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Contact between *Myrmarachne* (Araneae: Salticidae) and ants

F. Sara Ceccarelli
School of Tropical Biology,
James Cook University,
Townsville, QLD 4811, Australia

Summary

Myrmarachne (Araneae: Salticidae) is an ant-mimicking genus of jumping spiders. *Myrmarachne* species live close to their model ant species, yet they avoid making contact with the ants. However, contact can be unavoidable at times, so the question is what really happens when the ant and the spider make contact. This study found that the consequence of the contact very much depends on which body parts of both animals are involved. The most common form of contact was between the ant's antennae and the spider's first pair of legs. This resulted most frequently in the *Myrmarachne* running away. In contrast, when the spider's chelicerae were involved the ant would usually run away. The study concludes that even when there is contact between the two, *Myrmarachne* manages to avoid being attacked by the ant, thus remaining safe.

Introduction

Ant mimicry in terrestrial arthropods is relatively common, because ants possess characteristics making them ideal models for Batesian mimicry, amongst which are their aggressive nature and their noxious taste (Rettenmeyer, 1970). Thus ant mimicry has evolved many times in both insects and spiders (for reviews see Cushing, 1997; McIver & Stonedahl, 1993). For Batesian mimicry to be effective, the mimic must live in the proximity of its model. However, ants tend to be aggressive toward animals not belonging to their colony, thus posing a threat to their mimics (Halaj *et al*., 1997; Hölldobler, 1983; Hölldobler & Wilson, 1990).

Myrmarachne MacLeay, 1838 (Araneae: Salticidae) is a large genus of ant-mimicking spiders. There are over 200 *Myrmarachne* species worldwide (Prószyński, 2003), and at sexual maturity most of them are specialist mimics of one ant species, associating closely with their particular model species (Edmunds, 1978; Mathew, 1954). This means that occasional contact between the *Myrmarachne* and the ant is almost unavoidable, despite the fact that previous studies have shown that *Myrmarachne* avoids contact with ants (Edmunds, 1978; Mathew, 1954; Nelson *et al*., 2005). This study examines instances when contact does occur between *Myrmarachne* and ants, and attempts to answer the key questions of which body parts of the ant and the spider are most frequently involved during the contact, and what the reactions to contact are. This shows what the most likely outcomes are in the instances when *Myrmarachne* cannot avoid contact with ants, and whether those instances place the *Myrmarachne* in danger.

Material and methods

Individuals of four *Myrmarachne* species and four sympatric ant species were collected from locations in Townsville, Australia (19°13′S, 146°48′E), and brought into the laboratory, where videotape recordings were made of the behaviours of the animals within minutes of their capture. As the *Myrmarachne* species used are not yet named, they are referred to as *Myrmarachne* spp. A, B, C and D. The ant species used were: *Opisthopsis haddoni* Emery, 1893, *Polyrhachis* near *obtusa* Emery, 1897, *Tetraponera punctulata* Smith, 1877 and *Oecophylla smaragdina* (Fabricius, 1860). Henceforth the ants will be referred to by genus. The ants were the sympatric species most closely resembling the four *Myrmarachne* species. Based on visual resemblance, *Myrmarachne* spp. A, B, C and D were considered to be Batesian mimics of *Opisthopsis*, *Polyrhachis*, *Tetraponera* and *Oecophylla* respectively.

Recordings were made of one *Myrmarachne* individual and one ant in a 10 cm diameter plastic Petri dish using a low light, high resolution video camera connected to a video recorder. For each recording, a new Petri dish was used to avoid chemical cues from previous ants/spiders affecting the behaviour of the following pair. Ten replicates per *Myrmarachne* species were performed, using all four ant species at least twice with each *Myrmarachne* species. Each *Myrmarachne*–ant combination was left for 1 h 30 min. Later, the videotapes were analysed, recording every time when contact between the *Myrmarachne* and the ant occurred. When contact did occur, the following items were recorded (with abbreviations used on figures):

(a) The body part of the *Myrmarachne* making contact with the ant: one leg I (=1 leg I), two legs I (=2 leg I), chelicerae (=chel), prosoma (=pros), opisthosoma (=opis).
(b) The body part of the ant making contact with the *Myrmarachne*: one antenna (=1 anten), two antennae (=2 anten), mandibles (=mand), head (=head), thorax or abdomen (=tho/abd), leg (=leg).
(c) The intensity of the contact: soft or hard.
(d) The responses of both the ant and the *Myrmarachne*: *Myrmarachne* runs away (=*M* runs), ant runs away (=ant runs), both run away (=both run), *Myrmarachne* moves away (moving being defined as any movement other than running) (=*M* moves), ant moves away (=ant moves), both move away (=both move), ant attacks (attacks being defined as a very quick, jerky movement towards the spider (=ant att), no reaction (=nil).

