RAFFLES BULLETIN OF ZOOLOGY **64**: 70–75
Date of publication: 29 March 2016
http://zoobank.org/urn:lsid:zoobank.org:pub:CBF84197-175F-4838-B39E-E8F6DF048981

Pattern of co-occurrence between ant-mimicking jumping spiders and sympatric ants in a Bornean tropical rainforest

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Abstract. To evaluate the pattern of co-occurrence between ant-mimicking jumping spiders and sympatric ants in a tropical rainforest, we sampled these arthropods and also non-mimicking jumping spiders by net-sweeping from the understory vegetation in Sabah, Malaysian Borneo. We collected the spiders and ants from a total of 594 sample points, with ants occurring in 445 points (79.4%), non-mimicking jumping spiders in 308 (51.9%), *Agorius* ant-mimicking spiders in 40 (6.7%), and *Myrmarachne* ant-mimicking spiders in 59 (9.9%). Frequencies of occurrence of non-mimicking jumping spiders showed no significant difference in relation to ant-occurrence, whereas both of the ant-mimicking spider genera occurred significantly more frequently with ants. *Agorius* spiders co-occurred with a wider variety of different ant genera, compared to *Myrmarachne*, but logistic regression analyses and a null model test showed no specific associations between *Agorius* spiders and the sympatric ant genera. The mimetic resemblances of *Agorius* spiders are considered to be much less ant-like than those of *Myrmarachne* spiders, because their constriction of the cephalothorax is not as obvious as in *Myrmarachne*. These data provide support for the multi-model hypothesis (Edmunds 2000), which predicted that a poor ant-mimic should occur in ranges of many different ants, compared to good ant-mimic.

Key words. Ant-mimicry, Formicidae, Salticidae, Co-occurrence relationship, Multi-model hypothesis, Southeast Asian tropics

INTRODUCTION

Myrmarachne is a genus of jumping spiders (Salticidae) with over 200 named species, most of which occur in tropical regions of Southeast Asia (Proszynski, 2010; World Spider Catalog, 2016). All species of *Myrmarachne* closely resemble ants. They have an elongated body, a slender petiole-like ant waist, and create an antennal "illusion" by waving the forelegs. Furthermore, the ant-like resemblance of *Myrmarachne* is reinforced by distinct constriction between the cephalic and the thoracic regions, which gives the illusion of a three-part (head-thorax-abdomen) body like that of ants. Several studies have shown that *Myrmarachne* salticids are Batesian mimics of ants because they gain protection from visually hunting predators such as solitary wasps (Edmunds, 1993), mantises (Nelson et al., 2006), and other spiders (Cutler, 1991; Durkee et al., 2011; Huang et al., 2011; Nelson & Jackson, 2012). Batesian mimics might be expected to live near their models, so as to increase the efficacy of the mimic's protection from predators that are averse to the model (Edmunds, 2000; Pfennig et al., 2001, 2007). Indeed, some species of *Myrmarachne*, such as *M. assimilis*, *M. melanotarsa*, and *M. hanoi*, are observed routinely in the close company of the model ants (Nelson et al., 2004; Jackson et al., 2008; Yamasaki & Ahmad, 2013). However, the occurrence pattern of mimicking-spiders and its relationship with sympatric ant-occurrences has yet to be evaluated based on quantitative field research.

We investigated relationships of mimetic diversity in *Myrmarachne* spiders to ant species diversity in Danum Valley Conservation Area in Sabah, Malaysian Borneo. To this end, we sampled the spiders and sympatric ants by net-sweeping from understory vegetation from 594 sample points in the research area. Using samples obtained from net-sweeping, we analysed the relationship between the occurrence patterns of *Myrmarachne* spiders and sympatric ants to examine whether these were associated positively. Furthermore, because the spiders collected in our net-sweeping samples included non-mimicking jumping spiders and ant-mimicking jumping spiders of genus *Agorius*, we also examined the co-occurrence relationship of non-mimicking jumping spiders and *Agorius* spiders to sympatric ants, for

