

# Social parasites of ant colonies

How social parasites can thrive in ant nests  
and the consequences for their hosts.



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## Summary

Parasitism affect a wide range of organisms and the interactions between the host and the parasite can lead to an evolutionary arms race. Parasitism comes in different forms and one of them is social parasitism. In social parasitism, an organism parasitises on the relationship between members of the host species. Ant colonies are home to numerous social parasites that take advantage of how ant workers take care of the queen and her brood. In this thesis we will focus on socially parasitic ants and butterflies. Their ecology and the different ways and mimics used to be accepted into the colony of their host, are observed. Also the evolution of these parasitic life styles and possible evolutionary arms race are discussed and recent data is used to support the claims that are made.

Parasitic ants can be divided into different groups: species that feed on ant regurgitations (xenobionts), species that kill queen and take over a colony (temporary parasites), slave-makers and species that do not have workers and who's brood is cared for in a host colony (inquilines). The evolutionary pathways to these groups are complex and the exact way of evolution remains unsolved. The evolution of parasitic butterflies seems to be somewhat clearer: mutualistic species gave rise to predatory species which in turn gave give to cuckoo species. There was evidence for an evolutionary arms race between parasitic ants and their host but no evidence has been for one between parasitic butterflies and their host ants.

### Photos on cover (from left to right)

**1:** Caterpillar of the Alcon Blue *Phengaris (Maculinea) alcon* being fed by a worker ant of a *Myrmica spec.*

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Link: <http://tinyurl.com/n99oqda>

**2:** A queen *Polyergus mexicanus* with a host *Formica argentea* worker ant

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Link: <http://tinyurl.com/q3b3x6y>

**3:** *Paussus favieri* with a *Pheidole pallidula* worker ant

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Published in Mauritzi *et al.* (2012) *Behavior of Paussus favieri (Coleoptera, Carabidae, Paussini): A Myrmecophilous Beetle Associated with Pheidole pallidula (Hymenoptera, Formicidae)*

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## Introduction

Parasitism is Parasitic organisms are found all over the world and almost every organism is affected by at least one and often several parasitic species. Parasites reduce the fitness of their host organism without (immediately) killing them. Social parasites are a subset of parasites that, instead of parasitising on an individual, parasitise on the relationships between host species individuals. Amongst the best know examples of social parasites are cuckoos. Cuckoos lay their eggs in the nest of their host species and let the host birds take care of the cuckoo chicks. Cuckoos thus do not take care of their own young and the host is negatively affected by this form of parasitism. Host birds have to feed an additional nestling that is not their own, which requires a lot of energy, and the host's offspring are often killed in the process. This parasite-host interaction can lead to an evolutionary arms race in which both parasite and host evolve adaptations and counter adaptations in order to maximise their own fitness (Foitzik *et al.*, 2003). Social parasites can also parasitise on ant colonies. In order to be a successful social parasite of an ant colony, one needs to make use of the communication between workers, between the workers and the queen(s) and between the workers and the eggs and larvae. Ants use a wide range of chemical and acoustic cues to communicate with one another and these communication systems can be 'hacked' by other organisms (Buschinger *et al.* 2009; Sala *et al.*, 2014). For an overview of the social structure of an ant colony, see box 1.

Ants (Formicidae) are one of the, if not, the most abundant insect families on earth and over 12,000 species have been described. Studies performed in the Amazon forest of Brazil estimated ants to make up for about one-third of animal biomass in the area (Fittkau & Klinge, 1973). Ants inhabit all continents except Antarctica and can be found in a range of habitats and climate zones. Ants have symbiotic relationships with a variety of organisms. This abundant and diverse insect family is also affected by a wide range of specialised social parasites. Some examples of social parasites include caterpillars living of ant regurgitations (Pierce *et al.*, 2002), slave-making ants (Buschinger, 2009) and beetles that prey on ant brood (Maurizi *et al.*, 2012). Ants play an important role in shaping their environment. Ants play an important part in decreasing the number of defoliating caterpillars (Puntilla *et al.*, 2004) but the defoliating leaf-cutter ants of the genera *Atta* and *Acromyrmex* on the other hand can be a plague in forest plantations (Montoya-Lerma *et al.*, 2012). Ants are also the main or secondary food source for several animal species, such as bats (Levin *et al.*, 2009), several bird species and carnivorous insects (De la Mora & Philpott, 2010).

