Myrmecomorphy

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Myrmecomorphy, or the morphological and behavioral mimicry of ants, has evolved at least 70 times in the arthropods – 15 times in spiders, at least 10 times in plant bugs, and seven times in staphylinid beetles. More than 2,000 species of myrmecomorphic arthropods have been described thus far, belonging to over 200 genera in 54 families. Myrmecomorphy forms a subset of ant mimicry, which includes all species that resemble ants through convergence in morphological, behavioral, chemical, or textural characters (Fig. 117). The other major group of ant-mimetic species are the myrmecophiles, or those arthropods that associate closely with ants, but do not necessarily resemble them morphologically. Although some are also myrmecomorphic, most myrmecophiles have chemical and/or textural characters that facilitate a close relationship with their ant hosts. Here we describe signal properties of myrmecomorphic arthropods, present their taxonomic distribution, and discuss their adaptive significance.

Signal Properties of Myrmecomorphic Arthropods

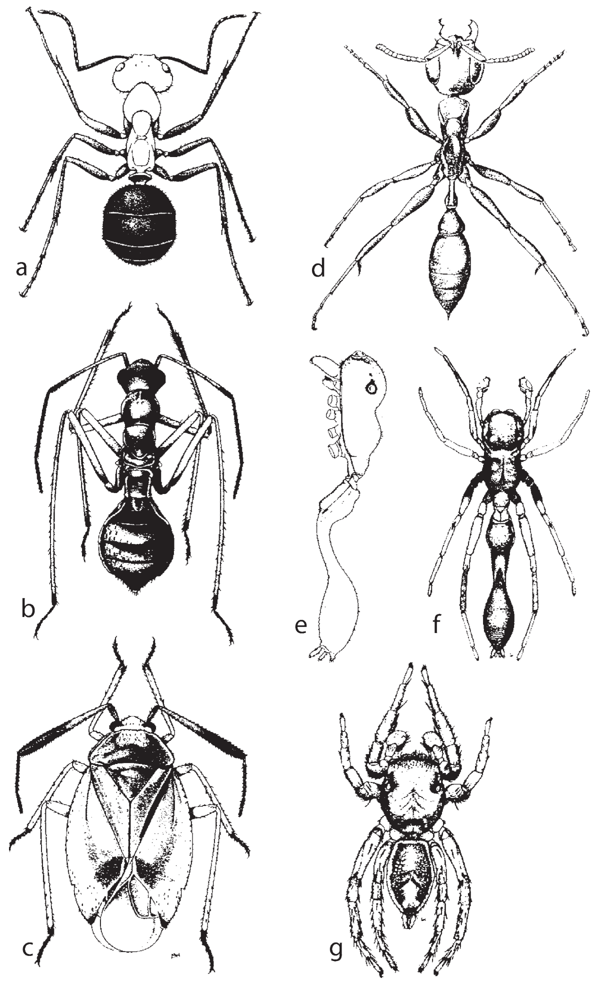
Mimicry can be defined as a system that involves an organism (the mimic) which simulates signal properties of another organism (the model) so that the two are confused by a third organism (the operator) and the mimic gains protection, food, or a mating advantage as a consequence of the confusion. Myrmecomorphic species express a variety of signal properties that enhance their resemblance to ants, involving shape, pattern, texture, color, behavior, and size. In this section, we review how mimicry is achieved for a representative sample of myrmecomorphic spiders and insects, and describe some examples of intraspecific variation.

