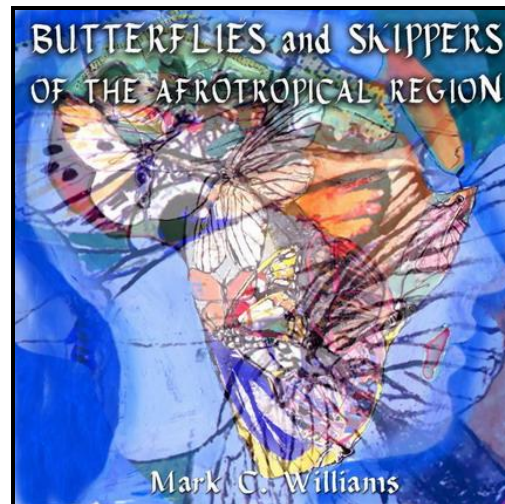


# AFROTROPICAL BUTTERFLIES



## BIBLIOGRAPHY OF MYRMECOPHILY IN LYCAENIDAE AND RIODINIDAE

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\* Indicates that a PDF is in my possession.

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**Abstract:** Myrmecophily is widespread in lycaenid butterflies, in which ants receive food resources and, in turn, protect caterpillars against natural enemies. This interaction ranges from obligate myrmecophily, in which immatures are invariably associated with ants and are dependent on ants for survival, and facultative myrmecophily, in which larvae are not dependent on ants for survival, but the presence of the latter may increase larvae survival. Lycaenids also include non-myrmecophilous butterflies, which do not have positive associations with ants and have developed strategies to avoid being attacked or preyed upon by them. In this study, we examined the relationship between the lycaenid *Michaelus ira* and two ant species associated with *Distictella elongata* (Bignoniaceae). This plant has extrafloral nectaries and is patrolled by *Camponotus crassus* and *Ectatomma tuberculatum*. Morphological analyses revealed that *M. ira* larvae have ant organs, such as dorsal nectary organs and perforated cupolas, structures associated with myrmecophily. We performed larval exposure experiments in the field, predicting that, in the absence of myrmecophily, the butterfly larva would present strategies to avoid ant attack. Results showed that larvae were attacked by both ant species. To escape ant molestation, larvae lived and fed inside silk-sealed *D. elongata* flower buds. We concluded that the *M. ira* bud-sheltering behavior was a defensive strategy against these ant species, while the dorsal nectary organs were apparently nonfunctional. Nonetheless, myrmecophily, in general, cannot be excluded in *M. ira* since relationships with other ant species may exist.

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**Abstract:** About 10,000 arthropod species live as ants' social parasites and have evolved a number of mechanisms allowing them to penetrate and survive inside the ant nests. *Myrmica* colonies, in particular, are exploited by numerous social parasites, and the presence of their overwintering brood, as well as of their polygyny, contributes to make them more vulnerable to infestation. Butterflies of the genus *Maculinea* are among the most investigated *Myrmica* inquilines. These lycaenids are known for their very complex biological cycles. *Maculinea* species are obligated parasites that depend on a particular food plant and on a specific *Myrmica* species for their survival. *Maculinea* larvae are adopted by *Myrmica* ants, which are induced to take them into their nests by chemical mimicry. Then the parasite spends the following 11 – 23 months inside the ants' nest. Mimicking the acoustic emission of the queen ants, *Maculinea* parasites not only manage to become integrated, but attain highest rank within the colony. Here we review the biology of *Maculinea/Myrmica* system with a special focus on some recent breakthrough concerning their acoustical patterns.

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**Abstract:** Social insect colonies are like fortresses, well protected and rich in shared stored resources. This makes them ideal targets for exploitation by predators, parasites and competitors. Colonies of *Myrmica rubra* ants are sometimes exploited by the parasitic butterfly *Maculinea alcon*. *Maculinea alcon* gains access to the ants' nests by mimicking their cuticular hydrocarbon recognition cues, which allows the parasites to blend in with their host ants. *Myrmica rubra* may be particularly susceptible to exploitation in this fashion as it has large, polydomous colonies with many queens and a very viscous population structure. We studied the mutual aggressive behaviour of *My. rubra* colonies based on predictions for recognition effectiveness. Three hypotheses were tested: first, that aggression increases with distance (geographical, genetic and chemical); second, that the more queens present in a colony and therefore the less-related workers within a colony, the less aggressively they will behave; and that colonies facing

parasitism will be more aggressive than colonies experiencing less parasite pressure. Our results confirm all these predictions, supporting flexible aggression behaviour in *Myrmica* ants depending on context.

