

On the association between *Myrmarachne* spp. (Salticidae) and ants*

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Summary

At Legon in Ghana each species of the ant-mimicking salticid genus *Myrmarachne* is positively associated with a different species of ant, *M. foenisex* with *Oecophylla longinoda*, *M. legon* with *Camponotus acvapimensis*, and *M. elongata* with *Tetraponera anthracina*. There is mutual exclusion between the three species of dominant ants at Legon, *Oecophylla longinoda*, *Camponotus acvapimensis* and *Pheidole megacephala*. The early instars of *Myrmarachne* mimic different, smaller, species of ant from the adults: young *M. foenisex* mimic *Crematogaster castanea*, young *M. legon* mimic *Acantholepis* sp. and *Cataulacus* sp., and young *M. elongata* mimic *Pheidole megacephala*. In *M. foenisex*, the model for the young spiders is positively associated with the model for the adults, so that it is easy for the young spiders to remain associated with an appropriate ant as they grow. In the other two species of *Myrmarachne*, the ant models show no association. However, the models for the young spiders (*Pheidole megacephala* and *Acantholepis* sp.) are so abundant that it is likely that some of the spiders associating with them will find the model for the adult. It is concluded that the development and evolution of populations and associations of ant species has been an important selection pressure in the evolution of species of *Myrmarachne*: each species of *Myrmarachne* has evolved a positive association either with one species of ant, or with a group of mutually tolerant species of ants, or with positively associated species of ants.

Introduction

Myrmarachne is a widespread genus of salticid spiders which closely resemble ants in form and be-

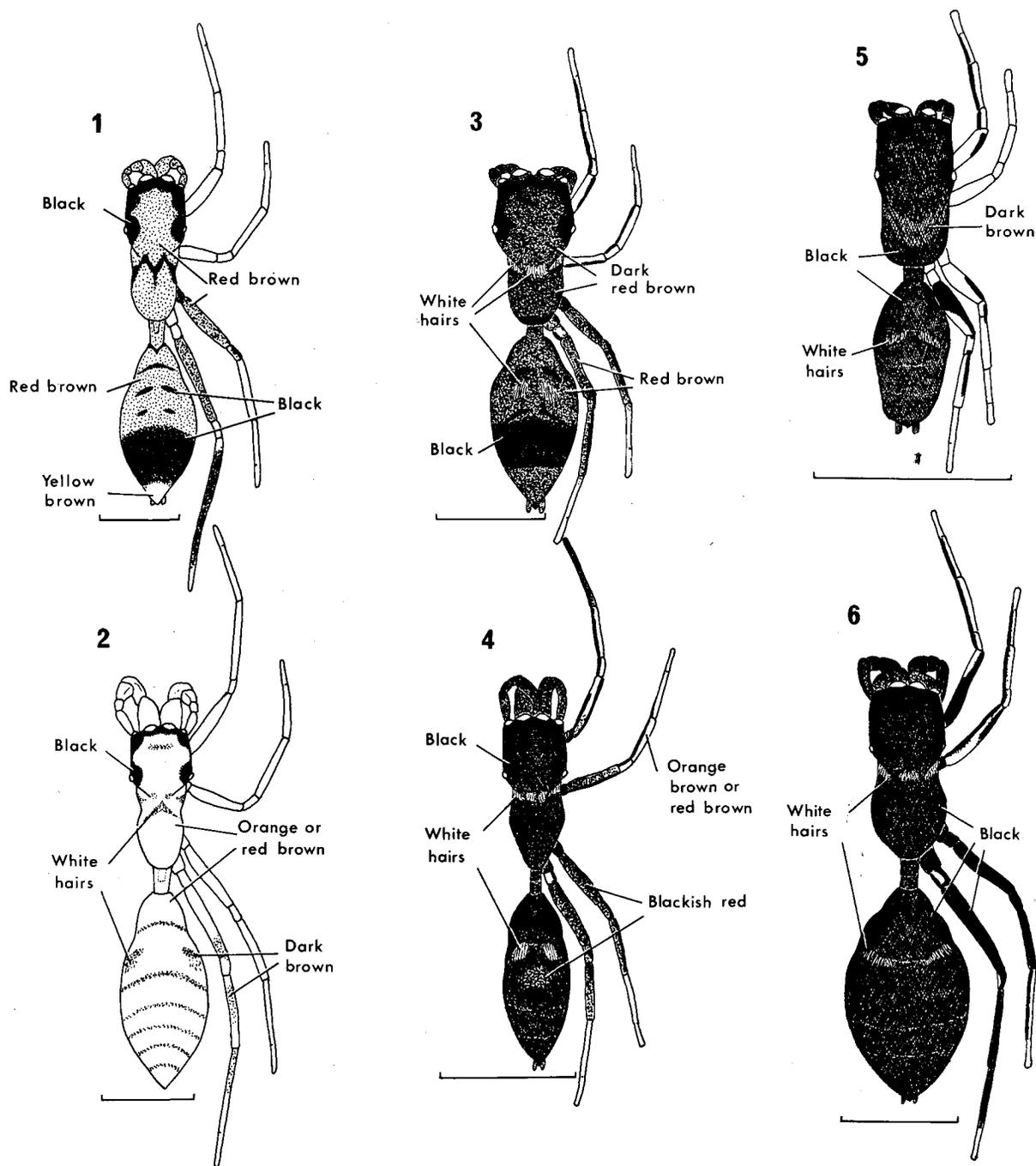
haviour. *Myrmarachne* is commonly found living amongst foraging ants, but the nature of the association between spider and ant has only been studied intensively in the Indian species *M. plataleoides* Cambr. which mimics the weaver ant *Oecophylla smaragdina* (Fabr.) (Mathew, 1954). There is some published information on the African *M. foenisex* which mimics *Oecophylla longinoda* (Latr.) (Collart, 1929 a, b, 1941), but little is known of the numerous species of black *Myrmarachne*. The purposes of this paper are to review our knowledge of the biology of *Myrmarachne*; to incorporate unpublished information on several African species of the genus; and to attempt to assess the nature of the relationship with ants. The original work was done in Ghana between 1968 and 1973 at the University campus, Legon. The three commonest species there are *M. foenisex* Simon, *M. legon* Wanless and *M. elongata* Szombathy, but I also made observations on a few other species at Legon, and in the forest region near Mt. Atewa.