The responses listed above are not the only possible ones, but they are the only responses observed during this experiment. The average number of contacts between the ant and the *Myrmarachne* per hour was also calculated in order to assess how frequently contact occurred.

Data analysis was carried out using the statistics program R version 2.1.1. (R_Development_Core_Team, 2005). A recursive partitioning tree was constructed using the rpart package (Therneau *et al*., 2005) to find which variables were most closely correlated with which responses. This follows the Classification and Regression Tree (CART) analysis, which was popularised by Breiman *et al*. (1984) as a means of partitioning

data sets into similar groups. The partitioning predicts the correlation of one or more independent variables with a categorical dependent variable by building decision trees. Both "recursive partitioning tree", "decision tree" and "classification tree" are terms used interchangeably in this study. One classification tree was built using only the body parts of the ant and *Myrmarachne* as predictor variables, and another tree was built using all the independent variables measured.

To find out whether the number of contacts per hour was dependent on either the *Myrmarachne* or ant species, ANOVA was used. Chi-squared tests were also performed on the frequencies (count data) with which each part of the *Myrmarachne* and the ant made contact.

Results

The results of this study are presented following the main questions asked.

How often did contact occur between the spider and the ant?

The average number of contacts between a *Myrmarachne* and an ant was found to be 2.90 per hour. The average number of contacts per hour was dependent neither on the *Myrmarachne* species (ANOVA: $F_{3,22}=1.00$, $p=0.416$), nor on the ant species involved (ANOVA: $F_{3,22}=2.22$, $p=0.115$). In addition, there was no discernible interaction effect of *Myrmarachne* and ant species in determining the number of contacts per hour (ANOVA: $F_{9,22}=0.80$, $p=0.623$).

Which part of the spider made contact with the ant?

As shown in Fig. 1, taking the overall average for all four species, the body part of *Myrmarachne* that most frequently made contact with the ant was the first pair of legs (51% of the time with one leg, and 5% with both legs I). The chelicerae were the next most frequent *Myrmarachne* body part coming into contact with the ant (31% of the time). The next most frequent body part was the prosoma with 11% of contact and the opisthosoma with only 2% of contact with the ant. The frequencies of the *Myrmarachne* body parts making contact with the ant were significantly different between *Myrmarachne* species ($\chi^2_{12}=97.83$, $p<0.0001$). The main difference was that species B and D made contact with their legs more frequently than species A and C, whereas species C made contact more frequently with its chelicerae than the other species.

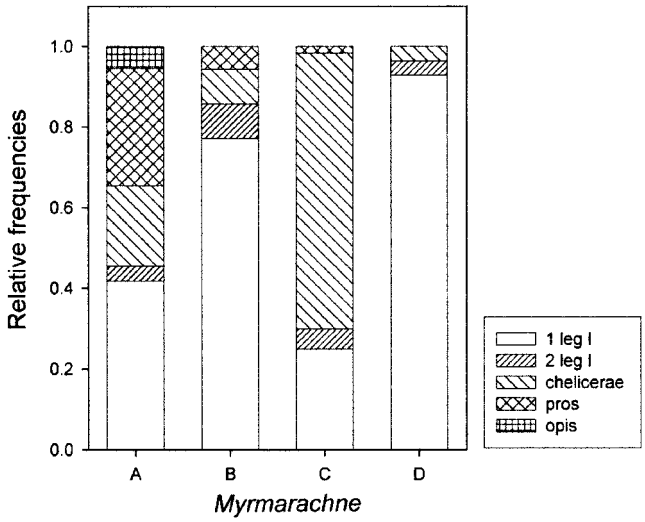

Fig. 1: Relative frequencies with which different parts of *Myrmarachne* contacted the ant for each *Myrmarachne* species (A, B, C and D). 1 leg I = one of the spider's first pair of legs; 2 leg I = the first pair of legs; chelicerae = *Myrmarachne*'s chelicerae; pros = spider's prosoma, opis = spider's opisthosoma.

Which part of the ant made contact with the spider?

