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Mating strategy and isolation between the two forms, macrogyna and microgyna, of *Myrmica ruginodis* (Hym. Formicidae)

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Abstract. 1. It is shown that the size distribution and degree of overlap between individual queens of the two forms of *Myrmica ruginodis*, microgyna and macrogyna, is exactly the same in southern England as was originally described from Scotland.

2. Distinguishing colonies of the two forms is not as easy as distinguishing between individuals, both types can be polygynous and approximately 25% of colonies contain a mixture of queens.

3. Males of the two forms can be distinguished solely on the basis of size and, in general, macrogyna colonies produce larger males, workers and gynes than microgyna colonies. There is little correlation between the sizes of males, workers and gynes in colonies within the macrogyna and microgyna groups.

4. If the two forms are separate species and mixing is a parasitic association (as suggested elsewhere), then there should be breeding isolation between the forms. This is tested by examining data from nine mating-swarms.

5. All the swarms contain a significant proportion of the microgyna form. There is no evidence of assortative mating, although larger males are more likely to get a mate than smaller ones. This behaviour, combined with the possibility that microgynes mate near to the nest, might prevent complete mixing during mating.

6. The status of the forms is discussed. Besides the possibility of a 'pre-parasitic' relationship it is suggested that the forms might represent a polymorphism, present in all populations, the balance between them being the result of selection determined by local environmental factors.

Key words. *Myrmica ruginodis*, macrogyna, microgyna, swarms, mating-strategy, Formicidae.

Introduction

The red ant species, *Myrmica ruginodis* Nylander, has two distinct forms. Brian & Brian (1949), working in Scotland, showed that nests containing more than one functional queen (polygynous colonies) specialized on stable habitats, usually those at a biotic climax, e.g. heather moorland, and contained small queens (microgynes). Whereas, monogynous or single-queened colonies usually had large queens (macrogynes) and used ephemeral habitat, e.g. forest clearings. Using bioassay, they demon-

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strated behavioural differences between the two sizes of queen and their workers; macrogynes were aggressive and would not tolerate the presence of other queens or workers, whereas microgynes were more passive and often tolerated the introduction of foreign workers and queens, even macrogynes.

Brian & Brian's study of *M.ruginodis* has been widely quoted in the contexts of eco-speciation, polygyny and the evolution of social parasitism (e.g. Wilson, 1971; Oster & Wilson, 1978; Brian, 1983; Sudd & Franks, 1987). The unusual separation of queens into two types, based upon behaviour and size, could represent an early stage in the evolution of a social parasite (e.g. Elmes, 1978a; Pearson, 1981) and even if not, it still requires an evolutionary explanation.

In recent years the evolution of social parasitism has stimulated much interest among social biologists. The similarity between the role of supernumerary queens in highly polygynous associations of *Myrmica*, and true social parasites was noted by Elmes (1973a), who considered that this supported the hypothesis formulated by Buschinger (1970): that many social parasites derive directly from polygynous host species [Buschinger (1990) points out that a similar idea was first published in 1909 by E. Wasmann]. Microgynes and the other social parasites of the genus *Myrmica* were considered to represent an evolutionary sequence (Elmes, 1978a).

In essence this hypothesis requires a process of sympatric speciation and several explanations have been developed along these lines (e.g. West-Eberhard, 1986; Bourke & Franks, 1990). The alternative, 'conventional' hypothesis supported by Wilson (1971) proposes the allopatric production of sibling species. These develop a parasitic association when their geographical isolation breaks-down and they come into direct competition with each other. Pearson (1981) suggested that *M.ruginodis* might represent the pre-parasitic phase in this process; in other words, we are witnessing the interaction between two previously isolated sibling species.

Buschinger (1990) envisages a similar pre-parasitic stage to that hypothesized by Pearson (1981) but produced by sympatric speciation within polygynous populations, which acts as a focus for the radiative evolution of several forms of social parasitism. In this scenario *M.ruginodis* might represent such a pre-parasitic stage.

Whichever of the two routes to social parasitism, sympatric or allopatric, is eventually shown to be the most probable, it is certain that the comparison of the biology of the two forms of *M.ruginodis* will provide important evidence. Despite this, there has been very little published on *M.ruginodis* since Brian & Brian (1949). A less widely known work of Brian & Brian (1955) suggested that macrogynes and microgynes swarm separately and show assortative mating between pairs. Otherwise, there is a population study (Elmes, 1978b), a study of the presence of microgynes in Japanese populations of *M.ruginodis* (Mitzutani, 1981) and a study of morphometrical variation in relation to geographic isolation (Elmes & Clarke, 1981).

The suggestion that microgynes of *M.ruginodis* are adapted to oceanic climates and are probably limited to the western seaboard of Europe (Brian & Brian, 1949) is wrong. Both forms are widespread: microgynes of *M.ruginodis* have been found in the arctic north, centre and east of Europe, where the climate is continental (Elmes, unpublished) and in Japan (Mitzutani, 1981).

Brian & Brian (1949) concluded that the two forms were distinct varieties, naming the one with large queens *Myrmica rubra* var. macrogyna and the other *M.rubra* var. *microgyna*. Under ICZN rules, variety is a rank that has no status in systematics, but for the purposes of this paper the names macrogyna and microgyna are used to distinguish the forms.

