

Biology and behaviour of the neotropical ant-mimicking spider *Aphantochilus rogersi* (Araneae: Aphantochilidae): nesting, maternal care and ontogeny of ant-hunting techniques

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(With 1 plate and 1 figure in the text)

Aphantochilus rogersi is an ant-mimicking spider that preys exclusively on cephalotine ants. The spiders oviposit in close proximity to nests of the model ant *Zacryptocerus pusillus*, and emergent spiderlings tend to remain in the vicinity of natal egg sacs. Females of *A. rogersi* actively defend their egg sacs against approaching workers of *Z. pusillus*, but the latter may sometimes destroy the eggs. Feeding specialization on these ants is confirmed by more than 300 observations of young and adult *A. rogersi* carrying ant corpses in the field. Although *A. rogersi* possesses several behavioural traits which may reduce the risk of being injured by ants during subjugation, field and laboratory observations showed that social defence by *Z. pusillus* may cause mutilation to the spiders. Tests in captivity revealed an ontogenetic change in the prey-capture techniques employed by *A. rogersi*. Early-instar spiderlings can apparently only seize the ant's petiole tightly if they are able to approach the ant from the front. As the ant is paralysed, the spiderling positions itself vertically in relation to the substratum. Larger spiders, on the other hand, attack ants most frequently from behind, and seem better equipped to seize the ant's petiole firmly with their larger chelicerae. Owing to their greater strength, late-instar spiders are able to lift the struggling ant aloft. The selection of a suitable oviposition site, the mother's ability to defend herself and the eggs from nearby ants, and the capacity to capture and subdue ants safely from emergence to maturity, are regarded as crucial traits inherent in the mimetic and feeding specialization by *A. rogersi*.

Introduction

Ant-mimicry (myrmecomorphy) is widely distributed across many different arthropod orders, and among spiders nine families have been recorded to contain myrmecomorphic species (McIver & Stonedahl, 1993). As in many different arthropod species, some ant-mimicking spiders have evolved an array of specific morphological and behavioural features which greatly enhance their striking resemblance to ants (Reiskind, 1970, 1977; Oliveira, 1986, 1988). Available evidence suggests that most ant-mimicking spiders are palatable prey items which live in the same microhabitats as ant models but usually avoid contact with the latter. Owing to the noxious traits of ants, many authors believe that ant-mimicking spiders are Batesian mimics receiving protection from predators which avoid ants (Edmunds, 1974; Reiskind, 1977; Oliveira, 1988; McIver & Stonedahl, 1993; and citations therein). Some ant-mimicking spiders, however, live in close proximity to ants and frequently prey upon their models (Hingston, 1928; Piza, 1937; Bristowe, 1941; Mathew, 1954; Oliveira & Sazima, 1984). Although ants represent an extremely abundant food resource, their structural and chemical

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weapons associated with co-operative behaviour in colony defence (see Hölldobler & Wilson, 1990) pose problems for spiders to capture them with safety. Nevertheless, a number of spider species (ant-like or not) from different families are known to prey regularly on ants (e.g. Hölldobler, 1970; Edwards, Carroll & Whitcomb, 1974; Harkness, 1977; Cutler, 1980; Oliveira & Sazima, 1985; Jackson & van Olphen, 1991, 1992).

Feeding specialization upon ants has been reported for *Bucranium* and *Aphantochilus*, two ant-mimicking genera in the spider family Aphantochilidae which prey on cephalotine ants (Piza, 1937; Bristowe, 1941; Oliveira & Sazima, 1984). The most common technique employed by adult *Aphantochilus rogersi* Cambridge when attacking the model ant *Zacryptocerus pusillus* (Klug) was described as "a rapid approach from behind, toward the back of the ant, followed by the seizure of the ant's petiole with the chelicerae and pedipalps" (Oliveira & Sazima, 1984: 147). While walking with its prey, *A. rogersi* may use the ant corpse as a protective shield against patrolling ants of the victim's colony (Oliveira & Sazima, 1984; Plate Id). Given that *A. rogersi* preys exclusively on cephalotine ants and risks living in close proximity to their models' nests, additional data on maternal behaviour and feeding by spiderlings are needed to understand better such a peculiar predator-prey relationship.

