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Specializations and Host Associations of Social Parasites of Ants

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1. Introduction

Ant societies dominate most terrestrial ecosystems at the scales at which they function (Wilson, 1990), and numerous similar-sized organisms have evolved adaptations to coexist with them (Wasmann, 1894; Wheeler, 1910; Donisthorpe, 1927; Hölldobler and Wilson, 1990; Huxley and Cutler, 1991). The occurrence of myrmecophily has probably been much underestimated in the field, but drawing on Donisthorpe (1927) and other studies, Elmes (1996) calculated that as many as 100,000 species of myrmecophile exist among the insects. Since this figure is more than double the number of vertebrate species known on Earth, myrmecophily can be regarded as a common phenomenon in ecology as well as one that has evolved independently, and convergently, across many Orders of insect (Hölldobler and Wilson, 1990).

Most known insect myrmecophiles are free-living commensals or mutualists, which live above ground within the foraging areas or territories of ants (Hölldobler and Wilson, 1990; Thomas, 1992a,b). They benefit from inhabiting these relatively enemy-free spaces (including freedom from hostile ants) and, in many cases, gain direct protection from their enemies. The functional and evolutionary ecology, and sheer diversity of the myrmecophilous adaptations of commensals and mutualists from several orders of insect are reviewed by Wasmann (1894), Donisthorpe (1927), Hinton (1951), Malicky (1969), Hölldobler and Wilson (1990), De Vries (1991a,b), Fiedler (1991, 1994, 1996, 1998), Pierce et al. (2002) and others. Although some adaptations are multifunctional, we loosely group them into three overlapping categories:

- **Evasive devices**, ranging from pacifying or non-threatening behaviours to morphological, behavioural or acquired-chemical disguise and camouflage.
- **Protection to withstand attack**, including some extreme morphological adaptations (e.g. highly sclerotized cuticles, onciform bodies with the vulnerable organs hidden underneath, setae, loose scales on wings, and many others).
Deliberate communication with ants through sound, touch and, especially, through a diversity of chemical secretions that ranges from rewarding ants with food (sugars, amino acids etc) to chemical mimicry (sensu Dettner and Liepert, 1994) or to the secretion of generalist allomones that either appease ants or alarm and agitate them. Chemical communication is the main means by which ant societies communicate with, and discriminate between, each other, and it is a major tool used by myrmecophiles from several insect orders to manipulate ant social behaviour: fine reviews are found in Hölldobler and Wilson (1990), Dettner and Liepert (1994) and Lenoir et al. (2001).

The interactions that have evolved between free-living commensal or mutualistic insect myrmecophiles and ants range from loose facultative associations to an obligate dependency for one or both partners. These interactions often appear complex and specialized (for butterflies alone, see Hinton, 1951; Malicky, 1969; Pierce, 1989; Pierce and Elgar, 1985; Pierce et al., 1987, 2002; De Vries and Baker, 1989; De Vries, 1990, 1991b; Fiedler and Maschwitz, 1987, 1988, 1989; Fiedler and Hölldobler, 1992; Thomas, 1992a,b; Fiedler, 1996), yet compared with myrmecophiles that inhabit ant nests or the other fiercely protected niches of ant societies, most are relatively simple and most free-living mutualists or commensals are comparatively generalist, interacting with ant species from several subfamilies, although a few are restricted to a single ant genus or species (Hölldobler and Wilson, 1990; Thomas, 1992a,b; Pierce et al., 2002).

In contrast, mutualistic species that inhabit ant nests are typically much more specialized and host-specific, whether they be the fungal gardens of Atta (leaf-cutting) ants (see Boomsma et al., Chapter 6, this volume) or the subterranean domestic herds of aphids and coccids on whose secretions certain species of Acanthomyops, Acropyga (and probably other genera) appear wholly to depend for food (Way, 1953, 1963; Hölldobler and Wilson, 1990). Some (we suspect many) of these associations are host-specific and it seems increasingly probable that subspecific adaptations and dependencies have (co-)evolved. The recent demonstration of colony-level associations between different genotypes of fungi and leafcutter ants – in which winged Atta queens carry their (colony-)specific strain of fungus with them on flights, transmitting this extreme mutualism vertically when new ant colonies are founded (Boomsma et al., Chapter 6, this volume) – has interesting parallels in Cladomyrma and Acropyga ant species, whose winged queens carry coccids taken from their natal nests in their mandibles during the nuptial flight (Hölldobler and Wilson, 1990).

2. Social parasites of ants

2.1 Definitions

We take a broad definition of the term social parasite to encompass all intruding arthropods that penetrate and inhabit, sometimes briefly, an ant society to exploit any resource that is valued and protected by the ant host,
rather than the narrower use of the term when applied only to parasitic ant species (see Hölldobler and Wilson, 1990). In contrast to the distinction between mutualist and commensal, that between mutualist and social parasite is clear-cut. Hölldobler and Wilson (1990) found no evidence that these relationships were anything other than one-sided, with the parasite winning all measured benefits and the ants none. Nor have we, in our studies on the butterfly *Maculinea rebeli*, whose caterpillars live within the brood chambers of *Myrmica schencki* nests where they displace the ant larvae and are fed directly by nurse ants. Although we predicted that the copious secretions of *M. rebeli*, which are continuously drunk by the nurses, might transfer increased fitness to workers at the expense of their own brood, it transpired that workers that tended *M. rebeli* lost weight and were shorter-lived than those tending the ants’ own brood, such were the demands imposed on the colony by the insatiable butterfly caterpillars (Wardlaw et al., 2000). The only apparent exception to this generalization is the special case of *Myrmica ruginodis* microgyna queens (see Brian and Brian, 1951, 1955) which confer distinct ecological advantages on colonies supporting them but which may be the first step in the evolution of a social parasitic ant (Elmes, 1978, and below).

We estimate that around 10,000–20,000 morpho-species of insect have evolved as social parasites of ants, thus accounting for a significant proportion of the world’s biodiversity (by comparison, about 10,000 species of bird and 4,500 mammal species exist). But despite the many species, most ant social parasites are exceedingly rare or localized in comparison to the abundance and distributions not only of their ant hosts but also of the other symbionts that interact with ants (Thomas, 1980, 1995; Hölldobler and Wilson, 1990; Thomas and Morris, 1994). Before exploring this, we briefly examine which types of ant society are most susceptible to social parasite attack.

### 2.2 The type of ant society most vulnerable to attack

It has long been accepted that one common form of social organization is especially vulnerable to intrusion, namely those ants whose colonies contain variable, usually multiple, numbers of queens (polygyny) and inhabit multiple nest sites (polydomy) (e.g. Buschinger, 1970; Alloway et al., 1982). Depending on the species, the number of queens in polygynous-polydomous colonies may range from zero to hundreds, and the local density of queens can vary intraspecifically between populations and over time. There is often a clear hierarchy in the social status of the queens: in the case of *Myrmica*, dominant alpha (α) queens occupy the central brood chamber where they receive maximum worker attention and lay most of the colony’s eggs, while beta (β) queens are relegated to the outer chambers awaiting promotion to α status (Brian, 1968, 1986; Evesham, 1984). Somewhat similar social structures have been found for other polygynous species, such as *Leptothorax nylanderi* (Plateaux, 1970) and *Solenopsis invicta* (Ross, 1989). In these and other species, daughter queens may be re-absorbed by their natal colony after the nuptial flight (e.g. Elmes, 1973), or enter a closely related one nearby. However,
colonies often recruit unrelated queens (e.g. Elmes, 1987; Pearson, 1982; Goodman and Ross, 1999), which can be interpreted as unrelated queens penetrating the society and acting as temporary social parasites (Elmes, 1974). Colony spread, in this system, is usually by fission, with daughter colonies budding off from core nests to exploit vacant habitat; initially these offshoots tend to be queenless, but may later recruit daughter queens from the mother colony or nearby nests (Elmes, 1991; Pedersen and Boomsma, 1999). There can also be a strong seasonal element to polydomy, with offshoots spreading in spring–early summer and retracting to merge with the donor nest in autumn (e.g. Herbers, 1985).

Compared to the societies of monogynous ants, polydomous-polygynous systems are loose, flexible and dynamic, leading sometimes to the development of massive supercolonies occupying >1 ha. This lifestyle imposes large reproductive costs to individuals, due to reduced kinship, but these are believed to be offset by shared benefits accrued at the colony level. Queens joining existing colonies obviously stand to benefit if their chances of individual colony foundation were small. Why the resident queens should tolerate joiners (even unrelated ones) is less clear, although some selective advantages have been suggested (Bourke and Franks, 1991, 1995). The ecological benefits at the colony level include an ability to withstand severe disturbances, resulting in colony fragmentation, and to spread rapidly, dominating new resources and pre-empting competitors, either seasonally or when fresh habitat becomes available following a perturbation. The greatest shared cost appears to be a periodic reduction in social cohesion, leading to increased vulnerability of the group to invasion by other organisms, including ant and non-ant social parasites that mimic the colony’s recognition signals.

Hölldobler and Wilson (1990) list three further attributes that may predispose ant colonies to social parasitism: they live in dense populations; inhabit cool or arid climates; and learn the species’ odour early in adult life, a theme developed by Lenoir et al. (2001). Our experiences suggest that the last two attributes seldom apply to the non-ant social parasites of ants (see also Pierce et al., 2002).

