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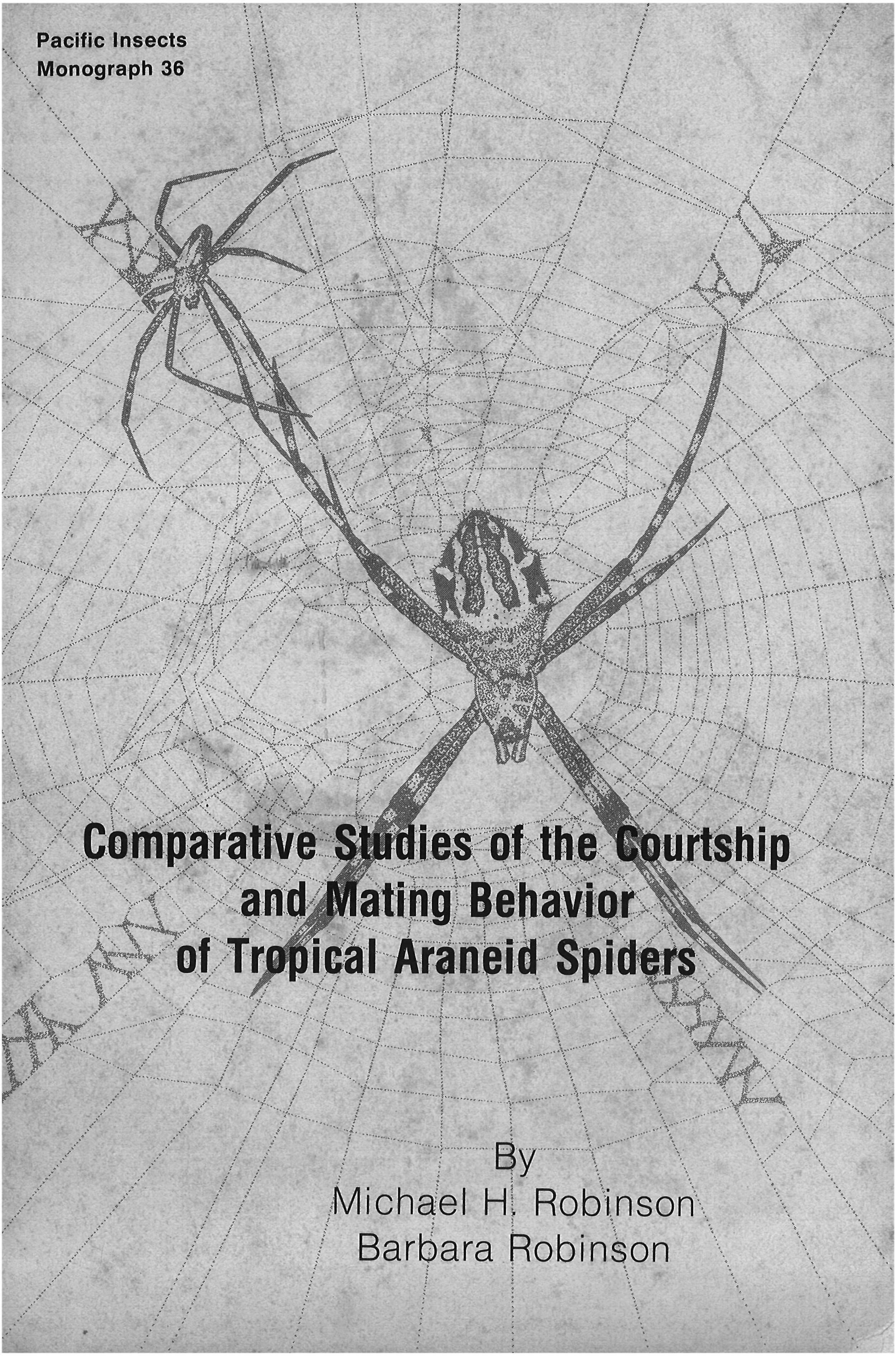

Comparative Studies of the Courtship and Mating Behavior of Tropical Araneid Spiders

By
Michael H. Robinson
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COMPARATIVE STUDIES OF THE COURTSHIP AND MATING BEHAVIOR OF TROPICAL ARANEID SPIDERS

By **Michael H. Robinson and Barbara Robinson**[1]

CONTENTS

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[1] Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama.

Abstract: The courtship and mating behavior of 53 species of orb-weaving spiders is described and illustrated. Fifteen genera are represented in the sample that was studied in 4 zoogeographic regions. Techniques of study and analysis are given alongside descriptions of the study areas. Following species-by-species descriptions, the results are compared and contrasted and the evolutionary and functional implications of the study are assessed in an extended discussion. A formal evolutionary scheme classifying the courtship behavior of araneid spiders is proposed in detail and correlated with other sources of evidence on the direction of evolutionary change within the family.

> One thing the early ethologists had in common was the wish to return to an inductive start, to observation and description of the enormous variety of animal behaviour repertoires and to the simple, though admittedly vague and general question: "Why do these animals behave as they do?" . . . We must hope that the descriptive phase is not going to come to a premature ending. . . . Contempt for simple observation is a lethal trait in any science, and certainly in a science as young as ours.
>
> —Niko Tinbergen (1959: 411–12)

Many of the early behavioral studies of spiders were concerned with courtship and mating. Fabre (1903) in Europe and the Peckhams (1890) and McCook (1889–1894) in the United States made pioneering observations on sexual behavior in spiders. Later, extensive studies involving spiders of many families were made by several major arachnological figures. Thus Bristowe (particularly 1926, 1929, 1930) and Gerhardt (papers between 1911 and 1933, see bibliography in Bonnet 1945: 362–63) covered a wide range of examples and arrived at broad generalizations about the nature and function of courtship activities in spiders. During this period a great many other scattered observations on spider courtship and mating were published. The studies at this stage were broadly comparative, but the weight of the comparisons was interfamilial. This is highly significant, since ethologists interested in the elucidation of behavioral evolution have repeatedly emphasized that this subject should be studied "mainly through comparison of groups of closely related species" (Tinbergen 1963: 428). In fact, intrafamilial comparisons that had a strong evolutionary bias did not really start until the studies of salticid courtship by Crane (1948a, b; 1949a, b).

We became interested in araneid courtship behavior as a result of our study of the general biology of *Nephila maculata* (Robinson & Robinson 1973, 1976a). When we saw the courtship of this species it became obvious that it did not conform to the extant generalizations about araneid courtship, and we then decided to study as wide a range of species and genera as was feasible. We have been engaged in this study, intermittently, since 1970 and have published a general summary of some of the major trends that we have discovered (Robinson & Robinson 1978a). In this paper we publish our detailed observations and examine the complexities of function, causation and evolution in the light of our results.

The use of behavioral traits, in comparative studies, to elucidate evolutionary trends involves the basic assumption that such traits are comparable to the morphological characters used by taxonomists in building phylogenies. Tinbergen (1959: 328) has commented on this point as follows: "Behaviour characters are in principle neither more nor less useful than morphological characters; they merely add characters to the total by which overall likeness is judged." However, he adds the caution (ibid.: 320) that it is specially important "when dealing with behaviour characters to investigate whether observed differences are genetically determined or merely reflect differences in environment." Separating environmental, ontogenetic and genetic influences on behavior is notoriously difficult. However, in choosing to study macrobehavioral aspects of courtship we have chosen a subject that is, in all probability, characterized by a very high degree of stability in terms of resistance to environmentally-induced modifications. Because spiders develop in discrete stages and mature at a distinctive molt, ontogenetic influences can at least be categorized. Most importantly, we were able to use virgins of both sexes during a substantial part of our investigations. When this was not possible (e.g., during the peripatetic stage of the study), we were able to use virgin males to "calibrate" or assess the behavior of those experimental males whose previous experience was unknown. This makes our study one of the very few broad field studies in which a large proportion of the subjects were naive (lacking prior experience) with respect to the principal behaviors under investigation. We return to the question of the nature of species-specific behavior in the Discussion.

A further problem that besets comparative studies is the difficulty of identifying the possible effects of convergence when interpreting the results. We feel that our basis for interpretative generalization is made more solid than is often the case by the size and scope of our sample. We studied over 50 species from 15 genera. In addition, these studies covered every tropical zoogeographic region, as well as some adjacent areas. We also brought to the study a background of knowledge of several other aspects of the behavior and ecology of many of the species involved.

Scope of the study

Our study was essentially a field study (see below) that concentrated on the broad behavior patterns involved in courtship across a wide spectrum of genera and species. Our main interest was in the detection of macrobehavioral differences and not in many of the other fascinating aspects of araneid courtship. Incidental to the main study, we gathered data on interactions between males during courtship and observed long-distance movements of males towards female webs, but we were in fact not studying competition between males nor female-finding by male araneids. Both these topics are important and largely unexplored aspects of araneid mating behavior and we hope our scattered observations on them will provide some insights for future workers in this field (see Discussion).

One of the main functions ascribed to courtship ceremonies in general is that of species identification (Morris 1956). Again, our study was not designed for the purpose of detecting fine-scale differences that might exist between closely related species. In areas where we studied a fairly large number of sympatric species within 1 genus, we were fortunate to find many cases of very striking differences. However, in species belonging to Group C, in which signalling is confined to vibratory movements of a mating thread, differences were much more difficult to detect with the techniques available to us (see below).

The most widely-asked question that we encounter from biologists aware of our interest in araneid courtship concerns the post-copulatory survival of males. During our study, we kept records of all cases of males being attacked and killed by females during or after courtship but attempted no large-scale quantification of risks. We can thus provide relatively crude estimates of the immediate hazards involved in different types of courtship. These could be the basis for selecting species suitable for a more systematic approach to this subject.

Kin-selection theory has developed rapidly in the last few years and has led to a widespread interest in the extent to which courtship and mating systems affect the parental (genetic) investment of a particular male. Clearly our extensive comparative data provide a good basis for speculation on this subject, but lack of basic information on the physiology of araneid reproduction prevents the formulation of firm conclusions at this stage (see Discussion).

MATERIALS AND METHODS

Methods of study

Our basic method was very simple indeed. We introduced males to females and watched the results. In reality, the process was far less simple than it sounds, since we had to find males that were ready to court and introduce them to females that were ready to be courted. Since males are often very small and frequently differ in color and shape from the adult female, matching pairs of the same species is not always easy, particularly (on a brief visit) when confronted with an unfamiliar spider fauna. Our methods for coping with these problems are described below. The nature of the preparations for courtship encounters differed according to whether we were working out of a semipermanent base or whether we were travelling and working out of hotels, motels and rest houses. At our 2 main study areas (Wau Ecology Institute, Papua New Guinea, and Smithsonian Tropical Research Institute, Panama), we studied courtship by using females in natural web-sites and supplemented these studies by using caged females. When travelling, all observations were made in the field.

Studies at Wau, Papua New Guinea

All our studies in Papua New Guinea were based at the Wau Ecology Institute (WEI), Morobe Province. The Wau Valley is rich in both species and numbers of araneid spiders. Because of its relatively aseasonal climatic regime (Robinson et al. 1974), it is an ideal place to conduct studies of courtship and mating, since adults of nearly all species are present in all months of the year. Our WEI house had an extensive garden consisting mainly of common local plants. For many of our studies we simply collected the species involved and released them in the garden, where they made webs in natural sites. Males collected elsewhere were placed on the web and we could watch the results with all our recording and cinematographic equipment within easy access. All except 2 species studied in Papua New Guinea occurred in the Wau Valley. These 2 species were collected near Port Moresby, transported to Wau for study, and maintained in cages.

The techniques that we have developed for the collection and maintenance of spiders in captivity are described in Robinson & Robinson (1975). In the course of our tropical studies, we also developed a number of techniques for the still and cine photography of spiders; these are described in the same paper and were extensively used in our courtship studies. Since slow-motion and frame-by-frame analysis of movie films reveals much that the unaided eye misses, we filmed all the species studied.

Studies in Panama

All studies in Panama were based at the Smithsonian Tropical Research Institute, Canal Zone. We used the same techniques that we used in Papua New Guinea, bringing spiders into the gardens and insectaries of residences at Barro Colorado I, Gamboa, Curundu and Arraijan.

Studies while travelling

When travelling we simply toured an area, looking for places with large populations of web-building spiders. When we found these, we sought accommodation nearby from which we could carry out intensive field studies. For peripatetic work of this kind, we streamlined our photographic equipment to bare essentials, as detailed in Robinson & Robinson (1975). The single item we found most useful was a polystyrene-foam icebox ('cooler'). This allowed us to carry films, cameras and living spiders without danger of their being overheated. Male spiders could be kept alive under the most difficult conditions if we had such an icebox, a water spray, and vials with cottonwool inserts in holes drilled through the stoppers.

Data recording

A major proportion of the study of each species was carried out as a team project. One of us watched the animals and gave a verbal commentary on the events, with time intervals, while the other made notes in longhand. When only one of us was present, we used a tape recorder for notetaking. We each acted as observer and notetaker randomly. The observer also acted as cinephotographer, since viewing spiders through a movie camera that is fitted for macrophotography is almost equivalent to the effect of birdwatching through binoculars. The notetaker acted as still photographer.

Special techniques

We have described the photographic techniques used in our spider studies elsewhere (Robinson & Robinson 1975). We developed almost all of these techniques in connection with the research on courtship and mating. We were confronted with a major technical obstacle in attempting to analyze the patterns of vibration set up by spiders in their courtship signalling. Attempts to measure vibrations in spiders' webs have all involved complex photoelectronic apparatus usable only in laboratory conditions and requiring that the subjects be insulated against vibrations from other sources (e.g., Krafft 1978). Such apparatus is clearly unsuitable for field use and, particularly, for peripatetic studies. Nor was detection of small-scale vibration patterns central to our aims (see above). We, therefore, restricted our attempts to analyze vibratory signalling to an analysis of the phasing of the movements involved. To do this we filmed courtship sequences and subjected the resultant movies to frame-by-frame analysis with a Kodak Ektagraphic MPS-8 projector; a variety of

Super 8 (mm) movie cameras was used for filming. When males are only a few millimetres long, as is the case with *Gasteracantha* species, it is impossible to achieve the necessary magnification without sacrificing depth of field. In practice, this means that movies of such tiny males are only intermittently in focus, as the slightest air movement is sufficient to move the long mating thread on which the male is operating. This is but one of the problems involved in attempting this kind of analysis.

Sample sizes

Our sample sizes varied considerably according to the availability of subjects. In the systematic account below, we make a special note if the description is based on less than 10 complete courtship sequences from 10 separate males. We include such designated cases based on small sample size only where the pattern revealed was distinct and interesting. On the other hand, we can think of no instance during our studies where the first-seen example of a courtship behavior proved exceptional in the light of further observations. Certainly, we frequently missed seeing some detail or other on first observation of several species, but never saw anything that later proved atypical.

With respect to mating itself, the problem of what constitutes a typical mating is less easy to resolve, since pseudomatings may occur. The criteria that we found helpful in resolving this are detailed below.

Finding spiders and matching pairs

In nearly all the species that we studied, adult males can be found associated with the webs of adult females at some stage in the seasonal cycle. Such males may be on the web itself, on foundation lines, the barrier web (if present), or on the remains of associated old webs. In addition, males may be found on vegetation near the web supports of a female's web or moving about nearby. Males thus in close proximity to a female may be in the preliminary stages of courtship, pausing between courtship bouts or apparently awaiting a period of sexual receptivity on the part of the female (see below). While males collected near the web are usually in a high state of sexual motivation and ready to court immediately if put on the web of a receptive female, this is not always the case. Such males are not identifiably naive and not necessarily the appropriate species. (We have seen a male *Nephila* approach a female *Argiope* across her web, remain at the hub for several minutes and then move off; more frequently, we have seen males of the appropriate genus but different species actually resting on females' webs, at the hub!) Males that consistently do not court when placed on a series of webs of female spiders will frequently do so after several days of isolation in vials. After establishing the identity of a male by obtaining a complete and successful courtship sequence, we were usually able to distinguish this species from others found in the area on the basis of some fairly conspicuous feature of coloration or shape. Having thus identified the males, we were able to search for immature individuals, raise them in captivity and obtain naive males. In a few species, we never found adult males in the wild and all our males were raised from immatures. In these cases, for example, the Wau *Gea* sp., we were able to use other cues to guess at the identity of the immature males. Cues such as web site, stabilimentum structure, web design, and the spider's defensive and predatory behaviors were all at one time or another useful, even when we knew the characteristic features of adult males. (It is noteworthy that at the final molt many male araneids actually become smaller and there is a radical change in coloration—see Robinson & Robinson 1976a, Robinson, B. & M. H. Robinson 1978). In addition to problems of matching males with females, there are problems involved in finding receptive females and, in fact, deciding whether females are adult or not. Females of several araneid species (and probably the majority, although only 5 species have been studied so far) can mature over a range of instars producing adults of conspicuously different sizes. The presence of males on the web is not an indication of maturity, since adult males will live on the webs of immature females (see below) in most of the subfamily Nephilinae. Eventually one learns to recognize the typical (larger) females, but only trial and error "introductions" can lead to the discovery of the subnormal mature females. Unreceptive females are not easy to identify without patience, since the first responses of even a receptive female may be indistinguishable from predatory responses. Again, patient trial and error is the only ultimate solution. Females that are known to have produced recent egg cocoons seem to be more ready to mate than others, but this view is entirely intuitive on our part: the reproductive physiology of araneids, particularly those tropical forms that we studied, remains a virtually unknown field. We have a similarly intuitive feeling that spraying the webs of females with water is stimulatory to both sexes. Certainly feeding the female will induce male approaches in those species where courtship may be opportunistic (see below).