In this thesis I will focus on two groups of social parasites that make ant nests their home: socially parasitic ants and socially parasitic butterflies. These two groups are the best researched social parasites of ants. It will be discussed how these parasites use the social structure of the ant colony to their own benefit, how the parasitic way of life is thought to have evolved in these groups and what the ecological and evolutionary consequences are for their host species with a special emphasis on the evolutionary arms race. Since ants are abundant, fulfil important ecological roles and can act as both pests and pest controllers, it is important to get a better understanding of these creatures and the social parasites that are associated with them. The study of social parasitism may also help us understand how complex ecological communities are formed and preserved.

### **Box 1: Social structure of ant colonies**

Ants are social insects and live in colonies with complex hierarchies.

Ants form colonies with one or multiple reproducing females called queens. These queens give birth to female offspring that are called workers. Worker ants take care of the eggs and larvae and the queen. They also collect food and defend the nest against intruders. Worker ants are often divided into different castes and perform specific tasks within the colony (see figure 1). A limited number of ant species, however, do not have worker ants. Worker ants generally do not mate but since ants exhibit haplodiploid sex-determination, workers are sometimes able to produce male offspring without mating. Workers of the ant species *Gnamptogenys menadensis* are known to both mate and reproduce and thus are also able of producing female offspring (Gobin *et al.*, 1999). In order to start new colonies most species of ant have a specific breeding period in which the queen produces fertile female and male offspring. These offspring are often winged and leave the nest in a process called the nuptial flight. During the nuptial flight the new queens mate, lose their wings and start a new colony or become a queen within an existing colony. Not all new queens are successful and a large amount of the insects is eaten by predators. Nuptial flights are known to be a primary food source for some bats (Levin *et al.*, 2009). When a new colony is founded the whole process can start over.



**Figure 1:** Three individuals of the Florida Harvester Ant *Pogonomyrmex badius* representing three different castes. From top to bottom: a queen, a minor worker and a major worker.

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Link: <http://tinyurl.com/o5c3a3p>

## Socially parasitic ants

The ~230 known social parasitic ant species rely on other ant species. This can range from building a nest inside the host's nest to being fully dependent of the host workers to feed their young. Four main types of social parasitism in ants can be distinguished: xenobiosis, temporary parasitism, dulosis (slavery) and inquilinism (Buschinger 1986, 2009).

### Xenobiosis

Xenobiotic ants or 'guest ants' make their nests inside of the nest of their hosts. They are smaller than the host species and their nest is usually not accessible by the bigger hosts (Buschinger, 1986; Martin *et al.*, 2007). Unlike the other socially parasitic ants, xenobiotic ants are usually distantly related to their host and in different genera or even subfamilies (Huang & Dornhaus, 2008). Xenobiotic workers obtain food by begging host workers or by licking food droplets exchanged between host workers (Buschinger, 1986). Most parasites make use of either chemical camouflage or chemical mimicry to enter and live in the host's nest. Chemical camouflage is the adoption of host odour by being around host ants and their nest. Chemical mimicry on the other hand is characterised by the production of host-like odour by the parasite itself. Most xenobiotic ants have one or few closely related species on which they parasitise. *Formicoxenus nitidulus* however is known to use chemical deterrents to stop host ants from attacking it. Since there is no need to obtain the host's odour by either chemical camouflage or chemical mimicry *F. nitidulus* can use this strategy to enter nests of at least 11 different host species (Martin *et al.*, 2007).

### Temporary parasitism

Queens of temporary parasites cannot start a colony themselves and need to take over the colony of a host species. This phenomenon is called dependent colony foundation. Temporary parasites usually have a couple of different host species to whom they are closely related. They are most often members of the same genus (Huang & Dornhaus, 2008). They kill or sterilise the host queen and let the host workers take care of the parasitic brood. The host queen is not producing eggs anymore and thus after a certain amount of time the nest consists of solely the parasitic species. Host workers are able to slow this process by producing eggs themselves (Chernenko *et al.*, 2013). A large amount of take-overs is without success (Chernenko *et al.*, 2013). See figures 2 and 3 for images of a temporary parasite and its host.