Resemblance between *Myrmarachne* and ants

Species of *Myrmarachne* closely resemble ants in shape: they have an elongated body with very narrow anterior region of the abdomen similar to the petiole of ants. The body colour is normally similar to that of nearby ants. Thus *M. plataleoides* is orange-brown or red-brown, similar to *Oecophylla smaragdina* (Mathew, 1954).

In the African *M. foenisex*, last instar immatures and adults at Legon are orange apart from the bases and tips of the legs which are transparent and colourless (Fig. 2). There are white hairs in a V just behind the eyes dorsally, and white hairs dorsolaterally towards the front of the abdomen. There is a blackish suffusion anteriorly and laterally on the carapace, and black lines mark off eight apparent segments on the abdomen. There are also dark brown or blackish markings on the legs. The colouration closely resembles that of *Oecophylla longinoda* at Legon. An adult male *M. foenisex* from the forest at Kade had similar markings but the body colour was dark red instead of orange. Two further males from Mt. Atewa both had blackish red carapaces with dark red chelicerae, a pale red-brown abdomen, and blackish petiole. The legs were brownish yellow, but legs III and IV had much black on them. This colour is

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Figs. 1-6: Typical colouration of adult and young of three species of *Myrmarachne*: 1, 2 young and adult *M. foenisex*; 3, 4 young and adult *M. elongata*; 5, 6 young and adult *M. legon*. Note that the young spiders are not all at the same instar: 5 is newly emerged from the retreat whilst 1 and 3 have moulted at least once since leaving the retreat. Scale lines: 1mm (Figs. 1, 3, 5), 2mm (Figs. 2, 4, 6).

similar to that of the dark forest morph of *Oecophylla longinoda* amongst which they were found. These forest ants have dark red-brown head, black thorax, and pale red-brown abdomen, with legs black towards the base, pale tips, and red-brown tarsi. The colony of ants from which the two spiders came was mixed, with about half the ants dark and half of typical reddish orange colour. Collart (1941) also gives several examples of dark brown *M. foenisex* taken from dark colonies of *Oecophylla* in the Congo.

M. legon has an entirely black body apart from white hairs medially just behind the eyes, a few pale hairs on the abdomen, and white patches laterally on the carapace just behind the posterior eyes (Fig. 6). In the active spider these white patches in the middle of the carapace give the impression that there is a constriction separating the head from the thorax, just as occurs in ants. Legs III and IV are largely black but with colourless tips; legs I and II are colourless but with black stripes on the femur, tibia and tarsus. The live spider closely resembles *Camponotus acvapimensis* in colour; this is a black ant with a large head and with a slightly greyish black abdomen.

M. elongata resembles the ant *Tetraponera anthracina* (Santschi) in colour; both have a very elongated abdomen and are reddish black (Fig. 4).

In addition to resembling ants in shape and colour, *Myrmarachne* also moves in a manner similar to that of an ant. Although it has eight legs and no antennae, the first pair of legs are normally held up in front of the body and waved, like the movements of the antennae of ants (Mathew, 1954), and the abdomen is often bobbed up and down, as also occurs in some ants (e.g. this behaviour occurs in the ant *Oecophylla longinoda* and in its spider mimic *M. foenisex*). The American ant mimic *Peckhamia picata* (Hentz) also bobs its abdomen up and down (Peckham & Peckham, 1889a). The similarity is so close that experienced entomologists can be deceived into mistaking the spider for an ant, but with experience it is possible to distinguish the spiders by their jerky movements and because they frequently turn their heads to look around. When alarmed, spiders and ants also behave differently: e.g. *M. foenisex* runs away or dodges round a leaf or stem, whilst the ant *Oecophylla longinoda* is more likely to attack or to stay put with the jaws held wide open.

Evidence for an association between *Myrmarachne* and ants

Each species of *Myrmarachne* is normally only found close to ants of its own colour, e.g. adult *M. platyleoides* are characteristically found only in colonies of *Oecophylla smaragdina* (Mathew, 1954; Marson, 1947).

At Legon I found more than 50 *M. foenisex*, always amongst *Oecophylla longinoda* ants, and a similar number of *M. legon*, always close to the black ant *Camponotus acvapimensis* Mayr. The spiders do not spend much time on the trunks and main branches of the trees which form important runways for ants, nor on the 'nests' of *Oecophylla*, but they are often found on leaves in the peripheral foraging area of the ants. I have also searched amongst foraging areas of numerous other ants but never found *M. foenisex* or *M. legon*. This suggests that each species of *Myrmarachne* lives in association with one or more species of ant. To confirm this, I undertook a survey of every shrub and small tree (up to 2m height) in a small area around the Department of Zoology, Legon, scoring each plant for species of ant present (if any), and for presence or absence of *Myrmarachne*.

