Behavioral mimicry in *Myrmarachne* species (Araneae, Salticidae) from North Queensland, Australia

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Abstract.   Batesian ant mimics – such as salticids belonging to the genus *Myrmarachne* – resemble their models to deceive potential predators, sometimes including the ants themselves. *Myrmarachne* species in addition to being striking visual mimics of ants also wave their first pair of legs in the air, much like the antennal movement of ants. Whether this leg movement is part of *Myrmarachne* species' mimicry is debated. In this study the leg I movement of four *Myrmarachne* species was investigated, with particular attention given to the frequency and amplitude of the leg waving. Correlations between the leg waving and other behaviors of *Myrmarachne* species were also looked at. There were interspecific differences in leg I movements, and the leg I waving also depended on other behaviors such as "bobbing" the opisthosoma. Thus the leg I movement of *Myrmarachne* species is behavioral mimicry of the antennal movement of ants, in other words increasing the spiders' resemblance to the ants to avoid predation. This "antennal illusion" displays characteristics of a plastic trait which has evolved under selection pressure.

Keywords: Behavior, antennal illusion, mimic, myrmecomorphy

Ant-mimicry in arthropods, the morphological, chemical and/or behavioral resemblance of specialized arthropod species to ants (Rettenmeyer 1970; McIver & Stonedahl 1993), is widespread and has - specifically in spiders - evolved repeatedly in families such as the Salticidae and the Clubionidae (for review see Cushing 1997). Batesian (Bates 1862) ant mimics must live in sympatry with their models, resembling their noxious or aggressive model thereby deceiving potential predators and thus gaining protection. The selection pressure exerted by predators is strong and, as a consequence, traits associated with Batesian mimicry are expected to evolve rapidly (Mappes & Alatalo 1997). The resemblance of Batesian mimics of ants to their models (also known as myrmecomorphs) can be both morphological and behavioral. A constriction in the middle of the carapace and a shiny opisthosoma shaped similarly to the ant's abdomen are some of the morphological adaptations of ant-mimicking spiders. The constricted carapace gives the spider the appearance of a three-segmented body like that of ants, whereas the shiny look of the opisthosoma - obtained through the presence of specialized or scale-like setae – and its shape further increase the mimic's resemblance to the ant (McIver & Stonedahl 1993).

Myrmecomorphs often reinforce their morphological resemblance to ants through ant-like behaviors. These behaviors include walking in a zig-zag motion (Reiskind 1977; Pekár & Král 2002), moving their opisthosoma up and down ("twitch abdomen" in Jackson 1982) in a manner similar to gaster bobbing in ants, and waving their first pair of legs in the air while walking on the remaining three pairs (Reiskind 1977). This movement of the first pair of legs in myrmecomorphs is generally thought of as behavioral mimicry, and has therefore been termed "antennal illusion" (Reiskind 1977). In some cases however, this leg movement is carried out by spiders to detect chemical cues from ants, as in the ant-eating zodariid spider *Habronestes bradleyi* (Pickard-Cambridge 1869) (Allan et al. 1996). Thus, the purpose of this leg I movement is not always clear as Pekár & Král (2002) stipulate in their study on *Zodarion*, suggesting that the "antennal illusion" of these spiders could be a form of threat display towards the ants rather than a means of detecting airborne chemicals. The leg I movement can vary greatly among species as well as between males and females of the same species, as was found in a species of *Sarinda* cited by Jackson & Drummond (1974) as *Sarinda linda* Reiskind (not listed in Platnick 2008).

Myrmarachne McLeay 1835 (Araneae, Salticidae) is a highly speciose genus of salticids whose species bear a striking resemblance to different ant species with which they associate closely and whose individuals also wave their first pair of legs in the air (Mathew 1954; Edmunds 1978; Jackson 1986). Since many ant species are aggressive and attack animals not belonging to their colony (Hölldobler & Wilson 1990), the close association of ant-mimics with ants can be dangerous (Halaj et al. 1997; Nelson et al. 2004; Nelson et al. 2005). *Myrmarachne* species, however, have developed special behaviors allowing them to deal with the aggressive nature of ants (Ceccarelli 2007) and, as myrmecomorphs have been shown to have higher rates of survival than non-ant associating spiders (Edmunds 1993; Nelson et al. 2004), establishing that these spiders are Batesian mimics. *Myrmarachne* species are diurnal, and rely heavily on visual, rather than chemical cues (Nelson & Jackson 2007), which means that they are unlikely to wave their legs I as a means of picking up chemical cues.

