l'intérieur des
sous-populations (Rst), à l'intérieur des nid par rapport à
la population totale (Rct), à l'intérieur des nids par
rapport aux sous-populations (Rcs), et pour les cultures.
(R=degré de parenté, c=nid, s=sous-population, t=popula-
tion). $Rcs = (Rct - Rst)/(1 - Rst)$

Three of the monodomous nests in the Sibbo population were
located on islands also inhabited by polydomous nests and 2
of these monodomous nests were also clearly polygynous. Thus
the status of these nests is not quite clear. These nests
are included in the polydomous groups in tables 2 and 3.

The value of Rct represents the total genotypic correlation
which consists of the components Rcs and Rst. The distribu-

tion of this total genotypic correlation over Rcs and Rst differs in populations having different colony types, indicating a proportionally greater genetic similarity within subpopulations in the polydomous colonies than in the monodomous ones. The relatedness values within entire islands (Rst), however, are roughly equal in both colony types. The variations in the relatedness values (Rct and Rst) in the polydomous colonies probably reflect a different spatial distribution of the islands in these populations.

The genetic differentiation between the populations expressed as fixation indices also indicate a larger population viscosity in polydomous colonies than in monodomous ones (table 3). Most of the total amount of differentiation (Fct) is explained by internest differentiation in monodomous populations, but by inter-island differentiation in polydomous ones. There is also a significant amount of inbreeding in polydomous populations, whereas no such inbreeding could be detected in monodomous ones.

	Fst	Fct	Fcs	Fit	Nests
Monodomous					
Tvminne	0.08	0.32	0.24	0.07 ± 0.2	20
Sibbo	0.08	0.26	0.19	-0.32 ± 0.21	5
Hitis I	–	0.33	–	0.08 ± 0.18	6
Polydomous					
Inkoo	0.14	0.19	0.05	0.34 ± 0.05	20
Sibbo	0.1	0.16	0.06	0.26 ± 0.07	17
Hitis II	0.14	0.19	0.05	0.18 ± 0.07	11

Table 3. Genetic differentiation in subdivided populations. Fst = between subpopulations (islands), Fct = between nests in each population. Fcs = between nests in each subpopulation. Fit = coefficient of inbreeding for each nest in the entire population, nests = number of nests studied. Tableau 3. Différenciation génétique dans les populations suivant différentes subdivisions. Fst = entre les sous-populations insulaires, Fct = entre les nids dans chaque population, Fcs = entre les nids dans chaque île, Fit = coefficient de consanguenité. Nests = nombre des nids étudiés.

DISCUSSION

The results show a difference between the mono- and polydomous colonies both in intracolony structure and population structure, as reflected by the relatedness estimates and the allele frequency variances. The differences in population structure indicated by the relatedness estimates are, how-

ever, probably boosted by the intracolony structure, as monogynous nests necessarily get a high intranest relatedness, and consequently a low degree of intercolony relatedness. This is not the case with the allele frequency data, as the genotype distributions within the nests do not affect this estimate. The significant amount of inbreeding in the polydomous colonies, also indicate that population viscosity may depend on colony type.

Genetic differentiation of populations is affected both by genetic drift/ migration and effective population size (Wright 1943, Nei et al 1977). Using the finite island model (Nei et al 1977), with the sample size corrections suggested by Pamilo (1983), the product Nm is 25 in monodomous populations, and 2 in polydomous populations (where N=effective population size, m=migration rate). According to Wright (1943) and Endler (1977) these values indicate no interisland differentiation for the monodomous populations and important interisland differentiation for the polydomous populations.

A correlation between social type and genetic parameters has also been observed in Formica exsecta (Pamilo and Rosengren 1984) and Formica sanguinea (Pamilo 1981, Marikovsky 1963), although their patterns differ from that of Formica truncorum.

The existence of such intraspecific differences in population structure has been discussed in relation to extrinsic factors (Hölldobler and Wilson 1977, Pamilo 1984, Rosengren et al 1985,1986). The question is, whether this structure is 1) a result of an inherent difference in behaviour, possibly dictated by genetical differences, 2) a result of environmental factors, such as availability of suitable nest sites, or competition, 3) a colony age dependent pattern.

Pamilo (1984) suggested a shifting balance between genetic and environmental determinants to explain the observed differences in a Formica sanguinea population. The differences in Formica sanguinea, however, were mainly quantitative whereas they are to be considered qualitative in Formica truncorum. Hölldobler and Wilson (1977) suggested that polygyny is favoured in patchily distributed habitats, but this does not explain the observed variations between the populations, unless important environmental differences between the studied islands have remained unidentified. A difference in the microhabitat structure nesting sites could affect colony structure (Rosengren et al 1985, 1986), but this does not explain the similarity within the single populations.

Dispersal patterns and inbreeding, as well as colony structure are also likely to affect sex ratio strategies (Hamilton 1971, Pamilo and Rosengren 1983, Alexander and Sherman 1977), as indeed has been observed by Rosengren et al (1986) for Formica truncorum.

The conclusion is that _Formica truncorum_ shows alternative colony tactics reflected in the genetic parameters of the populations, the next step would be to identify the ultimate and proximate reasons for this.

Ackknowledgements

References

ALEXANDER,R.D., SHERMAN,P.W. 1977. − Local mate competition and parental investment in social insects. Science 196:494-500

BUSCHINGER.A. 1974. − Monogynie und polygynie in Insektensozietäten. In G.H.Schmidt (Ed.), Sozialpolymorphismus bei Insekten. Stuttgart: Wiss. Verlagsgesellschaft.

ENDLER,J.A. 1977. − Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton

HAMILTON.W.D. 1971. − Selection of selfish and altruistic behavior in some extreme models. p 59-91. In J.F.Eisenberg and W.S.Dillon (eds.). man and beast: Comparative social behavior. Smithsonian Inst.Press, Washington

HÖLLDOBLER.B., WILSON.E.O. 1977. − The number of queens: an important trait in ant evolution. Naturwiss. 64:8-15

MARIKOVSKY,P.I. 1963. − The ants _Formica sanguinea_ as pillagers of _Formica rufa_ L. in nests. Ins.Soc. 10:119-128

NEI,M., CHAKRAVARTI.A., TATENO,Y. 1977. − Mean and variance of Fst in a finite number of incompletely isolated populations. Theor.Pop.Biol. 11:291-306

PAMILO,P. 1981. − Genetic organization of _Formica sanguinea_ populations. Behav.Ecol.Sociobiol. 9:45-50

PAMILO,P. 1982. − Multiple mating in Formica ants. Hereditas 97:37-45

PAMILO,P. 1983. − Genetic differentiation within subdivided populations of Formica ants. Evolution 37:1010-1022

PAMILO,P. 1984. − Genotypic correlation and regression in social groups: multiple alleles, multiple loci and subdivided populations. Genetics 107:307-320

PAMILO,P, ROSENGREN,R. 1983. − Sex ratio strategies in Formica ants. Oikos 40:24-35

PAMILO,P., ROSENGREN.R. 1984. − Evolution of nesting strategies of ants: genetic evidence from different population types of Formica ants. Biol.Linn.Soc. 21:331-348

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. Ges. 58:147-175