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THE SOCIAL BIOLOGY OF *MYRMICA* ANTS

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Résumé:

LA BIOLOGIE SOCIALE DES FOURMIS DU GENRE *MYRMICA*

Depuis plus d'une centaine d'années, les myrmécologistes ont utilisé de nombreuses espèces de *Myrmica* dans leur recherche sur les fourmis. Dans cet article, l'auteur passe en revue le travail accompli dans la station de recherche de Furzebrook en attendant la publication d'un travail plus important.

Le sujet a été découpé en six sections principales: structure des populations, polygynie et structure des colonies, variabilité des reines en ponte, contrôle royal et détermination des castes, production des sexués et enfin action des fourmis du genre *Myrmica* sur leur environment.

Summary:

Myrmecologists have used various *Myrmica* species for more than one hundred years in their investigations of ants. In this paper the author reviews the work done at Furzebrook Research Station as a preliminary to a wider monographic review.

The topics are separated into six main sections: the structure of populations, colony structure and polygyny, queen variability and oviposition, queen control and caste determination, sexual production and finally, the effect of *Myrmica* ants upon their environment.

INTRODUCTION

Myrmica ants are very common throughout the temperate northern hemisphere; more than 600 species and varieties have been described. They are medium sized ants with monomorphic workers measuring up to 10 mm in length. On average, queens are 1.25 the size and twice the weight of the workers. Males are intermediate to the sizes of the two female castes.

The genus has been used many times to study aspects of ant biology. Nearly 100 years ago it was used to investigate ant anatomy (eg. Janet 1899), such studies continue today (eg Billen 1986). *Myrmica* has been used to determine myrmicine chemistry (eg. Morgan & Wadhams 1972) and behaviour in response to pheromones (eg Cammaerts & Verhaeghe 1974). Since 1950 it was the main "tool" used by the late Michael Brian and his colleagues at

Furzebrook Research Station, to investigate the social physiology of ants. First the species *Myrmica rubra* L. was used to investigate caste determination and queen control (eg Brian 1974a) then the population structure of the N. European species were compared to investigate the adaptive significance of the colony processes that were worked out in detail by laboratory studies.

This paper briefly reviews the work of the Furzebrook group as a prelude to a general review of the biology of the genus *Myrmica*. The relevant papers are not treated in chronological order. For clarity the later results on the population structure of the various species are considered first, then aspects of the social biology are discussed showing its relevance in terms of the ants' ecology.

THE STRUCTURE OF *MYRMICA* POPULATIONS

In any temperate biotope, one can usually find two or three different *Myrmica* species. For example *Myrmica rubra* L. and *Myrmica scabrinodis* Nyl. live in close proximity on Scottish moorlands (Brian 1952a, 1956a,b) while 9 heathland sites from Hannover have a minimum of two and a maximum of 6 *Myrmica* species (Assing 1986). Similar results have been reported many times from grassland biotopes (eg Petal 1980, Brian *et al.* 1976). *M. scabrinodis* nearly always co-exists with *Myrmica sabuleti* Meinert on warm grassland sites in southern England (Elmes & Wardlaw 1982c).

Table I Niche overlap of seven common *Myrmica*.

temp. ^{0}C	species	SPEC	LOSA	SCH	SAB	SCA	RUB	RUG
16.3	SPECiodes	x	**22**	**37**	**31**	4	6	4
16.1	ruguLOSA	-4	x	3	**14**	0	**38**	5
16.0	SCHencki	**-20**	**-15**	x	**23**	**20**	9	12
15.6	SABuleti	**-15**	**-13**	**-21**	x	7	15	8
14.4	SCAbrinodis	3	-8	2	-3	x	**26**	**27**
13.2	RUBra	**13**	-4	1	3	-4	x	**20**
12.6	RUGinodis	**12**	-4	-9	**-11**	-5	**-17**	x

Calculated from Seifert (1986,1987). Right hand matrix is the percentage niche overlap (realised/potential). Left hand is the deviation (x100) from average, -ve value indicates displacement and +ve co-existence. Large values are emphasised.

Evolution seems to have favoured niche specialization in the genus *Myrmica* (Gallé 1986). A large amount of ecological data on the ants of East Germany was drawn together by Seifert (1986) who included data for seven common *Myrmica* species. Seifert's data allows these to be ranked for thermophily (mean summer temperatures at sites, Table I), producing a result that agrees with other less detailed studies (eg Gaspar 1972, Elmes & Wardlaw 1983a).

