



## The ecology of *Myrmica* ants in relation to the conservation of *Maculinea* butterflies

G.W. Elmes\*, J.A. Thomas<sup>1</sup>, J.C. Wardlaw<sup>1</sup>, M.E. Hochberg<sup>2</sup>, R.T. Clarke<sup>1</sup> and D.J. Simcox<sup>1</sup>

<sup>1</sup> Furzebrook Research Station, Institute of Terrestrial Ecology, Wareham, Dorset BH20 5AS, UK

<sup>2</sup> École Normale Supérieure, Laboratoire d'Écologie, URA 258 du CNRS, 46 rue d'Ulm, 75230 Paris Cedex 05, France

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*Maculinea* butterflies in Europe, and probably most of Asia, are host specific social parasites of various species of *Myrmica* ants. The latest summary of field data showing the pattern of host specificity by *Maculinea* is presented. *Myrmica* ants have been well studied in the laboratory but much less is known about the ecology of their natural populations. While the former is important in understanding the adaptive evolution of *Maculinea* larval behaviours, the latter is of more practical importance to conservationists charged with the protection of specific populations of *Maculinea*. The current knowledge of habitat partition, colony growth and colony reproduction within communities of *Myrmica* ants is summarized in relation to the ecology of *Maculinea* species. Concepts used in current population simulation models are explained. A key concept is the idea that community structure (both number of species and size and abundance of nests) is controlled by the quantity and quality of suitable nest sites. Some advice is given to conservationists who might need to manipulate *Myrmica* ant populations in order to maintain a robust population of a *Maculinea* species.

Keywords: *Myrmica*; *Maculinea*; populations; management; host specificity.

### Introduction

For most nature conservation projects involving *Maculinea* butterflies in Europe, the state of the local community of *Myrmica* ants is the key factor in determining the size, stability and persistence of the butterflies' populations. Furthermore, *Myrmica* ants are true keystone species in many temperate ecosystems, affecting the natural community at many levels (Elmes, 1991a,b). For example, many other rare lycaenid butterflies have symbioses with *Myrmica* ants (e.g. Malicky, 1969; De Vries, 1991a,b; Fiedler, 1998 this volume) and an understanding of their biology has an importance for practical nature conservationists beyond the management of *Maculinea* butterfly populations. The *Myrmica* genus has been well studied by ant biologists and, excluding taxonomic descriptions, more than 1000 scientific papers have been published on its biology. However, few lepidopterists or conservationists are familiar with this literature. Here we summarize and interpret relevant information in relation to the biology and conservation of *Maculinea* butterflies, and present new data on niche separation in *Myrmica* and host specificity among *Maculinea*.

*Myrmica* has a Holarctic temperate distribution with distinct European, Asian and North American faunas while *Maculinea* butterflies are restricted to the Palaearctic. Five of the six recognized *Maculinea* species are European, each of which is a parasite of a different *Myrmica* species (Thomas *et al.*, 1989). The sixth species, *Maculinea arionides* M. is present in east Asia where its larvae have been reported living in nests of *Aphaenogaster* species (Yamaguchi, 1988), a genus closely related to *Myrmica*. The distribution, precise number and location of *Maculinea* species is poorly known (see this volume). There are undoubtedly a number of undescribed species extant in central and east Asia (see Fiedler, 1998 this volume) and based upon the ant fauna on sites where Asian specimens have been observed flying, it is probable that many of these also depend upon *Myrmica* ants (Woyciechowski, unpublished). Although we restrict this paper to the biology of the European *Myrmica* species, field observations suggest that many of the generalizations can be applied directly to the Asian fauna (Elmes, unpublished).

There are 12 common free-living *Myrmica* species in western Europe, which could potentially act as hosts to

\*To whom correspondence should be addressed.

E-mail: G.elmes@ITE.AC.UK

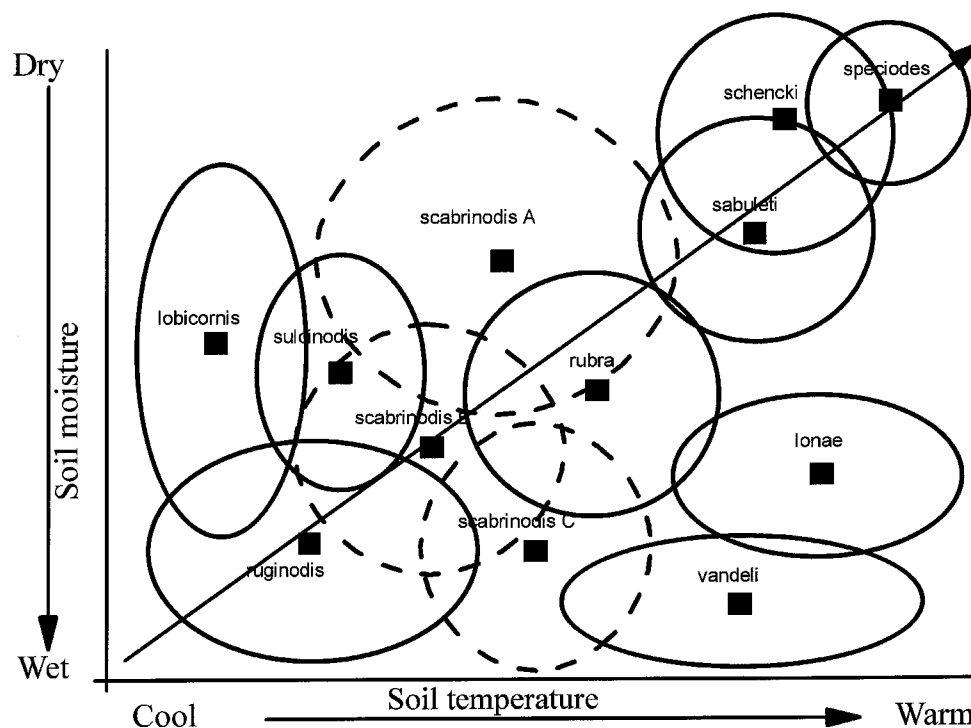


*Maculinea* larvae. Distinguishing between these can be difficult and identification is further confounded by the possible existence of several cryptic species or subspecies of *Myrmica scabrinodis* Nyl. (see Fig. 1; Elmes et al., 1994 and unpublished observations). Aspects of their biology such as morphology, individual behaviour, social physiology and colony genetics have been intensively studied because *Myrmica* ants are very amenable to laboratory experimentation. On the other hand, some aspects of their ecology such as colony fidelity, nest site persistence and community structure and stability, have been relatively poorly studied because field studies of these ants can be difficult.

