Male size dimorphism and alternative reproductive tactics in *Formica exsecta* ants (Hymenoptera, Formicidae)

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Formica exsecta Nyl. populations in southern Finland exhibit two distinct male size classes. This phenomenon, which also occurs in *Formica sanguinea* Latr., is seen both within single nests and at the population level. Small males (micraners) appear to mature later, to have sharper diurnal activity peaks and to disperse more widely than do large males (macraners). Micraners appear to predominate in crowded polydomous colonies characterized by strongly male biased sex ratios, while macraners are characteristic of monodomous populations with a sex ratio close to 1:1. We suggest that macraners represent a mating tactic based on limited dispersal, including inbreeding, and that they may be most common during the early stage of the colony cycle preceding polygyny, while micraners represent an outbreeding strategy associated with a decline in resource availability.

Index words: Formica, ants, male dimorphism, dispersal, inbreeding, mating tactics, reproduction, diurnal rhythm, polygyny.

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1. Introduction

Polymorphism in ant workers is closely linked to intracolonial division of labour and colony ergonomics, and hence may reflect colony level selection (Oster & Wilson 1978, Lumsden 1982, Wilson 1985, Franks 1985). Polymorphism or dimorphism has also been described in sexuals of eusocial insects including halictid bees (Houston 1970), termites (Roisin & Pasteels 1985, 1986) and ants (Buschinger 1975, Elmes 1976, Kutter 1977, Brian 1983). Colony level selection could be less relevant for some of those cases considering that polymorphism linked to alternative reproductive behaviours, different dispersal tactics, and variations in resource structure is common among non-social animals including insects (Gadgil 1972, Gadgil & Taylor 1975, Järvinen & Vepsäläinen 1976, Hamilton 1979, Thornhill & Alcock 1983, Austad 1984).

Sexual selection based on individual reproductives competing for mates has been postulated in social species (Davidson 1982, Hölldobler & Bartz 1985), and facultative polygyny coupled to intraspecific differences in nesting strategy (Pamilo & Rosengren 1984) could give rise to dispersal polymorphisms (Rosengren & Pamilo 1983, Fortelius 1985, 1987). Cases of male dimorphism are represented by *Hypoponera eduardy* (Kutter 1977) and *Formica naefi* (Kutter 1957), but reports on male polymorphism in ants have generally remained scarce. Here we describe the occurrence of male dimorphism in the common ant species *Formica sanguinea* Latr. and *Formica exsecta* Nyl. The latter case is analysed in some detail.

2. Material and methods

Nests of *Formica exsecta* Nylander 1846, a species forming small moundnests in open habitats, were sampled in the coastal area of Southern Finland. The sampling area included the following rural communities: Sibbo, Esbo,

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Table 1. Correlation coefficients (r) for thorax length versus interocular distance in micraners and macraners of *Formica exsecta* given with degrees of freedom (*df*) and level of probability (*P*). The test value (t_s) and level of probability (P_s) for the comparison of the correlation coefficients are also given (NS = non significant).

	r	df	P	t_s	P_s
Micraners	0.745	48	<0.001		
				1.263	0.206
Macraners	0.605	48	<0.001		NS

Sjundeå and Ingå. Males were also collected from nests of *Formica sanguinea* Latreille 1798, mainly on the Hangö peninsula. Sexual pupae were in both species sampled in July. Adult sexuals were usually collected between mid-July and the beginning of August and the high variability of emergence time was taken into account by examining many nests more than once.

Weights of individual ants were determined on a Cahn[R] 28 microbalance. Corresponding morphometric measurements were made using a Wild[R] M5 microscope with ocular micrometer. The following characters were measured: winglength; length of thorax viewed from the dorsal side (1. pronotum to the border between metanotum and propodeum or 2. the frontal border of mesonotum to the petiole scale); and interocular distance (the shortest distance between the medial borders of the compound eyes). The relationship between interocular distance and thorax length was virtually isometric and showed a strong linear correlation both for the entire sample (r = 0.96), and for micraners and macraners separately (Table 1).

Sex ratio estimates based on imagoes are unreliable because males often mature (and may fly away) before females (Pamilo & Rosengren 1983 and unpubl.). We therefore based sex ratio estimates mainly on pupae, but some samples included also a few callows. The pupae were sexed by removing the cocoon or by making the cocoon transparent in alcohol and examining the head under the microscope. Part of the sample contained prepupae which had to be dissected to examine the presence or absence of testes. We strived to examine at least 20 specimens from each nest, but 6 of a total of 97 samples contained only 10—19 pupae. Methodological problems associated with sex ratio estimates have been discussed by Rosengren & Pamilo (1986).