The proportion of niche overlap and potential "displacement" between the species pairs can be calculated (Table I) from the analyses presented by Seifert (1987), producing the comforting result that competition is most intense between species that share niche requirements. Displacement potential is greatest between species of the same genus, *Lasius* species being most likely to co-exist with *Myrmica* (Table II).

Table II Generic co-existence

	MYR	FOR	LAS
MYRmica	-57		
FORmica	-49	-194	
LASius	7	13	-35

Deviation from average niche overlap (x100) between genera (calculated from Seifert 1987)

All species of *Myrmica* are non-territorial (eg Brian 1952, 1956a) and can be considered to be "submissive" in terms of foraging (Savolainen & Vepsäläinen 1988, 1989, 1990). The distribution of potential nest sites is influenced by the size and aggressivity of territorial species; in English heathlands *Myrmica* colonies are marginalized by the territorial species (Brian *et al.* 1965) and are found at lower densities the nearer one gets to the nests of the aggressive *Formica polyctena* Först. (Savolainen & Vepsäläinen 1990). Foraging behaviour of submissive species is adapted to avoid competition; this ranges from habitat partition (Brian 1955a) to variation in daily rhythms (Savolainen & Vepsäläinen 1989) to varying annual cycles (Elmes 1982).

The size and abundance of *Myrmica* colonies in any habitat results from a combination of two factors, potential nest site abundance and food availability. Varying these can produce any combination of large and small colonies with any distribution, both within and between separate habitats. In high, cold moorlands, *Myrmica ruginodis* Nyl. has very little competition from other species and a wide variety of population structures were found (Elmes 1978a).

The ability to find and retain a nest site is very important in determining the pattern of *Myrmica* colonies (Brian 1952a), weak colonies can be evicted by congenerics (Brian 1952b) and there is considerable indirect evidence that there is a high turn-over of nest sites between conspecifics (Elmes & Wardlaw 1982a,b). There is good evidence that the physical characteristics of any particular nest site can influence the reproductive success of the colony using it; Elmes & Wardlaw (1982b) showed that various categories of *M. sabuleti* colonies (eg gyne-producers v those producing no sexuals) could be discriminated on the basis of the above-nest vegetation, which was interpreted as reflecting local microhabitat.

Nest densities can range from low (< $1/20m^2$) to more than $1/m^2$ (eg Elmes & Wardlaw 1982c). At low nest densities colony size is determined by the foraging efficiency of individual workers living in any particular nest site (Elmes 1973a) and by overall food availability, which can fluctuate greatly over a period of several years (Petal 1967). At high densities individual colonies suffer interference from neighbours, eg in a dense population of *M. rubra*, there was strong evidence that intra-specific competition resulted in nest-spacing (Elmes 1974a). Such competition should affect colony sizes (Elmes & Wardlaw 1982a).

Therefore in order to use the habitat in the way in which they do, one expects that *Myrmica* colonies should be mobile, highly defensive of their nest-site, should be able to rapidly colonize new nest sites and to be flexible in their reproductive strategy.

COLONY STRUCTURE AND POLYGYNY

Colony sizes of all *Myrmica* species can be very variable, ranging from very small (<50 workers) to very large (>5000 workers). In Europe the largest colonies normally belong to *M. rubra*: I have found one colony with > 6000 workers. In parts of Scandinavia and in the Pyrenees, I have seen very large mounds of *M.rubra* that probably contain >10000 workers. Worker numbers are always overdispersed (eg *M.rubra* in Figure 1) and can be described well by a negative binomial distribution (a simple log-transformation is a good approximation to this). The size that a colony can achieve is determined by the characteristics of the nest site (see previous section and Elmes 1973a). The rate at which it achieves its limiting size will be determined by various social factors (eg. Brian *et al.* 1981) and basically by food supply (Uchmanski & Petal 1982).

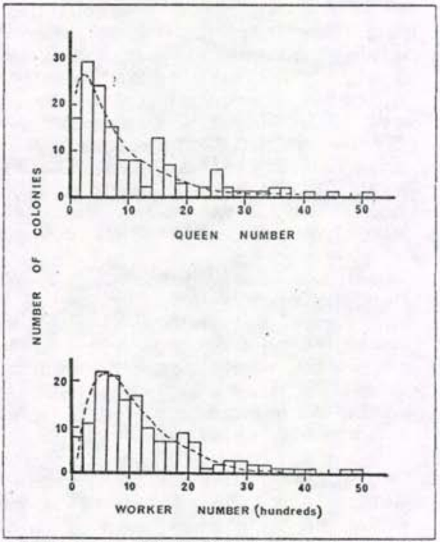


Figure 1 Distribution of queens and workers in *M.rubra*.

