groups. Species that are abundant and ecologically dominant generally make excellent models in mimicry systems, and so it is no surprise that so many myrmecomorphic arthropods have evolved since ants came on the scene some 100 million years ago. Myrmecomorphic species offer abundant opportunities for exploring ecological and evolutionary aspects of mimicry and can lead to a deeper understanding of related fields, such as ant social organization, systematics, and predator-prey relationships.

► Ants
► Mimicry
► Myrmecophiles

References

Edmunds M (1974) Defence in animals. Longman, Essex, United Kingdom, 357 pp

McIver JD, Stonedahl GM (1993) Myrmecomorphy: morphological and behavioral mimicry of ants. Annu Rev Entomol 38:351–379

Oliveira PS (1985) On the mimetic association between nymphs of *Hyalymenus* spp. (Hemiptera: Alydidae) and ants. Zool J Linn Soc 83:371–384

Reiskind J (1970) Multiple mimetic forms in an ant-mimicking clubionid spider. Science 169:587–588

Wickler W (1968) Mimicry in plants and animals. World University Library, London, England, 255 pp

Myrmecophiles

JAMES A. DANOFF-BURG
Columbia University, New York, NY, USA

One of several types of social insect symbionts, myrmecophiles are animals that live with ants for at least part of their life cycle. Other similar symbionts are termitophiles (guests of termites), melittophiles (guests of bees) and sphecophiles (guests of wasps). Of these, myrmecophiles and termitophiles are the most abundant, species-rich and morphologically diverse.

All of these social insect symbionts are thought to be nest parasites. Many previous studies have demonstrated that the guests take food from the hosts and may even prey upon them. Outstanding cases, such as more specialized species, that pass the entirety of their life cycle in the nest, may best illustrate why "nest parasite" is the most commonly cited role of social insect symbionts. Throughout their lifespan, these myrmecophiles receive regurgitations from nurse ants tending the ant larvae, and in the process, drain the resources that would have otherwise gone to the host ant larvae. The larval myrmecophile also preys upon the ant larvae, even in the presence of the nurse ants. Nonetheless, many myrmecophiles may not be solely parasitic on the hosts. More highly adapted species may even provide benefits to their host colonies for at least part of their life cycle, possibly indicating that they are mutualistic with the hosts.

A great number of taxa have evolved myrmecophilous lineages. Mites (Acarina), beetles (chiefly Staphylinoidea), flies (Phoridae) and a few other soil-dwelling insect species have the most myrmecophilous species and are also the most abundant. Myrmecophiles are found living in nests of nearly every species of ant. Colonies that are larger and more persistent at maturity, such as army and driver ants, have more species and individuals of myrmecophiles than smaller mature colonies, such as ponerine and dacetine ants. Additionally, the species found in larger colonies tend to be more specialized than are those living with ants that have smaller, less permanent colonies. Irrespective of the type of colony, the total relative abundance of myrmecophiles is low, often on the order of 1:5,000 ants. Myrmecophiles are found in nearly every area of the nest including the refuse middens, foraging columns, brood chamber and the queen chamber. A single species typically specializes in one of these niches within the nest.

Ecological Categories

Myrmecophilous species generally play one of three consistent roles in the nests of the ants. Symphilic species, the best integrated into the host nest, are species-specific guests who must live with a single species and frequently interact with the host ants. These species usually obtain all food from regurgitations or grooming interactions that they solicit from the hosts. Synoeketes (also called indifferently tolerated guests) are found in ant nests, but do not interact with the host ants. Instead, these guests use the resources that are provided by the nest, such as nest materials, frass, food refuse and other nest detritus. Host ants will attack these species if the myrmecophile is too apparent, forceful, or bothersome. Synecthrans (also called persecuted guests) are only occasionally found with ants and may merely raid the nest for food. This ecological category of myrmecophiles usually does not live within the nest, instead residing in the surrounding litter or soil. Other ant symphiles often classed as myrmecophiles include trophobionts (ant-tended phytophagous insects, usually Hemiptera and Lepidoptera) and ant parasites (mites, phorid flies, or parasitic wasps).