Authors often cite Brian & Brian (1949) as showing that macrogyna always has monogynous colonies and has a strict ecological separation from microgyna. In fact, they demonstrated only a tendency for these conditions. The first part of this paper tests the generality of Brian & Brian's results from Scotland by comparison with a similar study from southern England. In particular, the distinction between microgyna and macrogyna colonies and the recognition of microgyna males is considered.

The behaviour of ants during and following nuptial swarming has a great impact upon their subsequent life-histories, therefore the mating strategy of microgyna and macrogyna is examined in the second part of this paper. Observations are reported on the proportions of the two types in nine mating-swarms of *M.ruginodis*; assortative mating is tested between copulating pairs from one swarm. Following British nomenclature, young, un-mated

alate queens are called gynes to distinguish them from fertilized, functional queens.

All nine swarms followed the typical swarming behaviour of the genus *Myrmica*: mating swarms are usually local affairs, starting in mid-afternoon on a warm, humid, overcast day during August and early September (e.g. Donisthorpe, 1927), with swarms being highly male-biased (Leprince & Francoeur, 1986). Female bias in swarms were reported by Duelli *et al.* (1989) but their data probably represented captures of individuals flying to join mating swarms. Gynes fly to a swarm throughout the day, mate and leave, whereas males tend to arrive early, over a shorter period and remain with the swarm.

When the day cools, usually by early evening, gynes stop arriving at the swarm and the activity decreases. The males stay together, clustering on the undersides of leaves, or if they are on the ground, in cracks and crevices in the rocks and soil. This behaviour is not widely known although it was recorded for *M.ruginodis* by Brian & Brian (1955). The following day, if the weather conditions are favourable, the males resume flying by mid-afternoon and provide a focal attraction for fresh males and gynes.

The trait for late-summer swarming is remarkably constant over the entire range of this widespread genus and probably has an adaptive significance. Newly mated queens do not attempt to produce workers after swarming, instead they either join an existing colony or find a place to hibernate, sometimes in isolation and sometimes in groups. The following spring these unattached queens attempt to initiate new colonies, they have insufficient reserves to do this claustrally and spend a considerable time foraging (Hölldobler, 1938; Elmes, 1982). Some may still join existing colonies at this stage.

Swarms start when males leave the nest and assemble at some prominent local landmark, often the top of a shrub or tree on the summit of a hill (e.g. Hubbard & Nagell, 1976; Leprince & Francoeur, 1986; Pontin, 1986). The swarm of males release a chemical signal that can be smelt quite strongly by an observer at the centre of the swarm. I believe that the males release a pheromone that attracts the gynes: although reports of gynes producing male-attractants are more common, there are reports of males producing gyne-attractants (e.g. Brand *et al.*, 1973; Hölldobler, 1976).

Material and Methods

Nomenclature. Considerable confusion has resulted from the strict application of the rule of priority: in 1931 Santschi noticed that the original Linnaean name, *rubra*, was not used for any species of *Myrmica*. He decided that the original Linnaean description applied to *Myrmica ruginodis* Nyl. Therefore Brian & Brian (1949) used the name *M.rubra* quite correctly. Confusion arose when Yarrow (1955) examined the Linnaean collection and decided that the name rubra really belonged to *Myrmica laevinodis* Nyl.; the name *ruginodis* was revived, Brian & Brian's forms becoming *M.ruginodis macrogyna* and *M.ruginodis microgyna* with *M.rubra* = *M.laevinodis* (Yarrow, 1955).

Such varying nomenclature could be dismissed as taxonomic pedantry were it not for the considerable interest in these two species generated by: (a) the unusual morphological divergence of *M.ruginodis* queens, (b) the fact that *M.rubra* = *M.laevinodis* also has a microgyne form (e.g. Elmes, 1976), and (c) the intensive studies of caste determination by *M.rubra* (e.g. Brian, 1974). Many authors have assumed that published work on *M.rubra* = *M.laevinodis* (Yarrow, 1955) and *M.rubra* = *M.ruginodis* (Santschi, 1931) was done on a single species, despite the fact that the contrary was made clear many times (e.g. Elmes, 1973b).

Morphometrics. Population data are available for more than eighty colonies of *M.ruginodis* taken from four different moorland sites in the south of England. The sites were described and the population data were analysed by Elmes (1978b). Headwidths (taken as the maximum dorsal width immediately behind the eyes) were measured to nearest 0.02 mm for a sample of ten workers and all the queens, up to a maximum of five, from each colony. These specimens are stored at Furzebrook Research Station.

Samples of males and/or gynes were available for twenty-three of these English colonies and for seventeen colonies collected in Norway during 1977 (generally no queens were taken with the Norwegian material). The variability of workers in relation to queen size for a larger set of colonies that included these, were analysed using multivariate techniques (Elmes & Clarke, 1981). The headwidths were measured of a maximum sample of five gynes and five males from each of these forty colonies.

The M.ruginodis mating-swarms. Data are given for nine mating swarms of *M.ruginodis* (Table 1). Where possible the headwidths of a sample of 100 individuals of each sex was measured, though in most cases very few gynes were collected. 131 copulating pairs were collected from swarm 9; each pair was stored separately so that pair assortment could be investigated and the size of individuals successful in finding a partner could be compared with a similar number of unpaired individuals taken at random. In this case every individual caught was measured.