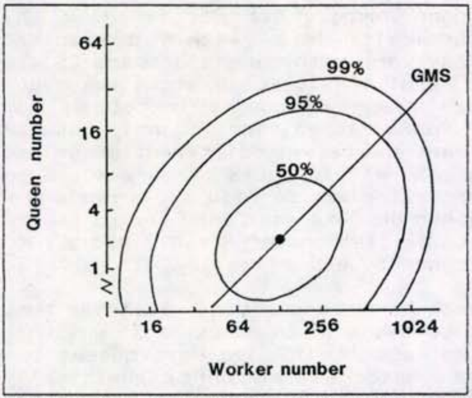


Figure 2 Probability distribution of workers and queens of *M.sulcinodis.*

All *Myrmica* species that I have studied are polygynous, that is some colonies contain more than one fully fertile, active queen. *M. rubra* are probably the "most polygynous" species, one colony was found that contained >600 queens (Elmes 1973a). Queen numbers are very positively skewed (eg Figure 1): for simplicity, a log-transformation is usually used to describe their distribution although strictly a stronger transformation is required.

In most population studies (eg. Elmes 1973a, 1974b, 1978, 1987, Elmes & Wardlaw 1982a, Elmes & Abbott 1974) there is a clear correlation between the number of queens and the number of workers in a colony. However, there is usually enormous variation around the correlation; this is illustrated for a *Myrmica sulcinodis* Nyl. population (Figure 2). There is no reason to suppose that either queen or worker number is the dependent variable, so the best description of the relationship is the geometric mean slope (GMS Figure 2).

The average number of queens per colony varies from <1 to >15 depending upon the species. This, at first sight would indicate that queen regulation in *Myrmica schencki* Emery, which has many colonies with 1 or no queens (Elmes & Abbott 1974), is quite different from that of *M.rubra*. However, when the "shape parameters" are calculated from the higher moments of the queen distributions (Figure 3), it is seen that the distributions for all the species can be described by the same mathematical function (known as a Pearson type III distribution). This suggests that they are therefore generated by a common biological process.

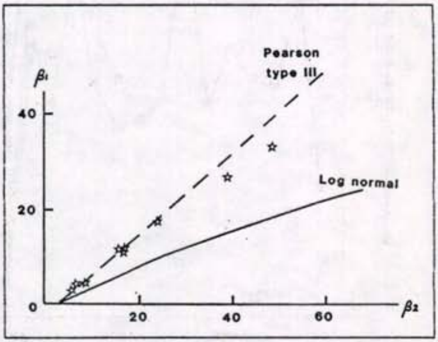


Figure 3 Shape parameters of queen distributions of 9 *Myrmica* species.

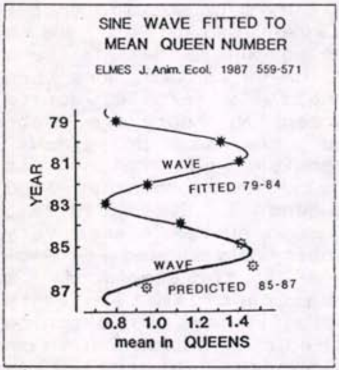


Figure 5 Regular Cycle in Queens.

Queen numbers are not fixed at any particular level within a species, they vary with time and space (Elmes & Petal 1989). For example the average number of queens in colonies of *M.rubra* varied significantly between years and between different grassland sites, within years (Figure 4). Such variation may be regular: a cycle for queen numbers was found in two separate populations of *M. sulcinodis* (eg. Figure 5, Elmes 1987).

What is the underlying mechanism that determines queen numbers? It was suggested that in some ways queens can be considered as acting parasitically upon the worker populations (Elmes 1973a) and I believe that there is now much more evidence that supports that point of view. Queens are periodically recruited into colonies (eg Elmes 1980a) and while daughters may be favoured there is much evidence to suggest that any queen will be accepted when a colony is in a "recruiting" phase. *Myrmica* queens probably live for no more than 3 years. Short longevity combined with frequent recruitment can explain all the population structures, variations and cycles outlined above.