Spiders

Spiders have a wide variety of body forms, but compared to ants, typically have relatively short, hairy bodies. Ants are generally elongate, have a medially constricted body with a distinct petiole, elbowed antennae, large compound eyes, and typically a shiny integument. Ant-like spiders on the other hand, are relatively elongate, have a medial constriction of the cephalothorax into a head and alitrunk, with a narrowing of the posterior cephalothorax or anterior abdomen to produce a petiole and gaster. Ant-like spiders often use the first or second pair of legs as if they were antennae, have pigmented spots on the cephalothorax that resemble large compound eyes, often have shiny setae or dense mats of reflective hairs to give a shiny illusion, and can have a transparent cuticle to give the illusion of a constriction. Many ant-like spiders match the color of their ant models closely. Populations of the jumping spider *Synemosyna aurantiaca* are color polymorphic, with yellow morphs resembling the ants *Pseudomyrmex flavidulus* and *P. oculatus*, and black morphs resembling *P. gracilis*. Correspondence in the color of individual structures in not uncommon, as in the species-specific mimic *Castianeira memnonia*, in which the yellow terminal segments of the front legs correspond to the bright yellow antennal apices of its otherwise black ant model, *Pachycondyla obscuricornis*. The evolution of ant-like behaviors in myrmecomorphic spiders is not surprising, given that behavior is often identified as the most conspicuous feature of ants. In both clubionid and salticid spiders, the first or second pair of legs are waved around in front of the spider, contacting the substrate in much the same way that ants use their antennae. The antennal illusion is often supplemented by a zigzag running gait, and in jumping spiders, there is a general reluctance to jump. In general, the spiders that are most difficult to distinguish from ants in the field are those that have a combination of morphological and behavioral ant-like features.

Insects

While insects are confronted with many of the same problems as spiders for evolving ant-like form, the possession of a similar body plan requires less profound modification. A major constraint to myrmecomorphy, however, is the one or two pairs of wings found in most adult insects. Consequently, the loss or reduction of wings in the adult is common in ant-like insect species, often accompanied by a constriction of the posterior thorax and/or anterior abdomen. In those species of myrmecomorphic insects that have retained their wings, oblique or transverse pale marks or bands of pale hairs typically interrupt the otherwise darkened forewings, to produce the illusion of a petiole. Still other species, such as alydids and mantids, resemble ants only in the immature form. Compared to many insects, ants have relatively large heads with well developed mandibles. In general, myrmecomorphic insects tend to possess relatively larger heads than their non-mimetic relatives, and the illusion of large mandibles in many ant-like plant bugs is accomplished by enlargement of the ventral region of the head, which also brings the head forward into a more ant-like horizontal position. Many ant-like insects mimic the elbowed antennae of ants through differential pigmentation or enlargement of various antennal segments. Myrmecomorphic insects often display microstructural and color modifications that enhance mimicry, including: (i) silvery, reflective hairs to increase body shine, or when arranged in bands, to act as an interruptive agent; (ii) changes in surface texture corresponding with smooth, roughened, or pitted areas on the ant's body; (iii) thoracic or abdominal spines to mimic those on the alitrunk and petiole of some ants; and (iv) color polymorphisms that match available ant models (Fig. 117).



Myrmecomorphy, Figure 117 Ants (top), myrmecomorphs (mimics; middle), and non-mimetic relatives (bottom). (a) *Formica obscuripes* (Formicidae), western North America. (b) *Coquillettia insignis* (Miridae), western North America. (c) *Pronotocrepis clavicornis* (Miridae), western North America. (d) *Pseudomyrmex tenuis* (Formicidae), Central and South America. (e, f) *Synemosyna aurantiaca* (Salticidae), Trinidad, Brazil. (g) *Habronattus mexicanus* (Salticidae), southern North America, Central America, Caribbean.

As in the spiders, morphological adaptations in ant-like insects are often accompanied by resemblance in behavior. Many staphylinid beetles are difficult to distinguish from their army ant hosts, due to very similar patterns of locomotion.

Regarding the behavior of alydid bugs, Oliveira (1985) remarks, "Nymphs of *Hyalymenus* have a highly differentiated ant-like morphology which is achieved by several structural adaptations. The similarity is greatly enhance by the nymph's ant-like behavior, notably the rapid zig-zag locomotion, the constantly agitated antennae, and the up and down movement of the abdomen (similar to an alarmed ant)".

Transformational Mimicry

Because their ant models are holometabolous, mimic species that develop gradually, like plant bugs and spiders, tend to resemble a range of appropriately sized models, usually representing two or more ant species or genera. This phenomenon is called transformational mimicry, and has been described for mantids, plant bugs, alydid bugs, running spiders and jumping spiders. Species that rely on transformational mimicry are typically genus-specific mimics, presumably because features that provide species-specificity on one life-history stage constrain the evolution of features that promote close correspondence to different ants in other stages.