Swarms 4–8 were sampled on a day when six species of *Myrmica* were flying on the Molsbjergs of Jutland. Swarm 4 was unusual in that it comprised a complete mixture of four of these species. A sample of 585 males comprised 477 *M.ruginodis*, eighty-six *Myrmica schencki* Emery, fifteen *Myrmica scabrinodis* Nyl. and seven *Myrmica sabuleti* Meinert while nine gynes comprised one *M.sabuleti*, four *M.scabrinodis*, three *M.ruginodis* microgynes and one *M.ruginodis* macrogyne. Five copulating pairs were captured: these comprised three *M.scabrinodis* × *M.scabrinodis*, one *M.schencki* × *M.schencki* and one *M.ruginodis* × *M.ruginodis* (macrogyna). Therefore, despite the mixture, this small sample indicated that the species were mating like-with-like. There was also some mixing in swarm 6, where a *Myrmica lobicornis* Nyl. male was caught, and in swarm 7 a small sample of thirty-nine males comprised thirty-seven *M.ruginodis* and one each of *M.sabuleti* and *M.rubra*.

Analyses. The distributions of headwidths were analysed by first assuming bimodality and calculating the means, variances and proportions of the two mixed distributions, using a computer optimization technique (Macdonald, 1980). The probability of the bimodal fit could then be compared with the probability of fit of a single normal distribution.

The overall shape of the distribution of headwidths of copulating individuals, from swarm 9, was compared with that of the random sample of the same sex using the Kolmogorov-Smirnov test (Sokal & Rohlf, 1981).

Results

Morphological isometry

Ninety-two colonies from the 132 nests of *M.ruginodis*, collected from southern English moorlands, contained queens; it was possible to measure headwidths of queens in eighty-nine of these, giving a total sample size of 225 queens. The frequency distribution of their headwidths was clearly bimodal: optimizing a bimodal fit suggested a class of queens (58%) with a mean headwidth of 1.00 ± 0.04 mm and the remaining 42% forming a second class with a mean headwith of 1.13 ± 0.04 mm. Individuals whose headwidth = 1.065 mm are intermediate in size between the two distributions. Using 1.065 mm

Table 1. Mating swarms of *M.ruginodis*.

No.	Date	Location	Mating-post	No. in sample			
				Micros		Macros	
				♀	♂	♀	♂
1	26.7.83	Mols Laboratory, Jutland, Denmark (M. G. Neilsen)	Picnic table	3	39	27	71
2	9.8.83	Furzebrook Research Station, U.K. (Elmes & Webb, 1985)	Light trap	3	11	9	89
3	9.8.86	Sourdeval, Normandy, France	Car roof	0	3	19	31
4	2.9.87	Lansbjerg, Mols, Denmark	Bush	3	57	1	43
5	2.9.87	Lansbjerg, Mols, Denmark	Bush	0	75	0	25
6	2.9.87	Lansbjerg, Mols, Denmark	Flat rock	0	36	1	27
7	2.9.87	Laadenbjerg, Mols, Denmark	Bush	0	12	0	25
8	2.9.87	Laadenbjerg, Mols, Denmark	Boulder	0	42	3	58
9	23.8.90	Edendale, Cumbria, U.K.	Road	8	71	111	155

to discriminate between microgyna and macrogyna misidentifies only 5% of each type.

When eight body measurements, frequently used for distinguishing *Myrmica* species, were compared for twenty microgyna, twenty macrogyna and twenty intermediate-sized individuals, there was little difference between the three groups other than that of size. Relatively wide post-petioles are characteristic of parasitic *Myrmica* (e.g. *Myrmica hirsuta* Elmes, 1978a); here the post-petiole shape, both width and height, was isometric, relative to headwidth, between the three size classes (Fig. 1). Similarly, relatively wide thoraces are indicators of a more developed flight ability; there was no evidence from these data that thorax/headwidth ratio varies between the classes. Although some slight differences between the three classes of queens could be detected using the other measurements (e.g. spine-length), these were not sufficient to suppose that microgyna are other than isometric reductions of macrogyna.

Recognition of Microgyna colonies

Although headwidth = 1.065 mm gives good discrimination between individual microgynes and macrogynes of *M.ruginodis*, it is harder to assign colonies to one or other of the types. One way is to use the average queen-headwidth and define microgyna colonies as those where average queen-headwidth ≤ 1.06 mm. On this criterion the *M.ruginodis* colonies (Fig. 2a) comprised forty-nine macrogyna (Fig. 2b) and forty microgyna (Fig. 2c); obviously this ignored the forty queenless colonies. However, in both

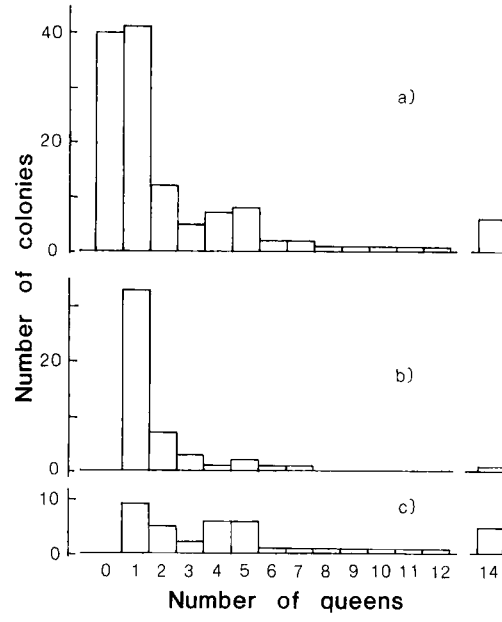

Fig. 2. Frequency histograms for the numbers of *M.ruginodis* colonies containing different numbers of fertile queens: (a) all 129 colonies sampled from southern England; (b) the forty-nine colonies with average queen-headwidth ≥ 1.065 mm; (c) the forty colones with average queen-headwidth < 1.065 mm.