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ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

comparison with co-occurring relationships of *Myrmarachne* spiders. *Agorius* spiders are regarded to resemble ants much less than *Myrmarachne* spiders, because constriction of the cephalothorax is not as obvious (Koh, 1989). Edmunds (2000) introduced the "multi-model hypothesis" to explain the coexistence of poor and good mimicry. The multi-model hypothesis assumed that when many potential model species live in a given habitat (e.g., many different species of ants), a poor, general ant-mimic should occur in ranges of many different ants, whereas a good ant-mimic, with a specific resemblance to one particular species or genus of ant, should normally occur in the range of that ant in order to be an effective mimicry. Edmunds (2006) examined whether the hypothesis applied to some good and poor ant-mimicking spiders in peninsular Malaysia. However, in this study he searched for ant-mimicking spiders and ants by eye, and the data presented cannot demonstrate statistical evidences for or against the hypothesis. A realistic test requires quantitative field data on co-occurrence patterns of ant-mimicking spiders to the sympatric ants as obtained by our field research. The present study addresses the question of whether a poor ant-mimic, *Agorius* spiders, should occur in ranges of many different ants, and whether a good ant-mimic, *Myrmarachne* spiders, should normally occur in the range of that ant in order to be an effective mimic.

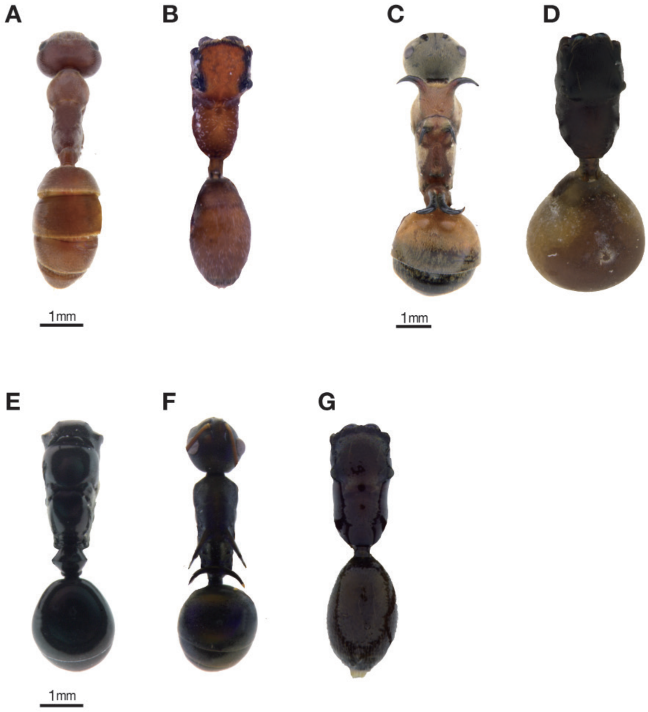

Fig. 1. Dorsal views of the model ants and their ant-mimicking spiders, showing the body parts removed legs and antennae. A, *Camponotus saundersi*; B, *Myrmarachne alticephalon*; C, *Polyrhachis olybia*; D, *Myrmarachne maxillosa*; E, *Polyrhachis boltoni*; F, *Polyrhachis phalerata*; G. *Myrmarachne malayana*.

MATERIAL AND METHODS

Study site. The study was undertaken at the Danum Valley Field Centre (DVFC), which lies on the eastern edge of the Danum Valley Conservation Area (4°55'N 117°40'E): a 438 km^2 area of primary forest within the Ulu Segama Reserve in south-eastern Sabah, Malaysia (north-east Borneo). Much of the Conservation Area is lowland (< 760 m) evergreen dipterocarp forest, where dipterocarps comprise up to 80% of the canopy trees (Newbery et al., 1992). The annual rainfall at Danum averages about 2800 mm per year, and annual mean temperature averages 26.7°C (Marsh & Greer, 1992). In this study, we used four main trails, Nature, Waterfall, East and West trails in DVFC as sampling transects.

Sample collections. Ants and spiders were collected by sweeping with a sweep net (50 cm diameter, 100 cm in depth) from the forest understory. Sweeps were conducted at about 2 m intervals along main trails of DVFC. We took 10-sweeps at each sample point in such way that ants and spiders were swept from leaves and twigs of an understory tree, isolating from other tree clumps. The captured ants and spiders in the net were put into a plastic bag, brought to the laboratory in the field center, kept in a freezer for several hours, then preserved in bottles filled with 75% alcohol. The sampling of ant and spider assemblages was conducted in September 2004, February 2005 and December 2006, and a total of 594 sample points were collected.

Identification of specimens. Ant specimens were identified to genus using the keys of Hashimoto (2003) and then determined to species or morphospecies using the reference collection of Asian ants established by the International Network for the Study of Asian Ants (ANeT) in Kagoshima University. *Myrmarachne* spiders were identified to species level using the keys of Yamasaki & Ahmad (2013). However, due to insufficient taxonomic studies for other groups of jumping spiders in Borneo, *Agorius* spiders were identified only to genus, and non-mimicking jumping spiders as family Salticidae. From samples collected here, a total of 115 ant species, belonging to 28 genera, and 10 species in *Myrmarachne* were identified. Voucher specimens of ants and spiders were deposited in ITBC of University Malaysia Sabah, and the Museum of Nature and Human Activities, Hyogo, Japan.