Sexual Dimorphism

While not common in ant-mimetic systems, sexual dimorphism has been described in several groups of spiders and some Hemiptera/Heteroptera. The adult males of the jumping spider *Zuniga magna* are striking mimics of *Pseudomyrmex gracilis*, while females closely resemble the ponerine *Pachycondyla villosa*. In both cases, the species-specific mimicry involves remarkably accurate structural and color correspondence between model and mimic. Many myrmecomorphic plant bugs are sexually dimorphic; brachypterous or apterous females are among the best morphological mimics of ants, while the macropterous males are comparatively poor pattern mimics.

Taxonomic and Geographic Distribution of Myrmecomorphy

Myrmecomorphy has been identified in nine families of spiders and 45 families of insects, representing 11 different orders. Over 200 spider and insect genera are known to contain myrmecomorphs, and the number of species involved is certainly in the thousands worldwide. Ant-mimicry has arisen at least four times in the spider families Clubionidae and Corinnidae (running spiders), three times in the Salticidae (jumping spiders), and several times each in the Aphantochilidae, Araneidae (orb-weavers) and Theridiidae (comb-foot weavers). In the plant bugs (Heteroptera: Miridae), morphological resemblance to ants has arisen no fewer than ten times, and this family contains the highest diversity of myrmecomorphic species among insects.

Myrmecomorphic arthropods are found in all major regions of the world except Antarctica and the extreme northern Holarctic. The number of species increases toward the tropics, mirroring the pattern observed for other mimetic species, for ants themselves, and for most other plant and animal groups.

Adaptive Significance

The adaptive significance of myrmecomorphy has not been clearly established in most cases. The most common mimetic hypotheses to explain myrmecomorphy are Batesian, Wasmannian, and aggressive mimicry.

Batesian Mimicry

For those ant-like species that do not live with or attack ants, the most widely supported hypothesis for myrmecomorphy is Batesian mimicry. The evolution of Batesian mimicry is presumed to occur within the context of an interactive system involving model, mimic, and a predaceous operator(s). The system has four basic features: (i) certain arthropods (models) are unacceptable to predators and advertise this, (ii) predators (operators) learn about this unacceptability, (iii) generalization in predators takes place allowing acceptable species (mimics) to benefit by resemblance, and (iv) visual discrimination by predators is sufficient to select for increased mimetic resemblance. The behavioral and ecological conditions presumed to favor the evolution of Batesian mimicry include: (i) the model must be an unacceptable prey item to at least some predators, (ii) the mimic must be an acceptable prey item, (iii) the model and mimic must have similar temporal and spatial distributions, (iv) the model must be common relative to the mimic, (vi) the mimic must have signal properties that deceive visually oriented predators within a community of alternate prey, and (vii) predators must be able to learn. Our discussion on the evidence for Batesian mimicry addresses these conditions by describing the qualities of species within selected myrecomorphic systems, and offering observational and experimental evidence of functional Batesian mimicry in the field.

In the best known myrmecomorphic systems, models, mimics and predators tend to possess ecological and behavioral features consistent with a Batesian mimicry hypothesis. Like bees and wasps, ants have features that make them ideal models in Batesian mimicry systems. Ants are among the most common and conspicuous of insects, and workers of many species are aggressive and distasteful. Ants are entirely social, and have alarm pheromones used for common defense against enemies. Therefore, small vertebrate and invertebrate predators must hunt them with caution. Although a variety of small predators attack or specialize on ants, these species are comparatively rare, and typically use special hunting tactics.

Myrmecomorphs that do not attack ants are almost always found in the same microhabitat as their models, but do not associate closely with ants, and often show avoidance reactions to them. Although little quantitative work has been done to estimate population sizes of mimics in relation to their models, observational evidence suggests that ants are almost always more common than co-occurring mimics. Most evidence suggests that free-living myrmecomorphs are relatively palatable – spiders serve as important prey items for birds and lizards, and myrmecomorphs are no exception to this general rule.

