Relationships of *Maculinea* butterflies with *Myrmica* ants

Beauties and Beasts

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In order to survive, butterflies of the *Maculinea* genus must occur together with *Myrmica* ants, whose nests provide the environment for a significant part of their development

Relationships between various organisms and ants are not a rare occurrence. Ants, a large proportion of which are predatory, are dominant insects and their numbers and feeding habits affect the behavior and evolution of their potential prey.

Dangerous liaisons

Some organisms have developed systems to defend against predatory ants, whereas others enter into very specific pacts with ants. All or part of the life cycle of such organisms, known as myrmecophiles, actually takes place inside an ants' nest or surrounded by ants tending it. Among invertebrates, the organisms exhibiting such myrmecophilous lifestyles are mainly insects, e.g. beetles (*Coleoptera*), flies (*Diptera*) and butterflies. In the latter group myrmecophily is most widespread in the *Lycaenidae* family, which numbers around 5,000 known species. The most important evolutionary step in the development of the often spectacular forms of myrmecophily in *Lycaenidae* was to "decipher" the ants' codes of communication. That has allowed the butterflies to become part of the hosts' social environment.

The nature of the ties developed between *Lycaenidae* and ants varies widely. A weak relationship - known as myrmecoxeny - mainly involves simply pacifying the ants' aggression, whereas the formation of stronger bonds (facultative or obligatory symbiotic relationships, predation and social parasitism) is a long-term process that often

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The *Lycaenidae* family numbers around 5,000 species. The Common Blue (*Polyommatus icarus*), pictured here, is facultatively (optionally) myrmecophilous

requires caterpillars to adopt sophisticated strategies. *Lycaenidae* have adapted morphologically, physiologically, biochemically and behaviorally to establish relationships with ants. Their larvae have a thick and firm cuticle providing excellent protection against ant bites and stings. The dorsal part of the caterpillars' bodies is rounded, while the underside is flattened and adjacent to the ground. The head is small and can be easily hidden under a fold of skin. *Lycaenidae* larvae move slowly without any rapid movements which might provoke an aggressive reaction from the worker ants.

Lured by nectar

The most important feature of myrmecophilous *Lycaenidae* caterpillars, however, lies in their highly-specialized epidermal glands (called myrmecophilous glands), whose secretions can manipulate the ants' behavior and thus facilitate interspecies bonding. The most important types of glands are *pore cupolas*, tentacular glands, and the dorsal nectar gland. *Pore cupolas* - glands scattered on the body surface of butterfly larvae and pupae - secrete attractants which reduce the workers' aggression. Tentacular glands occur in *Lycaenidae* caterpillars accompanied by ants on food plants. The dorsal nectar gland (Newcomer's organ), characteristic of *Lycaenidae* larvae exhibiting the most advanced myrmecophily, produces a nutritious carbohydrate secretion that is licked off by ants and thus helps a strong relationship develop between the myrmecophile and its host.

Protected larvae

Many species of *Lycaenidae* are defined as myrmecoxenic. Their caterpillars do not maintain a regular relationship with ants, and their only active myrmecophilous glands are *pore cupolas*. Other *Lycaenidae* develop relationships with ants characterized by what is known as mutualism, comparable with the close trophobiotic bonds between aphids and ants. The larvae and pupae of these butterflies secrete an energy-providing substance from their dorsal gland, and in return they receive protection from predators and parasites.

Facultative mutualistic relationships are somewhat casual in nature, and such caterpillars are not bound with specific species of hosts. This is the most common form of *Lycaenidae* myrmecophily. The caterpillars of obligatory myrmecophiles, on the other hand, secrete a liquid from the dorsal gland throughout their lives, which ensures them permanent protection by ants. Their larvae are cared for by workers of a specific ant genus or species. There are also some obligatory myrmecophilous *Lycaenidae* species that exploit ants through predation or social parasitism. This group includes the genus *Maculinea* (= *Phengaris*), which has four representatives in Europe. These butterflies spend most of their larval and pupal forms inside ants' nests, where the caterpillars feed on ant larvae (in predatory forms) or are fed by workers (in labor parasites). The hosts of the best studied species of the *Maculinea* genus are *Myrmica* ants.

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Lying motionless in the undergrowth, *Lycaenidae* larvae await adoption by *Myrmica* ants. This moment is crucial to the future life of the butterfly. Pictured here is a *Maculinea alcon* of the *rebeli* form as it is being adopted by *Myrmica schenecki*

Waiting to be adopted

During the first stage of development, in their first 2-3 weeks the larvae lead an endophytic lifestyle, feeding on seed buds. Having reached the final, fourth larval stage, yet still weighing no more than 2% of their final mass, they drop out of the flowers onto the ground. Lying motionless or only moving very slightly through the undergrowth, they await adoption by *Myrmica* ants. This moment is crucial to the future life of the butterfly larvae because their further development is only possible inside the nests of specific *Myrmica* species.

