GENETIC POPULATION STRUCTURE IN POLYGYNOUS FORMICA ANTS

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SUMMARY

Genetic population structures, both mating and interaction structures, were investigated in three polygynous *Formica* ants by examining how genotype frequencies are distributed among the nests in their populations. The study is based on electrophoretically analysed enzyme polymorphisms. The patterns of genotypic variation among single-nest workers suggest that polygyny is functional in all the three species. The observed genotype frequencies indicate outbreeding within the study areas, and no spatial microdifferentiation in gene frequencies is detected. The coexistent gynes in nests of both *F. transcaucasica* and *F. polyctena* are genetically related to each other, and the same holds for worker nest mates. These results support the hypothesis that polygyny is favoured by kin selection. The lack of genetic relatedness among gyne nest mates in the highly polygynous *F. aquilonia* suggests that additional factors, such as mutualism or parental parasitism, are probably involved in the evolution of polygyny.

1. INTRODUCTION

POLYGyny, the existence of many egg-laying females (gynes) in a single nest, is rather a common phenomenon in ants. Of the European ant species about one half are classified as polygynous (Buschinger, 1974). It is known in social wasps and bees that, although the total productivity of a nest may increase, productivity per gyne decreases in multigyne associations (Richards and Richards, 1951; Michener, 1964). Similarly, in *Formica* ants the rate of egg-laying per individual is smallest in polygynous species (Gösswald, 1941; Schmidt, 1972). An apparent reduction of offspring numbers in multigyne associations has frequently led people to consider nests as superorganisms and to explain the evolution of polygyny through selection at the level of colonies or populations (Sturtevant, 1938; Oster and Wilson, 1978; see Crozier, 1979 for a review).

Lin and Michener (1972) have suggested that multiple foundress associations in wasps may be selected for because of beneficial mutual relationships. Mutualism could also serve as an explanation for pleometrotic nest founding in ants, but pleometrosis (= cooperative nest founding by several females) is not known to lead to permanent polygyny in ants (Hölldobler and Wilson, 1977). Another approach has been offered by Elmes (1973), who specially considered the relationships between gynes and workers. His observations in *Myrmica* ants support the view that the gynes can be considered as parasites on the colonies that readopt them.

Although polygyny could be favoured by mutualistic relationships, or maintained by parental parasitism, its evolution is also affected by trait group selection due to population subdivision. A population of polygynous

nests can be considered a structured deme (see Wilson, 1980), in which genetically determined social traits may increase in frequency due to gene frequency variance between the nests. If the coexistent gynes are related to each other, the between-nest variance is greater and the conditions for such trait group selection are more favourable.

Genetic aspects of the evolution of polygyny were underlined by Craig and Crozier (1979), who discussed the problem in the light of Hamilton's (1964a, b) theory of social evolution by kinship associations. In another recent article, Hölldobler and Wilson (1977) stressed the ecological constraints on the evolution of polygyny. They suggested that polygyny in ants is either associated with short-lived nest sites or with stable but patchily distributed habitats. It is reasonable to assume that the evolution and maintenance of polygyny in ants is connected both with the genetic structure of the populations and the ecological circumstances.

The aim of the present study is to examine genetic population structures in three polygynous *Formica* ants (Hymenoptera, Formicidae). One of them, *F. transcaucasica* Nasonov (= *F. picea* Nyl.), is a typical habitat specialist in the classification of Hölldobler and Wilson (1977). It inhabits bogs, the nests being located in the peat. The other two species, *F. aquilonia* Yarrow and *F. polycтена* Foerst., can also be classified as habitat specialists but, at least in northern Europe, their habitat is not patchily distributed. Both species form large polydomous societies (associations of cooperating nests) in coniferous and mixed forests (such habitats may have been patchy during the last ice age). The species build mound nests of needles and small twigs and the mounds have well-organized systems of foraging routes (e.g., Rosengren, 1971). The two species are highly polygynous, and the number of single-nest gynes may be up to tens or hundreds. In the present study, the population structures of the three species are examined by means of enzyme marker genes.