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**Abstract:** The immature stages of *Aricoris propitia* (Stichel) are described and illustrated for the first time, using both light and scanning electron microscopy. Females oviposit in at least seven host-plant families, always in the presence of fire ants (*Solenopsis saevissima* (Smith) complex), without being attacked by them. Larvae are tended by ants during all larval and pupal stages. From the fourth instar on, larvae feed at night and rest during the day inside underground shelters constructed by ants on the host plant roots, and where pupation occurs. Several observed features, including ant-mediated oviposition, persistent ant attendance throughout all instars, and high spatiotemporal fidelity indicate that *A. propitia* is a myrmecophile obligately associated with fire ants. We propose *A. propitia* as an extraordinary model for studies on ant-butterfly evolutionary history in the Neotropics.
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**Abstract:** Symbiotic interactions between butterfly larvae and ants, termed myrmecophily, require a range of behavioural and morphological adaptations (ant-organs). Here, using light and scanning electron microscopy, we

describe the complete life cycle of two species of *Theope* (Lepidoptera: Riodinidae) that have contrasting ways of life. *Theope thestias* larvae are facultatively tended by several ant species, whereas *Theope pieridoides* have obligate symbiotic interactions with *Azteca* ants that inhabit a myrmecophytic tree. Morphological differences associated with their different degrees of intimacy with tending ants are visible from hatching. In *T.thestias*, the untended first-instar larva has elongated bifurcated setae and a few tiny perforated cupola organs (PCOs), whereas in *T.pieridoides*, the ant-tended first instar has short dendritic setae, larger and more numerous PCOs, and functional tentacle nectary organs (TNOs). Throughout ontogeny, *T.pieridoides* always shows more conspicuous ant-organs than *T.thestias*, with the exception of balloon setae, which are larger and more numerous in *T.thestias*. In addition, mature *T.pieridoides* larvae have an anterior set of ant-organs, including a new type, here described and termed anterior glandular openings (AGOs). Based on the behavioural responses of ants in contact with these structures, a new interpretation for the mechanism whereby *Theope* larvae can manipulate the behaviour of their tending ants is proposed. Until now, three ecological syndromes can be defined among *Theope* species: (1) oligophagous larvae with facultative myrmecophily; (2) monophagous larvae with obligate myrmecophily; and (3) polyphagous larvae with obligate myrmecophily. These results suggest that differences in the degree of specificity in the ant-plant interactions may have an important role in the evolution of host-plant use in *Theope*.