The spiders

The spiders that we worked with are not all identified to species. We have been faced with the problem that confronts almost all tropical biologists: that is, taxonomists with specialist knowledge for certain groups and/or regions do not exist. They are not even being trained. To complicate matters, type specimens are widely scattered, frequently in museums of European (ex-colonial-power) countries, and the literature is fragmentary and difficult for the nonspecialist. Ultimately, the neglect of taxonomy in the major scientific centers of the world will almost certainly bring advances in field biology to a grinding halt. At present, in many areas we are not merely failing to advance taxonomic studies but utterly failing to keep up with past work. We were extremely fortunate to have the help of Professor H. W. Levi (Museum of Comparative Zoology, Harvard University) in determining our New World material and the late Fr. Chrysanthus in determining the Papua New Guinea material. For the other regions we have been helped by several people (see Acknowledgments), but many identifications are tentative and provisional; these are so designated in the species-by-species account. Where a species identification is absent, we have used a

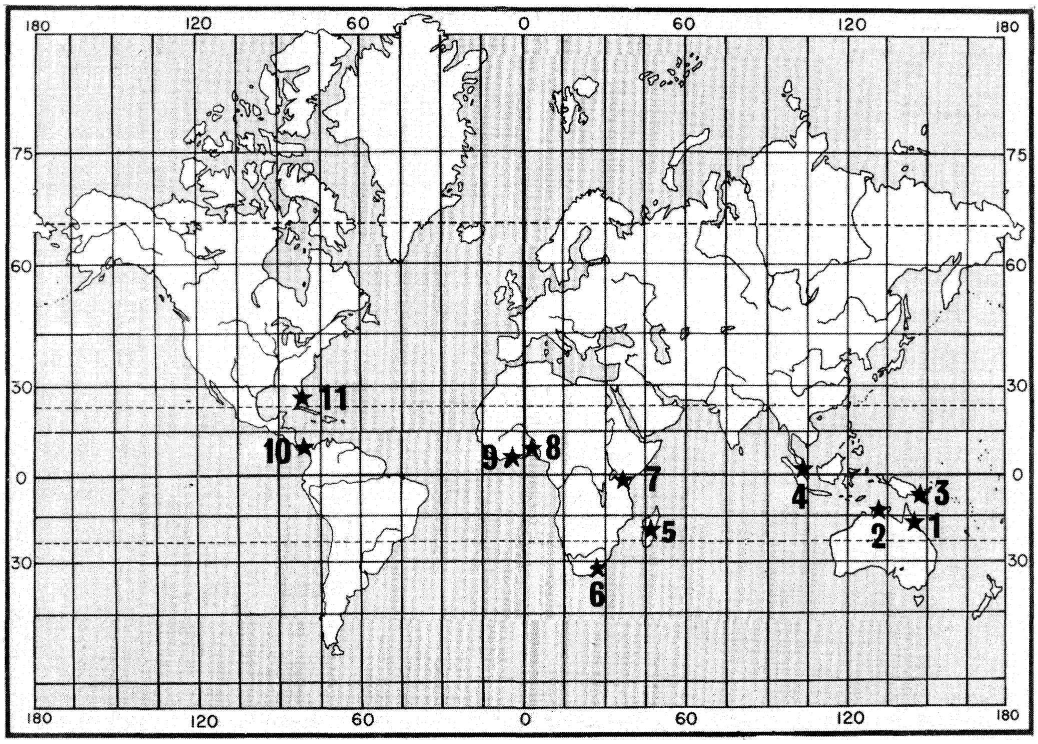

FIG. 1. Map showing approximate geographic location of the study areas. The species studied at each numbered location are listed in TABLE 1.

code name. Specimens of all species that we studied are in our collection or have been deposited in the Museum of Comparative Zoology, Harvard University, USA, and the Australian Museum, Sydney, Australia.

The study localities

FIG. 1 shows the approximate geographic location of our study areas throughout the world and TABLE 1 lists the species studied at each area. The known ranges for all the identified species are obtainable from both Roewer (1942) and the various volumes of Bonnet (1945–1961). We here give an expanded description of the study areas in the hope that this may be of some value to future workers in this field. The degradation of habitats is proceeding so rapidly in all the tropical countries that we visited that this information may only be of ephemeral value; we hope not.

Africa. In West Africa we worked in Ghana and Nigeria. In Ghana the campus of the University of Ghana, at Legon, proved to have a rich araneid fauna, and areas of uncut grass around the buildings as well as the arboretum were good study areas. *Nephilengys cruentata* was studied in the buildings of the departments of Zoology and Botany, where it is a highly successful commensal of man. The plain north of Legon

TABLE 1. Species studied at each numbered location. See FIG. 1.

1. Queensland, Australia
    - *Nephila edulis* (Labillardière)
    - *Argiope aetheria* (Walckenaer)
2. Darwin, Northern Territory, Australia
    - *Argiope* sp. N.T. riverine
3. Papua New Guinea
    - *Herennia ornatissima* (Doleschall)
    - *Nephila maculata* (Fabricius)
    - *Nephilengys malabarensis* (Walckenaer)
    - *Argiope aemula* (Walckenaer)
    - *Argiope reinwardti* (Doleschall)
    - *Argiope picta* Koch L.
    - *Argiope aetheria* (Walckenaer)
    - *Argiope* sp. Wau no. 5
    - *Argiope ocyaloides* Koch L.
    - *Gea* sp. Wau no. 1
    - *Gasteracantha taeniata* (Walckenaer)
    - *Gasteracantha theisi* Guérin
    - *Gasteracantha brevispina* (Doleschall)
    - *Gasteracantha* sp. Wau no. 1
    - *Gasteracantha* sp. Wau white
    - *Zilla* sp. Wau no. 1
    - *Zilla* sp. Wau no. 2
    - *Cyclosa insulana* (Costa)
    - *Cyclosa* sp. Mt Kaindi no. 1
    - *Cyclosa* sp. alpine grassland no. 1
    - *Cyclosa bifida* (Doleschall)
    - *Cyclosa* sp. Wau no. 5
4. Singapore
    - *Argiope* sp. Singapore no. 1
    - *Gasteracantha* sp. Singapore
5. Malagasy Republic
    - *Nephila madagascariensis* (Vinson)
6. Natal, Republic of South Africa
    - *Argiope aurocincta* Pocock
    - *Argiope cuspidata* Thorell
    - *Gasteracantha versicolor* (Walckenaer)
    - *Isoxya tabulata* (Thorell)
7. Kenya
    - *Gasteracantha falcicornis* Butler
    - *Isoxya cicatrosa* C. L. Koch
8. Nigeria
    - *Nephila pilipes* (Fabricius)
    - *Nephilengys cruentata* (Fabricius)
    - *Argiope flavipalpis* (Lucas)
    - *Gasteracantha curvispina* Guérin
    - *Aetrocantha falkensteini* Karsch
9. Ghana
    - *Nephilengys cruentata* (Fabricius)
    - *Argiope flavipalpis* (Lucas)
10. Panama
    - *Nephila clavipes* (Linnaeus)
    - *Argiope argentata* (Fabricius)
    - *Argiope savignyi* Levi
    - *Gasteracantha cancriformis* (Linnaeus)
    - *Micrathena sexspinosa* (Hahn)
    - *Micrathena schreibersi* (Perty)
    - *Micrathena clypeata* (Walckenaer)
    - *Micrathena duodecimspinosa* (O.P.-Cambridge)
    - *Cyrtophora nympha* Simon
    - *Mecynogea lemniscata* (Walckenaer)
    - *Eriophora fuliginea* (C. L. Koch)
    - *Cyclosa caroli* (Hentz)
    - *Mangora bimaculata* (O.P.-Cambridge)
11. Florida, USA
    - *Argiope aurantia* (Lucas)
    - *Argiope florida* Chamberlain & Ivie
    - *Micrathena sagittata* (Walckenaer)

(as far as the escarpment) is spider-rich at some times of the year. We also worked at the Cocoa Research Insititue at Tafo, where the local practice of planting cocoa in thinned forest provides a very rich environment. In Nigeria we worked at the research center of the International Institute of Tropical Agriculture, just outside Ibadan. There, an extensive research area of forest, secondary growth, and agricultural plots provided an ideal study area. In eastern Africa we worked in Kenya and we found that the Nairobi City Park was rich in spiders at a time when the surrounding country was suffering drought and desiccation. We worked there for some time until we were attacked by a gang of armed robbers who stole our exposed research film (as well as all our airtickets, money and passports, etc.). After this incident we carried out studies on the shores of Lake Naivasha (Rift Valley) and on the Kenya coast, north (Malindi) and south of Mombasa. In the Republic of South Africa we worked in the province of Natal at Umdoni Park, on the coast south of Durban, and around the campus of Pietermaritzburg. In Zululand we carried out studies in relict forest close to the St Lucia estuary.

In the Malagassy Republic we found *Nephila madagascariensis* in parks and gardens throughout the capital city, Tananarive, particularly at the national Parque Zoologique (which is a wonderful area for finding a variety of araneids). We also found this species and *Nephilengys cruentata* in the forest at Perinet.

Australia. Our studies in Australia were confined to Northern Territory, working out of Darwin, and Queensland, working out of Cairns. When we visited Darwin it was extreme dry season and the only spiders were in coastal mangroves, around springs and in the lush river valleys that cross the desertic landscape. We drove 113 km south along the Darwin to Alice Springs road and searched every river that the road intersected; at Robin Falls we found an abundance of spiders along the river some 100 m from the road. In Queensland, MHR found spiders on the edge of canefields on the main coast road south of Cairns and in parklands on the Atherton tablelands near Mareeba, as well as at Mossman, Atherton, Mt Molloy, and Fishery Falls.

Asia. We worked on the island of Singapore, at the Raffles Botanic Gardens, Cluny Rd, at Bukit Timah, and in the forest around the MacRitchie Reservoir of the Singapore City Council.

Papua New Guinea. As mentioned earlier, all our studies were based at Wau Ecology Institute in the Wau Valley, Morobe Province. We collected spiders from many localities in the Wau Valley, but principally from the slopes of Mt Kaindi between WEI and Blue Point. The many coffee plantations in the valley have abundant spider populations (see, for instance, Robinson & Robinson 1974a). We found a species of *Cyclosa* close to the summit of Mt Kaindi and along 1.5 km of the Bulldog Road. Another species of *Cyclosa* was found in the grasslands beyond Kaisenek, south of Wau. Two of the species that we studied seemed entirely restricted to the MacAdam Memorial Park, Wau. We collected 2 araneid species when working out of Port Moresby; one at the University of Papua New Guinea campus and botanic gardens and the other in coastal mangroves flanking the road to Rigo, southeast of Port Moresby; this area is designated Bootless Point, Port Moresby.

Panama. All the species that we studied in Panama are widely distributed and seasonally abundant in the highly forested area of the Canal Zone. In particular, the *Micrathena* species are almost exclusively confined to forest, and Panama is particularly rich in species of this genus (Chickering 1961). Most of the species are present along the Gamboa Pipeline Road. It is hoped that present plans for a nature reserve in this area can be realized when the land reverts to the Republic of Panama.[2] In addition to the Gamboa Pipeline Road, the Canal Zone Forest Preserve, particularly

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[2] Written before the land reverted to Panama in October 1979.

at Green Park and the Las Cruces Trail, was an important locality. We also collected spiders for study from the Madden Boy Scout Camp area (Camp Chagres) and the road to the Federal Aviation Agency at Cerro Galera, Canal Zone. In the Republic of Panama we collected at the Fortuna damsite (in Chiriqui Province) and from areas around the Bayano Lake, particularly from the El Llano-Carti Road.

United States. We worked out of the Archbold Biological Station, Lake Placid, Florida, approximately within a 16-km radius of the station.

Terminology

As pointed out in our treatment of the mating behavior of *Nephila maculata,* there is considerable divergence in the usage of the words *courtship* and *mating,* not only among arachnologists but among biologists in general (Robinson & Robinson 1973: 34). We have chosen here to regard courtship as the sequence of more or less complex behavioral interactions that occur between male and female prior to copulation or copulation attempts. We regard the term mating as applicable both to the state induced by successful courtship and to the act of insemination. Both these usages are fraught with problems but do less offense to current usage and have fewer proscriptive problems, in our view, than the alternatives that we have seen. Clearly courtship does not always lead to copulation or copulation attempts. A female spider often responds to the male by simple predation and, although he may persist in courtship attempts for some time, he is eventually driven off or killed without even attempting to copulate. We can cover these exceptions by calling them unsuccessful courtships. When a female responds favorably to the male and permits copulation attempts but the male, for some reason, is unsuccessful, our definition of mating becomes stressed. If mating is regarded as synonymous with copulation, the attempt that failed is unsuccessful mating. On the other hand, the spiders are mated in the sense that they have paired to the extent that copulation attempts are being made (and permitted). In fact, in some cases the pair may remain together for a considerable time during which intermittent copulation attempts can be made and these may eventually be successful. Such protracted copulation attempts could be regarded as functioning as the final stages of courtship. It is perhaps simplest to ignore such complications at this stage, since we attempt to resolve them in our final discussion of the function of courtship. Perusal of the spider courtship literature shows that terminological complexities are not only unresolved but are largely unrecognized by many authors (see discussion in Robinson & Robinson 1973: 34).

We use the terms *mating thread* and *copulation thread* interchangeably for structures built by male spiders that are attached onto or built into the webs of the female spiders. These threads are used to transmit vibratory signals to the female and on them, following successful courtship, copulation or copulation attempts occur. We define *acceptance posture* as any position assumed by a female spider, in response to courtship, that signals and/or facilitates the onset of copulation attempts. Acceptance postures may be assumed at the hub of the female's web or on a mating thread.

Mating threads may consist entirely of male silk or may be composite structures of male and female silk in those cases where the male lays down his thread on top of a female's web element. Mating threads are usually laid down in several movements from origin to insertion, and although they appear to be single strands they may actually consist of several successive elements.

A number of movements used by males during courtship are currently without a descriptive terminology. Of these, the most ubiquitous is a movement in which one tarsus is moved over the surface of another like a bow being moved over a stringed musical instrument. This movement is frequently unilateral and almost always involves legs I and II. Examination of film records shows that although one tarsus is usually held still while the other is moved against it, this is not always the case and complex compound movements occur. We call movements of one leg against another *tarsal rubbing* irrespective of whether the movement is made by only one or by both of the legs involved. Throughout this paper we use the abbreviation TR and its derivative TRing as a simple convenience. Since many movements involved in courtship are leg movements, we here designate a simple code of abbreviations for legs, based on Roman numerals and capital letters. Thus we number the legs from anterior to posterior as I, II, III, and IV, and use L and R to signify anatomical left and right. Since spiders direct legs I and II forwards and legs III and IV posteriorly, we refer to anterior leg pairs and posterior leg pairs, meaning both legs I and II, and legs III and IV, respectively. When the tarsi of 2 legs meet side by side on a thread we call this *looping.* We use the term *tapping* to describe leg movements in which the tarsus is lifted conspicuously off a surface (mating thread or female body) and brought down again, often repeatedly. *Stroking* differs from tapping in that the tarsus is moved along the surface that it contacts, lifted off and then again moved into sliding contact with the surface. *Twanging* is here used to refer to a movement on mating threads in which the thread is rapidly tensioned and then the tension is suddenly released. *Tugging* is slow-motion twanging, i.e., the release of tension is not sudden. *Bouncing* movements are those in which the body of the spider moves up and down on a line or the web due to alternate flexions and relaxations of all the legs in contact with the line. *Bobbing* is low intensity bouncing. *Juddering* refers to a feverish on-the-spot shaking of the entire body of the spider. We use the word *bowing* to describe any leg movement that is made against a surface in the manner of a violin bow against the strings of the instrument. *Scrabbling* is used to refer to movements made by males, particularly of *Argiope* species. The movements may be of the pedipalps against the ventral abdominal region of the female in the region of the epigyne. The movement is made with the embolus of the male pedipalp reflexed posteriorly; in this attitude the bulbous part of the pedipalp contacts the female but the backward-pointing embolus could contact protrusions from the surface of the abdomen. In scrabbling, the male pedipalps may be moved independently in scrubbing fashion but the male may also move the body back and forth. We also refer to clawing movements of the legs against a surface as scrabbling. *Rapping* is used to describe up and down movements of the pedipalps against the epigynal region. The movements are crudely analogous to the movement of a clenched fist knocking on a door. In rapping, the embolus is reflexed backwards, except immediately prior to insertion attempts.

Some movements appear to be movements of the male body even though they are based on leg movements. These include bouncing, in which the body is moved vigorously up and down. Bouncing may occur on the spot during movements on the web of the female spider or on a mating thread. Bouncing on mating threads may be so vigorous that the male actually "loops the loop" around the thread. Bouncing can be coupled with locomotion in a *bouncing gait*. *Shaking* is an oriented vigorous flexion of the web that is very similar to (if not identical with) the movements given by araneids to intruders moving across the web surface (see descriptions in Lubin 1973, and Buskirk 1975). *Jerking* and *plucking* involve essentially similar movements but are of lower amplitude.