2. MATERIAL AND METHODS

(i) *Material*

The data on *F. transcaucasica* come from a population at Siikajärvi, Vihti, southern Finland. The population inhabits an open bog with a total area of about 20 ha. The nests are mainly located at the peripheral areas of the bog, and the material for the present study was collected from 55 nests within an area of 25 m × 25 m, which also included two small ponds (fig. 1). The nests were excavated in order to find the gynes. During the first sampling (15, V, 1980), the bog was still frozen from a depth of 10 cm downwards, and during the second sampling (22, V, 1980), from 20 cm downwards. The ants were aggregated in the peat above the ice and the gynes were easy to find. The third sampling was done on 8, VI, 1980 when the ants were already active and dispersed so that it was difficult to detect the gynes. Most of the nests excavated contained eggs, which indicates that they were not mere wintering shelters but real summer nests (see Rosengren, 1969, for a discussion of winter and summer nests in another bog ant, *Formica uralensis*).

F. aquilonia and *F. polycтена* gynes were collected in late April and early May 1979, when they could be found in the upper parts of the mound,

FIG. 1.—Allele frequencies among workers in the nests of *Formica transkaucasica*. The dark sector gives the frequency of the S allele and the light sector that of the F allele.

or on the mound surface. Two populations of each species were examined. The Espoo population of *F. aquilonia* at Solkulla was examined within an area of 6.5 ha (altogether 80 nests), and the Vantaa population at Keimola within an area of 5 ha (8 nests). The *F. polycтена* material came from 10 nests within 5 ha in Kauniainen and 18 nests within 30 ha in Siuntio.

Genetic variation was examined by horizontal starch gel electrophoresis (Pamilo *et al.*, 1978), using the buffer system of Varvio-Aho and Pamilo (1980). In *F. transkaucasica* two polymorphic enzymes, malate dehydrogenase (*Mdh*) and esterase (*Est*), were detected. The latter could not be scored from workers. In *F. aquilonia* and *F. polycтена*, phosphoglucose isomerase (*Pgi*) was found to be polymorphic. The genetic basis of the electrophoretic variation observed was confirmed by studying haploid males. While the workers and gynes showed a certain proportion of heterozygotes, the males always had a one-banded staining pattern as did the diploid homozygotes. The *Pgi* heterozygotes often showed just a broad band, but in successful stainings a three-banded pattern could be seen. In *F. transkaucasica*, a clear three-banded pattern was detected in the *Mdh* heterozygotes, whereas the heterozygotes for *Est* showed only two bands.

(ii) *Statistical procedures*

Mating structure is analysed by calculating the deviation from the genotype frequencies expected in a panmictic population by a fixation index

$$F = 1 - H_o/H_e, \quad (1)$$

where H_o is the observed heterozygosity and H_e that expected from $H_e = 1 - \sum x_i^2$ x_i denoting the frequency of the allele i . The deviation between the observed and expected genotype frequencies can be tested by $\chi^2 = NF^2$ with one degree of freedom (Li and Horvitz, 1953). The statistic is maximized ($\chi^2_{\max}$) when N is the total number of individuals examined. When the nest mates are genetically related to each other, they include redundant information and represent a number of independent individuals smaller than N .

Interaction structure measures inter-nest differentiation, *i.e.*, how closely the nest mates are related genetically to each other with reference to the population average (see Wade, 1980; Pamilo and Crozier, 1981). A general measure of differentiation in subdivided populations is the standardized variance of the gene frequency (Wright, 1943)

$$F_{ST} = \frac{s_x^2}{\bar{x}(1 - \bar{x})}, \quad (2)$$

where s_x^2 is the variance of the allele frequency among the nests and $\bar{x}$ is the mean frequency in the population.