Although understanding ant behaviour and colony social physiology is of high socio-biological and evolutionary interest and underpins our understanding of the interactions which occur between caterpillars and

ants, an awareness of the ant population level processes is the key to the practical conservation of *Maculinea* populations. For example, the presence of a queen (queenright) in the *Myrmica sabuleti* Meinert host nest can significantly reduce the survival chances of an adopted predatory caterpillar of *Maculinea arion* L. (Thomas and Wardlaw, 1990). This tells us much about the nature of the relationship with ants but it does not really help practical conservationists, because, using current knowledge, it is almost impossible to manipulate precisely the number of queens in wild ant colonies. In contrast, the knowledge that *M. arion* populations can flourish only on sites supporting high densities of small host colonies is of practical use because it is possible to manipulate colony density (Thomas et al., 1998 this volume).

A common misunderstanding is that the relationship



**Figure 1.** A schematic representation of the niche preference of common European *Myrmica* species based on only two parameters – soil moisture and soil temperature (see text for details) – in locations approximately geographically central to western Europe. The positive diagonal represents the main correlative axis between these two variables and is effectively the gradient used in the model of Hochberg et al. (1994). The squares indicate the optimal conditions for individual nest sites, which in our models would be reflected by a maximum value of  $R_{\text{species}}$  (see text). The ellipses indicate the limits at which nest sites would have average values for  $R_{\text{species}}$ ; colonies occupying nest sites within these limits can probably defend the nest sites against congeneric competitors. Conversely, colonies occupying nest sites outside these limits have low values of  $R_{\text{species}}$  and experience strong competition from other *Myrmica* species for which the nest is more suitable. Beyond a certain displacement from the optimum, the value of  $R_{\text{species}}$  falls below 1.0 and the nest site becomes untenable even in the absence of competition. Note that *Myrmica scabrinodis* is shown as three types or ‘species’, this reflects real ecological differences observed in the wild, but to date, no morphological separation can be made of these types.



between *Maculinea* and *Myrmica* involves co-evolution. This is not the case. Adaptive convergence has been achieved by the butterfly in response to the ants' behaviour, which has evolved in response to other social and ecological factors. The mistake arises because field and modelling studies have shown that *Maculinea* populations can have major impacts upon extremely localized communities of *Myrmica* ants (Hochberg *et al.*, 1992, 1994; Clarke *et al.*, 1997). However on the scale at which genetic exchange occurs between ants, only a minute proportion of colonies are affected by the butterflies, and on a global scale the impact of *Maculinea* upon *Myrmica* host ants is infinitesimally small.

### The host species of the European *Maculinea*

First, we emphasize that meaningful data for host specificity by *Maculinea* species must relate to recorded adult emergences or, at least, to the presence of mature prepupal larvae and pupae in the ant nests. The identity of species retrieving young caterpillars and the presence of half-grown caterpillars in a nest in autumn are no guide to host specificity, nor is the ability of *Myrmica* to rear the butterflies in captivity; see Thomas *et al.*, (1989) for detailed reasoning. Many past errors

have also occurred through misidentification of *Myrmica* species.

Unfortunately there has been occasional confusion due to the manner in which the data showing host specificity was presented by Thomas *et al.* (1989, Figure 1). Some readers have taken the line (a bar of zero height) indicating *Myrmica* species recorded as coexisting with the butterfly and hence regarded as 'potential hosts', to mean those species were recorded as actual hosts. Since publication of Thomas *et al.* (1989) we have enlarged the data set considerably, sampling many more *Myrmica* nests and for most species, sampling over a wider geographical range. We summarize the latest information in Table 1. We found no significant deviations from the original patterns for 'primary hosts' except for *Maculineaalcon* Denis and Schiff., which has been shown to use a different host in different parts of its range (Elmes *et al.*, 1994). We suggested that *M.alcon* might consist of three or more 'cryptic' species, each with similar status to *M.rebeli*; this has in part been confirmed by recent genetical studies (Gadeberg and Boomsma, 1997). We have anecdotal evidence which suggests that *M.rebeli* might also include one or more similarly cryptic species further east in its range.

With this caveat, Table 1 shows that each species has a single primary host and one or more secondary hosts

**Table 1.** Data for host-specificity by the five *Maculinea* species of Europe gathered between 1974 and 1996. A record is only counted if an adult emergence was recorded from a *Myrmica* nest or if excavation showed that the nest contained *Maculinea* pupae or full-grown, pre-pupal larvae. Ten potential host species of *Myrmica* are listed. For each *Maculinea* species we give the total number of *Myrmica* nests searched (usually a random sample of the species present but these were not always fully excavated), the number of *Maculinea* sites examined and countries containing the sites (UK = United Kingdom, F = France, E = Spain, S = Sweden, PL = Poland, NL = The Netherlands). No entry beneath a *Myrmica* species indicates that the species has not been recorded coexisting with the *Maculinea* species, a zero indicates co-existence but no recorded emergences. Otherwise, the total number of nests containing at least one full-grown *Maculinea* is given and the total number of mature *Maculinea* recorded in those nests is given in parentheses. ? = *Myrmica* species present but no adult emergences recorded and no random searching made. *M.alcon* has been separated into three cryptic species according to Elmes *et al.* (1994).

<i>Maculinea</i>	Countries	Sites	Nests searched	Potential host <i>Myrmica</i> species												
				<i>schencki</i>	<i>sabuleti</i>	<i>scabrinodis</i>	<i>rubra</i>	<i>ruginodis</i>	<i>vandeli</i>	<i>lonae</i>	<i>lobicornis</i>	<i>sulcinodis</i>	<i>aloba</i>			
<i>arion</i>	UK, F, S	4	503		50 (60)	4 (4)		0								
<i>teleius</i>	F, PL	4	242		2 (2)	34 (41)	3 (5)	0		1 (1)						
<i>nausithous</i>	F, E, PL	5	250		0	0	30 (71)	0		0						
<i>rebeli</i>	F, E	10	321	71 (299)	1 (6)	1 (4)	0	1 (3)	0		0	0	0			
<i>alcon 1</i>	NL	3				0	1 (2)	8 (38)			0					
<i>alcon 2</i>	E, F	4	175			16 (98)	0	0								0
<i>alcon 3</i>	S	2				?	18 (68)	?								



from among the list of potential host ant species. In general a trivial number of adult butterflies emerge from secondary host nests although in some populations this could be important for long-term survival (Thomas and Elmes, in prep.). We suggest that compared to the more 'primitive' predatory species, the 'advanced' cuckoo species, *M. alcon* and *M. rebeli* which are highly adapted to coexisting with ants, are more strongly host-specific within a geographical region. The feeding habits of *Maculinea nausithous* Bergsträsser caterpillars are unclear. *M. nausithous* is probably a predatory species: it has been observed eating ant larvae in the laboratory (N. Elfferich, pers. comm. and our own unpublished observations), but on the other hand, all cuckoo species will eat ant larvae under certain laboratory circumstances (unpublished). The relatively low average number of *M. nausithous* caterpillars per worker in nests of *Myrmica rubra* L., also suggests that the caterpillars are predatory, but, the fact that it has so far been recorded only from *M. rubra* (Table 1) might indicate that it at least, also has some of the social attributes of the cuckoo species.