### Dulosis

Just like temporary parasites, queens of dulotic ('slave-making') ants create nests by means of dependent colony foundation. Dulotic ants and their host species are often in the same tribe but mostly but not necessarily in different genera (Huang & Dornhaus, 2008). In *Polyergus breviceps* it is observed that host workers became less aggressive towards the parasitic queen due to chemicals secreted by Dufour's gland (Topoff *et al.*, 1988). As opposed to temporary parasites dulotic ants raid nests of the host species and take pupae back to their nest in order to maintain a work force of host ant workers. These raids are often accompanied by the loss of many adult host ants of the raided colony. We can distinguish facultative and obligatory dulosis. Facultative dulotic species like *Formica sanguinea* (Hölldobler & Wilson, 1990) do not need to enslave host workers from other nests in order to survive as a colony. Obligatory species on the other hand cannot survive without

'slaves'. Obligatory dulotic *Polyergus* workers have sickle-shaped mandibles that are useful in killing during raids but not so useful in feeding their own young. In this case *Polyergus* ants need the enslaved *Formica* (*Serviformica*) workers to rear the *Polyergus* larvae (Hölldobler & Wilson, 1990).

### Inquilinism

Inquiline ants differ from other ants due to the fact that they usually do not have any workers (Buschinger 1989, 2009). Unlike temporary parasites and dulotic species inquiline queens do not get rid of the host queen. Instead they let the host queen continue producing eggs and thus workers. These workers take care of both the host and the parasite brood. Inquiline queens do not need to produce workers anymore and usually just produce new queens and males. Inquiline species mostly have a single host species and they are usually in the same genus as their host (Huang & Dornhaus, 2008).



**Figure 2:** Red wood ants *Formica* (*Formica*) *rufa*. This species is a temporary parasite.

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Link: <http://tinyurl.com/oleovxw>



**Figure 3:** The Large black ant *Formica* (*Serviformica*) *fusca* is a host species for some temporary parasites and dulotic ants.

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Link: <http://tinyurl.com/qzcvm8t>

### **The evolution of social parasitism amongst ants**

Xenobiosis, temporary parasitism, dulosis and inquilinism are all thought to have evolved multiple times and possibly in different ways (see figure 5). Dulosis is thought to have evolved at least six times within the tribe Formicoxenini alone (Beibl *et al.*, 2005).

How the different forms of social parasitism evolved remains an unsolved question (Buschinger, 1986, 2009).

Xenobiotic ants differ from the other parasitic ants by the fact that they are not as closely related to their host as the other parasitic ants are (Huang & Dornhaus, 2008). This could mean that xenobiotic species have another origin than the inquiline, temporary parasitic and dulotic ants. Those forms of parasitism might be more closely related and one form of parasitism could evolve into the other (Buschinger, 1986, 2009).

Xenobiosis may have evolved from different ant species living in close proximity of one another, with one of the species finding the nest of another species a good place to start a colony. This could over time evolve into a parasitic relationship in which the parasite cannot live apart from its host. (Hölldobler & Wilson, 1990; Buschinger, 1986)

The idea that xenobiosis could be a precursor for inquilinism is deemed unlikely since inquilines are closely related to their host whilst xenobionts are not (Huang & Dornhaus 2008). Buschinger (2009) also was unable to find evidence of xenobiosis leading to inquilinism and phylogenetic data points towards a different origin.

Temporary parasitism, dulosis and inquilinism may be more closely linked to each other. All three share the fact that they are closely related to the host and several theories on the evolution of these parasitic life styles have been proposed.

Temporary parasitism may have its origins in polygynous (multiple queens) colonies that are polydomous (multiple sub-colonies). Polygynous colonies are formed when one or several new queens start a new nest within their mother's colony instead of starting a colony of their own. Having multiple queens can result in a big colonies consisting of different sub-colonies. This phenomenon is called polydomy. Such a system could give rise to a sub-colony that is genetically different and that exhibits behaviours that differ from the other ants in the supercolony. The Common Red Ant *Myrmica rubra* is an example of a species observed to have different queen morphs in its polygynous colonies and differences in mating behaviour between sub-colonies have been observed (Heinze, 2008; Buschinger, 2009).