### 2.3 Properties of social parasites

Our main generalizations are made at the conclusion of this chapter. Here we note that, in addition to being rare in comparison to hosts, most lines of social parasite are embedded among clades of mutualistic species, and are presumed to have evolved from similar ancestors which were pre-adapted to invading ant societies through the defensive, pacifying and communicative devices that had evolved to promote symbiosis.

It is also increasingly clear that social parasitism has evolved independently many times among myrmecophiles, often within closely related taxa. For example, the butterfly Family Lycaenidae contains about 6000 species, of which most are mutualists and perhaps 300 (5%) species are social parasites; yet the latter are so polyphylitic that social parasitism is thought to have arisen
A final generalization is that many remarkable examples of convergent evolution exist between different lines of social parasite from several orders of insect (Coleoptera, Diptera, Lepidoptera, Hymenoptera, and to a lesser extent Orthoptera and others). Although almost every niche within an ant colony has been exploited by one type of myrmecophile or another, certain distinct forms are apparent, most of which are described and illustrated by Wassman (1894, 1912), Donisthorpe (1927) and Hölldobler and Wilson (1990). Later, we extend Hölldobler and Wilson's (1990) argument that the comparatively few morphological and behavioural forms found among the estimated 10,000–20,000 species of social parasite relate to distinct functional types that exploit ant colonies in one of a relatively small number of ways.

3. Four evolutionary routes to inquilism and other specialized forms of social parasitism

Hölldobler and Wilson (1990) identify four evolutionary pathways leading to social parasitism, and in some cases ultimately to inquilism, in which the parasite is so embedded in its host society that it lives the entire life cycle there. Three involve the most pre-adapted organisms of all – other ants. The majority confirm Emery's Rule (1909), which states that a parasitic species of ant is generally a close relative of its host ant species (see Savolainen and Vepsäläinen, 2003). One evolutionary route towards inquilism stems from ants that originally lived as commensals alongside or in the artefacts of other ant species, the eventual host typically being the larger and more dominant of the two. Emery's Rule frequently applies because this relationship often involves close mimicry of the host by the parasite, and the morphology, behaviour, physiology and communication systems of closely related ants provided the most similar models in the first place.

A second distinctive route involves slave-making ants, which raid the nests of close relatives, carrying off brood into their own nests to rear to adulthood as slave labourers. The spectrum of behaviours between various slave-making types of ant and their hosts, synthesized into a convincing evolutionary pathway that culminates in social parasitism, are so fully reviewed by Buschinger (1986) and Hölldobler and Wilson (1990, pp. 452–64) that it is unnecessary to repeat them here. Worth noting, however, is the fact that slave-making ants employ a very different strategy for penetrating host colonies to any other known social parasite of ants. Whereas the vast majority of the latter employ some combination of evasion, stealth or mimicry to enter host nests, slave-makers are well armoured and solicit aggression by attacking their host's workers, whilst releasing powerful alarm pheromones that cause the defending ants to panic and attack one another. This locks up much of the colony in combat, diminishing the protection otherwise available to the potential slave brood. Unlike typical alarm pheromones, which fleetingly trigger a wave of alarm across a colony, those of slave-making species are longer-chained, less volatile,
and prolong the confusion for tens of minutes. Until recently, this strategy was thought to be unique to slave-making species. However, another striking example of convergent evolution was recently described in the parasitoid wasp *Ichneumon eumerus*, which oviposits in the final instar of the socially parasitic butterfly *Maculinea rebeli* inside *Myrmica* colonies. Whereas *M. rebeli* employs close mimicry to inhabit the brood chambers of its host, *Myrmica schencki*, the heavily sclerotized *I. eumerus* adults induce fierce fighting in *M. schencki*, immobilizing up to 80% of a colony and leaving the *M. rebeli* larvae temporarily unprotected (Thomas and Elmes, 1993). Interestingly, *I. eumerus* releases a cocktail of similar chemicals to those of slave-makers – some compounds attract the ants to the wasp to amplify contact, some generate extreme aggression, and others repel the ants so that they mainly attack each other – but they are even longer-chained and more persistent, allowing the single parasitoid hours or days to seek and attack its host (Thomas *et al*., 2002).

The third route to social parasitism of ants by ants is very different. We have long argued that surplus β queens in polygynous ant colonies could, if not closely related to the ω queens, result in conflicts of interest in which low-caste queens might benefit from cheating by producing sexual eggs. In this way surplus queens might be considered as social parasites of their own worker force (Elmes, 1974, 1976, 1978; Buschinger, 1970, 1986). With local reproductive isolation, this might eventually lead to the sympatric evolution of permanent parasitic queens within their own nests, before spreading to infest other colonies of the same species. Elmes (1978) illustrated a hypothetical evolutionary pathway using social parasites of *Myrmica* ants (reviewed by Radchenko and Elmes, 2003). Starting with highly polygynous populations producing miniature but fully functional microgyne forms that confer ecological advantages on their colonies (represented by the microgyna form of *M. ruginodis*; see Brian and Brian, 1951), non- functional microgyne forms, such as those found in some *M. rubra* colonies, might be produced, especially when there is no longer an ecological advantage for microgyny. Elmes (1978) envisaged that microgyne forms of *M. rubra*, which are morphologically similar to normal queens but which produce only sexuals and pseudogyne forms, were the first step in the evolution of a true social parasite; indeed, these were described later by Seifert (1993) as a separate species, *M. microrubra*. This might lead to highly specialized species, such as *Myrmica karvajevi* that has several host species, via intermediate host-specific forms such as *Myrmica hirsuta*, which is found occasionally (and only) in *M. sabuleti* colonies. Although, the idea of rapid sympatric speciation contradicted the belief in the universality of slow allopatric speciation (e.g. Mayr, 1963), the concept is finding increasing favour (e.g. West-Eberhard, 1981; Hölldobler and Wilson, 1990). Recently, the hypothesis was given empirical support by Savolainen and Vepsäläinen (2003), who found that *M. microrubra* are most closely related to, and probably derived from, their parent populations, while *M. hirsuta* are close to their host but more similar to each other, possibly indicating a single speciation event.

The fourth route to social parasitism is the focus of our recent work (Thomas *et al*., 1998a; Elmes *et al*., 1999). It involves arthropods other than ants which, by definition, cannot fulfil Emery’s Rule. On the contrary, the same
ant genus or species may be host to a diversity of convergent lines from very
different insects. For example, we have found the Palaearctic ant Myrmica
scabrinodis parasitized by Maculinea teleius and M. alcon (Lepidoptera), by
Microdon myrmicae (Diptera) and by Atemeles emarginatus (Coleoptera) as
well as by Myrmica karavejevi and Myrmica vandeli; indeed, in certain hot-
spots we have found Maculinea teleius and Microdon myrmicae, or Microdon
and Atemeles, or Atemeles and M. hirsuta parasitizing the same individual nest.

Most of the pioneering studies of social parasites were concerned with
behavioural interactions between host and parasite, including Atemeles and other
staphylinid beetles (Wasmann, 1912; Donisthorpe, 1927; Hölldobler, 1967),
Maculinea butterflies (Chapman, 1920; Frohawk, 1924), and Leptothorax ants.
Ecological studies of social parasitism are much rarer, with the genus Maculinea
providing the only examples of studies on the population dynamic interactions
between a social parasite and its host, and of the ecological consequences of
these (e.g. Thomas, 1980; Thomas et al., 1998a; Elmes et al., 1999). These
studies – which were initiated to answer the nature-conservation question ‘Why
are most social parasites rare?’ – showed that host-specificity was a key factor for
the survival of the social parasite (e.g. Thomas et al., 1989; Elmes et al., 1999;
Schönrogge et al., 2002).

4. Host specificity in social parasites

4.1 Why are social parasites rare?

Despite many descriptions of the fine-tuning of specializations and the
reconstruction of plausible evolutionary pathways leading to social parasitism
(Hölldobler and Wilson, 1990), a key ecological question remains: Why – when
equipped with such successful mechanisms to trick and exploit ants, and when
listed hosts are often among the commonest species in their zoogeographical
regions – are most social parasites exceedingly rare in comparison to their hosts?
Why, for example, does the UK Red Data Book (RDB) for insects list a
disproportionately high proportion of social parasites from all Orders among its
most threatened species (Thomas and Morris, 1994)? Why did Heath’s (1981)
RDB for butterflies include all five socially parasitic species among only 15 species
listed in the rarest category for Europe? Why do the 13 independently evolved
lines of socially-parasitic lycaenid butterflies figure so prominently in the IUCN
world list (Pierce et al., 2002)? Why have we and our co-workers (A. Radchenko,
personal communication), having excavated several thousand western Palaearctic
Myrmica colonies in careers spanning 25–40 years, encountered ant social
parasites, including microgynes, so infrequently? For example, Myrmica hirsuta
appears to live only on sites with very high densities of M. sabuleti, where it infests
<1% of host nests (Elmes, 1994); and we have found M. karavejevi in only three
localities, despite its host, M. scabrinodis, being arguably the commonest Myrmica
species in western Europe. Other field myrmecophilists describe similar
experiences (see e.g. Hölldobler and Wilson, 1990), and we give further examples
later (see Microdon mutabilis, M. myrmicae).
Few infestation patterns have been quantified in the field; nevertheless, we tentatively recognize three population structures among social parasites:

1. **High infestation, low transmission.** The five European species of *Maculinea* butterfly and the hoverflies *Microdon mutabilis* and *M. myrmicae* typically live in discrete, closed, high-density populations, where they infest – and may destroy – up to 30–40% of host ant colonies in each generation (Thomas and Wardlaw, 1992; Thomas, 1995; Schönrogge et al., 2002; our unpublished data). However, their populations are typically restricted to small (<10–<0.1 ha) patches that are occupied for many generations, whilst elsewhere in the landscape their hosts may be widespread (sometimes ubiquitous), resulting in fewer than one in ten-thousand host nests being infested at this scale (our calculation).