Statistical analysis. The occurrence of ants and spiders in each sampling point was coded into presence-absence matrix, and the following procedures were applied to the matrix. We used a Chi-square test to compare the frequency of occurrence between non-mimicking jumping spiders and ant-mimicking spiders in co-occurrence relationships to the sympatric ants. These analyses were performed using Statistical software JMP version 10 (SAS Institute, Cary, NC, USA). We used Shannon's index (Shannon, 1948) for measurement of the variety of ant genera co-occurring with *Agorius* and *Myrmarachne* spiders, and assessed the significance of the differences between the indices of *Agorius* and *Myrmarachne* by randomisation test ($p < 0.05$), as described by Solow (1993). The analyses were performed using the software package Species Diversity & Richness 4.0 (PISCES Conservation Ltd). To measure degree of co-occurrence association between ant-mimicking spiders and ants, we used binary logistic regression analyses for each pair of the genus and species. The analyses provided one of three possible results; an odds ratio value of 1 indicates

Table 1. Comparisons by the chi-square test for occurrence frequency of non-mimicking spiders, *Agorius* and *Myrmarachne* ant-mimicking spiders in relation to the sympatric ant-occurrence.

Spiders	**Ants**		**Chi-square Test**
	Present	**Absent**	
Non-mimicking			
Present	235 (39.6%)	210 (35.4%)	*p* = 0.420
Absent	73 (12.3%)	76 (12.8%)	(χ^2 = 0.65, df = 1)
Agorius			
Present	36 (6.1%)	409 (68.9%)	***p* = 0.013**
Absent	4 (0.7%)	145 (24.4%)	(χ^2 = 6.20, df = 1)
Myrmarachne			
Present	51 (8.6%)	394 (66.3%)	***p* = 0.022**
Absent	8 (1.3%)	141 (23.7%)	(χ^2 =5.21, df = 1)

Table 2. Statistical measures of co-occurrence association between genus pairs of ant-mimicking spiders and the sympatric ants in logistic regression analyses and null model tests.

Ant genus	***Agorius***		***Myrmarachne***	
	OR (95% CI)	**C-score**	**OR (95% CI)**	**C-score**
Polyrhachis	1.18 (0.84–1.65)	–0.986	**1.60 (1.21–2.12)**	**–2.968**
Crematogaster	1.00 (0.70–1.42)	–0.071	1.06 (0.80–1.41)	–0.083
Camponotus	1.36 (0.93–1.99)	–1.607	**1.53 (1.13–2.08)**	**–2.545**
Dolichoderus	0.96 (0.59–1.56)	0.169	1.19 (0.84–1.53)	–1.384
Paraparatrechina	1.09 (0.63–1.87)	–0.364	0.95 (0.58–1.53)	0.637
Technomyrmex	1.30 (0.79–2.13)	–1.063	**1.55 (1.06–2.27)**	**–3.011**

OR: odds ratio, 95% CI: confidence intervals at 95%.
Bold number indicates significant association ($p < 0.05$)

Table 3. Species combinations found with significant co-occurrence association for *Myrmarachne* and ant species occurred more than 10 sample points.

Ant species	***Myrmarachne alticephalon* (19)**	
	OR (95%CI)	**C-score**
Camponotus saundersi (57)	3.18 (1.95–5.17)	–5.11
Ant species	***Myrmarachne maxillosa* (13)**	
	OR (95%CI)	**C-score**
Polyrhachis olybia (16)	6.72 (3.59–12.61)	–7.73
Ant species	***Myrmarachne malayana* (11)**	
	OR (95%CI)	**C-score**
Polyrhachis boltoni (18)	6.38 (3.24–12.56)	–7.24
Polyrhachis phalerata (47)	4.28 (2.23–8.21)	–5.46