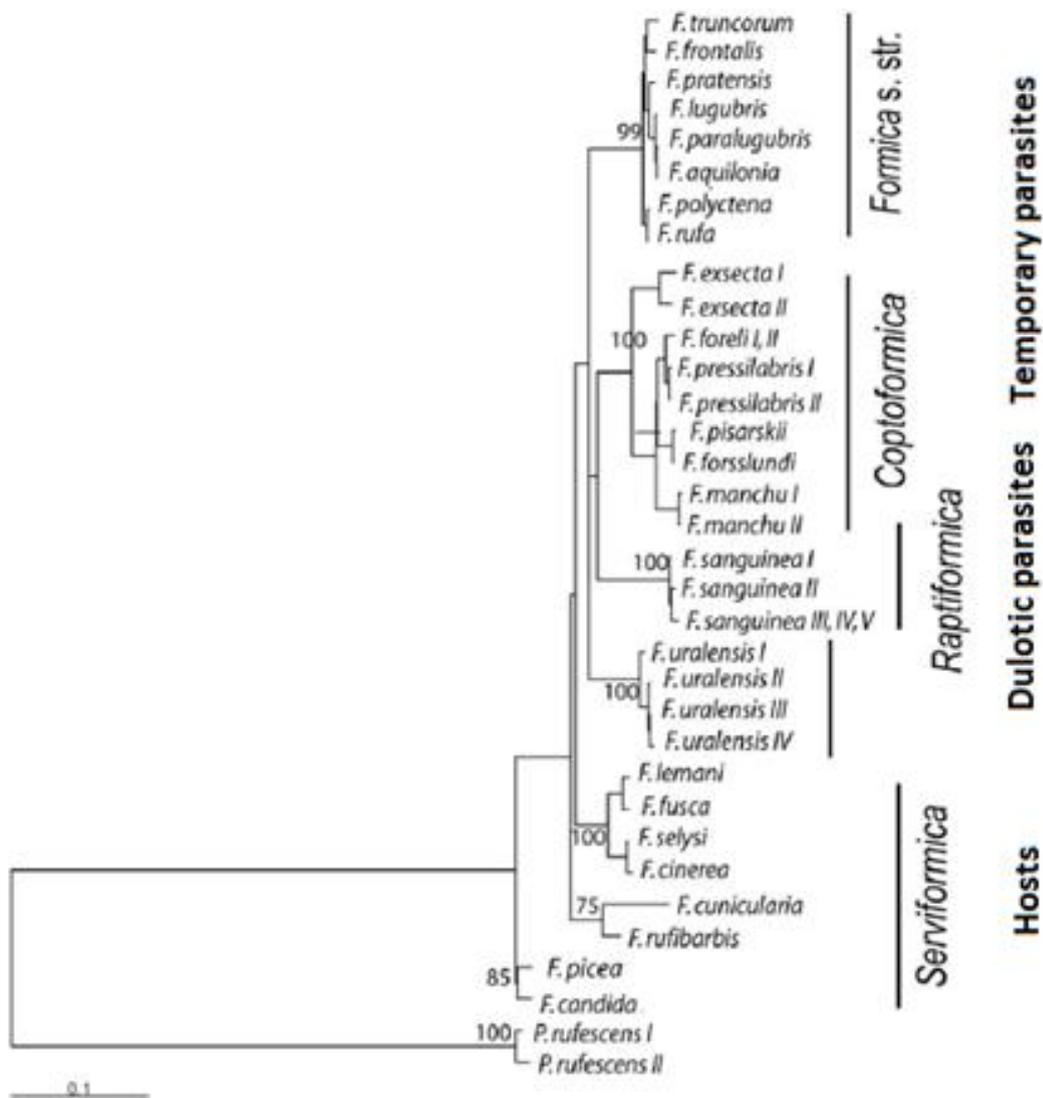
Over time these distinct sub-populations could develop into temporary parasites that show dependent colony foundation (Buschinger, 2009).

There are several hypotheses on the origins of dulosis. One of them is the 'transport hypothesis'. In this hypothesis temporary parasitism in polygynous and polydomous colonies gives rise to dulosis. Brood transport between the sub-colonies often occurs. This enables a sub-colony to obtain workers from different sub-colonies. This hypothesis may explain why dulotic species are often closely related to their host species and why they have dependent colony foundation. There is however not a lot of evidence in support of this idea. The fact that brood transport within a polydomous colony is non-violent whilst raiding nests by dulotic ants is has casted more doubts on this hypothesis (Beibl *et al.*, 2005). The second hypothesis is the 'predatory hypothesis' (Darwin, 1859; Buschinger, 1986). According to this hypothesis, brood of other nests is brought into the nest as a food source. Some of the brood may develop into workers and benefit the colony. This accidental slavery could over