The present study provides the first field account of nesting and maternal care in *A. rogersi*, and extends earlier observations on ant-hunting behaviour by describing in detail the prey-capture techniques employed by spiders at different developmental stages.

Materials and methods

Field work was undertaken from January 1994 to October 1995 at Cesário Lange ($\approx 23^{\circ}16'S$, $47^{\circ}59'W$), State of São Paulo, south-east Brazil. The climate of the region is characterized by a dry/cold season (April to September) and a rainy/hot season (October to March), and temperature ranges from 10 to 32 °C. The study area consisted of a 30 × 8 m plot of secondary growth vegetation containing a few trees and several shrubs. In the field, behavioural observations of *A. rogersi* and ants were carried out on small shrubs (up to 1.8 m tall) near trails of the arboreal model ant *Z. pusillus* (body length 3–5 mm). Some spiders and ants were brought to the laboratory for more accurate descriptions of their interactions. In captivity, each adult spider was maintained in a 30 cm high glass jar (20 cm diameter) containing a piece of moist cotton and a small potted plant. Behavioural interactions between spiders and ants were recorded after the introduction of 1–3 workers of *Z. pusillus* into the glass jar.

The morphological development of *A. rogersi* was followed in the laboratory at approximately 25 °C. Data on development were taken at 2-day intervals from captive juveniles emerging from one egg sac collected in the field, and from 2 ovipositions obtained directly from captive mature females. Newly-emergent spiderlings from egg sacs were considered as 'first instar' spiderlings. The body length of the spiders from instar I to V varied approximately from 2 to 7 mm. The length of the cephalothorax through different developmental stages ranged as follows: instar I, 1.25–1.47 mm ($n=6$); instar II, 1.61–1.83 mm ($n=7$); instar III, 2.03–2.17 mm ($n=4$); instar IV, 2.39–2.58 mm ($n=2$); instar V, 3.69–3.88 mm ($n=3$). After emergence, the spiderlings were confined individually in glass vials (6.0 cm long × 5.0 cm in diameter) containing a piece of moist cotton. Spiderlings were fed at 3-day intervals with one *Z. pusillus* worker, and their prey-capture behaviour was recorded. All behavioural data were gathered during intermittent sessions lasting 15–60 min.

Results

Nesting and maternal care

Aphantochilus rogersi does not make protective shelters of webbing and in the study area the spiders were commonly seen walking on foliage, or stationary on/under a leaf. A mating pair of *A. rogersi* was observed on a leaf at 12:05h, in February 1995. The spiders faced each other with ventral sides in

