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SPECIALISTS AND GENERALISTS: THE ECOLOGY AND BEHAVIOR OF SOME WEB-BUILDING SPIDERS FROM PAPUA NEW GUINEA

I. *Herennia ornatissima*, *Argiope ocyaloides* and *Arachnura melanura* (Araneae: Araneidae)

By Michael H. Robinson and Yael D. Lubin¹

Abstract. Studies of the ecology and behavior of 7 species of web-building spiders from Wau, Morobe Province, Papua New Guinea, will be published in 3 parts. The studies emphasize predatory strategies and predatory behavior. Part I deals with 3 specialized araneid species, *Herennia ornatissima*, *Argiope ocyaloides* and *Arachnura melanura*. *H. ornatissima* builds ladderlike elongate webs close to tree trunks, is cryptically colored and a specialized arboricole. Its predatory behavior units, particularly its prey-wrapping and transportation postures, are strongly modified compared with its nonarboricolous relatives. *A. ocyaloides* differs from the majority of *Argiope* species in being somberly marked on its dorsal surfaces and is probably an obligate arboricole. It builds a less specialized web than *H. ornatissima* and has a typical *Argiope* pattern of predatory behavior. Its stabilimenta differ markedly from those of most *Argiope* species and the difference can be correlated with the necessities of the tree-trunk habitat. *Arachnura melanura* is one of a small group of tailed araneids and is probably a flower-mimic. Its predatory behavior is affected by the presence of the long tail situated behind the spinnerets. Webs, web sites, egg cocoons, habitat preferences, prey composition (where known) and sexual dimorphism are described for each of these species. The evolutionary steps that could have led to specialized arboricolous adaptations are discussed in detail. New stringent definitions of stabilimenta and other forms of web "decorations" are given.

During our studies at Wau, Papua New Guinea (MHR 1970-1971, 1973-1974; YDL 1970-1971), we carried out separate, overlapping and joint research projects. The results of most of these studies have already been published (Lubin 1973, 1974; Robinson et al. 1974, Robinson & Robinson 1972, 1973a, 1974, 1976a, 1976b, 1977; Robinson 1975, 1977). The present publication is based on both joint and overlapping studies. It is separated into 3 parts, to be published serially. The studies reported in this series involve 5 species of araneid spiders and 2 species of psechrids.

Part I deals with 3 species of araneids: *Herennia ornatissima* (Doleschall), *Argiope ocyaloides* L. Koch, and *Arachnura melanura* Simon. Part II deals with 2 psechrid species: *Psechrus argentatus* (Doleschall) and *Fecenia* sp. [nr *angustata* (Thorell)]. Part

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III reports our studies of 2 *Gasteracantha* species (Araneidae): *G. theisi* Guérin, and *G. taeniata* (Walkenaer). Our individual contributions to these studies vary in their relative proportions from species to species, but we used common methods of study overall (developed over a period of collaboration). Our research was mainly concentrated on analyses of predatory behavior and to a lesser extent covered the general biology of the species.

All the species that we studied are generally or locally abundant in the Wau Valley. As far as we know, they are also wide-ranging throughout Papua New Guinea. Both *Herennia ornatissima* and *Argiope ocyaloides* build their webs on the trunks of trees. There seems to be no generally accepted adjective to describe this habit, but herein we use the term *arboricolous* (epidendric, truncicolous, corticolous are all possible alternatives with a respectable etymology).

Of the two, *H. ornatissima* has the most specialized web. This parallels, structurally at least, the complex ladder-webs that have been discovered in recent years (Robinson & Robinson 1972, Eberhard 1975). Elements of the predatory behavior of *Herennia* are quite modified, judging by patterns found in related genera, and these modifications are directly explicable in terms of the unusual web site and web structure. *A. ocyaloides* has a less specialized web, but its body coloration is unusual among *Argiope* species and this seems to be a direct specialization for arboricolous living.

The beautiful tailed spider, *Arachnura melanura*, at first seemed to be rare in the Wau Valley. However, once we tracked down the preferred web site of this highly cryptic species, we were able to find sufficient numbers to do a field study. The predatory behavior of *Arachnura* has not previously been described. Existing notes on the biology of members of this genus (Jones, in McKeown 1963; Forster & Forster 1973) are useful but fragmentary. *A. melanura* behaves very much like a small *Argiope*, but the presence of the long tail, situated behind the spinnerets, imposes a number of conspicuous constraints on its predatory behavior. The species also has other behavioral peculiarities that can be related to its specialized defensive adaptations.

Our interest in the psechrids arose from the fact that the *Fecenia* sp. builds elliptical webs with sticky and nonsticky components. These more-or-less perpendicular webs seemed to us to be the functional equivalent of araneid orb webs. Thus we found a cribellate spider that built a web broadly comparable in size, situation and overall structure to those of some of the Wau *Argiope* species whose predatory behavior has been described by B. Robinson & M.H. Robinson (1974). *Fecenia* was therefore intrinsically interesting, as a convergent (cribellate) orb-weaver with an undescribed predatory repertory, and was also interesting as a basis for interfamilial comparisons. The second psechrid, *Psechrus argentatus*, is an extraordinarily common species in the Wau Valley. It builds a horizontal sheet web that in many ways resembles an agelenid web. We decided to study this species, hoping that comparison with the related *Fecenia* would allow us to assess the influence of web structure on behavior. In fact, both species proved to possess predatory techniques that have elements in common with orb-weavers of the genera *Nephila*, *Nephilengys*, *Herennia* and *Argiope*.

In 1971, when we commenced our study of the 2 *Gasteracantha* species, there was

no published account of the predatory behavior of any species in this genus. We were interested in analyzing the total pattern. As it transpired, both species differ from *Gasteracantha cancriformis* studied by Muma (1971) in not employing attack wrapping with any kind of prey. In addition to this difference, we found some deviations from the general pattern of predatory behavior found in the other araneids that have been studied in detail.

MATERIALS AND METHODS

The spiders were studied at Wau, Morobe Province, Papua New Guinea, at a number of localities. Studies of *H. ornatissima*, *G. taeniata*, *G. theisi* and *A. melanura* were all carried out in the grounds of Wau Ecology Institute (WEI). *H. ornatissima* is abundant on tall trees in the arboretum of the Institute, and on other tree species that are abundant in the Institute's coffee plantations. *A. ocyaloides* appears to have a relatively restricted distribution in the Wau Valley and we have only found it on the trunks of *Araucaria* spp. and *Casuarina* spp. in plantations. It undoubtedly occurs elsewhere, but we have not found it on native hardwoods. We carried out the study of this species at the MacAdam Memorial Park, Wau.

As well as carrying out field studies of the spiders, we brought some into captivity and raised others from the egg. We raised *H. ornatissima* and *Fecenia* sp. in captivity. Special techniques used in behavioral investigations of these species are described in the species-by-species account below.

All the species were identified by the late Fr Chrysanthus; brief notes on all except *Arachnura* are given in Robinson et al. (1974). Specimens are deposited with the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.

STUDIES OF ARANEID SPECIES

Herennia ornatissima

NATURAL HISTORY AND ECOLOGY

Distribution

Herennia ornatissima is 1 of 4 species of *Herennia* recognized by Roewer (1942: 925–26), who places it in the subfamily Nephilinae. There seem to be few details available about its general biology, although Simon (1892: 757–59) saw the spider in Sri Lanka (Ceylon) and accurately describes the location of the web, its shape, general characters and the location of the egg-cocoons relative to the web. Robinson & Robinson (1973a: 52–54) give brief notes on the basic pattern of the species' predatory behavior, appearance and web form. At the time these authors did not draw attention to the specialized nature of the web. Although they had described a complex straplike web with a side-to-side viscid element as a ladder web (Robinson & Robinson 1972), they did not apply this description to the *Herennia* web. The many similarities between the structure of the *Herennia* and that of the New Guinea ladderweb spider (now

identified as belonging to the genus *Tylorida*, H. W. Levi, in litt.) led us to reexamine the *Herennia* web and study the species in detail.

Web location

In Papua New Guinea, we always found *H. ornatissima* on the boles of trees. Its elongate webs are built very close to the bark (see below). At Wau, the species is most common on tall trees, from close to ground level to a height of at least 10 m. The spider also occurs on the shade trees (*Lucaena glauca*) in coffee plantations, but seems to be restricted to the lower portions of these where the trunks are at least 15 cm in diameter. We never found this species on the rocky outcrops which were common on the sides of Mt Kaindi and elsewhere in the Wau Valley. On Singapore I and in Malaysia, however, MHR saw an abundant *Herennia* sp. building its webs close to more-or-less perpendicular rock faces. At Manaas Wildlife Sanctuary in Assam, we saw an *Herennia* sp. building on tree trunks, and MHR saw extensive occupation of this web site in Sri Lanka by *Herennia ornatissima*.

Web structure

Simon (1892: 758) states that in Sri Lanka *H. ornatissima* “is very common, living on trees with smooth grey bark or on walls, where it builds a more-or-less regular, but small, orb web that is stretched parallel to the substrate and close to it; the hub is concave, attached to the substrate and forms a cup consisting of a disc of dense silk” (this translation uses present-day terminology).²

The web of adult females is, in fact, a most irregular orb (FIG. 1) but in other respects conforms to Simon’s (1892) description. The hub is a concave depression of dense matted silk. It seems reasonable to call this structure a *hub-cup*, although we don’t know if it is constructionally the homologue of a hub. The hub-cup is frequently close to the upper edge of the web and may be above the entire viscid prey-capture area. The spider seems to take advantage of natural depressions in the bark of the tree (scars, rotted-out branch bases, and so on) in siting the hub-cup. Its location within the web is, therefore, extremely variable. The hub-cup shown in FIG. 1 is atypical in location since it is almost central. The webs are frequently (always?) built so that the upper margin, or the upper limit of the functional web (i.e., the part containing viscid elements), is not directly above the lower margin. The upper margin is often attached to some prominence on the tree, so that the web-plane is inclined inwards (towards the bark) from this point to the lower margin. A most interesting feature of the *Herennia* webs that we have seen on trees is that the web plane follows the circumferential curvature of the tree trunk. At first sight this seems to present a mechanical problem: how can the spider build a web that is curved from side to side? Webs are built during the hours of darkness and the process is extremely difficult to

2. “L’espèce type, que j’ai observée à Ceylan, où elle es très commune, se tient sur les troncs d’arbres à écorce grisâtre et lisse ou sur les murailles, où elle file une toile orbiculaire assez régulière, mais petite, tendue parallèlement au plan du position, sur lequel elle est presque appliquée et auquel elle adhère par son centre, qui est un peu déprimé, en forme de coupe . . .”