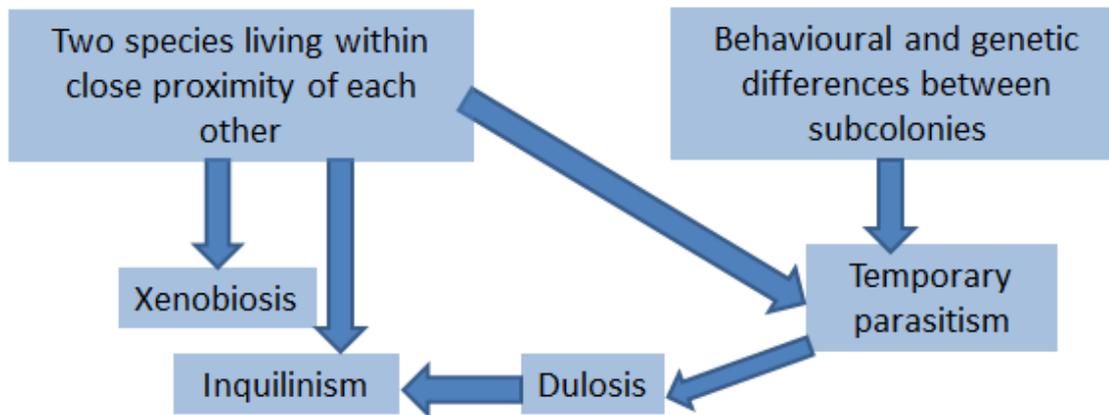
course of time evolve into facultative and even obligate slavery. This hypothesis, however, does not explain why dulotic species need to take over a host nest to start a new colony (Buschinger 1986, Stuart, 2002) and nor do most dulotic species raid nests for food (Stuart, 2002; Beibl *et al.*, 2005). The final hypothesis is the 'territorial aggression hypothesis' (Hölldobler & Wilson 1990) in which colonies of the same species attack each other's colony. The victorious colony may take the brood of the colony that lost and use this as a way to gain workers. This behaviour may progress towards interspecific behaviour and could eventually lead to real dulosis. Several ant species that will take the brood from the losing colony back to their nest in cases of territorial aggression (Hölldobler & Wilson 1990). This could be the basis from which dulosis evolved but can still not explain why all known dulotic species have dependent colony foundation (Buschinger, 1986, 2009). In order to try and answer this question Pollock & Rissing (1989) suggested the following: when colonies are young there are often conspecific colonies nearby. Young colonies often show aggression towards one another and over time one colony persists. During these wars between the colonies the brood of the losing colony is confiscated. Host ants of dulotic species are often polygynous and polydomous. Those species therefore provide a renewable resource for their dulotic parasites. If a young colony is able to penetrate a host colony and take over it is stronger than the conspecific colonies due to the higher number of workers. In this way dependent colony foundation and dulosis could evolve. When facultative dulosis in one way or another has evolved it can progress into obligatory dulosis. Workers of obligatory dulotic ants often have mandibles that are so adapted to raiding colonies that they cannot feed themselves or the larvae. In this case the colony will soon die out if no ants are enslaved (Buschinger, 1986). Host and parasite are often closely related. This could be due to both common ancestry and due to the possibility that chemical communication with related species is easier.

In Palearctic *Formica* species we can find host species (subgenus *Serviformica*), temporary parasites (Subgenera *Formica* s. str. and *Coptoformica*) and facultative dulotics (subgenus *Raptiformica*). Recent mtDNA studies give us a phylogenetic tree that may help us understand the evolution of these different life styles (Goropashnaya et al. 2012). The phylogenetic data seems to indicate that temporary parasites evolved from the host-like species and that temporary parasites gave rise to facultative dulotic parasites. It is however unable to tell us in which way it evolved exactly (see figure 4).

It has been proposed that inquiline species may derive from temporary parasites or dulotic species. These ancestral parasites may have lost their workers and became fully dependent on the workers of the host colony (Hölldobler & Wilson 1990). Buschinger (2009) however, was unable to find any clear evidence for this idea and hypothesises that a separate origin of inquilines is more probable. *Acromyrmex insinator* is an inquiline that can have a small worker caste. These workers are much more vulnerable to fungal pathogens than their host species counterparts. This may be due to the fact that inquiline workers are not exposed to external pathogens as much as the host workers. When infected, the worker caste is vulnerable to disease. This could be an extra factor for early inquiline species to lose their worker caste (Sumner *et al.*, 2003).



**Figure 4:** Maximum likelihood phylogenetic tree of Palearctic *Formica* species based on mtDNA. The subgenera and their accompanied differing (parasitic) life styles are written vertically, right of the phylogenetic tree. Adapted from Goropashnaya *et al.*, 2012.



