Quick guide

Myrmecophiles

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What are myrmecophiles? The term myrmecophile means 'ant lover', from the Greek 'myrmex' (ant) and 'philos' (loving). In the most general sense, any organism that is dependent on ants at least during part of its lifecycle is a myrmecophile. This definition encompasses plants that attract ants with food bodies or extrafloral nectaries, homopterans such as aphids, membracids, and scale insects that provide ants with honeydew, as well as fungi and bacteria that are cultivated or housed by some ants. The majority of myrmecophiles, however, are insects and other arthropods that benefit from the vast resources an ant colony provides in one way or the other. Here we limit our discussion to only those myrmecophiles that are animals living inside ant nests, the so-called ant guests, or inquilines.

What is so special about ant nests? Edward O. Wilson eloquently described large colonies of ants, such as leaf-cutting ants, army ants, or wood ants, as factories constructed inside fortresses. In fact, such colonies are extremely well defended by the ants, so from the perspective of a myrmecophile, they provide 'enemy free space' in an area effectively devoid of predators — that is, once the myrmecophile has figured out how to circumvent aggression from the ants themselves. Furthermore, ant nests provide homeostatic environments where temperature and humidity are controlled by sophisticated ventilation systems, sheltering the queen and the rest of the colony from the elements. Socially organized with a highly effective division of labor, ants have become ecologically dominant in most terrestrial ecosystems, where they successfully compete for resources as scavengers, predators, herbivores, and mutualists. This means that ant nests are an abundant niche where food is often plentiful. Furthermore, these fortresses are typically stable and long-lived, as colonies of many ant species can persist for several decades. It thus comes as no surprise that ant colonies are such a desirable place to call home for a variety of organisms.

How diverse are myrmecophiles? In 1894, Erich Wasmann, an Austrian Jesuit priest and one of the pioneering students of myrmecophiles, documented 1,177 ant guests, and the list has grown at an astonishing rate ever since. Myrmecophily has evolved independently in a large number of taxonomic groups, including flies (Figure 1A), beetles (Figure 1B and C), crickets (Figure 1D), butterflies (Figure 1E), bristletails, millipedes, isopods, snails, mites, aphids, scale insects, wasps, and even snakes. The taxonomically most diverse groups of myrmecophiles are mites and staphylinid beetles.

Ant species with the largest colonies generally harbor the highest diversity of myrmecophiles, while most species with small colonies rarely entertain guests. The reasons for this pattern are similar to those governing the dynamics of island biogeography: large colonies provide a larger variety of microhabitats and can sustain larger and more stable populations of guests over longer time periods.

A particularly striking diversity of myrmecophiles is associated with army ants (Figure 1A–C). Colonies of army ants contain between tens of thousands and millions of workers, which form large raiding parties that overwhelm and kill other arthropods. In a recent overview, Rettenmeyer *et al.* (2010) listed over 300 animals that depend on a single army ant species, *Eciton burchellii*. Most of these species are inquilines, including mites, beetles, scuttle flies, and bristletails. Army ant myrmecophiles are not only extremely diverse taxonomically, they are also abundant. One study estimated that an average *Eciton burchellii* colony harbors 20,000 mites. The nomadic colonies of army ants really are travelling circuses.

What are the interactions between myrmecophiles and ants? Different myrmecophiles interact with the ants in different ways, ranging from parasitism to mutualism. Some prey on the ants or their brood, some are ectoparasites or endoparasites, some are commensals and some are mutualists, providing the ants with beneficial services in exchange for safe housing. Some myrmecophiles are spectacular mimics