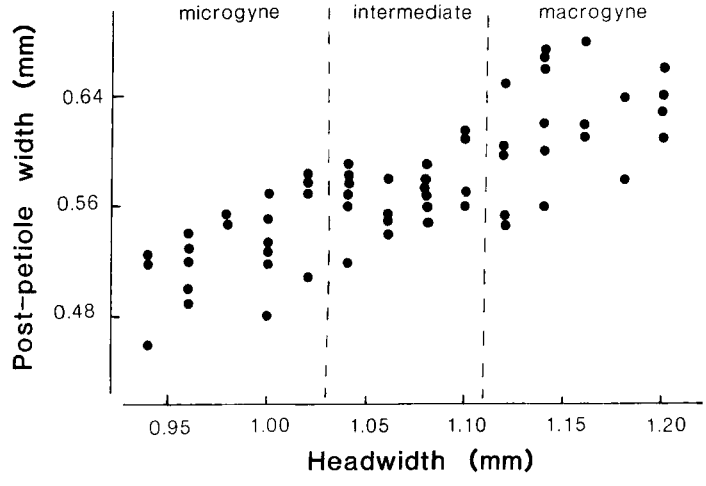

Fig. 1. The width of the post-petiole plotted against the headwidth of sixty *M.ruginodis* queens of three categories, being twenty microgynes, twenty macrogynes and twenty intermediates.

macrogyna and microgyna colonies the distribution of queen-numbers was similarly overdispersed; microgyna simply had a greater mean and variance. Obviously the death of a queen in a macrogyna colony is much more likely to produce a queenless colony than the loss of a queen in a microgyna colony. Therefore extrapolation of these distributions to the zero class suggested that the thirty-six queenless colonies originally were macrogyna.

Microgyna colonies had significantly more queens, 6.9 compared to 2.1 in macrogyna colonies ($P < 0.01$ calculated from log-means), but there is no evidence that the worker-numbers differed significantly, 295 compared to 444 ($P = 0.13$ calculated from log-means).

When the size of queens in forty-two monogynous colonies and forty-seven polygynous colonies (shown in Fig. 2a) were considered separately (Fig. 3b), the distributions were very similar to the Scottish samples of Brian & Brian (Fig. 3a). In both cases the monogynous colonies had unimodal headwidth distributions and the polygynous colonies had bimodal distributions. Optimizing a bimodal fit to the data for polygynous colonies (Fig. 3b), suggested that 65% of the queens were microgyna (mean headwidth 1.00 ± 0.03 mm) and the remaining 35% were macrogyna (mean headwidth of 1.12 ± 0.04 mm).

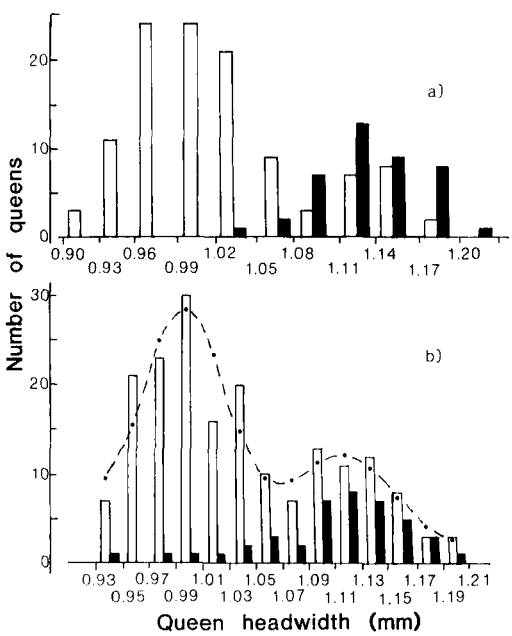

Fig. 3. The frequency distribution of headwidth sizes of *M.ruginodis* queens in polygynous colonies (open bars) and monogynous colonies (filled bars): (a) data from Scotland, extracted from Brian & Brian (1949); (b) data from southern England.

If queens with a headwidth ≤ 1.06 mm are considered as microgynes, then the forty-seven polygynous colonies (Fig. 4) comprised twenty-three colonies that were exclusively microgyna and thirteen entirely macrogyna while eleven had a mixture of queen sizes.

Breeding consistency of Microgyna

Size of workers. Overall there was a significant correlation between the average size of workers and average size of queens in the eighty-nine colonies of *M.ruginodis* ($r = 0.32$, $P < 0.01$). Multiple regression showed that 25% of the variation in the average size of workers was explained by worker-number and 10% by queen-size. No significant proportion of the variation in worker-size could be attributed to queen-number or differences between the sites where nests were collected.

Assuming a separation of the colonies into forty-nine macrogyna and forty microgyna (see above), then, on average, microgyna workers were smaller than macrogyna, 0.99 ± 0.05 mm compared to 1.03 ± 0.06 mm ($P = 0.002$). However, there was no significant correlation between average size of queens and average size of workers within the two classes, indicating that the overall correlation simply reflected the average size-difference between microgyna and macrogyna.