A simpler organizational scheme to help label those species that fall into more than one of the above three categories classifies myrmecophiles as either integrated or non-integrated species. Integrated species are those that play a role in the social life of the colony, including symphiles who occasionally attack the hosts and trophobionts. The roles played by these species can range from procuring food (e.g., trophobionts), to grooming the hosts, and providing what may be psychoactive chemicals (e.g., symphiles). Non-integrated species normally do not interact with the hosts and, instead, use the nest or the ants themselves as an ecological niche to be exploited. This category includes synoeketes, synecthrans and parasites.

Evolutionary Trends

Several trends are consistent with these ecological categories. Obligate, strongly integrated symphiles tend to be host-specific and are found with a single or a few closely related host species. These species are strongly adapted to living in nests of only one particular host species, whereas non-integrated synecthrans are usually not host-specific. They are, instead, found with whatever ant species presents the necessary ecological resources needed by the guest. Most species of myrmecophiles are integrated into the host nest, as this mode of living tends to produce a greater number of species through the processes of resource tracking and coevolution with the host ants. Therefore, as host ants speciate, any well-integrated, species-specific myrmecophile may also speciate and come to specialize on the newly evolved host species. Non-integrated species generally do not have strong parallel evolutionary relationships with their host ants because they generally are not species-specific.

Chemical Communication

Strongly integrated myrmecophiles tend to have a great diversity of adaptations that help to either mimic or crack the communication code of their hosts. These adaptations can include chemical, morphological and behavioral traits. Because they help to break the code, these adaptations often become useful as integrating mechanisms that enable the myrmecophile to enter and become a part of the colony. Non-integrated myrmecophilic species may have, at most, a single, rudimentarily developed integrating mechanism.

Presumably because most communication in the ant colony is done chemically, most well-integrated symphilic myrmecophiles are able to chemically communicate with the host ants. Myrmecophiles both send and receive chemical messages with the host ants. Typically, communications from the host ants to the myrmecophiles are intercepted signals between nestmate ants, rather than pure, interspecific communications. Species that ancestrally possess extensive glandular systems, such as staphylinid beetles of the subfamily Aleocharinae, have evolved prominent structures associated with the glands, such as trichomes and brushes. Complicated processes of chemical exudation have evolved in these species such that some myrmecophilous species use a sequence of three chemicals to first defend against, then appease, and then convince an ant to adopt them and carry them into their nest. These exudates often trigger actions by the ants that mimic the normal brood care behavior of the host ants. Well-integrated, obligate symphiles are frequently able to secrete chemicals that generally resemble the cuticular hydrocarbons of the host. In so doing, they are able to mimic the chemicals that are thought to form the basis of colony odor and nestmate recognition, thereby gaining at least initial entrance to the colony.

Morphological Mimicry

Morphological adaptations can include similar color patterning to the host, development of prominent glandular trichomes and the evolution of specialized body plans. Myrmecoidy, the most unique morphological specialization among myrmecophiles, involves a suite of characteristics including a petiolate abdomen, narrow body, long legs and an expanded basal antennal segment to resemble geniculate antennae. Typically, well-integrated, host-specific symphilic species adopt some aspects of myrmecoidy. In contrast, most synoeketes and synecthrans have either retained their generalized bauplan or have evolved a limuloid, heavily-sclerotized defensive (or trutztypus) form (Fig. 118).

Limuloid species, such as many staphylinid beetles, are characterized by reductions in the appendages and head and development of overlapping, sclerotized body regions so that the insects appear teardrop-shaped. When attacked, species with defensive forms retract their appendages into grooves and feign death until the agitated ant departs. Specializations of the cuticle of the guest so that they resemble their hosts are also common. For example, host-specific phoretic mites have cuticular surfaces that so closely mimic those of their hosts that it is hypothesized that the ants are incapable of detecting the presence of the mites.