Two surveys were made, on 2 February 1973 and on 24-26 May 1973. Since they gave very similar results the data have been combined for statistical analysis. In addition I have included results of a preliminary survey of 49 plants round the Zoology Department on 25 January 1973 and of 22 plants round the Botany Department on 27 January 1973. A total of 17 *M. foenisex* were found on the 665 plants searched, all of these amongst *Oecophylla* ants. However, two or more spiders were found on some plants, so scoring each plant for presence or absence of *M. foenisex* and of *Oecophylla*, we get the figures given in Table 1, first line. These figures can be tested for positive or negative association by means of a $2 \times 2 \chi^2$ test (Southwood, 1966), and the result indicates a highly significant positive association between *M. foenisex* and *Oecophylla longinoda* ($p < 0.001$). By contrast, there is a negative association between *M. foenisex* and the other very common ant in the area, *Camponotus acvapimensis*.

For *M. legon* the data in Table 1 indicate strong positive associations with *Camponotus acvapimensis* ($p < 0.001$) and with *Acantholepis* sp. ($p < 0.001$), and a negative association with *Oecophylla* ($p <$

0.01). Similarly *M. elongata* has positive associations with *Pheidole megacephala* ($p = 0.029$) and with *Tetraponera anthracina* ($p = 0.0009$).

There is also a negative association between *Oecophylla* and the other dominant ants in the area, *Camponotus acvapimensis* and *Pheidole megacephala* (see Table 2). This is because dominant ants exclude other ants from their foraging areas, and there may be inter- or intra-specific territorial battles between neighbouring colonies which ensure this exclusion (Majer, 1976; personal observation). *Oecophylla* is a particularly aggressive dominant ant as judged by personal observation of its behaviour and by the small number of joint occurrences with *Camponotus* and *Pheidole* indicated in Table 2 (5 and 8 respectively compared with expectations of 58.3 and 53.4). *Oecophylla* will apparently tolerate only one species of ant in its foraging area, the small *Crematogaster castanea* F. Smith, which appears from its positive association to be an obligate associate of *Oecophylla*. By contrast *Camponotus acvapimensis* has a positive association with another black ant, *Cataulacus* sp., and is also often found with *Acantholepis* sp., but in the latter

case the number of joint occurrences is almost exactly what one would predict assuming that there is no association (31 compared with an expectation of 34.2). Probably *Acantholepis* is so small that *Camponotus* ignores it rather than attacking. *Pheidole* has a positive association with *Acantholepis*, but the reason for this is unknown. It has a negative association with *Camponotus* ($p < 0.02$), but the number of joint occurrences is high (55 compared with an expectation of 68.4 assuming no association), indicating that these two species are not so rigorous in their exclusion of other ants as is *Oecophylla*.

Thus each of the three species of dominant ant has associated with it a different species of *Myrmarachne* which resembles it in colour. These three species of dominant ant (*Oecophylla*, *Camponotus* and *Pheidole*) together foraged over 80% of the plants surveyed (533 out of 665). Of the remaining plants, 12.5% (83) had no ants present, whilst the others had other much less common ants such as *Tetraponera anthracina*, *Cataulacus* sp. and *Crematogaster gambiensis* André. Only one of these, *Tetraponera*, had a *Myrmarachne* associated with it (see above), but it is

Spider	Ant	Ant present spider		Ant absent spider		χ^2 (1 d.f.)	p	Association
		Present	Absent	Present	Absent			
<i>M. foenisex</i>	<i>Oecophylla longinoda</i>	13	161	0	491	33.62	< 0.001	+
<i>M. foenisex</i>	<i>Camponotus acvapimensis</i>	0	223	13	429	5.24	< 0.05	-
<i>M. foenisex</i> (small, < 4mm)	<i>Crematogaster castanea</i>	2	19	0	644	-	= 0.0019*	+
<i>M. legion</i>	<i>Camponotus acvapimensis</i>	21	202	2	440	33.04	< 0.001	+
<i>M. legion</i>	<i>Oecophylla longinoda</i>	0	174	23	468	7.10	< 0.01	-
<i>M. legion</i>	<i>Acantholepis</i> sp.	11	91	12	551	16.86	< 0.001	+
<i>M. legion</i>	<i>Cataulacus</i> sp.	3	28	20	613	2.07	n.s.	Not demonstrated
<i>M. elongata</i>	<i>Pheidole megacephala</i>	3	201	0	461	-	= 0.0286*	+
<i>M. elongata</i>	<i>Tetraponera anthracina</i>	2	9	1	582	-	= 0.00093*	+

Table 1: Associations between ants and *Myrmarachne* spp. at Legon.

Figures are based on surveys of 263 plants on 2 February 1973 and of 331 plants on 24-26 May 1973, but including in most cases a further 71 plants on 25-27 January 1973

* Fisher's exact test is given for those cases where more than one expected total in the 2 x 2 table is less than 5.

perhaps significant that *Tetraoponera* is an ant with a particularly virulent sting, and its associated spider *M. elongata* is blackish red and has a very long thin abdomen, exactly like *Tetraoponera*. Hence it appears that *Myrmarachne* species are most likely to be found in the foraging area of a dominant ant, and/or in the foraging area of an ant which is protected by a particularly virulent bite or sting. This in turn suggests that one of the advantages of the association to the spider is defence against predators: the predators avoid ants and fail to find the spiders because of their resemblance to ants.