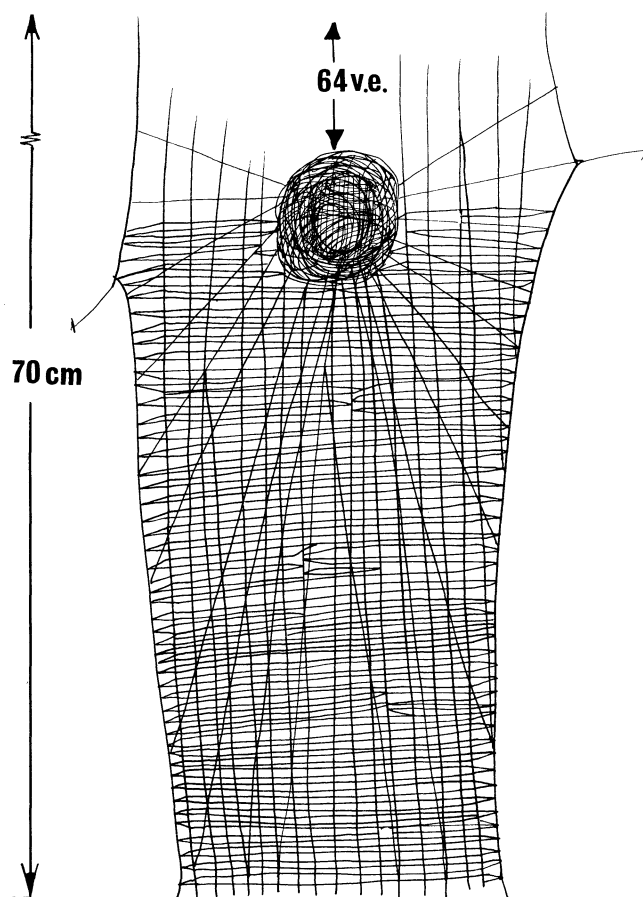


FIG. 1. Drawing of the web of an adult *Herennia ornatissima*, approximately to scale. Above the hub-cup, but not shown, were 64 viscid elements (v.e.) arranged from side to side, as in the lower web.

follow: the fine silk is difficult to see against the silvery tree bark (even when one is fortunate enough to encounter the spider actually working on its web and the light does not cause it to cease activity). Powdering the web with cornstarch (Eberhard 1976) helps to interpret the basic structure but does not, in this case, greatly help web photography because the background offers little contrast. FIG. 1 is based on extensive notes and sketches made on a powdered web. From this and from our notes on other webs, we can suggest an explanation for the side-to-side curvature of the web plane.

To facilitate explanation it is possible to regard the *Herennia* web as consisting of a number of perpendicular nonsticky structural threads across which the spider lays the side-to-side viscid element. Because the perpendicular threads are stretched between the attachments at each end, they form a taut system of supports for the viscid element that follows the basic curvature of the trunk. Like the ribs of an umbrella,

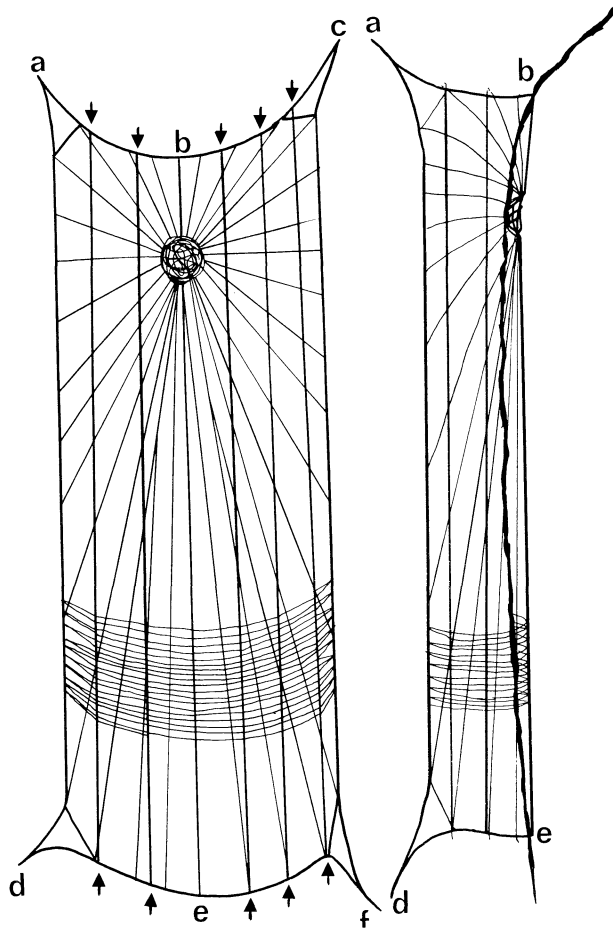


FIG. 2. Diagram illustrating how the *Herennia ornatissima* web could be constructed around the tree trunk without adhering to it. Left, plan view of entire web. Right, web showing the profile of the tree trunk (heavy black line) at the perpendicular midline; the tree is to the left of line b-e. It is suggested that the upper (a, b, c) and lower (d, e, f) web margins are in such relative positions that any line stretched from one to the other remains clear of the bark over its entire length. The perpendicular structural threads (between the arrows) are assumed to be laid down under tension—they serve an equivalent function to longerons in the frame of modern airplanes.

they give a curvature to the covering. This is shown diagrammatically in FIG. 2. The simplification involved in this explanation is not too extreme. The web certainly includes more or less perpendicular structural elements in addition to more conventional radii. We do not know whether these “pseudoradii” are laid down on top of the radii or vice versa; it would be structurally easier to conceive of them being built first so that they would keep the radii clear of the bark surface (see below). These “pseudoradii” are strongly reminiscent of the nondiverging “radii” that support the main ribbonlike sections of the ladder webs (Robinson & Robinson 1972, Eberhard 1975). The similarity does not stop there, since the viscid element in the *Herennia*

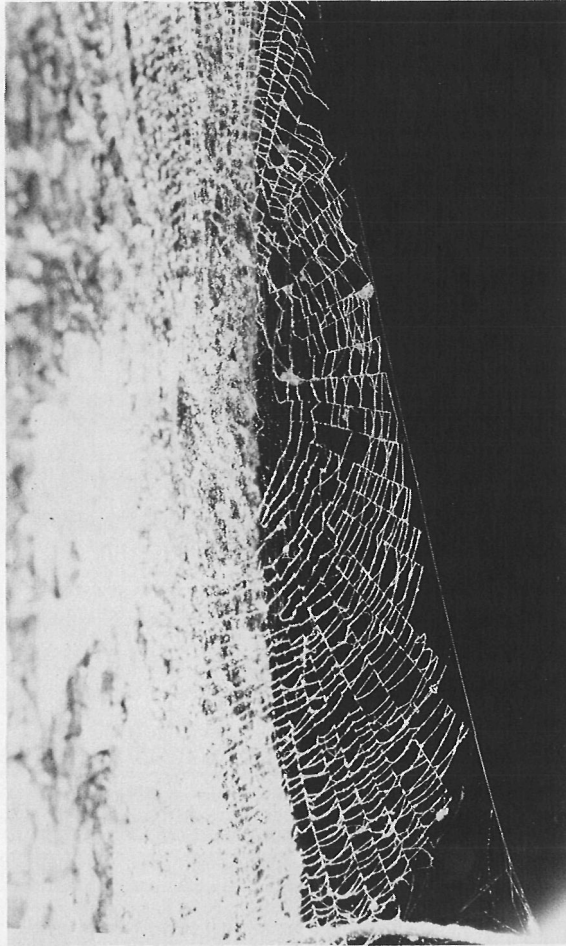


FIG. 3. Web of juvenile *Herennia ornatissima* (see text). Note that, although this web is clearly an orb, there are vertical structural threads in addition to normal radii.

web is like that of the ladder webs in being nonspiral (FIG. 1). It is tempting to think that the *Herennia* "pseudoradii" are inserted in the same way as the ladder web's parallel "radii," i.e., by the spider dropping from the upper point of insertion. If the web is to be clear of the bark, the upper insertions of the structural "ribs" must be outside a line drawn perpendicular to the lower edge of the web. Such upper insertions are frequently on the lower edges of side branches, stumps and callosities, where they are clearly not directly above the lower edge of the web. How does the spider determine where to build a web so that a line stretched from the upper margin will clear the bark surface for the length of the web? It must find a site where the perpendicular pseudoradii, under tension, will only touch the bark at their 2 ends. This could be done by trial-and-error testing, i.e., by the spider dropping on its dragline

from prospective upper margin sites. Web-site tenacity seems to be of a high order so that, having found a suitable site, *Herenmia* may tend to exploit it for longer periods than is usual for other araneids.

The web has the cup-shaped depression at the hub from an early stage of development. In captivity, spiderlings of the 3rd instar built tiny hub-cups clearly visible because of the dense whiteness of the matted silk. These were in webs that were built across plastic vials and not close to a substrate. In natural conditions, early instars make webs with numerous radii, and viscid elements that have large sections that are recognizably spiral in structure. FIG. 3 shows a web built by a 4th-instar female. This web is already much more perpendicularly elongate (rectangular) than would be the web of an *Argiope* or *Nephila* sp. at a similar developmental stage. Some perpendicular "pseudoradii" are present and the viscid element attaches to these at several points. Clearly this is a web that is transitional between the conventional orb and the adult ladder-web. It is noteworthy that adult female spiders, raised in captivity without normal web-building substrates (tree trunks), build webs that are less ladderlike than those of wild spiders building on natural substrates. Some of the elements of web architecture may thus be determined by the constraints imposed by the preferred web sites. Web-site preference is almost certainly genetically determined, but caged spiders showed no inclination whatsoever to build on sections of tree trunks placed in their cages. Whatever cues they use in determining suitable web sites were clearly absent, or suppressed by other factors, in the cage situation. Animals that would not build on tree trunks in captivity readily built on frames.

Web repair and web building is done during the hours of darkness, often in the early morning. Like *Nephila maculata* (Robinson & Robinson 1973a: 10-12), *H. ornatissima* often repairs only part of the web at a time. This repair is not easy to detect because viewing the white silk against whitish bark is difficult. We have seen more than $\frac{1}{2}$ the prey-capture area renewed in this way and outlined by old web on which innumerable moth scales provided contrast. The hub-cup seems to be added to from time to time and may not be renewed as frequently as the frame and viscid elements. It may, in fact, be accretionary. Renewal of part of the web or complete rebuilding of the capture zone occurred at a mean interval of 2.85 days (273 new or repaired webs built by 37 spiders in a period of 21 days). Web-site tenacity seems to be high. In this study we did not mark the spiders since this could have impaired their camouflage and increased susceptibility to predation. During the census all 37 webs were occupied for the 21-day period, except for 3 from which the spiders disappeared and did not reappear. We assume that the 34 consistently occupied webs were occupied by the same spiders, although supercession is possible in araneids (Enders 1974).

At no stage did we find *H. ornatissima* with ancillary web structures such as stabilimenta and barrier webs. Barrier webs are consistently associated with the webs of *Nephila* species. Their function is presumed to be protective since they are most frequently built dorsal to the spider (Robinson & Robinson 1973a). The barrier web could also serve to brace the hub, as suggested by Robinson and Robinson (1970a:

653) and Lubin (1975). In the case of *Herennia*, a barrier web would be difficult to site at a sufficient height above the main web, since it would need attachment points well above the substrate. In addition, the superb camouflage of the female spider (Robinson & Robinson 1973a, Fig. 5) would perhaps make a protective device less necessary. Similarly, the attachment of the hub-cup to the substrate renders any kind of additional bracing redundant. Linear stabilimenta occur very infrequently in the molting webs of some *Nephila* species. It has been argued that their function is then to brace the skeletal web (which lacks a viscid spiral) to provide a stable molting platform (Robinson & Robinson 1973b). This is clearly not necessary in this case, since the spider can molt hanging from the extremely stable hub-cup. The counter-suggestion, that the stabilimentum is an antipredator device that is particularly important at the time of molting (Eberhard 1973), is difficult to apply to the *Herennia* situation. It is noteworthy that *Argiope ocyaloides*, which also builds on tree trunks, builds a disc stabilimentum fairly regularly and occasionally builds a partial linear stabilimentum (see below). However, the hub of the *A. ocyaloides* web is free of the substrate and the spider is able to shuttle behind the disc. Disc stabilimenta are not known from *Nephila* or its relatives.