The activity rhythms of differently sized males were measured using infrared-sensitive transistors coupled to Sodecoprint[R] units, by pooling impulses from a running arena which the males reached from below through holes in the roof of their "nest". No workers were present. The device (figure in Rosengren & Fortelius 1986) was kept in a room maintained at constant humidity and temperature, on a 12:12 h light-dark cycle. Small and large males (20 in each batch) were tested separately. Field observations of alate activity were made by watching both natural nests and seminatural nests kept outdoors in a shady place. The latter nests consisted of natural nest material within glass-roofed containers harbouring workers, brood and alates (separate nests for females, macraners, and micraners). The number of alates on the surface of each nest was counted at 1h intervals. Air temperature was recorded with a Görtz[R], 183 8012 E00 thermograph.

3. Results

Like reproductive females, males of most European *Formica* species show little intraspecific size variability, at least as compared to workers. The high size variability of males in *F. sanguinea* and *F. exsecta* contrasts strongly with the usual situation and therefore demands an explanation.

Miniature males or "micraners" appear to be fairly rare in *F. sanguinea*, and the phenomenon could therefore be interpreted as "pathological". Micraners are found at the normal time of sexual production, but one nest of *F. sanguinea* produced small males in large numbers in late September and early October, about two months later than normal.

We concentrated our study on *F. exsecta*, a species in which small and large males (micraners and macraners respectively) both appeared to be very common within our study area. Measuring males from 27 different *F. exsecta* nests distributed within a large area of southern Finland not only confirmed this impression, but also indicated population level bimodality with respect to male size (Fig. 1). Based
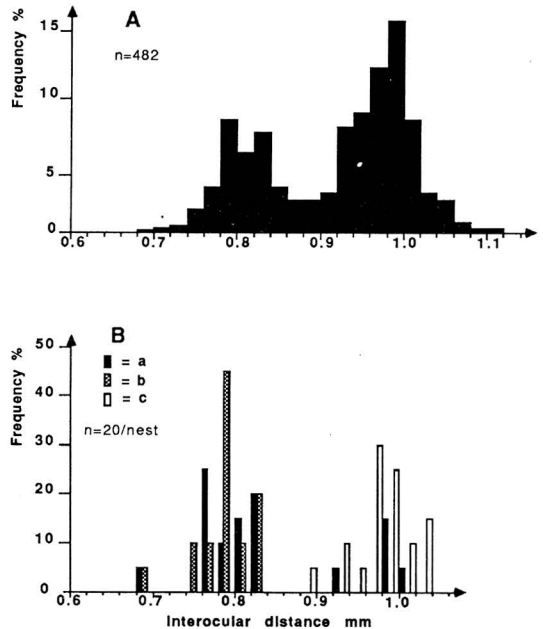

Fig. 1. Size frequency distributions in *Formica exsecta* males, illustrated by the interocular distance. — A. The bimodal population level distribution. Samples pooled from 27 randomly selected nests (about 20 males/nest). Sampling area about 2500 km[2] around Helsinki. — B. An example of three nests with different distribution types. a = mixture of size morphs, b = micraners only, c = macraners only.

on these measurements an interocular distance of 0.90 mm was chosen as an arbitrary division between micraners and macraners. Individual nests produce either a mixture of small and large males, or else predominantly just one of the two size morphs (Fig. 1). The pooled distribution of interocular distances fits the assumption of two separate but overlapping normal distributions ($\bar{x}_1 = 0.81$, $SD_1 = 0.04$ and $\bar{x}_2 = 1.0$, $SD_2 = 0.04$; $\chi^2(15) = 21.8$, $P > 0.1$). However, the groups are not separate enough to allow unequivocal classification of each individual male.

Worker samples from the same nests do not show any bimodality (Fig. 2), and scattered size measurements do not indicate any tendency to dimorphism in reproductive females either (Fig. 4 and unpubl.).

Micraners, but not macraners (as defined above), show a strong correlation between body size, as measured by interocular distance, and body weight (Fig. 3B). Also wing length and body size are much more strongly correlated in micraners than in macraners (Fig. 3A). Thus micraners show a significant correlation between wing length and body weight, whereas macraners do not. The wider range of weight measurements in macraners might be a consequence of their presumably longer life-span (below). The correlation coefficient (r) differs significantly between micraners and macraners in all the cases above, except for the relation between thorax length and interocular distance (Fig. 3 and Table 1 respectively). The range of size is wider in micraners than in macraners (Fig. 3), and this could partly influence the correlations, particularly in case 3A. Still the tendency seems clear and we can ask: What does it mean? One interpretation we find plausible is that the flight abilities of the micraners are under stronger (positive) selection than are those of the macraners.

Measurements of additional samples from individual nests, using thorax length (measure 2, in methods) as a measure of body size, confirm the presence of two size morphs and suggest furthermore that the size of macraners matches the size of females (Fig. 4) although macraners have a slightly higher size variance than females (Fig. 4C).