Males may move the abdomen up and down from the waist joint (pedicel); we call this movement *abdomen wagging,* abbreviated as AW and AWing. Since the apex of the abdomen is always attached to a substrate by the dragline, AWing may transmit vibrations to the substrate.

Spiders of groups A and B may spend long periods at the hub of the female's web indulging in a variety of courtship or courtship-related behaviors. We refer to the side of the hub on which the female rests as the lower side and the opposite side as the upper. Movement to below means movement onto the lower side. A common behavior at the hub is a bout of perambulation in which intermittent contact may or may not be made with the female. We discovered this phenomenon when we were in New Guinea and *walkabout* seemed an appropriate descriptive term (Oxford English Dictionary: "aboriginal pidgin"; a period of wandering). During a walkabout, if the male is on the upper surface of the hub, it may touch the female through the web.

In describing the orientation of mating threads, we always refer to the point nearest to the web, or the hub of the web if it is built within the web, as the *insertion* and the farthest point as the *origin.* In this usage we ignore the question of where the spider started to install the thread.

In our description of the courtship and mating behavior of *Nephila maculata* (Robinson & Robinson 1973: 43), we described mating that occurred without prior courtship, in circumstances when the female was otherwise occupied (molting or feeding), as "opportunistic." Since this form of mating occurs in at least 2 genera, we feel that the general term *opportunistic mating* can be applied to all cases where courtship is omitted as an antecedent to mating.

In referring to the structures that comprise an orb web, we have used British and U.S. terminology interchangeably. Robinson & Olazarri (1971: fig. 2) provide a concordance for these separate usages. Since mating threads are often attached to silk lines that support the web from nearby vegetation, such threads need designation. We have throughout used the terms *bridge thread* and *upper foundation thread* to indicate the entire length of silk that is the upper element of the web and spans from web support to web support, i.e., the silk extends beyond the frame of the web.

All species of *Argiope* and *Gea* rest by day in a posture in which legs I & II, and III & IV on each side are tightly apposed, side by side and held so that the 4 pairs form a St Andrews Cross. We refer to this resting posture as a *cross posture* or an *X posture.*

BASIC PATTERNS OF COURTSHIP

The species-by-species account that follows is arranged not by subfamilial categories within the Araneidae, but by the basic categories of courtship that were revealed by our studies (Robinson & Robinson 1978a). This gives an ordering of examples that facilitates functional and evolutionary interpretation, and this seems to us more useful than any other system of arrangement. We deal with topics that are incidental to the main theme (sperm induction, sexual dimorphism, differential longevity of the sexes, competition between males, and so on) after the main presentation.

We recognize 3 major patterns within araneid courtship. These are based on several factors as outlined in our previous summary paper (Robinson & Robinson 1978a), and shown in FIG. 2. Type A courtship (FIG. 2a) is conducted entirely at the hub of the female's web, involves a very considerable (but variable between species) amount of direct contact between the sexes prior to mating and has the least complex behavioral responses on the part of the female. A mating thread is not involved and mating takes place either at the hub of the web or its functional equivalent.

Type B courtship (FIG. 2b) takes place on the female's web and commences at the hub with a period of direct contact between the sexes. The male then cuts a hole in the web close to the hub, inserts a mating thread and conducts vibratory courtship on this thread. The overt female response is fairly complex; she moves a short distance from the hub onto the mating thread where she assumes an acceptance posture. Mating occurs on the thread, which is within the web boundaries but is a structure of the male spider.

Type C courtship (FIG. 2c) takes place with the male remaining outside the female's web and no contact courtship occurs prior to the assumption of an acceptance posture by the female. The male constructs a mating thread outside the female's web on which he conducts complex vibratory courtship. The female moves across her entire web and out onto the mating thread, where mating occurs.

Courtship can thus be categorized by where it occurs (hub, within the female's web, outside the web), by the principal sensory modality assumed to be involved (contact tactile stimulation, vibratory stimulation), by the presence or absence of a mating thread, and by the complexity of the overt female response (slight movement, complex movements).

MATING

There have been numerous attempts at classifying the copulatory postures of spiders. These may be of value for interfamilial comparisons but are of little relevance

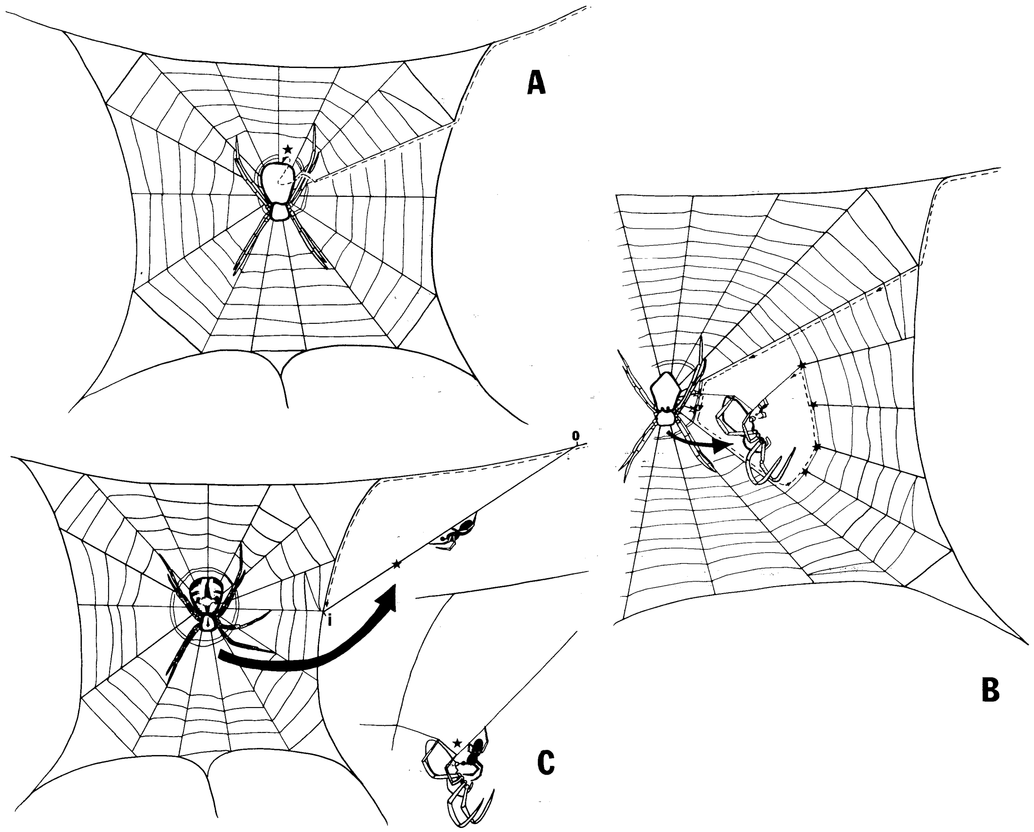

FIG. 2. Diagrammatic representations of courtship types. **A,** type A courtship: the ♂ approaches the ♀ at the hub and courts there; copulation occurs at the hub (see text); star indicates locus of copulation. **B,** type B courtship: after contact courtship the ♂ cuts a hole in the ♀ web and across it installs a mating thread, on which he conducts vibratory courtship; copulation occurs on the mating thread; the stars represent the points at which the ♂ cuts the radii to make the hole. **C,** type C courtship: the ♂ constructs a mating thread (o = point of origin, i = point of insertion) outside the web, on which he conducts vibratory courtship; copulation is initiated on the mating thread; the star represents locus of copulation on mating thread.

to our study. Montgomery (1903: 129–30) details "The mode of embrace in copulation" in at least 6 principal postures, with numerous subdivisions. Forster (1967: 42, Figs. 73–78) gives good descriptions and illustrations of a modern consensus on copulatory postures. All the postures that we have seen are classifiable into 2 basic types that are causally related. Thus, the predominant araneid posture is "mating position 3"; the postures found in *Argiope* species are simple modifications of this. Two *Micrathena* species that we studied adopt "mating position 1" (Forster, ibid.: Fig. 73).

The problem of deciding whether sperm transfer has taken place after a pedipalpal insertion is a difficult one. Swellings of the haematodocha are a guide but extremely difficult to see in most cases.[3] Ultimately the most critical test is that involving examination of the male's pedipalps before and after the presumed mating. We were seldom able to make such a test during our field studies. This may mean that some of the copulations that we recorded were in fact pseudocopulations that involved insertion but no sperm transfer. In some cases we were able to note that a spider with glistening sperm-charged pedipalps would insert one embolus and then emerge from a copulation with that pedipalp markedly changed in color. We think that such cases and our occasional observations of haematodochal pulsations allow us to equate insertion durations with mating durations over a fairly wide range of species. In the Discussion we raise the whole question of the problems created by our present ignorance of the physiology of reproduction in araneid spiders. This ignorance seriously affects our ability to assess the adaptive significance of several important aspects of courtship and mating behavior in araneids.

FORMAL ARRANGEMENT OF SPECIES-BY-SPECIES ACCOUNT

Since the descriptive section is long and complex, we preface each group of descriptions with a general introduction. This deals with overall features of the courtship in the genera and species involved and also details any general trends in the reproductive biology of subgroups within the group under consideration. Although we have tried to maintain a purely descriptive quality in this section, some interpretive remarks have inevitably crept into it; we hope that these contribute to understanding and clarity even though they anticipate the Discussion. We regard the large number of photographic illustrations as being virtually archival, since so many of the species that we studied live in habitats that are, unfortunately, under threat.

We have included a number of summary diagrams that illustrate the parallel behaviors of males and females of a given species in a representative courtship bout. These are not conventional ethograms and are included as an indication of com-

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[3] Since we completed the major part of this study (and wrote the above), we have been fortunate enough to return to Papua New Guinea for further research. There we were able to use the technique devised by Robinson & Smythe (1976) to observe spider copulations, in the field, through a specially mounted 20-power binocular microscope. This technique can only be used for species that copulate at a predictable location that is relatively stable, and is really feasible only for those species where the males are relatively small and copulation lasts for more than half a minute. These restrictions occur because at high magnification depth of focus is small and a stable base for the microscope cannot be set up in advance (in time) if copulation is brief or unpredictable in location. Similarly, when males are small relative to females, there is no danger of the field of view, centered on the pedipalps, being obscured by the body of the male. In the list of species that we studied, only those of group A and the *Gasteracantha* species can be studied in copula by this technique. The *Gasteracantha* spp. can be studied in this way because after copulation is started the female returns to the hub of her web carrying the male in copula. At the hub of the web a previously focussed microscope can be used to observe the copulation in fine detail. We have now used this technique to watch copulations in *Nephila maculata, Gasteracantha theisi* and *G. taeniata.* We have added brief notes to the more important new details revealed by these ongoing studies to the appropriate sections below. We intend to publish further details when the study is complete.

plexity. We have a major unsolved problem in defining what constitutes a typical courtship bout. The duration and sequential occurrence of the various elements is often very variable within the species. Morris (1956) discusses the problems involved in characterizing displays as "typical." We have simply used examples that involve all the behavioral elements that we have seen in the courtship of a particular species that, in our judgement, are part of normal courtship. We, therefore, speak of representative courtship rather than typical courtship.

Within each group, the genera and species are arranged either in a line of evolutionary progression, where we think that this is reasonably clear, or by the geographical localities in which the study occurred. When the species are arranged in an evolutionary progression, we place primitive species (by our assessment) first.

COURTSHIP AND MATING BEHAVIOR: GROUP A

Four genera are represented in this group: *Herennia, Nephila, Nephilengys,* and *Argiope.* Since some species of *Argiope* belong to this group while others belong to group B, we treat the descriptions of the *Argiope* species last, although they appear before the others in Roewer (1942). The status of *Nephilengys* is uncertain; Bonnet (1958) regards it as a synonym of *Nephila,* as do many recent taxonomists (H. W. Levi, pers. commun.). Our own view is that the species that we studied differ markedly in web structure, web siting, and ecology from all the *Nephila* species known to us (see Robinson & Robinson 1973: 52).

All the species in this group are large, with adult females ranging from ca 2 cm to 6 cm in length. All have marked sexual dimorphism in size. The spiders belonging to the subfamily Nephilinae (of Roewer 1942) are characterized by a tendency for males to accumulate on the webs of females before the latter reach sexual maturity, and those species that have been studied show intrasexual polymorphism in size (Bonnet 1929; Robinson & Robinson 1976a; Robinson & Robinson, unpubl.). Web sites vary from open sites for large aerial webs (*Nephila* spp.) to tree-supported aerial webs (*Nephilengys* spp.) and tree trunks and rockfaces (*Herennia* spp.). Courtship in all the nephilinids is characterized by frequent approaches down the ventral face of the female's abdomen to the epigyne, and frequent bouts of alternating insertions. Overt responses of females are minimal except in the case of *Herennia ornatissima.*

As noted above, males of all the *Nephila* and *Argiope* species that we studied accumulate on the webs of the females, often resting on the web proper and not merely on the frames. In the case of *Nephila, Nephilengys* and some *Argiope* spp., males may move onto the webs of immature females and live there for several weeks, effectively awaiting the maturation of the female. We think that this could usefully be called the *suitor phenomenon.* The males live kleptoparasitically (or commensally) on the females. The fact that we recorded this phenomenon in only some of the *Argiope* spp. does not mean that it does not occur in the others. In order to be sure that the males were on the web of an immature female, we had either to know the minimum size at maturity or see males on the web of a female that we saw molt at a later stage. When there is marked intrasexual polymorphism in size and life history details and these have not been determined (as is the case for all the *Argiope* spp. except 2), evidence other than from the molt itself is little better than suggestive. We believe that the suitor phenomenon may be widespread in spiders and would predict that it could well occur wherever males mature in a short time relative to females and the females are essentially nonvagrant. It could thus occur in trap-builders of several families and also in sedentary nonweb-builders. Our use of medieval terminology to describe this phenomenon is not without precedent. McCook (1890: 18) noted that males begin "their solicitations even before there is a reasonable hope for a favorable response," referring to "several gallants" waiting "in the outer courts of the habitation of the female."

When males of *Argiope* are waiting on the webs of females, they typically assume the normal diurnal predatory posture of the species. *Argiope* spp. males and females rest with their 8 legs arranged in 4 units in the form of a St Andrew's cross. Legs I and II, and III and IV, on each side, are closely apposed in pairs. For convenience, we refer to this simply as the *"X" posture.* The spaces between the pairs of legs form vees, and we use this term (topographically) to describe the position of the male during approaches to the female. Thus we refer to the right V, or posterior V, and so on.

All the *Argiope* spp. in this group build aerial webs in the herb layer and all, with the exception of *A. aurantia,* build cruciform linear stabilimenta. Sexual dimorphism in size is considerable and all exhibit more complex courtship than any of the nephilinids except *Nephila maculata.* Overt female responses to courtship are more complicated than in any of the species of *Nephila* and involve the adoption of postures at the hub that appear to facilitate the insertion attempts of the male and his movements onto the body of the female.

Male copulatory postures in all the nephilinids (except *N. pilipes*) are simple. The male stands erect on the female's abdomen, facing downwards. Copulatory postures in most *Argiope* spp. are adopted after a sideways twisting movement and the male becomes tightly appressed to the female's abdomen, venter to venter, but lying at an angle to the female's long axis. Insertions in *Argiope* species are always separated by violent withdrawal of the male from the female and an intervening recourtship (often perfunctory).