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***Lycaenidae* have "deciphered" ants' code of communication. The secretions of their epidermal glands enable their caterpillars to manipulate ants' behavior. Photographed here is a *Maculinea teleius* pupa with *Myrmica* ants**

It takes predatory species (Large Blue, *M. arion*; Scarce Large Blue, *M. teleius*; Dusky Large Blue, *M. nausithous*) a relatively long time to get adopted by worker ants. Before the caterpillars get transported to a nest, they spend around an hour enticing the ants with the sweet liquid secreted by their Newcomer's gland. The better chemical camouflage of the parasitic *Maculinea alcon* means that its caterpillars are taken to an ant nest within seconds of being found. Immediately after leaving the food plant where they began life, the larvae of all *Maculinea* species secrete a simple set of cuticular carbohydrates that are universal attractants for various species of *Myrmica*. However, *Maculinea* larvae undergo development and pupation in nests of only some host species. It is not until they are in the ant nest that they begin biosynthesis of chemical compounds with a profile most closely matching the surface hydrocarbons appropriate for the host species. And so if the larva finds its way to the nest of a wrong *Myrmica* species, it will be identified and most likely killed. In nests of the correct *Myrmica* species, on the other hand, predatory *Maculinea* species will feed on ant larvae while the hosts usually treat their guests with indifference. However, *Maculinea alcon* caterpillars are actually fed trophallactically and given regular care. The larvae gain 98% of their final mass inside the ants' nests.

The rate of development of *Lycaenidae* caterpillars is most likely conditioned genetically. They spend between 10 and 23 months in the ants' nests. The hatching of imagos takes place 2–3 weeks from pupation within the nest.

Several hosts?

The famous story of the extinction of *Maculinea arion* (Large Blue) in Great Britain has stirred increased scientific interest in this and related *Maculinea* species. The first observations carried out by Dr. Jeremy Thomas and others 30 years ago indicated that each *Maculinea* species is specific to one host *Myrmica* species. In recent years the European project named MacMan (*Maculinea Butterflies of the Habitats Directive and European Red List as Indicators and Tools for Habitat Conservation and Management*), pooling together the efforts of several dozen scientists, has made it possible to reassess this view and learn more about the biology and ecology of endangered butterflies. It turns out that in some central regions of *Maculinea* occurrence in Europe the butterflies are able to use several local host species thanks to their ability to synthesize a specific set of surface hydrocarbons (*multi-host mimicry*).

However, *Maculinea*'s specificity is more pronounced near the borders of its occurrence range. The two latest studies of the Alcon Blue (*Maculinea alcon*) have also shown that *Maculinea*'s specificity results from local co-evolution of the butterflies and their hosts in different geographical regions of their incidence. This co-evolution affects the profiles of both partners' surface hydrocarbons. The development of a chemical system that makes it difficult for the butterflies to access the host's nest triggers an evolutionary process of adaptation to exploit ants nests' of other *Myrmica* species that are most suitable chemically and most easily available.

Predators and labor parasites

All four *Maculinea* species occur in Poland: the predatory Large Blue (*Maculinea arion*), Scarce Large Blue (*M. teleius*) and Dusky Large Blue (*M. nausithous*), and the social parasite Alcon Blue (*M. alcon*). Apart from life strategies, individual species (and in the case of *M. alcon* its ecological forms) differ in terms of their habitat requirements, preferences for food plants and ant hosts, and chemical adaptations that allow their integration within the nest.

Predatory *Maculinea* species usually use several host species, while the parasitic ones usually have one or perhaps two hosts. In Poland the least specialized are *M. teleius* and *M. arion*, which use several *Myrmica* ant species. *Maculinea nausithous* is predatory, although it has certain features of a labor parasite and has just one host - *Myrmica rubra*. *M. rubra* is used by the majority of the European population of this *Maculinea* species. The labor parasite *Maculinea alcon* and its ecological forms are characterized by local specialization in Poland. In most territories the *alcon* form uses nests of *Myrmica scabrinodis* ants, as well as *M. vandeli* in the Świętokrzyskie Mountains, while the *rebeli* form uses *M. sabuleti* and *M. scabrinodis* in the Przemyskie Foothills and *M. schencki* in the Pieniny Mountains. *M. rebeli* pupae have also been found in one *M. rugulosa* nest.

Save the ants!

Maculinea populations are endangered across Poland and Europe. Environmental changes resulting from the trend towards intensive land use methods are to blame. Some of the butterflies' territories have been converted to arable fields, some have been allocated for building development, others have become overgrown with shrubs and trees. Active conservation is essential for the preservation of *Maculinea* territories, yet notwithstanding the existing legal mechanisms it is difficult to retain the current character of all habitats. According to many researchers, the key condition for the survival of *Maculinea* populations is the occurrence of food plants near nests of ants of the correct species, which are extremely sensitive to any environmental changes. Other researchers consider appropriate microclimate and vegetation structure to be more important for the butterflies. Research carried out in Poland shows unambiguously that at least in the case of three species - *Maculinea nausithous*, both forms of *M. alcon*, and *M. teleius* - conservation plans for individual populations must also consider the micro-environmental requirements of the ant hosts. One must also remember that protection of *Maculinea* territories is necessary to ensure the survival not only of these unique insects, but also other, frequently protected species that the butterflies interact with or which co-occur with them. ■

Further reading:

Stankiewicz A., Sielezniew M. (2002). Host specificity of *Maculinea teleius* Bgstr. and *M. nausithous* Bgstr. (*Lepidoptera: Lycaenidae*): The new insight. *Annales Zoologici, 53*, 403-409.

Stankiewicz A.M., Sielezniew M., Buszko J. (2005). *Maculinea alcon and M. rebeli in Poland: distribution, habitats, host ant specificity and parasitoids.* [In:] Settele J., Kühn E., Thomas J.A. (Eds.). *Studies on the Ecology and Conservation of Butterflies in Europe.* Sofia-Moscow: Pensoft Publishers.

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***Maculinea alcon* is a parasitic *Maculinea* species occurring in Poland, where it exists in two ecological forms and has a total of 5 host species. Pictured here is a male of the *rebeli* form**