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**Abstract:** The Alcon blue butterfly (*Maculinea alcon*) parasitizes the nests of several *Myrmica* ant species. In Denmark, it uses *M. rubra* and *M. ruginodis*, but never *M. scabrinodis*. To further examine the basis of this specificity and local co-adaptation between host and parasite, the pattern of growth and survival of newly-adopted caterpillars of *M. alcon* in *Myrmica* subcolonies was examined in the laboratory. *M. alcon* caterpillars were collected from three populations differing in their host use, and reared in laboratory nests of all three ant species collected from each *M. alcon* population. While there were differences in the pattern of growth of caterpillars from different populations during the first few months after adoption, which depended on host ant species and the site from which the ants were collected, there was no evidence of major differences in final size achieved. Survival was, however, much higher in nests of *M. rubra* than in nests of *M. ruginodis* and *M. scabrinodis*, even for caterpillars from a population that is never known to use *M. rubra* as a host in the field. The caterpillars of *M. alcon* thus do not show local adaptation in their pattern of growth and survival, but instead show a pattern that may reflect different nestmate recognition abilities of the host ants, related to their sociogenetic organisation. The pattern of observed host ant use in the field seems to result from a combination of differences in local host availability and locally adapted infectivity, modulated by smaller differences in survivorship in the nests of the different host ants.
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**Abstract:** Some phytophagous insects gain defense from natural enemies by associating with otherwise potentially harmful top predators. Many lycaenid butterfly caterpillars are involved in such interactions with ants: larvae provide carbohydrate rewards from the dorsal nectary organ (DNO) to associated ants in return for protection from natural enemies. The stability of these interactions involves signals that identify the lycaenid caterpillar as a mutualist. However, larvae of some lycaenid species, such as *Lycaena xanthoides*, are found in close association with ants but do not possess the reward producing DNO. Evaluating the relationship in a phylogenetic framework, we show that the association between *L. xanthoides* and ants likely evolved from a non-ant-associated ancestor. Behavioral trials also show that *L. xanthoides* larvae are capable of influencing ant behavior to increase ant tending when faced with a simulated predator attack, without providing DNO-derived rewards to ant associates. These results demonstrate that the DNO is not necessary to maintain associations between lycaenid larvae and ants. Third-party interactions may affect the evolution of mutualisms and consideration of underlying evolutionary history is necessary to understand contemporary species associations.
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**Abstract:** The choices made by ovipositing female butterflies play a key role in the survival of their offspring and consequently in the persistence of butterfly populations. These choices are even more crucial in the case of obligate myrmecophilous organisms such as *Maculinea* butterflies with larvae that, after a phytophagous period, need to be adopted by *Myrmica* ants to complete their life cycle. Because the worker ants' foraging range is limited, selecting an 'ideal' oviposition site requires that both the phenological stage of the larval food plant (short-term larval fitness) and the presence of suitable host ants (long-term larval fitness) are taken into account. Whether the female's selection of a valuable oviposition plant is influenced by the closeness of a *Myrmica* nest is unclear. We studied the oviposition



behaviour of a *Maculinea arion* population exploiting *Origanum vulgare* as a host plant. By following females, we collected phenological data on the visited plants that were either ‘chosen’ for oviposition or ‘avoided’ (flowers were visited and evaluated, but received no eggs), and we assessed the presence of *Myrmica* ants in the vicinity of each plant. Results suggest that plants are selected by *M. arion* females on the basis of their bud phenology and the presence of host ants and not of other environmental features. We thus hypothesize the evolution of an adaptive mechanism that affords females of this strictly myrmecophilous butterfly the ability to ensure the long-term survival of their brood by selecting host plants growing near a *Myrmica* nest.

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**PECSENYE, K., BEREZKI, J., JUHASZ, E., TARTALLY, A. & VARGA, Z. 2015.** Contrasting genetic structure in cuckoo and predatory *Maculinea* butterflies. *Conservation Genetics* **16** (4): 939-954.

**\*PELLISSIER, L., LITSIOS, G., FIEDLER, K., POTTIER, J., DUBIUS, A., PRADERVAND, J.-N., SALAMIN, N. & GUISAN, A. 2012.** Loss of interactions with ants under cold climate in a regional myrmecophilous butterfly fauna. *Journal of Biogeography* **39** (10): 1782-1790.

**Abstract:** Aim: Specialized mutualistic clades may revert and thus increase their autonomy and generalist characteristics. However, our understanding of the drivers that trigger reductions in mutualistic traits and of the consequences for the tolerance of these species to various environmental conditions remains limited. This study investigates the relationship between the environmental niche and the degree of myrmecophily (i.e. the ability to interact with ants) among members of the Lycaenidae. Location: The western Swiss Alps. Methods: We measured the tolerance of Lycaenidae species to low temperatures by comparing observations from a random stratified field sampling with climatic maps. We then compared the species-specific degree of myrmecophily with the species range limits at colder temperatures while controlling for phylogenetic dependence. We further evaluated whether the community-averaged degree of myrmecophily increases with temperature, as would be expected in the case of environmental filters acting on myrmecophilous species. Results: Twenty-nine Lycaenidae species were found during sampling. Ancestral state reconstruction indicated that the 24 species of Polyommata displayed both strong myrmecophily and secondary loss of mutualism; these species were used in the subsequent statistical analyses. Species with a higher degree of ant interaction were, on average, more likely to inhabit warmer sites. Species inhabiting the coldest environments displayed little or no interaction with ants. Main conclusions: Colder climates at high elevations filter out species with a high degree of myrmecophily and may have been the direct evolutionary force that promoted the loss of mutualism. A larger taxon sampling across the Holarctic may help to distinguish between the ecological and evolutionary effects of climate.