Using four *Myrmarachne* species as examples of Batesian mimics, this study investigates the nature of leg I movement in these salticids. The questions addressed are how do leg I movements differ between *Myrmarachne* species and sex, how do other behaviors influence these movements, and is there a relationship between leg I movement of each *Myrmarachne* species and antennal movement of the corresponding ant species? These questions help us understand the nature of leg I movement in a typical Batesian ant-mimic. If the leg I movement is a means of picking up chemical cues we would expect it to be much more random than if it is really a Batesian mimicry trait. In contrast, if the leg I movement is a component of Batesian mimicry we would expect this behavior to display properties similar to other traits under selection pressure, such as interspecific differences and plasticity.
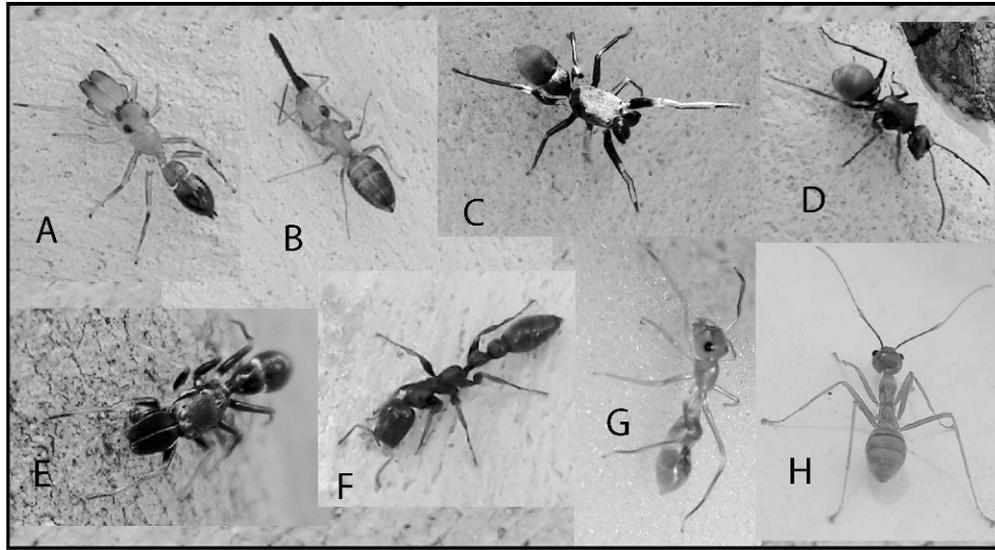
Figure 1.—Paired photographs of *Myrmarachne* mimics and their respective model ant species from Townsville. *Myrmarachne* sp. A (A) and model ant *Opisthopsis haddoni* (B); *Myrmarachne* sp. B (C) and model ant *Polyrhachis* nr.*obtusa* (D); *Myrmarachne* sp. D (E) and model ant *Tetraponera punctulata* (F); *Myrmarachne* sp. F (G) and model ant *Oecophylla smaragdina* (H) (modified from Ceccarelli & Crozier 2007).

METHODS

This study was carried out at the James Cook University campus in Townsville, North Queensland, Australia (19°13′S, 146°48′E) using sympatric species of local *Myrmarachne* (species used here designated sp. A, B, D, and F) and their respective model ant species. The *Myrmarachne* species are undescribed to date, but species integrity has been established through DNA analysis (Ceccarelli & Crozier 2007) and taxonomic work is under way. Mimic-model associations between *Myrmarachne* and sympatric ant species were determined visually by identifying the ant species that had the closest morphological resemblance to each *Myrmarachne* species (see Fig. 1). In addition, each *Myrmarachne* species was collected within a 5 meter radius of a determined model ant species' colony.

Voucher specimens of all species used in this study have been deposited in the arachnid and entomology collections of the Queensland Museum (Brisbane, Australia) with the following accession numbers: S66648 (*Myrmarachne* sp. A); S66649 (*Myrmarachne* sp. B); S66650 (*Myrmarachne* sp. D); S66651 (*Myrmarachne* sp. F); T133706–707 (*Opisthopsis haddoni* workers); T133693–696 (*Polyrhachis* nr. *obtusa* workers); T133697–699 (*Tetraponera punctulata* workers); T133700–702 (*Oecophylla smaragdina* workers). The numbers of individual females and males for *Myrmarachne* species used in this study are shown in Table 1. For the ants, 15 individuals from each species were used.

The animals were collected and brought into the lab for video recording. An individual *Myrmarachne* and one ant (random model or non-model) were videotaped inside a 10 cm diameter Petri dish. Recordings were made for 1 h, on each occasion using a different pair of animals as well as a new Petri dish, thus avoiding possible effects on behavior from chemical cues left from a previous encounter. The recording was carried out using a low light, high resolution video camera connected to a video recorder. The subsequent analysis was done using a SVHS player connected to a computer, using the program Adobe Premiere (version 4.2). The hour-long recordings were parsed twice, each time recording different variables from different parts of the tape.