Egg-cocoons

The egg-cocoons of *Herennia ornatissima* are attached to the bark of the trees in which the webs are built. The spider usually attaches the cocoon fairly close to the web site and all the ones that we found were within 0.5 m of the nearest occupied web. The cocoons were white in color and covered with a papery layer of completely opaque silk that forms an ovoid capsule around the egg mass. There is no distinct cushion of silk on which the eggs are laid (in contrast to the cocoons of *Argiope*, *Cyrtophora*, etc.). The outer layer of the egg-cocoon is quite different from the cocoons of the (presumably) closely related *Nephila* species that we have seen. *Nephila* cocoons are typically covered with an open-weave layer of golden-yellow silk through which it is possible to see the egg-mass (e.g., Robinson & Robinson 1976a, Fig. 3); on the other hand, *Nephila* cocoons resemble those of *H. ornatissima* in being flattened on one side and attached to a substrate, rather than suspended aerially from silk guys.

Defenses

The defensive behaviors of araneid spiders have been reviewed by Robinson & Robinson (1970a) and Tolbert (1975). Robinson & Robinson (1973a: 66) described 2 defensive responses that they observed in *Nephila maculata*. That spider responded to being lightly touched on its dorsal surface by flexing its legs over the dorsal surface of the body as though forming a defensive cage of stiff appendages. At the same time, the spider raised the 2 extremities of its body by flexing the abdomen and cephalothorax at the "waist." The flexed legs may also be used to brush off attackers. *H. ornatissima* assumes a similar posture when lightly stroked with an artist's paintbrush. This kind of stimulation could mimic the attacks of small parasitic insects. When the web is shaken violently, the spider settles deep into the hub-cup, flattening

its legs against the web plane. This "foxhole" posture presumably maximizes the crypticity of the spider. In response to strong prodding on its dorsal surface, the spider may jump off the web and fall, belayed on its dragline. This is perhaps the ultimate escape response. It is unpredictable in that the same type of stimulation does not always elicit the jumping response. [Tactile stimulation in the field is notoriously difficult to standardize. Tolbert (1975) experimented with tactile stimulation and induced in *Argiope* spp. a spectrum of defensive responses.] A cryptic animal should not indulge in escape responses until its primary defense has been penetrated or until a potential predator has approached to within a critical distance (see discussion in Robinson 1969a: 297-302). Violent prodding of the spider could mimic the effects of an actual attack, and the penetration of the primary defense. One spider jumped after the web had been twanged within 2 cm of its left leg I. This stimulation could, presumably, simulate the close approach across the web of a pedestrian predator.

H. ornatissima is much more nocturnal than any other nephilid that we know. Web renewal is always at night, and the spider will attack prey in the hours of darkness much more readily than it will attack prey by day (see below). Nocturnality is a behavioral correlate of crypsis and *Herennia* is by far the most eucryptic araneid spider that we know (many *Cyclosa* sp. are concealed by merging with a line of adventitious material that they build into their webs, but this is not strictly background-matching). The activities of web building and the movements involved in attacking prey would certainly reveal the otherwise well-camouflaged spider. When considering the cryptic coloration of *Herennia ornatissima*, we can make comparisons with other bark-living animals. On the same trees as *Herennia* at Wau, MHR found bark-mimicking spiders (sparassids and salticids), bark-mimicking beetles (cerambycids and curculionids), beautifully camouflaged pentatomids, mantids and phasmids and extraordinary lichenose geometrid caterpillars. The spiders, beetles, mantids and phasmids were all patterned above and unicolorous on their ventral surfaces. The ventral surfaces of all these arthropods are appressed to the substrate, and not visible from above, when the animal is in its cryptic posture. *H. ornatissima* has patterned dorsal surfaces and uncamouflaged ventral surfaces. The dorsal patterning is essentially similar to that found on the other bark-dwelling arthropods (compare with the sparassid *Pandercertes gracilis* in Mascord 1970, Fig. 53 & 54, for instance). *Herennia* has a bright circular spot of carmine red on the ventral surface of the abdomen; this is only visible from above when the spider is "headstanding" while prey-wrapping (see below). This spot, which surrounds a smaller black mark, was yellow in cage-raised specimens; its function is problematical.

Males

The males of *H. ornatissima* are much smaller than the females, ca $\frac{1}{4}$ of their length, and, like the males of all the *Nephila* species that we have seen, are quite distinctly colored as adults. They are glossy and basically reddish in color with some black markings dorsally. Adult males live on the webs of females, where they are easily

confused with the theridiid kleptoparasites that are of the same overall color. Courtship and mating in this species have been described by Robinson & Robinson (1978) as primitive. A detailed description is forthcoming (Robinson & Robinson, in press). Males live on the webs of adult females for considerable periods; 5 of 20 marked males were still with their original females at the end of 30 days, 2 moved from one web to another one close by, and 13 males disappeared without trace. During the observation period, 14 new males moved onto the study webs. At the time of this study, we were not alerted to the fact that males in some nephilid species live on after they have lost both intromittent organs. This phenomenon was discovered by Robinson & Robinson during studies of *Nephilengys malabariensis* and subsequently by the same workers in studies of *N. cruentata*. They called such functionally pedipalpsless males "eunuchs," considering that their postreproductive survival, on the web of a female that they had fecundated, might involve protection of parental investment by driving off other males (Robinson & Robinson 1978). This discovery of the eunuch phenomenon led MHR to look more closely at *Herennia* males during a brief (May 1977) visit to Wau. He discovered eunuchs among the males on the *Herennia* webs.

Kleptoparasites

Theridiid kleptoparasites occur on *Herennia* webs and are similar in appearance to those occurring on the webs of *Nephila maculata*, *Cyrtophora moluccensis*, and *Argiope aemula* at Wau. *Argyroides argentatus* occurs on the webs of all 3 species, and *Argyroides minaceus* on at least 2 of the 3. We were not able to obtain determinations of the kleptoparasites of *H. ornatissima* from Wau, but would not be surprised if they include both the species found on the webs of *N. maculata*.

Prey

The outstanding question about the ecology of *H. ornatissima* concerns the functional significance of the specialized fine-meshed web that is utilized in an equally specialized web site. Since the web touches the substrate at its margins, it could catch ambulatory insects that walked into contact with it. Flying insects that attempted to alight on the bark in the area covered by the web would also tend to be caught. What types of prey does it actually catch and what niche is the spider exploiting? There is no simple way to solve this problem. Prey traps designed to collect discarded prey remains, such as those used by Robinson & Robinson (1973a), are easy to attach to tree trunks and there are no problems about web-site tenacity. However, such traps proved impossible to ant-proof in situ. Regular visual censusing of a number of sample webs is clearly the solution; but, since the spider operates its web 24 h a day, and probably peaks in prey-capture activity during the hours of darkness, we did not make such a census. Instead, we noted the nature of prey found in *Herennia* webs whenever we intermittently, and quite randomly, inspected them. This provided an indication of some of the prey items that can be caught in this type of location by this type of web. Experimental presentations of a variety of insects to wild and captive *Herennia* provided circumstantial evidence for further speculations.

TABLE 1. Prey caught by a sample population of adult female *Herennia ornatissima* compared with prey caught by an arboreal lizard *Anolis distichus* and the spider *Nephila maculata*.

TAXA	NO. CAPTURED	% OF TOTAL	% CAPTURED BY <i>N. maculata</i> *	% CAPTURED BY <i>Anolis distichus</i> **
Hymenoptera				
Ants	6	8.1	3.1	75.5
Others	1	1.4		
Homoptera	4	5.4	4.52	4.3
Hemiptera	4	5.4		
Diptera	5	20.2	9.5	10.9
Dictyoptera				
Cockroaches	7	9.4	0.28	—
Mantids	1	1.4	—	—
Odonata	—	—	0.2	—
Coleoptera	12	16.2	26.7	2.0
Orthoptera				
Crickets	2	2.7	3.3	—
Grasshoppers	—	—		
Katydids	1	1.4		
Lepidoptera				
Butterflies	1	1.4	23.9	0.2
Moths	7	9.4		
Larvae	1	1.4		
Others	12	16.2	28.4	4.1
Total	74			

* From Robinson & Robinson 1973 (Table 4, p. 22).

** From Schoener 1968 (Table 10, p. 721, juveniles).

The prey census (TABLE 1) shows no preponderance of any taxon that would be suggestive of specialization, nor is any ecotype discernably dominant. Admittedly, the total number of insects is small ($N = 74$). This represents a catch of 0.09 insects per web day, which is clearly an underestimate. Previous studies of the prey of tropical orb-web spiders (Robinson & Robinson 1970b, 1973a; Lubin 1974) give a minimum figure of 1.5 insects per web day, which the authors admit to be an underestimate.

We expected to find that worker ants were an important item of prey for *H. ornatissima*. They are numerous on the trees that have webs on them. In addition they are active at all hours and are potentially trappable at the edges of the web where it touches the bark. However, only 8.1% of the prey items in our sample were ants and all of these were alates. We believe that the difference between expectation and reality is due to the fact that, because of the limitations of its predatory behavior, *H. ornatissima* cannot subdue ants even though its web may trap them.

This view is supported by a number of direct and indirect observations. Firstly we presented a small number of ants to mature *H. ornatissima* females during the study. These were taken from trees at WEI. They were not identified but, judging by mor-

phototypes, represented at least 5 species. Only 1 ant out of 15 was attacked; the others were approached, touched, and then ignored. This reluctance to attack ants led to a study of the reactions of araneid spiders to a variety of tropical ants. Robinson & Robinson (in prep.) have systematically presented a number of ant species, with different defensive adaptations, to a number of species of araneid spiders that differ in their predatory repertoires. One of the araneids used in these experiments was *Nephila clavipes*, which has a predatory repertoire resembling that of *H. ornatissima* and attacks all prey by biting (Robinson & Robinson 1973a). Reliance on a biting attack puts *N. clavipes* at a disadvantage when faced with many ant species, particularly those with chemical defenses (Robinson & Robinson, in prep.). *H. ornatissima* may be similarly disadvantaged. This would explain why the ants in the sample were alates, since, generally speaking, alates rarely have complex and powerful defenses. In contrast to those species that are restricted to a biting attack on prey, the species that are capable of attack wrapping have few problems with ants. *Argiope argentata*, a much smaller spider than *Nephila clavipes* but one with attack wrapping in its predatory repertoire, effectively subdued all species of ants in the experiments of Robinson & Robinson (in prep.). *Herennia* is not well adapted to be an ant specialist.

Of course the prey sample (TABLE 1) is too small to be other than merely suggestive. One way of determining the types of insects potentially available to this spider would be to run sticky traps on tree trunks at sites similar to those used by *H. ornatissima* for its webs. We did not do this but Robinson (in prep.), using sticky traps that eliminated captures of ambulatory insects, showed that in Panama a wide variety of insects alight on tree trunks. Cockroaches, gryllids, beetles, homopterans and hemipterans were trapped in substantial numbers. Although sticky traps are likely to produce biased results (Southwood 1966, Robinson & Robinson 1973a), they provide at least a conservative estimate of prey availability. We conclude that arboricolous predators can obtain an abundance of insect prey other than ants.