2. **Low infestation, high(ish) transmission.** *Myrmica microrubra* (= *M. rubra* microgyne s.* sensu Elmes, 1976), although more frequent in certain landscapes than others, are found widely throughout their host’s distributions, but within few nests on any one site, to which little cost is apparent. Despite their sympatric origins (Savolainen and Vepsäläinen, 2003), we envisage that *M. rubra* microgyne spread from one host (super-)colony to infest neighbouring colonies in each region. If confirmed, they would be superior dispersers but poorer invaders of new host colonies than *Maculinea* and *Microdon*. *Anergates atratus* (Hölldobler and Wilson, 1990) and, in our experience *Atelemes* spp., have a similar population structure.

3. **Low infestation, very low transmission.** In theory, this represents an evolutionarily unstable strategy, at least at the very low infection rates described. Nevertheless, in our experience, several European social parasites, including *Myrmica hirsuta* and *M. karavejevi*, exhibit this type of infestation, as may many other advanced species of social parasite. For example, Hölldobler and Wilson (1990), in a different context, comment thus on the incidence of ant–ant social parasites: ‘The great majority of workerless [= highly integrated] parasites have been found at only one or two localities, and are extremely difficult to locate even when a deliberate search is made for them in the exact spots where they were first discovered. Usually they give the impression, quite possibly false, that they have no more than a toehold on their host populations and that they exist close to extinction.’

We addressed this conundrum first in a category 1 (high infestation–low transmission) species, the butterfly *Maculinea arion*, and attributed its rarity to a combination of factors: considerably greater host-ant specificity than had hitherto been realized, plus the need for two sequential hosts to coexist, the first (initial food-plant) sufficiently widely distributed to infest host ant colonies, the second (*Myrmica sabuleti*) in sufficient local abundance (>55% of biotope foraged) to support a closed population of this sedentary species (Thomas, 1980, 1984a,b, 1991, 1995; Thomas et al., 1989, 1998a; Thomas and Wardlaw, 1992; Elmes and Thomas, 1992; Elmes et al., 1994; Hochberg et al., 1992, 1994; Clarke et al., 1997). More generally, Pierce et al. (2002)
considered social parasitism to be an evolutionary dead-end within the Lycaenidae, resulting in such extreme specialization that species were unable to track rapid ecological perturbations. While this is essentially the argument advanced by Thomas (1980, 1984a, 1991) for the decline of *M. arion*, it does not explain why most social parasites were so rare in the first place, including in the ecologically stable tropics (e.g. Hölldobler and Wilson, 1990). But nor did our or co-workers’ arguments concerning *Maculinea* explain the equal or greater rarity of the majority of other species that parasitize one common ant species without the constraint of a second host.

We will argue that even category 3 (low infestation–very low transmission) species may be successful exploiters of their hosts, but in order to succeed they have (co-)evolved such close adaptations to a local host genotype that, in extreme cases, they may be restricted to exploiting it at the level of a single supercolony of ant.

### 4.2 Hypotheses to explain variation in the strength of host speciality in social parasites

We suggest two hypotheses that may help explain variation in host specificity. Both are drawn partly from theory and partly from detailed knowledge of the functional biology of six social parasites species (described in detail in Section 6) and of a wider range of mutualistic myrmecophiles that has been studied in recent years.

**Hypothesis 1**

The deeper a social parasite penetrates towards the most protected and resource-rich niches within an ant society, the closer will it become adapted to or integrated with that society (Thomas and Elmes, 1998).

For this hypothesis we identify five zones (Fig. 17.1), four within the nest of a polygynous ant society, which are protected with increasing ferocity: foraging range/territory (score 1); outer nest/midden areas (score 2); outer nest chambers inhabited by β queens (score 3); main brood chambers (score 4); and inner chambers inhabited by α queens (score 5). Others exist – notably foraging columns which, although outside the nest, are well defended, and niches or chambers within or without nests where trophobionts (domestic aphids, coccids) or fungi are nurtured or seeds are stored – but five will suffice. Except under the most benign ecological conditions, when the cost of fighting outweighs the gain (e.g. high worker : brood ratio, low queen : worker ratio, neither food nor space limiting), polygynous ant societies attack intruding adults (non-kin workers, queens) of their species if they enter nest zones 3–5, often fighting to the death (Winterbottom, 1981; Brian, 1988). Greater tolerance is shown to the larvae of non-kin colonies or other congeneric species, which may be nursed and fed if introduced to brood chambers. However, they are the first to be butchered and fed to the conspecific brood when
**Fig. 17.1.** Ant niches inhabited at different stages of the life cycle by three types of social parasite.
the colony experiences food shortages; further starvation results in the sacrifice of kin eggs, followed by kin larvae from the smallest upwards, to feed the largest of their sibling larvae and ultimately just the workers (Gerrish, 1994; Elmes et al., 2004).

We suggest that any social parasite that depends solely on mimicking ant brood must achieve a closer match even than non-kin ants to its host’s recognition codes, or must mimic some attribute of a high-ranked member of the society, if it is to gain sufficient status to induce direct feeding by workers ahead of their own kin larvae. Unless strong reinforcing cues are involved (e.g. mimicry of adult, especially queen, signals), we find no evidence that the mere acquisition of a host colony’s ‘gestalt’ recognition odour (chemical camouflage sensu Dettner and Liepert, 1994; Vander Meer and Morel, 1998; Lenoir et al., 2002) can deliver competitive supremacy over hungry kin brood; instead, recent studies suggest that the biosynthesis of copious mimetic allomones is involved (Elmes et al., 2004; Schönrogge et al., 2004). We restrict this deduction to the many social parasites, exemplified by M. rebeli (see Section 5.2), that divert substantial amounts of food from ant larvae in order to grow from juveniles to adulthood. Although mouth-to-mouth exchange of regurgitated food or secretions (trophallaxis) is an important part of this feeding, the exchange of small beads of liquid – which is mimicked by many adult social parasites — between the mouths of worker ants to reinforce social acceptance is another matter: this deprives the host colony of negligible food and we have no evidence that it leads to conflict.

An alternative (or additional) strategy evolved by many other social parasites is to combine exceptionally well-armoured cuticles with evasion and stealth. By definition, the latter two methods of infiltration are incompatible with direct feeding by worker ants. The capability of social parasites to deploy armour during different life stages led us to formulate Hypothesis 2.

**Hypothesis 2**

The younger the stage of social parasite that exploits a host ant society, the more likely it will be closely adapted — and hence host-specific — to one host.

Here we divide social parasites into three periods of their lives, listed in the decreasing facility with which they can evolve both armour against attack and secretory organs to communicate with ants: adults of all Orders plus the nymphs of Hemimetabola (score 1); pupae and late instars of Holometabola (score 2); young instars (and eggs) of Holometabola (score 3).

To elaborate, the adults of many social parasites are heavily sclerotized and able to withstand modest ant attacks, enabling them to penetrate colonies of >1 ant species, especially if they move stealthily and acquire a weak camouflage of their host’s gestalt odour. (Free-living adults that emerge from pupae in ant nests may use other devices during their brief escape from the colony, such as rewarding workers with secretions or employing loose sticky wing scales to baffle them; Pierce et al., 2002.) The evolution of sclerotized cuticles appears also to be an adaptable trait in the nymphs of hemimetabolous
insects; yet despite their preponderance among the domesticized mutualists of ants, remarkably few true social parasites are from the hemimetabolous Orders of insect, Myrmecophila cricket species (Wasmann, 1901; Hölldobler, 1947; Akino et al., 1996) being an obvious exception. This defence is not available to the larvae of holometabolous social parasites, whose cuticles remain flexible enough for continuous growth. We divided holometabolous myrmecophiles into two categories of vulnerability: the later instars that are often large enough to develop thick ‘rubbery’ cuticles that withstand nips by ants, though not concerted attacks (Malicky, 1969), and the first instars which, from the ants’ perception, resemble thin-skinned packages of food conveniently located within their nest. Insect eggs, of course, can be heavily armoured, but hatching larvae take 2–3 days to bore out of the thickest-shelled examples, during which they are presumably vulnerable to ant attack (Thomas et al., 1991). We know of no social parasite that oviposits into ant nests which has invested in thick-shelled eggs, although the unusually clumped population structure inherent in cuckoo Maculinea species has led to the evolution of the thickest chorions described for any (including overwintering) species of Lepidoptera, presumably to negate Trichogamma parasitoid above-ground on their initial food-plants (Thomas et al., 1991).