During the first videotape pass, twenty instances were analyzed (the first ten at the start of the recording and the next ten starting from 30 min into the tape) when the spider showed a reaction to the presence of the ant. The analysis involved recording whether the spider was waving its first pair of legs, lifting them up without waving them, and/or bobbing its opisthosoma (as shown in Table 2). These data were recorded to find out how often *Myrmarachne* wave their legs I (as opposed to carrying out other forms of behavior) when encountering ants and provided us with count data on how frequently the spiders carried out each behavior.

The second videotape pass involved taking ten measurements per hour (every 6 min) of the frequency (cycles per second) at which *Myrmarachne* individuals waved their first pair of legs and the amplitude (in mm) of the leg movement.

Table 1.—Numbers of male and female *Myrmarachne* of each species used in this study

Myrmarachne species	A	B	D	F
Females	9	8	9	10
Males	6	7	6	5

Table 2.—Behavioral traits observed in *Myrmarachne* species

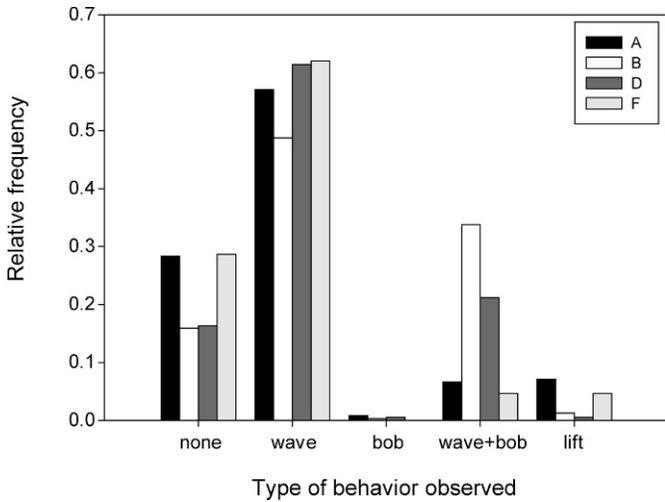| Behavior	Explanation
none	neither waving the legs nor bobbing the opisthosoma
wave	waving the first pair of legs up and down
bob	only bobbing the opisthosoma
wave + bob	waving the first pair of legs up and down and bobbing the opisthosoma at the same time
lift	first pair of legs raised in the air and held there without the up-and-down movement

Figure 2.—Relative frequencies of the type of behaviors (as described in Table 2) of all four *Myrmarachne* species (A, B, D, and F). (χ^2_{12} = 142.69, P < 0.001).

When measuring the frequency, one cycle was taken to be the movement of the leg from one point through both top and bottom extremities and back to the starting point. The amplitude was measured from the highest apex of the tip of leg I to the substrate. To avoid negative values, the substrate was chosen as a starting point for the amplitude measurement since the leg I waving often started from the substrate. At the same time co-occurring activities were recorded, namely whether or not the *Myrmarachne* was moving (walking or

