Ant-hunting behaviour in spiders with emphasis on *Strophius nigricans* (Thomisidae)

Paulo S. Oliveira and **Ivan Sazima**
Departamento de Zoologia,
Universidade Estadual de Campinas,
13100 Campinas, São Paulo,
Brazil

Introduction

Ants outnumber in individuals all other terrestrial animals and, although they represent a significant food resource, relatively few predators regularly feed on them (Wheeler, 1910). Despite the fact that ants are abundant, mobile and of generally easy location by predators, their strong mandibles, poisonous sting (Eisner, 1970; Blum, 1981) and co-operative behaviour in colony defence (Wilson, 1971) pose problems for capturing them with safety. Nevertheless, different ant-hunting animals have evolved various behavioural, structural and chemical adaptations to subdue these well-protected insects (see Alcock, 1979: 324-325). Among spiders, ant predation is known to occur in members of the Thomisidae (Shelford, 1902; Hingston, 1928; Mathew, 1954), Aphantochilidae (Piza, 1937; Bristowe, 1941; Oliveira & Sazima, 1984), Salticidae (Robinson & Valerio, 1977; Cutler, 1980), Theridiidae (Bristowe, 1939, 1941; Levi & Levi, 1958, Hölldobler, 1970) and Zodariidae (Hingston, 1928; Harkness, 1977). We have described elsewhere (Oliveira & Sazima, 1984) the ant-hunting tactic employed by the aphantochilid spider *Aphantochilus rogersi* Cambridge, a probable aggressive mimic of certain cephalotine ants. In the present paper we describe the ant-hunting behaviour of the thomisid *Strophius nigricans* Keyserling and indicate some general behavioural trends among ant-preying spiders based on comparisons with *A. rogersi,* as well as with some other species cited in the arachnological literature. Field observations on *Strophius* were made in secondary growth vegetation in Taiaçupeba, Mogi das Cruzes, São Paulo, Brazil (about 23°30'S, 46°10'W), during November 1982. The interaction between *S. nigricans* and ants was also observed under laboratory conditions, in sessions of 15-60 min, totalling about 8 hours.

Ant-hunting behaviour of *Strophius nigricans*

In the field, one male of *Strophius nigricans* was observed on leaves of a 120 cm tall shrub, carrying aloft a dead worker of the black formicine ant *Camponotus crassus* Mayr. *Strophius nigricans* is black in colour, the integument being covered with sparse white hairs which form thin transverse stripes on the round abdomen. Although the spider's shape is not ant-like, its close similarity in size and colour to *C. crassus* produced a striking visual deception when the thomisid was seen from above carrying its ant prey. The spider seized its prey by one of its legs and walked with it in rapid zig-zag movements, which was very similar to a 'true' ant carrying a dead companion. The spider was captured and brought to the laboratory, without loosening the grip on its prey.

In captivity, *S. nigricans,* with its ant prey, was placed in a glass vivarium (containing a small potted plant) together with three workers of *C. crassus* from the same colony. Whenever one of the ants approached the spider, it used the ant corpse as a 'protective shield', exposing it towards the approaching ant which then promptly went away. During *c.* 30 minutes the thomisid, still holding its prey, unsuccessfully pursued the ants on seven occasions. On one occasion, one of the ants slowly approached the spider and its prey, almost touching them. Then, the thomisid manoeuvred rapidly and seized the ant from behind at the petiole, simultaneously releasing the ant corpse in front of the new victim. As the ant struggled, fiercely biting the corpse, the spider adjusted itself, without releasing the prey, and probably strengthened its bite. After the first bite, *Strophius* kept its front legs extended upwards and backwards, as far as possible from the dying ant's mandibles. As the ant calmed down and released the corpse which it had held until then, it continued forcing the legs against the substrate in an attempt to get rid of the spider. The thomisid then held its prey aloft and isolated it from the substrate. Henceforth the thomisid, from time to time, touched the ant's antennae and front legs with its own front legs; if the ant's legs moved vigorously the spider promptly withdrew its legs backwards again. Finally, on two consecutive occasions, the ant's antennae moved very weakly after being touched by the thomisid's front legs. Soon after, *Strophius* manipula-