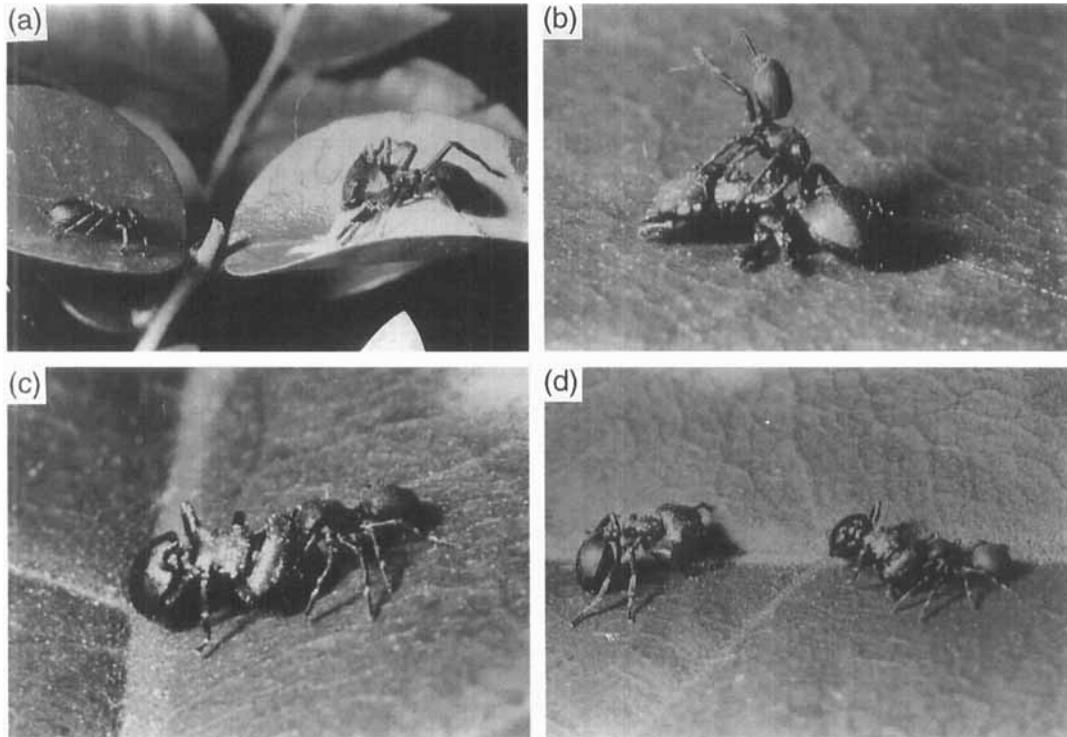


PLATE I. (a) Female of *Aphantochilus rogersi* (size ≈ 7 mm) guarding her egg sac and facing an approaching worker of *Zacryptocerus pusillus*, which eventually retreats. (b) Second instar spiderling of *A. rogersi* (positioned vertically with its head down) paralyzing a worker of *Z. pusillus* at the region of the petiole. (c) Second instar spiderling of *A. rogersi* feeding on a recently killed worker of *Z. pusillus* through the region of the compound eye. (d) Spiderling of *A. rogersi* using a recently killed worker of *Z. pusillus* as a shield against an approaching ant of the victim's colony.

contact. The male was much smaller than the female and the female's abdomen was considerably enlarged when compared to non-reproductive females. Ovipositions were observed in the field from the beginning (October) to the end (April) of the rainy/hot season. Females oviposit 30.9 ± 25.1 cm high on foliage (mean \pm S.D., $n = 29$), at a mean distance of 41.8 ± 26.7 cm ($n = 31$) from trails of the model ant *Z. pusillus*, and 1–2 m from a wood gallery containing a colony subunit of this ant species (parts of the colony can be dispersed among different nest cavities in the branches of a given shrub, and a whole mature colony may contain over 300 workers). The silk nest is white; the mother constantly guards the brood and vigorously defends the egg sac from approaching ants (Plate Ia, see below). After the emergence of the spiderlings, however, the mother abandons her egg sac. In captivity, the spiderlings emerged 23 days ($n = 1$) after oviposition and the mean number of spiderlings per oviposition was 31.0 ± 2.6 ($n = 3$). On two occasions, we saw unguarded egg sacs covered by fungi in the field. One of them was brought to the laboratory and only 18 spiderlings emerged from it; the remaining brood inside the silk nest (some eggs and newly-ecloded spiderlings) was found destroyed.

We found eight egg sacs being parasitized by ichneumonid wasps, which caused the death of some of the spiderlings and eggs. In seven egg sacs some of the spiderlings had already emerged, but in one of them the mother was still guarding her brood.

After emergence, the spiderlings do not show a strong tendency for dispersal, and in the field they were commonly seen on shrubs having remains of ovipositions. Dispersal through the wind by adult *A. rogersi* was seen once in the field at a leaf margin: the spider emitted a silk thread (≈ 40 cm long) which was caught by the wind and carried the spider aloft.

While guarding her egg sac, the mother spider actively defends it against intruders (Plate Ia). Even if experimentally forced 2–3 cm away from the silk nest with a small brush, she would immediately return to sit on it. The mother spider usually repels intruding ants from her egg sac by kicking them away with the front legs, or by attacking and killing them with the chelicerae. The dead ant can be either consumed by the mother spider, or thrown off the plant immediately. Although females guarding egg sacs rarely feed, on three occasions we saw spiders holding ant prey on their egg sacs in the field. When three workers of *Z. pusillus* were presented in captivity to a female on her egg sac, she killed two of them and captured a third one which was sucked empty after the spider returned to the egg sac. When simultaneously approached by several workers of *Z. pusillus*, however, the mother spider may fail to drive them away and end up temporarily abandoning the egg sac. Attacks by groups of ants may therefore be responsible for egg sacs found without females ($n=7$), as well as for the killing of a mother spider and the destruction of her brood in the study area. In the field, we observed one worker of *Z. pusillus* destroying an unguarded egg sac of *A. rogersi*.