Figure 2 shows that the part of the ant that most frequently came into contact with the *Myrmarachne* was the antennae (47% of the time with only one, and 3% of the time with both antennae). The next most frequent ant body part was the head (26%), followed by the rest of the body — thorax and abdomen (22%). The mandibles and the legs each made contact with the *Myrmarachne* only 1% of the time. There was a significant difference between the four ant species in the frequencies of ant body parts making contact with the *Myrmarachne* ($\chi^2_{15}=30.20$, $p<0.05$). The main difference was that *Oecophylla* made the most contact with one antenna, whereas *Tetraponera* had most contact with its head, thorax and abdomen.

What was the effect of contact on the spider and the ant?

The responses to coming into contact with each other for the *Myrmarachne*, the ant or both were similar for both groups. The most frequent response to contact was the *Myrmarachne* running away (35% of events), followed by the ant running away (33% of events). Both the

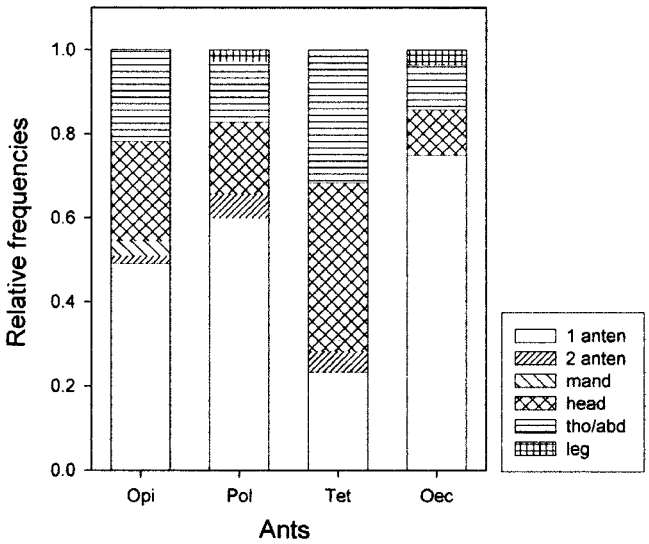

Fig. 2: Relative frequencies with which different parts of the ant contacted *Myrmarachne* for each ant species (Opi = *Opisthopsis haddoni*, Pol = *Polyrhachis* nr *obtusa*, Tet = *Tetraponera punctulata*, Oec = *Oecophylla smaragdina*). 1 anten = one antenna; 2 anten = two antennae; mand = mandibles; head = head; tho/abd = thorax or abdomen; leg = leg.

ant and the *Myrmarachne* ran away at the same time after 12% of interactions, and similarly after 2% of interactions they both moved away together (a category of movement excluding running). In 1% of events, the *Myrmarachne* only moved away from contact on its own, as opposed to 3% of the ant moving away. The ant attacked the *Myrmarachne* (fast movements towards it) on 3 occasions (2% of interactions). No visible response to the contact from either animal could be seen on 2% of interactions. The chi-squared test for differences between *Myrmarachne* species in the frequencies of the results showed that there was a significant difference between *Myrmarachne* species ($\chi^2_{21}=86.76$, $p<0.0001$).

The frequencies of the combinations of spider and ant body parts making contact are shown in Fig. 3. The most frequent contact between *Myrmarachne* and the ant occurred between one leg I of *Myrmarachne* and one antenna of the ant (39% of contacts). The second most frequent contact was between *Myrmarachne*'s chelicerae and the ant's head and the third most frequent was between *Myrmarachne*'s chelicerae and the ant's thorax/abdomen. These three combinations of spider–ant body parts were used to construct the histogram in Fig. 4, which shows the responses of the spider and the ant to each combination. For example, one leg I of the *Myrmarachne* and one antenna of the ant touching resulted most frequently in the *Myrmarachne* running away. On the other hand, the *Myrmarachne*'s chelicerae