The most likely predators that could serve as operators in Batesian mimicry systems are small vertebrate predators such as lizards and birds, and arthropod predators such as jumping spiders and wasps. These predators possess relatively good vision, necessary to select for the detailed structural and behavioral adaptations seen in many myrmecomorphic species. Vertebrate species are also well known to be capable of associative learning, including experimental studies involving mimetic insects. While associative learning has been demonstrated in social insects, similar data on arthropod predators are scanty at best, possibly because of the greater difficulty in choosing meaningful stimuli for arthropods that are solitary, more reclusive than bees and ants, or have unknown feeding habits. Nonetheless, a few studies have demonstrated the capacity for associative learning in arthropod predators, involving wasps, mantids, crab spiders, and assassin bugs.

Some of the most convincing observational evidence that supports Batesian mimicry in ant-like species comes from the existence of a number of remarkably close species-specific correspondences between model and mimic, particularly among the spiders. For example, the running spider *Mazax rettenmeyeri* features a unique ridge of erect hairs along the midline of the cephalothorax, which closely approximates the thoracic keel of its model *Camponotus sericeiventris*. Other characteristics of the mimic, such as color, shape and behavior, accentuate the resemblance between model and mimic. Many other species-specific pairs of model and ant mimic have been described worldwide.

Experimental evidence in support of Batesian mimicry includes feeding trials in which visually oriented predators behave similarly toward model and mimic. For example, in a study on the ant-mimetic plant bug *Coquillettia insignis* in north-eastern Oregon (USA), both the jumping spider *Sassacus papenhoei* and the assassin bug *Sinea diadema* accepted non-mimetic plant bug prey significantly more often than the ant-mimic *Coquillettia insignis*, while their behavior toward the model ant Formica fusca and toward the mimic was indistinguishable. In addition, the assassin bug *Siadema diadema* was able to learn and remember unpleasant experiences with the ant model. While about half of the field-collected specimens of this assassin bug attacked the ant-mimic *Coquillettia insignis*, after close confinement with the ant *Formica fusca*, individual assassin bugs that had previously attacked *C. insiginis* were significantly less likely to do so.

Wasmannian Mimicry

Myrmecophilic arthropods that also possess a body shape or texture that closely resembles their ant models are called Wasmannian mimics. Some observers have argued that the body shape and texture of ant-like rove beetles that associate with army ants evolved as a consequence of selection by the ants themselves. This view is consistent with the general observation that when encountering one another, doryline army ants and other swarm raiding species antennate the petiolar area of their nestmates, and that the same behavior performed by a myrmecomorphic rove beetle allows the mimic to function with the colony as if it were an ant. Yet among the rove beetles that associate with ants (myrmecophiles), most species that do not resemble ants occur entirely within the nest of their hosts, while all known ant-like rove beetles live with legionary ants, spending the majority of their adult lives on the surface, exposed to the full range of visually oriented predators that accompany the foraging raids. Hence, ant-like body form in some rove beetles may have evolved as a consequence of selection by both ants (Wasmannian mimicry) and by visually oriented predators (Batesian mimicry).

Aggressive Mimicry

Ants represent an abundant and conspicuous source of protein for potential predators, and many ant species care for other insect species, from which they extract nutrients. These features attract a considerable diversity of arthropod predators, and among these predators are some of the more remarkable examples of aggressive ant-mimicry. Aggressive mimicry differs from Wasmannian mimicry in that aggressive mimics do not live with their ant models, and typically associate with ants just closely enough to access their resource, either the ants themselves, or their symbiotic associates. Spiders of the genus *Aphantochilus* possess a shiny and granular integument, characters that are thought to facilitate acceptance by their cephalotine ant models, which are their only source of food. The adult crab spider *Amyciaea forticeps* attacks workers of the weaver ant *Oecophylla smaragdina*. Under normal circumstances, the crab spider does not closely resemble the weaver ant. While hunting, however, the spider adopts a behavior in which it looks like a dying or struggling weaver ant, and other workers often come nearer to investigate. The spider then pounces on its prey and quickly withdraws to a more remote location. Myrmecomorphic arthropods may also have evolved ant-like morphology and behavior to gain access to the Hemiptera that some ants tend for honeydew. Several authors have noticed a correlation between the distribution of ant-tended aphids and various species of the ant-like plant bug *Pilophorus*. It is widely believed that myrmecomorphy in *Pilophorus* serves as a temporary illusion, allowing the plant bugs to closely approach and seize their aphid prey.

Mimicry is very common in nature, and occurs in a bewildering array of plant and animal 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

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Myrmecophiles

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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