OR: odds ratio, 95% CI: confidence intervals at 95%
Frequency of occurrence of each species is shown by the numbers in parentheses

the occurrence patterns are associated randomly, whereas odds ratio values of greater than 1 and less than 1 indicate a positive and negative association, respectively ($p < 0.05$, 95% confidence interval). All logistic regression analyses also were performed in Statistical software JMP version 10 (SAS Institute, Cary, NC, USA). Additionally, we confirmed these results from the logistic regression analyses by null model tests (Gotelli & Graves, 1996), using null-model program EcoSim version 7.0 (Acquired Intelligence Inc. & Kesey-Bear). Herein, we used the C-score (Stone & Robert, 1990) as an index measuring the degree to which pairs co-occur, and swap algorithm and 'fixed-equiprobable' model for 5,000 randomisations of observed pattern in order to create null expectations for the C-score. The fixed-equiprobable model would be most appropriate for lists of species taken from standardised samples within areas of relatively homogeneous habitat (Gotelli, 2000). Following the approach of Sridhar et al. (2012), to facilitate the comparison of C-scores exhibited by each pair, we normalised (Z-transformed) their C-scores, which is calculated as: (observed C-score – mean of simulated C-scores)/standard deviation of simulated C-scores. The normalised values of greater than 1.96 and less than –1.96 indicate a negative and positive non-random co-occurrence pattern, respectively ($p < 0.05$, 95% confidence interval). In the logistic regression analyses and null model tests, we used only ant genera occurring in more than 60 sample points (>10% of the total), and examined only pairs of ant and *Myrmarachne* species occurring in more than 10 sample points (Table S1).

RESULTS

Of 594 total sample points, ants occurred in 445 points (79.4%), non-mimicking jumping spiders in 308 (51.9%), *Agorius* ant-mimicking spiders in 40 (6.7%), and *Myrmarachne* ant-mimicking spiders in 59 (9.9%). Chi-square test revealed that both *Agorius* and *Myrmarachne* spiders occurred significantly more frequently with ants than without ants (Table 1). On the other hand, frequencies of occurrence of non-mimicking jumping spiders showed no significant difference in relation to ant-occurrence. In total, 17 ant genera co-occurred with *Agorius* spiders and 15 with *Myrmarachne* spiders. The variety of co-occurring ant genera was determined using Shannon's index to be higher in *Agorius* (2.41) than in *Myrmarachne* (2.16). Randomisation test for the differences in Shannon's index revealed that ant genera co-occurring with *Agorius* were significantly more diverse (at 5% level) than those co-occurring with *Myrmarachne*. Ant genera with a frequency of occurrence of more than 10% of total sample points were *Polyrhachis* (244 occurrences, 41.1%), *Crematogaster* (232, 39.1%), *Camponotus* (118, 19.9%), *Dolichoderus* (93, 15.7%), *Paraparatrechina* (67, 11.3%), and *Technomyrmex* (60, 10.1%). Logistic regression analyses for occurrence patterns of the six ant genera to *Agorius* showed that the ant genera, except for *Crematogaster* and *Dolichoderus*, had positive associations with *Agorius*, but these associations were not statistically significant. Null model tests of co-occurrence also cannot detect significant association between these generic pairs. On the other hand, in *Myrmarachne,* significantly positive associations with *Polyrhachis*, *Camponotus* and *Technomyrmex* were revealed by logistic regression analyses and also null model tests (Table 2). Of the *Myrmarachne* species collected, *M. alticephalon* (19), *M. maxillosa* (13) and *M. malayana* (11) occurred at more than 10 sample points. Statistical measures of co-occurrence in logistic regression analyses and null model tests between the three *Myrmarachne* species and ant species occurring in more than 10 sample points showed significantly positive association of *M. alticephalon* with *Camponotus saundersi*, *M. maxillosa* with *Polyrhachis olybia*, and *M. malayana* with *Polyrhachis boltoni* and *Polyrhachis phalerata*, respectively (Fig. 1, Table 3).

DISCUSSION

Tropical rainforests support the most diverse ant fauna in the world (Hölldobler & Wilson, 1990). Indeed, a total of 115 ant species, belonging to 28 genera, were collected from our research site in a tropical rainforest. We thus expect to find ant-mimicking spiders in such a habitat to associate with the sympatric ants as predicted by the multi-model hypothesis.