Size of gynes and males. Five of the eighty-nine *M.ruginodis* colonies which contained queens (see above), also had samples of gynes and males, and a further three had samples of males. In addition, sixteen Norwegian colonies, whose queens were not collected, had samples of gynes and twelve had males (see Methods). The sample-size (five) was too small to look for a correlation between queen-size and gyne-size. However, three were macrogyna colonies (mean headwidth of queens *c.* 1.16 mm) and produced macrogynes (headwidth *c.* 1.14 mm) whereas the two microgyna colonies (queens *c.* 1.00 mm) produced microgynes (headwidth *c.* 0.96 mm). A similar result was found with the eight colonies producing males: six macrogyna colonies (headwidth *c.* 1.15 mm) produced large males (headwidth *c.* 1.01 mm) and two microgyna

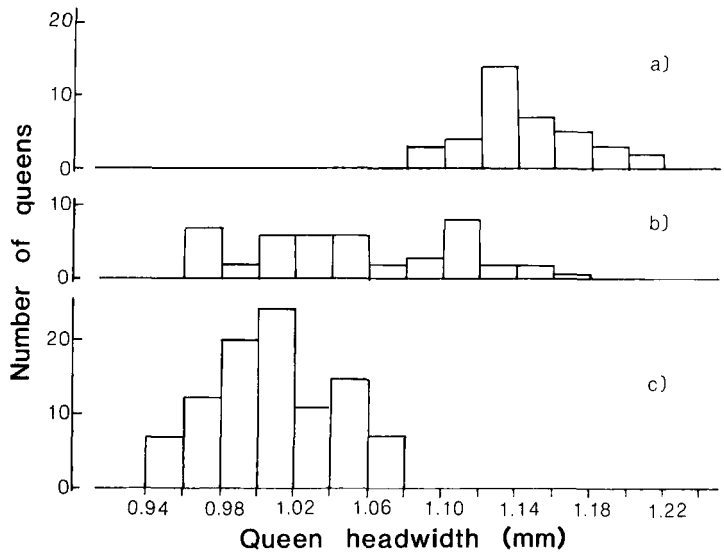

Fig. 4. The frequency distribution of the size of *M.ruginodis* queens in: (a) the twenty-three colonies having all queens with headwidth ≥ 1.065 mm; (b) the eleven colonies with a mixture of queen sizes; (c) the thirteen colonies having all queens with headwidth <1.065 mm.

colonies (headwidth *c.* 1.00 mm) produced small males (headwidth *c.* 0.92 mm).

Both gyne-size and male-size correlated well ($r = 0.68$, $n = 28$ and $r = 0.68$, $n = 26$ respectively, both $P < 0.001$) with the average size of workers in the colonies, calculated from the combined British and Norwegian samples. Therefore the average size of males in these colonies correlated well with the average size of gynes ($r = 0.83$, $n = 22$, $P < 0.001$, Fig. 5); when

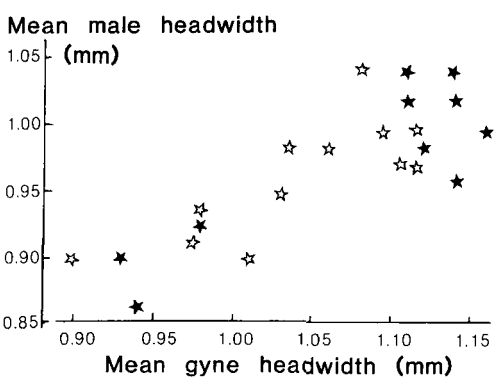

Fig. 5. The average headwidth of males plotted against the average headwidth of gynes in twenty-two colonies of *M.ruginodis*, being twelve from Norway (open stars) and ten from southern England (filled stars).

the two types of colony were distinguished, there was a significant correlation between gyne and male sizes within the microgyna group ($r = 0.80$, $n = 10$, $P = 0.005$) but no correlation within the group consisting of twelve macrogyna colonies ($r = 0.17$, $n = 12$, $P > 0.5$).

Discrimination of males

As there is a clear distinction between the two types of queen and male-size correlates well with the size of gynes produced in the same nest, it follows that it should be possible to discriminate between males on size alone. The sample of forty-nine males from colonies known to contain macrogynes had an average headwidth of 0.99 ± 0.04 mm (Fig. 6a) whereas the thirty-eight males from microgyna colonies averaged 0.92 ± 0.06 mm (Fig. 6b). The males from microgyna nests were more variable with the larger males originating from the three colonies that had intermediate-sized queens (1.00 −1.06 mm). Excluding these males the average size of microgyna males was 0.90 ± 0.05 mm.