PREDATORY BEHAVIOR

There has been a tendency on the part of some arachnologists to describe what we call predatory behavior as *feeding* behavior. This is completely misleading, since the araneid spider does not commence feeding until it has transported the prey from the capture site to the hub (or retreat) after the behaviors involved in attack and immobilization. The behavior of feeding can therefore be regarded as the end of a predatory sequence. For a discussion of definitions of predation, see Curio (1976: 1-2). *H. ornatissima* lacks attack wrapping in its predatory repertoire; it attacks all prey by biting. This was noted by Robinson & Robinson (1973a: 52-54). What they did not note was a very strong tendency for the spider to attack a wide range of prey more readily at night than by day, nor did they draw attention to the fact that the web site imposes constraints on the form of some of the predatory units, particularly on wrapping at the capture site, wrapping at the hub, and on transportation of prey.

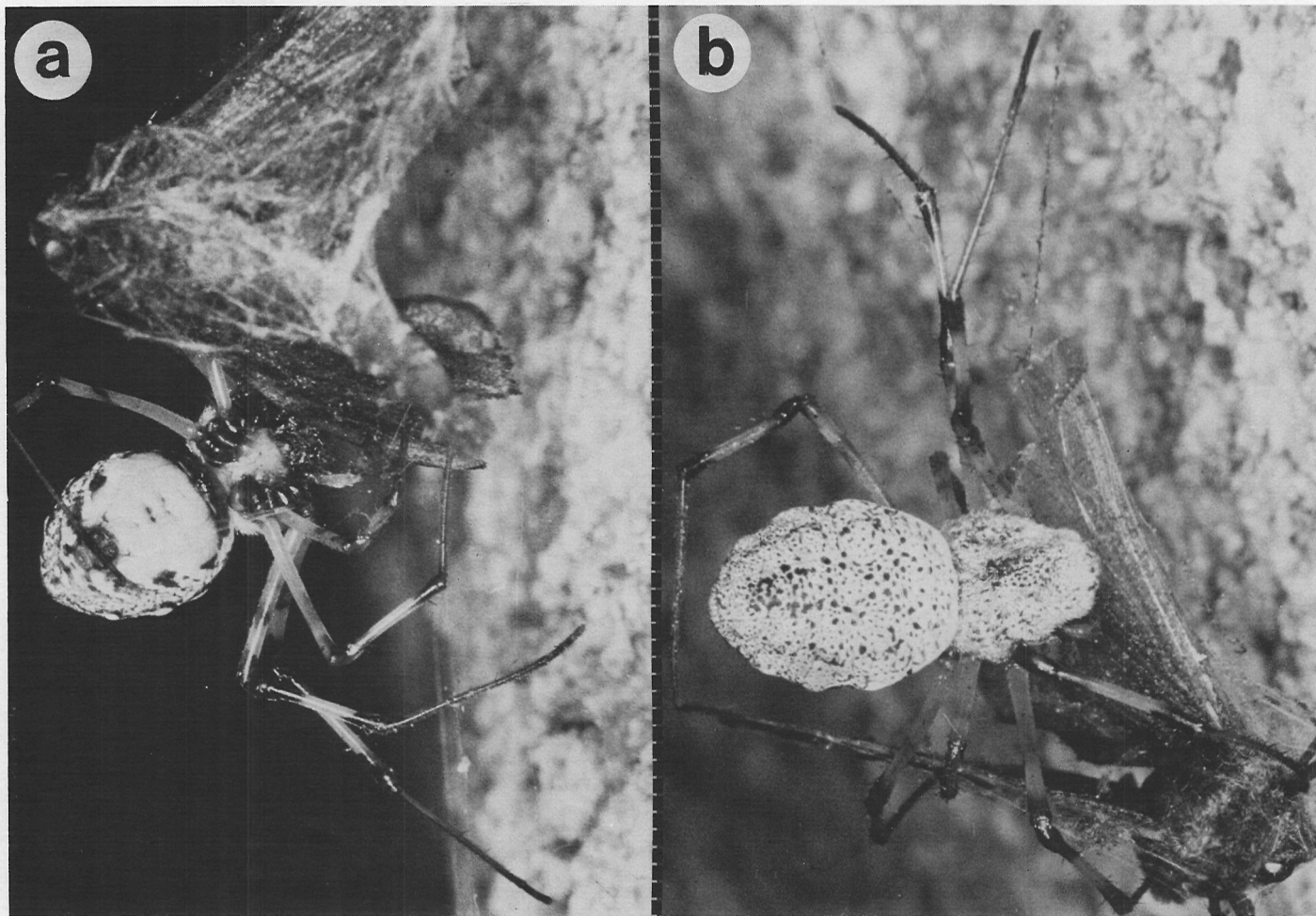


FIG. 4. Typical "headstand" wrapping postures of *Herennia ornatissima*. a, ventral view; b, dorsal view. Note the braced position of legs I and II.

TABLE 2. Circadian differences in attack tendencies and efficiency of prey capture in *Herennia ornatissima*.

PREY*	PRESENTATION BY DAY		PRESENTATION BY NIGHT	
	% attacked**	% captured	% attacked**	% captured
Blowflies	48.6	46.0	100	100
Moths	35.1	24.3	94.6	83.8
Tettigoniids	16.2	10.8	81.1	78.4

* One insect of each category presented by day and by night to each of 37 adult spiders. Percentages calculated out of total presentations, i.e., N = 37.

** If spider left hub-cup on a predatory excursion, this was scored as an attack irrespective of whether it reached the prey. The difference between % attack and % capture is due to escapes of prey.

Nocturnal and diurnal differences in attack tendencies of spiders

Some 37 adult female spiders were used in field experiments. Over a period of 1 week we presented various types of prey to spiders at the same web site by day and after nightfall. Each spider constitutes its own control, but the presentations were not randomized because of practical problems. Each kind of prey was presented first by day and then by night, on the following day another kind of prey was presented by day and then by night, and so on. We presented tettigoniids, moths, and blowflies in that order. In this test we scored whether or not the prey items were attacked, how they were attacked and the details of the predatory sequence. In tests where the spider did not respond, the observations were terminated after 5 min; if the insect escaped in less than 5 min, tests were stopped when it escaped. Prey items were crudely standardized (by eye) for size and for similarity in appearance but were not necessarily the same species or genus. Despite this standardization there were differences in activity after striking the web; some flies, for instance, struggled more vigorously than others.

In general, the insects that struggled without producing high intensity vibrations (tettigoniids) were much less likely to be attacked by day than by night (TABLE 2). Insects that buzzed or fluttered were still more likely to be attacked by night, but a greater proportion released diurnal attacks. Diurnal attacks were also much less likely to be successful than nocturnal ones; the spiders were slower to react to prey and insects escaped more frequently.

Attack behavior

Herennia may approach the prey directly or may shuttle through the web at the hub-cup and approach prey items on the backside of the web with its dorsal surface to the bark. We saw no consistency in this and cannot characterize the situations in which a "backside" approach is made. A small buzzing fly may be approached thus, as may a large convulsively kicking grasshopper. Approaches may be rapid runs or slow hesitant approaches much interrupted by plucking. The former is absolutely

characteristic of approaches to what we consider to be highly stimulative prey, i.e., those prey that even evoke attack by day. Approaches to particularly large prey were more frequently characterized by postures in which the spider had legs I raised off the web during most of the approach. When close to the prey, such spiders would tap it gently with legs I before attacking. This approach has been described in detail by Robinson & Robinson (1973a: 44, 46). Biting is almost always directed at the part of prey immediately adjacent to the advancing spider. Legs and projecting appendages are bitten briefly, and then the bite is transferred to the body itself, at an early stage. We saw some bite-and-back-off behavior (see Robinson & Mirick 1971); this always occurred when the prey item was comparatively large, but it was not consistently elicited by large prey. After a biting attack, the spider either wrapped the prey in situ or pulled it from the web at the capture site. Pulling out was observed only in the case of attacks on moths (15%) and flies (4.3%); otherwise, wrapping occurred. Wrapping was most complex when relatively large prey were involved. Grasshoppers more than $\frac{3}{4}$ the spider's length were subject to wrapping during which the spider assumed the complex postures seen in FIG. 4. Smaller prey of all kinds were wrapped as the spider stood astride them, usually facing the hub-cup.

Since the wrapping posture with large prey is the most strikingly unusual behavior of this species, it is worth describing in detail and comparing with the equivalent behavior in other araneids. Biting occurs with the spider in a head-down posture, but as wrapping starts the spider turns sideways, using the jawhold as a pivot point, until the long axis of its body is more or less lying across the web. As the first threads of silk are cast onto the prey, the spider does a "headstand" so that its body is nearly perpendicular to the upper surface of the web plane. From this position, alternating movements of the 4th legs carry silk down onto the surface of the prey. As wrapping progresses, the spider slowly cuts the prey free of the web and holds it with the short 3rd legs while silk is deposited around the entire prey package. This use of the 3rd legs is clearly visible in the photographs. Towards the end of the wrapping the spider moves to a position below the prey, still in a headstand and, as the prey is completely freed from the web, moves so that its body is interposed between the prey package and the web plane. The spider is thus facing the hub-cup, ventral surface uppermost and fending off the prey package with one or more legs III and IV. The spider cannot climb back to the hub with its ventral surface uppermost; before moving it spins on its long axis to regain a normal orientation and footing on the web. Essentially the spider does a "barrel-roll" while facing the hub. This behavior is illustrated in FIG. 5. We do not claim that all wrapping bouts directed at large prey follow precisely these stages; there are variations in the sequence which presumably result from the fact that the prey is not necessarily completely immobile. However, the behavior is sufficiently frequent in occurrence to be described as characteristic of this species.

We believe that these complex movements are an adaptation of normal prey-wrapping behavior to the essentially one-sided *Herennia* web. There is not space beneath

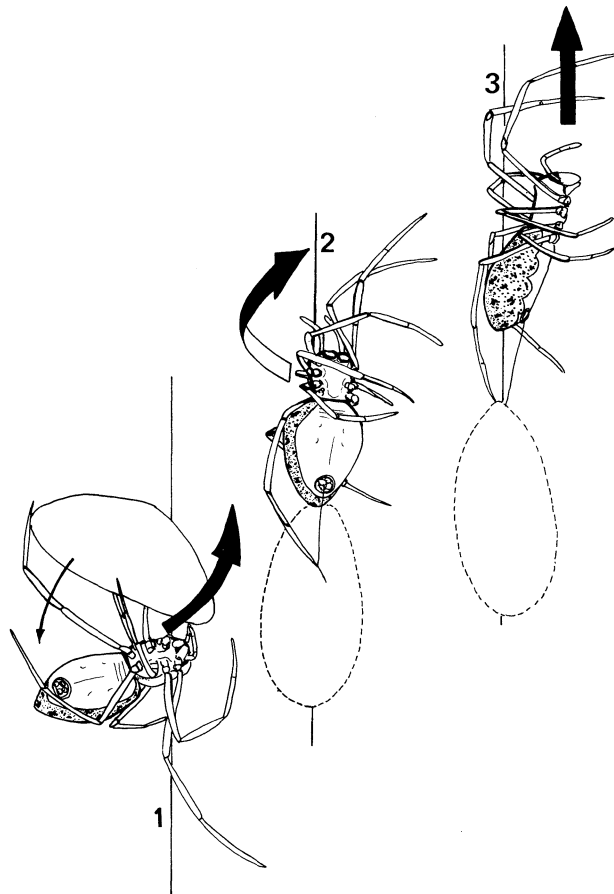


FIG. 5. The complex movements involved in passing from a "headstand" wrapping posture to a carry-on-silk movement in *Herennia ornatissima*, as executed on a one-sided vertical web. Stage 1: the spider moves (in the direction of the large arrow) upwards beneath the prey, with its ventral surface uppermost. Stage 2: the spider then rotates about its long axis (arrowed) to bring the dorsal surface uppermost. During this "barrel-roll" maneuver, the spider holds the prey package away from the web with leg IV. Stage 3: the spider is now correctly oriented to carry the prey up the web (see FIG. 6).

the web plane for "gymnastic" wrapping movements. Furthermore, if wrapping resulted in the prey being pushed against the substrate, as might well happen if the spider were working in the plane of the web rather than above it, the web could stick to the tree, or the prey might use the foothold to free itself. Descriptions of wrapping in other araneid species show that much of the activity takes place in and beneath the web plane. Certainly in these cases, the spider does not behave as though the web were one-sided. Details of wrapping behavior in *Nephila maculata* (Robinson & Robinson 1973a: 48, Fig. 21) provide an interesting comparison. The only fundamental

similarity lies in the fact that both species wrap using slow, alternating movements of the 4th legs. Post-immobilization wrapping in *Argiope* species differs to an even greater extent because these spiders roll the prey in the web; however, it is instructive to compare the postures illustrated in FIG. 4 with the posture shown by Robinson & Olazarri (1971, Fig. 5) for *Argiope argentata*. In that illustration (taken from movie film), the *Argiope* is hanging through the web with its 1st and 2nd legs braced in very similar positions to those shown here for headstanding *Herennia* (FIG. 4).