The within-group genetic relatedness, b , can be defined as the average proportion of identical genes shared by two group members. Hamilton (1972, see also Michod and Hamilton, 1980) suggested that $b = 2F_{ST}/(1 + F)$, where F_{ST} is calculated from (2) and F from (1). When using small sample sizes, the estimate should include a sample size correction (Pamilo and Crozier, 1981). I used two methods to estimate genetic relatedness among nest mates: an intraclass regression coefficient (Pamilo and Crozier, 1981; see also Craig and Crozier, 1979) and an analysis of variance intraclass correlation coefficient (*e.g.*, Cockerham, 1973; Donner and Koval, 1980). The coefficients take into account the sample size correction, and they are calculated from genotypic values, letting the electrophoretic genotypes have values 1 for FF , 0.5 for FS and 0 for SS (F and S refer to the alleles representing fast and slow migrating allozymes). The standard error of the regression estimate is calculated according to standard methods, although this yields conservative confidence limits especially when b is close to zero (Pamilo and Crozier, 1981). The significance of the difference of b from zero is tested with a randomization test by rearranging the observed genotype numbers randomly in groups according to the sample sizes used. The observed estimate is then compared to the distribution of 1000 randomly generated values.

The estimates from (1) and (2) and the regression estimate of relatedness are calculated by weighting the nests equally and the estimates must be understood as average values per nest.

Spatial patterns of genetic differentiation within local populations are analysed in three alternative ways. Association of neighbour nests is examined by internest relatedness between nearest neighbours by applying

	Workers			Gynes							Workers			Gynes					
	<i>Mdh</i>			<i>Mdh</i>			<i>Est</i>				<i>Mdh</i>			<i>Mdh</i>			<i>Est</i>		
Nest	<i>FF</i>	<i>FS</i>	<i>SS</i>	<i>FF</i>	<i>FS</i>	<i>SS</i>	<i>FF</i>	<i>FS</i>	<i>SS</i>	Nest	<i>FF</i>	<i>FS</i>	<i>SS</i>	<i>FF</i>	<i>FS</i>	<i>SS</i>	<i>FF</i>	<i>FS</i>	<i>SS</i>
1	38	4	—	3	—	—	—	2	1	29	18	1	—	5	—	—	1	3	—
2	8	14	1	—	1	—	—	—	—	30	3	6	—	2	—	—	1	1	—
3	17	2	—	8	—	—	—	3	—	31	15	8	3	16	—	—	4	5	2
4	23	—	—	—	—	—	—	—	—	32	3	12	—	1	1	—	—	—	—
5	9	13	2	—	—	—	—	—	—	33	18	—	—	—	1	—	—	—	—
6	15	10	—	—	—	—	—	—	—	34	6	5	—	—	1	—	—	—	—
7	3	9	—	1	—	—	—	—	—	35	12	8	—	—	—	—	—	—	—
8	11	11	—	—	—	—	—	—	—	36	12	7	—	3	—	—	—	—	—
9	19	—	—	—	—	—	—	—	—	37	18	—	—	2	—	—	—	—	—
10	18	—	—	1	—	—	—	—	—	38	19	—	—	—	—	—	—	—	—
11	25	12	2	1	—	—	—	—	—	39	6	13	—	—	1	—	—	—	—
12	17	—	—	2	—	—	2	—	—	40	14	4	—	1	—	—	—	—	—
13	18	—	—	3	—	—	—	—	—	41	10	7	—	—	—	—	—	—	—
14	10	5	2	16	7	4	21	4	—	42	7	12	—	—	—	—	—	—	—
15	14	6	—	1	2	—	3	—	—	43	10	4	—	—	—	—	—	—	—
16	13	—	—	—	—	—	—	—	—	44	20	—	—	—	—	—	—	—	—
17	17	10	—	1	—	—	—	—	—	45	11	9	—	—	—	—	—	—	—
18	15	—	—	—	—	—	—	—	—	46	13	7	—	—	—	—	—	—	—
19	19	1	—	15	—	—	7	6	1	47	11	6	—	—	—	—	—	—	—
20	20	—	—	6	—	—	2	3	—	48	15	—	—	—	—	—	—	—	—
21	19	—	—	—	—	—	—	—	—	49	7	7	—	1	—	—	—	—	—
22	16	4	—	3	—	—	2	1	—	50	10	1	—	11	5	—	—	—	—
23	20	—	—	5	—	—	3	2	—	51	10	4	—	—	—	—	—	—	—
24	20	1	—	1	—	—	1	—	—	52	20	—	—	—	—	—	—	—	—
25	22	—	—	2	—	—	1	—	—	53	11	6	—	1	2	—	—	—	—
26	20	—	—	1	—	—	—	—	1	54	2	3	8	—	1	—	—	—	—
27	10	1	—	5	—	—	4	1	—	55	13	3	—	2					