ted the ant with the chelicerae and legs, and turned it round so as to seize the suspended prey by the neck (Fig. 1a). Five minutes after the initial attack on the ant, the spider walked to a lateral branch and remained almost motionless with its ant prey. Again, whenever one of the two remaining *C. crassus* workers approached the thomisid, it immediately used the new ant corpse as a shield, making abrupt and successive movements with it towards the approaching ant, always maintaining the front legs extended backwards. The approaching ant usually went away after 1-3 such movements by the spider. Basically the same ant-hunting tactic was observed during two subsequent sessions involving *Strophius* and two other *C. crassus* workers. Ant corpses released by the thomisid were neither mutilated nor crushed, but their exoskeletons were completely emptied.

Comparison with other ant-hunting spiders

Both *Strophius nigricans* and *Aphantochilus rogersi* attack ants from behind, although the latter spider may, more rarely, capture them frontally (Oliveira & Sazima, 1984). Hingston (1928) and Mathew (1954) report that the thomisid *Amyciaea forticeps* Cambridge also captures the Indian red ant *Oecophylla smaragdina* (Fabricius) from behind. Attacking ants from behind is probably a safer tactic, since in frontal attacks the spider has an increased risk of being bitten on the legs before the ant is paralysed. This risk is avoided by *Strophius* both by 'offering' the corpse of a previous victim to be held between the mandibles of the struggling *Camponotus* and by extending its front legs backwards while paralysing the ant. Whenever *Aphantochilus* captures cephalotine ants frontally, the spider's first pair of legs are also kept away from the victim's mandibles until complete immobilisation (Oliveira & Sazima, 1984). Cutler (1980) noticed that the salticid *Habrocestum pulex* (Hentz) keeps its front legs extended laterally and forwards (without touching the ground) after frontal attacks on ants; with flies, however, the spider's legs are all on the ground. After biting and probably discharging the venom into the ant's petiole, both *Aphantochilus* and *Strophius* turn their prey round, in order to seize it frontally by the neck, only when the victim is apparently dead (Fig. 1). *Strophius nigricans* seems to evaluate the appropriate moment to do so by touching the victim's antennae with its front legs, making a sort of tactile inspection of the state of the dying ant.

The isolation of ant prey from the substrate, just after capturing it, is done by ant-hunting spiders basically through two techniques: (1) holding the victim aloft, so as to make it lose the support of its legs on the ground; (2) dropping on a dragline, with the ant held, and hanging on the end of the line. The first tactic was observed in *Aphantochilus* (Oliveira

