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Review Article

Ant-Mimicking Spiders: Strategies for Living with Social Insects

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Mimicry is a fascinating topic, in particular when viewed in terms of selective forces and evolutionary strategies. Mimicry is a system involving a signaller, a signal receiver, and a model and has evolved independently many times in plants and animals. There are several ways of classifying mimicry based on the interactions and cost-benefit scenarios of the parties involved. In this review, I briefly outline the dynamics of the most common types of mimicry to then apply it to some of the spider-ant associative systems known to date. In addition, this review expands on the strategies that ant-associating (in particular ant-mimicking) spiders have developed to minimise the costs of living close to colonies of potentially dangerous models. The main strategy that has been noted to date is either chemical mimicry or actively avoiding contact with ants. If these strategies warrant protection for the spider (living close to potentially dangerous models), then the benefits of ant associations would outweigh the costs, and the association will prevail.

1. Introduction

The phenomenon of mimicry has intrigued numerous biologists, prompting studies from natural history to behaviour, ecology, evolution, and most recently genomics, to name but a few [1]. Perhaps mimicry so readily attracts attention because it is an evident example of natural selection in action. Mimicry—or the resemblance of one organism (or certain aspects of) to another, taxonomically unrelated one—almost always involves three parties: the signaller (mimic), the signal receiver (or operator), and the model. The mimics in these cases must have a selective advantage over nonmimics, and therefore the particular phenotype is fixed in these populations. The classification of mimicry largely depends on the functions of the parties involved and has, based on this scheme, been subdivided down to 40 theoretical classes, or types of mimicry [2], though the focus is generally on the most common types: Batesian, Müllerian, and aggressive mimicry.

Batesian mimicry, named after H. W. Bates, pioneer in the study of mimicry in Amazonian butterflies [3], is defined by a palatable mimic gaining protection from predators (the signal receiver in this case), by resembling a noxious or unpalatable model organism. In Müllerian mimicry, the line of "palatability" between mimic and model is less clear, with emphasis being placed on a certain phenotype of various organisms being reinforced and acting as a deterrent for predators. A third type of mimicry commonly encountered in nature is aggressive mimicry, so-called because the mimic, rather than gaining protection from potential predators, more easily gains access to resources or prey (sometimes the model itself) through its resemblance to another organism. Although many cases of mimicry can easily be categorised, sometimes an organism displays different strategies, either at the same time or at different stages of its life, such as the cuckoo which was found to be a Batesian mimic as an adult, and an aggressive mimic in other birds' nests [4].

In Batesian mimicry, the mimic is under predator-mediated selection thus resembling a noxious or unpalatable model, whereas traits of aggressive mimics are under pressure to deceive their prey. This means that the sensory channel of the receiver (be it visual, chemosensory, or other) greatly influences the evolution of the mimic [5]. In cases where learning by the signal receiver is involved, it is also important that the mimics do not outnumber the models and that both models and mimics live in sympatry [6]. Be it for protection from predators or access to resources, mimicry has arisen numerous times throughout animals and plants as a recurrent evolutionary stable strategy [6]. This is evidence for strong selection for traits associated with mimicry, where the fitness of the mimic is expected to increase with a closer resemblance to the model [7, 8]. Studies based on theoretical population genetics have modelled Batesian mimicry traits and polymorphism within populations [9, 10]. The fact that Batesian mimicry may be a costly trait must also be considered together with an increased number of parameters such as the cognitive constraints of the signal receivers [11, 12]. Selection pressure on mimics to resemble a model very much depends on the visual system of the receiver [5]. In the particular case of Batesian mimicry, where mathematical models predict greater protection from predators with increasing resemblance to the model organism, the main question that arises is why are there still “imperfect” mimics or those that bear only a slight resemblance to any one model? One explanation given is that the term “imperfect” is subjective, dependent on the signal receiver; what may appear imperfect to a human observer may in fact be seen otherwise by potential predators [13]. Alternatively, an imperfect mimic may be an intermediate phenotype or one of polymorphism [14]. Certain conditions may relax the selection pressure towards a “perfect” phenotype, for example, if the model is very noxious [15] or if behavioural traits reenforce morphology [16]. The selection force towards one “perfect” phenotype is countered by polymorphism, which may arise due to kin selection [17], in some cases the potential cost of being too conspicuous [18] or through selection from receivers with opposing predatory preferences [19].