## The biology of a *Myrmica* community

### Colony structure

The life styles of all *Myrmica* species are quite similar. Most form small colonies of 200–500 workers which can be polygynous, containing from one to many functional queens (Elmes, 1973; Elmes and Petal, 1990; Elmes and Keller, 1993). *Myrmica rubra* forms the largest colonies (generally about 1000 workers) although sometimes all the species create large colonies in excess of 2000 workers (Wardlaw and Elmes, 1996). Colony structure can be labile, frequently changing in both space and time. Despite this, the colony is the most useful unit for describing the *Myrmica* ant population, both for ant studies and for the conservation of *Maculinea* butterflies. We define a *Myrmica* colony as being that group of ants found living together in the same nest structure (Elmes, 1973).

*Myrmica* ant colonies grow logistically (Brian, 1965; Elmes, 1973; Hochberg *et al.*, 1994) following the equation:

$$W_{t+1} = R * W_t / (1 + \theta W_t)$$

where  $W$  = number of workers in year  $t$ ,  $R$  = rate of natural increase and  $\theta$  = the restriction on unlimited growth. The maximum number of workers  $W_{\max} = (R - 1) / \theta$ . In our models (e.g. Hochberg *et al.*, 1994; Clarke *et al.*, 1997) we consider that  $\theta$  is a species constant and that a colony living in an optimum nest

site will have a maximum value of  $R$ , which may differ between species. The effective value of  $R$  for any colony is a function of nest site quality, which is a combination of the physical characteristics of the site and the resources in the surrounding foraging territory (see below). This type of model was used by Elmes (1973) who showed that it could lead to the highly skewed distribution of colony sizes found in all *Myrmica* ants (Wardlaw and Elmes 1996).

In monogynous or single-queened colonies, the size of a colony is usually limited by the number of eggs the queen can lay. This is seldom the case for polygynous *Myrmica* colonies. Queen number is dynamic: queens are frequently short-lived (Elmes, 1980; Seppa, 1994; Evans, 1996a) and there is a considerable turnover of queens which can lead to low levels of relatedness within colonies (Pearson, 1983; Seppa, 1996; Evans, 1996b) and pose difficult questions for evolutionary biologists (see Keller, 1993). However, at the functional level of a colony, it means that worker numbers are not restricted directly by lack of queens. In some populations queen numbers fluctuate in a regular manner, with all nests having many queens in some years and few in others. It was hypothesized that such cycles occur in all colonies, but in most populations the individual colonies are out of phase with each other so that, generally, the average number of queens per colony in a population, appears to be more or less constant (Elmes, 1987; Elmes and Petal, 1990). This may affect the size of the *Maculinea* population both directly (queen effect) and indirectly through competition for the resources of the host colony, because each additional queen imposes a real cost on the ant colony (Elmes, 1989) and in effect, reduces the value of  $R_{\max}$  (Elmes, 1973).

### Colony foundation

The nuptial flights of virtually all *Myrmica* populations occur between mid-August and mid-September regardless of their geographical location. The only exceptions appear to be species living in the tundra of the far north (Alaska), which complete their cycle some weeks earlier (M.G. Nielsen, pers. comm.). After eclosion, the gynes (young alate queens) must spend about six weeks in the parent nest, during which time they build fat reserves for hibernation. Males need only a week or so to mature and are ready for the nuptial flight earlier than sister gynes; consequently one often observes precocious mating swarms comprised mainly of males.

*Myrmica* nuptial flights are generally local affairs, sometimes occurring within a few tens of metres from



the source nests, although sexuals are often drawn in from a wider radius of some hundreds of metres (i.e. from  $\approx 10$  ha). Flights usually occur above some prominent physical feature – a hilltop, tree, shrub, boulder or area of bare ground. Most gynes probably dealate and attempt to nest close to the mating post although some disperse considerable distances. Freshly mated queens must overwinter before laying their first eggs, which is why nuptial flights occur shortly before the onset of winter. Some gynes hibernate solitarily, others in groups and others join existing colonies. All three strategies can be adopted by any of the species.

After hibernation new queens form incipient colonies. Unlike the larger queens of *Lasius* and *Formica* species, they do not have enough fat reserves to establish colonies claustrally and must forage to feed their first larvae. Consequently, solitary *Myrmica* queens are often less successful than groups of queens (Elmes, 1989). In spring and early summer many fertile queens can be trapped on the soil surface and it is probable that given the opportunity most will join an established conspecific colony (Elmes, 1982; Elmes, and Petal, 1990). On ground supporting established *Myrmica* communities, most colony formation is by fragmentation of existing colonies. The strong competition for nest sites (see below) ensures that most small colonies, including incipient nests, are either destroyed by fragments of neighbouring congeneric colonies or absorbed by conspecifics. Successful colony foundation by gynes is probably only commonplace in new isolated patches of habitat.

#### The brood cycle

The six week maturation time for gynes means that eclosion must occur by mid-July. However, the larvae of *Myrmica* like other boreal myrmecines develop slowly (Kipyatkov, 1993) and there is insufficient time for an egg laid in spring (usually mid-April) to grow to maturity by mid-July. Consequently, larvae destined to be gynes (and most male larvae) are produced during the previous summer and overwinter in the nest as third instar larvae. A gyne is thus physiologically two years old and has survived two winters before she lays her first eggs.

Eggs laid in spring pass through the first two larval instars and are ready for rapid growth when the overwintered larvae are beginning to metamorphose. Some young larvae develop rapidly to workers (rapid brood) and eclose a few weeks after the overwintered larvae. Some males are produced in this way. Other female larvae develop slowly and enter a diapause, this cohort

includes both worker and all gyne potential larvae (Brian and Hibble, 1964; Brian and Kelly, 1967). A cold period is required to break the diapause. In spring, the largest individuals develop into gynes although all can be 'switched' into workers at a late date under certain social conditions. The presence of active mature queens inhibits gyne production ('queen-effect' see Brian and Hibble, 1963). Oviposition continues until late September, when it ceases in response to short day lengths (Kipyatkov, 1979). At the onset of winter all larval growth ceases, the small 3rd instar larvae overwinter, but younger larvae and any eggs still present, perish. These small larvae are in a false diapause and do not need a cold period to complete development; in most *Myrmica* species these individuals cannot develop into gynes.