4.3 Ecological consequences of Hypotheses 1 and 2

Selection for greater host specificity \( (H_{sp}) \) due to increased penetration \( (P) \) or exploitation at a younger life stage \( (L_{stage}) \) seem unremarkable concepts in isolation. However, we suggest that each functions independently and that the net level of host specificity found in a myrmecophile will be described by a function of both variables:

\[
H_{sp} = f(P) \cdot f(L_{stage})
\]  

Although the functional dependencies are unknown, to illustrate the use of such an index we assume \( H_{sp} \) to be the simple product of \( P \) and \( L_{stage} \) from here on. Using the arbitrary scores given above to each category in Hypotheses 1 and 2, we obtain a highest value for host specificity of 15 (a social parasitoid that exploits or outcompetes resident \( \alpha \) queens during its earliest instars) and a lowest value of 1 (an adult myrmecophile inhabiting the foraging range of an ant colony). In fact, we know of no myrmecophile that can outcompete \( \alpha \) queens; slave-making ants that kill them are a different matter (Foitzik and Herbers, 2001). However, we predict that a holometabolous species of social parasite living as a young larva in ant brood chambers (\( H_{sp} \) value of 12) will evolve such close adaptation to (especially mimicry of) its host colony that it may be restricted to exploiting its host at a subspecific scale, rendering the parasite effective but rare. On the other hand, robust adult social parasites and perhaps the shallow-penetrating nymphs of Myrmecophilida crickets (\( H_{sp} \) values 3–4), should be able to exploit ants by employing more generalist, less restrictive adaptations, such as acoustic or tactile signalling (Hölldobler, 1947) and acquired ‘camouflage odour’ gained through exposure to the host colony,
that enable them to eat less-valued items in nests but ill-equipped to solicit large quantities of food at the expense of the host’s brood.

We do not expect these hypotheses to cover all variations in host specificity, but hope they may supplement the existing rules explaining patterns in social parasites. The population ecology and host specificity of many commensals and mutualists is known well enough from the field to test formula (1) on low-scoring \((H_{sp} = 1–2)\) myrmecophiles (see Section 6) (Thomas, 1983, 1992a,b; Thomas and Lewington, 1991; Pierce et al., 2002), but only six (out of perhaps 20,000) ant social parasite species have been studied in similar detail, of which five belong to one genus, *Maculinea* butterflies. Moreover, these six systems are not independent of our hypotheses, which were framed with some hindsight of their biology. Nevertheless, the six species encompass three very different types of system, with \(H_{sp}\) scores ranging from 4 to 12 (Fig. 17.1). Since many other social parasites exhibit strong convergent evolution in form towards one or other of these types, we tentatively suggest there may be a similar convergence in function.

In Section 5 we describe case histories of how one or two examples function, inasmuch as is known, in each of the three model systems.

### 5. Case histories of host specificity and the degree of social integration in three social parasite systems

#### 5.1 *Maculinea arion* and *Maculinea teleius* (Lepidoptera, Lycaenidae)

*High-virulence, low-transmission predators of ant brood, which enter host colonies in their final larval instar and mainly inhabit the outer nest chambers*

The biology of these butterflies is similar (see Fig. 17.1) apart from their use of different food-plants and *Myrmica* ant hosts. Both are low-scoring \((H_{sp} = 4–6)\), comparatively unspecialized social parasites with two sequential larval hosts: a specific initial food-plant (*M. arion*: *Thymus* spp. or *Origanum vulgare*; *M. teleius*: *Sanguisorba officinalis*) followed by parasitism of *Myrmica* ants in the final instar. Like all *Maculinea* species, the adults live above ground in mid–late summer and show no interaction with ants after eclosion from pupae in the outer cells of *Myrmica* nests, from which they emerge while the ants are quiescent in the early morning. Van Dyck et al. (2000) and Wynhoff (2001) suggest otherwise, but we find no evidence for ant-mediated oviposition in any *Maculinea* species (Thomas, 1984b, 2002; Thomas and Elmes, 2001), although *M. teleius* and *M. nausithous*, which share *S. officinalis* as a food-plant and often coexist on the same site, oviposit preferentially on different growth forms of *Sanguisorba* that coincide with the optimum ecological niches of their respective ant host species (Thomas, 1984b; Thomas et al., 1989, 2002).

*M. arion* and *M. teleius* eggs are laid between flower buds (Thomas et al., 1991) on which the first three larval instars feed. Each develops quickly for 3 weeks but gains little weight, following a shallow growth trajectory (Elmes et al., 2001). The fourth and final instar inhabits a *Myrmica* ant nest, where it lives for
at least 10 months and acquires 98–99% (M. arion) or 92–93% (M. teleius) of its ultimate biomass without further moults (Thomas and Wardlaw, 1992). Other known Maculinea species show the same striking deviation from Dyar's law of constant insect growth between instars, and consequent loss of allometry between head and body size, a deviation that has evolved independently in Lepidochrysops, another genus of lycaenid social parasites that feeds initially on plants (Elmes et al., 1991a,b, 2001). This is perhaps explained by selection for small size at the time of entry into ant nests, to facilitate initial mimicry of ant larvae and transport by workers, balanced by the development in the (much larger) final instar of mutualist lycaenids – from which these social parasites clearly evolved (Fiedler, 1998; Pierce et al., 2002) – of high densities of myrmecophilous glands and, perhaps crucially, of cuticles about 20 times thicker than in typical non-myrmecophilous lepidopteran larvae (Malicky 1969; Elmes et al., 2001).

After the third and final moult, the 1–2 mg (M. arion) caterpillar remains on its food-plant until about 18.00 hours, when it drops 2–3 cm to the ground and awaits discovery by an ant. This places it in the optimum foraging niche of all Myrmica species at their time of peak foraging, enhancing its chances of discovery by a Myrmica worker rather than by those of other genera by >200-fold (Thomas, 2002). Early reports that M. arion (Frohawk, 1924) and M. teleius (Schroth and Maschwitz, 1984) caterpillars actively seek host ant nests before adoption derive from experimental artefacts (Thomas, 1984a,b, 2002; Fiedler, 1990); instead, the larvae await discovery by a Myrmica worker within 1–2 cm of their food-plant. The classic (Frohawk, 1924; Purefoy, 1953) hour-long adoption interaction between M. arion and Myrmica then ensues, when the caterpillar’s dorsal nectary organ (DNO) and secretory pores are constantly ‘milked’ by the worker and the caterpillar perhaps acquires some of the ant’s gestalt odour (Thomas, 2002). Eventually, the caterpillar rears up, probably mimicking a Myrmica larva (Cottrell, 1984), which causes the Myrmica worker to carry it into the ant nest and place it among the brood. Adoption of M. teleius appears identical (Thomas, 1984b; Fiedler, 1990).

M. arion caterpillars quickly leave the brood to spin a silk pad on the roof of an outer chamber, where they rest for most of the next 10 months. In form, they possess the typical flattened body of the final instar of a mutualistic lycaenid, which conceals the mouth and other vulnerable parts (Fig. 17.2a). Most other adaptations of mutualists are recognizable, apart from tentacle organs that agitate ants, but modified for social parasitism. Thus the cuticle of M. arion is even thicker than that of a typical lycaenid; the churring sounds produced by all Maculinea species differ greatly from those of typical lycaenids and mimic the adult stridulations of the genus Myrmica, but not any particular Myrmica species (De Vries et al., 1993); and the secretions, which are abundant, coat the body in a cocktail of hydrocarbons that mimic the recognition signals of Myrmica (K. Schönrogge, E. Napper, G.W. Elmes, J.A. Pickett and J. A. Thomas, unpublished).

M. arion and M. teleius are obligate predators of ant brood that rely much on armour, evasion and stealth to exploit Myrmica colonies. M. arion feeds
Specializations and Host Associations of Social Parasites of Ants

a. PREDACIOUS SPECIES (e.g. *M. arion*)
   CUCKOO SPECIES (e.g. *M. rebeli*)

b. INEFFICIENT
   1 butterfly per 250 ants (laboratory)
   1.2 butterflies per ant nest (field)
   EFFICIENT
   1 butterfly per 50 ants (laboratory)
   5.6 butterflies per ant nest (field)

c. SCRAMBLE COMPETITION
   Efficent
   1 butterfly per 50 ants (laboratory)
   5.6 butterflies per ant nest (field)
   CONTEST COMPETITION

   % Surviving
   Caterpillars adopted per nest
   Caterpillars per nest
   Weeks

   d. Erratic 1-year growth
   e. Destroys ant colony
   f. 3–6.5 higher survival with host *Myrmica*
   g. Minimum co-existence with host ants for population to persist

   Model: high (55%)
   Field: % egg population in host ant’s range

   No. of sites
   Minimum predicted by model

   h. Small/erratic populations
   i. Host-specificity

   can use host ant populations widely across Europe

   large/stable populations

   adapted to local host ant population in Europe:
   restricted range
   local speciation?

Fig. 17.2. A comparison of the traits, costs and benefits in two systems of social parasitism – predatory and cuckoo feeding – within the genus *Maculinea.*
erratically, gliding slowly to the brood chamber, then briefly ‘binge feeding’ on large larvae before returning to its pad where it may rest for up to 10 days digesting the meal. *Myrmica* colonies are small compared to those of many ants, but caterpillars use this resource in the most efficient way possible for a predator of larvae (Thomas and Wardlaw, 1992). By eating the largest available prey, they initially kill only those larvae that will soon pupate and be lost as food. At the same time, the fixed number of larvae in the second (overwintering) cohort of *Myrmica* brood is left to grow larger before it is killed. When this occurs, large individuals are again selected, leaving small ones to grow on. With the range of colony sizes available on a typical site, Thomas and Wardlaw (1992) calculated that this increased the carrying capacity of nests by 124%, although for 2 weeks after adoption it incurs a cost of increased mortality in nests that contain queen ants, due to the probability of contamination by gyne pheromones from the largest larvae, while the caterpillars grow from their mean adoption weight of 1.3 mg to 8 mg (Thomas and Wardlaw, 1990). It is perhaps to reduce this vulnerable period that *M. teleius*, for which no queen effect is reported (E. Figurny, 2000, personal communication), enters ant nests at three-times the size (mean weight 4.3 mg) of any other *Maculinea* species.