Figure 4.—Notched boxplot of the frequency of leg I waving for each *Myrmarachne* species and sex. Species and sex are coded as: AF = females of species A, AM = males of species A; BF = females of species B, BM = males of species B; DF = females of species D, DM = males of species D; FF = females of species F, FM = males of species F. (ANOVA for species: $F_{(3,57)}$ = 6.41, P < 0.001; ANOVA for sex: $F_{(1,57)}$ = 1.10, P = 0.298; ANOVA for species-sex interaction: $F_{(3,57)}$ = 0.56, P = 0.643).
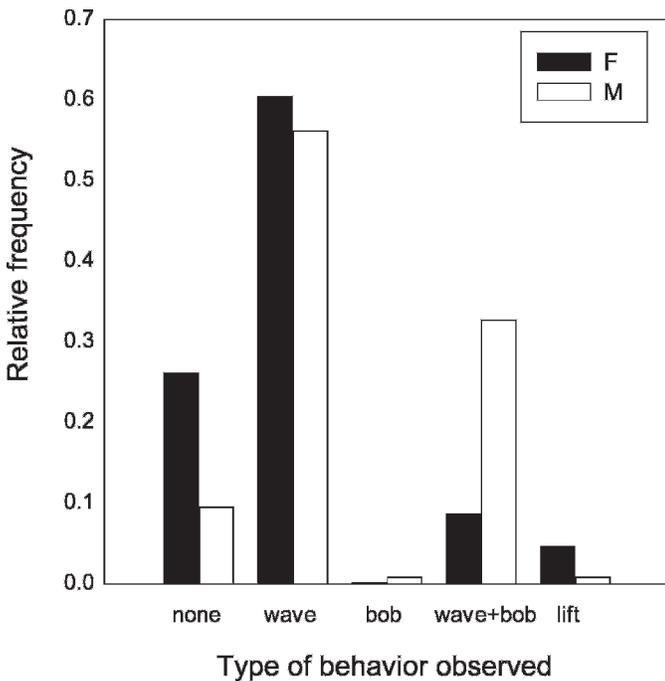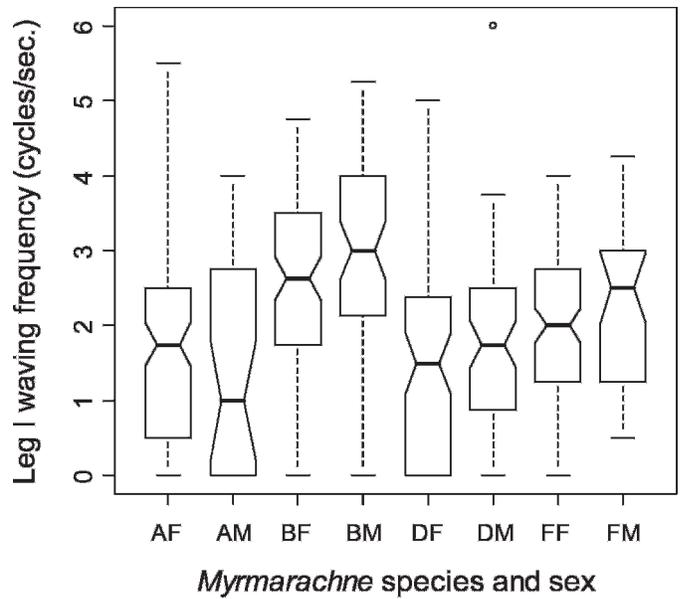

Figure 3.—Relative frequencies of types of behaviors (as described in Table 2) of *Myrmarachne* females and males. Females are represented by the black bars and males by the white bars. (χ^2_4 = 114.07, P < 0.001).
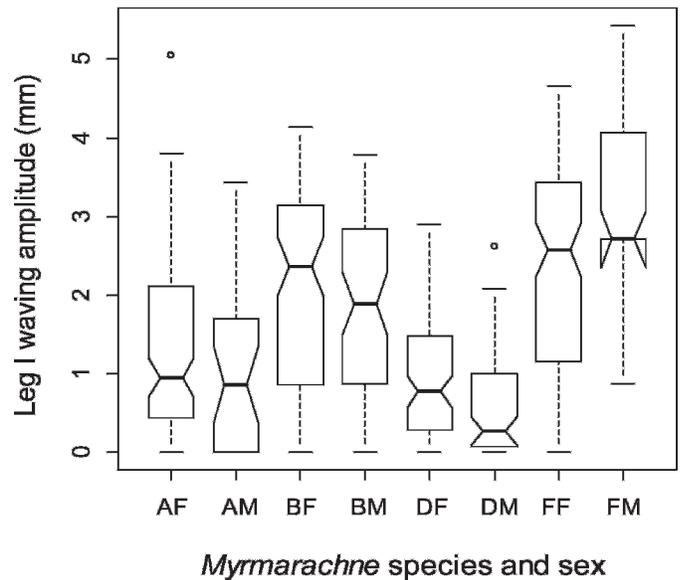