Excluding the males taken from the mating swarm from the Pennines in 1990 (Table 1) which were sampled in a different way, 634 *M.ruginodis* males have been measured. The distribution of their headwidths is apparently

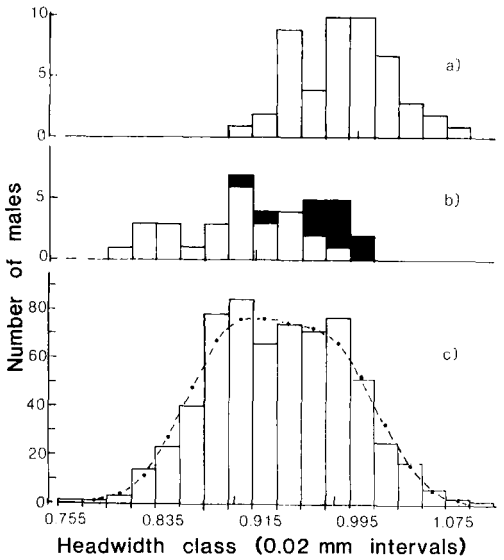

Fig. 6. Frequency histograms of the headwidths of male *M.ruginodis*, plotted at intervals of 0.02 mm. Means are indicated by the short vertical bars within the distributions. (a) The forty-nine males from macrogyna colonies; (b) the thirty-eight males from microgyna colonies, individuals from the three colonies with queen-headwidth > 1.00 mm < 1.065 mm are filled; (c) 634 males that have been measured, excluding those from swarm 9. The fitted line is the optimized fit under the assumption that the distribution consists of a mixture of two separate distributions.

unimodal but is not normal; there is $< 10\%$ chance that the data can be described by normal distribution with the overall mean 0.94 ± 0.06 mm. However, the best fit, assuming a bimodal basis, had a $> 82\%$ chance of being a true description of the data (Fig. 6c). This assumed that 52% of the males were small (headwidth 0.90 ± 0.04 mm) and 48% were large (headwidth 0.98 ± 0.04 mm). These estimated means are very similar to those measured for males from colonies of known origin (Figs 6a and 6b). If the headwidth ≥ 0.94 is taken to separate males of macrogyna origins from microgyna males, then on average 16% of each type will be wrongly classified.

Composition of the M.ruginodis swarms

The numbers of microgyna gynes (headwidth ≤ 1.06 mm) and males (headwidth < 0.94 mm) in the samples measured from each swarm are given in Table 1 and the distributions of headwidths of males in Fig. 7. These indicate that only swarm 3 (from Normandy, France) could have consisted just of macrogyna, all the other swarms appear to be mixed. Generally 40–50% of males were microgyna, depending upon how individuals with headwidth = 0.94 mm were assigned. Swarms 1 and 9, which had the best

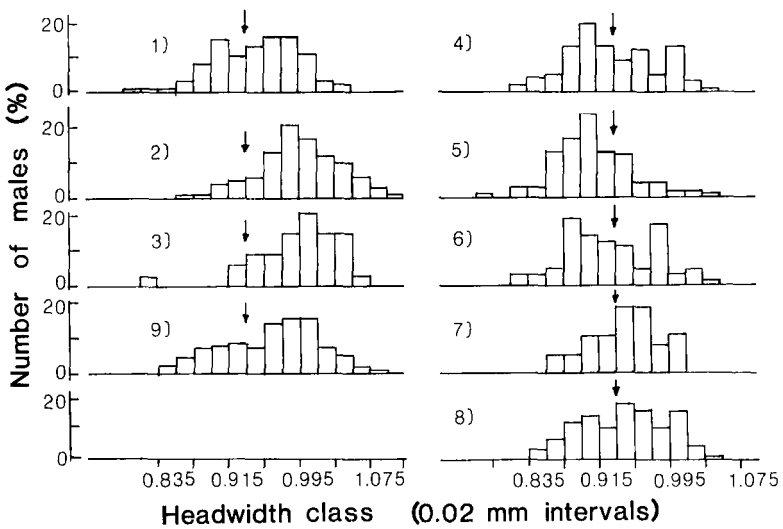

Fig. 7. The frequency distribution (per cent) of headwidths of males (0.02 mm intervals) sampled from nine mating swarms of *M.ruginodis* (see Table 1). The size (0.94 mm) which best separates males of microgyna and macrogyna origins is indicated by arrows.

sample of females, comprised < 10% microgynes although microgyna males constituted > 30% of the swarms.

In swarm 9, copulating pairs were taken continuously throughout the duration of the swarm (2 h) at the rate of approximately 1 pair/min. Plotting the size of males and gynes against the order in which they were captured (time) gives no indication that their size varied with time (virtually zero correlations in both cases). Therefore there is no evidence that large individuals arrived at the swarm site first, or vice versa.

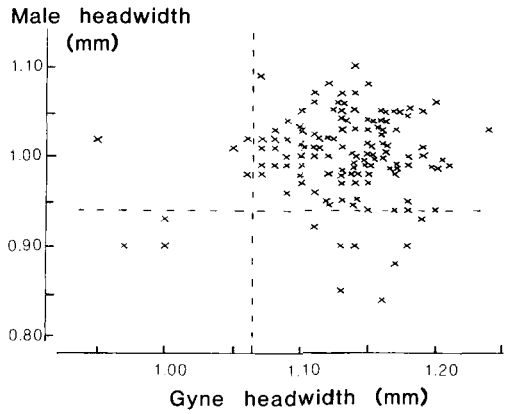

Fig. 8. Scatter plot of the headwidths (mm) of males and gynes taken in copulation from *M.ruginodis* swarm 9. Separations between macrogyna and microgyna are indicated by the dashed lines.