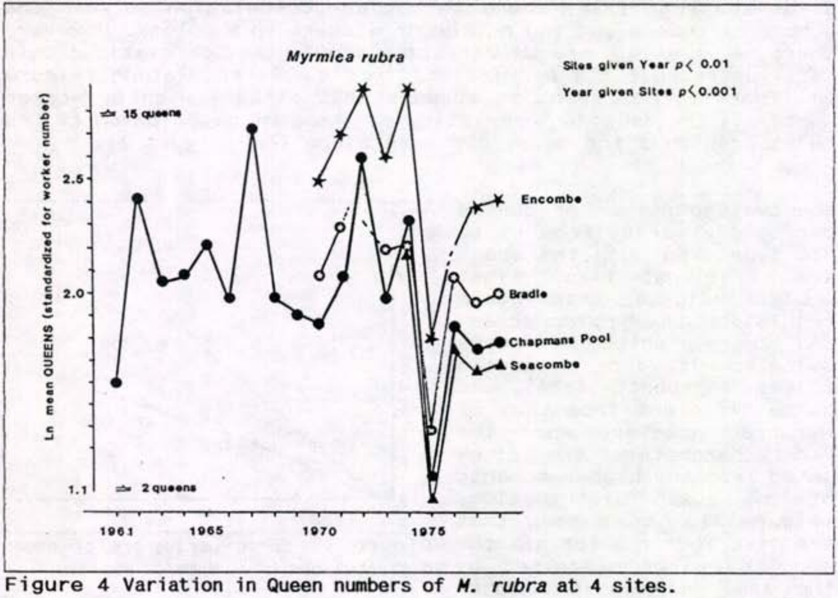
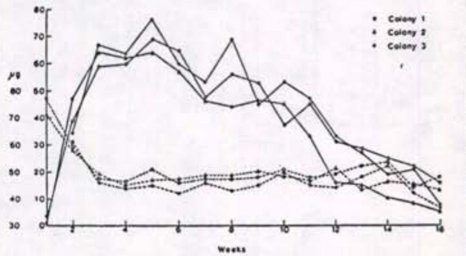


Figure 4 Variation in Queen numbers of *M. rubra* at 4 sites.

QUEEN VARIABILITY AND OVIPOSITION

The vast majority of laboratory studies have been made on *M. rubra*. However, tests on other species (eg. Elmes & Wardlaw 1983b) suggest that the results can be generalized throughout the genus.



— Average egg number per week (continuous line) and average egg weight (in micrograms, broken line) for three colonies each of four queens.

Figure 6 Egg production by *M. rubra* queens.

Average-sized queens of *M. rubra* can produce in excess of 600 eggs during a growing-season (Figure 6, Brian & Hibble 1964). The first 50-100 eggs laid by a queen, are considerably heavier than her subsequent production (c 30µg versus 20µg). The size and quantity of the eggs laid also varies with the size of the queen (specifically her ovariole mass, Elmes 1976). The eggs follow a developmental strategy (Figure 7a) that has been worked out in detail over a period of years starting with Brian (1955b).

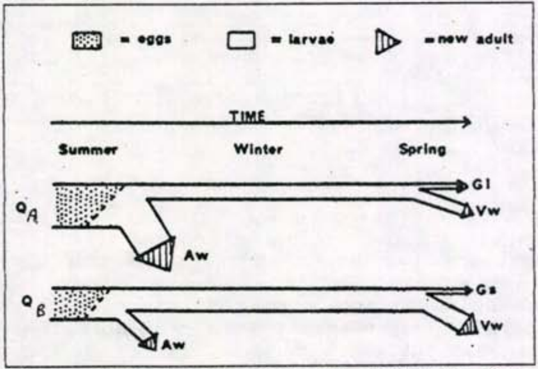
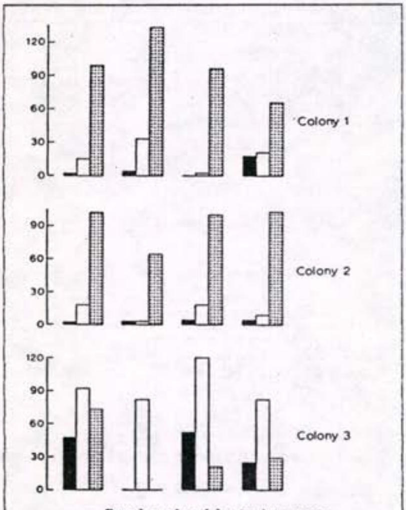


Figure 7 The developental path of *Myrmica* larvae. There is no growth during the winter period.