Figure 5.—Notched boxplot of the amplitude of leg I waving for each *Myrmarachne* species and sex. Species and sex coded as: AF = females of species A, AM = males of species A; BF = females of species B, BM = males of species B; DF = females of species D, DM = males of species D; FF = females of species F, FM = males of species F. (ANOVA for species: $F_{(3,57)}$ = 12.20, P < 0.001; ANOVA for sex: $F_{(1,57)}$ = 0.005, P = 0.944; ANOVA for species-sex interaction: $F_{(3,57)}$ = 1.63, P = 0.192).
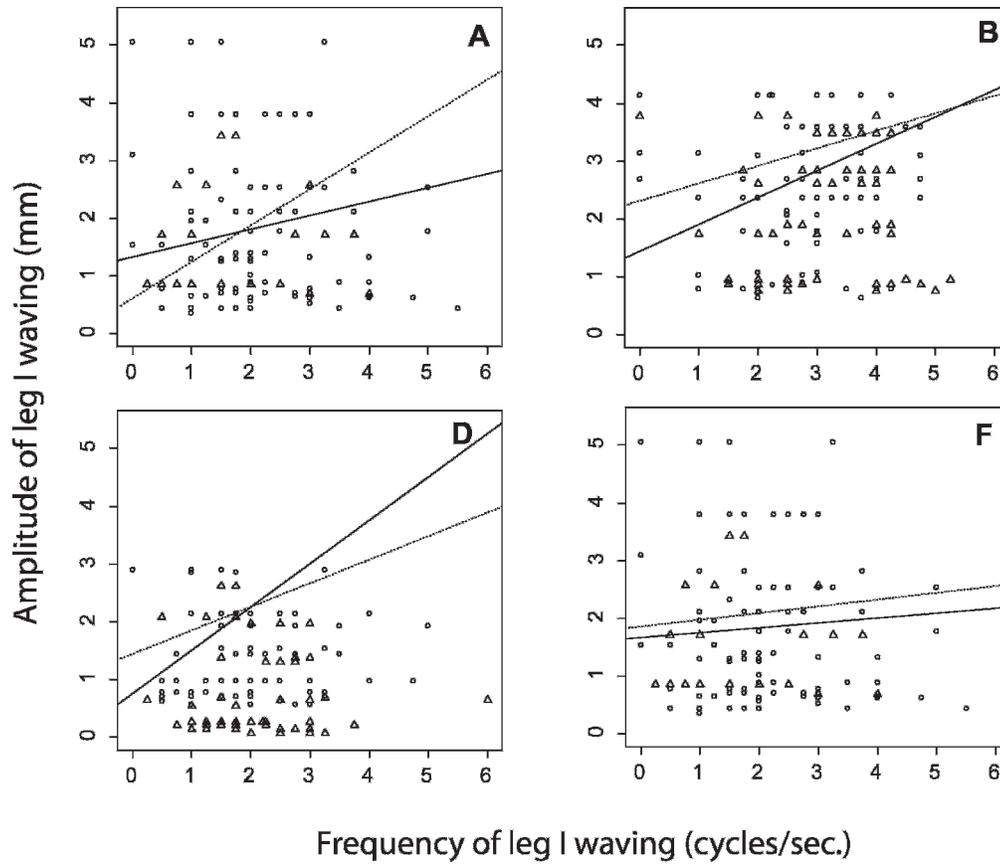
Figure 6.—Scatterplots of frequency of leg I waving (in cycles per second) on the x-axes, versus the amplitude of leg I waving (in mm) on the y-axes for each *Myrmarachne* species separately. The species are "A," "B," "D," and "F" as shown on the top right-hand corner of each graph. Data for females is represented by the circles, with the solid best-fit line, whereas data for the males is represented by the triangles and the dashed best-fit line.

running), whether it was bobbing its opisthosoma and whether or not it had the ant in its field of vision (i.e., it was facing the ant with its anterior median eyes). Again, these variables were recorded to find any possible correlations with the leg I movement. This part of the study was also carried out to find interspecific differences in *Myrmarachne* with regard to the average speed and amplitude of the leg waving. The same measurements were recorded for the frequency (cycles/second)

and amplitude of antennal movements in the model ant species.

Data analysis was carried out using the program R version 2.1.1 (R_Development_Core_Team 2005) with the rpart package (Therneau et al. 2005) to build recursive partitioning trees to identify the variables most closely associated with the different groups of antennal illusion and bobbing. Recursive partitioning analysis was popularized by Breiman et al. (1984),

Table 3.—Results of Mantel test for distance matrices of leg/antennal frequency and amplitude for each *Myrmarachne* and ant species. Values shown in table are Mantel's r based on Pearson's product-moment correlation followed by the significance value. Significant correlations ($P < 0.05$) are shown in bold.