**PELLISSIER, L., LITSIOS, G., GUISAN, A. & ALVAREZ, N. 2012.** Molecular substitution rate increases in myrmecophilous lycaenid butterflies (Lepidoptera). *Zoologica Scripta* **41** (6): 651-658.

**Abstract:** Is species diversification driven by neutral- or niche-based processes? Butterflies of the Lycaenidae family have developed mutualistic interactions with ants. This biotic requirement increased the spatial fragmentation of populations of lower effective population size ( $N_e$ ) compared with autonomous species. The nearly neutral theory predicts that species with smaller  $N_e$  should fix more mutations because of the increased strength of drift. Taking into account the phylogenetic relatedness among species, this study shows that species with a stronger dependence on ants displayed more intra-specific Single Nucleotide Polymorphisms compared with species with low or no myrmecophily. This phenomenon can cause more pronounced genetic differentiation between populations and could ultimately promote speciation in a similar manner as on physical islands. The large species diversity observed in this family could be the consequence of this neutral process enhancing the diversification of lineages.

**PELLISSIER, L., RASMANN, S., LITSIOS, G., FIEDLER, K., DUBUIS, A., POTTIER, J. & GUISAN, A. 2012.** High host-plant nitrogen content: a prerequisite for the evolution of ant-caterpillar mutualism? *Journal of Evolutionary Biology* **25** (8): 1658-1666.

**Abstract:** The amount of nitrogen required to complete an insect's life cycle may vary greatly among species that have evolved distinct life history traits. Myrmecophilous caterpillars in the Lycaenidae family produce nitrogen-rich exudates from their dorsal glands to attract ants for protection, and this phenomenon has been postulated to shape the caterpillars' host-plant choice. Accordingly, it was postulated that evolution towards myrmecophily in Lycaenidae is correlated with the utilization of nitrogen-rich host plants. Although our results were consistent with the evolutionary shifts towards high-nutrient host plants serving as exaptation for the evolution of myrmecophily in lycaenids, the selection of nitrogen-rich host plants was not confined to lycaenids. Butterfly species in the nonmyrmecophilous family Pieridae also preferred nitrogen-rich host plants. Thus, we conclude that nitrogen is an overall important component in the caterpillar diet, independent of the level of myrmecophily, as nitrogen can enhance the overall insect fitness and survival. However, when nitrogen can be obtained through alternative means, as in socially parasitic lycaenid species feeding on ant brood, the selective pressure for maintaining the use of nutrient-rich host plants is relaxed, enabling the colonization of nitrogen-poor host plants.

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**PFEUFFER, E. 1998.** Zur Myrmekophilie des Idas-Blaulings (*Lycaeides idas* L.). Beobachtungen an den Dammen der Lechstauufen im Unteren Lechtal. *Berichte des Naturwissenschaftlichen Vereins fuer Schwaben* **102**: 41-56. [Formica]

**PIERCE, N.E. 1984.** Amplified species diversity: a case study of an Australian lycaenid butterfly and its attendant ants. *Symposia of the Royal Entomological Society of London* No. 11: 197-200. [Jalmenus evagoras; Iridomyrmex; Australia]

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**PIERCE, N.E., 1989.** Butterfly-ant mutualisms. *In*: GRUBB, P.J., & WHITTAKER, J.B. [Eds]. *Toward a more exact ecology*. Blackwell Scientific Publications. Oxford & London: i-x, 1-468. Chapter pagination: 299-324. [Jalmenus evagoras; Iridomyrmex anceps; Australia]

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**Abstract:** Larvae and pupae of the obligately myrmecophilous social parasites *Microdon myrmicae* (Diptera: Syrphidae) and *Maculinea alcon* (Lepidoptera: Lycaenidae) were found using exclusively *Myrmica aloba* (Hymenoptera: Formicidae) host ants in NE-Portugal. *Ichneumon eumerus* (Hymenoptera: Ichneumonidae) was also found developing in *Ma. alcon* pupae in nests of *My. aloba* at the same site. These are the first records of *Mi. myrmicae* and *I. eumerus* for Portugal, and from *My. aloba* nests. Earlier records that *My. aloba* is the only known host ant of *Ma. alcon* in Portugal are confirmed. Further studies on the biology of these isolated peripheral populations are necessary for their well-planned protection.