Interaction with ants, and prey-capture techniques

Aphantochilus rogersi and *Z. pusillus* were active only at daytime, and a shrub housing an ant colony normally had 1–8 workers walking on leaves at the peak of ant activity (10:00–12:00 h). The commonest behaviour of individual *A. rogersi* when approached by an ant on a leaf, is to run to the opposite leaf surface, or to jump off the leaf and hang on the end of a silken line. If holding an ant prey, the spider may use it as a shield held toward the approaching ant (Plate Id), flee to a safer place, or even drop on a silken line with its prey. In captivity, on one occasion we saw a spider exhibiting shielding behaviour towards a patrolling *Z. pusillus* but, as the ant did not go away, the spider released its prey and subsequently killed the approaching ant. In another instance, one spider carrying a recently captured worker of *Z. pusillus* had one of its legs mutilated after being attacked by a patrolling ant of the victim's colony. Three mutilated *A. rogersi* were observed in the field; two of them had seven legs and one had only five legs. Although other ants such as *Camponotus crassus* Mayr and *C. aff. blandus* (Fr. Smith) (Formicinae) were also seen in the neighbourhood, we never observed them interacting with *A. rogersi*.

Aphantochilus rogersi preyed exclusively on the ant model *Z. pusillus*, and we observed young and adult spiders carrying corpses of this ant species on 306 occasions in the study area. In all, nine adult *A. rogersi* and many spiderlings (up to 53 on a single day) were found on the foliage near three colonies of *Z. pusillus*. Spiders may take from a few hours to three days to consume their ant prey entirely, which are then discarded with no crush or mutilation in the exoskeleton. Spiders may suck empty their prey through the compound eye region (Plate Ic), or through the head-thorax joint.

The hunting techniques employed by *A. rogersi* varied according to the developmental stage of the spiders (Fig. 1). Two methods of prey-capture were observed:

(1) Frontal attack—the spider approaches the ant frontally and bites between the thorax and abdomen (petiole region), the prey being seized with the chelicerae and first pair of legs. As the ant is paralysed, the spider positions itself vertically in relation to the substratum (Plate Ib). After the complete immobilization of the ant (legs folded to the body), the spider places all its legs on the substratum and carries the prey. After a few minutes, the spider turns the ant round and sucks it through the region of

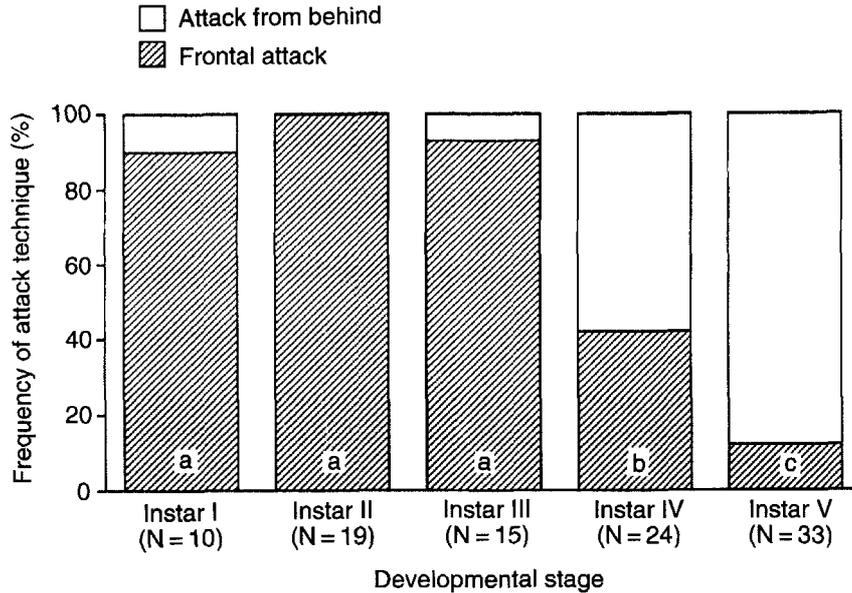


FIG. 1. Prey-capture techniques employed by ant-hunting *Aphantochilus rogersi* at different developmental stages, when confronted with workers of *Zacryptocerus pusillus* during captivity tests. Percentages designated by the same letter are not significantly different (*G*-tests).

the compound eye (Plate 1c). This hunting technique is significantly more frequent in I, II and III instar spiderlings (Fig. 1). On four occasions, the spiderlings attacked ants from behind but then immediately turned their bodies through 180° to firm the grip as in a frontal approach (Plate 1b). On three other occasions, the bite was initially aimed at the head-thorax joint of the ant, but the spiderlings rapidly switched the strike and paralysed the prey at the petiolar region. Successful frontal attack aimed at the head-thorax joint was observed only once.