Essentially, the first fertilized eggs, laid in early summer, either develop slowly and enter a true (secondary) diapause before winter or they eclose rapidly to form summer-workers (Aw = Aesteval-workers in Brian's terminology). Larvae from eggs laid later in summer are often "trapped" by the onset of winter and enter a pseudo or primary diapause. During the following spring the overwintered large, secondary diapause larvae can develop into gynes (G) or spring workers (Vw = Vernal workers), depending upon their treatment. The smaller primary diapause larvae can only develop into spring workers.

The proportion of eggs forming summer workers, primary and secondary diapause larvae varies between queens, within and between colonies (Figure 8, Brian & Kelly 1967). Small queens produce fewer offspring and relatively fewer summer workers and more spring workers (Figure 7b). The new gynes are similarly sized to their mothers, indicating a strong genetical component (Elmes 1976).



— Brood produced by twelve queens, four from each of three colonies classified according to whether it metamorphosed into workers (black), remained in primary diapause (white) or went on to secondary diapause (dotted).

Figure 8 Variability between queens.

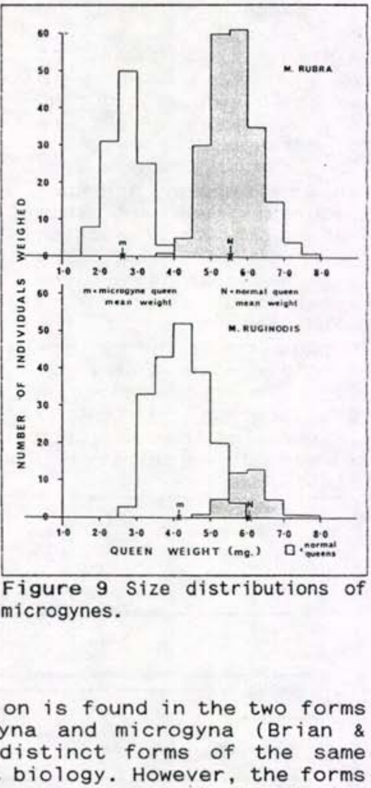


Figure 9 Size distributions of microgynes.

The clearest example of size variation is found in the two forms of *Myrmica ruginodis* Nyl., macrogyna and microgyna (Brian & Brian 1949). These represent two distinct forms of the same species, each form having a distinct biology. However, the forms are not segregated there being a large number of mixed colonies (Elmes *unpublished*). There is considerable size overlap between the two forms of *M. ruginodis* but the microgyne form of *M. rubra* is even more distinct (Figure 9, Elmes 1973b, 1976). There is some evidence that *M. rubra* microgynes are separate parasitic species (Pearson 1981).

In fact, it has been suggested that microgyny is a step towards the evolution of true social parasites, eg *Myrmica hirsuta* Elmes (1978b), which are abundant in the genus *Myrmica*. Surplus queens are a drain on the economy of a colony (Elmes 1973a), interfering with queen oviposition and reducing the overall production of the group (Figure 10, Elmes 1989).

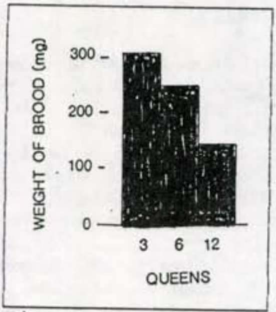


Figure 10 Production by different queen numbers with constant workers.

It appears that polygyny has considerable adaptive value, enabling individual colonies to adjust their egg production to rapidly changing nest-sites (see earlier sections). In turn this gives great flexibility at the population level (see first section). The disadvantage is that by recruiting unrelated queens, it is easy for individuals to "cheat" driving the system towards a purely parasitic one. In order to avoid this queens have evolved the ability to produce "plastic" eggs that are easily controlled by all queens, making it difficult for any one to monopolise the brood production. This is explored in the next section.

LARVAL ONTOGENY AND QUEEN CONTROL

The detailed developmental patterns of overwintered, third instar male and female larvae of *Myrmica ruginodis*, were worked out by Brian (1954, 1955c). He showed that both queens and males followed the same basic embryological development, similar to that of other hymenoptera. The adult system forms within the growing larva and is already well developed by the time of pupation. The development of the legs were used to measure the growth of the adult system (Brian 1954).