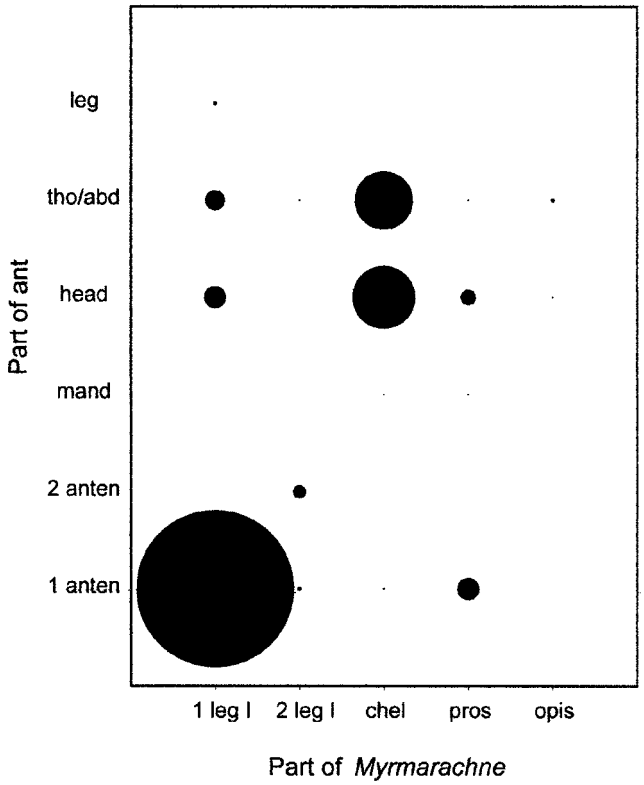

Fig. 3: Frequencies of contact between the different body parts of *Myrmarachne* and different body parts of the ants. Parts of *Myrmarachne* coded as: 1 leg I=one of the first pair of legs; 2 leg I=the first pair of legs; chel=chelicerae; pros=prosoma; opis=opisthosoma. Parts of ants coded as: 1 anten=one antenna; 2 anten=two antennae; mand=mandibles; head=head; tho/abd=thorax or abdomen; leg=leg. Frequencies are indicated by the size of the bubble.

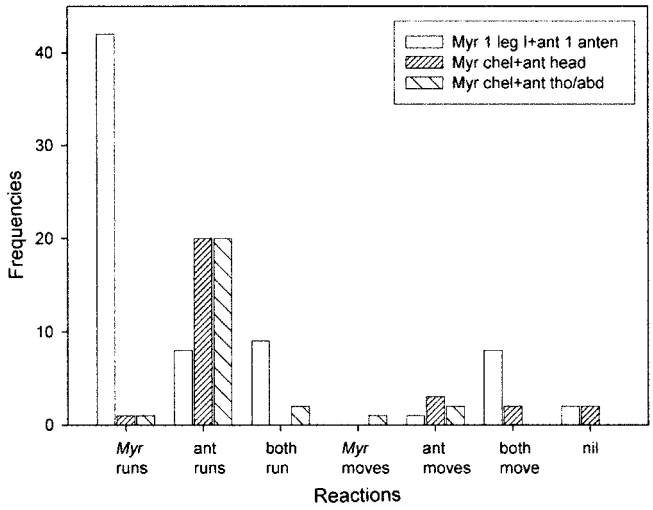

Fig. 4: Total frequencies with which the responses of *Myrmarachne* and ants occurred following the three most frequent contact combinations (one leg I of *Myrmarachne* and one of the ant's antennae, *Myrmarachne*'s chelicerae and the ant's head, *Myrmarachne*'s chelicerae and the ant's thorax or abdomen.

making contact with either the ant's head or its thorax or abdomen was most closely associated with the ant running away. In nature, similar observations have been made, where female *Myrmarachne* were seen "pushing" ants (mainly small ones from the genus *Crematogaster*) that got too close to the *Myrmarachne*'s retreat, presumably endangering the salticid's eggs. The *Myrmarachne* "pushed" using its chelicerae, but the action did not involve any biting. Rather, it was a very quick jerky forward movement towards the target, making strong contact (FSC, pers. obs.).

Recursive partitioning analysis

The recursive partitioning analysis shows the strongest predictor variables for responses of the *Myrmarachne* and the ants. At each node of the classification trees are given the independent variables deemed most likely to be correlated with the dependent variable at the end of the node. The independent variables are split at the nodes, the labels showing those following down each side of the tree.