Transportation of prey

Prey are transported to the hub in 1 of 2 ways. The insect may be held in the chelicerae in front of the spider or it may be suspended, trussed in silk in a prey package, from the spinnerets, behind the spider. In general, small or nonbulky prey are carried in the jaws and large prey on silk (see transportation in Robinson 1969b, Robinson & Olazarri 1971). The spider carrying prey in its jaws can walk forwards (head first) to the hub or it can back up the web. Of the prey small enough to be carried in the jaws, the larger items are more likely to be carried by the spider backing up the web. This process of backing up the web with prey held in the jaws also occurs in *Nephila maculata* (Robinson & Robinson 1973a: 48, 50, Fig. 22).

Only the carry-on-silk movement showed any clear differences from the postures involved in this behavior in other araneid spiders. An *Herennia* carrying prey on silk has a distinct "tail-up" attitude in which the abdomen is strongly flexed, so that the apex is well above the level of the head on the longitudinal axis (FIG. 6). In addition, the legs are stilted; the overall effect of these 2 factors, combined with the attitude of the 4th leg holding the silk line from the prey package, is to hold the latter well clear of the web. Most species of araneid spiders, transporting prey on silk, climb up the underside of a sloping web so that gravity swings the prey package away from the web plane. Since *Herennia* climbs up the outside of a more or less perpendicular web, it must run a greater risk of getting its prey package entangled.

Attachment of prey at the hub

Prey carried on silk behind the spider is simply attached to the perimeter of the hub-cup as the spider turns to assume its normal head-down predatory posture. The silk from the prey package is continuous with the spinnerets and the spider simply dabs the spinnerets against the hub silk as it turns, attaching the line from 2 to 5 times (i.e., in a semicircle). Prey carried in the jaws is subject to more complex treatment. When the spider backs up the web with wrapped prey in her jaws, she simply headstands at the hub and casts a few skeins of silk onto the package. This is sufficient to attach the package to the dragline silk of her spinnerets and it can then be attached in the same way as prey carried on silk, that is, to several points on the hub. Prey carried head-first in the jaws is wrapped at the hub; the spider often does this on stilted legs, facing down the web, and then simply attaches the prey once.

Multiple captures are not left in the web at the capture sites, but are transported



FIG. 6. Adult ♀ *Herennia ornatissima* carrying a large tettigoniid back to the hub-cup up the web. Note that the abdomen is strongly angled upwards from the waist (pedicel) and that the right leg IV, from which the prey is dangling on a silk line, is raised up to hold the prey free of the web. The spider is ca 10 mm long.

to the hub region and hung there. In this, the spider's behavior resembles that of all the *Nephila* species that have been studied.

Argiope ocyaloides

NATURAL HISTORY AND ECOLOGY

Distribution

In Papua New Guinea this species has been recorded from Maffin Bay, West New Guinea, by Chrysanthus (1971) and a specimen collected at Bulolo by B. Gray was identified as *A. ocyaloides* by Chrysanthus (in litt. to B. Gray).

Chrysanthus remarks (1971: 14) "this species has never been mentioned after the first description (Roewer 1942: 742; Bonnet 1955: 692)." Gray's Bulolo specimen was found on Klinki Pine (*Araucaria hunsteinii*) in a plantation and this led us to search Klinki Pine plantations at Wau. We found the spider in 1973 at MacAdam Memorial Park, Wau. The species is extremely cryptic and nowhere seems to be very common. Its unusual web site seems reason enough for its being overlooked for so long. The spider is not figured in either Clyne (1969) or Mascord (1970), although it was first recorded from Australia.

Web location

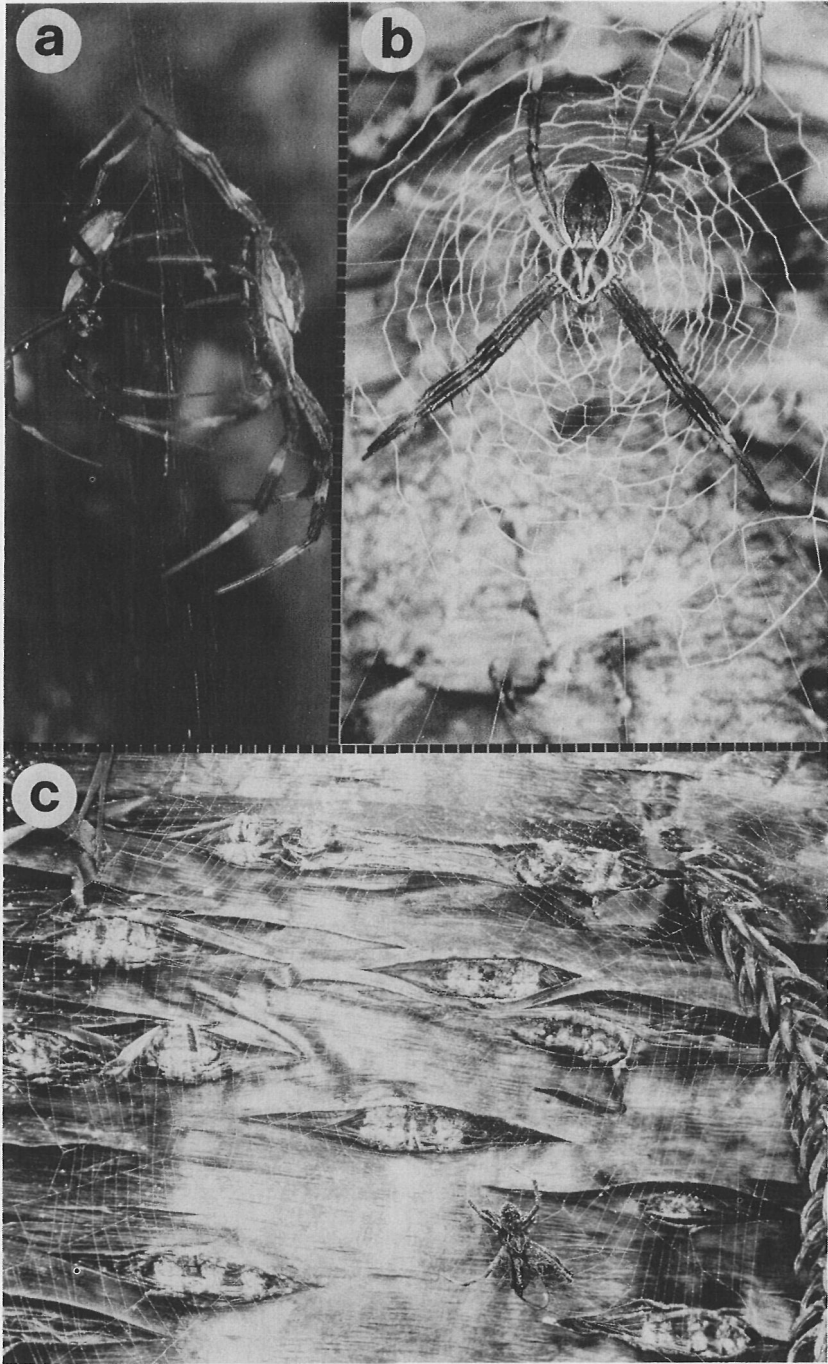
All the webs that we found were on the trunks of trees, most commonly on the trunks of *Araucaria hunsteinii* but also on the more gnarled bark of *Casuarina* sp. nearby. The bark of the Klinki Pine peels off in curling masses at irregular intervals and the lower parts of the trunk are frequently scarred with stumps of defunct lower branches. These projections are utilized as web supports by the spider, which builds a noncurved web above the trunk. The web may clear the trunk by 2-3 cm at its closest point. At the same location we found *Argiope reinwardti* on both kinds of trees and were unable to detect any differences in preferred web sites of the 2 species on these trees. We have never found *A. ocyaloides* anywhere but on trees and consider it to be an obligate arboricole (see Discussion).

Web structure

The web is a virtually unmodified *Argiope*-type orb. It has a closed hub that is usually slightly above the midline, unbranched radii, and a relatively widely-spaced viscid spiral, and is coarse meshed. We did not attempt to quantify basic web parameters because the web is in no way exceptional in its basic structure. FIG. 7 shows the

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FIG. 7. a, ♂ and ♀ *Argiope ocyaloides* at the hub of the web during courtship (the web seen end-on lies between the two; the ♂ is on the inside surface). The ♀ is ca 10 mm long. Note the relatively large size of the ♂ (left). b, a recently molted *A. ocyaloides* ♀, showing the fine lacelike disc stabilimentum. Note the camouflage patterning on the dorsal surface of this spider. c, web of mature *A. ocyaloides* ♀ sited above the trunk of an *Araucaria* tree, showing the mesh size and typical form.



spider on its web and typical examples of web location and web structure. It is noteworthy that the spider almost invariably sits on the outside of the hub with its ventral surface towards the substrate. The small number of spiders (about 4%) that we found facing outwards (i.e., on the inside surface of their webs) could have shuttled inwards in response to web disturbance. The dorsal surface of the spider is disruptively patterned (FIG. 7b); the ventral surface is pale brown with faint yellow markings.