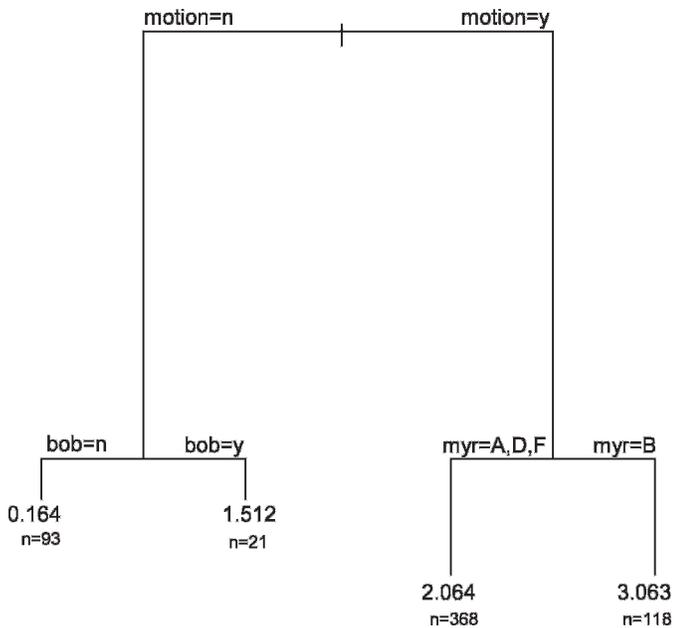|	*Myrmarachne* species			
Ant species	A	B	D	F
Opisthopsis haddoni	**r = 0.23**	r = −0.03	r = 0.06	r = 0.03
	P = 0.002	P = 0.676	P = 0.089	P = 0.299
Polyrhachis nr. *obtusa*	r = 0.04	r = 0.12	**r = 0.11**	r = 0.07
	P = 0.254	P = 0.056	**P = 0.012**	P = 0.143
Tetraponera punctulata	r = −0.01	r = 0.07	r = −0.01	**r = 0.12**
	P = 0.517	P = 0.106	P = 0.564	**P = 0.015**
Oecophylla smaragdina	r = 0.002	r = 0.0007	r = 0.06	r = 0.07
	P = 0.471	P = 0.488	P = 0.066	P = 0.081

Figure 7.—Recursive partitioning tree of frequency (cycles/second) of leg I waving (values at the end of the branches) by all *Myrmarachne* species, and the variables that are most closely correlated with a particular frequency value. "motion" refers to whether the *Myrmarachne* was moving (y) or not (n), "bob" refers to whether the *Myrmarachne* was moving its opisthosoma up and down (y) or not (n), "myr" is the species of *Myrmarachne* (A, B, D, and F). The letter n at the end of the frequency value represents the number of times that frequency value was placed in correlation with the predictor variables.

and is now widely used in various areas of science (e.g., Lehmann et al. 2003; Karels et al. 2004). This analysis is used to find correlations between mixed (categorical and/or numerical) variables, and the resulting tree shows the dependent variable at the end of the branches and each predictor variable at the nodes. The closer the variable is to the root node of the tree, the higher its predictive value on the outcomes. Repeated measures ANOVA was carried out to determine if there were significant differences in the frequency and amplitude of leg I waving between *Myrmarachne* species and sex. Chi-squared contingency tests were also carried out to find possible differences in behavioral mimicry (count data on the categories described in Table 2) between *Myrmarachne* species and males and females. In addition, a Pearson's correlation test was carried out to find possible correlations between leg I waving frequency and amplitude. This was done to see whether – in the case of a significant correlation – an index of leg I frequency over leg I amplitude could be used as a general measure of leg I movement. Further, Pearson's correlation tests were then carried out to find possible correlations between the leg I movements of *Myrmarachne* species and the antennal movements of their respective model ant species. In case of non-significant results for the Pearson's correlation tests on the leg I/antennal indices, a Mantel's test on distance matrices for frequency and amplitude of model ant antennal movement and *Myrmarachne* leg I movement was also performed on the data.

RESULTS

In this study, when the four *Myrmarachne* species reacted to the presence of ants there was a significant difference in the way they carried out the different behaviors, including the leg I waving (see Fig. 2). *Myrmarachne* species B and D waved their legs I and bobbed their opisthosoma more frequently than species A and F, whereas the latter lifted their legs I without waving more often than species B and D. There was a significant difference between *Myrmarachne* males and females in how frequently they carried out each type of behavior (see Fig. 3). The main difference between males and females was that males bobbed their opisthosoma and waved their first pair of legs more frequently than females.

The frequency (measured in cycles/second) as well as the amplitude of the leg I movement was significantly different between the *Myrmarachne* species but not between *Myrmarachne* males and females (see Figs 4 and 5). There was a positive correlation (Pearson's $r = 0.337$, $P < 0.001$) between the frequency and amplitude of the leg I waving for all *Myrmarachne* species. This correlation gives an indication of the intensity of the movement: the higher up the spider moved its first pair of legs, the quicker it moved them up and down. This trend was consistent throughout all species and both sexes (see Fig. 6). This correlation allowed for the calculation of a general leg and antennal waving index (frequency divided by amplitude).