**Figure 5:** Flow chart showing some possible ways of how the different parasitic life styles (xenobiosis, temporary parasitism, inquilinism and dulosis) in ants may have evolved. Based on figure in Buschinger 1989.

### Ecological and evolutionary consequences for host species

Social parasitic ants can have a huge effect on the host colony: food can be stolen, brood can be taken and queens can be killed, resulting in the death of the colony. The host-parasite relationship could lead to an evolutionary arms race. Delattre *et al.* (2012) tried to test this by looking at aggression rates and found that if the response rates were scaled to take into account the cuticular chemical differences between the foreign ant and the host colony, the host ants did react more aggressively towards parasitic intruders. However this behaviour was also shown by ants that were not known to be host species of the parasitic intruder ants. In another study it was demonstrated that *Temnothorax longispinosus* showed innate increased aggression of colonies after encountering dead individuals of their dulotic parasite *Protomognathus americanus*. After being exposed to these bodies for over two weeks, they stopped showing an increased state of aggression. This may be due to the fact that increased aggression has certain costs (Pamminger *et al.*, 2011). *Temnothorax longispinosus* is also the first ant species where a 'slave rebellion' was recorded. In this case up to two-thirds of the healthy parasite pupae of *P. americanus* were destroyed by the host workers. This could result in lower brood raiding pressure on nearby host species colonies (Achenback & Foitzik, 2009). Overall we can say that adaptations and counter adaptations (and thus an evolutionary arms race) are observed. It is important to note there are not that many clear examples of host adaptations against parasites. This could be due to the fact that a lot of parasites occur quite locally and have a much less common than their hosts. Therefore only a small percentage of host nests are actually affected by a specific parasite species. This may not be enough for evolutionary adaptations to develop in the host species (Buschinger, 2009).

## Socially parasitic butterflies

The majority of butterfly species of the Lycaenidae family are known to associate with ants (myrmecophilous) during their larval and pupal stages. This can be anything mutualism to predatory larvae living of ant brood (Pierce et al, 2002). Of the Lycaenids with a described life history, about 2% are known to be parasitic or predatory (Cotrell et al. 1984). Some species of parasitic butterflies, such as the Alcon Blue *Phengaris alcon*, face serious population declines and are therefore considered flagship species for conservation (Elmes & Thomas, 1992; Als et al. 2004).

### Myrmecophilous butterflies

As many as 75% of Lycaenidae species associate with ants during their larval and/or pupal stage (Pierce *et al.*, 2002). Of these species about 3% are parasitic or predatory and the others are either facultative or obligate mutualists (Pierce et al, 2002). All known lycaenid larvae are known to have special organs and morphological features that are associated with myrmecophily. This is true even for Lycaenid species that do not associate with ants (Pierce *et al.*, 2002; Alvarez *et al.* 2014). Ant-associated adaptations during the larval stage include the presence of a dorsal nectary organ, tentacle organs and pore cupola organs (Pierce *et al.*, 2002). The dorsal nectary organ, which is present in most Lycaenids, produces nutritious droplets that can be consumed by ants. It is sometimes called the 'honeydew gland' and shows similarities to honeydew secretion in ant-tended aphids (Pierce *et al.*, 2002, Ivens *et al.*, 2012). The dorsal nectary organ of the larvae of facultative myrmecophilous Common Blue *Polyommatus icarus* secretes more droplets when the larva is attacked. This in turn results in a higher presence of ants that can protect the larva from predators and parasitoids (Leimar & Axén, 1993). Presence of caterpillars with a dorsal nectary organ has also shown to boost ant worker survival in laboratory conditions (Fiedler & Saam, 1993). Tentacle organs can be found in many but not all Lycaenid larvae (Pierce et al, 2002). Tentacle organs are small organs that can be extruded and emit chemicals to attract the ant's attention (Saarinen, 2005). They emit chemicals that alert ants (Henning, 1983). Pore cupola organs are small glands that release ant-appeasing chemicals. It is one of the ways the larvae can feed themselves near ant-tended aphid colonies without being attacked. The presence of ants helps to protect the larvae from predators. It is thought that all Lycaenids possess these organs (Pierce et al, 2002). Acoustic cues emitted by the larvae also play an important role in ant-Lycaenid communication (Sala et al 2014). Pupae too often possess stridulatory organs. These organs may play a role in ant-Lycaenid communication but are also found in non-myrmecophilous Lycaenid species (Alvarez et al., 2014). Myrmecophilous butterfly larvae can be phytophagous (feeding on plants) or aphytophagous (feeding on other things than plants) and have some change their feeding behaviour during their larval development (Sala et al., 2014). Aphytophagous larvae can feed on ant-tended aphids (Lohman *et al.*, 2009), ant regurgitations (Pierce et al. 2002, Als et al. 2004) or ant brood (Pierce *et al.*, 2002, Sala *et al.*, 2014). Larvae that spend a part of their life cycle inside ant colonies and feed on brood or regurgitations are considered social parasites of ants (Als *et al.*, 2004).