The recursive partitioning trees show that the strongest predictor variable for responses by the spider and the ant was the part of the *Myrmarachne* making contact with the ant. Contact between *Myrmarachne*'s chelicerae and any part of the ant's body was most closely correlated with the ant running away. Considering only the body parts of the *Myrmarachne* and the ant as predictor variables (Fig. 5), the ant also ran away most frequently if the *Myrmarachne*'s leg I touched any of the ant's body parts other than one antenna. If one antenna of the ant made contact with any of the *Myrmarachne*'s body parts (other than the chelicerae), the most closely correlated response was the *Myrmarachne* running away. The second classification tree, using all the measured variables as potential predictor variables (Fig. 6), shows that the responses could also be correlated with variables such as ant species, *Myrmarachne* species and

Myrmarachne sex. For example, *Myrmarachne* running away was associated with the ants *Oecophylla*, *Polyrhachis* and *Tetraponera*. If the ant involved was *Opisthopsis*, females of *Myrmarachne* species B and D were correlated with *Myrmarachne* running away. On the other hand, *Opisthopsis* with a male *Myrmarachne* from species B, C or D was correlated most closely with the ant running away.

Discussion

Previous studies have shown that contact rarely occurs between *Myrmarachne* and ants (Edmunds, 1978; Mathew, 1954; Nelson *et al.*, 2005). When there is an interaction between an ant and a *Myrmarachne*, contact comprises only 3.17% of the salticid's total responses to the ant when they are both in a confined space (Ceccarelli & Rowe, in prep.). This study has shown that when contact between an ant and a *Myrmarachne* does occur, it is most likely to be between one of the ant's antennae and one of the *Myrmarachne*'s front legs. These body parts have different functions in the two animal groups. The antennae of ants are sensory organs used in chemical communication, usually between workers of the same colony (Hölldobler & Wilson, 1990). If the ants detect a chemical from an animal other than their nestmates, they are likely to react aggressively, as a defence mechanism (Hölldobler & Wilson, 1990). *Myrmarachne* have been shown to use their legs I for tapping insects such as moths as a part of their prey capture technique (Jackson, 1986). However, *Myrmarachne* are not generally known to prey on ants (Jackson & Willey, 1994), so their use of the first pair of legs during contact with ants is not likely to be for predatory purposes. This study has shown that *Myrmarachne* are most likely to run away following contact between their leg I and one of the ant's antennae, probably because of the inherent danger of the ants reacting aggressively.

The other frequent point of contact between the *Myrmarachne* and the ant is the chelicerae of the former making contact with the head, thorax or abdomen of the latter. Ants that get too close to *Myrmarachne* do occasionally get "attacked" by the salticid and, as shown in this study, when the *Myrmarachne*'s chelicerae make contact with the ant, the most common response is the ant running away.

Although ants are said to be aggressive, and a potential danger to other animals of similar size (Halaj *et al.*, 1997; Nelson *et al.*, 2004, 2005), this study has shown that ants are only aggressive toward *Myrmarachne* following 2% of all instances of contact. In addition, the ants' aggression never resulted in any harm being done to the *Myrmarachne*. It is reasonable to assume that in

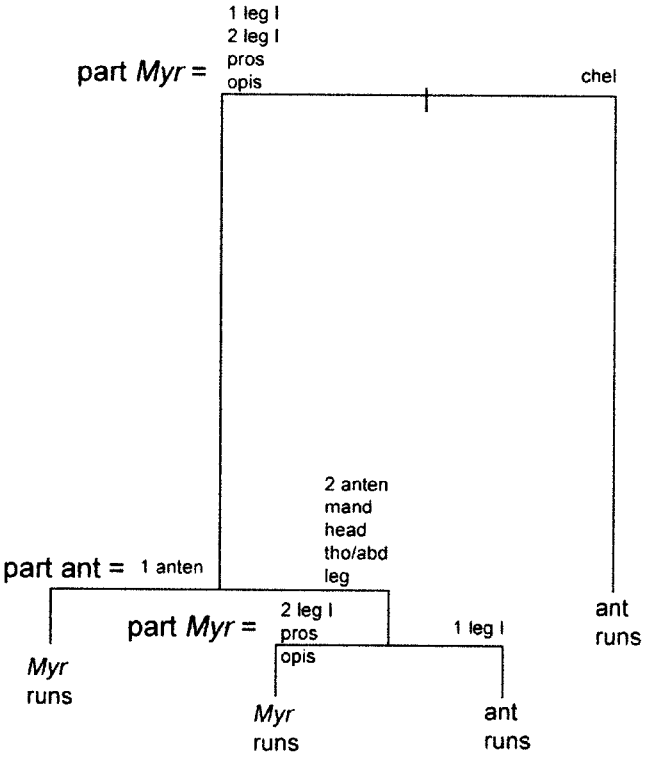

Fig. 5: Recursive partitioning tree of *Myrmarachne* and ant responses to contact, constructed using only the part of the spider and part of the ant making contact as predictor variables. Responses are shown at the end of the branches. Body parts of *Myrmarachne* (**part *Myr***) are: 1 leg I=one of the first pair of legs; 2 leg I=the first pair of legs; chel=chelicerae; pros=prosoma; opis=opisthosoma. Body parts of the ants (**part ant**) are: 1 anten=one antenna; 2 anten=two antennae; mand=mandibles; head=head; tho/abd=thorax or abdomen; leg=leg.