We did not find barrier webs associated with any *A. ocyaloides* webs. We regularly found immature spiders of both sexes with disc stabilimenta. The disc stabilimenta were sufficiently unusual to attract our attention to this spider long before it was identified. We found delicate "crotched" disc stabilimenta on tree trunks in webs occupied by nondescript juvenile argiopids. We tried to raise these in captivity but found the adults before we were successful. FIG. 7b shows the typical disc of an immature *A. ocyaloides*. This differs from the discs of *A. argentata*, *A. savignyi* (Robinson & Robinson 1970a, Fig. 6) and other *Argiope* species that we have seen (at least 24) in that the white ribbon-silk of which it is composed is very fine and narrow. Instead of a conspicuous opaque mass of silk laid down on top of the hub silk, this is an intricate "design" of fine lines. [It is worth mentioning here that there is considerable confusion over the use of the term stabilimentum. The term was probably first used by Simon (1892) and applied to radial structures of zigzag silk in the webs of *Argiope* and *Cyclosa* spp. It has since been used to describe a variety of structures built into orb webs of araneids and uloborids, including tufts of silk on foundation lines and egg-sac detritus strings (Eberhard 1973). Robinson & Robinson (1970a) gave a restrictive definition, applying the term only to zigzag bands of ribbon silk. Restriction of usage has merit insofar as there may be many functionally different structures described by the same term if a broad definition is used. McCook (1889: 59, 99) applied a variety of terms to zigzag *Argiope aurantia* stabilimenta, but clearly called the opaque silk sheet covering the hub a shield. This term should be retained to distinguish between a homogeneous layer over the hub and the zigzag disc stabilimentum. The shield and the disc could serve different functions.] Linear stabilimenta belong to a later developmental stage in most *Argiope* sp., but see Ewer (1972) for a contrary viewpoint. Immature males build linear stabilimenta at a much earlier stage than do females (Robinson, B. & M.H. Robinson 1978). In the webs of *A. ocyaloides* we saw 3 linear stabilimenta in over 12-months of sporadic observations. These were incomplete elements of a St Andrew's cross type of stabilimentum and could be regarded as vestigial because of their rarity.

The situation in *A. ocyaloides* is thus one where the disc is present in juvenile webs but much reduced in the density and area of silk involved. We found linear stabilimenta to be extremely rare. Unfortunately, these facts do not really further the enquiry into stabilimentum function that has proceeded largely on a deductive basis. Robinson & Robinson (1970a, 1973b) have argued strongly for the disc being a protective reinforcement of the hub, behind which the spider can shuttle. In an aerial web, it may be a relatively conspicuous structure and an effective shield. In a web

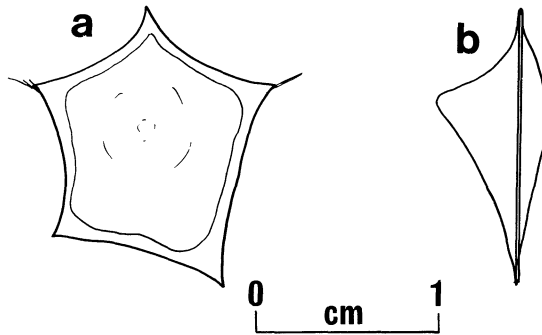


FIG. 8. Egg-sac of *Argiope ocyaloides* seen frontally (a) and laterally (b).

close to a dark substrate, reduced conspicuousness may be highly adaptive. Proponents of the concealment function of the linear stabilimentum can argue that the virtual absence of this stabilimentum in *A. ocyaloides* webs is a consequence of its function being assumed by protective coloration of the spider itself. On the other hand, the proponents of the stabilization theory can argue that the *A. ocyaloides* web has the most stable foundations of any *Argiope* web, being but a short distance at all corners from a solid substrate, and therefore needs no stabilizing devices.

Egg-cocoons

The egg-sacs of this species are laid on silk supports very close to the bark of tree trunks, but some distance from the web site. The spider tends to site them close to branch scars and other bosses or depressions. The outermost surface is off-white, the inner surface is dirty-white. The shape and size of a typical egg-sac is shown in FIG. 8. Seven egg-sacs that we dissected contained a mean number of 66.4 eggs or spiderlings. The heaviest egg-sac was approximately $\frac{1}{4}$ the weight of a fat adult female.

Males

Sexual dimorphism in size is common in *Argiope* species (Robinson & Robinson, in press); in addition there is frequently intrasexual polymorphism in size (B. Robinson & M.H. Robinson 1978). Males of *A. ocyaloides* are often more than $\frac{1}{2}$ the size of adult females and are therefore much larger in proportion to the females than those of any other *Argiope* species that we have seen. Such males are not only proportionally larger but absolutely larger. (This is a small species; the adult female ranges from 8–11 mm in length.) Males assemble on the upper foundation threads of female webs and remain there for some time. The courtship and mating of *A. ocyaloides* is described by Robinson & Robinson (in press). FIG. 7a shows an adult male and an adult female.

Defenses

Juveniles with discs in their webs shuttle from one surface of the web to the other, interposing the disc between themselves and the potential predator. Shuttling occurs in response to tactile stimulation. Adult females respond to disturbance of the web by moving onto the upper foundation lines where they hang motionless; in such circumstances the spiders are extremely inconspicuous. The spiders also "pump" at the hub (i.e., flex and extend all their legs rhythmically), but we could not consistently evoke this response. Dropping from the web did not occur during our observations.

Prey

We made no attempt to census prey, but the spider can deal efficiently with a wide variety of insects and, in experiments, was able to subdue all the ant species that we presented to it. The web is much further from the tree trunk than that of *H. ornaticissima* and thus more suitable for catching flying or jumping prey than for catching ambulatory insects. The spider no doubt specializes on those insects that alight on tree trunks. The sticky-trap samples of Robinson (in prep.) are relevant to the consideration of the prey potentially available to this species.

PREDATORY BEHAVIOR

Argiope ocyaloides is a typical *Argiope* species as far as its predatory behavior is concerned. Its predatory behavior includes all the component units described for other species (see review in Robinson 1975). We presented free-living individuals with grasshoppers, moths and calliphorid flies and recorded the details of the behavior sequences given in response to these prey items. All the insects were presented alive. The grasshoppers and calliphorid flies were attack-wrapped, then bitten. The moths were bitten and then pulled from the web or wrapped in situ. The fact that the flies were wrapped first is noteworthy because Robinson & Olazarri (1971) and Ades (1972) found that *Argiope argentata* bit and pulled out, or bit and wrapped, a proportion of the blowflies with which they were presented. The blowflies used in the experiments were much larger in proportion to the *Argiope ocyaloides* than they were in relation to *A. argentata*. Most of the blowflies that we presented were equal (or almost so) in length to the adult female spiders. This may explain the total reliance on wrapping attacks.

Watching attacks on moths convinced us that an important element of attack biting on these insects has previously been underemphasized (see, for instance, detailed account in Robinson & Olazarri 1971: 11), although it is noted in passing (Robinson & Robinson 1976b: 267). We think that biting attacks on moths should really be called *bite/clasp* attacks because, as the spider sinks its jaws into the prey, several of its long legs enfold the insect, coming in from behind it (often through the web), to clasp the prey tightly against the spider's own body. The moth is thus simultaneously seized in the jaws and imprisoned in a cage of legs. We were particularly struck by this aspect

of the biting attack because we found exactly similar behavior in *Psechrus* and *Fecenia* (see Part II of this series).

Grasshoppers in the 80–120 mg range were substantially larger than the spider. These were attacked without hesitation in nearly all cases. Some of the spiders cut radii above the struggling insects, thus causing them to drop through further layers of viscid spiral and become further enmeshed in the web (see Robinson, Robinson & Graney 1971: 306–07). In addition, several spiders attacked by dropping below the prey and *throwing* swathes of silk over it from a distance. Once the prey was initially enswathed, the spiders finished the prey-packaging process by running around the long axis of the grasshopper, laying down multistrand silk. This is the functional equivalent of prey rolling that other *Argiope* species carry out on smaller prey. In prey-rolling, the spider remains in one place and lays down multistrand silk as it turns the prey on an axis formed by web attachments or the tarsi of its 3rd legs. Web-cutting above the prey, silk-throwing, and running around the prey depositing silk are all adaptations to dealing with prey larger than the spider. They are used by *A. ocyaloides* with a facility that suggests that it may normally encounter prey of this size. The spiders carried the grasshoppers to the hub on silk rather than in their jaws. In 2 cases, the grasshopper was derricked up to the hub. This modification of the carry-on-silk process is another adaptation to the treatment of large prey. It involves the spider hauling the prey up to the hub on a successive series of silk lines, a little at a time. The prey is not necessarily cut free of the web, but dragged up through it. This suggests that particularly large prey may be sufficiently rewarding for the spider to sacrifice the future catching capacity of the web in order to get them safely to the feeding site.

We presented a number of ant species to this spider. All were effectively attacked, but we did not follow the predatory process after the initial wrap/bite attack. After wrap/bite, the spider frequently retires to the hub for long periods before returning to the prey to complete the sequence and transport it to the hub; watching complete predatory sequences is thus a time-consuming process. All prey items are left in situ in the web, after being attacked, if the spider is already feeding at the hub. They are not transported until the spider has completed feeding on the first-caught prey item.

Arachnura melanura

NATURAL HISTORY AND ECOLOGY

Distribution

Roewer (1942: 751) gives the distribution as India, Malacca, Java, and Celebes. Bonnet (1955: 372) gives Malaya, and the species was recorded from New Guinea by Chrysanthus (1961, 1971). We found isolated adult females at Wau in 1970–1971. In 1973–1974, MHR found the species to be common in the coffee plantations of the Wau Ecology Institute. It was found elsewhere in the Wau Valley in coffee plantations by MHR during a brief visit in 1977. No males were found at any time.

Web location

Recognizing the preferred web site of *A. melanura* was the key to recognizing the spider as common. In fact, the spider builds within the branch-crown of bushes and small trees and is thus occupying a niche that is quite different from that of spiders that build between trees and small bushes (e.g., both *Gasteracantha* species described in Part III). The typical situation is much easier to recognize than to categorize. On coffee bushes there tend to be small gaps in the outer layer of foliage and in such gaps *Arachnura* webs can be found. The web plane of such webs can be regarded as lying across the flight path of insects flying into, or out of, the inner nonleafy part of the crown. We never found the spider in the herb layer nor in rocky or grassy situations. Jones (in McKeown 1963) found *Arachnura higginsi* living in holly bushes in Tasmania. Forster & Forster (1973: 166) report that the webs of *Arachnura feredayi* in New Zealand are "usually strung close to the ground."

Web structure

The web of *Arachnura* is a relatively fine-meshed conventional orb, except that the 2 sectors at each side of the 12 o'clock radius contain no spiral elements (FIG. 9). They are thus free sectors, as in the web of *Zygiella x-notata*. The *Arachnura* situation differs from *Z. x-notata* (see, for instance, Levi & Levi 1968: 61) in that the spider sits at the closed hub of the web and above it there is a radius with a free sector on each side of it, rather than a free sector that is partly bisected by a signal line. The 12 o'clock radius in *A. melanura* is used by the spider as a site for attaching dead leaves and plant debris (FIG. 9). Mature females string their egg cocoons along this radius. The web usually slopes and may sometimes nearly approach the horizontal. The spider sits on the lower surface, and there may be a tangle of apparently unorganized threads beneath the spider (below the web plane). We regard this as a possible barrier web. Forster & Forster (1973: 166) state that the web of *A. feredayi* "is surrounded by irregular threads." However, not all the spiders had this thread tangle and it could for example represent the remains of previous webs at the particular site.

Judging by the number of egg-sacs seen in webs, we can assume considerable web-site tenacity; we would guess at least a one-week interval between egg cocoons, giving a minimum of 7 weeks at 1 site. Sometime in the first few hours after nightfall, the spider usually takes down the old viscid spiral and spends the night in a "skeleton web" of radii and frame members. The viscid spiral is renewed shortly before dawn or later if rain intervenes. Jones (in McKeown 1963: 51) observed a similar regime in Tasmania.

Egg-sacs

The egg-sacs of *Arachnura melanura* are roughly ovoid, bilaterally compressed structures of brownish-golden silk and often have plant detritus attached to them. They separate fairly easily into 2 sections along an axial circumference. The outer layer consists of papery silk with an inner cushioning of more fibrous wooly material.