(2) Attack from behind—the spider approaches the ant from the rear and bites between the thorax and abdomen. The prey is seized with the chelicerae and lifted from the substratum. After the ant is immobilized, the spider turns it round and starts feeding through the compound eye region. This hunting tactic is progressively more frequent toward instars IV and V of *A. rogersi* (Fig. 1).

Discussion

The subject of ant-mimicry has recently been reviewed by McIver & Stonedahl (1993) and its adaptive significance has not yet been clearly assessed for most groups of ant-mimicking arthropods. Available observational and experimental evidence suggests that most ant-mimicking spiders do not feed on ants, and presumably receive Batesian protection against predators which avoid ants (e.g. Edmunds, 1974, 1978). A few species have been reported in which aggressive ant-mimicry is also a possibility, with the spider somehow deceiving its model in order to prey on it (e.g. Mathew, 1954; Oliveira & Sazima, 1984).

Irrespective of the selective agents involved, however, a spatial association between mimics and

models is a condition for the evolution of mimicry (Edmunds, 1974; McIver & Stonedahl, 1993). In fact, presumed Batesian ant-mimicking spiders generally occur in the same microhabitats as their models (see Reiskind, 1977; Oliveira, 1988). Edmunds (1978) provided statistical evidence that different species of *Myrmarachne* (Salticidae) are each positively associated with one ant species or with a group of ant species which they resemble, being most likely found in the foraging area exploited by their models. On the other hand, ant-mimicking spiders that prey exclusively on ants tend to show a more pronounced spatial association with their models, since the latter constitute the spiders' only food source (Mathew, 1954; Oliveira & Sazima, 1984).

The present field study complements earlier observations on the interaction between *Aphantochilus rogersi* and cephalotine ants (Piza, 1937; Bristowe, 1941; Oliveira & Sazima, 1984), and confirms the close spatial association between the mimic and its ant models as well as the extremely specialized diet of the spider. Female spiders oviposited in close proximity to nests of the model ant *Zacryptocerus pusillus*, and emergent spiderlings tended to remain in the vicinity of natal egg sacs. Moreover, feeding specialization on the ant model was further supported by more than 300 observations of young and adult *A. rogersi* carrying ant corpses in the field. These findings are relevant in view of the remarkable structural resemblance between *A. rogersi* and cephalotine ants (Oliveira & Sazima, 1984), and the scarcity of quantitative field data on ant predation by ant-mimicking spiders. The results are also in contrast with less specialized, non-mimetic, ant-eating spiders which may prey on several ant species (Cutler, 1980; Jackson & van Olphen, 1991, 1992).

The behavioural interactions observed both in the field and captivity enhanced the trade-off inherent in such a mimetic and feeding specialization by *A. rogersi*. In this presumably two-component mimicry, *A. rogersi* may receive both Batesian protection against predators, as well as the benefit of a nearby predictable food source which they may exploit with a relative impunity (see Oliveira & Sazima, 1985). As stressed by Edmunds (1978), however, the close spatial association with ants brings two main disadvantages for ant-mimicking spiders: first, the spiders must cope with the risk of being injured or eaten when attacking their models, and second, the ants may attack the spiders while they mate, or even destroy their eggs.

Although *A. rogersi* possesses several behavioural traits that may reduce the risk of being attacked by its models, such as quickly dodging under a leaf, 'shielding behaviour' and dropping on a dragline (Oliveira & Sazima, 1984), the current study clearly shows that social defence by the ants may cause mutilation of the spider's leg. The observation of several mutilated *A. rogersi* in the field suggests that this type of ant-induced injury can be common, and that *Zacryptocerus* ants are not at all defenceless (see also Oliveira & Sazima, 1984). Similarly, Mathew (1954) reports that ant-eating *Amyciaea forticeps* (Thomisidae) may also be eaten by its ant model *Oecophylla smaragdina* if it fails to escape through a dragline.