Other species of *Myrmarachne* found at Legon

In addition to *M. foenisex*, *M. legon* and *M. elongata*, I found two other species of *Myrmarachne* at Legon.

A single *M. uvira* Wanless was found with *Camponotus flavomarginatus* Mayr, both species being grey in colour. An immature *Myrmarachne* was found with *Pheidole megacephala*, both being dark brown; the identification of this spider is uncertain but it is possibly *M. vanessa* Wanless (det. F. R. Wanless). I do

not know with which species of ant these two species of *Myrmarachne* normally associate, so they will not be considered further.

Food and hunting activity

M. plataleoides feeds largely on small Diptera and Hemiptera (Marson, 1947), and the American mimic *Peckhamia picata* also feeds largely on small insects such as Diptera (Peckham & Peckham, 1889b). In Ghana I have found *M. foenisex* eating on twelve occasions. The prey comprised two small moths, two small dipterans, and one green hemipteran (the remaining seven prey items were too much digested to be identified except to establish that they were not ants). I have also observed *M. foenisex* pounce on a moth unsuccessfully. *M. elongata* has been found eating three times, twice the prey was a mosquito, and once a small moth. Hence species of *Myrmarachne* feed on small insects that settle on vegetation, but they have never been reported to prey on their ant associates. *M. plataleoides*, however, will take ant pupae if the occasion for doing so arises (Mathew, 1954). *M. legon* also takes nectar from

Ant species A	Ant species B	A present		A absent		χ^2 (1 d.f.)	p	Association
		B present	B absent	B present	B absent			
<i>Oecophylla longinoda</i>	<i>Camponotus acvapimensis</i>	5	169	218	273	91.34	< 0.001	-
<i>Oecophylla longinoda</i>	<i>Pheidole megacephala</i>	8	166	196	295	73.72	< 0.001	-
<i>Oecophylla longinoda</i>	<i>Crematogaster castanea</i>	20	154	1	490	49.92	< 0.001	+
<i>Camponotus acvapimensis</i>	<i>Pheidole megacephala</i>	55	168	149	293	5.29	< 0.02	-
<i>Camponotus acvapimensis</i>	<i>Cataulacus</i> sp.	20	203	11	431	12.58	< 0.001	+
<i>Camponotus acvapimensis</i>	<i>Acantholepis</i> sp.	31	192	71	371	0.38	n.s.	none
<i>Pheidole megacephala</i>	<i>Acantholepis</i> sp.	55	149	47	414	29.33	< 0.001	+
<i>Pheidole megacephala</i>	<i>Tetraoponera anthracina</i>	6	160	5	423	2.71	n.s.	none
<i>Acantholepis</i> sp.	<i>Cataulacus</i> sp.	3	99	28	535	0.41	n.s.	none

Table 2: Associations between different species of ants at Legon based on surveys of January, February and May, 1973

extra-floral nectaries (e.g. of *Morinda lucida* Benth.), but whether this is to obtain nourishment to supplement the diet, or whether it is simply to obtain water, is not known. In captivity all the species that I have kept ate *Drosophila* and other small flies but they never attacked ants. However, both *M. plataleoides* and *M. foenisex* sometimes enter *Oecophylla* nests and feed on ant larvae (Collart, 1941; Mathew, 1954), and more recent observations suggest that this may occur regularly (summarised by Wanless, 1978). *M. foenisex* has also been reported to feed on honey-dew from coccids (Collart, 1929a, b).

In order to assess peak hunting times a grapefruit tree overrun with *Oecophylla* was thoroughly searched to head height at different times of the day over a period of 18 days in March 1969. The results (Fig. 7) indicate a peak of hunting activity between 14.00 and 16.00 hours, with little hunting between 10.00 and 14.00 hours. When not hunting the spiders normally rest in silken retreats under leaves or made by stitching two leaves together. Females with eggs or young appear to spend much more time in their silken retreats instead of actively hunting, but I do not have good quantitative data to support this statement.

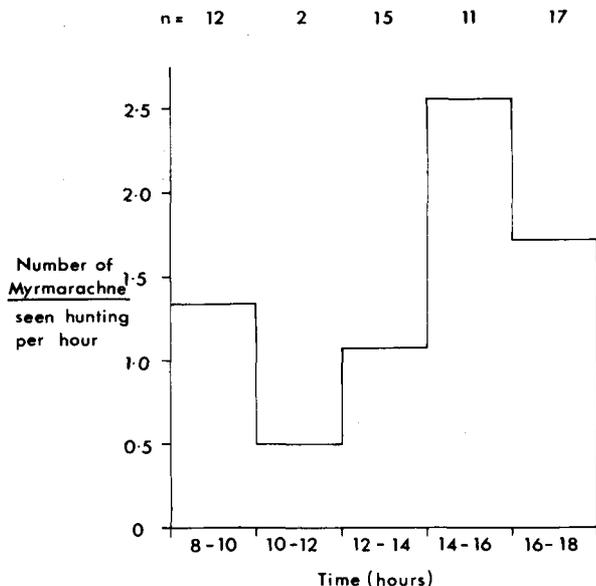


Fig. 7: Hunting activity of *Myrmarachne foenisex* on a grapefruit tree at Legon, Ghana, March 1969.