Mate selection

Only from swarm 9 were sufficient copulating pairs (131) collected to test for assortative mating. Testing between the two forms was difficult because only seven microgynes were taken copulating and only four of these were definitely microgyne (headwidth < 1.00 mm). There was no correlation between the sizes of males and gynes forming pairs (Fig. 8, $r = 0.07$). Three of the microgynes and about 7% of the macrogynes paired with microgyna males. Therefore, although there was some cross-pairing between macrogyna and microgyna, most pairs (> 90%) were macrogyna × macrogyna.

A comparison of the distribution of headwidths of copulating males with the random sample (Fig. 9) showed that these two distributions were very unlikely to have been drawn from the same population ($D = 0.31$, $P < 0.001$ Kolmogorov-Smirnov Two-sample Test). Clearly fewer microgyna males copulated, only 8% of the sample compared with 31% present in the swarm. However, the selection in favour of large males seemed to go beyond simply favouring macrogyna males instead of microgyna: if all the males are pooled into a single sample and ignoring the tails of the distribution, the proportion copulating in each size class increases significantly with size ($r = 0.87$, $n = 12$, $P < 0.001$).

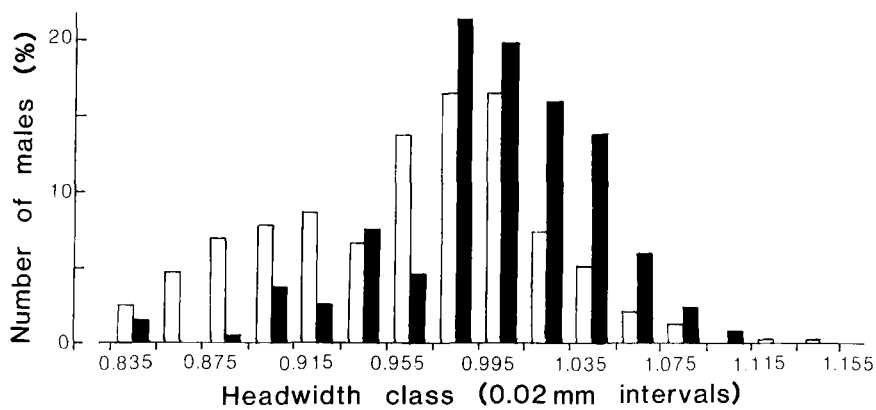

Fig. 9. The frequency histogram (0.02 mm intervals) of the headwidth of male *M.ruginodis* from swarm 9 taken in copulation (solid bars) compared with that of a random sample of unpaired males (open bars). The two distributions are significantly different.

Discussion

The range of variation and the average size of queens within most European *Myrmica* species is consistent over a wide geographical range (Elmes, unpublished). *Myrmica ruginodis* appears to contradict this rule because it has a large range of queen-size and the average size varies from place to place. However, if *M.ruginodis* queens are separated into two groups, based on size (Brian & Brian, 1949), the average and the range of sizes within each group varies little over the species' range. The apparent overall variability between geographical locations is merely the result of the proportion of microgynes in the local population.

This is illustrated here by the detailed comparison of data from Southern England with the original data from Scotland (Brian & Brian, 1949). Mean headwidth measurements for Scottish populations of *M.ruginodis* were 1.02 $\pm$ 0.06 mm for microgyna and 1.13 $\pm$ 0.04 mm for macrogyna, with a headwidth = 1.06 mm being both morphologically and behaviourally intermediate. Analysis of English samples gave 1.00 $\pm$ 0.04 mm, 1.13 $\pm$ 0.04 mm and 1.065 mm respectively. The similarity between the two sets of data, separated by 600 miles and 30 years, is remarkable.

Brian & Brian (1949) were unable to discriminate between males, although they showed that males from microgyna nests were usually smaller than those from macrogyna nests. Here it was shown that males can be distinguished solely on the basis of size and that there is no reason to suppose that microgyna of either sex are other than isometric reductions of macrogyna.

As in Scotland, microgynes from Southern England usually live in polygynous associations while macrogynes often live monogynously. However, contrary to popular belief, this separation is not clear-cut in either study. Here, almost 25% of all polygynous nests contained only macrogynes and a further 25% contained a mixture of both types of queen. Consequently, discrimination between microgyna and macrogyna colonies is problematic; the forms cannot be distinguished simply on the basis of queen numbers.

The taxonomic status of the two forms remains undetermined. Pearson (1981) argued that if macrogyna and microgyna were separate species, then they had evolved allopatrically. Mixed colonies were the 'pre-parasitic' consequences of competition between the two forms, with the microgynes acting parasitically. This is the opposite view to that of Brian & Brian (1949) who concluded that the bimodality of queen size in polygynous colonies mainly resulted from pleometrotic colony foundation by macrogyna (i.e. colonies started by groups of young, newly mated queens). They suggested that a few mixed colonies occurred when macrogynes occasionally gained access to the more tolerant microgyna nests (although Brian & Brian's behavioural assays of tolerance have not been repeated, many other laboratory observations confirm that microgyna are nearly always less aggressive than macrogyna). This idea is really based upon mixing being 'accidental', although, following Pearson's arguments, it could be construed as macrogyna acting parasitically.

The morphometrical analyses, indicating that both males and queens can be distinguished, combined with the behavioural (aggressive) differences could, arguably, indicate that macrogyna and microgyna are distinct species. In this case the mixed colonies might result from some sort of parasitization. However, if this is the case there should be considerable breeding isolation between the two forms.