Three stages were recognised: A:- the period during which the leg-buds grow and distend, B:- the period during which the bud produces the 3 distal segments in telescoped form, C:- the final elongation of the leg within the intercuticular haemolymph. The larva feeds and grows steadily during the A & B phase but stops feeding during C, when growth is terminated by the ejection of the meconium forming the prepupa.

Throughout the third instar life, the brain gradually migrates from the larval head capsule into the prothorax, where it is enveloped by the developing adult head. When the brain is completely in the prothorax, it stimulates hormonal reactions which result in moulting (Brian 1959). Therefore, the position of the brain is a useful indicator of maturity (Brian 1954) which can be independent of corporal development. If corporal development and brain migration are kept in synchrony (Skellam *et al.* 1959) a fully mature adult is produced.

Synchrony almost always occurs in males but in female larvae the two systems can get out of phase. If either the brain maturity is accelerated in relation to growth, or growth is retarded in relation to brain development the larva metamorphoses before it is completely developed. In this way workers and a variety of female intercastes can be formed (Brian 1954).

Given the evolutionary arguments for a worker caste in ants, why has the genus *Myrmica* evolved a "plastic" system of caste determination rather than a more easily controlled genetically based system? I think that the reason is the need for a very flexible population structure (see earlier sections) which has selected for polygyny, low internal colony relatedness and the ability to respond quickly to habitat change. In turn this demands that colonies should be able to switch production between worker and reproductive at short notice (see following section). The plastic system is open to manipulation by both queens and workers and has lead directly to the interaction between workers and queens that M.V. Brian called "Queen Effect".

In very general terms queen effect operates because workers can recognise the presence of a queen in the nest. Although workers can recognise the shape of queens, awareness is mainly the result of chemical signals. These are contact pheromones and can only be passed from queen to worker to worker by touch (Brian 1970), they appear to be produced only in the abdomen of fertilized queens and are probably related to the ovaries (Brian 1973a, Coglitore & Cammaerts 1981). Queen effect seems universal in its action among species of genus *Myrmica.* It has been shown that queens of one species can stimulate workers of a second to show "queen effect" in their treatment of larvae of a third species (Elmes & Wardlaw 1983b).

In the absence of a queen, the workers favour the largest, most mature larvae and treat them in a way that maximises their chances of developing fully into a gyne or male. Workers can recognise gyne-potential larvae (Brian 1975a). When an active queen is present workers adopt an opposite strategy (Brian & Carr 1960); they favour the smaller, less mature larvae and treat them in a manner that speeds-up growth, while inhibiting growth in the larger larvae. The net result is early metamorphosis producing workers rather than gynes. Reduction in male growth simply produces smaller males or death.

Queen effect starts right from the time eggs are laid (Brian 1962, Brian & Hibble 1964, Brian & Kelly 1967) through larval pre-winter development (Brian 1975b) and continues throughout post-winter development (Brian 1973b). Workers can manipulate the temperature and feeding regimes of larvae (eg Brian 1956c, 1957, 1973b&c) which can affect the growth rates of larvae. On the other hand, growth and maturity can be affected chemically (Brian & Hibble 1963, Brian & Blum 1969, Brian 1974b, Brian *et al.* 1974).

When queen effect was first discovered the natural interpretation was that it was the way in which the queens controlled their workers and "made them do what they wanted". This is now considered simplistic, the process being a two-way interaction between queens and workers. My view is that workers recognise the presence of queens and manipulate the colony in their interests so that in a sense the workers are "using" the queens. This would explain many of the related problems of sexual investment in polygynous colonies where queens turn-over regularly (Elmes & Petal 1990).

SEXUAL PRODUCTION

To a large extent the production of gynes is controlled separately from the production of males. In the previous section it was shown how workers are produced at the expense of gynes. This is enabled both by the social control of queens and by physical manipulation of environment by the workers, which can regulate the food supply and incubation temperatures. However, these last two are liable to be manipulated drastically by chance climatic effects, which, if occurring at a critical phase in larval development, can switch gyne-larvae to workers.
Males develop from unfertilized eggs, in most species of *Myrmica* both queens and workers can lay male-eggs (Brian 1953). Many species appear to specialize in processing food by workers into highly nutritious trophic eggs (Brian & Rigby 1978). Queen effect causes workers to switch from producing reproductive eggs to trophic eggs (Brian 1969).