number exceeding ten per nest is not very common. The distribution of the gynes in the gyneright nests (table 1) fits a discrete log-normal distribution, with zero term truncated ($\chi^2_{(2)} = 2.91$, $0.30 > P > 0.20$). All the gynes detected were inseminated, having sperm in the spermatheca.

Three alleles were found segregating at the *Mdh* locus. One of them was detected only in a single heterozygous gyne, its frequency being 0.003 (in all calculations requiring biallelic data this allele is combined with the *S* allele). The two common alleles had frequencies 0.88 (the *F* allele) and 0.12 (the *S* allele) in the gynes. Esterases were assayed in only 98 gynes, the two alleles segregated with frequencies 0.72 and 0.28. From these allele frequencies we obtain the expected heterozygosities 0.21 at *Mdh* and 0.41 at *Est*. The deviations from the observed heterozygosities, 0.23 and 0.38, yield fixation indices $F = -0.093$ and 0.062 , respectively. The deviations are not statistically significant ($\chi^2_{\max} = 1.38$ and 0.38).

1040 individual workers were sampled from 55 nests. On the basis of worker genotypes at *Mdh*, there were 18 single-genotype nests, 31 two-genotype nests and 6 nests with three genotypes (table 1). The frequencies of the *F* and *S* alleles were 0.86 and 0.14, giving an expected heterozygosity $H_e = 0.24$, which exactly equals the observed one, so that $F = 0$.

In gynes, the standardized allele frequency variance is $F_{ST} = 0.24$ for *Mdh* and 0.22 for *Est*, indicating that about 77 per cent of the total genic variation within the population can be found within single nests and 23 per cent is due to internest variation. The F_{ST} coefficient overestimates genic correlation by a factor inversely related to the sample size (see Pamilo and Crozier, 1981). The mean estimate of genetic relatedness among coexistent gynes (mean over *Mdh* and *Est*) is $\bar{b} = 0.26$ (table 2), the correlation method giving the estimate 0.23. The randomization test suggests that at both loci the relatedness estimate is significantly different from zero ($P = 0.03$ and 0.01).

The positive affinity of nest mates is also seen in workers. The mean estimates of genetic affinities in the 55 nests sampled are $F_{ST} = 0.19$ and $b = 0.33 \pm 0.07$ (mean $\pm$ SE). Taking the same set of nests used for estimating the genetic relatedness among gynes, a value $b = 0.24 \pm 0.11$ is obtained.

TABLE 2

Interaction structures given as estimates of genetic affinity of nest mates

		F_{ST}	$b \pm SE$
<i>F. transcaucasica</i>			
Gynes	<i>Mdh</i>	0.24	0.24 ± 0.16
	<i>Est</i>	0.22	0.29 ± 0.20
Workers	<i>Mdh</i>	0.19	0.33 ± 0.07
<i>F. aquilonia</i> /Espoo			
Gynes	<i>Pgi</i>	0.08	0.01 ± 0.11
Workers	<i>Pgi</i>	0.08	0.09 ± 0.09
<i>F. aquilonia</i> /Vantaa			
Gynes	<i>Pgi</i>	0.05	-0.02 ± 0.14
<i>F. polycтена</i> /Siuntio			
Gynes	<i>Pgi</i>	0.35	0.45 ± 0.18
Workers	<i>Pgi</i>	0.25	0.29 ± 0.15
<i>F. polycтена</i> /Kauniainen			
Gynes	<i>Pgi</i>	0.21	0.19 ± 0.34
Workers	<i>Pgi</i>	0.27	0.30 ± 0.23

No genetic microdifferentiation is evident within the study area (fig. 1). Genetic relatedness between neighbouring nests, calculated as a regression coefficient $b = 0.002 \pm 0.087$, reveals no affinity between the adjacent nests. Neither do the geographic distance and the pairwise allele frequency difference show any significant dependence (the regression coefficient of 0.003 is non-significant). Studying the geographic continuity reveals no significant departure between the observed and expected mean edge length in a Gabriel connected graph ($t = 0.03$, $df = \infty$, ns). Nor does the distribution of the edge lengths depart from that expected on the basis of random differentiation ($G = 7.21$, $df = 9$, ns).