*M. arion* also gains an estimated 31% ergonomic advantage by refraining to feed for several weeks after its host breaks hibernation in spring, during which the caterpillars lose about 6% in weight while their food supply (ant larvae) grows by 27% (Thomas and Wardlaw, 1992). An ability to starve or fast during normal growth periods appears to be a third ergonomic adaptation. Large caterpillars, which exhaust their food supply in spring, exert such low attraction over the broodless workers that the colony frequently deserts, leaving the social parasite behind. In due course, an offshoot of this polydomous ant genus colonizes the vacant nest, importing a fresh supply of ant larvae. Thomas and Wardlaw (1992) estimated that this occurs in 80% of the nests that successfully produce a *M. arion* adult. Nevertheless, overcrowding is a major cause of mortality in *M. arion*, which experiences steep scramble competition, generally resulting in 100% mortality when >4 larvae are adopted into a single *Myrmica* nest (see Fig. 17.2C, taken from Thomas and Wardlaw, 1992).

Before our studies it was believed that *M. arion* was equally successful as a parasite of any *Myrmica* species, and some suggested that other ant genera, including *Lasius*, were secondary hosts (e.g. Ford, 1945; Hinton, 1951). We found that although oviposition was indiscriminate and caterpillars were adopted with equal facility into any of up to five *Myrmica* species that foraged under the initial food-plant, the mean survival of *M. arion* in the field was 6.4 times higher in colonies of *M. sabuleti* than with any other *Myrmica* species (Fig. 17.3; Thomas, 1977, 1980, 2002; Thomas et al., 1989, 1998a; Thomas and Elmes, 1998), perhaps because they secrete species-specific mimetic allomones while invading the brood chambers to feed (see *M. rebeli*). Similarly, *M. teleius* survival was 2.9 times higher with *M. scabrinodis* (which quickly kills *M. arion*) than with any other *Myrmica* species that adopted it in the field (Fig. 17.3; Thomas et al., 1989; Thomas and Elmes, 1998; Elmes et al., 1998). Models based on 6-year life tables and natality measurements predict that a
Fig. 17.3. Host specificity in five species of *Maculinea* butterfly, with data for the cuckoo species *M. alcon* presented for populations from three regions of Europe. Data are shown as the proportion of individuals surviving (total = 100) in each of six ant species that commonly adopt *Maculinea* larvae (from Thomas et al., 1989; Thomas and Elmes, 1998; unpublished results).
population of *M. arion* species will persist (λ > 1) only if >55% of the larval population is adopted by *M. sabuleti*, and declines rapidly to extinction if other (secondary) host species predominate (Fig. 17.2G; Thomas, 1991; Thomas et al., 1998a): field data from across Europe support this prediction (Fig. 17.2G; Thomas, 1995, 1999; Thomas and Elmes, 1998; Thomas et al., 1998a). In other words, although individual *M. arion* occasionally survive with ‘non-host’ *Myrmica* species, it is species-specific at the population level.

There is no evidence, however, of subspecific adaptation by predatory *Maculinea* species. On the contrary, following extinction in the UK and the Netherlands, *M. arion* and *M. teleius* have respectively been re-established using donor populations from Sweden and Poland (Thomas, 1995; Wynhoff, 2001). Moreover, observed population dynamic interactions between Swedish *M. arion* and UK *M. sabuleti* colonies on six sites have closely followed model predictions of annual fluctuations and equilibrium levels for up to 22 generations, despite parameterization from interactions with old UK populations of *M. arion* (Thomas, 1995, 1999, unpublished results). This suggests that neither local adaptation by the social parasite, nor local resistance by the host, nor a coevolutionary arms-race between both partners have evolved to any significant extent in these predacious *Maculinea* systems.

### 5.2 *Maculinea rebeli* and *Maculinea alcon* (Lepidoptera, Lycaenidae)

*High-virulence, low-transmission cuckoo-feeders in ant brood chambers, which enter host colonies in their last larval instar*

Like the other *Maculinea* (see Fig. 17.1), these close relatives oviposit on specific food-plants (*M. rebeli*: xerophytic *Gentiana* species, mainly *G. cruciata*; *M. alcon*: wet grass or heathland *Gentiana*, mainly *G. pneumonanthe*), but the lifestyle diverges radically after abandoning their food-plant. Caterpillars are again retrieved by any *Myrmica* species to encounter them beneath gentians, but are picked up and carried into the ant’s nest within 1–2 s of being found, without the elaborate interactions of *M. arion* or *M. teleius* (Elmes et al., 1991a). Deep inside the nest they inhabit brood chambers and become intimately integrated with the host society, receiving frequent grooming and, on begging (Fig. 17.2A), being fed by the nurse ants with trophic eggs, solid food and by trophallaxis (cuckoo feeding). For a month caterpillars may also eat some ant brood, but have little direct impact on numbers: thereafter, owing to *Myrmica* nurses’ segregation of all brood by size, the >10 mg caterpillars are kept apart from the brood and fed entirely by adult ants (Elmes et al., 1991a,b). As they grow, their morphological resemblance to a predatory or phytophagous lycaenid diminishes, for they develop thinner-skinned cylindrical bodies (Fig. 17.2A) with very high densities of secretory pores (Malicky, 1969).

Two atypical populations apart (Als et al., 2001, 2002), both cuckoo species exhibit much higher levels of host specificity at the individual and population level than their predacious congener (Figs 17.2F, 17.3; Thomas and Elmes, 1998). Working mainly with *M. rebeli* from the Pyrenees and
southern Alps, where *Myrmica schencki* is host (Thomas *et al*., 1989), we have come to understand some of the processes whereby this system functions.

On leaving its gentian, *M. rebeli* secretes a simple mixture of surface hydrocarbons that weakly mimic those of *Myrmica* (Fig. 17.4A; Akino *et al*., 1999; Elmes *et al*., 2002). Its profile is closest to *M. schencki*, and vice versa (Fig. 17.4B), but is sufficiently similar to all *Myrmica* species for the caterpillar to be quickly retrieved by the first worker to touch it (Akino *et al*., 1999). At this

**Fig. 17.4.** Chemical mimicry of *Myrmica schencki* by *Maculinea rebeli* larvae. A Hydrocarbon profiles of *M. rebeli* after leaving food-plant before exposure to ant; after 6 days with *M. rebeli*; and of the model, *M. schencki* larvae. B Similarity between hydrocarbon profiles of *M. rebeli* and five *Myrmica* species that commonly adopt larvae, including its natural host, *M. schencki* (from Akino *et al*., 1999).
stage we doubt whether it is possible for a *Maculinea* larva to evolve a species-specific retrieval cue, since a *Myrmica* forager will gently retrieve the larva of any congener that is artificially placed in its territory (Gerrish, 1994).

On reaching the domain of the nurse ants, greater discrimination occurs. About 90% of caterpillars survive the first 48 h in the brood chambers of their closest model, *Myrmica schencki*, but only 45–60% survive on average with other ‘non-host’ *Myrmica* species (Fig. 17.5; Schönrogge et al., 2004). Thereafter, individuals that pass this initial period of integration usually survive well with any *Myrmica* species, so long as the colony remains well-fed and benign. But if, as occurs often in the field (but seldom in the laboratory), the colony experiences food shortage or other stress, we find that *M. rebeli* continues to survive well with *M. schencki*, at the expense of the ant brood and workers, whereas its caterpillars are cut up and fed to the ant larvae in colonies of ‘non-host’ *Myrmica* species (Elmes et al., 2004; Fig. 17.5).

How is such discrimination achieved? We knew already that after 6 days with *M. schencki*, *M. rebeli* possesses a more complex profile of surface hydrocarbons that closely matches its host (Fig. 17.6; Akino et al., 1999). We originally assumed that this resulted from the absorption by the caterpillar of background odours from the nest (chemical camouflage). This now seems naive, for if *M. rebeli* can absorb the odour of one *Myrmica* colony, it should be equally successful at parasitizing any species after the initial period of integration.