Mimicry occurs in all forms of terrestrial and aquatic plant and animal life [6]. For example, among vertebrates, marine fishes count with at least 98 cases of mimicry, including Batesian, Müllerian, aggressive, and social (or cases where the mimic aggregates with the school of models) [20]. Perhaps the most diverse and varied forms of mimicry can be found in arthropods, due to their impressive diversity resulting from relatively short generation times, which increase the recombination events, which in turn allow for more genetic diversity. Among terrestrial arthropods, ants are a common model system [21, 22]. Here, I intend to focus on an exceptional group of arthropods, namely, the spiders, and their varied forms of ant mimicry. Even though the majority of spiders are web builders [23], the most striking examples of ant associations can be found in cursorial spiders. Thorough and up-to-date reviews of ant-mimicry in spiders already exist [24–27], so my aim here is not to replicate the information found in these papers, but rather to focus on the various strategies that can be found in these spiders minimising the costs and maximising the benefits of living with or close to ants. I will do this by first talking briefly about ant association and then introducing various examples of benefits and costs to the spiders. Throughout, ant-mimicry will refer to cases of morphological and/or chemical mimicry and “ant associations” include mimics as well as spiders that do not mimic ants but nevertheless gain some advantage living close to ant colonies.

2. Ant Associations in Arthropods

Being social insects, ants form large colonies with numerous individuals, thus satisfying the condition of mimicry where any mimic should be at lower densities than the model [6]. For the purpose of Batesian mimicry, ants are also good model organisms because they are unpalatable for many other animals due to characteristics, or combinations thereof, such as formic acid, stings, strong mandibles that bite, and in general an aggressive nature [21, 22, 28]. So acquiring morphological and/or behavioural resemblance to ants confers a certain degree of protection from predation to otherwise palatable arthropods.

Morphological and/or behavioural resemblance to ants, also known as myrmecomorphy, has evolved at least 70 times in more than 2000 described species belonging to 54 arthropod families in groups such as spiders, plant bugs, and staphylinid beetles [21]. In spiders alone, myrmecomorphy can be found in numerous species belonging to 13 different families [24, 25]. Myrmecomorphic spiders have morphological and/or behavioural modifications that increase their resemblance to ants. These include a generally narrower body and longer legs compared to other spiders: at times a constricted carapace or abdomen giving the impression of a three- instead of two-segmented body. The cuticular surface of myrmecomorphic spiders is often strikingly similar to that of their model ant species as well, including hairs and coloration and fake eye spots. As spiders have four pairs of legs while ants have three and one pair of antennae, myrmecomorphic spiders often raise their first pair of legs and wave them as an “antennal illusion” [29, 30] and also carry out an up-and-down movement of the gaster, akin to some ants when they are recruiting nestmates [30–32].

The family of spiders with perhaps the most striking examples of myrmecomorphy is the jumping spiders (Araneae: Salticidae). Here again, myrmecomorphy has evolved independently various times [33], and the most speciose genus of myrmecomorphic salticids is *Myrmarachne*, which has more than 200 described species and many more undescribed [34].

Arthropods that are not morphological mimics of ants can nevertheless form close associations with colonies. These arthropods are generally referred to as myrmecophiles, and their association to ant colonies can vary in extent [24, 25]. The ecological advantage for myrmecophiles is that the nests of many ant species are relatively stable microhabitats where resources can be readily available, and a certain degree of protection is conferred as well [24, 25]. Some examples of this will be given in the following section.

3. Benefits of Ant Associations for Spiders

The fact that ant mimicry exists in such varied forms across many invertebrate taxa implies that the benefits must outweigh the costs. As social insects, ants form colonies, often containing thousands and in some cases millions of individuals [22], and in many cases their nests are sophisticated structures and spaces in the environment. This has advantages for invertebrates that associate so closely with ants that they actually live inside the ants’ nests. The nest provides a stable environment, often with plenty of resources to feed on, be it other inquilines, materials the ants gathered or bred, or the ants/larvae themselves [35]. For example, the linyphiid spider *Masoncus pogonophilus* feeds on collembolans that also live inside its host ant nests [36], while the salticid spider *Cosmophasis bitaeniata* enters ants' nests to feed on their larvae [37].