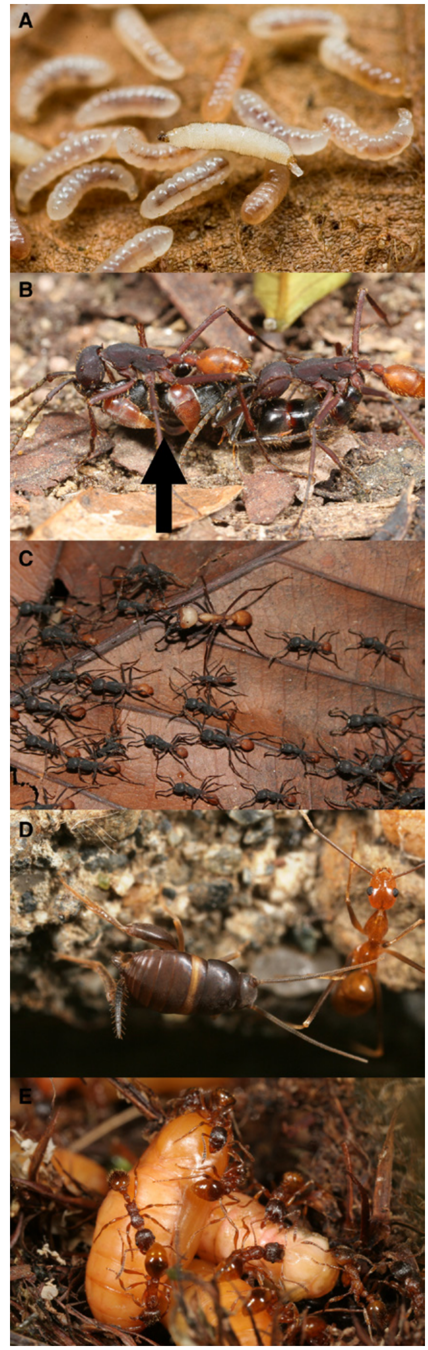

Figure 1. Exemplar myrmecophiles.
(A) Adult female scuttle fly *Vestigipoda longiseta* among the brood of its army ant host, *Aenictus* spec. (photo courtesy of Munetoshi Maruyama). (B) Two limuloid *Cephaloplectus* beetles (arrow) hitching a ride on a *Pachycondyla* prey ant being carried by two *Eciton vagans* army ant workers. (C) A staphylinid beetle of the genus *Ecitophya* runs in the raiding column of the army ant *Eciton burchellii* (just below the major worker). (D) The cricket *Myrmecophilus albicinctus* in a nest of the yellow crazy ant *Anoplolepis gracilipes*. (E) Workers of the host ant *Myrmica rubra* are tending pupae of the alcon blue butterfly, *Maculinea alcon*. (Photos B–E by Daniel Kronauer.)

of ant larvae (Figure 1A), the ant version of a cuckoo. Less integrated guests, on the other hand, often simply avoid direct contact with the ants and spend most of the time in the periphery of the nest.

The effect a myrmecophile has on its host ants often correlates with the level of integration into the host colony, with more detrimental species typically being less well integrated. This is either because myrmecophiles become less virulent as they evolve to integrate into the ant society, or because the ants recognize and attack more harmful myrmecophiles.

Wasmann originally devised a scheme to classify myrmecophiles on the basis of their level of integration and their interaction with the ants. Although this classification has heuristic value in describing interactions, given the great variety of myrmecophilic lifestyles, many species do not naturally fit into one of his rather rigid categories. It has also become apparent that parasitism and mutualism only represent the extremes of a continuum, and that the outcome of any given interaction is dynamic and depends on a variety of parameters. Accordingly, Wasmann's original classification is less used today.

The level of integration into the host colony can also correlate with the level of specialization on a particular ant host. For example, ant crickets of the genus *Myrmecophilus* can be specialists or generalists with respect to their ant host species. *M. albicinctus* is a specialist that exclusively lives in nests of the yellow crazy ant, *Anoplolepis gracilipes* (Figure 1D). The crickets freely walk around the ants without being attacked, and they engage in intimate behavioral interactions with the ants, such as trophallaxis, the sharing of liquid food from mouth to mouth. The crickets cannot survive when removed from the ant colony and they are attacked and killed when introduced into the nests of other ants. *M. formosanus*, on the other hand, occurs with a wide range of ant host species. The crickets feed independently, escape the frequently attacking ants by swift movements, and readily survive outside of ant colonies.

How do myrmecophiles integrate into ant societies? Ants can be fierce hosts and myrmecophiles have adopted a variety of tactics to evade or avoid ant attack. An ant colony is a world of odors, and the prime mechanism to fit in seamlessly is to smell like the host. Ants use a colony-specific, complex profile of cuticular hydrocarbons to tell nestmates from foreigners. Many myrmecophiles acquire this signature by grooming the ants and rubbing against the nest material until they are chemically camouflaged. Some myrmecophiles, like the staphylinid beetle *Atemeles pubicollis*, produce specific chemicals that seem to mimic the brood pheromone of their hosts, and trick the ants into adopting the beetles as one of their own. The beetles also have a second gland that releases an ant appeasement substance used to suppress aggressive behavior.

Behavioral mimics are also common when it comes to soliciting food from the ants, and some species, like *Myrmecophilus* ant crickets, adjust their movements to match those of their host species. Recently it has also been suggested that larvae and pupae of *Maculinea* butterflies mimic the stridulation calls of queen ants to be more attractive to workers. In terms of morphological adaptations, many ant guests have short or hidden appendages that are difficult to snag, and a recurrent theme among myrmecophiles is a smooth and teardrop shaped ('limuloid') body form, which probably slips easily through the grip of the ants' mandibles (Figure 1B).

Some ant guests also strikingly resemble their ant hosts in overall body shape and coloration, a phenomenon known as Wasmannian mimicry. While Wasmann suggested that this form of mimicry is mainly adaptive to deceive the ants themselves, others have argued that it has most likely evolved in response to potential predators, such as birds, which would otherwise be able to pick out tasty myrmecophiles among unpalatable ants. In this case Wasmannian mimicry would not be much different from Batesian mimicry. A classic example of Wasmannian mimicry is the staphylinid beetle *Ecitophya*, which lives in the colonies of neotropical army ants (Figure 1C).

What are the life cycles of myrmecophiles? Their life cycles are as diverse as the myrmecophiles themselves, ranging from simple to complex. Ant crickets, for example, reproduce and spend their entire life inside the ant colonies. They probably disperse to other host nests simply by walking along the ants' foraging trails. Other myrmecophiles have complex life cycles that enable them to track the phenology of their hosts. The alcon blue butterfly, *Maculinea alcon*, for example, deposits eggs on gentian flowers in the summer. The caterpillars initially feed inside the flower before eventually letting themselves down to the ground. If they are lucky, they are picked up by a *Myrmica* ant and carried back to the nest. Here they are assiduously fed by the ant workers, which are unable to discriminate the parasites in their midst. Like several other myrmecophilous butterflies, *M. alcon* has an unusually long period of larval development, with larvae overwintering inside the ant nest. In early summer of the following year, the larvae pupate (Figure 1E) and about a month later the adult butterflies emerge. The butterflies then rush to leave their foster parents behind, in an effort not to be attacked and torn to pieces. These are only a few well-studied examples. For many myrmecophiles, however, the information on life cycle and natural history is still very incomplete.

Where can I find out more?

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