FIG. 9. Photograph of the web of an adult ♀ *Arachnura melanura* showing the simple hub and 2 vacant sectors, 1 on each side of the 12 o'clock radius. Note the plant detritus that the spider has attached to the 12 o'clock radius above its resting site; the dead leaves cover 2 egg-sacs.

Dissecting old capsules fails to reveal the sort of egg-cushion built into one side of *Argiope* cocoons. On the other hand, the structure is totally unlike the typical *Nephila/Gasteracantha* type of cocoon, in that the outer silk is clearly a discrete, opaque layer. The maximum number of cocoons seen on any 1 web at Wau was 7. Since the eggs take around 3 weeks to hatch, an egg string of 7 presumably includes a number of egg-sacs from which the spiderlings have emerged.

Males

We found no males at any stage. McKeown (1963) quotes a letter from Coleman that gives sizes and weights for adults of both sexes of an unnamed *Arachnura*. The male was said to weigh 0.6 mg and the female 83.2 mg; allowing for inaccuracy in the balance, it was assumed that the female was 120 to 160 times as heavy as the male. The body length of the male is given as 1.5 mm, that of the female as 17 mm.

Defenses

We think that the primary defense of the female spider lies in its appearance when at rest. The elongate tail is undoubtedly an encumbrance in prey capture (see below),

and we can conceive of no reproductive function for this extension of the abdomen. It is probably an elaboration for defense against visually hunting predators. This view is buttressed by the fact that the resting spider protracts legs I and II side by side ahead of the body. These 4 legs, in apposition, appear as a single unit that enhances the apparent length of the body. Legs III and IV are normally laid inconspicuously against the sides of the abdomen, bent slightly so that the tarsi grip the hub-silk (FIG. 10). Such leg-concealment postures are commonly associated with crypsis and plant-part mimicry (Robinson 1969c, 1970 reviews many examples). Visually hunting predators may use insect appendages as prey recognition cues, so leg concealment makes adaptive sense. Difficulty arises over assigning *Arachnura* to a particular category of visual defense. At Wau, it exists in 2 color forms: daffodil yellow and a deep chocolate brown. The yellow form could be regarded as a flower mimic with the long tapering body essentially similar to a *Rhododendron* flower. The brown form is less convincing in this role. Spiders of both color forms merge in with the line of plant detritus and appear, to a casual glance, as just another piece of detritus. Certainly if a predator learns to associate the web with the presence of the spider, it might attack several items of nonprey before hitting the spider. [Robinson & Valerio (1977) report that salticids that have been alerted by an *Argiope argentata* moving on the web will then leap on immobile prey packages that are roughly spider-sized and attack them. Salticids could well be diverted by the detritus masses in the *Arachnura* web.]

There is yet another possibility. Robinson (1969c: 230-32) suggested that some tropical arthropods gain protection against predators by evolving bizarre shapes. They perhaps thus deviate from the range of generalization that the predator has acquired in the process of learning to recognize food items. In short, they may be so unlike that which is recognizably edible as to be ignored. This could be the case with *Arachnura*. At rest, with the legs in their cryptic posture, this spider is totally unlike an orb-web spider! Only when it moves does it betray its characteristic structures and its animate nature. Interestingly enough, *Arachnura* moves in a totally bizarre way (see below).

The spider responds to disturbances of the web by high intensity web-shaking. In addition to convulsive movements of the first 2 pairs of legs that produce violent agitations of the web, the spider see-saws back and forth, rocking about a point somewhere on the ventral cephalothorax. The tail of the spider moves up and down conspicuously, but the movement actually involves the whole body, of which the tail is a major part. This is quite different from pumping (Robinson & Robinson 1970a). FIG. 11, based on movie film, shows the extent of this rocking. The violent movements may serve to dislodge any predator that tries to approach across the web, and they certainly dislodge large unwanted prey that might otherwise prove dangerous. In defense, the spider also jumps off the hub and drops to the ground where it remains motionless for considerable periods before ascending its dragline to the hub again. We were not able to consistently evoke this response.

Movements involved in prey capture, approach to attack the prey, withdrawal to

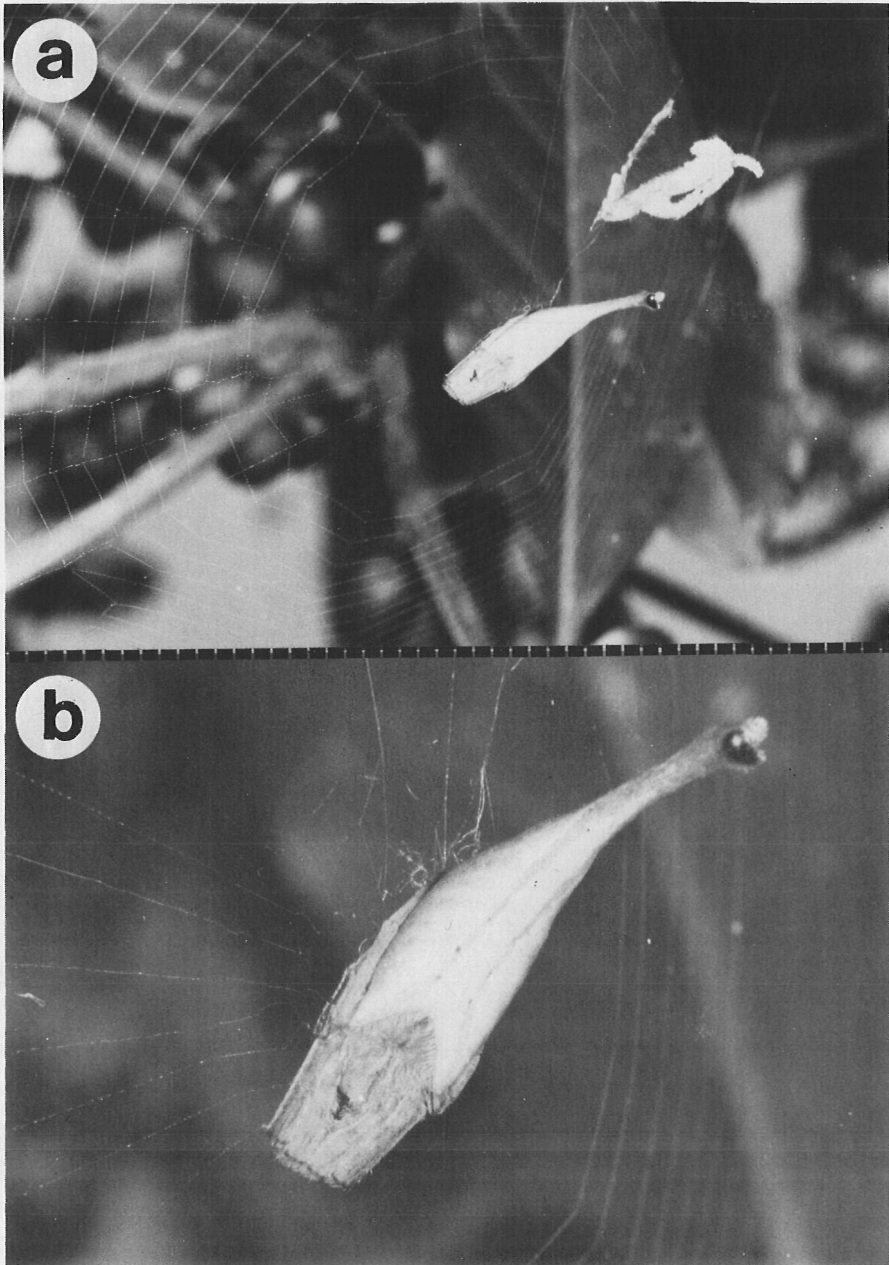


FIG. 10. *Arachmura melanura* ♀. a, cryptic posture of ♀ in her web; note the similarity in outline between the spider and the detritus on the 12 o'clock radius. b, close-up of the same spider showing how the legs are concealed by apposition to the body and/or each other (see text). The spider is ca 15 mm long.

the hub after a wrap/bite attack, and transportation of prey, often involve locomotion that has an end-to-end rocking component. The spider also makes this movement at the hub after resuming its normal predatory posture, or when feeding. The movement looks mechanical and unspiderlike; it could well be either intimidating or uninteresting to predators.

The tail can be curled to some extent and we saw the tail of 1 individual after being touched retract until only a small stump remained. McKeown (1963) suggests that curling the tail over the back is aggressive, and Mascord (1970) states that when the spider curls its tail it is not unlike a scorpion. (Scorpion mimicry, at first sight a somewhat fanciful suggestion, should not be dismissed, since scorpions of this size can have very fierce stings. They could thus be very powerful models for a mimicry situation.)

Prey

The only prey we found in sporadic observations on a number of webs in coffee bushes were bees, wasps and flies. The spider is diurnal and is probably exploiting the insects that fly in among the outer branches of trees and bushes. These must include plant-feeding homopterans, heteropterans, and their predators and parasites, as well as other insects (with folivorous larvae) on oviposition flights.

PREDATORY BEHAVIOR

A. melanura is an advanced araneid with regard to its predatory behavior [in the sense of Robinson (1975)]. It has all the basic components of predatory sequences seen in *Argiope* species (see Robinson 1975). Attacks are made on most insects by use of the wrap/bite attack couplet. Its wrapping behavior is awkward (see below) but rapid and includes silk-throwing and prey-rolling elements. Small prey (e.g., *Drosophila* sp., nematocerans, etc.) are simply seized in the jaws and pulled from the web. Moths and butterflies are bitten first (bite/clasp) and then are either simply pulled from the web, or wrapped first and then cut from the web. The spider interrupts predatory sequences, leaving the prey in situ and returning to complete the sequence after remaining at the hub for a variable period. This interruption of predatory sequences is not seen in genera that lack attack wrapping in their predatory repertoire (*Nephila*, *Herennia*, *Nephilengys*, *Micrathena*, *Gasteracantha*).

The spider's tail seems to impose some restrictions on its predatory activities, although we were not able to quantify this. The spinnerets are about $\frac{1}{4}$ to $\frac{1}{3}$ of the way to the apex of the abdomen, i.e., the tail lies behind them (see FIG. 10). In wrapping, the spider's 4th legs pick up swathes of silk and cast them onto the prey. During wrapping, the spider hangs on the undersurface of the web and the tail is strongly arched away from the web plane (FIG. 12). This posture presumably minimizes the encumbering effect of the tail. In throwing, which is used against large and vigorous prey, swathes of silk are cast over the insect from a distance, trapping it against the web plane. *Arachnura* throws mainly from a head-up position below the

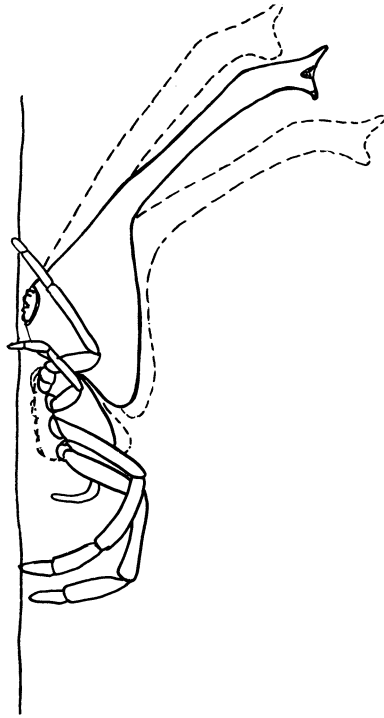


FIG. 11. The rocking movements of *Arachnura melanura*. The dotted outlines, based on stop motion analysis of movie film, delimit the extremes of movement seen in this case.

prey. Throwing passes imperceptibly into rolling as the spider moves closer to the prey. Rolling characterizes the later stages of wrapping as the prey package becomes free from entangling web elements and begins rotating in response to the wrapping movements of legs IV. This behavior is described in detail in Robinson & Olazarri (1971: 7-9, Fig. 4) for *Argiope argentata* and is virtually the same in the case of *A. melanura*.