The difference between micraners and macraners is probably caused by environmental cues experienced during larval development. Such a control of size could also lead to a continuous unimodal size distribution, whereas our observations suggest bimodality. Micraners may be energetically less costly to produce, but the idea of "tradeoff" between small and
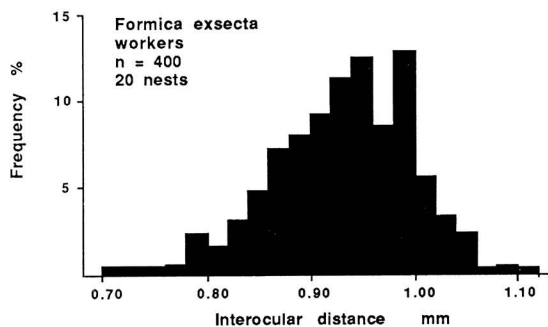

Fig. 2. Pooled distribution of interocular distances in random samples of workers (20/nest), representing 20 of the 27 nests used for the data of Fig. 1.

large males (Davidson 1982) can not by itself explain the bimodal size distribution. We suggest that the bimodality indicates two different reproductive behaviours. Thus it is possible that the large sized macraner phenotype is selected to match the size of females because of competition for mates on the natal patch. Mating on the ground favours large size in ant males (Davidson 1982), and males competing for females on the nest surface have been observed in other species of the genus *Formica* (Rosengren & Pamilo 1983).

The strong correlation between size, weight and wing length in micraners (above) suggest that the micraners have the advantage of being good flyers. Good flight ability would allow long range dispersal, and also the option of approaching females in the air, thus avoiding mating competition on the ground. A mating tactic based on good flight ability may require population-level syncronization of nuptial flights and hence narrow activity peaks in individual males. The alternative tactic of males waiting for females within or near the nest, followed by copulation on the ground may, by contrast, favour broadening of the active period. At the moment we have very few observations of female mating behaviour in natural conditions. The working hypothesis sketched above is however consistent with the following observations:

1. Micraners emerge later than macraners in nests which produce both morphs, as shown in Fig. 5 and by earlier observations on the emergence time of adult males (Pamilo & Rosengren 1984). It can be argued that this state of things is advantageous both to macraners and to micraners and may improve
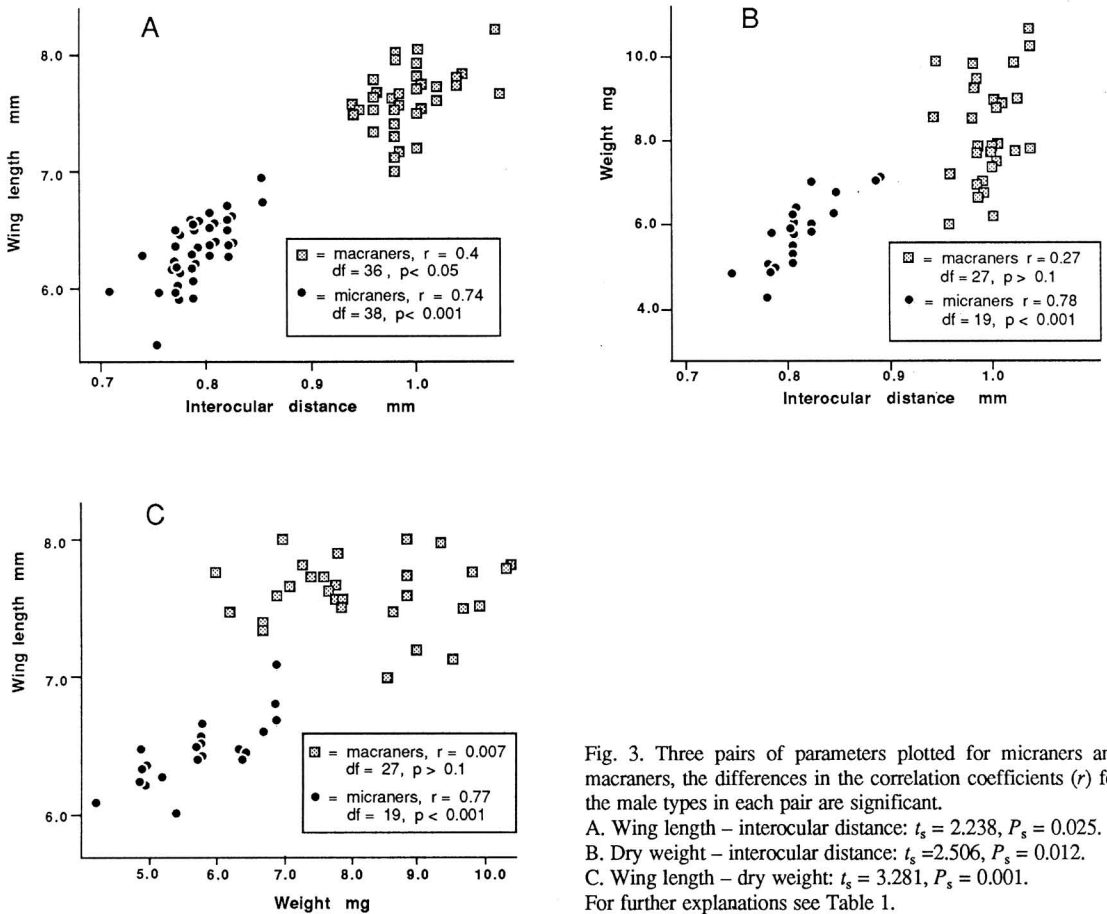
Fig. 3. Three pairs of parameters plotted for micraners and macraners, the differences in the correlation coefficients (r) for the male types in each pair are significant.
A. Wing length – interocular distance: $t_s = 2.238$, $P_s = 0.025$.
B. Dry weight – interocular distance: $t_s = 2.506$, $P_s = 0.012$.
C. Wing length – dry weight: $t_s = 3.281$, $P_s = 0.001$.
For further explanations see Table 1.