Different individual queens invest different proportions of their eggs as rapid and diapause brood, but as a rule of thumb roughly 50% of eggs mature into new workers in the year they are laid and 50% the following year, a ratio we have used in our population simulation models (Hochberg *et al.*, 1994, 1997; Clarke *et al.*, 1997). *Maculinea* larvae have little effect upon rapid brood production, but either prey upon or out-compete the cohort of overwintered larvae. The absence of overwintered larvae in nests of many other ants such as *Formica* species may make them unsuitable hosts for *Maculinea* caterpillars and we have argued that the presence of overwintered brood early in spring was important in the evolution of a predatory life style by *Maculinea* (Thomas and Wardlaw, 1992; Elmes *et al.*, unpublished).

#### Nest sites and territoriality

In most biotopes, there is strong intraspecific competition for nest sites and, because most *Myrmica* species have overlapping niches, there is also strong interspecific competition (Brian, 1952a,b). Nests can be constructed in rotten wood, sphagnum moss, grass tussocks and soil (the most common place); soil nests may be under stones or simply underground. Many nests, particularly in moist, densely vegetated habitat, have small raised solaria but others have no surface evidence of their presence other than a small entrance hole. Given the correct combination of environmental circumstances, all *Myrmica* species will construct any of these types of nests, although in any habitat a particular style will dominate.

Nest density depends mainly upon nest site availability, which is a function of habitat. In plagioclimax habitat such as grazed grassland (a common habitat for



*M. arion* and *M. rebeli*), nest densities may exceed  $1 \text{ m}^{-2}$  (Elmes, 1974; Elmes and Wardlaw, 1982; Gallé, 1986) with individual nests (each system of underground galleries) being more or less permanent structures which are occupied and fought over by a succession of separate colonies. On the other hand, nest sites are clumped and transient in forest clearings, usually centred on rotten tree stumps, and persisting only as long as the vegetation remains open (Brian and Brian, 1952). On moorland and in marshes (the main habitats of *M. alcon*, *M. nausithous* and *M. teleius* Bergsträsser), the situation is intermediate. Some nest sites, particularly those on exposed tussocks of grass, persist for many years, but others are transient, often being suitable for occupation only for a few months. The population of ant colonies in such habitats may be high but it is also quite mobile (e.g. Elmes, 1978).

Colony foundation by groups or (single) gynes is important in the initial colonization of new isolated habitat, but in habitats containing established populations of *Myrmica* ants it is relatively rare. With nest sites at a premium, and the resulting strong competition, any new site is usually colonized rapidly by a fragment (bud) of an existing colony, which soon becomes a separate entity from the parent colony. At the population level, this means that once one or more *Myrmica* species have colonized an area, invasion by other species is unlikely unless the physical conditions of the habitat are changed or unless very large areas of new habitat are created. For example, on the scale of management operated by many conservationists, if only 1 ha of new habitat is created in the centre of an area containing a mature population of *Myrmica* (perhaps by clearing and burning scrub), it will be colonized rapidly by fragments of surrounding colonies (Thomas, 1995) with relatively little aerial invasion by gynes.

The ability of ants to maintain a territory varies between species. Three classes of territorial behaviour have been defined by Vepsäläinen and Pisarski (1982). Some species strongly defend a territory, others do not defend a physical boundary but will defend a food source once it has been located (encounter species), while others defend only their nest and will generally avoid territorial conflict (submissive species). However, the response is plastic and depends to some extent upon the competing species (e.g. Mabelis, 1984). For example, *Formica polyctena* in Finland is highly territorial and excludes *Tetramorium caespitum* L. which adopts an encounter role, whereas *Myrmica* species are submissive (Savolainen and Vepsäläinen, 1988, 1989). Nevertheless, submissive behaviour pays in these circumstances because some *Myrmica* colonies are permit-

ted within the territories of the dominant *Formica* (Savolainen and Vepsäläinen, 1990). On the other hand, in Dorset heathlands, *T. caespitum* is dominant and highly territorial while *Myrmica* adopt an encounter role and are excluded from *T. caespitum* territories (Brian et al., 1965).

To generalize: *Myrmica* colonies are prevented from nesting within the territories of ants of a similar size, such as *T. caespitum* and *Lasius niger* L., but are usually tolerated within the large territories of the much larger aggressive *Formica* species. All *Myrmica* defend their small nest sites but never any foraging area. As a result it is commonplace to find colonies, even those of different *Myrmica* species, nesting close to each other, sometimes even coexisting under the same stone. In the face of competition from more dominant genera, *Myrmica* adopt a submissive role but act as encounter species defending food sources against congeners and less dominant species. Most species are ground foragers searching up to 2 m from the nest (Elmes, 1975) but *Myrmica ruginodis* Nyl. and *M. rubra* can forage in shrubs up to 8 m from their nest (Stradling, 1968; McGlynn, 1994).

In our models we use a simple algorithm to determine whether a *Maculinea* larvae is found by a foraging worker. The probability of a worker searching any spot is directly proportional to the number of workers in the colony and inversely proportional to the square of the distance from the nest. Once a food source is found, foraging workers can soon recruit others to exploit it (Cammaerts-Tricot and Verhaeghe, 1974; Cammaerts, 1979; De Vroey, 1980). This is important for cuckoo species such as *M. rebeli*, in which many caterpillars often occur on the same foodplant and leave it at the same time (Elmes et al., 1991); once one individual is found by a foraging ant, the others are quickly found by foragers recruited from the same colony (unpublished).

The quality of any nest site (effective  $R$ , see above) depends also upon the productivity of the surrounding foraging territory. If nest site density is low, colonies have uncontested exploitation of all food within the area foragers search over. But if density is high, foraging territories of adjacent colonies overlap and the resources are shared, reducing the effective  $R$  for all nest sites which leads to generally smaller colonies. Proactive management of habitat for *Maculinea* should vary according to whether many small or fewer large colonies of the host ant are required. A management which takes local patches of habitat through a series of rapid successions rather than maintaining a plagio-climax, generally leads to high densities of small ant colonies. For example, British *M. arion* populations are



more successful on habitats supporting a high density of small colonies rather than fewer large colonies. This might be due to the poor survival of caterpillars in colonies of *Myrmica sabuleti* which contain queens (Thomas and Wardlaw, 1990, 1992); a higher proportion of colonies are queenless when colony sizes are small (Elmes, 1980).