Although females of *A. rogersi* actively defend their egg sacs against approaching workers of *Z. pusillus*, our field and laboratory observations show that the ants may sometimes destroy the egg sac when the mother spider fails to drive them away. The degree to which egg-guarding by *A. rogersi* females can reduce brood damage from fungi or parasitoid ichneumonid wasps is unknown (see also Foelix, 1982). Edmunds (1978) reports that ant-mimicking *Myrmarachne* remain with the eggs until the spiderlings emerge from the retreat, and he further suggests that spiderlings of *M. legon* may also receive some protection from their mother until dispersion. *Myrmarachne* normally mates in the protection of a silken retreat, but the ant model *Oecophylla longinoda* may expel male and female *M. foenisex* from their retreat and eat the eggs (Edmunds, 1978). Although mating in *A. rogersi* takes place in the open, we have no information as to whether this makes the mating pair more vulnerable to attacks by nearby ants.

Very little is known about prey preference and prey-capture techniques during development in hunting spiders, and this is probably because predation events are difficult to witness in the field and prey items are often discarded at scattered points of capture (Turnbull, 1973). The predictable foraging area of ant-mimicking spiders that prey on ants (i.e. close to nests of ant models) makes them suitable organisms for this type of investigation. To our knowledge, the current study with *Aphantochilus rogersi* is the first to show an ontogenetic change in the prey-capture techniques employed by an ant-hunting spider. The peculiarity of the ant-hunting behaviour of *A. rogersi* is based on the fact that the spiders will feed on a single prey species from emergence to maturity, and therefore adjustments in predatory technique through development are not related to prey switching but rather to predator size.

Since ant predation is associated with the risk of injuries or death (see above), the success of a given ant-hunting method would depend not only on the efficacy of the attack and subsequent immobilization of the prey, but also on the safety it renders against attacks from the ant itself. Many adult ant-hunting spiders attack their prey from behind, and in doing so they probably avoid the risk of being bitten on the legs before the ant is completely paralysed (Hingston, 1928; Mathew, 1954; Oliveira & Sazima, 1984, 1985; Jackson & van Olphen, 1992). Interestingly, spiders that attack ants frontally usually spread out and raise their legs during subjugation, presumably to avoid contact with the ant's mandibles (Edwards *et al.*, 1974; Cutler, 1980; Jackson & van Olphen, 1992). Both attack tactics have been observed in young and adult *Aphantochilus rogersi*, but the present study clearly showed that attacks from the rear become more frequent as the spider grows larger (see also Oliveira & Sazima 1984). We believe that this tendency is related to the place where the spider firms its bite on the ant's body, the ability to keep the legs away from the ant's mandibles, as well as with the spider's capacity to lift the struggling ant from the substratum. These three factors seem to depend largely on the size of the spider. Early-instar spiderlings apparently can only seize the ant tightly if they are able to grab hold of the ant's petiole during a frontal approximation. In fact, on seven occasions, early-instar spiderlings were observed to switch their strike as a result of an unstable seizure of the ant. Moreover, since the small spiderlings are unable to isolate the struggling ant from the substratum, they have to keep their bodies in a vertical position until complete immobilization of the ant (see Plate Ib). Larger spiders, on the other hand, are apparently better equipped to seize firmly the ant's petiole with their larger chelicerae and need not risk a frontal approximation in order to hold their prey tightly. Owing to their greater power, late-instar spiders can easily hold the struggling ant aloft, so as to make it lose contact with the substratum (see also Oliveira & Sazima, 1985).

In conclusion, we have shown that the peculiarity of the mimetic and feeding specialization by *Aphantochilus rogersi* has shaped many aspects of its behavioural biology. Social insects are locally abundant organisms which, once located, can constitute a predictable prey item both in space and time. A hunting spider that succeeds in overcoming an ant species' defensive traits should therefore face relatively little competition for a nearly unlimited food resource (Nentwig, 1986; Reichert, 1992). This is particularly important at early stages of development, when food deprivation can account for a high rate of juvenile mortality (Turnbull, 1973). Consequently, the selection of a suitable oviposition site close to an ant model's nest, the mother's ability to defend herself and the eggs from nearby ants, and the capacity to capture and subdue ants safely from emergence to maturity, can all be regarded as crucial traits intrinsic to this rare mode of life among spiders.