Courtship and mating

Mathew (1940) has described the courtship and mating behaviour of *M. plataleoides* and *M. manducator* (Westwood) in India. Typically the males associate with last instar immature females, and build silken retreats adjoining that of their female. When she has moulted and become adult, the male then moves into her retreat and mates. The courtship movements consist of much stroking of the head and appendages by the first legs and palps. If a wandering male comes across a retreat containing a female he tries to enter this and mate with her. The initial movements involve many jerky movements and tactile exploration with the palps and first legs. Occasionally Mathew observed males meeting females in the open. Under these conditions the jerky movements and tactile exploration are more prolonged, and the final act of mating can occur either in the open or after the female has built a silken retreat whilst the male waits nearby. Mathew considers the more elaborate movements made by wandering males to be the normal 'on guard approach' behaviour that occurs when a male meets another male, another spider, or even an ant. In such a situation the male must be prepared to retreat (if the intruder is a larger spider or an ant), to attack (if it is another male), or to court and copulate (if it is a female). Hence these initial movements are not part of courtship but enable the spider to recognise first the species of the other individual, and second, if it is another *Myrmarachne*, its sex.

With *M. legon* in Ghana, I once introduced a male to a female who was in her retreat. He approached her, there was much waving and touching of front legs, he then entered and (as far as I was able to see through the silk) they mated. Twice I kept a male and a female *M. legon* together in the same small container for two weeks without either being harmed. However, when a male approached a female in the open he chased her repeatedly. Similar behaviour was observed with *M. elongata*: when male and female met in the open, the female was chased, but when the female was in a retreat the male built another retreat close by and they lived together for two weeks until the female died (for some unknown reason, but she had not been mutilated by the male). Hence it seems probable that courtship and mating in these two species is similar to that in *M. plataleoides* and *M.*

manducator. Ledroux (in Wanless, 1978) also reports no elaborate courtship before mating in *M. legon*, and Collart (1941) describes mating in *M. foenisex* without preliminary courtship.

I have not observed mating in *M. foenisex*, but when a male *M. foenisex* approaches another arthropod of similar size (e.g. an ant or another *Myrmarachne*), it does so slowly with much jerky movement and waving of the first legs. As it gets close it opens its chelicerae to 150°. If the other animal is an *Oecophylla* the male then retreats; if it is another male *M. foenisex*, the two may approach with wide open chelicerae until these touch, then one of the two retreats, turns and flees. No fighting was observed, but on the two occasions when this behaviour was seen it was the smaller male (with smaller chelicerae) which retreated. Once the smaller male was partially inside his retreat and he tried to pull the silk down over the opening, but he then turned and fled leaving the larger male to take over the retreat. Thus the enormous chelicerae of *Myrmarachne* males are probably used by rival males for display and, perhaps, for fighting.

Sex ratio

Casual observation suggests that the sex ratio of *Myrmarachne* is biased in favour of females, a fact which gives trouble to the taxonomist who requires males for examination of chelicerae and pedipalps. A survey of a large colony of *Oecophylla longinoda* on a grapefruit tree at Legon in March 1969 resulted in my recording 16 male and 75 female *M. foenisex* (17.6% males). The figures include only actively hunting spiders and omit spiders resting or guarding eggs in retreats, hence they could reflect different activity patterns. The figures also include repeated observations of the same individuals on different days, and it is possible that some of the spiders recorded as females were subadult (last instar) males. A more careful search of several other *Oecophylla* colonies in 1973 yielded seven adult females (≥ 8 mm long) and no males. Experience with *M. legon* confirms that in this species also females are more often found than males. Assuming that the sex ratio at birth is equal, the most likely explanation for the excess of females amongst the adults is that females live longer than males.

Fecundity

The elongated body and narrow abdomen of *Myrmarachne* may be an advantage with respect to predators which fail to recognise them as potential prey (see below), but they also imply that the spider cannot lay as many eggs as can a salticid of normal shape. Bristowe (1939) shows that there is a correlation between size of spider and number of eggs laid: thus the small salticid *Euophrys frontalis* (Walckenaer) lays 19 eggs, *Salticus scenicus* (Clerck) and *Heliophanus cupreus* (Walckenaer) each lay 25 eggs, the larger *Aelurillus v-insignitus* (Clerck) lays 35 eggs, and the very large *Phidippus audax* (Hentz) (= *P. morsitans*) lays 180 eggs (Peckham, 1889).

Amongst ant-mimicking salticids, one of the largest species is *M. plataleoides*, but accounts of how many eggs it lays vary from 5-6 (Mathew, 1954), 8-12 (Bhattacharya, 1938; Marson, 1947), 15-20 (Mathew, 1934, 1954), to 30 (Marson, 1946). The explanation for this discrepancy is probably that the first clutch is normally large, typically 15-20, but that subsequent clutches are much smaller, with as few as 5-6 eggs being laid (Mathew, 1934, 1954). For the large African species, *M. foenisex*, Collart (1941) examined 22 clutches with between 16 and 36 eggs (average 25) whilst I have two clutches with 11 and 12 eggs. For the slightly smaller *M. legon* I have recorded clutches of 2, 3, 5, and 6, and the American ant mimic *Peckhamia picata* typically lays only 3 eggs (Peckham & Peckham, 1889a; Peckham, 1889).

Thus myrmarachnids probably lay fewer eggs than non-ant-mimicking salticids, and small species of *Myrmarachne* lay very small clutches. Such species must therefore be K selected (MacArthur & Wilson, 1967); mortality of young must be low, and longevity of adult females high in order to increase the average number of eggs laid per female.