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**Abstract:** *Myrmica* ant colonies host numerous insect species, including the larvae of *Maculinea* butterflies and *Microdon myrmicae* hoverflies. Little is known about the interspecific relationships among these social parasites and their host ants occurring in sympatric populations. We investigated communities of social parasites to assess the strategies allowing them to share the same pool of resources (i.e. *Myrmica* colonies). The present study was carried out at five sites inhabited by different social parasite communities, each comprising varying proportions of *Maculinea teleius*, *Maculinea nausithous*, *Maculineaalcon*, and *Microdon myrmicae*. We investigated their spatial distributions, host segregation, the degree of chemical similarity between social parasites and hosts, and temporal overlaps in colony resource exploitation. Spatial segregation among social parasites was found in two populations and it arises from microhabitat preferences and biological interactions. Local conditions can drive selection on one social parasite to use a *Myrmica* host species that is not exploited by other social parasites. *Myrmica scabrinodis* and *Myrmica rubra* nests

infested by larvae of two social parasite species were found and the most common co-occurrence was between *Ma. teleius* and *Mi. myrmicae*. The successful coexistence of these two species derives from their exploitation of the host colony resources at different times of the year.

**WITEK, M., SKORKA, P., SLIWINSKA, E.B., NOWICKI, P., MORON, D., SETTELE, J. & WOYCIECHOWSKI, M. 2011.** Development of parasitic *Maculinea teleius* (Lepidoptera, Lycaenidae) larvae in laboratory nests of four *Myrmica* ant host species. *Insectes Sociaux* **58** (3): 403-411.

**Abstract:** *Maculinea* butterflies are social parasites of *Myrmica* ants. Methods to study the strength of host ant specificity in the *Maculinea-Myrmica* association include research on chemical and acoustic mimicry as well as experiments on ant adoption and rearing behaviour of *Maculinea* larvae. Here we present results of laboratory experiments on adoption, survival, development and integration of *M. teleius* larvae within the nests of different *Myrmica* host species, with the objective of quantifying the degree of specialization of this *Maculinea* species. In the laboratory, a total of 94 nests of four *Myrmica* species: *M. scabrinodis*, *M. rubra*, *M. ruginodis* and *M. rugulosa* were used. Nests of *M. rubra* and *M. rugulosa* adopted *M. teleius* larvae more readily and quickly than *M. ruginodis* colonies. No significant differences were found in the survival rates of *M. teleius* larvae reared by different ant species. Early larval growth of *M. teleius* larvae differed slightly among nests of four *Myrmica* host species. Larvae reared by colonies of *M. rugulosa* which were the heaviest at the beginning of larval development had the lowest mean larval body mass after 18 weeks compared to those reared by other *Myrmica* species. None of the *M. teleius* larvae was carried by *M. scabrinodis* or *M. rubra* workers after ant nests were destroyed, which suggests a lack of integration with host colonies. Results indicate that *Myrmica* species coming from the same site differ in their ability to adopt and rear *M. teleius* larvae but there was no obvious adaptation of this butterfly species to one of the host ant species. This may explain why, under natural conditions, all four ants can be used as hosts of this butterfly species. Slight advantages of particular *Myrmica* species as hosts at certain points in butterfly larval development can be explained by the ant species biology and colony structure rather than by specialization of *M. teleius*.

**WITEK, M., SLIWINSKA, E.B., SKORKA, P., NOWICKI, P., SETTELE, J., & WOYCIECHOWSKI, M. 2006.** Polymorphic growth in larvae of *Maculinea* butterflies, as an example of biennialism in myrmecophilous insects. *Oecologia Berlin* **148** (4): 729-733.

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