Subfamily NEPHILINAE

Herennia ornatissima (Doleschall) FIG. 3–4

Robinson & Robinson (1973: 52, Fig. 25) give a brief description of the web, appearance and predatory behavior of this specialized arboricolous species, while Robinson & Lubin (1979) give a more extensive account of its ecology and behavior. The species builds elongate ladder webs close to the trunks of trees or against rocky outcrops. These webs are built so that they clear the substrate by only a short distance

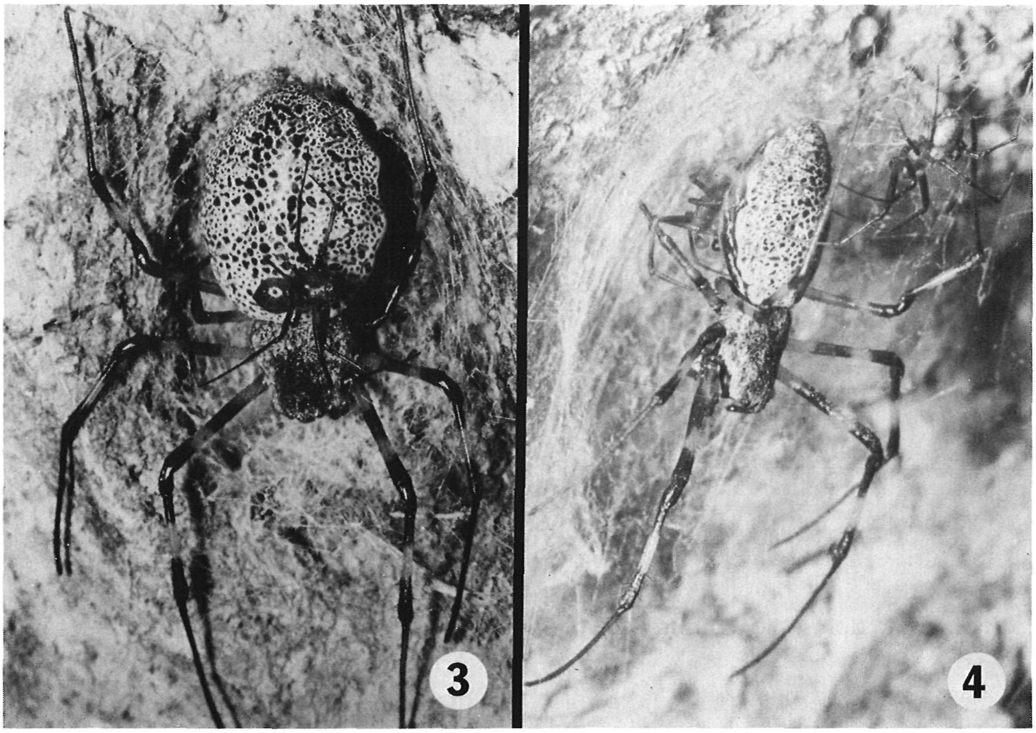

FIG. 3–4. *Herennia ornatissima.* **3,** ♀ in hub cup on tree trunk; ♂ on dorsal surface of abdomen is moving over ♀ in early stages of courtship. **4,** lateral view of ♀ with ♂ in copula beneath her; note the difference in color between his pedipalps; the left one (raised) is already discharged, the right pedipalp is inserted; a 2nd ♂ is touching the dorsal surface of the ♀ abdomen from the web surface; the ♀ is in an access posture (see text).

and the adult spider rests in a silken depression at the hub that touches the substrate. Robinson & Lubin (ibid.) call this a *hub cup.* The adult female spider is cryptically colored on its dorsal surface, while the adult male is red with black markings.

Approach behavior. Males approach the female at the hub cup and establish themselves on her web where they remain for long periods. We would guess that at least 2 males are frequently resident for several weeks after a female has become mature, but we have seen up to 7 males on the web at a time. This complement of resident males may include "castratos" or "eunuchs" that visibly lack the terminal portion of their pedipalps (see below). Introducing new males onto maleless webs gave no indication of the existence of any specialized communicatory behaviors performed during the approach stage. The males simply walked slowly, but directly, towards the female's resting place. When other males are present the situation is complicated; the approaching male often becomes involved in interactions with the residents. These interactions involve a number of conspicuous behaviors on the part of the invader and the residents (see below). *H. ornatissima* is much more likely to attack mildly stimulatory prey by night than by day (Robinson & Lubin, ibid.); we made no observations on male approaches by night, but no males were attacked by females during diurnal approaches.

Courtship. The female of this species rests in the concave, silken hub cup with the ventral surface of her body tightly appressed to the silk and no space beneath her that would permit the male to approach the epignye. During courtship, males make frequent approaches to the female, touching her on the legs and on the dorsal surfaces of the abdomen and cephalothorax. A receptive female responds by raising her body partly out of the hub cup, thus allowing the male access to the epigyne. This movement is usually followed by repeated visits to the ventral surface of the epigyne where rapping occurs, followed by insertion attempts, and ultimately copulation takes place after a variable number of rapping/insertion-attempt bouts.

Behaviors that occur prior to the adoption by the female of an access posture include a complex combination of units without any clear pattern. Several days of walkabouts and male/male interactions may precede the first male/female contacts, but we have several records of newly introduced males moving down from the web margin and commencing contact courtship within a few minutes of introduction. One male had achieved access to the ventral face of the female's abdomen only 2 minutes after introduction. (We assume part of the variability in all courtship sequences depends on the level of sexual motivation in the female.) Males frequently make slow, hesitant, tapping movements on the silk surrounding the hub cup during the initial stages of a courtship bout and then move onto the edge of the hub cup where the upper surface of the female's body is more or less level with the web plane (because she is resting in a depression). Here, slow tapping on the female herself may occur and the male may rest half on and half off the female's abdominal apex. When the male moves about on the body of the female, he often appears to be rubbing the pedipalps against her body surface in the same way that he does prior to rapping and insertion attempts. (We have also seen this behavior in males of *Argiope aemula* and *A. argentata*; it could be tactile "searching" for the epigyne.) FIG. 3 shows a male moving over the surface of a female prior to her adoption of an access posture. At a later stage in courtship, movement over the female is accompanied by attachment of silk lines to her body; we cannot be sure that this takes place at the preaccess stage.

Periods on the female body may be interspersed with walkabouts around the female, during which the male enters the V's between the female's legs and taps, or strokes, individual legs. Some bouncing on the web occurs in close proximity to the female. Tapping is most frequently unilateral, but occasionally both legs I are used simultaneously.

When the female adopts an access posture, this is often accompanied by stilting legs I, II and IV while the short legs III are lifted off the web and held against the sides of the abdomen (see description of acceptance posture of *Argiope aemula*). In some acceptance postures, legs I and II were stilted and legs IV remained in the normal resting position; this arrangement lifted the anterior part of the female off the hub cup, but left no posterior access for the male. Once the female has assumed this position, the male may gain a position on the ventral face of the female's abdomen in several ways. Commonly he climbs onto the dorsal surface of the abdomen and then circles, sidestepping, around her. This latitudinal movement may be done close to the abdominal apex or close to the waist. The male may squeeze through the gap between the abdominal apex and the web with his dorsal surface uppermost and then "barrel-roll" onto her ventral surface. When access is restricted to the anterior, the male may ascend the surface of the hub cup as far as the female's dragline attachment and there swing off the web onto her body. Circlings from above were most frequently seen in the early stages of ventral approach. We had the impression that the male was attaching his dragline to the female but we could not see dragline silk on the female with the naked eye, or on photographs or movie film. Analysis of movies shows characteristic silk attachment movements, both on the dorsal and ventral surfaces of the female and, at intervals, on the rim of the hub cup. Despite this, no silk is visible. However, we have one movie sequence in which the male is standing inverted, half beneath the female and clearly resting his left leg IV on a surface (not visible) behind the female and above the level of her abdomen. Clearly this is not the female's dragline. Since the male in question had made spinneret-dabbing movements on the dorsal surface of the female's abdomen and on the web behind the female, we have no doubt that during circling he was laying down a system of silk scaffolding on and around the female. (Similar silk deposition by *Argiope aemula* was only confirmed by photography, see FIG. 20.)

Repeated approaches to the epigyne lead to insertion attempts and copulation. It is extremely difficult to see what the male is doing beneath the female's abdomen, but we were fortunate enough to get a good camera angle on the occasion of 2 bouts of approach, insertion attempts and copulation. One of these lasted over 2 h, the other over 45 min. These were the only times when we could see the male clearly in profile during his excursions. On other approaches we could see a red shape beneath the female and noted sporadic pedipalpal movements, but could not distinguish left and right pedipalps or see whether or not the embolus was inserted. Often all one could see of a male in copula were the tips of his tarsi folded over the dorsal edge of the female's abdomen; a back view of an embrace. One film sequence lasting 2½ min. shows the epigyne protruding very conspicuously at the end of a period of circling and rapping. It is tempting to think that this is an erection of the membranous parts consequent to courtship stimulation (see below). It could simply result from a change in the female's angle to the camera resulting in the region moving into more distinct profile, but this seems unlikely, since the leg and body postures are not detectably different from those seen at the start of the sequence.

Copulation. In the clear sequences mentioned above, insertions were distinguishable and the pedipalp that was inserted was identifiable, since it was held lower than the unemployed one (FIG. 4). Unfortunately, for many copulations that occurred when the female was low in the hub cup it is still a matter of difficulty to decide whether the left or right pedipalp is the one inserted. We have noted, during the 45-min. clear session, a period of 17 min. 10 s in which the left pedipalp was down and the right one up. All other bona fide insertions were less than this. The shortest insertion was 88 s.

Interactions between males. As males accumulate on the female's web they interact and are particularly responsive to each other's movements. They orient towards each other and indulge in shaking duels. Overt fighting occurred when one male ran up to another that did not flee. Suddenly a complex ball of 2 intertwined males would fall some way down the web before resolving itself into 2 separate males again. We saw no limbs lost in such fighting although males on webs often lack one or more legs. Usually when one male runs at another it leads not to fighting but pursuit and fleeing. A fleeing male may drop out of the web belayed on its dragline and climb back later. Eunuchs fight and respond aggressively to other males. We have one record of a eunuch moving under a female and interacting with the male already beneath the abdomen. This interaction led to the eunuch being chased some 8 cm across the web. Clearly such encounters could interrupt copulations and disrupt courtship. In body length the largest males may exceed the smallest males ca 1:0.7.

Nephila maculata (Fabricius) FIG. 5–6

Details of the courtship and mating behavior of *N. maculata* are given in Robinson & Robinson (1973, 1976a). Here we summarize the main features of the process so that the reader can make comparisons. The species is one of the largest araneid spiders and perhaps the largest of the genus *Nephila.* Details of the ecology and behavior of *N. maculata* are given in Robinson & Robinson (ibid.). Males aggregate on the large aerial webs of females before the females mature. There is striking sexual dimorphism in size and considerable intrasexual size polymorphism. This species has the most complex courtship of any *Nephila* species that we have seen (or whose courtship has been described).

Approach behavior. Males moving across the web for the first time have a considerable expanse of web to cross before they reach the vicinity of the female, who rests at an eccentric hub located in the upper part of the web. They move slowly with their legs I more or less constantly off the web, but they tap the web from time to time, with the tarsus of 1 of the first legs. The males may take several minutes to move 20–30 cm, pausing frequently. Should the female pluck or otherwise move during this approach, the males freeze or even drop off the web belayed on their dragline. Eventually the males reach a position close to the female, usually close to the upper margin of the web, and adopt a head-down resting posture. From these resting positions males make walkabouts, interact, and approach the female. Vollrath (pers. commun.) has discovered that males living on the webs of *N. clavipes* behave kleptoparasitically and steal food from the female; males of *N. maculata* probably do likewise. We have seen a male feeding from the opposite side of a large insect as it was being fed upon by the female. Hingston (1923: 74) described the males living as dependents on female *N. maculata* in India.

Courtship. No special postures are adopted by the female to provide access for the male, contrary to the description by Hingston (ibid.) who claims that she swings, like a door, away from the web by releasing the legholds on one side "the object being to lay herself open so as to receive without obstruction the advances of her mate." We have seen more than a hundred copulations and have never seen such a posture. When the female is at the hub there is ample clearance for the male to descend the ventral face of her abdomen without contacting the web. It is thus difficult to formally demarcate the beginning of courtship, since the male may make repeated perambulations of the upper web and approaches to the female before moving onto her body. Insofar as these movements may serve to habituate the female to his presence they can be considered to be part of courtship (see Discussion). During walkabouts and approaches to the female, the male walks more or less normally but occasionally pauses to tap with a leg I, or indulge in short bouts (up to 15 min.) of on-the-spot juddering. Eventually the male will approach close enough to tap or stroke the apex of the female abdomen and/or legs IV. After a variable period of approach behavior the male climbs onto the female and the next phase of courtship commences.

When the male moves onto the female he moves down onto the cephalothorax to indulge in a remarkable behavior. He commences a strikingly complex silk-binding behavior. He moves about the dorsal surface of the cephalothorax passing his abdomen like a shuttle between the bases of the female's legs and attaching dragline silk to her as he moves. This process may be continued intermittently for hours and complex gussets of silk are built up between the legs and between the base of the abdomen and the dorsal surface of the cephalothorax. The male even ventures over the pedipalps of the female and across the face of her chelicerae. Thakur & Tembe (1956: 331) made passing reference to this behavior in their account of the biology of *N. maculata* in India, stating that the "male does construct a web on the back of the female."

Binding behavior may be omitted completely when a male is present at the moment when an immature female molts for the last time. Then the male will go down to mate with the freshly ecdysed adult as she hangs from her old exoskeleton, expanding her limbs and hardening. This we call opportunistic mating. Males will also make direct approaches to the epigyne of feeding females without indulging in prior binding behavior. This can be regarded as another category of opportunistic mating. Examples of opportunism in other species are given below. Approaches to the epigyne may occur intercalated between bouts of binding and they eventually become more and more persistent until copulation occurs. Such approaches are made by 2 basic routes. Most frequently the male simply moves up to the apex of the abdomen on its dorsal surface and then descends the ventral surface by walking forwards down it, belayed on his dragline. He may also simply circle around the circumference of the abdomen (compare with *Herennia ornatissima* below). Retreat by circling is very

NEPHILA MACULATA

FEMALE BEHAVIORS	MALE BEHAVIOR ON FEMALE
female at hub	male on dorsal surface female abdomen
	move to dorsal cephalothorax
	deposit silk under bases of legs IV-L, III-L, IV-R
	rest dorsal abdomen
	deposit silk cephalothorax, then on legs IV-R, III-L, III-R, II-R
	circle beneath abdomen
	circle to dorsal abdomen
	down to dorsal cephalothorax
	deposit silk on bases of legs IV-R, III-R, I-R, I-L, II-L
	rest dorsal abdomen
	circle beneath abdomen
	beat on epigyne
	10
	15
	long insertion LEFT pedipalp
disturbed by author's bounces	circle to dorsal abdomen
rest on hub	rest
	down to dorsal surface cephalothorax
	deposit silk on leg bases I-R, II-R, IV-L, III-L
	dorsal surface abdomen
	circle to ventral abdomen
	beat on epigyne
	17
prey hits web, female plucks	10
predatory excursion	circle to dorsal surface
	rest
back to hub	
	onto dorsal surface cephalothorax
	deposit silk

FIG. 5. Conventional summary diagram of courtship in *Nephila maculata*. Abbreviations in this and subsequent conventional summary diagrams are as follows: L = left; R = right; LHS = left hand side; RHS = right hand side; ×1 = once, ×2 = twice, etc. Numbers refer to total discrete rappings by pedipalps per bout.

common indeed. Presumably this is the quickest route from the vulnerable (to female grooming movements) ventral surface onto the relatively safe dorsal surface.

The behavior of the male at the epigyne has general features that are seen in all the courtship activities of the *Nephila* spp. that we have studied. These are extremely difficult to see with the unaided eye, as Hingston (1923) remarked when he made preliminary observations on the courtship of the species. Using a movie camera in close-up mode certainly helps solve this problem and we feel that this behavior is sufficiently important to the general process of *Nephila* courtship to merit an expanded description here as a general summary of the process. This allows us to concentrate on noting differences of detail in the description of this phase of courtship in the other species described below.

We have already mentioned that the male makes repeated short approaches to the epigyne during pauses in the process of silk binding. These approaches and subsequent longer periods spent at the epigyne are characterized by similar groups of behavior units. These can be characterized as insertion attempts but we now feel (see Discussion) that they are in all probability a very important part of the stimulatory phase of courtship. They are almost always prolonged and they involve repeated contact with the epigyne or the area immediately surrounding it. The male stands on the ventral face of the female's abdomen, belayed on his dragline, in a mirror-image posture facing her. According to the degree of sexual dimorphism in size, and whether the male is a micromale, normal, or macromale, his anterior legs may rest on the apex of the abdomen or as far forwards as the sternum of the female. The pedipalps are usually more or less directly above the epigyne itself. (The epigastric furrow often bears a tuft of long stiff hairs.) The male stands more or less erect and starts rapping on the epigyne with the pedipalps. This behavior shows some differences of detail from species to species, but involves the movement of the bulb(s) against the surface of the female. It may, in part, be carried out as the male crouches close to the body of the female; if so, he straightens up again at the end of a bout. Sooner or later these rappings begin to include brief insertions. These last 1 or 2 s and the embolus can be clearly seen in an inserted position (see FIG. 6). Withdrawal is accomplished by the raising of the inserted pedipalp but this is often accompanied by the male rising up on his legs so that the entire body moves conspicuously away from the female and appears to be straining upwards. That this is probably the case is indicated by the fact that there is a distinct recoil when the embolus is freed (see below). In our earlier description of this behavior (Robinson & Robinson 1973: 41), we suggested that such brief insertions "may represent unsuccessful attempts." We now feel that they almost certainly do not involve sperm transfer. If they represent unsuccessful insertion attempts, this certainly does not preclude a courtship function. Their very universality bespeaks a courtship function: *Nephila edulis, N. pilipes, N. madagascariensis, N. clavipes* all have similar behaviors, so much so that Charezieux (1961) appears to have confused this behavior with copulation in the case of *N. madagascariensis* (see below).

We are currently investigating whether prior "insertion attempts" by one male facilitates courtship and/or copulation by subsequent males to determine whether this phase of courtship has a stimulatory effect. Preliminary results are positive.