The *Myrmica* ant community

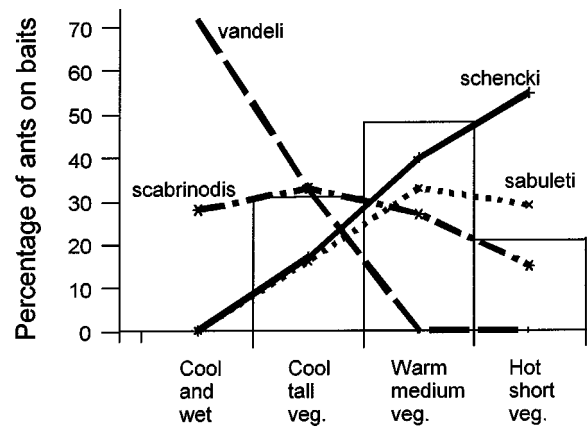
*Myrmica* species are similar in basic morphology and social behaviour (see above), and specific adaptation has been largely physiological (Elmes, 1982; Elmes and Wardlaw, 1983). We suggest that the strong competition that typically exists between *Myrmica* colonies, has led to speciation in an attempt to maximize *R* in response to particular combinations of nest site conditions. Although other factors are undoubtedly important, the simplest expression of this is a two dimensional gradient in soil (nest site) warmth and humidity; however these factors are often correlated which makes untangling of their effects difficult. Each species is more or less adapted to a different optimum (Fig. 1), for example, *M. ruginodis* is adapted to cool-moist conditions and *M. schencki* to warm-dry conditions at the nest site (which to an extent includes the surrounding foraging territory, see above). Within the framework of Figs 1 and 2, soil moisture ranges from wet = 'surface soil more or less damp throughout the year' to dry = 'surface soil well-drained and normally dry, moist soil at a depth of >20 cm in an average summer', and temperature from cool = 'top 5 cm of the soil averages 18°C in summer' and warm = 'top 5 cm soil averages about 24°C in summer'.

When the niches of the initial foodplants of *Maculinea* species are classified on a similar scale to that in Fig. 1, they are invariably found to be much broader than the niches of single *Myrmica* species (Fig. 2). Here, field data for *M. rebeli* from the Haute Alpes, France show that the larval food plant overlaps the range of four potential host *Myrmica*; Thomas *et al.*, (1998 this volume) gives similar data for *Thymus* and the host ants of *M. arion*.

Take, for example, an hypothetical area of land bounded by the distribution of a *Maculinea* foodplant, and which contained the full range of nest sites as defined in Fig. 1. If the average insolation of this area could be reduced instantly, by increasing shade (e.g. change of aspect or taller vegetation) or translocation to a higher altitude or more northerly latitude, the soil temperature axis would in effect, be extended left and all nest sites would become too cold for their present occu-

pants. The species at the right-hand side of the figure would be lost and their nest sites pre-empted by a species from the left of the figure, although due to the interaction between soil temperature and moisture, the survivors might generally prefer drier sites than previously. Many nest sites at the cooler end would become untenable for any *Myrmica* species, with the net result that both species diversity and overall colony abundance would be reduced. Increasing general insolation would have a similar effect but lead to a different fauna.

How does this theoretical concept translate to a real community of *Myrmica* species? First the geographical position will determine the overall insolation and range of soil moisture of the habitat. Superimposed upon this, individual potential nest sites will vary according to microtopography and microphysiography. Thus, in terms of a colony's ability to increase, each site will have a species-specific value of *R* ( $R_{species}$ ). We propose that  $R_{species}$  is maximal when a nest site coincides with the centre of the species' range, as defined in Fig. 1. Take, for example, *M. rubra*: as nest site conditions



**Figure 2.** Data for niche distribution of four *Myrmica* species measured at a *Maculinea rebeli* site in the Haute Alpes, France. The site (area over which the foodplant *Gentiana cruciata* was distributed) was divided subjectively into three areas (based upon the vegetation and soil characteristics which affect nest site suitability for *Myrmica* species, see text and Fig. 1). Approximately equal numbers of plants were present in each area except for the cool-wet area which contained fewer gentians. The percentage of the total gentian population which was at a suitable flowering stage and carried *M. rebeli* eggs is illustrated by the boxes – note that no gentians in the coolest area carried eggs (in most cases the flowers were insufficiently developed for oviposition). Baits were set at gentians and the percentage of baits within each sub-area, attracting the four different *Myrmica* species, is illustrated.



become cooler, the effective value of  $R_{rubra}$  decreases but  $R_{ruginodis}$  increases. At a certain point it will be equally suitable (or unsuitable) for both *M. rubra* and *M. ruginodis* and optimal for *M. scabrinodis*, and inter-specific competition for the site will be strong.

If all potential nest sites within an area are identical in terms of  $R_{species}$ , the stable community should consist of only one or two *Myrmica* species (see Thomas *et al.*, 1998 this volume for a practical example). As the heterogeneity in  $R_{species}$  increases, a greater potential number of species can compete for the nest sites. However, we have shown recently that the actual spatial arrangement (or degree of clustering of similar sites) can have significant effects upon the distribution and persistence of the competing species (Clarke *et al.*, 1997, 1998 this volume). Finally,  $R_{species}$  varies in time either in response to unique local factors or more general (climatic) factors, which affect all nest sites in the same way. This temporal variability could result in an increase or decrease in the diversity of *Myrmica* species, depending upon the starting conditions and frequency of variation. We are in the process of modelling this for *Myrmica* ant communities.

Hitherto, we have applied only a simplified version of this concept to our current models (e.g. Hochberg *et al.*, 1992, 1994, 1997). We consider just the host species and lump all other potential hosts as a super-population called 'other *Myrmica*'. A uniform nest density of 1 nest per 11 m<sup>-2</sup> is maintained and each nest site is assigned a position on a temperature/humidity gradient (equivalent to the positive diagonal of Fig. 1) and is given a value of  $R$  for each species accordingly. In current models,  $R_{species}$  does not vary in time and obviously a nest site is untenable when the effective  $R_{species}$  is less than 1.0. Colonies die (or abandon the site) with a probability according to their size and with a small density independent mortality factor. Parasitism by *Maculinea* caterpillars can be thought of as a disease suffered by the colony, which reduces the effective  $R_{species}$  of primary hosts relatively more than that of secondary hosts. Infested colonies shrink in size and suffer higher mortalities because they are less able to defend their nest site due to fewer workers.

### The manipulation of *Myrmica* populations

In early programmes to conserve *Maculinea*, the focus was too often directed towards the butterflies' egg laying behaviour in relation to the conspicuous flowering foodplant populations (Elmes and Thomas, 1992). But most *Maculinea* population changes are attributable to changes in the status of their *Myrmica* host ants

(Thomas, 1980, 1995), which is not surprising when one recalls that about 85% of the butterfly's life is spent underground or that >98% of its biomass is acquired as a social parasite of *Myrmica*. This is not to say that plant populations are unimportant (e.g. Elmes *et al.*, 1996), but low plant numbers are the key constraint on only a minority of sites of all *Maculinea* species.