colony-level fitness: A) larvae of sexuals are fed with glandular food representing stored, probably limited, resources. Thus the production of either morph would be a result of prevailing food access. B) males (at least macraners) emerge before females of a given nest and macraners live longer than micraners (unpubl. preliminary observations). Macraners may thus be able to mate with females from the same or a nearby colony (which requires that they emerge before the females), while micraners (assuming long range dispersal and considering the high variance in development time between sexuals from different colonies) do not need this option. C) the later appearance of micraners is likely to coincide better with the average mating time of females in the population because of the general rule that males emerge before females. Preliminary observations indicate that the spermathecae of flying females are empty but this does not exclude the possibility that at least part of the matings occur on the nest.

2. Our field observations suggest that micraners are good flyers capable of aerobatic maneuvers including hovering in the air like flies. Micraners hovering in the air were frequently observed also in captivity. Micraners released from seminatural nests in open air were in all cases observed to rise high in the sky before disappearing from sight. Macraners "swarming" on a natural moundnest were observed to behave differently. They flew in most cases only short stretches close to the ground, in effect "jumping" between tussocks of grass within the natal habitat patch. Some did not even attempt to fly, but climbed vegetation close to the nest and remained sitting there for hours. The result of a preliminary laboratory test agrees with the above observations. A higher proportion of macraners, as compared to micraners, bumped to the floor after leaving the nest by flight, although the difference was nonsignificant, and males of both categories flew a significantly longer distance than females (Table 2).
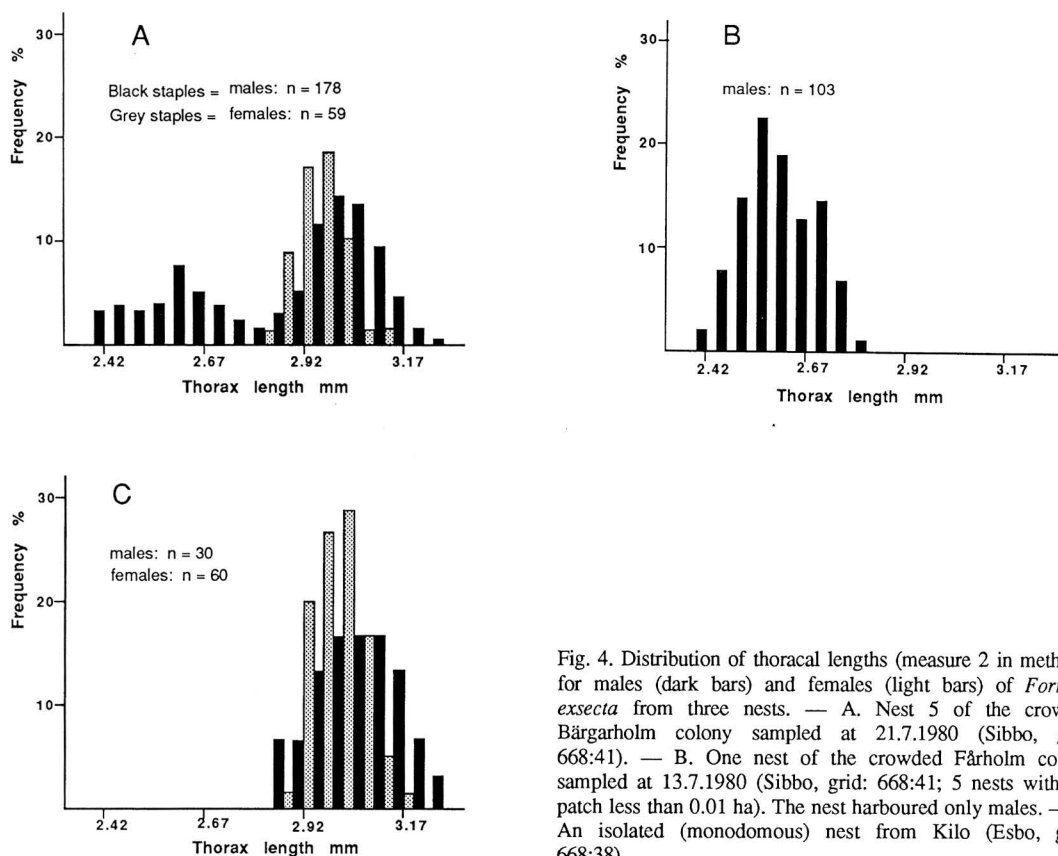
Fig. 4. Distribution of thoracal lengths (measure 2 in methods) for males (dark bars) and females (light bars) of *Formica exsecta* from three nests. — A. Nest 5 of the crowded Bärgarholm colony sampled at 21.7.1980 (Sibbo, grid: 668:41). — B. One nest of the crowded Fårholm colony sampled at 13.7.1980 (Sibbo, grid: 668:41; 5 nests within a patch less than 0.01 ha). The nest harboured only males. — C. An isolated (monodomous) nest from Kilo (Esbo, grid: 668:38).