In all nine mating-swarms of *M.ruginodis*, with the possible exception of swarm 3, there was a proportion of both types of males. However, if this represents a mixing of two species, this in itself is not unusual for *Myrmica* ants (e.g. Collingwood, 1958; Leprince & Francoeur, 1980, swarm 4 and Elmes, unpublished: a swarm comprising a complete mixture of *M.scabrinodis* and *M.sabuleti*). However, in the cases that I have seen there were no cross species couplings among the few copulating pairs that were collected, suggesting that this seldom happens. It might be that *Myrmica* gynes produce specific pheromones that deter alien males at close quarters, as reported for genus *Pogonomyrmex* (Hölldobler, 1976). On the other hand, the gyne might eight physically reject the males or it may be that copulation is physically difficult because of genital shape.

The data from swarm 9 indicated that within any size class the proportion of males that successfully achieved copulation increased linearly with the size of the males. In other words, while microgyna males have very little chance

of pairing compared to macrogyna males, when part of a large 'normal' swarm, large macrogyna males have a greater chance of finding a mate compared to small macrogyna males and, similarly, large microgyna males compared to small microgyna males. However, the few microgyna females present in the swarm had a good chance of pairing with a macrogyna male, so that this type of swarm would produce a number of cross-matings. Within the group of macrogyna males and females there was no evidence of assortative mating.

This is quite contrary to the results of Brian & Brian (1955), who found a good correlation between the size of males and gynes forming pairs, which they interpreted as showing assortative mating. However, they mixed data from three separate mating posts sampled over the entire period of swarming. One of these mating posts was dominated by microgyna and the other two by macrogyna. I believe that they were detecting the predominance of like × like matings within the three swarms and the overall significant correlation was due to the difference between the two forms rather than assortative mating within either of the forms. This can be partly tested by the absence of correlation within the macrogyna × macrogyna and microgyna × microgyna 'quarters' of their Table 1 (Brian & Brian, 1955). Unfortunately it is not possible to assign their data to the separate swarms.

The simplest interpretation of these pairing results is that gynes do not choose their mate, rather there is some sort of contest between the males with the outcome being biased in favour of larger males. Therefore, in swarms of *M.ruginodis* where males greatly outnumber the gynes (the usual situation), small males have very little chance of pairing. This is very similar to the situation in the common toad, *Bufo bufo*. Reading & Clarke (1983) hypothesized that small male toads should find ways of pairing with females before they reached the breeding grounds.

Interestingly, Brian & Brian (1955) reported that *M.ruginodis* microgynes were much more likely than macrogynes to mate as they left their nest, before flying to a mating-swarm. The scarcity of microgyna from swarm 9, in relation to the number of microgyna males, might be used to argue that they must in fact be mating before joining the swarm. However, *M.ruginodis* microgyna nests usually have very male-biased sex ratios and in some years entire populations produce no gynes at all (Elmes, unpublished) so that microgyna might simply have been very rare in that particular area in 1990.

So, why do microgyna males join a mating-swarm at all? There are several possibilities: if most microgynes are mated as they leave the nest the predominance of males ensures that most microgyna × microgyna pairings occur there (the indirect evidence from Brian & Brian Table 1 suggests that there is no assortative mating within microgyne parings, so that it is probable that bigger microgyna males are more successful in this situation). If no gynes are sensed close by when swarming begins, the males have nothing to loose by flying to join a swarm, a strategy that gives them a low but finite chance of mating. In some circumstances macrogyna males may be rare, so that microgyna males have a good chance of coupling, even with macrogyna.

From the view of the queens this strategy ensures that most microgynes pair with a microgyna male. They remain close to the parent nest and are available for readoption by the parent nest or a close neighbour, maintaining high local relatedness. Many of the microgynes that reach a proper swarm probably mate with macrogyna males. The macrogynes probably rarely mate near their nest, although this possibility cannot be discounted; most fly to a swarm and mate with a macrogyna male or possibly a microgyna male when these are very numerous.

This combination of local mating proclivity by microgyna and the tendency for large males to win a mate in a swarm is sufficient to ensure a high proportion of like × like matings. Assuming reasonable viability, the small proportion of cross-pairings should be sufficient to maintain the genes for macrogynes in microgyna dominated populations and vice versa. Cross pairings might also be very important in ensuring the spread of the microgyne form into new isolated sites that are much more likely to be colonized by the macrogyna form. Careful genetical investigations will eventually resolve these issues.

Another question is why does any colony, of either type, produce small males if larger ones win a mate more frequently in a swarm. Apart from the probability that the microgyna mating behaviour is linked in a complex genetical way with reduced body size, there must be some

trade-off between individual size and total numbers produced by a colony. If males are producing a gyne-attractant, it may be that a large swarm of smaller males is more successful at 'attracting' females than a smaller swarm of larger males.

It can be argued that the absence of a clear-cut mating separation between the two forms of *M.ruginodis* and the high probability of cross matings between them, compared with hybridization in swarms of mixed species, are expected of two recently diverged species as hypothesized by Pearson (1981). Macrogyna and microgyna might indeed be in some 'pre-parasitic' competitive relationship that gives rise to the high proportion of mixed colonies. However, my intuitive belief is that genetical study will show that the forms represent a polymorphism for behaviour linked with size, that is maintained by the partial but incomplete breeding isolation. The exact proportion of each form and the number of 'hybrids' being a rapidly, selectable population trait that is determined by environmental factors.

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