Parental care

The female *M. plataleoides* normally remains with her eggs until they hatch, and indeed until the young have moulted for the second time, but whether or not she actively guards them is unknown (Mathew, 1934). Marson (1947), however, reports that female *M. plataleoides* die after laying eggs and that the male then guards them and even chases off ants, but this may be an atypical situation. My observations con-

firm that in captivity *M. foenisex* and *M. legon* females also remain with the eggs until small spiders emerge from the retreat about a week after they have emerged from the cocoon. Marson's report of a male chasing off an *Oecophylla* was probably an observation of the male encountering and intimidating an *Oecophylla* by its 'on guard approach' posture, but it would be interesting to have confirmation. The only observation of relevance that I have is of a male and female *M. foenisex* having been driven out of their retreat by *Oecophylla* and remaining nearby whilst the eggs were eaten.

When the young spiders emerged from their retreat, one female *M. legon* chased them away but did not attempt to eat them. However, by the next day two of the three young were missing. A second female was kept with her young for two weeks after they had emerged from their retreat, and all six young survived. Thus it appears that the young spiders may receive some protection from their mother until they disperse.

Life cycle

Eggs of *M. plataleoides* hatch in about a week producing immobile, almost globular first instar larvae (Mathew, 1934). These moult after about two days into spiderlings which continue to subsist on their yolk reserves. The spiderlings moult to the third instar after another week and then leave the silken retreat. They climb upwards, spin out silk, and balloon on the wind. According to Mathew there are a further four moults before the adult stage is attained, but Bhattacharya (1938) reports a further six moults. It is likely that there is some individual variation in the number of moults, but it would be useful to know the normal number of ecdyses and duration of the immature stages. According to Mathew (1934) it takes a minimum of 11 weeks from egg to adult, but if there is a shortage of food, and if there are more moults as reported by Bhattacharya, then it must take considerably longer.

According to Mathew (1934), third instar young are dark brown and are often found with the similarly coloured ant *Prenolepis* or with dolichoderine ants. The fourth instars are often more reddish but retain a dark tip to the abdomen, like the ant *Solenopsis*. The fifth instars are paler yellowish brown and resemble *Plagirolepis* or *Oecophylla*, whilst the final instar im-

matures and adults both mimic *Oecophylla*. Thus all stages of the spider mimic ants, but three or four different species of ants are mimicked at different stages of the life cycle. Furthermore, the young spiders are typically found amongst colonies of the ant which they appear to mimic: the smallest spiders are not found with *Oecophylla* but with *Prenolepis*. Bhattacharya's account of the ants mimicked during development is slightly different: according to him the early instars mimic *Solenopsis geminata* (Fabr.), half-grown spiders mimic *Anoplolepis (Plagirolepis) longipes* (Jerdon), and last instars and adults mimic *Oecophylla*, but he does not report finding young spiders with these ants, and Marson (1947) reports that the immatures do not associate with *Solenopsis* or *Plagirolepis*. Marson concludes that whilst adult *M. plataleoides* resemble *Oecophylla*, associate with them, and hence derive protection from the resemblance, the young spiders simply have a general resemblance to ants which may be of some protective value, but they do not mimic or associate with any particular species of ant. Clearly there is scope for a more thorough investigation of this species.

In Ghana I have studied immature stages of *M. foenisex*, *M. elongata* and *M. legon*. *M. legon* third instar young emerge from their retreats at about 2mm length. The body is black apart from a dark brown transverse mark dorsally on the carapace and a pair of small white marks dorsally on the abdomen (Fig. 5). The legs are transparent with some black marks on legs I, III and IV. I was unable to rear these small spiders, but wild caught spiders of 3, 3.5 and 4mm length were examined. In these spiders the brown mark is replaced by a small patch of white hairs and the legs are darker. Thus in *M. legon* there is little difference in colouration between young and adults. However, whilst the adults associate with and closely resemble *Camponotus acvapimensis*, the 3-6mm long immatures closely resemble another but smaller black ant, *Cataulacus* sp. Although the figures do not indicate a positive association between *M. legon* and *Cataulacus* (Table 1), *Cataulacus* is itself positively associated with *Camponotus acvapimensis* (Table 2). The young spiders are too small to mimic either of these two species of ant, but they closely resemble the very small ant *Acantholepis* sp., which is very common on low growing plants. *M. legon* has a positive association with *Acantholepis* (Table 1), but

Acantholepis shows no association with *Camponotus acvapimensis* (Table 2). However, of the 102 plants colonised by *Acantholepis* 31 also contained *Camponotus acvapimensis*. Hence it is possible to envisage how the close association with *Camponotus* arises as the spiders grow: initially they associate with the small black *Acantholepis*, then as they grow they come to associate with the larger *Cataulacus* or *Camponotus* both of which often forage on the same plants as does *Acantholepis*. What we do not know is if the association is brought about by means of the spiders choosing to associate with certain species of ants, or because spiders which associate with other species of ants suffer more intense predation.

The smallest *M. foenisex* found was 4mm long. One spider of this size was eventually reared to maturity: it moulted four times and became adult after 15 weeks. If Mathew's (1934) report of four moults after emergence from the cocoon in *M. platyleoides* is correct for *M. foenisex* as well, then this 4mm spider must have been recently emerged. However, it was substantially larger than newly emerged *M. legon*, and I therefore suggest that the African *Myrmarachne* studied here probably have five free-living instars before the final moult.