Wrapping is followed by biting, after which the prey may be immediately removed from the web by a cutting-out process or (see above) the spider may interrupt the predatory sequence and retire to the hub for a variable period before cutting the prey from the web. The spider carries the prey packages back to the hub in its chelicerae or suspended on a silk thread. During any part of the predatory sequence the spider may make rocking or see-sawing movements, as noted above (defenses). The following verbatim field notes of an attack on a 68 mg grasshopper detail this point: "Down web to prey, tap prey with legs I, wrap 10-15 secs, roll 16-23 secs, bite 24-43 secs, wrap 44-48 secs, back to hub bouncing, prey left in situ, rock at hub, intermittently, down 3 min 10 secs bouncing, wrap briefly, cut out bouncing, cut

above, cut below, carry in jaws on dragline, 3 min 18 sec wrap at hub, head up, turn and hang bouncing, feed 3 min 30 secs."

Biting attacks on moths and butterflies clearly involve the bite/clasp behavior mentioned in the section on *Argiope ocyaloides*. This is shown in FIG. 12.

DISCUSSION AND CONCLUSION

The 3 araneids dealt with in this section show a range of features that can be regarded as specializations. *Herennia ornatissima* has both a specialized web and an excellent camouflage coloration. *Argiope ocyaloides* is unusual in its web siting and dull cryptic coloration compared with other members of this genus. *Arachnura melanura* is one of a very small group of tailed araneids that, as far as we know, includes only 9 species of *Arachnura* (Roewer 1942), *Cyclosa bifida* and the undetermined Neotropical araneid figured in Robinson (1970, Fig. 4). *C. bifida* is common at Wau and is truly tailed and entirely dark brown or black. When in a motionless state at the hub of its web, it looks like a small piece of broken twig. The whole range of tailed spiders can be regarded as specialized plant-part mimics. The morphological (and hence energy) investment in this kind of visual defense must be considerable. Perhaps the payoff is that it allows the spider to exploit highly exposed, but lucrative, web sites.

H. ornatissima has all the predatory behavior units found in related *Nephila* and *Nephilengys* species, but the detailed form of these units is clearly adapted to the specialized nature of its web, as described above. The fact that the adult female spider spends the hours of daylight tightly appressed to the hub-cup not only affects her readiness to attack prey, but has also affected the courtship behavior of the species. To copulate, the male must reach the ventral surface of the female abdomen which is normally pressed against the hub-cup. The male, in fact, has a typical *Nephila* courtship, but one in which he makes contact with the female's legs and dorsal surface until she stands erect and allows him to pass beneath her body (Robinson & Robinson, in press).

The degree of specialization found in *H. ornatissima* presumably evolved in a series of adaptive steps. We assume that the ancestral form was a generalized *Nephila*-like spider that built a more or less conventional (aerial) orb web and that lacked background-matching camouflage coloration. We can hypothesize some of the steps from this form to the *Herennia* situation. The first step may simply have involved building a relatively unmodified orb web with its upper edge attached to a tree and the remainder conventionally aerial. Once in this type of web site, the spider would gain protection from both predators and insolation by resting at an eccentric hub attached to the bark, preferably near a projection or underneath a side branch. Genetic fixation of these behaviors would be adaptive. This is exactly the situation now found in *Nephilengys* species. (It is noteworthy that these species-specific traits of *Nephilengys* constitute a preadaptation to the exploitation of web sites formed by human dwellings; webs that function well when extended from trees work extremely well when built from the overhangs of house roofs.) Once the spider was resting at the hub on

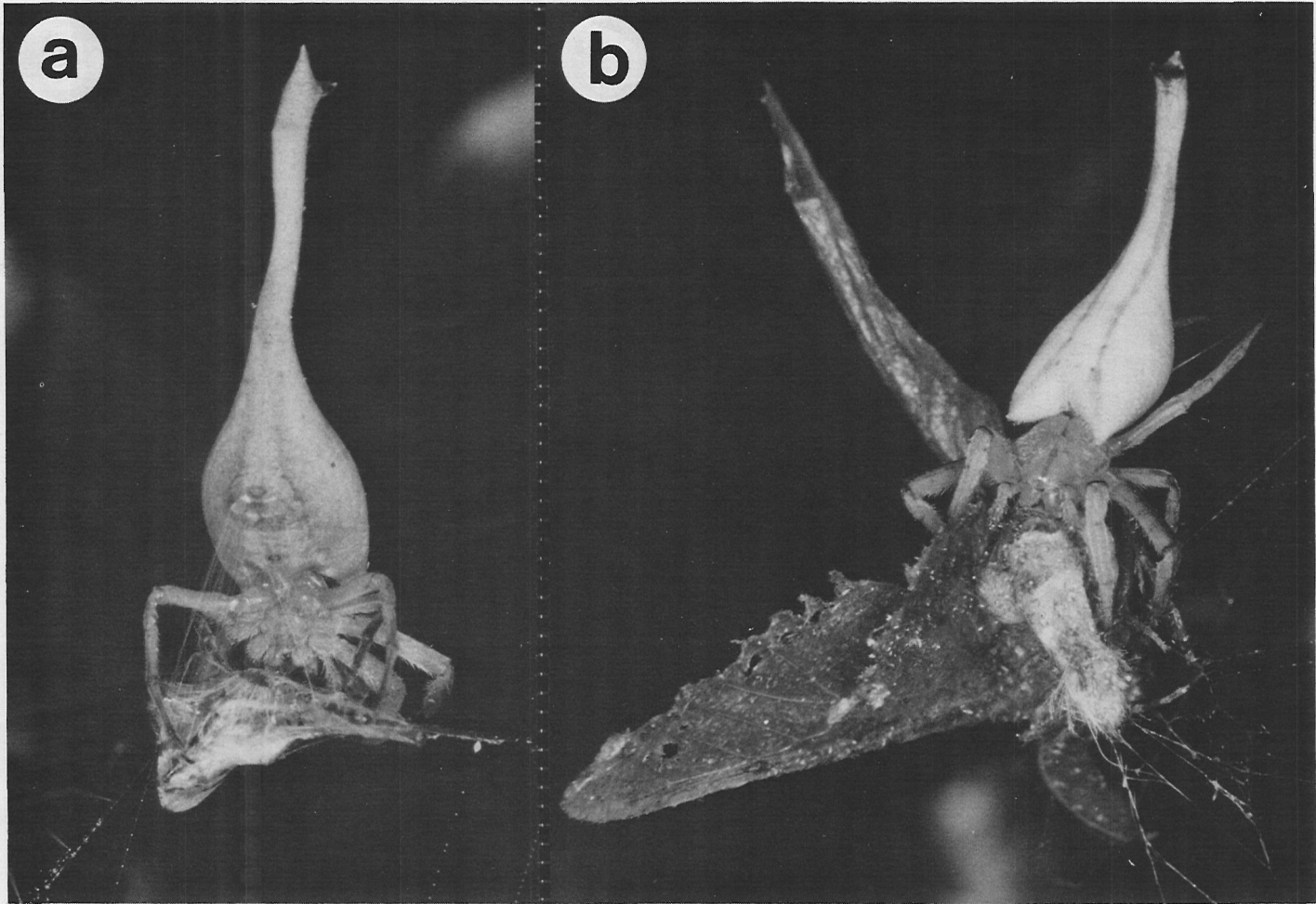


FIG. 12. Attack behaviors of *Arachmura melanura*. a, wrapping an orthopteran. Multi-strand silk is being moved onto the prey by the 4th legs and the extension of the tail beyond the spinnerets is clearly visible. b, a bite/clasp attack on a large moth. Note how the legs surround the prey.

the surface of a tree, selection would favor any steps to eucrypsis. The camouflage coloration could thus have evolved prior to the extreme specializations of ladder-web building. We have seen *Caerostris* spp., in Ghana and Malagassy Republic, that build aerial webs in tree crowns and that are beautifully cryptic (see also Edmunds 1974, plate 6d). Once the spider was building a ladder web close to the tree trunk, a thimble-shaped silk retreat like that of *Nephilengys* (Robinson & Robinson 1973a: Fig. 24) would be less advantageous and selection would favor any steps to its conversion to a hub-cup. If something like these steps were actually involved, then *Herennia* was primarily adapted to life on trees and these adaptations now enable it to live on rock faces and walls. It is not easy to read the tree trunk to rockface progression in reverse; if the spider evolved on rockfaces, it is difficult to see why the spider lost its orbicular web. *Argiope reinwardti* may provide an instance of the kind of flexibility in web-site utilization that could have a high potential for leading to specialization. The species builds a normal web on rockfaces, in herbage and on tree trunks (see Robinson et al. 1974: 124).

We have been fortunate to see a large number of *Argiope* species under natural conditions in all the major temperate and tropical faunal regions (MHR has seen at least 24 species and 2 species of *Gea*). From this experience, we feel that adaptive radiation within the genus has not led to any complex specializations of web structure or habitat preference. *Argiope ocyaloides* has probably the most narrowly specialized habitat of any species that has had its basic natural history described. It is the only species that we know that does not have either white to silver markings or strongly developed transverse bars on the dorsal surface of the abdomen. Its web structure is distinguished by the marked reduction in the density of the disc stabilimentum and the extreme rarity of linear stabilimenta. It is interesting to compare *A. ocyaloides* with *A. reinwardti*, since the latter can facultatively exploit the tree-trunk habitat. *A. reinwardti* has a strongly barred abdomen and builds dense, white, disc stabilimenta. Its linear stabilimenta are well developed and relatively common (Robinson, B., & M.H. Robinson 1974). Although the argument is now a posteriori, it is tempting to attribute the differences between the 2 species to the difference in the degree of web-site specialization.

The occurrence of 2 arboricolous araneids in Papua New Guinea is interesting. We know of no araneids occupying this niche in either the Neotropic, Nearctic or Ethiopian faunal regions. *Nephilengys cruentata* (in Africa and Asia) and *Nephilengys malabariensis* (Australia, Papua New Guinea) certainly build their webs very close to trees, often with a silken retreat beneath a side branch, but the larger orbs are usually 30 cm or more from the bark. These spiders may be exploiting many of the insects that alight on trees, but their niche is presumably broader than those of *H. ornatissima* and *Argiope ocyaloides*. *Nephilengys* is perhaps arboriphilic rather than arboricolous. Reptiles and amphibians may fill a niche closely similar to that of *Herennia* in the Neotropics, at least. In the Wau Valley, we know of no lizard feeding on insects on tree trunks, although there are certainly skinks in this niche at the coast. The arbo-

ricolous mantids and spiders (sparassids, salticids and thomisids) must be partly competitive with the 2 arboricolous araneids, but all are diurnal except the sparassids. The possession of an elongate web must greatly extend the area of prey detection of the araneids compared to these other predatory arboricolous arthropods. These studies suggest that it is impossible to understand one group within an ecosystem without knowledge of a diverse assemblage of other components. This may be a particularly important consideration in tropical studies.

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