## Parasitic butterflies

The best studied parasitic butterflies are the species of the genus *Phengaris* (which includes the species of the former genus *Maculinea*). The genus is divided into species that feed on ant regurgitations ('cuckoo larvae') and species with larvae that prey on ant brood ('predatory larvae') (Als et al. 2004). *Phengaris* species only oviposit on flowering parts of one or a few plant species (Als et al, 2004; Patricelli et al. 2011).

After hatching the larvae feed on flowering parts of their host plants until they reach their fourth larval stage (Solazzo *et al.*, 2013). During this stage they let themselves drop to the ground. From here *Myrmica* ant workers pick up the larvae and take them to their nest, where they complete their larval and pupal life stage (Als *et al.*, 2004; Nash *et al.*, 2008). The larval life stage is divided into a pre-adoption (free-living) and a post-adoption stage (living in an ant nest). These two stages are characterised by different feeding habits and a range of other ecological and behavioural differences (Sala *et al.*, 2014).

Several strategies are used in order to get the attention of *Myrmica* workers to take them to the ants' nest. Chemical mimicry is one of tactics used. The cuticular chemistry of the Alcon Blue *P. alcon* is found to mimic that of its host's brood and chemical analyses show more similarities between the parasite and its host than between the host and a closely-related ant species (Nash *et al.*, 2008; see figure 6). There are differences between *P. alcon* individuals and this partly explains differences in adoption time, with a greater chemical dissimilarity between host and parasite leading to longer adoption times (Nash *et al.*, 2008). Nutritious droplets secreted by the dorsal nectary organ also play a role in the adoption process of larvae of the Scarce Large Blue *P. teleius*, whilst this was not observed in its sister species the Dusky Large Blue *P. nausithous* (Fiedler, 1990). Larvae of all European *Phengaris* species possess pore cupola organ. They lack tentacle organs, possibly because these organs are not needed in a relatively predator-free area like an ant nest (Fiedler, 1998). Acoustic cues also play an important role in the adoption process. A study by Sala *et al.* (2014) shows that larvae of *P. alcon* and *P. teleius* both emit sounds that mimic stridulations made by their host ant queen. In the post-adoption stage the sounds emitted by the predatory *P. teleius* start to become more dissimilar from the queen's stridulation sounds than in the pre-adoption stage. The opposite was found to be the case in cuckoo species *P. alcon*. This may be explained by the fact that cuckoo larvae need to communicate with the ants more often in order to get fed. Predatory species do not need to exploit these elaborate acoustics in order to prey on ant brood.



**Figure 8:** A: Gas chromatograms of surface extracts of the caterpillar of an Alcon Blue *Phengaris (Maculinea) alcon*, the host ants *Myrmica rubra* and *M. ruginodis* and non-host *M. scabrinodis* larvae. B: Host ant *M. rubra* carrying the cuckoo caterpillar of the Alcon Blue *P. (Maculinea) alcon*. From Nash *et al.*, 2008