The body of 4 mm *M. foenisex* is red-brown, with much black dorsally at the edges of the carapace and over the posterior half of the abdomen, though the tip is clear yellow-brown. The first two legs are yellow-brown with colourless basal segments; leg III is also yellow-brown distally, but red-brown proximally and with a black basal segment; leg IV is also clear yellow-brown but with black on the femur, tibia and tarsus, and with a transparent basal segment. The next instar young lack the black patch on the abdomen and are more orange, like *Oecophylla*, but the black on the last two pairs of legs does not disappear until after another moult. Thus young *M. foenisex* are both smaller and darker brown than *Oecophylla*, but they are similar in size and colour to the small brown ant *Crematogaster castanea*. This ant appears to be an obligate associate of *Oecophylla*, and is one of the few species that *Oecophylla* will tolerate in its foraging range. It has a highly significant positive association with *Oecophylla* (Table 2). The *M. foenisex* associated with *Oecophylla* in Table 1 included two individuals of only 4 mm length: both of these were on plants which also contained *Cremato-*

gaster castanea. Hence there is a significant positive association between small *M. foenisex* and the ant it appears to mimic (see Table 1, third line). Out of the 17 *M. foenisex* found during the survey, 8 were on plants containing *Crematogaster castanea* as well as *Oecophylla*. Three of these 8 were 5 mm long or less whilst of the 9 *M. foenisex* found in *Oecophylla* foraging areas with no *Crematogaster*, only one was less than 5 mm long. Thus it appears that young *M. foenisex* have a clear positive association with *Crematogaster castanea*, but as they grow they range further so that they may live in *Oecophylla* foraging areas that are not used by *Crematogaster*.

Young *M. elongata* associate with *Pheidole megacephala*, whilst adults live with *Tetraoponera anthracina*. Spiders just under 3 mm long have the body colour red-brown with white hairs on the abdomen and mid-dorsally on the carapace. There is black dorsally round the front edge of the carapace and as a band on the abdomen, much as in young *M. foenisex*. The legs are transparent or tinged with yellowish but with black marks. The next instar young have most of the body black with red-brown persisting only at the front of the abdomen and on the pedipalps. The legs are more orange. The final instar and adult spiders are black with some reddish showing through on the body, whilst the legs are orange-brown or reddish brown with black markings. The young spiders resemble the brown ant *Pheidole* in colour, the adults resemble the reddish black ant *Tetraoponera*. A problem must arise during the life of this species since young and adults are associated with different species of ant which do not associate with one another as do *Crematogaster castanea* and *Oecophylla longinoda*. However, of the 11 plants foraged over by *Tetraoponera*, 6 were also overrun by *Pheidole megacephala*. Hence although there is no positive association between these two ants, there is no exclusion either (Table 2), and whilst many of the young *M. elongata* living amongst *Pheidole* may be unable to find *Tetraoponera*, some are likely to succeed.

On the basis of these three species of African *Myrmarachne* it is reasonable to conclude that young spiders associate with certain species of ant just as do adults, and that in some cases the ant models of the young and of the adults are positively associated with one another so that the change in the association of the spider as it grows can easily be achieved. In other

cases the ant associate of the young spider is common and widespread so that some of the young spiders are likely to come into contact also with the ant associate of the adult spiders. But we do not know if the spiders actively choose to live near certain species of ants or if those that live amongst the 'wrong' species suffer a higher mortality than those which live amongst the 'right' species.

The entire life cycle of *M. platalaeoides* takes a minimum of 11 weeks (Mathew, 1934). I have not reared any of the African species through from egg to adult, but *M. elongata* takes 7 weeks from the 3 mm long penultimate instar to adult, which is close to the time taken for *M. platalaeoides*. My incomplete data on *M. legon* and *M. foenisex* also correspond with Mathew's observations of *M. platalaeoides*. Adults can be kept alive in captivity for a considerable period, and I have a record of a female *M. legon* still alive and apparently healthy after six months in captivity as an adult.

Body colour varies to some extent with environmental conditions, but no systematic study appears to have been made of this. Mathew (1954) reports that *M. platalaeoides* found away from *Oecophylla* or reared on Diptera become darker than normal spiders. One female *M. legon*, black when captured in January 1973, had changed colour considerably by June: legs III and IV were by then predominantly orange-brown, as also was the ventral surface of the abdomen and the anterior half and tip of the abdomen dorsally. It is not known what causes this change in colour, but similar variation occurs in the field in *M. foenisex*: forest *Oecophylla* are often much darker in colour than savanna ants, and the *M. foenisex* found with them are also darker than savanna spiders (see above).

Advantages and disadvantages of the association with ants

The close resemblance between *Myrmarachne* and ants suggests that either the spider gains protection against predators (defensive batesian mimicry), or that the ants are deceived by the resemblance into mistaking the spider for an ant, and that this enables the spider to attack and prey on ants (aggressive mimicry). Aggressive mimicry probably occurs in the thomisid ant mimic *Amyciaea* whose movements appear to attract ants, but which then pounces and feeds on any that come too close (Hingston, 1927;

Mathew, 1954). *Myrmarachne*, however, has never been observed to feed on ants either by Mathew, Marson (1947) or Komatsu (1961); it was observed once by Hingston (1927), but this is probably very unusual. I have kept three species of *Myrmarachne* with their host ants in small containers (7.5 x 2.5 cm specimen tubes) for 24 hours on several occasions, and both spider and ant have always survived the experiment. Under similar conditions small Diptera are normally eaten either by the spider or the ant. *M. foenisex* and *M. platalaeoides* appear to feed largely on small insects such as moths, hemipterans and flies, but they occasionally take ant pupae (see above). Thus there is no evidence that species of *Myrmarachne* regularly prey on adult ants or that they are aggressive mimics.