Table 2. The results of a simultaneous test comparing the flight distances of *Formica exsecta* micraners, macraners and females in the morning (07.00–09.00). Seminatural nests containing each category (the same batches as in Fig. 8) were housed in a large room and the ants flew spontaneously from their nests toward the window. Mere flight attempts were not included.

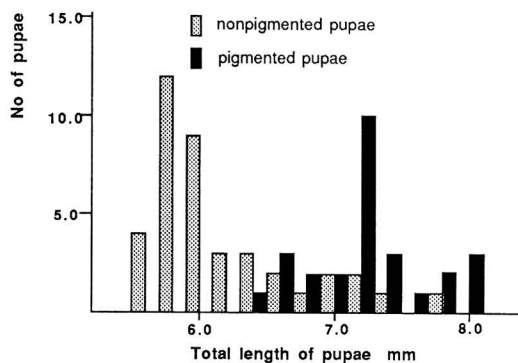|	fly > 3m	fly < 3m	
micraners	20	19	$\chi^2 = 3.24$
macraners	14	30	$P > 0.05$
macraners	14	30	$\chi^2 = 7.78$
females	4	43	$P < 0.01$

Fig. 5. Size frequency distribution of pigmented and nonpigmented *Formica exsecta* male pupae sampled 29.6.1979 from one moundnest (Pojo, grid: 667:31). A specimen was considered pigmented if the dark pigment was visible through the cocoon. Pigmentation takes place a little before emergence (younger pupae are white). Dividing the total range into halves (classes 5.6—6.8 mm versus 7.0—8.2 mm) and comparing the proportions of pigmented pupae indicate that macraners emerge significantly earlier ($\chi^2 = 32.3$, $df = 1$, $P<0.001$).

3. Laboratory recordings of diurnal activity in an artificial light regime (Fig. 6) and observations of alate activity in seminatural nests subject to the natural light rhythm (Fig. 7) suggest that micraners and females have narrower activity peaks than
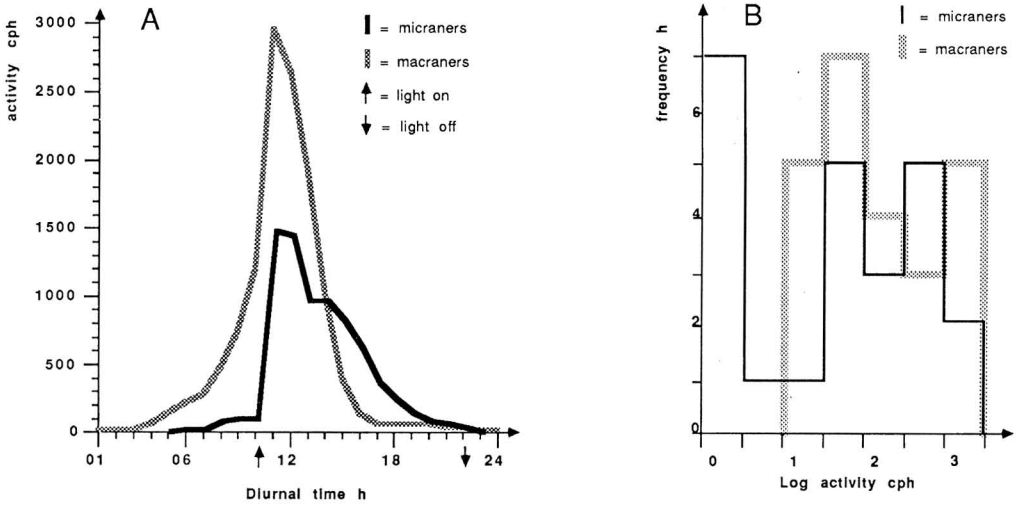
Fig. 6. Machine recordings of diurnal activity of *Formica exsecta* micraners and macraners in a thermostated room with a 12:12 h light:dark cycle (cph = machine counts/h). — A. Mean activity for several 24 h cycles, $n = 5$ for micraners and $n = 4$ for macraners. Note the strong dependence on light in micraners. — B. Frequency distribution of hours with a given log activity during a 24 h cycle (based on the same recordings as A). The distributions, demonstrating the high number of hours, with very low or no activity at all in micraners, differ on a statistically significant level (Kolmogorov–Smirnov test: $D = 0.567$, $P<0.001$).