(ii) *Formica aquilonia*

In the Espoo population, 168 gynes from 18 nests, and 296 workers from 21 nests were electrophoresed. The gynes assayed represent only a sample of the colony gynes. Of the 105 gynes dissected, 90 (86 per cent) had sperm in the spermatheca, being thus able to lay diploid eggs. The observations of R. Rosengren (personal communication) concur with this; he found 55 inseminated gynes out of 64 examined (86 per cent).

Two alleles were found segregating at the *Pgi* locus. The observed allele frequencies were 0.73 (the *F* allele) and 0.27 (the *S* allele) among the gynes, and 0.82 and 0.18 among the workers. The expected heterozygosities in gynes and workers are 0.39 and 0.29, respectively. The observed heterozygosities 0.34 and 0.31 (table 3) thus give fixation indices $F = 0.12$

TABLE 3

Numbers of the Pgi genotypes in the nests of F. aquilonia

Gynes					Workers				
Nest		<i>FF</i>	<i>FS</i>	<i>SS</i>	Nest		<i>FF</i>	<i>FS</i>	<i>SS</i>
Espoo	1	10	4	2	Espoo	4	11	7	—
	2	3	2	—		5	9	6	—
	3	17	5	2		14	8	3	—
	4	—	—	2		20	9	4	—
	5	3	2	1		24	7	8	1
	6	—	3	—		27	7	5	—
	7	4	—	—		28	12	3	—
	8	5	4	—		30	3	6	1
	9	3	1	—		32	6	—	—
	10	4	—	—		34	14	3	—
	12	1	1	—		38	13	6	—
	13	17	3	—		39	14	1	1
	14	—	1	—		45	14	5	—
	15	22	10	3		46	6	9	4
	16	6	—	1		55	11	2	—
	22	9	7	—		57	11	3	—
	23	4	6	—		62	8	2	—
Vantaa					63	11	4	1	
	1	3	2	9	64	6	5	—	
	2	3	4	3	66	13	1	—	
	3	1	5	4	67	7	5	—	
	4	—	1	1					
	5	4	6	9					
	6	—	5	7					
	7	1	2	5					

and -0.05 . These values do not differ significantly from zero ($\chi^2_{\max} = 2.37$ and 0.74).

The interaction structure of the population is studied in the same way as in *F. transcaucasica*, but only those nests from which at least four gynes (12 nests) or 10 workers (20 nests) are included.

The analysis of allele frequencies by the F_{ST} statistic suggests that about 7.7 per cent of the genic variation is between and 92.3 per cent within the nests (table 2). After a sample size correction, the values of F_{ST} become close to zero. Similarly, the correlation and regression estimates of genetic relatedness among gynes yield values very close to zero (table 2), suggesting that single-nest gynes are not more related to each other than to other gynes in the study area. The randomization test shows that the b estimate does not differ significantly from zero ($P = 0.88$).

The relatedness estimate among workers is considerably greater than among gynes, $b = 0.09 \pm 0.09$, the estimate being significantly different from zero (randomization test $P = 0.002$).

Similar results were obtained in the Vantaa population, from which 75 gynes from seven nests were examined. The allele frequencies among them were 0.32 and 0.68 (table 3), the expected heterozygosity thus being 0.43. This yields a fixation index $F = 0.17$ ($\chi^2_{\max} = 2.05$, ns). On the basis of F_{ST} , 4.9 per cent of the total genic variation is due to the inter-nest component. The genotypic estimate of genetic relatedness is slightly negative, $b = -0.02 \pm 0.14$, but not significantly different from zero ($P = 0.75$).