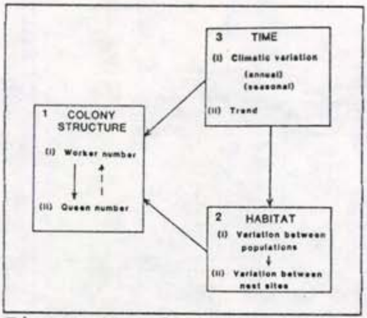


Figure 11 Relationship between population, habitat and climate.

In a study of male production, Smeeton (1981) showed that many male-eggs are produced in late summer by wild colonies of *M. rubra*. Her work suggested that most males are produced from worker-eggs, particularly from those laid by young workers that eclosed in early summer (Smeeton 1982a). Egg production was maximal when a small number of larvae were present, ie excess capacity, whereas it was reduced when many larvae were present (Smeeton 1982b). The condition of the workers affected the amount of eggs laid (Smeeton 1982c), this was particularly determined by the food availability when the laying workers were themselves larvae. Once the male-eggs are incorporated in the brood pile they are not singled out for attack by the workers (Brian 1981). When food is short they "compete" with the smaller female larvae and may die of starvation or eclose at a smaller size.

Consequently the proportion of sexuals produced by any colony results from a combination of environmental and social factors acting over several years. Changes in climatic and habitat conditions (Figure 11) determine population size. If social conditions in a colony were ripe for gyne production one might expect to find both gyne and male larvae among the overwintered brood (Figure 12, Elmes and Wardlaw 1982b). However, if environmental conditions were poor in spring many of the gyne-larvae would be switched to workers. These "failed gyne" workers tend to be larger than normal and contribute most to male-eggs during the following summer (Smeeton 1982a). Male production might be reduced but would only fail completely in extreme conditions. Consequently the colony produces a male-biased sex-ratio and has a higher potential male production the following year. Using the scheme in Figure 12 many other possibilities can be envisaged.

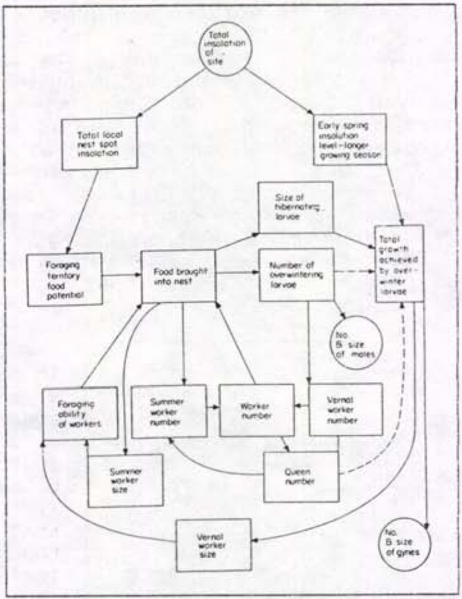


Figure 12 Interaction between sexual production and environment.

Male and gyne production should track each other but appear independent of each other in any year. Social factors can only be detected when a long run of data is available and the climatic and other physical variation can be eliminated statistically. Analysis of a long term data set for *M. sulcinodis* (Elmes *unpublished*) show cycles in sex-ratios that track the cycle in queen numbers (Elmes 1987a&b).

It is my opinion that the niche specialisation for nest sites that has occurred within the context of very variable environments, has given rise to the large number of *Myrmica* forms. In turn this life cycle demands polygyny, which is best regulated, in social terms, by flexible caste determination. This system results in considerable internicine struggle, it being very important who controls the part of the nest containing the egg-mass - the core (Brian 1986a). Workers establish the position of the core to which only certain individuals have access - both workers and queens (Elmes & Brian 1991), but it is not clear whether the workers determine which queens have access to the core or *vice-versa*. However, workers have low fidelity, they bond to the queen that is the most attractive to them even if she comes from a foreign colony (Brian 1986b).

All these factors result in male-biased sex-ratios which can be considered a cost to be set against the benefits of the life-style.

RÔLE IN THE ENVIRONMENT

At first sight, one might think that the relatively small colonies of *Myrmica* have little impact upon their environment. However, studies have shown them to have many interactions with plants and animals. Although small, *Myrmica* nests can be numerous and exist at high densities (first section). Being scavengers, *Myrmica* bring back large quantities of organic material which is incorporated in the soil around their nests. A comprehensive study of the soil of ants nests was made in Poland (Jakubczyk *et al.* 1972, Cezerwinski *et al.* 1971:- reviewed Petal 1980). They compared the soil of the nests of two Lasius species with *Myrmica* species (Table III).