It is now clear that *M. rebeli* caterpillars synthesize additional hydrocarbons after adoption that improve and amplify their mimicry of *M. schencki* and are

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**Fig. 17.5.** Survival of *M. rebeli* larvae in four phases during the first 3 months after leaving its initial food-plant, when coexisting with three species of *Myrmica*: *M. schencki* (natural host, solid line); *M. sabuleti* (dashed line); *M. rubra* (dotted line) (from Elmes et al., 1991a, 2004; Schönrogge et al., 2004).
Fig. 17.6. The order within the hierarchy in *Myrmica schencki* societies in which Maculinea rebeli larvae are retrieved after perturbation, 2 h and 6 days after entry to ant nest (from Thomas et al., 1998b; unpublished results).

thought to encompass cues from higher castes, possibly queens (Schönrogge et al., 2004). Whatever the exact model, the effect is to elevate the status of the parasite in *M. schencki*’s hierarchy, so much so that, whereas *M. rebeli* is the last item to be retrieved by agitated nurses if a nest is disturbed within a few hours of the caterpillar’s retrieval, the same caterpillars – although no larger than medium-sized ant brood – are among the first items to be rescued, alongside pupae and well ahead of large and small *M. schencki* larvae, if the disturbance is repeated 6 days later (Fig. 17.6; Thomas et al., 1998b). *M. rebeli* behaves differently in the nests of non-host *Myrmica* species: caterpillars switch off their ill-matching secretions and rely solely on absorbing the ants’ background odour (Schönrogge et al., 2004). This presumably results in a weak signal because their social status remains low, so much so that when the disturbance bioassay was repeated using apparently well-integrated 6-day Spanish *M. rebeli* in *M. sabuleti* nests, its caterpillars were the last items to be
rescued (if at all) after perturbation (J.A. Thomas et al., unpublished). It is not surprising, therefore, that they are first to be sacrificed when a non-host species is short of food (Fig. 17.5; Elmes et al., 2004). Indeed, the hungry parasite may experience a double jeopardy because – presumably to win attention – it switches on its schencki-like secretions when starving, at exactly the time when the non-host Myrmica workers are most xenophobic (Schönrogge et al., 2004; Elmes et al., 2004).

We can now compare some costs and benefits of the predacious and cuckoo systems in Maculinea social parasites (Fig. 17.2). At first sight, the cuckoo species enjoy most benefits. By inducing direct feeding by worker ants (Fig. 17.2A), they jump the food chain compared with brood predators, increasing the capacity of a standard-sized Myrmica colony to support these 120–150 mg butterflies by four to five-fold (Fig. 17.2B; Elmes et al., 1991a,b; Thomas and Wardlaw, 1992). Moreover, when caterpillars are overcrowded inside nests (a common event in the field; Thomas et al., 1998a), the predacious species experience severe scramble competition, often resulting in 100% mortality despite their ability to draw a neighbouring colony into vacant nests (Fig. 17.2C; Thomas and Wardlaw, 1992). Cuckoo species, on the other hand, merely experience contest competition at high densities, because the nurse ants select the maximum number of individuals they can feed, which survive at the expense of the others (Fig. 17.2C; Thomas et al., 1993). Moreover, both M. rebeli (Thomas et al., 1998b) and M. alcon (Schönrogge et al., 2000; Als et al.,

Fig. 17.7. Polymorphic growth (1- and 2-year development) by larvae of Maculinea rebeli in Myrmica schencki ant societies (from Thomas et al., 1998b).
2002) have evolved a remarkable fixed polymorphism in larval growth that further smoothes density-dependent starvation: one-third of caterpillars grow quickly and pupate after 10 months in the ant nest, while two-thirds of individuals feed slowly, taking 22 months before pupation (Figs 17.2D, 17.7).

Moving from individuals to populations, the predatory species have an apparent benefit of higher (but not very high) survival in non-host Myrmica species (Fig. 17.2F), which theoretically provide refuges if local conditions become catastrophic for the host species (Thomas, 1999). Against this, in both theory and practice, cuckoo species can inhabit more sites within a region because, due to their efficient exploitation of and lower damage to hosts (Fig. 17.2F), they can persist in suboptimal patches where host densities are very low (Fig. 17.2G; Hochberg et al., 1992, 1994; Clarke et al., 1998; Elmes et al., 1996; Thomas and Elmes, 1998; Thomas et al., 1998b). Furthermore, the over-compensating effect of density-dependent ‘scramble’ mortalities means that populations of predatory species are not only smaller but also more erratic than those of cuckoo species, and hence more prone to extinction (Fig. 17.2H; Thomas et al., 1998b).

The main cost of the cuckoo lifestyle is that increased specialization restricts each social parasite to a narrower, regional part of its host’s range. We have seen in M. arion and M. teleius that any population of their respective host species seems suitable, at least across western Europe. However, local adaptations are apparent in M. rebeli and M. alcon. For example, M. rebeli from the Pyrenees is more (100%) host-specific to M. schencki than those from the Hautes-Alpes (J.A. Thomas et al., unpublished), and host shifts occur over greater distances. Thus M. rebeli exploits Myrmica sabuleti from the north Alps eastwards (Meyer-Hozak, 2000; Steiner et al., 2003), an ant with which it experiences 100% mortality in the Pyrenees, and in the central High Alps, M. rebeli apparently exploits Myrmica sulcinodis (Steiner et al., 2003). Similar host shifts are found in M. alcon (Elmes et al., 1994): in south and east Europe it exclusively parasitizes Myrmica scabrinodis, but from the Pays Bas northwards it exploits M. ruginodis (Belgium, Netherlands, Finland) or M. rubra (northern Finland, Sweden). Some of these represent substantial evolutionary shifts because – as with pathogens, true parasites and parasitoids – they represent not only a change of food but also of the social parasite’s main enemy and environment. In our examples, Myrmica schencki has the most different hydrocarbon profile from M. sabuleti of any Myrmica species studied (Elmes et al., 2002), and kills Maculinea rebeli from north-east Europe as quickly as M. sabuleti kills M. rebeli from south-west Europe (J.A. Thomas et al., in preparation). Similarly, M. scabrinodis is chemically and behaviourally very different from M. ruginodis and M. rubra (which are rather similar) (Elmes et al., 2002), and those M. alcon populations that exploit M. scabrinodis seem to be wholly incompatible with the latter two species, and vice versa for northern M. alcon (Elmes et al., 1994; Thomas and Elmes, 1998; Als et al., 2001, 2002). These major functional types, each restricted to a different region of Europe, may be well down the path towards cryptic speciation.

Host-switching across M. alcon’s range has been studied in Denmark, straddling the boundaries of the ruginodis and rubra populations (Gadeberg
and Boomsma, 1997; Als et al., 2001, 2002). Here, Als et al (2001, 2002) found isolated populations that were specialist exploiters of either *M. rubra* or *M. ruginodis*, and also two more generalist populations that survived with – but were less well adapted to – both ants on the same site (as elsewhere in northern Europe, *M. scabrinodis* remained unsuitable on them). Early genetic analyses of Danish *M. alcon* showed considerable variation between populations but no clear-cut pattern that matched host-specificity (Gadeberg and Boomsma, 1997). It is too early to determine whether the two generalist populations are recent hybrids between *rubra* - and *ruginodis*-exploiting populations, surviving briefly in evolutionary time in optimal habitat (which results in less-stressed colonies) for both host ants, or whether they evolved from a ‘pure’ *rubra* - or *ruginodis* - exploiting population. We suspect the former due to the absence of other examples of generalist cuckoo populations apart from on the boundary of this comparatively minor host shift. On the other hand, Nash et al. (2002) report patterns of chemical mimicry in *M. alcon* profiles that suggest local adaptation to individual host populations in Denmark, as well as variation in host ant profiles compatible with coevolutionary arms-races at the population scale. Further (especially molecular genetic) research is clearly needed to elucidate the evolution of host specificity in *M. alcon* and *M. rebeli*, but on current evidence we conclude that their specializations constrain regional populations of each butterfly to regional populations of a host.

5.3 Microdon mutabilis and Microdon myrmicae (Diptera, Syrphidae)

*High-infestation, low-transmission predators in ant brood chambers, which enter host colonies as eggs*

The approximately 350 described species of *Microdon* syrphid resemble most social parasites in having no larval resource other than social insects. *M. mutabilis* adults live a few days above ground, ovipositing in the outer edges of ant nests. The larvae migrate to inner brood chambers, where they live as predators for 2 years before pupating in the outer chambers (Fig. 17.1; Donisthorpe, 1927; Schönrogge et al., 2000).

We studied the ecology of *M. mutabilis*, seeking to understand why this *Red Data Book* species is so rare – inhabiting the same very localized, typically <0.1 ha sites for many generations – when its listed hosts include several of the most ubiquitous and abundant ants from three subfamilies in Europe (e.g. *Formica fusca*, *Lasius niger*, *Myrmica ruginodis*).

We found in the UK that *M. mutabilis* exploits one of two species, *Formica lemani* or *Myrmica scabrinodis* (another ubiquitous ant not previously listed as a host), but exclusively one host species per population. Knowledge of *Maculinea* suggested that a larval parasite of such different subfamilies would require specific adaptations that were unlikely to coexist in one species, and we duly found morphological differences in the young stages that unequivocally established the existence of two sibling species: *Microdon mutabilis* parasitizing *F. lemani* and the new *Microdon myrmicae* with *Myrmica scabrinodis* (Schönrogge et al., 2002).
This, however, failed to explain the extreme local distribution of either parasite in comparison to its host.

A chance remark by *Microdon* specialist Boyd Barr – that he successfully reared *M. mutabilis* only when eggs were introduced to the same colony from which their mother had emerged – led us to test the hypothesis that this social parasite had evolved adaptations to local genotypes of its host. Experiments supported this (Fig. 17.8), confirming 100% survival when eggs were introduced to the natal colony or an adjoining one, but usually 100% mortality in *F. lemani* colonies from only >1–2 km away, even though all these ‘distant’ nests were themselves infested with *M. mutabilis* whose eggs, in turn, were killed in the reciprocal tests (Elmes *et al*., 1999). This extreme host specificity functioned only through the maternal line. To eliminate the remote possibility of an artefact, a redesigned experiment was repeated by Karsten Schönrogge twice, including in another locality: the result was the same except that mortality in most ‘distant’ nests was 65–80%.