When the leg waving of each *Myrmarachne* species was compared to the antennal movements of the respective model ants, no significant correlation was found, whether between the frequencies, amplitudes or indices. The Mantel test for leg I waving frequency and amplitude of *Myrmarachne* species versus the antennal waving frequency and amplitude of ant species showed significant correlations between *Myrmarachne* sp. A and *Opisthopsis haddoni*, *Myrmarachne* sp. D and *Polyrhachis* nr. *obtusa*, and *Myrmarachne* sp. D and *Tetraponera punctulata* (see Table 3). There is only one case where a correlation between the antennal movements of the model and the leg I movement of the mimic is found (*Myrmarachne* sp. A and *Opisthopsis haddoni*).

The strongest predictor variable for the frequency of *Myrmarachne*'s leg I waving was found to be whether the spider was moving (walking or running). The species of spider and whether or not the spider was bobbing its opisthosoma were the next most important factors influencing the leg I waving frequency. Thus, the lowest frequencies of leg I waving were most closely correlated with the spider being stationary and not bobbing its opisthosoma. When spiders were walking or running, the higher frequencies of leg I waving were more closely correlated with individuals belonging to *Myrmarachne* sp. B (see Fig. 7). The highest leg I amplitude was correlated most closely with *Myrmarachne* spp. B and F moving (walking or running) whereas the lowest leg I amplitude was correlated with species A and D not moving. The sex of the spider was only a determining factor for leg I amplitude when species B and F were stationary (see Fig. 8).

DISCUSSION

When *Myrmarachne* species reacted to sympatric ants, they commonly waved their first pair of legs, lifting them without the up-and-down movement, and/or "bobbed" their opistho-
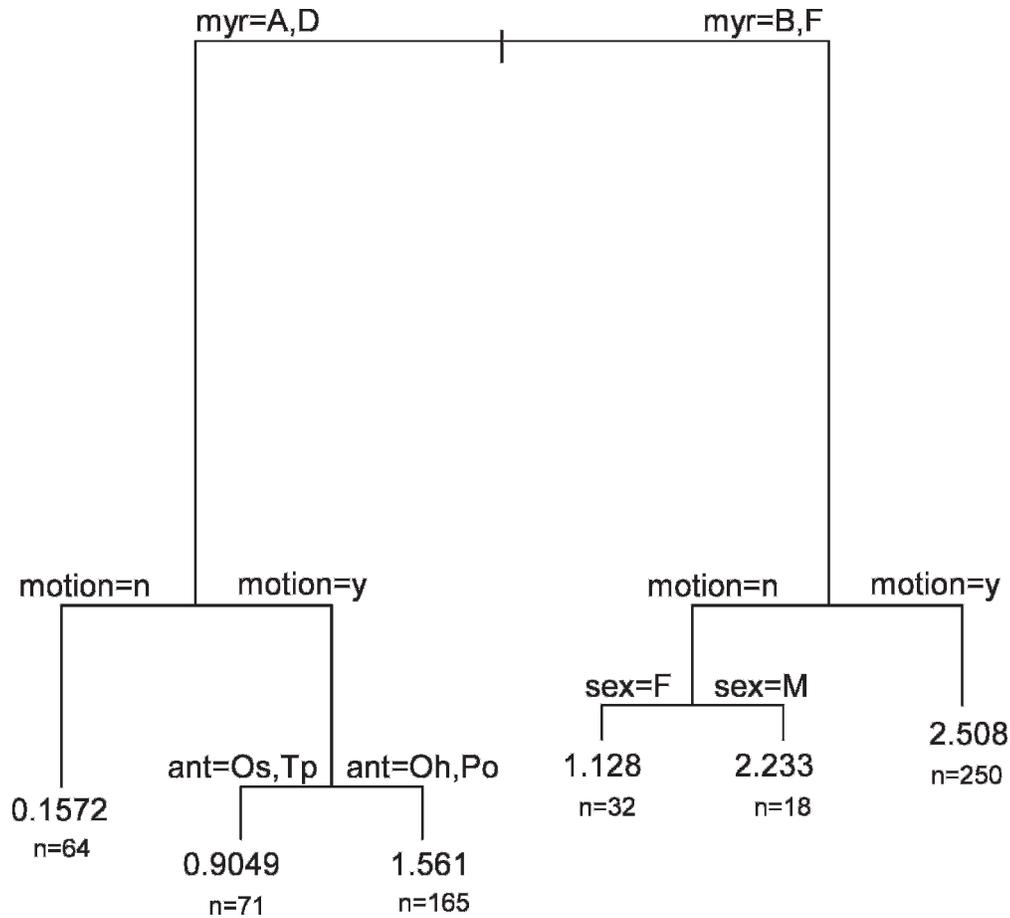
Figure 8.—Recursive partitioning tree of amplitude (in mm, values at the end of the branches) of leg I waving by all *Myrmarachne* species. "Myr" is the species of *Myrmarachne* (A, B, D and F), "motion" refers to whether the *Myrmarachne* was moving (y) or not (n), "sex" is the sex of *Myrmarachne* (M = male, F = female), and "ant" refers to the ant species (Oh = *Opisthopsis haddoni*, Po = *Polyrhachis* nr. *obtusa*, Tp = *Tetraponera punctulata*, Os = *Oecophylla smaragdina*) present in the Petri dish with the spider. The letter n at the end of the amplitude value represents the number of times that amplitude value was placed in correlation with the predictor variables.