Copulation. Since our first report on copulation durations in this species, we have

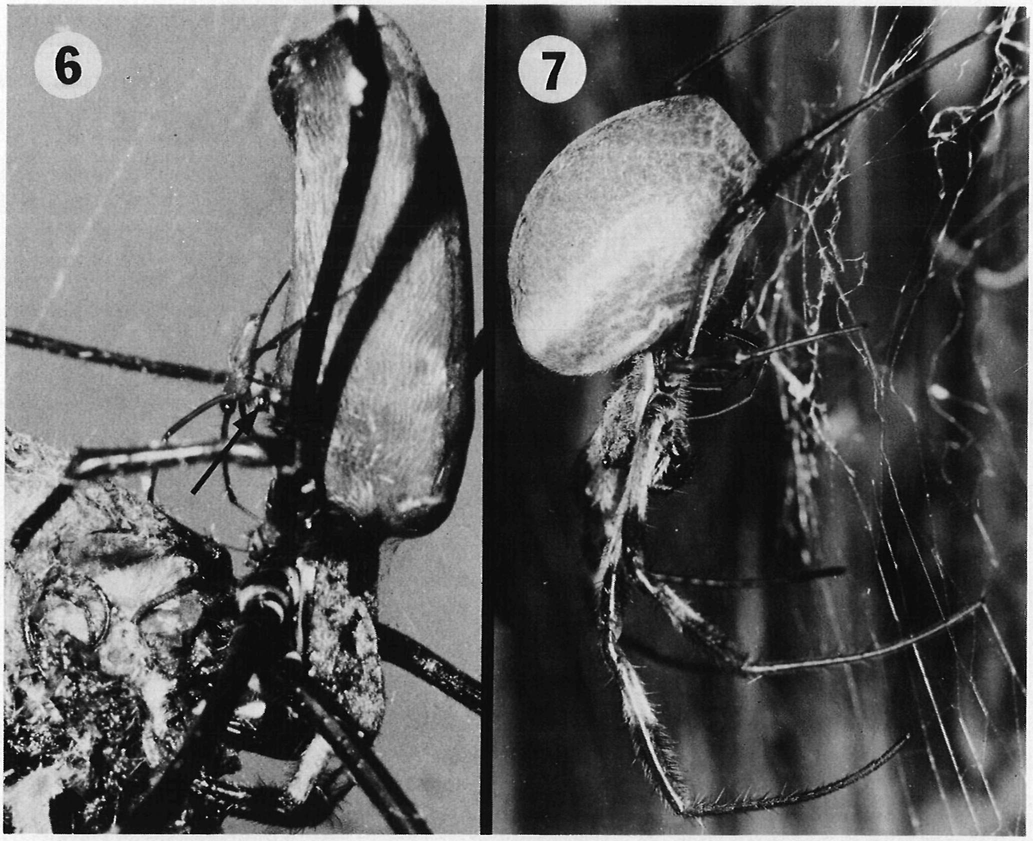

FIG. 6–7. **6.** Copulation stance of ♂ *Nephila maculata.* The right pedipalp is held in line with the body, the left pedipalp (arrow) is inserted. **7.** *Nephila edulis.* Copulating ♂ on body of ♀. Note ♀ rotund abdomen. Embolus of left pedipalp is inserted perpendicularly. Legs I and II of ♂ reach onto sternum of ♀.

seen long copulations (Robinson & Robinson 1976a) and expect to resolve the matter of copulation duration during our present study. (Added July 1979: Using a 20-power binocular microscope for field observations of copulating *N. maculata,* we have been able to determine that long copulations (often of over an hour) involve continual and regular haematodochal pulsation. Very few brief insertions are accompanied by the expression of the haematodocha and many of them seem to be mislocations of the embolus. We expect to report on copulation in this species in much greater detail in a later publication. We have also seen insertions, accompanied by haematodochal pulsations, made by a male on a female that subsequently molted. Should such a phenomenon prove to be more than an isolated aberration, it could be of considerable importance for an understanding of courtship and mating in this species.) Insertion attempts prior to the long copulations followed repeated rapping on the epigyne and bouts of alternating short insertions. As noted above, withdrawal is often followed by a very distinct recoil, as if the tip of the embolus stuck in the epigyne. Males collected at random often have the tip of an embolus broken off, but we have not seen males lacking the entire terminal segment, as in the eunuchs of *Herennia* and *Nephilengys.* Females of *Nephila* spp. are often found with embolus tips in their epigyne (Bonnet 1930). Following copulation the male simply walks off the ventral surface of the female, onto the web or onto the upper surface of her body. We have seen only 1 male killed during approaches to the epigyne; he was killed after an insertion attempt.

Interactions between males. Males vary considerably in size since they mature over a range of at least 3 instars (Robinson & Robinson 1976a: 10). Males interact at all stages of courtship, fighting and chasing occur regularly during such interactions. While 2 males are thus engaged, a 3rd male may sneak onto the female undetected and commence direct courtship. Size is not the only factor deciding the outcome of interactions in this species. This situation has been studied in detail in the case of *N. clavipes* (Vollrath, in prep.).

Nephila edulis (Labillardière)[4] FIG. 7–8

This Australian species is in the same weight range as *N. maculata* but is shorter and characteristically more rotund (FIG. 7). We studied it in North Queensland on the Atherton Plateau, near Cairns. There it was found building large aerial webs between trees and large bushes. The webs have little or no prey capture area above the hub and are often sited 1 or 2 m above the ground. At the hub the spiders build a "gibbet" of prey remains and silk. Barrier webs dorsal to the spider are common and quite well developed. Sexual dimorphism in size is not so extreme as in *N. maculata* (compare FIG. 6 and 7). Intrasexual polymorphism in males is quite marked. In the field we saw up to 5 males on a single female's web.

Approach behavior. Approach behavior in this species closely resembles that described above for *N. maculata.* Males advance up radii towards the hub, making a number of tentative inward excursions before finally proceeding to a resting position near the female. Locomotion is hesitant and accompanied by unilateral and bilateral tapping movements of leg(s) I. Something we have seen in no other *Nephila* species is an approach in which a dragline was progressively attached further and further along a radius from an attachment point on a nearby branch. This dragline formed an oblique approach to the inner part of the female's web and the male could retreat onto it from a point some 5 cm from the hub, where the female was stationed. It formed an analogue, in positioning and origin, to the mating threads of some species (see below). It was not used in courtship but merely as an approach pathway that was presumably much safer than the web itself. We only saw this behavior once but noted that resident males move not only on both sides of the web but on their own lines between the web and the well-developed barrier web. In many cases males seemed to take up residence resting on the spider's gibbet.

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[4] See also Austin & Anderson (1978).

Courtship. Courtship is relatively simple compared with *N. maculata,* but has a number of interesting features. Males of this species spend a considerable time on the upper surface of the web in walkabouts before approaching the female for contact. Initial contact in over 75% of the courtship bouts that we saw was through the hub; the male passed partway through the hub silk and slowly tapped and stroked either the apex of the female's abdomen or one of her legs IV. This process was repeated at short intervals, with the male slipping partway through the hub and retreating again after a few tapping strokes. Similar advance/retreat contacts were also made from the lower surface of the web and the male made some vibratory movements while resting the 1st legs on the female's dragline (at rest, this is a short thread from the spinnerets to an attachment on the hub silk). Silk deposition occurred during the walkabout on the upper surface of the web and during approaches to the apex of the abdomen.

During close approaches to the female's abdomen or legs IV, or contact with these, males made high intensity juddering movements. These were difficult to decipher, but out of over 18 min. of movies on this species we have a clear sequence of 25.8 s of juddering that we were able to analyze. In this time the spider made 6 bursts of high-intensity juddering. The body and legs were in the postures shown in Fig. 8. From this it can be seen that the juddering resulted in the drumming of the male's abdominal apex against the hub silk and movements of his anterior legs against the female's abdomen and/or her dragline. We were able to distinguish the following numbers of component movements in the 6 bouts: 9, 3, 9, 10, 12, 7. After the last bout the male moved onto the female's body.

In all the cases where we had the appropriate camera angle to allow us to discern this, movement onto the female's abdomen was clearly preceded by the male spreading his pedipalps apart. The male may move onto the dorsal surface of the abdomen and there make close pedipalpal contact with the surface "as though feeling for the epigyne." We noted similar movements in the behavior of male *Herennia ornatissima.* From the dorsal surface the male may circle around to the ventral surface or back up onto the web and start again. In early excursions down the ventral face of the female's abdomen, the male as he moves may press his pedipalps into contact with the female all the way down to the epigyne. He assumes an extremely low profile (crouching) as he descends. This is strikingly different from the approach of *Nephila maculata* and *N. clavipes,* where the males walk down on normally erect legs. The male maintains this crouching posture as he raps on the epigyne region, but not during copulation (see below). Some of our film of rapping in this species is, felicitously, in sharp profile view and makes it apparent that much of the rapping is carried out on a cuticular prominence slightly above the epigyne itself.

Copulation. A copulation is shown in Fig. 7. The contrasts with *N. maculata* are largely a result of the comparatively large size of the *N. edulis* male, whose legs I and II reach well forward onto the sternum of the female and whose legs IV extend all the way back to the lateral margins of the spinnerets. The male stands erect during copulation in contrast to his posture during rapping and insertion attempts. We were

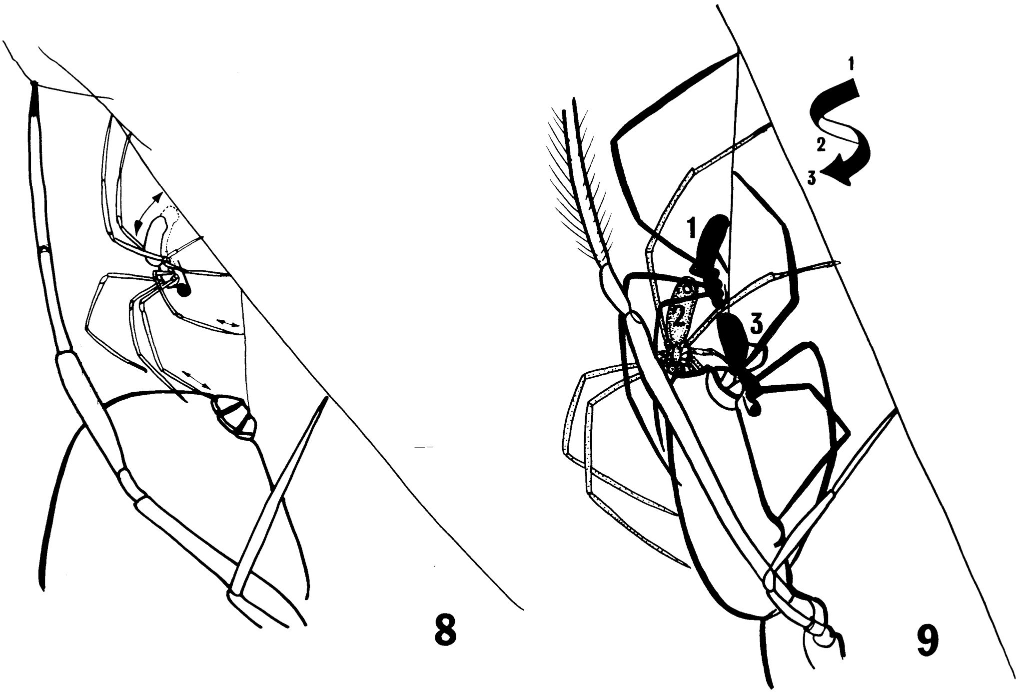


FIG. 8–9. **8.** Male *Nephila edulis* juddering against ♀ (see text); apex of abdomen drums against hub silk. **9.** Movement of ♂ *Nephila pilipes* onto body of ♂ by barrel-roll around her dragline; 1, 2, and 3 are successive stages in this movement. Arrow on right shows that 180° turn about long axis occurs.

able to see pumping movements behind the pedipalpal bulb on one occasion and noted that these appeared to coincide with dorsoventral movements of the male's body ("press-ups"). The longest copulation that we saw was fractionally over 11 min. We saw no attacks on males at the moment of withdrawal, but one male was brushed at and chased during insertion attempts.

Interactions between males. We have only one brief set of observations on interactions between 3 males of differing sizes. The smallest of these established "possession" of the female after a series of shaking bouts conducted at a distance. No contact occurred between the males and no chases occurred.

Nephila pilipes (Lucas) FIG. 9–10

This medium-sized *Nephila* species is widely distributed in Africa. We studied it in Ibadan, Nigeria, in forest-fringe habitats. We also found some specimens inside shaded forest. The web is built of golden silk. Males are polymorphic in size and females of conspicuously different sizes were being actively courted (we have no means of knowing whether all were mature).

Approach behavior. Males move across the web for the first time in a manner similar to that described for the 2 *Nephila* species detailed above. The walk is hesitant and accompanied by much leg waving and occasional bouncing. Leg waving and slow tapping are not necessarily confined to the direction of progression across the web; the wavings may be partly lateral and web members to the left or right of the route may be tapped. At Ibadan, dry season conditions appear to have stressed the males, since in early morning approaches we saw 2 males interrupt movements across the web to move back onto nearby leaves where they drank from water (dew?) droplets. A further male moving in the barrier web was also seen drinking during the same period (about an hour after sunrise). One male became partly entangled in an element of viscid spiral during an approach but freed himself with no loss of limbs. This is the only time we have seen this occur with any *Nephila* male.

Courtship. Movements of males established on the web as suitors involve extensive silk deposition around the hub and female dragline. A web subjected to several days of male activity is easily recognizable by the large numbers of fine lines laid down irregularly at the hub. These are particularly conspicuous if the web is back-lit. Much of the male walkabout activity takes place above the hub; the males shuttle through when making direct approaches to contact distance. Activity on the lower surface of the web is also characterized by silk deposition. This may be nothing more than the result of making multiple, frequent, dragline attachments, but we have notes of a single female dragline, 3 cm long, having 7 oblique male threads visible as attachments like spokes of a wheel. In addition, a segment of film shows a male advancing down the web towards the female, apparently walking on air for at least 13 cm. He must have been on a dragline above the surface of the female's web. This observation and the somewhat similar incident seen in a *N. edulis* courtship could be important clues about the possible origins of mating threads.

Approaches down the ventral face of the abdomen started, quite regularly, with the male standing with his long 1st and 2nd legs touching the apex of the female's abdomen, vibrating on the spot and stroking. Then to get from standing on the web in a similar orientation to the female to the 180° shifted position of standing venter-to-venter on the female, the male frequently twisted around, using the female's dragline as a foothold for his barrel-roll. This movement is used by a wide range of male spiders in groups A and B and is illustrated in FIG. 9. Walking on the undersurface of the hub during approaches to the female preceding contact and/or movements onto her was characterized by brisk jerkiness and AWing. We noted that during AWing the male's dragline was visibly taut and that vibrations could be induced in the hub silk by the movements of the silk consequent on the AWing. We have one movie sequence showing a very distinct juddering bout (see above) prior to the male mounting the female's abdomen. We have no record of this in our notes and think that it was probably so brief and fast as to have escaped our notice. It could be a regular feature of initial contact.

When the male eventually moves down towards the epigyne, the body is held more or less tightly appressed against the female and the reflexed pedipalps are scrubbed

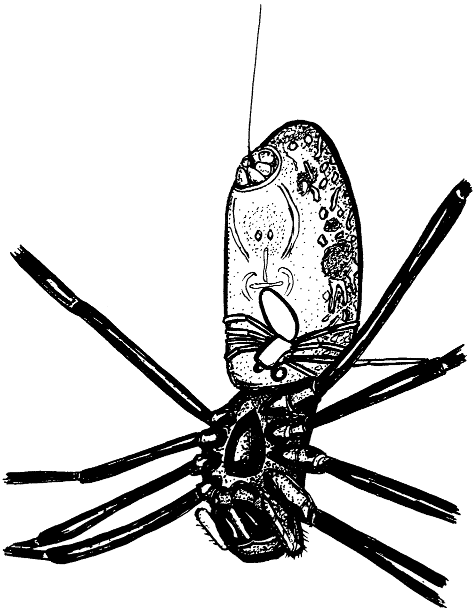


FIG. 10. Copulatory posture of ♂ *Nephila pilipes* on abdomen of ♀. Note that he is appressed to her and twisted sideways. His left pedipalp is inserted.

against her ventral surface. As this movement merges into insertion attempts, the male stands partly erect and often raises the apex of the abdomen. Rapping in the vicinity of the epigyne occurs in typical *Nephila* manner.

We found one female that had just ecdysed and was suspended below her old cuticle in an immediate post-molt posture. A large male was standing on the dragline that supported her and had both legs I and II resting on her abdominal apex. He made 1 approach to the epigyne before we removed him so that we could test the male-attracting powers of a newly emerged female. Next morning she had 3 established suitors in a new web. This is another case of an opportunistic mating attempt. (Significantly, the old molting web had an extremely complex stabilimentum; this is the 3rd *Nephila* species now known to build an occasional ribbon stabilimentum since our first discovery of this phenomenon in *N. maculata.*)

Copulation. We saw numerous brief insertions and 3 veritable copulations. The insertions were made by males standing partly erect, and withdrawals produced the conspicuous recoil seen in other species and first noted by Robinson & Robinson (1973: 41). The longest of these insertions was 2 min. 31 s. Our basis for believing that short insertions of this kind are not necessarily true copulations, although possibly involving sperm transfer, is much more securely based in this case than in the case of the other *Nephila* spp. (see above, and Robinson & Robinson 1976a: 20). This arises from the fact that the male has a distinct copulatory posture. We were excited to discover this complex copulatory posture that is quite unlike that seen in the other nephilinids so far described (above and Bonnet 1930, Gerhardt 1933b, Charezieux 1961, McKeown 1963). At the moment of insertion the male instantly twists sideways and drops flat against the body of the female, encircling her body with most, if not all, of his legs. In this posture he is flattened against the substrate and presents a minimal profile. This is shown in FIG. 10. This posture has remarkable parallels with the copulatory posture found in the *Argiope* species that we have seen. Yates (1968: facing 73) has a figure showing a male of *N. fenestrata* in a similar posture, but does not comment on this. We saw males adopt variants of this posture on 3 separate females differing widely in size. The longest such copulation was 27+ min., the shortest 18 min. 47 s.