We only partly understand how this remarkable system functions (and our detailed results have yet to be ratified by peer review). We know, nevertheless, that the same individual *F. lemani* colonies (about one-third of the total) within a site are infested for generation after generation by *M. mutabilis*. We know also that these successive infestations are by the same family lines: although females fly quite often, their dispersal is so low in the field that an individual seldom departs more than 1–2 m from her natal nest, to which she returns to oviposit, while marked males patrol up to 10–30 m away (K. Schönrogge *et al*., in preparation). This is consistent with a template for

![Fig. 17.8. Extreme host specificity in egg survival by *Microdon mutabilis* in colonies of its host ant, *Formica lemani*, at different distances from the natal nest from which the mother social parasite emerged (from Elmes *et al*., 1999).](image-url)
selection for mimicry (or other adaptation) in *M. mutabilis* at the population or supercolony scale of its host. Less easily explained is why, given the substantial predation of host larvae by *M. mutabilis*, should any vulnerable genotype not be replaced by more resistant colonies of *F. lemani* long before local adaptation can evolve. We envisage – and have some evidence of – two processes resulting from the social manipulation of host colonies by *M. mutabilis*: one mechanical, one genetic.

As with *M. arion*, an inevitable consequence of ‘cropping’ one colony of a polydomous ant species in high-density, optimum habitat is that adjoining colonies bud to occupy the depleted nest site. With *F. lemani*, this might result in mixed ‘colonies’ within the same nest, in which case these heterogeneous colonies should be more tolerant of aliens especially if, due to the depletion of ant brood, the workers can easily obtain food for the survivors (Fig. 17.5). A further adaptation is required if the social parasite is to (co-)evolve very locally with one subset, or with a particular subspecific mixture, of its host genotype. Unlike *M. arion* caterpillars, which select the largest available brood, *M. mutabilis* (K. Schönrogge et al., in preparation) and at least one congener (Duffield, 1981) prey exclusively on small ant larvae. In theory, this is the least efficient way for a predacious social parasite to exploit its host (Thomas and Wardlaw, 1992), and perhaps explains why *M. mutabilis* and *M. myrmicae* larvae take 2 years to pupation (Schönrogge et al., 2000). On the other hand, the selective cropping of small larvae from an ant colony results in a high probability that the individuals that escape will switch in development to become gyne (queen-ant) females, due to the surplus food available from a worker population geared to feed many mouths (Brian, 1968, 1988). And indeed, we found twice as many queen pupae (but many fewer worker pupae) in colonies of *F. lemani* infested by *M. mutabilis* compared with similar-sized uninfested ones (K. Schönrogge et al., in preparation). In other words, however complex the local genotype to which it is adapted may be, *M. mutabilis* has evolved a mechanism for maintaining – even exporting – rather than eliminating it. This, we believe, is a *sine qua non* for any social parasite that evolves specialization at a sub-metapopulation scale of its host.

### 6. Testing and calibrating the two host-specificity hypotheses

Our six case-histories, representing three systems for exploiting ants found commonly among social parasites, show variations in host specificity that contributed to the two hypotheses described in Section 4.2. Before testing each idea against the wider literature, we recognize that published host lists for other social parasites have almost certainly accumulated similar confusions and errors to the many that existed for *Maculinea* and *Microdon mutabilis* before detailed ecological studies began (see Table 17.1 for summary of types of error, and Thomas et al., 1989, for a fuller critique). If so, host specificity will often be underestimated in other species, especially those that exhibit extreme (subspecific) host specificity at the regional scale but also host shifts across their
global ranges: as Schönrogge et al. (2002) found with Microdon, this can result in a list of multiple hosts being published for certain of social parasites, giving the false impression that the morpho-species is a generalist.

With that proviso, in Fig. 17.9 we summarize the published specialization of >150 comparatively well-studied species of myrmecophile on a graph whose axes represent the two variables in our hypotheses. Current data are too crude to quantify the strength of a species’ interaction with ants beyond placing it in one of the 12 classes ($H_{sp}$ scores: minimum 1; maximum 12) that result from each possible combination of our four categories of colony penetration (x axis) and three categories of life cycle (y axis). For clarity, we have shifted the location of certain species within each ‘box’ to generate smoother patterns of host specificity, which we group into five classes ranging from myrmecophiles that interact with >1 subfamilies of ant to those that specialize on a local population or supercolony.

We obtained patterns consistent with both hypotheses across a spectrum of myrmecophiles, from commensals to inquilines. At one extreme are the many free-living commensals and mutualists that typically penetrate ant colonies (if at all) only to pupate in the outer edges: these typically interact with >1 subfamilies of ant. The mutualist Plebejus argus, on the other hand, inhabits the outer cells of nests from its 1st larval instar onwards, but does not exploit colony resources: its modest specializations restrict it to interactions with a single ant genus (black species of Lasius) (Jordano et al., 1992; Jordano and Thomas, 1992). At the other extreme, we have the microgyne queens of M. rubra and Microdon mutabilis, whose regional or individual populations appear to be adapted to very local populations, possibly individual supercolonies of a single host species. In between we find intermediate levels of host-specificity among species of social parasite whose interactions are less intense. For the present, we have located the 59 ant–ant inquilines listed by Hölldobler and Wilson (1990) as being specific to a single species of ant towards the most specific corner of their ‘box’; we predict that most of these will fall into higher categories of host specialization once their ecology is better known.

Atemeles pubicollis, the first and best-studied of all social parasites, presented an obstacle to our hypotheses. The classic work of W.M. Wheeler, Horace Donisthorpe, K. Hölldobler, Bert Hölldobler and others demonstrates that this staphylinid beetle sequentially exploits two subfamilies, Formica polystena and various species of Myrmica, during a life that is spent almost entirely with ants and includes trophallactic feeding of larvae inside brood chambers (Hölldobler and Wilson, 1990). We suspect that it is the exception that may help prove the rule. We suggest that A. pubicollis scarcely qualifies as a social parasite while it coexists with Myrmica, for this occurs only in the well-sclerotized adult stage which uses Myrmica nests merely as overwintering quarters. Atemeles undoubtedly possesses several attributes that enable it to live with Myrmica: stealthy movement, a gland that secretes generalist appeasement allomones, and the ability to absorb a colony’s gestalt odour and to indulge in trophalaxic bonding with workers. However, it poses no significant threat to Myrmica resources and scores only 2–3 in this period in our rough $H_{sp}$ guide, comparable to other adult myrmecophiles that coexist with ants from different subfamilies (Fig. 17.9). Its ‘score’ rises steeply...
Increasing host specificity

Life-stage

- Adult/hemi-metabolous nymphs
- Pupa
- Late instars
- 1st instar & egg

No host specificity

Increased host penetration

Increasing specificity

Specificity of ant interaction

- Sub-family
- Genus
- Species
- Local region
- Sub-species
- Population
- Super-colony

Maximum host specificity

- Nest brood chambers
- Outer nest
- Middens etc
- Foraging range
- Territory

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Specializations and Host Associations of Social Parasites of Ants

Fig. 17.9 opposite. A provisional attempt to classify the host specificity of >150 myrmecophiles with comparatively well-described ant associations according to the twin hypotheses that increased host specificity results from increased penetration of ant societies and by interacting with ants in early stages of the life cycle (homometabolous Orders only). Species that interact with ants in different ways at different life stages are entered twice under each of the relevant life-history stages. Specialist myrmecophiles that join ant trails or attack ant-defended domestic herds (aphids, coccids etc) outside the nest are omitted. Black symbols = social parasites (including ant–ant inquilines); open symbols = mutualists, commensals.


Key to species:
1. Telectomyrex schneideri
2. Microdon mutabilis
3. Myrmica microrubra
3a. Myrmica hirsuta
4. M. karawevi
5. Atemeles pubicollis (juvenile)
6. Lomechusa strumosa
7. Maculinea rebeli
8. M. alcon
9. Microdon myrmicae
10. Maculinea nausithous
11. Spindasis takanonis
12. Dentarda dontata
13. D. markeli
14. D. hagens
15. D. pygmaea
16. Thestor dicksoni
17. Cremastocheilus spp (juveniles)
18. Maculinea arion
19. M. teleius
20. M. arionides
21. Allotinus apries
22. Niphanda fusca
23–30. eight Lepidochrysops spp
32. Cremastocheilus spp (adults)
33. ten temporary ant–ant social parasite spp (Hölldobler and Wilson. 1990, pp. 438–444)
34. Hetaerius ferrugineus
35. 59 spp workerless ant inquiline spp (Hölldobler and Wilson, 1990, pp. 438–444)
36. Plebejus argus
37. P. pylaon
38. Ialmenus evagoras
39. Claviger testaceous
40. Myrmecaphobius excava
collis
41–100 species lycaenid butterfly mutualists/commensals that interact with >1 subfamilies ant (Thomas, 1992a; Thomas and Lewington, 1991; Pierce et al., 2002).
42. Thecla betulae, Quercusia quecus, Calliphrys rubi, Polyommatus icarus, Lysandra coridon, L. bellargus
43. Atelura formicarra
44. Atemeles pubicollis (adult)
45. Myrmecophila acervorum.

to 12 for the vulnerable immature period, when adult females leave their hibernation nests to oviposit in Formica colonies, and when the Atemeles larvae, like cuckoo Maculinea, outcompete the ant larvae for worker attention within ant brood chambers. During this stage, A. pubicollis shows closer, albeit imperfect, agreement with our hypotheses in being restricted to one host species, F. polyctena, but not, on current knowledge, to local genotypes of its host. We may be guilty of data-fitting in our treatment of Atemeles in that we plot it twice, once representing its phase as a roving adult generalist, exploiting ants for protection and minor amounts of food, and again as a specialist immature social parasite adapted to grow from egg to pupa by tapping the food supply of a single host species (Fig. 17.9).