A common problem in the conservation of *Maculinea* is that most practitioners and advisers are lepidopterists or general ecologists, who have little experience of the biology of *Myrmica* (Elmes and Thomas, 1992). They frequently question whether *Myrmica* populations can be manipulated to aid the conservation of *Maculinea*. The answer is yes, but it is not easy. In this section, we cannot give precise instructions for management to produce particular *Myrmica* ant communities because this can only be done on a case by case basis. However, see other papers in this volume for several successful practical examples of such management. Instead we try to highlight a few of the general principles to be remembered and some of the major pitfalls which should be avoided.

Broadly speaking, there are three main reasons why a *Maculinea* population is small or starts to decline:

- (i) Foodplants are widespread on a site but there are insufficient host ants throughout the site (either too few or too small colonies) to sustain the butterfly population. In habitat where the plant community needs to be in a very early successional stage, as was the case for most British *M. arion* populations (see Thomas *et al.*, 1998 this volume), it can be the hardest situation to remedy. It requires a detailed understanding of the ants and careful long-term management, such as mowing or grazing, to produce an altered but stable ant community in which the host ant predominates. Although the habitat management techniques are usually easier in the wetland habitats occupied by *M. nausithous* and *M. teleius*, detailed knowledge of the ants is still required.
- (ii) There are sufficient host colonies but too few overlap with the foodplant population to sustain the butterfly population. Here there are two choices, either manipulate the whole environment to spread the ants into areas where plants are growing or spread the foodplants into the ant habitats. The former is effectively the same as (i), but because the host ants are not evenly distributed throughout the site, the practical manipulation of the management regime might be even more localized and delicate. The latter particularly concerns





*M. arion*, *M. rebeli* and *M.alcon* sites that contain areas which either lost both plants and ants in the past, or never contained either, but now happens to support a large population of host ants due to recent management changes (e.g. scrub and woodland clearance). In some parts of the *Maculinea* species' ranges, it may take decades or even centuries in the case of *Thymus*, before the foodplants recolonize these areas naturally. In these circumstances the translocation of plants has proved effective (Thomas, 1995). The decision as to which is done depends upon a range of both ecological considerations and wider conservation issues. Altering the plant distribution probably has less impact upon other rare plant and animal populations present on the site, but could result in a larger but less stable *Maculinea* population (Hochberg *et al.*, 1994). On the other hand, altering the management to manipulate the *Myrmica* ant community produces a modified biotope which might or might not be desired for the conservation of other fauna and flora (Elmes and Thomas, 1995).

- (iii) There are sufficient host ant colonies overlapping with foodplants to sustain (theoretically) a butterfly population, but the food plant is so abundant that too many young caterpillars are, by chance, either recruited into secondary host ant nests or are never found by ants. This is quite a common situation for both *M. nausithous* and *M. teleius* where the ant populations are concentrated towards the edges of hay meadows whereas the centres of fields which may contain low densities of *Myrmica* often support the highest densities of *Sanguisorba*. This situation is perhaps the easiest to remedy because there is no need to manipulate the ant population. Oviposition can be forced into the desired areas by selective cutting of the flowering stems of foodplants before the butterflies emerge and oviposit.

In order to decide which of these situations applies, it is essential that *Maculinea* conservationists must become reasonably competent *Myrmica* taxonomists. The paper by Wardlaw *et al.*, (1998 this volume) in conjunction with the specialist keys cited therein should assist the beginner. If it is decided to manipulate the ant community, the next essential is to understand some key elements of *Myrmica* ecology (see above). First, it is important to remember that *Myrmica* colonies are highly dynamic (see above) and that changes can occur on a timescale that is an order of magnitude faster than the fluctuations observed in the foodplant populations

(e.g. Thomas, 1995). Under most conditions, flowering *Thymus*, *Origanum* and *Gentiana cruciata* populations have particularly slow dynamics as well as broader niches, in comparison to *Myrmica*, and although flower production by *G. pneumonanthe* and *Sanguisorba* track environmental changes more quickly, the overall populations of these plants seldom change at the rate exhibited by ants. Also it should be remembered that habitat changes that appear trivial to human eyes, can force major changes in *Myrmica* populations, due to their narrow and differing niches compared to most flowering plants.

Two other important factors affect the type and frequency of management required – the successional stage of the habitat occupied by the particular *Maculinea* 'community-module' and its position in the overall geographical range of the community. In general most *Maculinea* populations live in habitat in early to mid-seral stages and are susceptible to successional changes following perturbation or changed management. Such changes tend to occur more rapidly in wetter habitats and consequently over their whole range, *M.alcon*, *M. nausithous* and *M. teleius* are more susceptible to successional change than *M. arion* and *M. rebeli*. Even among these three there are differences. For example, if the mowing regime on wetland areas being managed for *M. teleius* and *M. nausithous* is not carried out for a few years, the *M. scabrinodis* colonies which live under *Sanguisorba* plants growing in the shorter open vegetation are more likely to be lost than those of *M. rubra*, which inhabit a broader, less transient niche among the taller, more overgrown marginal vegetation and support *M. nausithous*.

The niches of all *Myrmica* and to a lesser extent all (flowering) foodplants become much narrower towards the edge of each *Maculinea* species' range, and in most circumstances, we consider that the niche availability of the host ant restricts the *Maculinea* community dynamics more severely than niche requirements of the foodplants. For example, at the centre of its range in Europe, *M. arion* is associated with long grass in lowlands and montane meadows in highlands where its host, *M. sabuleti*, flourishes; habitat succession in both of these circumstances is rather slow. However, at the northern edge of *M. arion*'s range, *M. sabuleti* populations occupy potentially unstable biotopes maintained as very short-turf plagioclimaxes (see Thomas *et al.*, 1998 this volume), and consequently populations of *M. arion* respond more quickly to environmental change than is the case with core populations.