After withdrawal, the males backed up the female's ventral surface rather than circled round her (compare with *N. maculata*). These differences could be related to differences in the proportions of male:female size (see Discussion).

Interactions between males. We saw 5 males on one web and observed numerous aggressive interactions involving chases and web-shaking duels. We saw 1 micromale sneak a copulation attempt, while 2 macromales were indulging in a 3-min. bout of mutual threat and a chase. One male moved onto a female when a male was already in copula; the copulating male was apparently undisturbed by this incursion; the intruder moved off the female and did not return.

Nephila madagascariensis (Vinson)

This striking species is in the same size range as *N. maculata* and has been the subject of a great deal of biological research [Bonnet (1958) gives references up to that date]. Courtship in this species is described by Bonnet (1930), Gerhardt (1933b), and Charezieux (1961). Both sexes are polymorphic in size (Bonnet 1929) and variation in the size of males is considerable, since they mature over a range of at least 3 instars. We saw considerable variation in the field and found males on the webs of immature females. The species thus exhibits the suitor phenomenon. When we visited the Malagasy Republic we were not engaged in a study of araneid courtship and have only incidental observations on this species. We made no systematic introductions of males to females and are not in a position to resolve the discrepancies between the various published reports on the courtship of *N. madagascariensis.* These principally concern detail rather than the broad pattern of the courtship. Our observations confirm the observations of Bonnet (1930), Gerhardt (1933b) and Charezieux (1961) that the male approaches the epigyne down the ventral face of the female's abdomen and then makes insertion attempts by beating downwards on its surface. There is nothing comparable to the complex silk deposition of *N. maculata.* One pedipalp is inserted at a time and this one is conspicuously held down, with the embolus visibly at right angles to and entering the epigyne. Withdrawal is accomplished with a distinct recoil after the male has apparently strained to pull the embolus free (see descriptions of a similar phenomenon in the withdrawal behavior of *N. maculata,* Robinson & Robinson 1973). Much of the concern of the early students of the courtship of this species centered around whether or not the female could be mated more than once, since there was a general feeling that the epigyne was often blocked by a fragment of embolus after a single mating (Bonnet 1930: 63–64, Gerhardt 1933b: 57). Part of the controversy is the question of the duration of copulations: Charezieux (1961: 378) clearly regards the duration as extremely brief, "L'acte copulateur se caractérise donc par sa grande brièveté: une à deux secondes par série de martelements, chaque série pouvant être repetée plusieurs fois au cours de la copulation." Some of the problem may hinge on his definition of copulation, but we think that part of the problem is in confounding precopulatory stimulation of the epigyne region, including brief (1- or 2-s) insertions, with copulation itself. We have already emphasized this point above, and have seen this repetitious rapping and brief-insertion activity, conducted at the epigyne, in all the *Nephila* spp. that we studied. However, we regard the 2 insertions of over 1 min. that we saw as true copulations. We did not see approach behavior or preliminary approaches to the female; these are variously described by the above-mentioned authors but are probably similar to this phase of courtship in other *Nephila* spp. In summary, our observations show that this species has a courtship of the simple kind seen in *N. edulis* and *N. clavipes.*

Nephila clavipes (Linnaeus) FIG. 11–13

This is the only New World (Neotropics and Nearctic) species of the genus *Nephila.* The genus is represented by several species in each of the other faunal regions (except Antarctica). There are a considerable number of studies of various aspects of its biology, e.g., predatory behavior (Robinson & Mirick 1971), thermoregulatory behavior (Krakaeur 1972, Robinson & Robinson 1974b, Carrel 1978), web structure (Peters 1954), and reproductive biology (Farr 1976). Peters (1954) gives an excellent description of the web, web site, and basic ecology of the species. The spider is known by the English common name of golden web spider, and its large, fine-meshed, aerial web is of golden silk. Barrier webs are commonly present dorsal to the spider and aggregations of several individual webs with shared structural lines are a frequent feature of the species' biology. The suitor phenomenon is well developed.

Approach behavior. No feature of the *N. clavipes* approach behavior seems unique to this species. The descriptions for the other species could all be applied to *N. clavipes,* with the single exception that we have not seen the construction of a dragline to the heart of the female's web from nearby vegetation as described for *N. edulis.*

Courtship behavior. Males in residence as suitors make extensive walkabouts on the upper surface of the hub. Such walkabouts are punctuated by bouts of jerky walking that our notes characterize as "ritualized." On the other hand, arriving males may approach the female within minutes of reaching the web. Approaches to contact distance may be made down the lower surface of the web or, frequently, by the male slipping through the hub somewhere close to the female's dragline attachment. Silk deposition occurs during walkabouts and on approaches to contact distance. Since males (even the largest) are relatively small, they often descend the female's dragline

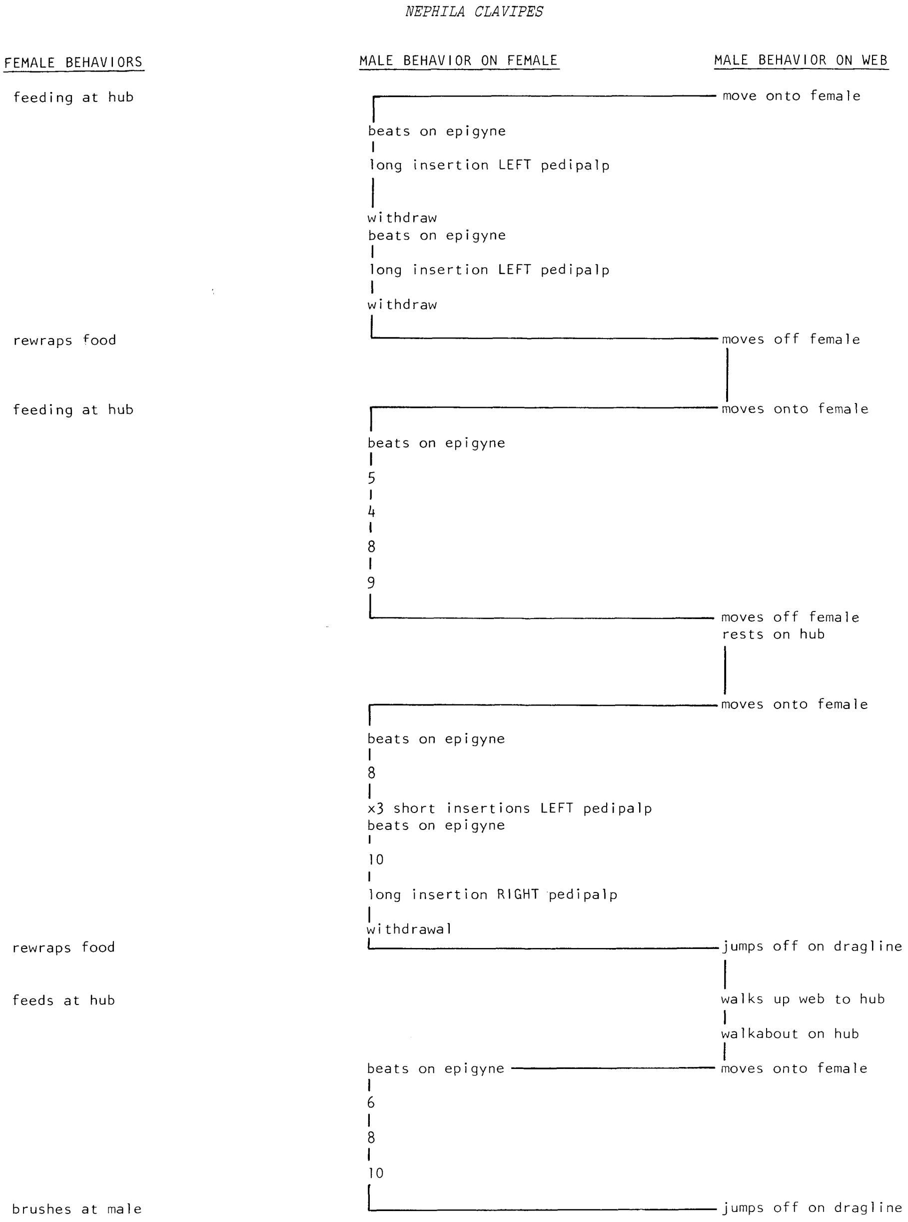


FIG. 11. Conventional summary diagram of courtship in *Nephila clavipes*. For explanation of abbreviations, see FIG. 5. Nos. refer to total discrete rappings by pedipalps per bout.

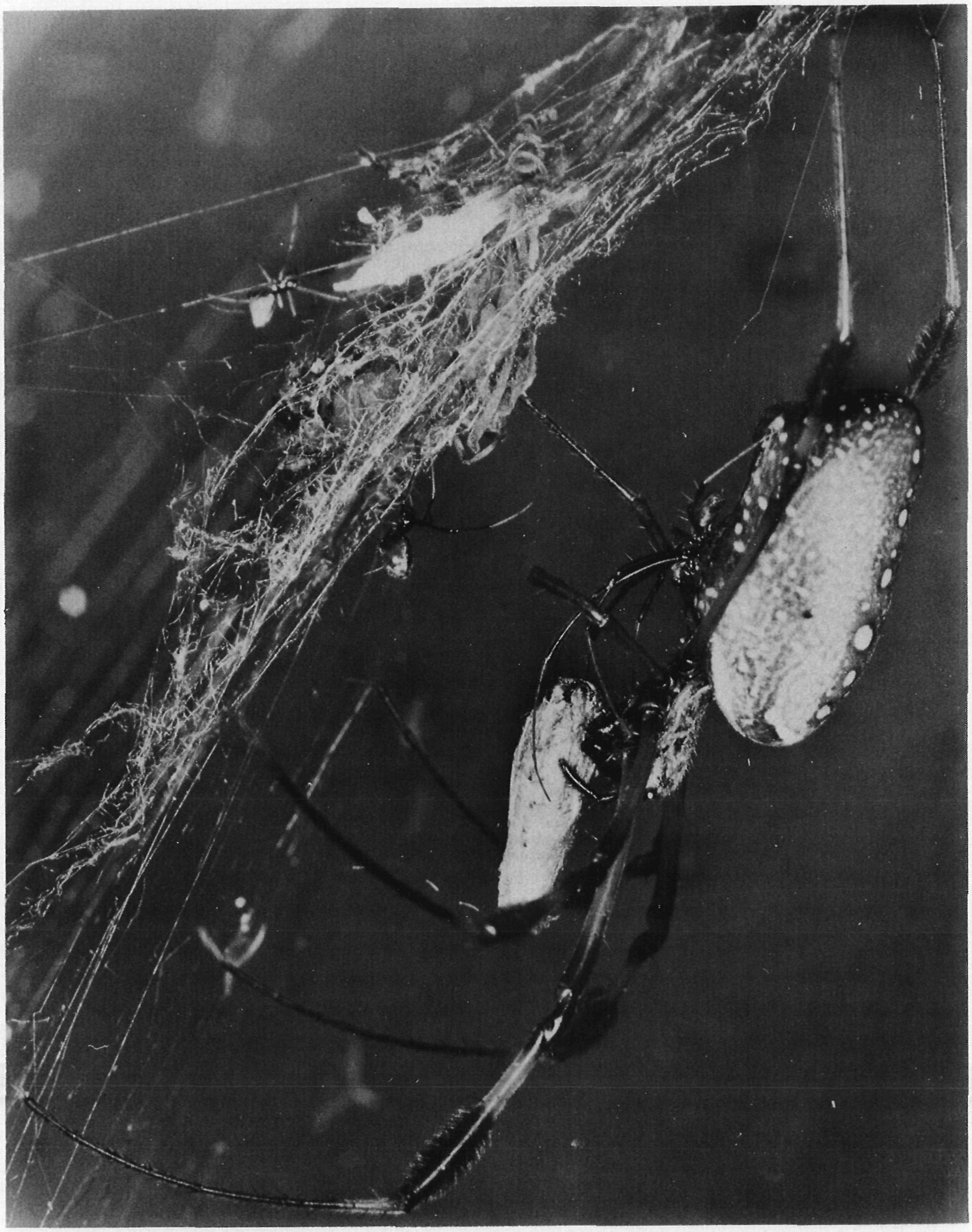


FIG. 12. *Nephila clavipes* in copula. Inserted left embolus is almost perpendicular to the ♀ abdomen. (At least 2 theridiid kleptoparasites are visible in the picture.)

onto the ventral face of the female's abdomen. Leg touching and abdomen stroking are relatively uncommon and beating on the epigyne region in repeated approaches dominates the contact courtship of this species. High-intensity bouncing on or near the female's abdominal apex and/or dragline was observed in only 9 cases of the 85 approaches that we have watched since observing this phenomenon in other species (and therefore being alerted to its existence). We could have missed other occurrences and suspect that large-scale use of film analysis will be necessary to further refine studies of nephilinid courtship.

Approaches down the ventral face of the female's abdomen are made in an erect or semierect posture and crouching is absent. Rapping on the epigyne region precedes insertion attempts and is subsequently interspersed between such attempts.

Males that have been inactive for some time react to some kinds of female activity by moving down onto the female's abdomen and making insertion attempts. In particular, they more or less consistently respond to successful female predatory excursions in this way. It has recently been shown (Vollrath, pers. commun.) that the movements involved in attack, transportation and storage activities in the predatory sequence set up a characteristic vibration pattern in the web. Theridiid kleptoparasites time their robberies as if they were aware of the host's activities, and it seems reasonable to assume that they use these characteristic vibrations as cues. Selection should favor any steps towards the evolution of a similar ability on the part of males, since it would no doubt enhance their fitness. The latter point would seem to be eminently susceptible to experimental investigation. Blanke (1974) showed a correlation between prey capture by the female and the timing of courtship in *Meta segmentata* (Cl.).

The movements involved in insertion attempts and successful insertions are slightly simpler in *N. clavipes* than they are in *N. maculata.* FIG. 12 shows that the embolus is directed perpendicular to the female's abdomen rather than obliquely.

Towards the end of a series of courtship bouts that has included copulations, the female seems to become increasingly irritable and will brush at the male or move violently on the spot during his approaches. We only saw one male actually seized in all our observations; he was bitten and dropped.

Copulation. The copulatory posture in this species is an erect one. The male may ride the female in copula if she is involved in attacks on prey during a successful insertion. We have seen such a male apparently undisturbed throughout an entire successful predatory sequence on a large grasshopper (3 min. from start to finish). Even when the female wrapped the insect in silk, and silk strands were moved under the spider's abdomen onto the prey, the male did not leave his copulatory position.

In a copulation/courtship sequence that we saw with the sun behind the spider, we were able to see pulsations behind the bulb of the inserted pedipalp and attempted to time these. This is a task that requires almost painful visual concentration since the bulb is tiny and barely translucent. We counted 19 contractions during one half-minute period and 23 during a second period. At one stage in this copulation the spider was flicking a leg I apparently in synchrony with the pulsations. The leg was

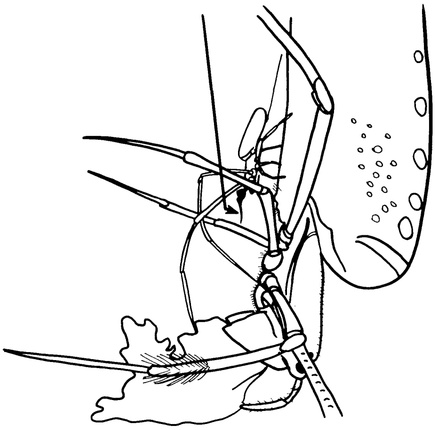


FIG. 13. Withdrawal of embolus by ♂ *Nephila clavipes*; note that embolus points forwards (see text).

held at an angle with the tarsus not grounded and the male was indulging in movements analogous to "knee-kicks." At another stage, the apex of the male's abdomen was bobbing rhythmically. We suspect that the pedipalpal pulsations are hydraulic and the effect becomes systemic. Rovner (1975) noted that the haematodocha of the inserted pedipalp of a wolf spider expanded synchronously with erecting leg spines, "both presumably caused by the same hydraulic mechanism."

Withdrawals often produce a recoil, and analysis of a particularly clear film sequence shows that sometimes the male pulls back on the inserted pedipalp rather than simply lifting it up. This gives a very strong impression of the embolus being gripped by the epigyne. After removal, in such cases, the embolus is facing anteriorly as though it had been pulled forward by the spider backing away from its trapped end (FIG. 13). The same pedipalp may be inserted for at least 2 long insertions.