Table III Contents of Nest Soils.

The ratio (nest-soil/control) of nutrients and micro-flora in nests of 3 European ants (Lf= *Lasius flavus*, Ln= *Lasius niger*, Myr= *Myrmica*). 0= still occupied, 1= abandoned for 1 year, 2= abandoned 2+ years. (Petal 1980).

				Myrmica nests		
Measure	Ln	Lf	Myr	0	1	2+
K_2O	2.0	3.7	4.0	6.3	3.6	1.0
P_2O_5	2.0	4.0	4.0	5.0	6.7	1.0
N				1.3	1.2	1.0
Catns.	1.0	1.5	1.8	1.5	2.6	
Bact.	22.8	2.1	10.2	16.5	1.1	0.7
Fungi	12.1	0.8	3.8	5.5	11.0	6.5
Yeasts	1.3	0.2	0.2	0.2	0.4	0.8

Both *Myrmica* spp. and *Lasius flavus* had considerably more organic material and nutrients in their nest soil, compared with controls. The accumulated nutrients were soon lost from the abandoned mounds of *Myrmica* spp., soil from those nests abandoned for two years had no more nutrients than the control samples (Table III). Petal (1980) concludes that the different levels of micro-flora in the soil from the nests of the different species is explained by their diet and general biology. *Myrmica* collect insect prey throughout the year and the remains, once incorporated in the soil, stimulate the growth of ammonifying bacteria. A benefit of the high levels of these micro-organisms is that it enables *Myrmica* spp. and *Lasius niger* to cope with high levels of mineral nitrogen pollution (Petal *et al.* 1975, Petal 1983).

Ants affect vegetation in two ways. 1. By modification of the plant community colonizing nest sites: Elmes & Wardlaw (1982b) could find no evidence that the plants above *Myrmica sabuleti* nests were responding either to gross physical factors. They considered that microhabitat features determined both the plant composition and the suitability of the nest-spot for a nest. The particular combination of plants might modify the suitability of a "spot" for the ants, probably by altering the shading effect of microclimate. If the ants occupied the site for a long period and accumulated nutrients as reported by Petal (1980) then it is conceivable that the flora might be altered by the ants.

2: Seed relocation: Beattie & Culver (1983) thought that the relocation of seeds of the myrmechochores and other plants to nests of *Myrmica discontinua* resulted in greater survival of seedlings. They showed that the nests of *M.discontinua* were richer in NPK than the nearby mounds of *Formica canadensis*. Seeds of *Viola* spp. survive better in nests of *Myrmica* spp. (Beattie & Culver 1978). *Myrmica* ants help disperse seeds of *Trillium* spp. in Japan (Ohara & Higashi 1987) and *Carex* spp. in Europe (Kjellson 1985).

Apart from their rôle as predators, that can have a large impact upon the populations of other invertebrates (Petal 1967), *Myrmica*, like most other ants, have developed complicated relationships with other invertebrates, especially Lycaenid butterflies (Malicky 1969).

One of the most complex relationships is between the parasitic Lycaenid genus *Maculinea* and *Myrmica* ants: in Europe there are five species of *Maculinea* and each is parasitic on a different *Myrmica* species (Figure 13, Thomas *et al.* 1989). Of especial interest is the relationship between *Maculinea rebeli* Hir. and its host *Myrmica schencki*, which feeds the caterpillars directly (Elmes *et al.*a&b). *Maculinea rebeli* has "learnt to use the complex relationship between the *Myrmica* queens, workers and larvae and they "deceive" the ants into believing that they are particularly attractive ant-larvae. Consequently they show growth patterns and competitive interactions, both with themselves and ant brood, that are analogous to those normal in *Myrmica* nests.

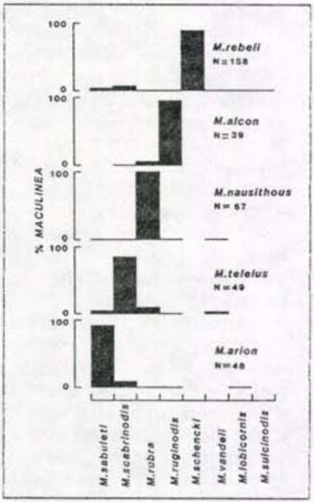


Figure 13 The distribution of *Maculinea* in different species of *Myrmica* nest.

I believe that such studies will show that *Myrmica* ants are very important in maintaining the "health" of the traditional cultural habitats of Europe.

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