macraners. Strong timing of mating activity by light acting as a "Zeitgeber" is compatible with outbreeding (Hölldobler & Bartz 1985), while relaxation of rhythmicity may indicate selection for a mating tactic based partly on inbreeding.

4. Previous results show that males from *F. exsecta* nests producing pure male brood are, other things being equal, significantly smaller than males from nests producing mixed brood (Pamilo & Rosengren 1984). This is consistent with our working hypothesis because males from nests producing only males have no other option than dispersal. Micraners appear to be more characteristic of polydomous-polygynous populations than of monodomous populations (Pamilo & Rosengren 1984). This association was confirmed also in the present study by selecting nests producing all-male broods from monodomous and polydomous populations (Table 3). The data of Table 3 show a significant difference in male size between mono- and polydomous colonies (Student's t-test: $t = 3.6$, $df = 14$, $P < 0.01$). Our data suggest that the coupling between polydomy and high production of micraners is caused not by polydomy per se, but by crowding of the patch followed by low resource availability. This has also been suggested by Charnov (1982) for parasitic wasps. The polydo-
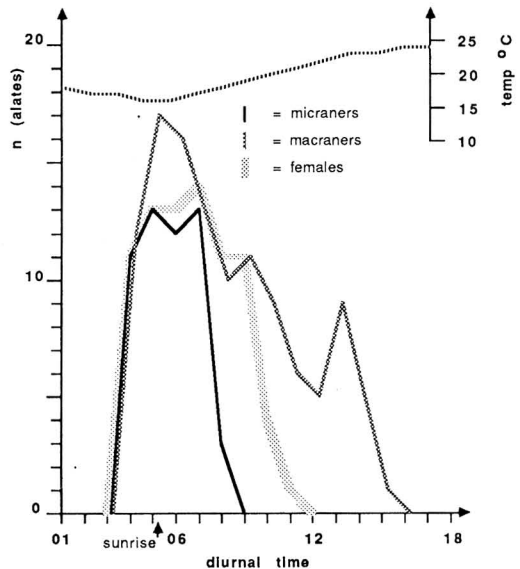

Fig. 7. Periodicity of micraners (interocular distance: mean ± $SD = 0.805 \pm 0.036$ mm), macraners (0.989 ± 0.036 mm) and females of *Formica exsecta* relative to the prevailing diurnal cycle (early August). The number of alatae rising to the surface of three seminatural nests were counted each hour throughout a 24 h period.

Table 3. Comparison of thoracal lengths (measure 1 in methods) and interocular distances of male imagos from individual nests of monodomous and polydomous *Formica exsecta* populations (20 males/nest). The nests, all of which were sampled in the summer 1984, contained only male sexuals. A nest was arbitrarily classed as a monodomous if alone on a patch > 1 ha, but as polydomous if five or more nests occurred within a patch < 0.5 ha. The samples marked with * constitute the ones from Stora Halstö and Sibbo Fagerö, where the resource availability was presumed to differ from that in the other polydomous colonies.

	Thorax		Head		Pooled
	Mean	SD	Mean	SD	
Monodomous					
Jakobsbacken, Sjundeå	2.25	0.05	0.99	0.04	Thorax:
Lilla Halsö, Ingå	2.21	0.07	0.99	0.02	mean = 2.24
Åbovägen, Esbo	2.18	0.08	0.98	0.04	SD = 0.06
Rövarland, Ingå	2.19	0.07	0.96	0.02	
Pikkala, Sjundeå	2.25	0.05	1.01	0.04	Head:
Kitö-Snättvik, Sibbo	2.19	0.06	0.99	0.03	mean = 1.0
Krokholmsträsk, Sibbo	2.38	0.05	1.06	0.03	SD = 0.03
Kilo, Esbo	2.26	0.08	1.00	0.03	
Polydomous					
Klobbacka, Ingå	1.78	0.09	0.81	0.03	Thorax:
Klobbacka, Ingå	1.88	0.09	0.85	0.03	mean = 1.94
Fårholm, Sibbo	1.80	0.10	0.82	0.03	SD = 0.2
Bärgarholm, Sibbo	1.86	0.10	0.84	0.03	
Bärgarholm, Sibbo	1.82	0.08	0.82	0.03	Head:
Stora Halstö, Ingå	*1.91	0.24	0.85	0.09	mean = 0.90
Stora Halstö, Ingå	*2.28	0.08	1.00	0.03	SD = 0.07
Sibbo Fagerö	*2.23	0.09	0.97	0.04	