soma. This versatile range of behaviors carried out at different frequencies by the four *Myrmarachne* species and between males and females is evidence for behavioral plasticity in these spiders. The up-and-down movement of the opisthosoma - here referred to as "bobbing" - has been observed and commented on before (Jackson 1982) and much resembles the abdominal movements of ants recruiting nest-mates for the defence of the colony (Hölldobler 1983; Mercier et al. 1997). The lifting of the first pair of legs also resembles the high-held antennae of ants during aggressive displays (Hölldobler 1983; Hölldobler & Wilson 1990). The detailed analysis of the leg waving behavior revealed further interspecific differences in the frequency (or rate, measured as cycles/second) and amplitude with which the *Myrmarachne* species moved their first pair of legs. This motion resembles the antennal movement of ants, yet the leg I waving of each *Myrmarachne* species did not closely match the antennal movements of their respective model ant species. Correlations between the antennal movement of each ant species and the leg I movement of the respective *Myrmarachne* mimic species would have been unrealistic, since there are anatomical and morphological differences between ants' antennae and spiders'

legs, and therefore similar movements from these two appendages cannot be expected.

In nature, each *Myrmarachne* species closely associates with an ant species (Edmunds 1978), and the visual similarity of the spider with the ant is striking (Mathew 1954; Jackson 1986). *Myrmarachne* species are Batesian ant mimics, since they do not routinely prey on ants (Jackson 1986; Jackson & Willey 1994), and they are not preyed on as often as non-ant mimics (Edmunds 1993; Nelson et al. 2004; Nelson et al. 2005). The *Myrmarachne* species' leg waving behavior analyzed in this study is likely to be a Batesian mimicry trait, which – like other phenotypic traits in Batesian mimicry – is under strong selection pressure exerted by predation (Mappes & Alatalo 1997). Thus we found interspecific differences and behavioral versatility and plasticity since all these features arise through selection pressure during evolution. The differences between males and females in how often they perform the leg I waving behavior can be explained by the fact that male *Myrmarachne* spiders spend more time exposed to predators when outside their retreats searching for females (Jackson 1982), and must therefore be more convincing mimics than females. In addition, *Myrmarachne* individuals that were walking or

running waved their first pair of legs at a higher rate and amplitude, an observation which is consistent with the hypothesis that the leg I movement complements other ant-like traits when the spider is moving around and therefore more exposed to predators.

Waving the first pair of legs has been observed in several other species of spiders, such as *Habronestes bradleyi* (Pickard-Cambridge 1869) (Allan et al. 1996), *Zodarion germanicum* (Koch 1837) and *Z. rubidium* Simon 1914 (Pekár & Král 2002), and *Sarinda linda* Reiskind (Jackson & Drummond 1974). However the purpose of this leg movement is not the same for all species. In *H. bradleyi*, waving the first pair of legs was found to be a means of detecting alarm pheromones from ants for the spider to prey on (Allan et al. 1996), and in *Zodarion* species it could be a threat display towards the ants (Pekár & Král 2002). Jackson and Drummond (1974) found that males wave their first pair of legs more often than females. So the question arises whether this leg movement is higher in males that are trying to detect female pheromones. However, according to Gaskett (2007) the receptors that detect female pheromones are located on the pedipalps and not on the legs. Furthermore, Nelson and Jackson (2007) showed that *Myrmarachne assimilis* Banks 1930 males use visual, rather than chemical cues to detect the presence of females. Since *Myrmarache* species do not normally prey on ants, and rely on visual rather than chemical cues, waving their first pair of legs is unlikely to be used as a means of detecting airborne chemicals. In the cases where the spiders wave their first pair of legs to mimic the antennal movement of ants, this behavior has been referred to as "antennal illusion" (Reiskind 1977). All the evidence – including the outcomes of this study – support the hypothesis that leg I waving in *Myrmarachne* species is in fact an "antennal illusion," or a trait that has evolved to reinforce the spiders' Batesian ant mimicry.

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