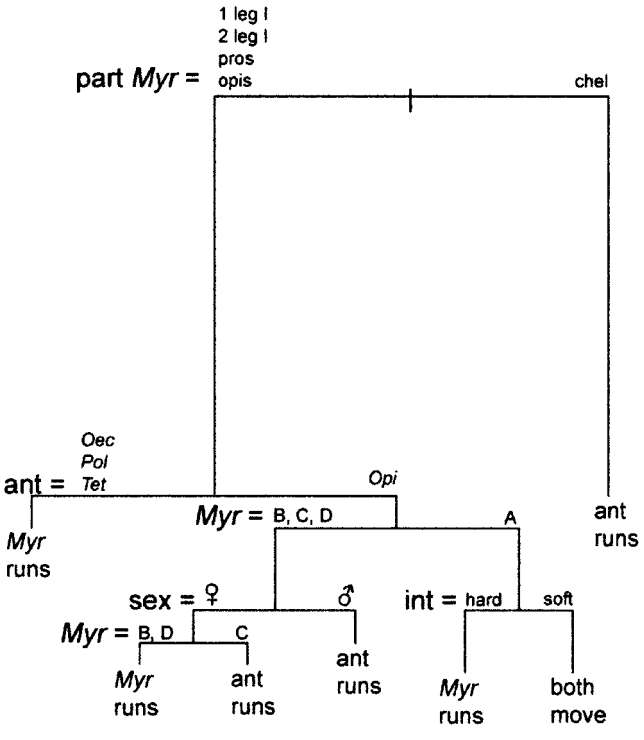

Fig. 6: Recursive partitioning tree of *Myrmarachne* and ant responses to contact between the ant and the spider, constructed using all measured variables as potential predictor variables. Responses are shown at the end of the branches. **Part *Myr*** refers to the part of the *Myrmarachne* making contact (1 leg I=one of the first pair of legs, 2 leg I=the first pair of legs, chel=chelicerae, pros=prosoma, opis=opisthosoma); **ant** is the ant species (Oec=*Oecophylla smaragdina*, Pol=*Polyrhachis* nr *obtusa*, Tet=*Tetraponera punctulata*, Opi=*Opisthopsis haddoni*); ***Myr*** is the *Myrmarachne* species (A, B, C or D); **sex** is the *Myrmarachne* sex (♂ or ♀); **int** refers to the intensity of contact (soft or hard).

this experimental situation, the ants may not have behaved as they normally would when they are amongst their colony. As social insects, ants rely on continuous chemical, visual and tactile feedback from other members of their colony to carry out functions such as colony defence (Hölldobler & Wilson, 1990). This means that the individual ants inside the Petri dish may have behaved less aggressively than they would in nature. However, there is no apparent reason to assume that the *Myrmarachne* would not be able to recognise ants as a potential danger, even outside their natural habitat.

Myrmecomorphic salticids (such as *Myrmarachne*) have a high rate of survival when compared with other types of salticids that encounter ants, possibly as a result of some form of behavioural mimicry (Nelson *et al*., 2004, 2005). The fact that *Myrmarachne* runs away from ants, or ''pushes'' them with its chelicerae, suggests that the salticid has developed these mechanisms for avoiding serious injury or death from the ants. The fact that *Myrmarachne* never really attack ants (as they would prey) also suggests that their behaviour is matched to that of the ants in that the *Myrmarachne* do not elicit an aggressive response from the ants.

The relative frequencies with which different parts of the spiders' bodies made contact with the ants (and vice-versa) differed in the four species of spiders (and ants). The various responses to contact also occurred at different frequencies in the four *Myrmarachne* species. These interspecific differences in *Myrmarachne* not only reflect versatility in their behaviours, but also a degree of plasticity in these ant-associating salticids, necessary for survival when living in the vicinity of potentially dangerous ants.

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