mous colonies on Stora Halstö and Sibbo Fagerö inhabited large areas suitable for additional nests of the species while the colonies on Bärgarholm and Fårholm were concentrated into miniature patches (cf. tables 3 and 4). Males on Sibbo Fagerö and Stora Halstö tended to be large compared to those from Fårholm and Bärgarholm (Table 3).

5. Polydomous colonies of *F. exsecta* have strongly male biased sex ratios while monodomous colonies of the species have population level sex ratios close to 1:1 or female biased (Pamilo & Rosengren 1983). Our present results, based on a larger number of sampled nests (in most cases not identical with the nests sampled in the previous study), confirm those conclusions (Fig. 8). The high variability of population sex ratio for our polydomous colonies (Table 4) points to the possibility that male frequency may be positively correlated with nest density (nests/ha). The most probable reason for this effect is that resource availability (which may be low in crowded patches) influences the sex ratio as demonstrated in other *Formica* species (Luther 1985, Rosengren & Pamilo 1986). A connection between sex ratio of ants and resource availability has independently been suggested by Nonacs (1986).
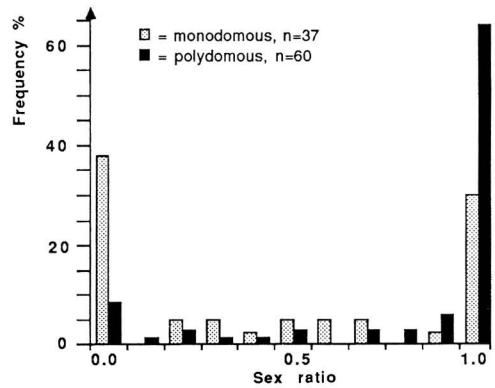

Fig. 8. Distribution of colony sex ratios (proportion: males/total). The graphs summarize the data from the localities listed in Table 4 (data from 1983 and 1984 combined). The material is mainly based on pupae (usually 20 or more/nest), *n* refers to the total number of sampled nests containing sexual brood.

Switching the sex ratio toward male bias, and male size toward the micraner morph, could thus have the same proximate cause and may represent different aspects of the same strategy.

Table 4. Population sex ratio (mean ± SD) given as the numerical frequency of males (no. of males/ males + females). Departure from the 1:1 ratio (Wilcoxon rank test) refers, however, to investment ratios based on dry weight. We have used a weight ratio males:females of 0.77 for the monodomous population and 0.54 for the polydomous populations (based on data in Pamilo & Rosengren 1983). The latter figure is probably too small for the Halstö and Sibbo Fagerö colonies. Further Information in Table 3, Fig. 8 and the text.

Locality	Year	Area sampled (ha)	No of nests	Nests /ha	% Sex nests	Sexed nests	Sexed specimens	Frequency of males	P - dep. from 1:1 ratio
Polydomous									
Stora Halstö	1983	2	26	13	?	14	322	0.78±0.42	<0.05
	1984	2	26	13	96	16	279	0.76±0.40	<0.01
Sibbo Fagerö	1984	1.3	19	15	74	12	264	0.78±0.33	<0.05
Bärgarholm + Fårholm	1984	0.02	11	550	85	8	158	0.98±0.51	<0.01
Esbo	1984	0.1	17	170	59	10	186	0.91±0.16	<0.05
Monodomous									
Ingå + Sibbo	83–4	>3000	?	1	?	37	911	0.48±0.43	NS

4. Discussion

We have so far discussed male dimorphism in *F. exsecta* in terms of alternative male mating tactics, an explanation often assumed to implicate genetic differences underlying the phenotypic traits studied (but see Austad 1984). We do not however presuppose genes for male size as an explanation for the difference between macraners and micraners and actually find this explanation unlikely. It may therefore be more heuristic than correct to include selection on males, e.g. when competing for mates, as an explanation of our findings considering that selection as an evolutionary mechanism must be based on heritable differences between the males discussed. The success of a given male phenotype compared to another male phenotype may however (also when the difference is based on nurturing conditions alone) effect the fitness of the colony (or mother queen) responsible for a given blend of male phenotypes. Poor performance of males could, through selection on mothers (or colonies), influence nurturing schedules for males and thus maximize the mean fitness of males e.g. by adapting male phenotypes to different mating niches. The situation would, if this interpretation is correct, represent a close analogy to the evolution of different worker castes within a colony. Alternative male mating tactics, controlled by colony-level epigenetic rules, is however only one of several possible explanations and we have to examine other hypotheses as well:

1. Observations on orphaned *F. exsecta* nests suggest that worker-produced males could occur in this species (Pamilo & Rosengren 1983). Do micraners develop from eggs laid by workers and macraners from eggs laid by queens? This is difficult to examine in polygynous nests, but observations of male production (macraners) in orphaned nests indicate that at least this is not a universal rule. To explain the data this hypothesis requires an additional hypothesis that the queens lose control of male production in polydomous colonies. We have no data with which to test this hypothesis.