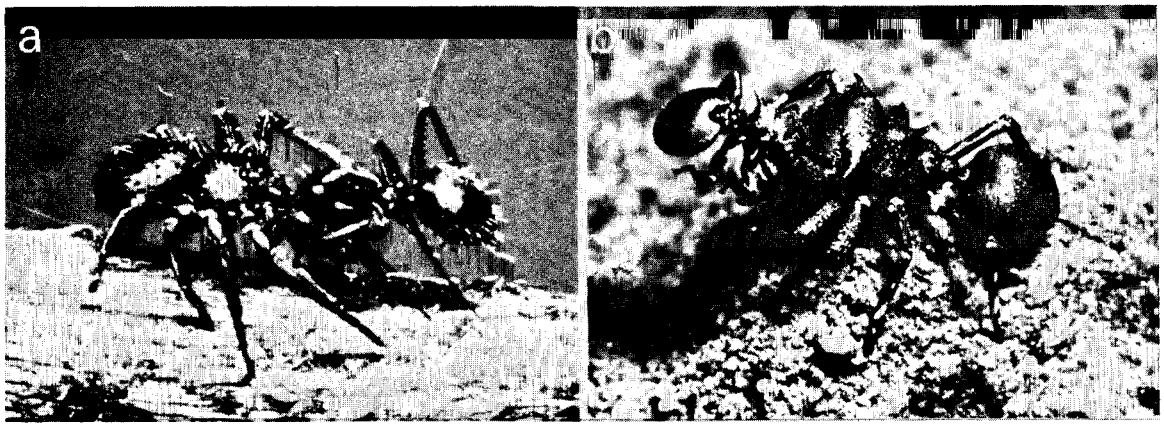

Fig. 1: Ant predation by two thomisoid spiders. **(a)** The thomisid *Strophius nigricans* carrying aloft, by the neck, a dead worker of the formicine ant *Camponotus crassus*. **(b)** The aphantochilid *Aphantochilus rogersi* carrying, in the same way, a dead worker of the cephalotine ant *Zacryptocerus pusillus*. Sizes of spiders 4 mm and 6 mm respectively.

& Sazima, 1984) and *Strophius*, and it clearly reduces the victim's escape probabilities. The drop and hold technique is known to be employed by certain Costa Rican salticids after pouncing on *Pseudomyrmex* ants (Robinson & Valerio, 1977), by the thomisid *Amyciaea forticeps* when subduing the red ant *Oecophylla smaragdina* (Mathew, 1954), and by *Aphantochilus rogersi* under situations where the victim's companions become alarmed (Oliveira & Sazima, 1984). Robinson & Valerio (1977) argue that dropping on a dragline allows certain salticids to attack prey that are protected by social defence; the victim's companions attracted by the alarm pheromone find the dragline but are unable to descend the thread. After having observed on several occasions *Amyciaea* sucking red ants hung on what he called a "safety cable", Mathew (1954: 253) writes the following about this tactic: "This is certainly safer since red ants move about in the vicinity and, if one of them surprises the spider, the latter would have no way of escape as was noticed previously in one of my observation cages".

There is another method by which some ant-hunting spiders can overcome the co-operative behaviour of their prey, and which we have called 'shielding behaviour' (Oliveira & Sazima, 1984). Both *Aphantochilus* and *Strophius* may use the ant corpse as a protective shield towards patrolling ants of the victim's colony. This behaviour lures, at least momentarily, the alarmed ants and provides the spider with a few additional seconds of security before taking refuge in a less crowded place. However, if shielding behaviour fails and the spider is detected as an intruder, it can still avoid being attacked by running away (and these spiders are usually much faster than ants) or, as observed with *Aphantochilus*, by dropping with its prey on a dragline (Oliveira & Sazima, 1984). Safety against attacks from patrolling ants can also be achieved by hunting during periods of low colony activity. The zodariid *Zodarium frenatum* (Simon) hides during the day and preys on *Cataglyphis* ants at night, when the solitary guard outside the nest happens to be a likely victim for the spider (Harkness, 1977). Besides all the behavioural tactics presented here, ant-hunting spiders must also, in order to capture and successfully subdue their prey, cope with the various chemical deterrents used by ants against their enemies (see Eisner, 1970; Blum, 1981).

Keeping prey intact seems to be a general characteristic of ant-hunting spiders. These predators suck empty the body contents of their prey and release the corpses without crushing or mutilating them. This fact could result from the hard integument of most ants, and its consequences may be advantageous to ant-preying spiders in two ways. First, while carrying its ant prey intact, the spider becomes extremely similar to an ant carrying a dead companion (Fig. 1; see also Bristowe, 1941; Mathew, 1954; Hinton, 1977; Oliveira & Sazima, 1984). Such resemblance may deceive (provided the spider and ant are somewhat similar in size and colour) the spider's potential predators which avoid or hesitate preying on ants (e.g. spider-hunting wasps, birds and lizards). Recent studies on ant-naive hatchlings of the iguanid *Anolis lineatopus* have shown that these lizards do reject ants on sight in prey choice experiments and that they are susceptible to the ants' weapons; moreover, older juveniles still are reluctant to take ants and feed on them according to prior experience with stinging ants (Vogel & Brockhusen-Holzer, 1984). Thus, ant-like appearance can provide the spider some Batesian protection or, at least, some chance to escape while its potential predator hesitates. The second advantage, as we have observed with *Strophius* and *Aphantochilus*, is that the spider may use the ant corpse as a protective shield towards patrolling ants of the victim's colony.