We tentatively conclude that both hypotheses apply independently across a range of myrmecophiles. While each hypothesis is unremarkable in itself, in certain combinations they may entail such extreme specialization for a social parasite to function successfully that it must evolve adaptations to its host at subspecific, population, or even supercolony scales. This inevitably places severe geographical constraints on the deepest-penetrating inquilines, explaining why most are exceedingly localized or rare. These extreme life-forms may also evolve frequently but be subject to frequent extinctions.
Table 17.1. Nine types of error or causes of confusion encountered in determining host specificity at the scale of individuals or populations during studies of *Maculinea* or *Microdon* species (from Thomas *et al.*, 1989, and subsequent data). Prior to our studies, species in both groups were thought to exploit ants in different subfamilies or genera.

<table>
<thead>
<tr>
<th>Type or error</th>
<th>Example</th>
<th>Species affected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Speculation</td>
<td><em>Lasius flavus</em> is secondary host of <em>M. arion</em> (Ford, 1945; Hinton, 1951)</td>
<td>All social parasites</td>
</tr>
<tr>
<td>Misidentification of ant</td>
<td>On <em>Maculinea</em> hosts: ‘La fourmi que j’ai dénominée Tetramorium caespitum est en réalité la Tapinoma erraticum et celle que je supposais être une Myrmica se trouve être la Tetramorium caespitum’ (Powell, 1918)</td>
<td>All non-ant social parasites</td>
</tr>
<tr>
<td>by specialists in taxon of</td>
<td></td>
<td></td>
</tr>
<tr>
<td>social parasite</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Revision of ant taxonomy after</td>
<td><em>Formica fusca</em> listed for <em>Microdon mutabilis</em> before <em>F. lemani</em> was</td>
<td>All hosts, especially <em>Myrmica, Lasius, Formica</em> in</td>
</tr>
<tr>
<td>host name published, especially</td>
<td>recognized (Donisthorpe, 1927). <em>Myrmica sabuleti/M. scabrinodis</em> or</td>
<td>Europe</td>
</tr>
<tr>
<td>sibling ant spp.</td>
<td><em>M. rubra/M. ruginodis/M. laevinodis</em> used as synonyms</td>
<td></td>
</tr>
<tr>
<td>Cryptic speciation of social</td>
<td><em>Microdon mutabilis/myrmicae; Maculinea alcon/rebeli</em> (Schönrogge <em>et al.</em>, 2002)</td>
<td>Especially well-integrated social parasites</td>
</tr>
<tr>
<td>parasite ‘species’ each with</td>
<td></td>
<td></td>
</tr>
<tr>
<td>different host</td>
<td></td>
<td></td>
</tr>
<tr>
<td>‘Adoption’ by non-host ants</td>
<td>Young <em>Maculinea</em> larvae retrieved into the nests by any <em>Myrmica</em> species but survive only with one species: sampling nests in late autumn reveals <em>Maculinea</em> larvae with all <em>Myrmica</em> species. Also, social parasites taken as prey sometimes mistaken for adoption.</td>
<td><em>Maculinea</em></td>
</tr>
<tr>
<td>Occasional survival in benign</td>
<td>Occasional individuals survive in ‘non-host’ nests but too rarely to</td>
<td>All social parasites</td>
</tr>
<tr>
<td>colonies</td>
<td>support a population</td>
<td></td>
</tr>
<tr>
<td>Laboratory artefacts</td>
<td>Pampered laboratory ant colonies are typically in such a benign social</td>
<td>All social parasites (e.g. <em>M. rebeli</em>, see Fig. 17.6).</td>
</tr>
<tr>
<td></td>
<td>state that any intruder is tolerated</td>
<td></td>
</tr>
<tr>
<td>Host species later replaced by</td>
<td>The damage to host colonies can be so great, especially prior to pupation,</td>
<td>Especially predatory social parasites</td>
</tr>
<tr>
<td>other ants</td>
<td>that original host ant deserts, leaving the pupa in an abandoned nest that is sometimes colonized by a non-host ant species</td>
<td></td>
</tr>
<tr>
<td>Host shifts across species’</td>
<td><em>M. rebeli</em> and <em>M. alcon</em> each parasitize a total of three different host species, each in a different parts of Europe. <em>Predatory Maculinea</em> also parasitize different <em>Myrmica</em> species in Japan than in Europe</td>
<td><em>Maculinea; Microdon</em> possibly all social parasites</td>
</tr>
</tbody>
</table>
7. Questions for the future

We envisage three areas of research to test or extend the following ideas.

7.1 Case studies of functional ecology and host specificity in additional systems of social parasite

To date, the functional and population ecology of just six out of perhaps 10,000–20,000 species of social parasite has been studied in sufficient detail to test our hypotheses with confidence. Similar research is urgently required for different types of social parasite, especially those that apparently possess low infestation–high transmission and low infestation–low transmission population dynamics. Owing to powerful convergent evolution, we suspect that few radically different strategies for social parasitism exist beyond β queens that cheat, slave-making systems, specialist plunderers of ant middens or food-sources (domestic aphids, coccids, fungi, seeds etc) or the three systems described here. It is also important that the ecological studies of lycaenid (Lepidoptera) social parasites are balanced by more of other Orders, focusing especially on the many species whose basic life-history traits are already described, but for which no detailed account exists of host specificity in the field at the regional and population level.

7.2 Do hot-spots exist for social parasites?

Hölldobler and Wilson (1990) predicted that ant–ant social parasites were likely to be commonest in cool temperate climates due to geographical variation in the vulnerability of host ants; we predicted that non-ant social parasites would be commonest near the centre of their host’s range, where the carrying capacity of colonies was highest (Thomas et al., 1998a). At more local scales, it has been noted that an exceptionally high diversity of social parasites exists on a few particular sites or landscapes, for example in the Saas valley, Switzerland (Hölldobler and Wilson, 1990). We doubt that these hot-spots arise by chance, and suggest three factors that might amplify the evolution, accumulation and abundance of social parasites both in individual ant colonies and in competing ant species on certain sites.

1. Social parasites thrive (and probably evolve) in localities where the ecological conditions encourage ants to exist in polydomous-polygynous populations over very long periods of time.

2. Once a polydomous ant species’ colony is infested by one social parasite, its social structure and that of neighbouring colonies is inevitably altered, in some systems making it more homogeneous (Foitzik and Herbers, 2001), in others more heterogeneous and in theory more benign (see M. mutabilis), and hence more vulnerable to invasion by other social parasites, especially species that inhabit different niches in the ant nest and are unlikely to compete with the original invader.
3. One ecological impact of predatory and cuckoo social parasitism is to reduce the realized niche of its host, to the benefit of competing ant species whose fundamental niches partly overlap with that of the parasitized species (Thomas et al., 1997, 1998a).

We have yet to model systems containing two competing ants each infested by a different social parasites, but we are sufficiently familiar with the spatial dynamics of 1-social parasite, and >1-competing ant models (Hochberg et al., 1994; Clarke et al 1997; Thomas et al., 1998a) to expect that populations of social parasites and host ant species are likely to show increased stability and persistence on sites in which two competing ants are infested by different parasite species (e.g. M. rubra and M. scabrinodis by Maculinea nausithous and by M. teleius, M. alcon or M. myrmicae, respectively).

7.3 Does local coevolution between social parasites and ants generate speciation in ants?

To our knowledge, only Nash et al.'s (2002) studies of whether ants experience local evolutionary arms-races with their social parasites are sufficiently advanced to confirm that local patterns exist in the hydrocarbon profiles (= colony recognition signals), not only of Maculinea alcon but also of its host Myrmica ruginodis, that are consistent with Thompson’s (1994; Thompson and Calsbeek, Chapter 14, this volume) Mosaic theory of coevolution. In addition, the intense population dynamic interactions between Microdon mutabilis and Formica lemani, and the very local intraspecific gradients in the extreme aggression of F. lemani to Microdon eggs, which is mirrored in gradients of aggression between the ant colonies themselves (Elmes et al., 1999; K. Schönrogge et al., in preparation), suggest that powerful coevolutionary forces are in play. Logic and some data (e.g. Fig. 17.9) suggest that these interactions generate co-adapted genotypes of social parasite and ant host that approach or achieve incompatibility between community modules of the same species in neighbouring landscapes, perhaps resulting in Hawaiian scales of local diversity in both ants and their social parasites, but extending over continents. It will be a task for future researchers to establish whether this is true. For now, we suspect that it is no coincidence that certain of those ant genera, such as Myrmica, which are particularly susceptible to social parasitism, are also believed to comprise many cryptic, sibling species and parasitic forms (Radchenko et al., 2003).

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Thompson, Phil De Vries and many others for discussions and insights on many aspects of social parasitism. Our frequent citations of ‘The Ants’ are testimony to our huge debt to Bert Hölldobler and E.O. Wilson, both for their original experiments and for the synthesis of ideas which provided a foundation for much in this chapter. Finally, we are indebted to Graham Holloway, Mark Fellowes and Jens Rolff for inviting us to write this chapter.

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