Interactions between males. Vollrath (in prep.) has made an extensive study of the size distribution of males on females' webs and their interactions. Farr (1976) made a study of some of these phenomena in *Nephila clavipes* populations in Florida. Here it is sufficient to remark that males interact aggressively, that size is not necessarily a guarantee of dominance and that sneak matings occur.

Nephilengys malabarensis (Walckenaer) FIG. 14–16

Simon (1892: 744–54) notes that this species differs in several anatomical features from more "typical" *Nephila* species and appears to regard it as a link with the genus *Argiope*: "dans les espèces qui passent aux *Argiope,* particulièrement chez *Nephila malabarensis* Walck." (1892: 744). He notes (ibid.: 754) that the web has a long tubular retreat and is built on old walls. The habit of colonizing human buildings is common to both *N. malabarensis* and *N. cruentata* (in our experience, the latter is a strikingly

FIG. 14. Web site of *Nephilengys malabarensis.* The web extends below the tree to the left (not shown); the spider is feeding on a tettigoniid beneath her retreat (in the leaf).

successful commensal of man in many parts of Africa, Sri Lanka and India). The original preferred web site of both species was almost certainly the one where we have found them in undisturbed habitats, i.e., building against the trunks of medium to large trees in such a way that the main orb is aerial, but the retreat is against the bark (FIG. 14). They usually build beneath massive side branches or where the trunk slopes sufficiently for the angled orb to be well clear of the tree at its base. Having evolved a web that fitted against a solid surface at its upper (retreat) edge and one that became aerial below this attachment (shelter), the spider was preadapted to exploit walls, eaves under roofs, verandas and porches (Robinson & Lubin 1979). The species is originally arborphilic rather than arboricolous (compare with *Herennia* above). Both species of *Nephilengys* show the suitor phenomenon and both have eunuchs regularly occupying their webs. We found *N. malabarensis* in mangroves near Port Moresby and studied courtship in captive specimens only. *Nephilengys malabarensis* is not elongate in the manner of *N. maculata* and most *Nephila* species, but more similar in shape to *N. edulis* (compare FIG. 6, 7 and 14). Although dark and glossy, the female has a striking red mark occupying more than ½ the ventral surface of the abdomen; this is one of several features shared with *Herennia ornatissima* (see also Simon, ibid., on this general point).

Approach behavior. As in the case of *Herennia ornatissima,* we noted no specialized approach behaviors; males introduced onto the outside of the web sometimes spent a considerable time on the frame threads moving on the perimeter of the web and laying down dragline before taking a radial route to the female in her retreat. We saw some hesitant approaches and some leg-waving and tapping but, in general, the males walked boldly to the region near the retreat to assume their suitors' stance.

Courtship. Most nephilinids hang from a sloping, off-perpendicular, web. *Nephilengys* females of all species stand within an almost horizontal silk tunnel, and access to their ventral surface is much more limited in these circumstances. Early courtship reflects this factor; it is, at least in part, a process of inducing a modified stance in the female within her retreat. This is another parallel with *Herennia* courtship. Males perform jerky, high-stepping walkabouts on the upper surface of the web near the retreat and shuttle through to the retreat entrance. There they may encounter the forward-directed legs I and II of the female, if she is facing the web, or the apex of her abdomen if she is facing inwards. Tapping at either of these extremities may be followed by entry into the retreat or further walkabouts near the retreat's entrance. [Robinson & Robinson (1973: Fig. 24) illustrate the relationship of the retreat of *N. cruentata* to the main orb. That of *N. malabarensis* is essentially similar.] We have records of 2 separate males biting through the retreat wall and entering through the side. Entering through the mouth of the retreat may take the male over the body of the female, along the floor of the retreat (beneath her dorsal surface), along the sidewalls or along the roof (if there is room beneath the spider's ventral surface). If the female is facing inwards, the male may tap and stroke the apex of the abdomen and/or the dragline. From such active contact he may shift to merely resting in contact with part of the female. We have some footage of juddering movements made at this stage of courtship (see FIG. 15 and compare with FIG. 8). During walkabouts and approaches to contact distance, males made several leg-rubbing movements that we described in our notes as TRing. After examining movies of some of these incidents we are not sure that this original evaluation is correct. The movements lack the repetitive briskness seen in communicatory tarsal rubbing and may well have been grooming of the tarsi of the anterior legs that had contacted the female. The movements are accompanied by pedipalp rubbing, in which the pedipalps were rubbed against each other. Robinson & Robinson (1978a) suggested that tarsal rubbing may be a ritualized form of grooming movement and that such grooming was probably an accompaniment of courtship, since the tarsi are probably rich in sense organs involved in contact chemoreception and need to be kept clean. The presence of these movements as a regular feature of *N. malabarensis* courtship might represent an early stage of such ritualization.

During an approach to a feeding female that was holding a large grasshopper in

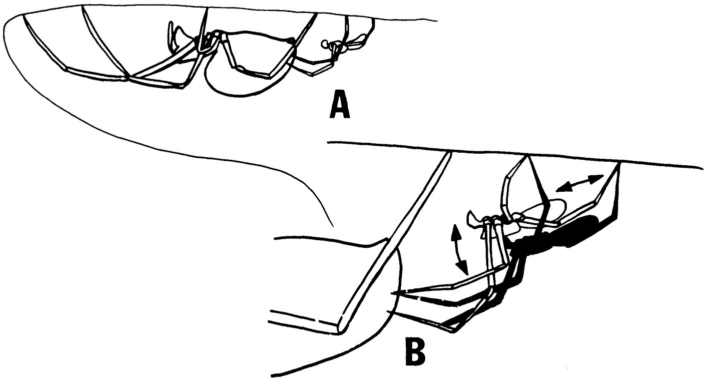


FIG. 15. *N. malabarensis*: **A,** ♀ in retreat with ♂ in juddering posture; **B,** detail of juddering ♂, showing successive movements.

front of her body across the tunnel, one male tapped the insect and then moved down its body in a low crouch with its pedipalps in close contact with the body surface of the insect. After a brief period of such movements, the male stood erect as though withdrawing from an insertion, backed off the insect and then did a series of 12 juddering movements close to the insect. We have critically examined the film of this incident and are not certain what the male was doing with its pedipalps, although one is certainly raised with the embolus down at one stage in the process. The incident is too brief to be a feeding act. We are inclined to think that this represents an attempt to copulate with the dead insect. Close proximity to an attractive (actively courted before and after) female may have confused the male. We have seen absolutely unmistakable insertion attempts made by an *Argiope* male on a prey item being consumed by the female he was courting. We thus feel that this interpretation is not too fanciful (see Discussion). We give here our field notes on a similar incident that occurred several days later: "10.54, male jerks on the spot, leg rubs and then moves closer to the female, rests there then does further walkabout with jerking, silk attachment ×3 and rest, then moves down onto corpse of prey abandoned by female but still in web—makes scrabbling movements close to surface, then abandons 11.05."

After approach/contact/retreat repetitions, we noticed a change in posture in the female in the one case where we could see clearly through the retreat walls (FIG. 16). It is tempting to think of it as an access posture. Certainly its adoption was followed by male excursions onto the female and by insertion attempts, but we could not say that all other such excursions were preceded by adoption of this posture. We never saw rapping and insertion attempts clearly but would guess that they resemble those units in other nephilinids. We saw several approaches that started from the dorsal surface of the female, after which the male ran around her body to finish up facing the epigyne.

In addition to the access posture, we saw 2 other female behaviors that occurred

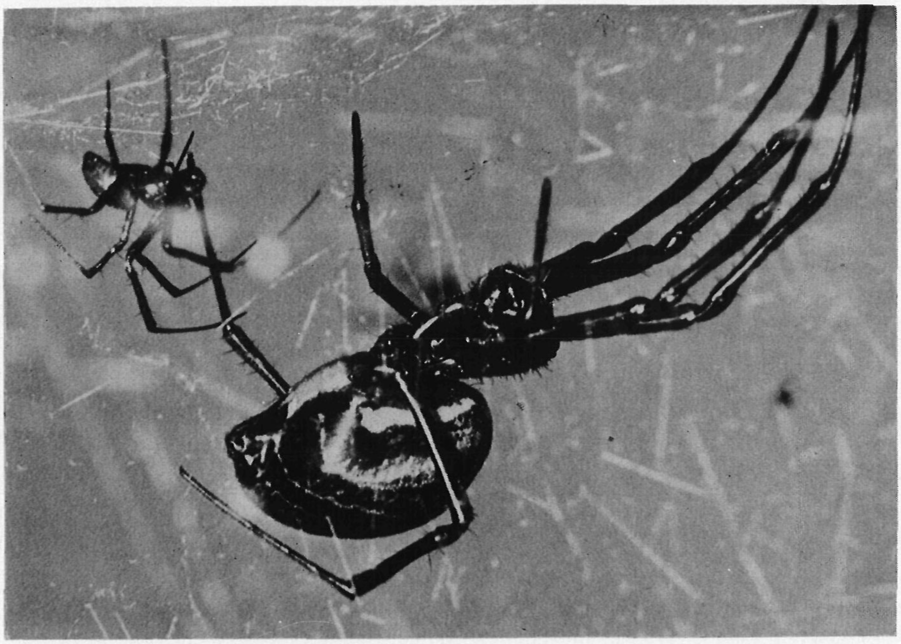


FIG. 16. Access posture of ♀ *Nephilengys malabarensis.* Note that her abdomen is hanging well below the roof of the retreat, allowing the ♂ to move onto her ventral surface.

during bouts of male approach/contact and could be responses to it or sexual signals of some kind. These involved movements of the pedipalps and of the abdominal apex. The pedipalp movements are simple up-and-down movements of both pedipalps out of synchrony with each other. At first we thought the female was rubbing the pedipalps against each other, but our film shows a distinct gap between them. The abdominal movements were not simply up-and-down movements as in male AWing, but also had a side-to-side component. They could certainly have transmitted vibrations to the web silk. We saw no evidence of male behavior being affected by these acts.

Copulation. We never saw the details of copulation in this species or *N. cruentata.* We saw males approach the epigyne and then emerge from the tunnel clearly having mated. Thus, the first time we saw this we recorded it as follows: "male no. 1 immediately moves along ventral face of female abdomen, scrabbles vigorously, circles abdomen at waist level then scrabbles again, insertion may have occurred—one pedipalp has embolus straight down, moves out backwards onto hub silk. Male now has one pedipalp in which the embolus is all twisted and points permanently forwards, bulbus (?) extruded . . . (12 minutes later) male bites off one pedipalp, the used-up one, wraps it . . . in jaws . . . and hangs it from the web." After another such presumed copulation, we saw the male repeatedly groom at the disfigured pedipalp with the tarsi of legs I and II as though trying to push the end off. This male was subsequently captured, and overnight, in a holding vial, he removed this part.

From these and similar data we assume that copulations are brief; we have no timings on insertions but in no case did the male spend longer in the retreat than 2 min. If the male went immediately into copulation and withdrew immediately to the outside this would, at the most generous estimate, put the copulation time well below that of other nephilinids.

Interactions between males. Males interact aggressively and overt fighting occurs. During such fights the subordinate male may end up dropping off the web on his dragline. Prior to fighting and chasing, males may carry out duels of web-shaking.

Nephilengys cruentata (Fabricius) FIG. 17

This species was common on the buildings of the International Institute for Tropical Agriculture (IITA) at Ibadan, Nigeria, and in the departments of Zoology and Botany at the University of Ghana, Legon, Ghana. We have only 11 h of observations on it and saw only male/male interactions and approaches to the female in her retreat. However, we did census webs at both localities and include these data here.

The species has polymorphism in male size, males show the suitor phenomenon and eunuchs occur. The males approach the female in her retreat (shown in FIG. 17) and move about juddering close to the retreat mouth and on its outer walls. It is almost certain that mating occurs within the retreat after contact courtship. Males on the web interact vigorously and we saw chases and fights. Eunuchs stay close to the retreat and may rest for long periods, clinging to its outer surface. Females are somberly colored but marked with large bright red to yellow patches on ther ventral surfaces. Robinson & Robinson (1973) give an illustration of the web and notes on predatory behavior.

At IITA, Ibadan, we censused 20 webs that contained a total of 28 males. Of these, 7 were entire, 5 had one pedipalp missing, and 16 were eunuchs. At Legon we censused 30 webs, of which 17 had associated egg-cocoons and 18 had males present. Of the 25 males present in the 18 webs, 14 were eunuchs, 9 were entire and 2 were unilaterals.

Subfamily ARGIOPINAE

Argiope aemula (Walckenaer) FIG. 18–21

Some notes on the natural history of this species are given in B. Robinson & M. H. Robinson (1974) and Robinson et al. (1974). It is a large, striped species and was the 1st *Argiope* whose mating behavior we studied. This was fortunate, since courtship proved to be complex and exciting. Our entire study was stimulated by our observations on *N. maculata* and *A. aemula* during our first visit to New Guinea (1970–1971). The webs of this and all the following *Argiope* species are more symmetrical than those of the preceding nephilinids. Thus, to reach the hub where courtship

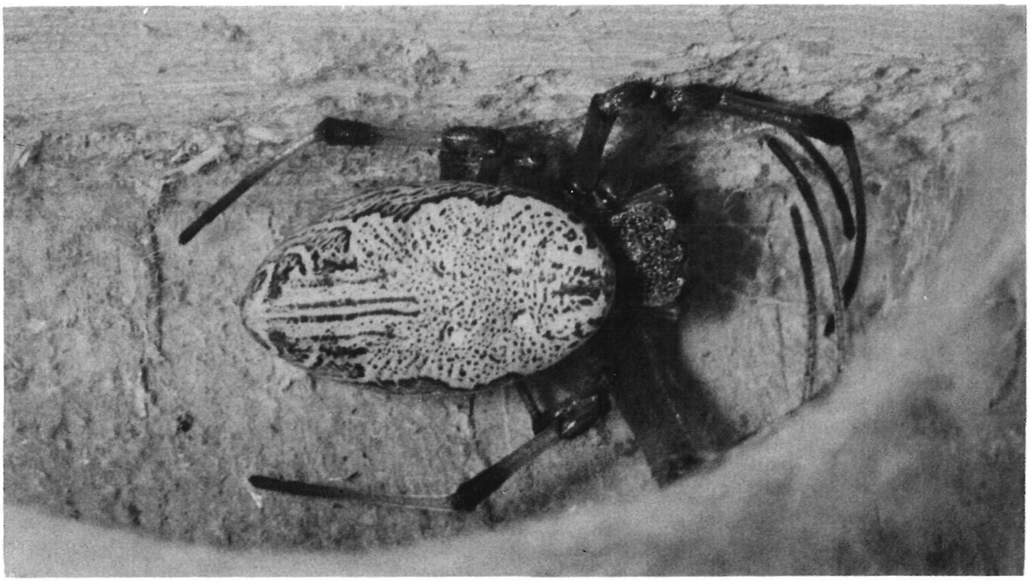


FIG. 17. Female *Nephilengys cruentata* in her retreat, seen from below. There is no space between her ventral surface and the substrate.

takes place, the males have to traverse an extensive area of prey-capture zone. Furthermore, there is no extensive "neutral " zone above the hub or retreat and a barrier web may be entirely absent from the adult web. All the species with group A courtship, with the exception of *A. aurantia,* have a cruciform stabilimentum when this structure is present in its complete form.

Approach behavior. Males move onto the foundation lines of the web from surrounding vegetation, via web supports or by draglines that they stream out when moving from place to place. On arrival at a web, they do not always pass immediately down the web to the hub, but often assume resting positions hanging from the upper foundation thread. In such rest positions, the males assume cruciform postures that are similar to the diurnal predatory postures of both males and females. Males may return to the web periphery and assume such hanging postures after visiting the hub, where they apparently assess the mating readiness of the female. A number of males resting on webs of females build miniwebs within the frame of the females' webs. These consist of a frame, radii and a temporary spiral. We have not found them with a viscid spiral, and they are much smaller than webs built normally by penultimate instar males. A frequent site for such webs is a web corner that is often roughly triangular, being bounded by an upper and lateral foundation thread on the outside and a 2nd-order foundation thread on the hubside.