Microgeographic differentiation between nests is analysed in the Espoo population in which a greater number of nests was studied. The allele frequency distribution within the study area indicates no areal differentiation. The regression coefficient of the allele frequency difference on the metric distance between the nests does not differ significantly from zero ($t = 1.21$, $df = 188$), and the analyses of the Gabriel connected graph indicate no departure from randomness ($t = 0.48$, $df = \infty$, ns, and $G = 3.75$, $df = 5$, ns).

(iii) *Formica polyctena*

Like *F. aquilonia*, *F. polyctena* is highly polygynous, forming large colonies living in interconnected nests. However, it is, at least in Finland, not as highly polygynous as *F. aquilonia* (R. Rosengren, pers. comm.). Of the 280 gynes dissected for the present study, 80 per cent were inseminated.

The two populations of *F. polyctena* studied were almost monomorphic for the F allele at the *Pgi* locus (table 4). Its frequency among the gynes was 0.93 in Siuntio (104 gynes from 13 nests) and 0.96 in Kauniainen (29 gynes from five nests). The allele frequencies among workers were 0.97 in Siuntio (118 workers from 15 nests) and 0.95 in Kauniainen (53 workers from eight nests), respectively.

The expected heterozygosities are 0.13 from the gyne data and 0.05 from the worker data in the Siuntio population, and 0.08 and 0.10 in Kauniainen, respectively. Due to the low frequency of the S allele and the small number of nests studied, the estimates of genetic population structure (both mating and interaction structure) become rather imprecise and liable to sampling errors. The estimates of genetic relatedness among nest mates are rather high, the value of b ranging from 0.19 to 0.45 (table 2). All the

TABLE 4

Numbers of the Pgi genotypes among gynes in the nests of F. polycтена

Nest		FF	FS	SS	Nest		FF	FS
Siuntio	1	16			Kauniainen	1	6	
	2	16				2	6	
	3	3				3	6	
	4	2	7			4	3	2
	5	5				5	6	
	6	2	2	1				
	7	5						
	8	8						
	9	8						
	10	8						
	11	10						
	12	5	1					
	13	5						

estimates are significantly different from zero (randomization test P always <0.005), except the relatedness among gynes in Kauniainen which cannot be meaningfully tested because of the small number of heterozygotes.

4. DISCUSSION

It has been suggested that inbreeding, especially in family-structured populations, might have a role in the evolution of sociality and in development of multigyne associations (Hamilton, 1964*b*; Michod, 1979; Breden and Wade, 1981). Inbreeding in ants could arise from intranidal mating, although with polygyny this does not indicate mating between close relatives, or from a viscous population structure with spatial differentiation within the total population. The fixation indices in the present study showed no significant deviations from panmixia, indicating that there is no significant inbreeding within the local study areas (it has to be noted that the test is not very powerful (Ward and Sing, 1970)). Intranidal mating is partly suppressed by nests producing one-sex progenies, especially in *F. polycтена*, or releasing females and males at different times (Pamilo and Rosengren, 1981).

A population of *Formica* ants can be divided into lower-level subgroups termed federations, colonies and families (Zakharov, 1974; see also Pamilo *et al.*, 1978), especially in the polydomous *F. aquilonia* and *F. polycтена*. The present study gives no evidence for there being genetic subdivision within the given study areas. In this respect, the results differ from those in *F. sanguinea*, which showed extensive microdifferentiation within one population (Pamilo, 1981). Clearly, the differences in the population structures between species and populations of *Formica* ants are not only differences in polygyny or polydomy but also differences in genetic parameters.