So, with the important exception of sites that are near the species' edge-of-range (where populations can



decline in two seasons from more than a thousand butterflies to local extinction), when faced with preserving a declining *Maculinea* population, conservationists must remember that inappropriate management may be worse than no management. Before any manipulation is considered, an assessment should be made of the distribution of *Myrmica* ant colonies in relation to the foodplants where eggs are laid. Empirical evidence supports our model predictions for minimum and optimal ant densities under foodplants: in the cases of *M. rebeli* and *M. alcon*, a minimum of 10% and optimum of 30–40% of flowering foodplants within foraging range of the host *Myrmica* species is indicated. For *M. nausithous*, using a host ant species that has atypically large colonies, the minimum is 15% and optimum 100%. But in the cases of *M. arion* and *M. teleius*, a minimum of 50% and optimum of 100% foodplant must be in foraging range of the host ants. If the coincidence falls below the mid range of 25% for *M. rebeli* and *M. alcon*, 50% for *M. nausithous* and 75% for *M. arion* and *M. teleius*, then judicious manipulation of the host ant population should increase the numbers and persistence of the butterfly populations.

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### References

- Brian, M.V. (1952a) The structure of a dense natural ant population. *J. Anim. Ecol.* **21**, 12–24.
- Brian, M.V. (1952b) Interaction between ant colonies at an artificial nest-site. *Ent. Mon. Mag.* **88**, 84–8.
- Brian, M.V. (1965) *Social Insect populations*. London: Academic Press.
- Brian, M.V. and Brian, A.D. (1952) Insolation and ant population in the West of Scotland. *Trans. R. Ent. Soc. Lond.* **102**, 303–30.
- Brian, M.V. and Hibble, J. (1963) Larval size and the influence of the queen on growth in *Myrmica*. *Ins. Soc.* **10**, 71–82.
- Brian, M.V. and Hibble, J. (1964) Studies of caste differentiation in *Myrmica rubra* L. 7. Caste bias, queen age and influence. *Ins. Soc.* **3**, 223–38.
- Brian, M.V. and Kelly, A.F. (1967) Studies of caste differentiation in *Myrmica rubra* L. 9. Maternal environment and the caste bias of larvae. *Ins. Soc.* **14**, 13–24.
- Brian, M.V., Hibble, J. and Stradling, D.J. (1965) Ant pattern and density in a southern English heath. *J. Anim. Ecol.* **34**, 545–55.
- Cammaerts, M.C. (1979) Recruitment to food in *Myrmica rubra*. *Biol. Behav.* **4**, 159–72.
- Cammaerts-Tricot, M.C. and Verhaeghe, J.C. (1974) Ontogenesis of trail pheromone production and trail following behaviour in the workers of *Myrmica rubra* L. (Formicidae). *Ins. Soc.* **21**, 275–82.
- Clarke, R.T., Thomas, J.A., Elmes, G.W. and Hochberg, M.E. (1997) The effect of spatial patterns in habitat quality on community dynamics within a site. *Proc. R. Soc. Lond. B.* **264**, 347–54.
- Clarke, R.T., Thomas, J.A., Elmes, G.W., Wardlaw, J.C., Munguira, M.L. and Hochberg, M.E. (1998) Population modelling of the spatial interactions between *Maculinea*, their initial foodplant and *Myrmica* ants within a site. *J. Ins. Conserv.* **2**, 29–37.
- De Vries, P.J. (1991a) Call production by myrmecophilous riodinid and lycaenid butterfly caterpillars (Lepidoptera); morphological, acoustical, functional and evolutionary patterns. *American Museum Novitates* **3025**, 1–23.
- De Vries, P.J. (1991b) Mutualism between *Thisbe irenea* larvae and ants, and role of ant ecology in the evolution of myrmecophilous butterflies. *Biol. J. Linn. Soc.* **43**, 179–95.
- De Vroey, C. (1980) Food competition in meadow ants. *Ins. Soc.* **27**, 278–9.
- Elmes, G.W. (1973) Observations on the density of queens in natural colonies of *Myrmica rubra* L. (Hymenoptera: Formicidae). *J. Anim. Ecol.* **42**, 761–71.
- Elmes, G.W. (1974) The spatial distribution of a population of two ant species living in limestone grassland. *Pedobiologia* **14**, 412–18.
- Elmes, G.W. (1975) Population studies on the genus *Myrmica* (Hymenoptera, Formicidae), with special reference to southern England. Unpublished PhD thesis, University of London, 334 pp.
- Elmes, G.W. (1978) Populations of *Myrmica* (Formicidae) living on different types of *Calluna* moorland – a semi-natural habitat of southern England. *Memorab. Zool.* **29**, 41–60.
- Elmes, G.W. (1980) Queen numbers in colonies of ants of the genus *Myrmica*. *Ins. Soc.* **27**, 43–60.
- Elmes, G.W. (1982) The phenology of five species of *Myrmica* (Hym. Formicidae) from South Dorset, England. *Ins. Soc.* **29**, 548–59.
- Elmes, G.W. (1987) Temporal variation in colony populations of the ant *Myrmica sulcinodis* I. Changes in queen number, worker number and spring production. *J. Anim. Ecol.* **56**, 559–71.
- Elmes, G.W. (1989) The effect of multiple queens in small