Most species of myrmecophiles have not evolved any morphological adaptations, instead retaining the ancestral species bauplan. Morphologically generalized species tend to be either synoeketes or synecthrans, and are rarely well integrated into the colony. These species must instead manipulate the host behavior using either chemical or behavioral specializations.

Myrmecophiles, Figure 118 **Myrmecophiles, particularly well-integrated species such as these *Dinardilla mexicana* and *Sceptobius dispar* (Coleoptera: Staphylinidae: Aleocharinae), frequently interact with their host ants. The obligate symphiles require the presence of the hosts to live and are rarely found outside their company.**

Behavioral Traits

A myrmecophile may have evolved behavioral traits that allow it to interact peaceably with the host ants. These are found in all types of guests, irrespective of how well integrated they are. Strigilation occurs when the myrmecophile either licks or scrapes the oily secretions from the surface of the ants and serves to acquire what is likely the host odor as well as to provide some food to the guest. Guests often perform a vigorous bout of strigilation when first introduced into a novel nest. This behavior frequently stops the attacks that invariably occur when a myrmecophile first enters a new colony. Behavioral traits such as episodic walking that is similar to that of ants, as well as antennation upon greeting, are frequently manifested in well integrated guests. Whether these traits are selected by the hosts or another species that may be predatory on the guests, such as antbirds, is not clear. It is unlikely that the operator of selection is identical in all cases.

Most research on myrmecophiles conducted at present focuses on Lycaenidae caterpillars, which are trophobionts and are tended by the ants for the honeydew and a diversity of chemical exudates by the caterpillars. The caterpillars are frequently studied within the field of myrmecophily, in part because most species are easily accessible on the branches of a plant. The adult butterflies are not tended nor are they ant associates. The caterpillars are not, strictly speaking, symphiles because they do not live with the ants, but instead are only tended by the hosts. Most of the adaptations of these caterpillars involve chemical cues, including the secretion of many chemicals from a spectacular diversity of specialized exudatory organs. As an example, the caterpillars often produce an alarm pheromone used by the host ants, so that if they are attacked, they signal for help from the host ants.

References

Kistner DH (1979) Social and evolutionary significance of social insect symbionts. In: Matthews RW (ed) Social insects, Vol. I. Academic Press, New York, NY, pp 339–413

Hölldobler B, Wilson EO (1990) The ants. Chapter 13. Harvard University Press, Cambridge, MA

Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annu Rev Entomol 47:733–771

Myrmeleontidae

A family of insects in the order Neuroptera. They commonly are known as antlions.

► Lacewings, Antlions and Mantidflies

Mystax

A patch of hair or bristles located above the mouth, especially in robber flies (Diptera: Asilidae). In robber flies it is also called a mouth beard.

Mythicomyiidae

A family of flies (order Diptera).

► Flies

Mythology and Insects

RON CHERRY
University of Florida, Belle Glade, FL, USA

The study of insects and other arthropods in mythology falls into the realm of cultural entomology. However, in order to approach this subject, it is necessary to understand what mythology is. Quite simply, mythology is the study of myths. One definition of a myth commonly used in everyday conversation is that a myth is something false or imaginary. This definition has nothing to do with mythology. As used in mythology, a myth is a story, presented as having actually occurred in a previous age, explaining the cosmological and supernatural traditions of a people, their gods, heroes, cultural traits, religious beliefs, etc. Mythology is also closely related to religion as exemplified by the saying, "One man's religion is another man's mythology."

Myths in general may be categorized into certain types such as creation myths, emergence myths, etc., and this is also true of many insect myths. For example, the creation of the Milky Way Galaxy by a beetle is explained in a creation myth of the Cochiti tribe of North America. The Negritos of the Malay peninsula have a diving myth in which a beetle dives into mud and brings up earth which become land. The Navajo of North America have an emergence myth in which the origin of the Navajo from the earth is explained in a myth