### The evolution of socially parasitic butterflies

The parasitic Lycaenidae are thought to have evolved from mutualistic living species (Fiedler, 1998; Als *et al.*, 2004). Therefore in order to get a better understanding of the evolution of the parasitic Lycaenids, we need to understand how mutualistic ant-Lycaenid interactions evolved. Ants can provide a safe environment to live in by attacking potential predators, so living in proximity of ants, without being attacked, can have an evolutionary advantage. Pore cupola organs are possessed by all known Lycaenids and are thought to be the first organs that have especially evolved to be accepted by ants by secreting appeasing chemicals (Pierce *et al.*, 2002). Relationships between ants and the Lycaenid larvae would be intensified if the interaction would be mutualistic instead of solely commensal. The evolution of glands secreting nutritious droplets (that could feed ants) may have been the start of a mutualistic relationship. Some specialised organs like the dorsal nectary organ and the tentacle organ are hypothesised to have been lost independently during evolution in some lineages (Pierce *et al.*, 2002). Some Lycaenidae species take the mutualism a step further by having their larval or pupal diapause inside ant nests (Fiedler, 1998). From there predatory larvae may have evolved (Fiedler, 1998; Als *et al.*, 2004). A predatory way of feeding could have paved the way for cuckoo parasitism. Cuckoos have been demonstrated to have a much smaller negative impact on the host ant colony than predatory species, leading to an ant nest to harbour more caterpillars if a predator switched to a cuckoo life style (Thomas & Elmes, 1998). Cuckoos were hypothesised to be descendent from predatory species and mtDNA studies revealed that this is indeed the case. (Als *et al.*, 2004). The same study also shows that the parasitic *Phengaris* clade is indeed derived from mutualistic ancestors. The predatory *Phengaris* clade is estimated to have given rise to the cuckoo *Phengaris* species about 5 million years ago (Als *et al.*, 2004). These parasitic butterflies can only occur in areas where both their host plants and host ants occur. Since the range of host ants and host plants doesn't nicely overlap, parasitic butterflies show a patchy distribution (Nash *et al.*, 2008). The patchy distribution and dependence on two other species are factors that make conservation of these butterflies difficult (Elmes & Thomas, 1992; Nash *et al.*, 2008).

### **Ecological and evolutionary consequences for host species**

Whilst mutualistic ant-lycaenid interactions have shown to enhance worker ant survival (Fiedler & Saam, 1993), parasitic species have a negative impact on the ant colony by eating brood and by consuming food that was meant for the ant larvae (Pierce *et al.*, 2002; Sala *et al.*, 2014; Nash *et al.*, 2008). Just like in the parasitic ants this could lead to an evolutionary arms race between parasite and host. Just as with the parasitic ants it is hard to find clear evolutionary consequences for the host species (Buschinger, 2009). A way for the host to make it harder for other species to intrude is to decrease the within-colony relatedness. By doing this there are fewer chemical differences within the colony and intruders will be more easily recognised (Solazzo *et al.*, 2013). In *Myrmica rubra* however the opposite was observed. Populations of the *M. rubra* expressed lower levels of within-colony relatedness when the populations were infested by *Phengaris nausithous*. This may be due to the fact that *P. nausithous* larvae eat more smaller brood (future workers) than large brood (future queens), resulting in higher levels of polygyny and a lower within-colony relatedness (Solazzo *et al.*, 2013).

## Conclusion

Both parasitic ants and parasitic butterflies use a range of different tactics to be accepted in the ant nest. Parasitic ants are observed to use chemical mimicry, chemical camouflage, repellents and, in case of slave-raiding, brute force. Caterpillars use appeasing chemicals, nutritious droplets, chemical and acoustic mimicry. The use of chemical mimicry is something that both groups have in common. The main difference between the two groups is that the butterflies are only parasitic during their larval life stage.

Socially parasitic ants have evolved several times independently but the details on how they did are still unclear. Butterflies that are mutualistic with ants gave rise to a clade that predated on ant brood. This predatory clade eventually gave rise to butterflies with cuckoo larvae. Some examples of an evolutionary arms race have been found between socially parasitic ants and their hosts but not between butterflies and their hosts.

Similar social parasites can be found in other insects, such as cuckoo bees that parasitise on other bees. Most studies in this field only focus on describing new host or parasite species for a parasite and host respectively and do not look at the effects on host species. It would be interesting to see if the ecology and evolution of these parasites resembles that of the parasites described in this thesis.

Within the discussed groups a lot is still unclear too. Less than half of Lycaenid butterflies have a documented life history (Pierce *et al.*, 2002) and even within *Phengaris*, the most studied Lycaenid genus, the larval life of some species is unknown (Als *et al.*, 2005). Unknown (parasitic) species of ants new to science are still being found, even in the Netherlands (Boer & Noordijk, 2005). Also more research has to be done to examine the possible evolutionary arms race between the parasitic butterflies and their host ants. The effects of social parasites on host brood survival are still not well recorded and DNA studies on ants could help unravel some evolutionary pathways to different forms of parasitism. Within the ants most evidence for an evolutionary arms race is from after the year 2000 and continuing this research will probably contribute to our understanding of the ecology and evolution of social parasites.

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