There is evidence to suggest that *Myrmarachne* derives protection from predators as a result of its resemblance to ants. In the first place, many birds which normally eat insects do not touch ants, presumably because they are too hard or are distasteful. It is reasonable to suppose that such birds would also avoid attacking *Myrmarachne* because they would mistake these for ants. However, there are some predators that regularly eat ants, and one might suppose that *Myrmarachne* would suffer increased predation from these predators relative to other spiders which do not mimic ants. Mathew (1934) points out that when a bird or other possible predator approaches a group of *Oecophylla*, the ants in turn approach it with jaws held open, and they may attack. If the intruder is an ant predator (such as a woodpecker or a lizard) it is thus easy for it to pick up as many ants as it wants. The behaviour of *Myrmarachne* is very different: as soon as a large predator approaches, the spider dodges under a leaf or hides in a crevice. In consequence the predator is far more likely to kill ants than the spider. If the spider is pursued it eventually drops on a silk thread to the ground and later climbs back to its original position.

Associating with ants may also give protection from spider-hunting wasps such as *Sceliphron* and *Pison* since these may not be able to find *Myrmarachne* as easily as they can find non-ant-mimicking salticids. For example, seven out of nine *Sceliphron* nests in Ghana contained salticid spiders, but none of the 32 salticids in them was an ant mimic. *Pison*, however, often captures *Myrmarachne*

spp., but there is some evidence to suggest that it is less likely to do so if the spider is living with an aggressive ant (such as *Oecophylla*) than if it is with a more placid ant (such as *Camponotus*) (Edmunds, 1974, and in preparation). Thus there are several lines of evidence suggesting that mimicry of ants by *Myrmarachne* results in reduced predation by vertebrates and by wasps.

One disadvantage of living with ants is that the ants may themselves attack the spider. The ants do not appear to mistake the spider for one of themselves, probably because they recognise fellow ants by chemical and tactile cues rather than by eyesight. But the spiders have acute eyesight and quickly avoid any ant that approaches by dodging under a leaf or jumping on to another leaf. When ants come close to a *Myrmarachne* they assume an aggressive posture, and if the spider fails to escape it will be eaten (Mathew, 1954). If *M. foenisex* is kept in a jar with *Oe. longinoda* the two can survive for several days, the spider making no attempt to kill the ant and itself evading capture during the day by its good eyesight and quick evasive responses, and at night by resting in a silken retreat.

Another problem of living close to ants is that the ants may disturb and attack the spiders whilst they are mating, and ants may find and destroy eggs. Mathew (1940) found that in *M. plataleoides* and *M. manducator*, mating normally occurs in a silken retreat, and the male may even wait whilst the female builds a retreat before he copulates with her (see above). Mating spiders are likely to be vulnerable to attack by ants, and this behaviour ensures that mating normally only takes place in the protection of the silken retreat.

Finally, indirect evidence for the advantage to spiders of resembling ants is the detailed similarity of both young and adult spiders to ants. The different colours of young and adult *M. foenisex*, *M. legon* and *M. elongata*, together with different colours and species of ant with which they associate, suggest that the association with ants is an effective anti-predator defence. Evidence for the strength of predator selection in perfecting the resemblance between mimic and model is the infrequency of finding a *Myrmarachne* with the 'wrong' species of ant, and the occurrence of different colour morphs of mimic wherever the model has a different colour. Thus the

dark forest form of *M. foenisex* replaces the typical form wherever the dark forest form of *Oecophylla longinoda* is common (see above). It is interesting to note that in another presumed batesian mimic of *Oecophylla longinoda*, the mirid heteropteran *Xenotomorpha carpenteri* Poppius, I have also found an orange form with the orange *Oecophylla* colonies at Legon but two dark red-brown insects with the dark forest form of *Oecophylla* at Mount Atewa, Ghana (*Xenotomorpha* determined by C. Lyal). There is also variation in the colour of *M. legon*: whilst the spiders collected at Legon and associated with *Camponotus acvapimensis* were black, as described above, two spiders were found with pale hairs on the abdomen such that the overall appearance of the body was grey. One was with *C. flavomarginatus* Mayr at Legon, the other with *C. sericeus* (Fabr.) at Nungua, two species of ant which are similar to *C. acvapimensis* in general appearance but are grey rather than black (ants determined by D. Leston). Thus it appears that where the spiders associate with a different colour form or species of ant, they have evolved a correspondingly coloured morph.

Conclusions

Study of three species of *Myrmarachne* in Ghana has provided statistical evidence for the positive association with ants which they most closely resemble, thus supporting the hypothesis that the association between *Myrmarachne* and ants is one of defensive batesian mimicry (Edmunds, 1974). Furthermore, the young spiders also associate with and mimic different species of ant. It is clear that the evolution of species of *Myrmarachne* and of their immature stages has been determined by the ants present in the area. For adult *Myrmarachne*, selection has favoured resemblance to, and association with, dominant or exceptionally well protected species of ant; whilst for young *Myrmarachne* selection has favoured resemblance to and association with ant species that are either very common or are themselves associated with the model for the adult. In this way it is possible for the young spider to change its ant associate without having to move through territories of other ants to which it has no resemblance and where it would be conspicuous to predators. It is probable that the majority of species of *Myrmarachne* are associated

with one or a few species of ants as adults and with one or more different species of mutually tolerant ants as immatures.

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