Our results found that frequencies of occurrence of non-mimicking jumping spiders in the same site showed no significant difference in relation to ant-occurrence, whereas the occurrence of both of *Agorius* and *Myrmarachne* ant-mimicking spiders were positively associated with sympatric ant occurrence. Furthermore, we found that *Agorius* ant-mimicking spiders co-occurred with a greater variety of ant genera, compared to *Myrmarachne*, but *Agorius* spiders showed no specific associations with any particular ant genera. On the other hand, *Myrmarachne* ant-mimicking spiders showed significantly specific associations to the ant genera *Polyrhachis*, *Camponotus* and *Technomyrmex*. In this study we conducted further co-occurrence analyses for the three most frequently encountered species of *Myrmarachne* spiders with the sympatric ants. The analyses can detect significantly species-specific associations of *Myrmarachne alticephalon* with *Camponotus saundersi*, *M. maxillosa* with *Polyrhachis olybia*, and *M. malayana* with *P. boltoni* and *P. phalerata*. Although we do not present the data here, we objectively assessed shape, color and size of similarities between *Myrmarachne* species and ant species collected here using image-processing methods in computer vision (Hashimoto et al., in prep.). Our assessment of mimetic resemblance for *M. alticephalon* showed that it had the closest similarity to *C. saundersi* among the sympatric ant species. The assessment also revealed that *M. maxillosa* and *M. malayana* had close mimetic resemblance to two or more species of genus *Polyrhachis*, such as *M. maxillosa* to *P. olybia* and *P. armata*, and *M. malayana* to *P. phalerata*, *P. boltoni* and *P. furcata* (attributable to polymorphism in the color pattern of *M. maxillosa* and *M. malayana*). Although insufficient taxonomic studies for *Agorius* spiders prevent us from examining their co-occurrence pattern at species level, the co-occurrence pattern between *Myrmarachne* species and their presumed ant-models and that between *Agorius* spiders and sympatric ant genera, conform with the prediction of the multi-model hypothesis.

In summary, we found that occurrence patterns of *Agorius* and *Myrmarachne* ant-mimicking spiders in tropical rainforest in Borneo were associated positively to that of sympatric ants, with the good and poor ant-mimics associated with the ants as predicted by the multi-model hypothesis. To our knowledge our study is the first to have identified a positive co-occurrence association between ant-mimicking spiders and ants at a local habitat scale, based on quantitative field research. However, further analyses, such as field surveys examining relationships in spatial occurrence of prey of ant-mimicking spiders to the sympatric ants, and predators of the spiders to the ants, will be needed to fully understand co-occurrence pattern in the mimic-model relationship. Such surveys will be time-consuming because occurrence frequency of ant-mimicking spiders was much less than that of the sympatric ants and no-mimicking spiders, as observed by our study. Despite the difficulty gathering and analysing sufficient quantitative data on co-occurrence patterns of ant-mimicking spiders to their model ants, such ecological studies should give even more insight into the evolution of ant mimicry and its function in driving high species diversity of ant mimics in tropical rainforests.

ACKNOWLEDGEMENTS

We would like to thank the management and staff of the Institute of Tropical Biology and Conservation, University Malaysia Sabah for provision of field and laboratory facilities. Thanks also to the Danum Valley Management Committee and the Danum Valley Field Center management and their staff for their guidance and assistance both in the field and at the Research Center. Our study was conducted in accordance with the Memorandums of Understanding signed between University Malaysia Sabah and Museum of Nature and Human activities, Hyogo, which was supported by Grants-in-Aid (no.16657028, 19570094, 24570109) from the Japanese Ministry of Education, Science and Culture.

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SUPPLEMENTARY MATERIAL

Table S1. *Myrmarachne* and ant species occurred more than 10 sample points.

Ant species	***M. alticephalon***	***M. maxillosa***	***M. malayana***
	(19)	(13)	(11)
Camponotus arrogans (16)	0	1	1
Camponotus bedoti (18)	0	3	0
Camponotus saundersi (57)	9	2	1
Camponotus sp.38 (14)	0	1	0
Crematogaster coriaria (14)	0	0	1
Crematogaster modiglianii (47)	1	0	2
Crematogaster sp. C2 (40)	5	0	1
Crematogaster sp. O1 (11)	0	0	0
Crematogaster sp. O2 (19)	0	0	0
Diacamma intricatum (10)	1	0	1
Dolichoderus beccarii (12)	0	0	0
Dolichoderus sp. A1 (16)	2	0	0
Gnamptogenys menadensis (13)	1	0	1
Lophomyrmex longicornis (24)	0	0	0
Paraparatrechina sp. 4 (13)	1	0	0
Paraparatrechina sp.1 (11)	0	0	0
Polyrhachis armata (12)	1	0	0
Polyrhachis banghaasi (15)	1	0	0
Polyrhachis boltoni (18)	1	0	5
Polyrhachis danum (15)	0	0	0
Polyrhachis muelleri (13)	1	0	1
Polyrhachis olybria (16)	0	6	1
Polyrhachis phalerata (47)	0	1	6
Polyrhachis sp.N1 (12)	0	2	0
Polyrhachis vindex (42)	1	2	1
Rhoptromyrmex wroughtonii (15)	0	0	0
Technomyrmex butteli (14)	0	1	0
Technomyrmex convexifrons (12)	0	0	0
Technomyrmex dubius (10)	1	0	1