Thus different spider species have managed to solve effectively the problems inherent in the habit of feeding on ants. Some of these solutions are similar and seem to have arisen independently in unrelated spider taxa (e.g. attacking from behind, drop and hold tactic); others are peculiar to certain related species and may reflect phylogenetic affinities (e.g. shielding behaviour in the thomisoids *Strophius* and *Aphantochilus*); and still other, extremely specialized, solutions (e.g. aggressive ant-mimicry in *Aphantochilus*) appear to be the product of a regular and obligatory intimate contact of the spider with its prey.

Acknowledgements

We are grateful to Drs E. Curio, K. S. Brown, Jr and W. H. Stubblebine for reading the manuscript; to Dr F. von Brockhusen-Holzer for reading the

manuscript and for giving us access to an unpublished manuscript on predation by *Anolis* on ants; to I. M. P. Rinaldi and B. A. M. Soares for identifying the spider; and to W. R. Silva for helping to process the photographs. Both authors received financial support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq); I. Sazima also acknowledges support from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grant 83/0235-0).

References

ALCOCK, J. 1979: *Animal behavior. An evolutionary approach.* Sunderland, Sinauer.

BLUM, M. S. 1981: *Chemical defenses of arthropods.* New York, Academic Press.

BRISTOWE, W. S. 1939-1941: *The comity of spiders* **1**: 1-228; **2**: 229-560. London, Ray Society.

CUTLER, B. 1980: Ant predation by *Habrocestum pulex* (Hentz) (Araneae: Salticidae). *Zool.Anz.* **204**: 97-101.

EISNER, T. 1970: Chemical defense against predation in arthropods. *In* E. Sondheimer & J. B. Simeone, *Chemical ecology:* 157-217. New York, Academic 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). *Entomologist's mon.Mag.* **112**: 111-121.

HINGSTON, R. W. G. 1928: Field observations on spider mimics. *Proc.zool.Soc.Lond.* **1927**(4): 841-858.

HINTON, H. E. 1977: Mimicry provides information about the perceptual capacities of predators. *Folia ent.mex.* **37**: 19-29.

HÖLLDOBLER, B. 1970: *Steatoda fulva* (Theridiidae), a spider that feeds on harvester ants. *Psyche, Camb.* **77**: 202-207.

LEVI, H. W. & LEVI, L. R. 1958: The genera of the spider family Theridiidae. *Bull.Mus.comp.Zool.Harv.* **127**: 1-99.

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.

OLIVEIRA, P. S. & SAZIMA, I. 1984: The adaptive bases of ant-mimicry in a neotropical aphantochilid spider (Araneae: Aphantochilidae). *Biol.J.Linn.Soc.* **22**(2): 145-155.

PIZA, S. de T. 1937: Novas espécies de aranhas myrmecomorphas do Brasil e considerações sobre o seu mimetismo. *Revta Mus.paul.* **23**: 307-319.

ROBINSON, M. H. & VALERIO, C. E. 1977: Attacks on large or heavily defended prey by tropical salticid spiders. *Psyche, Camb.* **84**: 1-10.

SHELFORD, R. 1902: Observations on some mimetic insects and spiders from Borneo and Singapore. *Proc.zool. Soc.Lond.* **1902**(2): 230-284.

VOGEL, P. & BROCKHUSEN-HOLZER, F. von 1984: Ants as prey of juvenile *Anolis lineatopus* (Rept., Iguanidae) in prey choice experiments. *Z.Tierpsychol.* (in press).

WHEELER, W. M. 1910: *Ants: Their structure, development and behavior.* New York, Columbia University Press.

WILSON, E. O. 1971: *The insect societies.* Cambridge, Mass., Belknap Press.