The present observations indicate that all, or almost all, the gynes are inseminated, and the genotypic diversity within the worker population indicates that polygyny is functional. The data from *F. transkauucasica* and *F. polycтена* concur with the previous findings in *Myrmecia pilosula* (Craig and Crozier, 1979) and *Formica sanguinea* (Pamilo and Varvio-Aho, 1979;

Pamilo, 1981) that coexistent gynes, and also workers, are genetically related to each other. This supports the interpretation that polygyny is favoured by kin selection. All the three species shared the same feature that the genetic relatedness among the gynes approximately equals that among worker nest mates, as was also found earlier in *F. sanguinea* (Pamilo, 1981). This fits the assumption that the coexistent gynes may have arisen from a single nest, although we have to remember that the estimates are average relatednesses and in reality may vary from nest to nest. The relatedness among gynes estimates the true interaction structure of the breeding population, whereas that among workers depends on the number of gynes and possible differences in their egg-laying, on the relatedness among those gynes, and on the number of males with which the gynes have mated.

The relatedness estimates of the highly polygynous *F. aquilonia* are interesting as they suggest that the nests are not genetically differentiated, i.e., single-nest gynes are not more related to each other than to average gynes within the local population. This result raises the question recognized by Williams and Williams (1957): "The crucial point is the lack of genetic relationship between conspecific queens. If this were a regular occurrence, reproductive competition between the queens would necessarily promote the loss of the sterile castes and would have to be opposed by selection at a higher level."

The problem can be approached by distinguishing between the cases when the nests split by swarming with multiple gynes and when the number of gynes increases through adoption of new fertile females. Also, the problem can be considered either from the viewpoint of the gynes or the workers.

It has been speculated that polygynous nests may react to increasing intranest genetic heterogeneity by splitting, which would help to maintain high genetic relatedness among the nest mates (Crozier, 1979; Pamilo, 1981). In such a mode of nest founding, the gynes act as a group of coequal individuals, and polygyny might be favoured either by mutualistic cooperation or by kin selection between genetically differentiated gyne groups. These alternatives are not mutually exclusive, but they do not suffice to explain the *origin* of polygyny.

When the gyne number increases through adoption of new females, as is the case in *F. aquilonia* and *F. polystena*, there is an asymmetric relationship between the old and new gynes. The old gynes can be considered as donors offering an already existing nest for the recipients. The building and maintenance of a new nest, especially a big mound nest, requires significant resources in terms of worker numbers, resources that would take several years for a lone gyne to accumulate, and small and new Formica nests do not normally produce sexuals (see Brian, 1979). Further, the risk of failure for lone gynes is very great. It may therefore be far more advantageous for new gynes to join an established nest than to seek to found their own; this will result in many young gynes each year attempting to invade established nests. If we apply Wilson's (1980) model of structured demes to the present data, we find almost identical conditions for social evolution as by applying genetic relatednesses and Hamilton's (1964a) kin selection model. But by applying Wilson's alarm call model, these conditions become much less stringent (see also Johnson and Brown, 1980). More

information on the costs and benefits of multigyne associations in different ecological conditions is needed to solve these problems.

Evolution of polygyny should not be opposed only by gyne competition but also by worker interests. If the development of the sterile caste is based on kin selection, the workers should care for a brood related to themselves. Under polygyny this condition is easily violated. The relatedness of the brood to workers can be estimated approximately by the worker-to-worker relatedness, which was positive in all the species, although rather close to zero in *F. aquilonia* as is also the relatedness of the female brood to the workers (Pamilo and Rosengren, 1981).

An alternative hypothesis to kin selection would be to consider gynes as parasites of their worker force. This approach could explain both the evolution of insect sociality in the first place (Charnov, 1978) and the evolution of polygyny (Elmes, 1973). The model of the gyne population as an entity parasitic upon, but otherwise uncontrolled by, the workers accords with the indication from our work (Pamilo and Rosengren, 1981) that the sex ratio in the *Formica rufa* group, including *F. aquilonia* and *F. polyctena*, is probably controlled by the gynes, whereas in many other ants there is indication for great worker effects (Trivers and Hare, 1976).

The parasitism hypothesis does not solve the problem of intergyne competition raised by Williams and Williams (1957), but there is now accumulating evidence for intergyne relatedness in several polygynous ants which serves to explain reduced competition between them. We can conclude that the alternative hypotheses are not mutually exclusive, and actually they may explain different aspects of the evolutionary process.

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