- groups of *Myrmica rubra*. *Actes Colloques Ins. Soc.* **5**, 137–44.
- Elmes, G.W. (1991a) The social biology of *Myrmica* ants. *Actes Colloques Ins. Soc.* **7**, 17–34.
- Elmes, G.W. (1991b) Ant colonies and environmental disturbance. In *The Environmental impact of burrowing animals and animal burrows*. (P.S. Meadows and A. Meadows, eds). Oxford: Clarendon Press.
- Elmes, G.W. and Keller, L. (1993) Distribution and ecology in queen number of ants of the genus *Myrmica*. In *Queen number and sociality in insects* (L. Keller, ed.) pp. 294–307. Oxford: Oxford University Press.
- Elmes, G.W. and Petal, J. (1990) Queen number as an adaptable trait: evidence from wild populations of two red ant species (genus *Myrmica*). *J. Anim. Ecol.* **59**, 675–90.
- Elmes, G.W. and Thomas, J.A. (1992) Complexity of species conservation in managed habitats: interaction between *Maculinea* butterflies and their ant hosts. *Biodivers. and Conserv.* **1**, 155–69.
- Elmes, G.W. and Wardlaw, J.C. (1982) Variations in populations of *Myrmica sabuleti* and *M. scabrinodis* (Formicidae: Hymenoptera) living in southern England. *Pedobiologia* **23**, 90–7.
- Elmes, G.W. and Wardlaw, J.C. (1983) A comparison of the effect of temperature on the development of large hibernated larvae of four species of *Myrmica* (Hym. Formicidae). *Ins. Soc.* **30**, 106–18.
- Elmes, G.W., Thomas, J.A. and Wardlaw, J.C. (1991) Larvae of *Maculinea rebeli*, a large blue butterfly, and their *Myrmica* host ants: wild adoption and behaviour in ant nests. *J. Zool. Lond.* **223**, 447–60.
- Elmes, G.W., Thomas, J.A., Hammarstedt, O., Munguira, M.L., Martin, J. and van der Made, J.G. (1994) Differences in host-ant specificity between Spanish, Dutch, and Swedish populations of the endangered butterfly, *Maculinea alcon* (Denis et Schiff.) (Lepidoptera). *Memorab. Zool.* **48**, 55–68.
- Elmes, G.W., Clarke, R.T., Thomas, J.A., and Hochberg, M.E. (1996) Empirical tests of specific predictions made from a spatial model of the population dynamics of *Maculinea rebeli*, a parasitic butterfly of red ant colonies. *Acta. Oecol.* **17**, 61–80.
- Evans, J.D. (1996a) Temporal and spatial variation in reproduction in the facultatively polygynous ant *Myrmica tahoensis* (Hymenoptera: Formicidae). *Ins. Soc.* **43**, 309–17.
- Evans, J.D. (1996b) Queen longevity, queen adoption, and posthumous indirect fitness in the facultatively polygynous ant *Myrmica tahoensis*. *Behav. Ecol. Soc. Biol.* **39**, 275–84.
- Fiedler, K. (1998) Lycaenid–ant interactions of the *Maculinea* type: tracing their historical roots in a comparative framework. *J. Ins. Conserv.* **2**, 3–14.
- Gadeberg, R.M.E. and Boomsma, J.J. (1997) Genetic population structure of the large blue butterfly *Maculinea alcon* in Denmark. *J. Ins. Conserv.* **1**, 99–111.
- Gallé, L. (1986) Habitat and niche analysis of grassland ants (Hymenoptera: Formicidae). *Entomol. Gener.* **11**, 197–211.
- Hochberg, M.E., Thomas, J.A. and Elmes, G.W. (1992) A modelling study of the population dynamics of a large blue butterfly, *M. rebeli*, a parasite of red ant nests. *J. Anim. Ecol.* **61**, 397–409.
- Hochberg, M.E., Clarke, R.T., Elmes, G.W. and Thomas, J.A. (1994) Population dynamic consequences of direct and indirect interactions involving a large blue butterfly and its plant and red ant hosts. *J. Anim. Ecol.* **63**, 375–91.
- Hochberg, M.E., Elmes, G.W., Thomas, J.A. and Clarke, R.T. (1997) Mechanisms of local persistence in coupled host–parasitoid associations: the case model of *Maculinea rebeli* and *Ichneumon eumerus*. *Phil. Trans. R. Soc. Lond. B.* **351**, 1713–24.
- Keller, L. (1993) *Queen Number and Sociality in Insects*. Oxford: Oxford University Press.
- Kipyatkov, V.E. (1979) The ecology of photoperiodism in the ant *Myrmica rubra* (Hymenoptera, Formicidae). I. Seasonal changes in the photoperiodic reaction. *Entomol. Rev.* **58**, 10–19. (Translation of Russian: *Entomol. Oboz.* **58**, 10–19.)
- Kipyatkov, V.E. (1993) Annual cycles of development in ants: diversity, evolution, regulation. In *Proceedings of the Colloquia on Social Insects*; (Vol. 2) (V.E. Kipyatkov, ed.) pp. 25–48. St Petersburg, Russia.
- Mabelis, A. (1984) Interference between wood ants and other ant species. *Neth. J. Zool.* **34**, 1–20.
- Malicky, H. (1969) Versuch einer Analyse der ökologischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden (Hymenoptera). *Tijdschrift voor Entomol.* **112**, 213–98.
- McGlynn, K. (1994) The foraging behaviour of the common ant, *Myrmica rubra* (L.). Unpublished PhD thesis, University of London, 339 pp.
- Pearson, B. (1983) Intra-colonial relatedness amongst workers in a population of nests of the polygynous ant, *Myrmica rubra*. *Behav. Ecol. Soc. Biol.* **12**, 1–4.
- Savolainen, R. and Vepsäläinen, K. (1988) A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* **51**, 135–55.
- Savolainen, R. and Vepsäläinen, K. (1989) Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. *Oikos* **56**, 3–16.
- Savolainen, R. and Vepsäläinen, K. (1990) The effect of interference by formicine ants on the foraging of *Myrmica*. *J. Anim. Ecol.* **59**, 643–54.



- Seppa, P. (1994) Sociogenetic organization of the ants *Myrmica ruginodis* and *Myrmica lobicornis* – number, relatedness and longevity of reproducing individuals. *J. Evol. Biol.* **7**, 71–95.
- Seppa, P. (1996) Genetic relatedness and colony structure in polygynous *Myrmica* ants. *Ethol. Ecol. Evol.* **8**, 279–90.
- Stradling, D.J. (1968) Some aspects of the ecology of ants at Newborough Warren National Nature Reserve, Anglesey. Unpublished PhD thesis, University of Wales.
- Thomas, J.A. (1980) Why did the Large Blue become extinct in Britain? *Oryx*, **15**, 243–7.
- Thomas, J.A. (1995) The ecology and conservation of *Maculinea arion* and other European species of large blue butterfly. In: *Ecology and conservation of butterflies* (A.S. Pullin, ed.) pp. 180–97. London: Chapman and Hall.
- Thomas, J.A. and Elmes, G.W. (in prep.) Higher productivity at the cost of increased host-specificity when myrmecophilous butterfly larvae exploit ant colonies through trophallaxis rather than by predation.
- Thomas, J.A. and Wardlaw, J.C. (1990) The effect of queen ants on the survival of *Maculinea arion* in *Myrmica* ant nests. *Oecologia* **85**, 87–91.
- Thomas, J.A. and Wardlaw, J.C. (1992) The capacity of a *Myrmica* ant nest to support a predacious species of *Maculinea* butterfly. *Oecologia* **91**, 101–9.
- Thomas, J.A., Elmes, G.W., Wardlaw, J.C. and Woyciechowski, M. (1989) Host specificity among *Maculinea* butterflies in *Myrmica* ant nests. *Oecologia* **79**, 452–7.
- Thomas, J.A., Simcox, D.J., Wardlaw, J.C., Elmes, G.W., Hochberg, M.E. and Clarke, R.T. (1998) Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. *J. Ins. Conserv.* **2**, 39–46.
- Vepsäläinen, K. and Pisarski, B. (1982) Assembly of island ant communities. *Ann. Zool. Fennici.* **19**, 327–35.
- Wardlaw, J.C. and Elmes, G.W. (1996) Exceptional colony size in *Myrmica* species (Hymenoptera: Formicidae). *Entomol.* **115**, 191–6.
- Yamaguchi, S. (1988) *The life histories of 5 myrmecophilous lycaenid butterflies of Japan*. Kodansha of Japan.