2. Inbreeding in ants and bees is known sometimes to give rise to diploid, usually sterile, males, which can be larger than normal males (Ross & Fletcher 1985). The explanation is unlikely in *F. exsecta* considering that the two morphs are nearly equally common in our study area, and that enzyme electrophoresis has not detected any heterozygous (diploid) males in this species (Pamilo & Rosengren 1984).

3. Micraners and macraners could represent two sibling species emerging through Emery's rule (Starr 1979, Brian 1983). The explanation is unlikely considering that we have seen hundreds of females without detecting any evidence of female dimorphism. Our SEM studies to confirm differences in chaetotaxonomic or other characters have similarly yielded only negative results (unpubl.). But it is worth noting that the widely distributed *F. exsecta* is characterized by large females and dimorphic males

while most other European species of the *exsecta*-group, many of which are sibling species, are characterized by microgynes and monomorphic males of the micraner type (Collingwood 1979).

Nuptial flight and mating in *F. exsecta* occurs exceptionally early in the morning, starting at sunrise. Our data are still insufficient to permit firm conclusions regarding the connection between the male morphs and differences in mating and dispersal behaviour. But our indirect fragmentary evidence suggests the following solution to this puzzle.

Most species of ants are considered to be strongly outbreeding (e.g. Hölldobler & Bartz 1985, Trivers 1985, but see Alexander & Sherman 1977). However, field observations and genetical data suggest that this generalization may not be true in the case of moundbuilding *Formica* ants (Rosengren & Pamilo 1983, Pamilo & Rosengren 1984). A switch from a monodomous and monogynous to a polydomous and polygynous nesting structure occurs in several of those species including *F. exsecta* (Pamilo & Rosengren 1984). This switch is problematic from the point of view of evolutionary theory, because it results in reproductive competition within nests and because the workers of a nest or group of communicating nests will have different mothers and fathers. Genetical data indicate that monodomous colonies of *F. exsecta* are often inbred (Pamilo & Rosengren 1984). They also tend to produce macraners, especially if both male and female brood occur within a single nest. It thus seems that the switch to polygyny may coincide with a cycle of inbreeding, increasing relatedness. Macraners may be poor dispersers and may therefore more often mate with relatives from the same or a nearby nest. Inbred females remaining in their natal nest or habitat patch will have closely related offspring. This cycle of inbreeding may switch to a cycle of outbreeding as soon as the polydomous-polygynous colony exceeds the carrying capacity of the patch, or resource availability becomes poor for other reasons.

This can lead to local resource competition among related females and so is expected to favour a male-biased sex ratio (Charnov 1982, Pamilo & Rosengren 1983). It becomes more difficult for males to find a mate in the natal patch, and dispersal thus becomes a better option. As we have argued above, this can favour a small body size. There is probably a correlation between the size of a male and the amount of sperm it can produce and a macraner may, compared to a micraner, have a greater ability to monopolize the spermatheca of a queen (see Crozier and Page 1985 for a discussion of this aspect). Multiple mating (polyandry) reducing the level of relatedness between nest mates has been demonstrated in some *Formica* species, to some extent also in *F. exsecta* (Pamilo 1982, Pamilo & Rosengren 1984) but it is difficult to assess the significance of this problemacy for the fitness of different male size morphs or for the colony-level scenario discussed. Good dispersal and aerobatic ability could also be an option for the females, but reduction in body size may in this case be constrained by the energetic reserves needed for egglaying. A complication here is that single *F. exsecta* females start new nests through temporary parasitism (Collingwood 1979) implicating that the *Formica* foundress, unlike species with claustral nest founding, do not need bulky store tissues for raising its first brood to maturity. There are circumstantial evidences, however, that the foundress has to kill the queen of the host colony by brute force (Adlerz 1913) and this could contribute to selection against reduced body size in foundresses.

The scheme sketched above relates the colony cycle (including the switch from monodomy-monogyny through monodomy-polygyny to polydomy-polygyny) to adaptive changes in the frequency of different male morphs. The colonies produce macraners at the beginning of the colony cycle because of their good mating success, and switch to produce widely dispersing micraners later, when the local population density increases.

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