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REFERENCES

- Bristowe, W. S. (1941). *The comity of spiders* 2. London: Ray Society.
- Cutler, B. (1980). Ant predation by *Habrocestum pulex* (Hentz) (Araneae: Salticidae). *Zool. Anz.* **204**: 97–101.
- Edmunds, M. (1974). *Defence in animals*. Harlow: Longman.
- Edmunds, M. (1978). On the association between *Myrmarachne* spp. (Salticidae) and ants. *Bull. Br. Arachnol. Soc.* **4**: 149–160.
- Edwards, G. B., Carroll, J. F. & Whitcomb, W. H. (1974). *Stoidis aurata* (Araneae: Salticidae), a spider predator of ants. *Fla Entomol.* **57**: 337–346.
- Foelix, R. F. (1982). *Biology of spiders*. Cambridge, MA: Harvard University Press.
- Harkness, R. D. (1977). Further observations on the relation between an ant, *Cataglyphis bicolor* (F.) (Hym., Formicidae) and a spider, *Zodarium frenatum* (Simon) (Araneae, Zodariidae). *Entomol. Mon. Mag.* **112**: 111–121.
- Hingston, R. W. G. (1928). Field observations on spider mimics. *Proc. zool. Soc. Lond.* **1927** (4): 841–858.
- Hölldobler, B. (1970). *Steatoda fulva* (Theridiidae), a spider that feeds on harvester ants. *Psyche* **77**: 202–207.
- Hölldobler, B. & Wilson, E. O. (1990). *The ants*. Cambridge, MA: Belknap Press.
- Jackson, R. R. & van Olphen, A. (1991). Prey-capture techniques and prey preferences of *Corythalia canosa* and *Pystira orbiculata*, ant-eating jumping spiders (Araneae, Salticidae). *J. Zool. (Lond.)* **223**: 577–591.
- Jackson, R. R. & van Olphen, A. (1992). Prey-capture techniques and prey preferences of *Chrysilla*, *Natta* and *Siler*, ant-eating jumping spiders (Araneae, Salticidae) from Kenya and Sri Lanka. *J. Zool. (Lond.)* **227**: 163–170.
- Mathew, A. P. (1954). Observations on the habits of the two spider mimics of the red ant *Oecophylla smaragdina* (Fabr.). *J. Bombay Nat. Hist. Soc.* **52**: 249–263.
- McIver, J. D. & Stonedahl, G. (1993). Myrmecomorphy: Morphological and behavioral mimicry of ants. *Annu. Rev. Entomol.* **38**: 351–379.
- Nentwig, W. (1986). Non web-building spiders: prey specialists or generalists? *Oecologia* **69**: 571–576.
- Oliveira, P. S. (1986). Ant-mimicry in some spiders from Brazil. *Bull. Soc. Zool. Fr.* **111**: 297–311.
- Oliveira, P. S. (1988). Ant-mimicry in some Brazilian salticid and clubionid spiders (Araneae: Salticidae, Clubionidae). *Biol. J. Linn. Soc.* **33**: 1–15.
- Oliveira, P. S. & Sazima, I. (1984). The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae). *Biol. J. Linn. Soc.* **22**: 145–155.
- Oliveira, P. S. & Sazima, I. (1985). Ant-hunting behaviour in spiders with emphasis on *Strophius nigricans* (Thomisidae). *Bull. Br. Arachnol. Soc.* **6**: 309–312.
- Piza, S. de T. (1937). Novas espécies de aranhas myrmecomorphas do Brazil e considerações sobre o seu mimetismo. *Rev. Mus. Paul. N.S.* **23**: 307–319.
- Reiskind, J. (1970). Multiple mimetic forms in an ant-mimicking clubionid spider. *Science (Washington DC)* **169**: 587–588.
- Reiskind, J. (1977). Ant-mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae). *Biotropica* **9**: 1–8.
- Riechert, S. E. (1992). Spiders as representative 'sit-and-wait' predators. In *Natural enemies: The population biology of predators, parasites and diseases*: 313–328. Crawley, M. J. (Ed.). Oxford: Blackwell.
- Turnbull, A. L. (1973). Ecology of the true spiders (Araneomorphae). *Annu. Rev. Entomol.* **18**: 305–348.