In the case of myrmecomorphic spiders, the main benefit is that they gain protection from ant-averse predators that would otherwise feed on them. Several experiments have been carried out to show that myrmecomorphic spiders are Batesian mimics because they gain protection from potential predators such as wasps [38], mantises [39], and other spiders [40–42] and that ant-aversion is even innate in some predators [39, 43]. Salticids as predators alone were suggested to be a driving force for myrmecomorphy in jumping spiders [44]. To date, there is little evidence that myrmecomorphy serves in protecting the spider directly from the ant, as the ants' primary sensory channel seems to be chemical [45]. On the other hand, most myrmecomorphs do not routinely prey on ants, although there have been cases reported where the myrmecomorphs do prey on ants [46–48].

Within Batesian ant-mimicking spiders, several alternative or supplementary strategies have been described that confer protection from potential predators. One of these strategies is transformational mimicry, meaning that the model mimics different species as it grows [49]. Several *Myrmarachne* species are transformational mimics, thus always being approximately the same size as their model ants [50]. Another strategy involves the common occurrence among males of several *Myrmarachne* species that have enlarged chelicerae (thought to be a sexually selected character [51]), a phenotype that could be seen as reducing their resemblance to ants. However, these males were found to be "compound mimics" resembling ants carrying a "parcel" in their mandibles [52]. Additionally, *Myrmarachne melanotarsa*, a spider unusual in that it lives in aggregations, resembles, as a group, a whole ant colony [53]. Selection has acted on these varied strategies found among myrmecomorphs, increasing their resemblance to ants, yet forces countering the selection of "perfect" resemblance to ants also exist, as polymorphism has been recorded in various *Myrmarachne* species [54, 55].

So the benefits for spiders of associating with ants come mainly in the form of increased chances of survival for the individuals. These increased survival chances are either due to an easier access to readily available resources or heightened protection from predators. If these benefits did not exist, selection would not have favoured the traits allowing these spiders to associate with ants. However, for the spiders there are not only benefits to these associations, but also costs. For the associations to persist in evolutionary terms, the benefits must still outweigh the costs, meaning that the costs are kept minimal. The next section deals with the spiders' strategies that minimise the various costs.

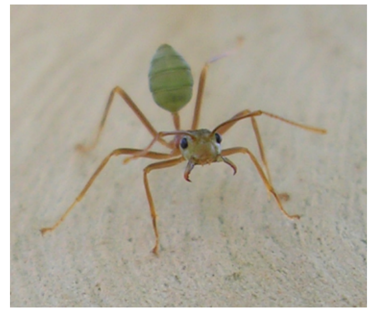
4. Minimising Costs of Ant Mimicry

The costs of ant mimicry for spiders come in varied forms. First of all, for myrmecomorphs there is the fact that morphological modifications, such as a restriction of the abdomen, mean that females can lay fewer eggs than non-myrmecomorphic spiders ([25] and references therein). A major problem that myrmecomorphic spiders face is that while their resemblance to ants confers protection from ant-averse predators, they are more prone to fall victims to predators that specialise on eating ants [19, 56]. To counter this problem, jumping spiders of the genus *Myrmarachne* have developed signals using their first pair of legs, aimed at deterring ant-eating salticids from attacking [57]. This "display posture" of holding the first pair of legs almost fully extended, elevated 45°, and held out to the side 45° [57] was also noted in other studies on *Myrmarachne* when the spiders were in the presence of ants [58], and it resembles the aggressive display posture of worker ants from certain species such as *Oecophylla smaragdina* (see Figure 1). This display posture, while being efficient in deterring salticid predators, seems to be adopted by *Myrmarachne* as a general measure when threatened, before fleeing, and may also affect ants—such as *O. smaragdina*—that have a more sophisticated visual system [59, 60].

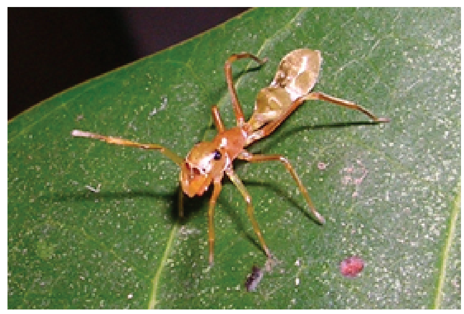
Perhaps the biggest challenge for ant-associating spiders comes from living close to ant species, most of which would react aggressively towards inquilines or mimics themselves. In fact, spiders may easily be killed or injured by their own model [61]. The negative effects of ants on spiders are not only restricted to the individuals' survival, but also the spiders' reproductive success in some cases, in that they are less likely to mate if the ants are close by [62]. Certain spiders that have developed a close association with ants deploy chemical mimicry to be able to live among and at times exploit the ants [63]. *Cosmophasis bitaeniata* even acquires the hosts' cuticular hydrocarbons specific to the ant colony with which it lives [64], as the cuticular hydrocarbons are transferred to the spider while feeding on the ant larvae [65]. In the case of this spider, the host ant species, *Oecophylla smaragdina*, is particularly aggressive [59, 60, 66] (see Figure 1), and chemical mimicry is a form of protection. Through chemical mimicry, many nonant nestmates are able to enter ant colonies and take advantage of the ants and/or their mutualistic relationships [67]. Some myrmecophiles are small enough to live among the ants undetected without chemical mimicry [36], while others, such as *Gamasomorpha maschwitzi*, have alternative strategies to chemical mimicry which are to date poorly known but could consist of acoustical, behavioural, and/or morphological adaptations [68].

For those spiders that do not live in, or enter into the ants' nests, there does not seem to be as much danger as of being killed by an ant. However, for the myrmecomorphs that are Batesian mimics, the premise is to be in the model ants' vicinity, which nevertheless poses a considerable danger [61]. As there is no known case of chemical mimicry in myrmecomorphic spiders [69], their defence strategies need to rely on different approaches, which are mainly behavioural. It has long been observed that ant-associating spiders such as *Myrmarachne* generally avoid contact with ants [45, 58, 61, 70], and this holds true not only for myrmecomorphs, but also for aggressive mimics such as *C. bitaeniata*, despite its chemical protection [35, 58]. Upon seeing an ant approach, myrmecomorphic spider species of the genus *Myrmarachne*

(a)



(b)



(c)

Figure 1: Ant-associating salticids (a) *Cosmophasis bitaeniata*, chemical, aggressive myrmecophile and (c) *Myrmarachne smaragdina*, myrmecomorphic Batesian mimic, and their common model ant species (b) *Oecophylla smaragdina* in an aggressive display posture.

actively move away from the ant, regardless of the ant species, and contact occurs in fewer than 3% of the cases when the spiders react to the presence of the ants [58]. These spiders are able to distinguish between ants and conspecifics, due to their remarkable visual acuity [71]. They also react differently to ants depending on whether the ants are facing them, side-on, moving, or stationary but generally do not let the ant get closer than approximately 2 cm [58]. At times, however, contact is unavoidable, and the spiders flee even upon contact, only very rarely reacting aggressively, perhaps as a last resort [72]. Active avoidance of ants is common in myrmecomorphic spiders, and the behavioural reactions of myrmecomorphs towards sympatric ant species are different depending on the species of spiders (as was shown with *Myrmarachne*). Innate behavioural traits are different between species due to selection (as is the case in morphological traits). Aversion to ants is innate in arthropods such as mantises [39], and avoidance of ants could therefore also be an innate trait in myrmecomorphic jumping spiders such as *Myrmarachne*. If that is the case, the fact that each species of *Myrmarachne* reacts differently to the presence of ants suggests that these behavioural traits are under selection pressure [58].

5. Conclusions

There are advantages and disadvantages for ant-associating spiders related to living near or inside ant colonies. When looking purely at ant mimicry, it is clear that there is an arms race between the parties involved in terms of evolutionary costs and benefits. Varied strategies have evolved in ant-mimicking spiders allowing them to reap the benefits of resembling ants. In addition, these spiders have innate and/or learned behaviours that reduce the costs of having models that are often aggressive and a real danger to the spiders themselves. Despite the considerable studies that have been carried out recently, ant mimicry in spiders is definitely a topic which deserves more attention and in-depth studies. In particular, with the increasing use of genomics, it is possible to carry out studies relating the underlying genetic mechanisms to phenotypic adaptations to ant mimicry, as have been carried out by D. Charlesworth and B. Charlesworth [72] which would give even more insight into the evolution of mimicry.

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