The spider approaches the hub along a radius and our studies show that in this species approaches along the lower side of a radius exceed those on the upperside by almost 2:1. As the male walks down the radius, one leg IV is extended more or

ARGIOPE AEMULA

FEMALE BEHAVIORS	MALE BEHAVIOR ON FEMALE	MALE BEHAVIOR ON WEB
female at hub		male approaches down 11 o'clock radius
		plucks x5
		shuttle to upper surface hub
		rest in X (30 min. +)
		walkabout upper surface hub in posterior Vee
		rest
		walkabout upper surface hub in posterior Vee
		walkabout touching legs through hub
stilts body		III, IV-L, then III, IV-R
		rest
		walkabout, touching legs
		rest
		walkabout
bounces on the spot		14 repetitions walkabout/rest all on upper surface hub
		shuttle onto lower surface hub
at rest at hub		walkabout
		scrabble at legs III, IV-R
		rest
		walkabout, scrabble at sides of abdomen
		in left Vee, then legs right Vee
		rest
		30+ repetitions of walkabout
		scrabble at legs body
		onto female dorsal surface
	trails dragline across female	
	left Vee to right Vee	
grooms intensively	right Vee to left Vee	
	onto web	
		walkabout in Vee posterior
		scrabble at legs apex abdomen
		onto female dorsal surface
	trails dragline across female	
	anterior Vee to posterior Vee	
	left Vee to right Vee	
	rest on dorsal abdomen	
	circle under female L - R	
	onto hub	
		walkabout on hub
		rest
		walkabout
		onto dorsal surface of female
female's legs III off web	repetitions of dragline	
	deposition to total of 47	
	side-to-side moves	
	down ventral surface abdomen	
	insertion scrabbling	
	onto web	
		walkabout
		onto female
	down ventral surface of female	
	insertion scrabbling	
bend at waist, drop slightly	insert	
place legs III on male	twist sideways	
scrabble at male, start to wrap	male jumps off on dragline	

FIG. 18. Conventional summary diagram of courtship in *Argiope aemula*. For explanation of abbreviations, see FIG. 5.

less stiffly behind the spider. Since it does not make walking movements we believe that it is holding out the dragline behind the male. The spider walks along the radius with legs I and II and may be merely fending itself off the viscid spiral elements with the posterior legs. Having repeatedly examined film of this approach walking, we think that the spider may be pulling itself forwards "hand-over-hand," with the 2 sets of anterior legs doing most of the work. Certainly many approach walks leave behind a trail of snarled, stuck together, and displaced viscid spiral elements. This disruption, usually to one side of a radius, appears to be caused by the trailing posterior legs. We have at least one record of the spider cutting away a substantial area of viscid spiral after seeming to become entangled on its way down to the hub. Once the male reaches the free zone, it almost always shuttles to the upper surface of the web if it is approaching down the lower surface. During approach walks along radii, the males characteristically make jerking movements while briefly pausing. Film shot at 24 frames per second (fps) does not allow these movements to be analyzed.

The history of the movements of one male that we followed for several hours provides an interesting example of approach behavior and its possible species-recognition function. We introduced this male onto the upper foundation thread of an *A. aemula* web at 0900 h on 13 December 1973. It immediately went down to the hub on the lower side of a radius, jerking it as it went. At the hub it shuttled to the upper surface and courted sporadically until 1045 h when it left via the upper foundation thread and moved off "at great speed." At 1051 h it arrived at an *A. picta* web some 2.25 m away and descended to the hub of this web, jerking during the descent. The approach elicited no overt response from the adult *A. picta.* At the hub the male went through initial courtship and then moved onto the body of the female. [This movement is typical of the 2nd stage of *A. aemula* courtship (see below) but does not occur in *A. picta* courtship.] At 1128 h the male left the *A. picta* web, unmolested, after nearly 37 min. of activity at the hub of the wrong species. It moved onto the web of another female *A. aemula* nearby, descended to the hub, and performed a walkabout, left this web at 1140 h and moved onto the *A. picta* web again. At the hub, the male eventually climbed over the female, at which time she shook her anterior legs and he dropped off; he eventually regained the web and walked to a 2nd *A. picta* web some 2.5 m away. This female flailed her legs during his approach and he left the web and moved along a line towards an immature *A. aemula.* This attacked him at the edge of the web. He then constructed a skeletal complex of threads and remained inactive for the rest of the day. The male was active from 0900 h to 1208 h and in this time visited females of *A. picta* at the hub on 3 occasions and females of his own species on 2 occasions. We have one record from this period of a *N. maculata* male visiting an *A. aemula* female at the hub and subsequently remaining on the upper foundation line of her web for an entire day.

Courtship. Courtship in this species is complex and involves exhaustive silk-binding behavior that is more comprehensive than that seen in *N. maculata.* TRs and TRing are entirely absent from the courtship of this species. On arrival at the hub, the male starts courtship with sporadic walkabouts on the upper surface of the hub. During these, the male's route is largely confined to the area within a circle containing the outstretched legs of the female. The male tends to move along the line of the outstretched legs during these perambulations, and as the walkabouts proceed, starts to reach through the hub silk and touch the female's tarsi.

Gradually, walkabouts on the upper surface become interspersed with shuttling onto the lower surface and more contact with the female. Unless the female reacts

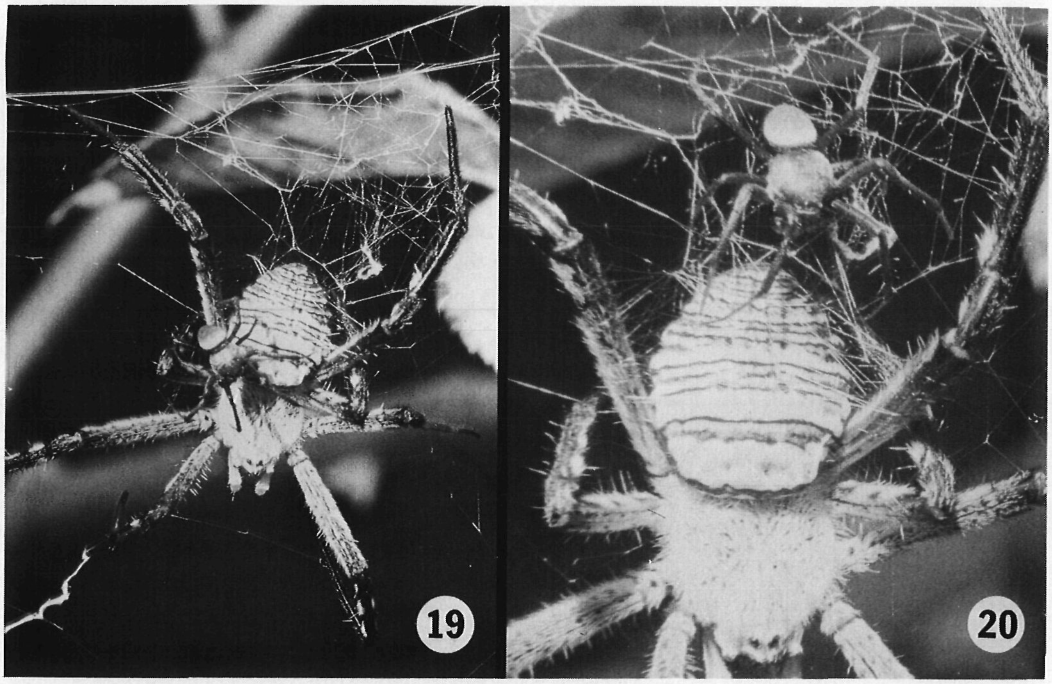


FIG. 19–20. *Argiope aemula*: **19,** ♂ on dorsal surface of ♀ during binding (see text); note many threads extend across abdomen and legs and that the ♀ legs III are against the sides of her abdomen. **20,** detail of binding silk on legs and abdomen of ♀; notice the many more than 20 threads attached to ♀ leg IV on her right side.

violently, she is then subjected to more frequent touching from her side of the hub. Then the male climbs onto her dorsal surface and traverses it from side to side. Traverses may be roughly longitudinal, latitudinal or oblique. Analysis of still photographs and occasional glimpses of sun-glinting silk in movie sequences show that silk is being laid down in all these movements and it is attached both to the surrounding web and onto the legs and body of the female. Strands may connect the leg elements to the dorsal surface of the spider. FIG. 19 and 20 give some idea of the complexity of binding. The male moves from the web across the female and onto the web, and may start from the posterior V between the left and right legs III and IV, or from the lateral V's (left and right) between legs I and II, and III and IV, or from the anterior V. In the latter case, the male climbs onto the female over her pedipalps and chelicerae and walks over her eyes. Eventually, if he is successful, the female stilts her legs and stands away from the web. At this point, the tarsi of her short 3rd legs are taken entirely off the web and held against the undersurface or side of her abdomen. These 2 postural changes considerably increase the clearance beneath the female's body. The stilting is clearly an overt female behavior response to courtship. The movement of the 3rd legs is more difficult to interpret. The male certainly

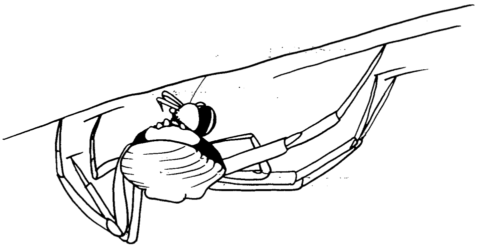


FIG. 21. Tilted acceptance posture of *Argiope aemula* as seen from above. The ♂ is in copula, twisted through 90° (see text).

attaches lines to these and from time to time pushes against them from the hub's surface. Thus the female could merely permit the male to move them off the web, or actively move them herself in response to his particular stimulation of them. She could also move them as a response to general stimulation. We cannot be sure. We also saw a variant of the female acceptance posture in which the body was tilted to one side by differential stilting of the left and right legs (FIG. 21).

As the male moves over the surface of the female, his body is arched. This arching brings the extremities, the pedipalps and the spinnerets, into contact with the female's body. This is suggestive of a fairly tight binding being effected by the silk being stretched close to the female or of the silk binding being laid down against the body surface, or both. Once the female has adopted an acceptance posture, the male circles beneath her in addition to moving from side to side. At this stage, judderings against the apex of the female's abdomen and/or the dragline, or simply on the hub silk, become quite frequent and the male starts to make sorties onto the female that involve insertion attempts. These are made both from the posterior V, and from the lateral V's. Insertion attempts are very distinctive indeed, and easily separable from the movements involved in binding (although the latter also involve touching of pedipalps against the female body surface). Two features are diagnostic of insertion attempts: the anterior legs are always strongly flexed and obviously not in walking postures, and the spider rocks vigorously to and fro during the attempts. This fore-and-aft movement is presumably necessary to drive the embolus into the epigyne from the side rather than from above, as in nephilinids (see above). Insertion attempts take place both (appropriately) on the ventral surface and on the dorsal surface. We have seen many different males on the dorsal surface apparently stimulated by the raised and protuberant anterior and lateral edges of the abdomen. These are, in effect, crenulated and may possess some of the tactile properties of the boss-like epigyne.

In addition to assuming an acceptance posture the female may respond at the silk-binding stage of courtship by grooming herself free of the silk. This grooming can take some time and she gives particular attention to the pedipalps, eye region, and frontal aspects of the cephalothorax. Such grooming bouts do not necessarily presage an unsuccessful courtship. One courtship that we watched lasted over 85 min. Before the female adopted her 1st acceptance posture, there were 31 complete side-to-side movements, then 32 with ventral circlings among them. The female cleaned off the silk 7 times. The judderings occurring in the later stages of this long courtship include at least 12 bouts in contact with the abdominal apex, dragline or legs IV, and 6 noncontact bouts of which 3 were on the upper surface of the hub. The male made a total of 16 insertion attempts, of which 2 were inappropriately oriented to the lateral abdominal margin. We did not score all the walkabouts but noted 18 on the upper surface of the web and 33 on the lower surface. After a right pedipalp insertion, this male went on to further courtship and a successful left insertion. We do not know what constitutes a "typical" courtship in terms of duration and number of different elements, but the one above is certainly not unusual.

Copulation. There are, as far as we are aware, no detailed descriptions of *Argiope* spp. copulations in the literature. This is understandable, since the movements involved after insertion are very rapid indeed and do not yield easily even to cinematographic analysis. It is necessary to film the male in profile on the female's abdomen in order to see the insertion and then transfer to a view of him through the hub silk to see details of the assumption of the complex copulatory posture. This presents considerable technical difficulty. The following account is a composite based on analysis of filmed sequences of a number of different copulations and direct observations of many more. The assumption of the copulatory posture occurs in a fraction of a second and by direct observation it is impossible to resolve the components.

Insertion in *A. aemula* seems to take place when the male drives the embolus from a position anterior to the erected epigyne. We have only 2 clear movie sequences of this, but in both cases the bulbus of the pedipalp was close to the abdominal surface (perhaps touching it) and the embolus must, therefore, have been more or less parallel to the surface, directed at the anterior side of the epigyne rather than down onto it from above. The anteroposterior insertion movements of the entire male body must move the pedipalps backwards and forwards, which again suggests a kind of near-horizontal insertion. Certainly the spider does not make conspicuous press-up movements nor does it make knocking movements with the pedipalps.

Immediately on insertion the male turns around through 90°. From a venter-to-venter position facing in the same direction as the female, the male comes to lie across her body with the anterior edge of the cephalothorax over the epigyne and the apex of the abdomen close to the edge of the female's abdomen. In this position the male appears to be crouching against the female's body surface with the edge of his body corresponding to the inserted pedipalp closest to her surface and the other sometimes slightly raised. (Thus, if the left pedipalp is inserted, the left side of his body is closest to the female's cuticle and vice versa. Designating the direction in which the male turns can be confusing. When the male turns to face the left after inserting a left pedipalp, its body swings to the right. Adding to this confusion is the fact that, since the pair are venter to venter, the male's right is to the female's left and vice versa.) The male appears to turn about the locus formed by the inserted pedipalp and as he

TABLE 2. Summary of courtship and mating behaviors in tropical araneid spiders.

SPECIES	BEHAVIORS*																				
	Multiple insertion	Juddering	Walk to epigyne	Opportunistic mating	Courtship at hub	Suitor phenomenon	TR walkabout	TR contact	Hub mating thread	Insertion twist	Postcopulation attack on web	Acceptance posture	TR vibratory courtship	Postcopulation courtship	Copulation duration**	Outside thread	Jerk or twang	AWing	Copulation at hub	Postcopulation attack on mating thread	Leap apart
GROUP A																					
Nephilinae																					
Herennia ornatissima	+	+	+	?	+	+	0	0				⊕			<1–17						
Nephila maculata	+	+	+	+	+	+	0	0			R	0			<1–48						
Nephila edulis	+	+	+	?	+	+	0	0			R	0			<1–11			+			
Nephila pilipes	?	+	+	+	+	+	0	0		+	R	0			<1–27						
Nephila madagascariensis	+	?	+	?	+	+	0	0			?	0			<1–??						
Nephila clavipes	+	0	+	+	+	+	0	0			R	0			<1–22						
Nephilengys malabarensis	?	+	+	?	+	+	0	0			R	⊕			<1–2						
Nephilengys cruentata	?	+	+	?	+	?	0	0			?	?			???						
Argiopinae																					
Argiope aemula		+	+	?	+	?	0	0		+	+	⊕		+	<1–(2)***						
Argiope reinwardti			+	?	+	?	0	0		0	+	⊕		+	<1–			+			
Argiope argentata			+	?	+	+	+	+		+	+	0		+	<1–(38)†						
Argiope aurantia			+	+	+	+	0	0		0	+	+		+	<1–(1.5)						
GROUP B																					
Argiopinae																					
Argiope picta					+	0	+	+	+	+	+	+	+	+	<1						
Argiope aetheria					+	0	+	+	+	+	+	+	+	+	<1						
Argiope sp. Wau no. 5					+	0	0	?	+	+	+	+	+	+	<1			+			
Argiope sp. N.T. riverine					+	0	+	+	+	+	+	+	+	+	<1–6			+			
Argiope sp. Singapore no. 1					+	0	+	+	+	+	+	+	+	+	1–35 sec			++			
Argiope savignyi					+	0	0	0	+	+	+	+	+	+	<1			+			

TABLE 2. Continued.

SPECIES	Multiple insertion	Juddering	Walk to epigyne	Opportunistic mating	Courtship at hub	Suitor phenomenon	TR walkabout	TR contact	Hub mating thread	Insertion twist	Postcopulation attack on web	Acceptance posture	TR vibratory courtship	Postcopulation courtship	Copulation duration**	Outside thread	Jerk or twang	AWing	Copulation at hub	Postcopulation attack on mating thread	Leap apart
															BEHAVIORS*						
Argiope florida					+	0	+	+	+	+	+	+	+	+	<1			+			
Argiope flavipalpis					+	0	0	0	+	+	+	+	+	+	<1			+			
Argiope aurocincta					+	0	0	?	+	+	+	+	+	+	35 sec			+			
Argiope cuspidata					+	0	+	+	+	+	+	+	+	+	28 sec			?			
Argiope ocyaloides					+	0	+	+	+	+	+	+	0	+	32 sec			+			
GROUP C																					
Argiopinae																					
Gea sp. Wau no. 1												+	+	+	<1	+	+	0		+	
Gasterocanthinae																					
Gasteracantha taeniata												+	?	+	40–80	+	?	0	+	0	+
Gasteracantha theisi												+	?	+	33–130	+	?	0	+	0	+
Gasteracantha brevispina												+	?	+	58–104	+	?	0	+	0	+
Gasteracantha sp. Wau white												+	?	+	43–76	+	?	0	+	0	+
Gasteracantha sp. Singapore												+	?	+	6 & 28	+	+	0	+	0	+
Gasteracantha falcicornis												+	?	+	18–112	+	+	0	+	0	+
Gasteracantha curvispina												+	+	+	28–68	+	+	0	+	0	+
Gasteracantha versicolor												+	+	+	63–97	+	+	0	+	0	+
Gasteracantha cancriformis												+	+	+	38–131	+	+	0	+	0	+
Isoxya tabulata												+	+	+	75	+	0	0	+	0	+
Isoxya cicatrosa												+	?	?	?	+	?	?	?	?	?
Aetrocantha falkensteini												+	?	?	?	+	?	?	?	?	?
Micrathena sexspinosa												+	+	+	<1–1.5	0	0	++			+
Micrathena schreibersi										+		+	0	+	1–2.75	+	0	++			+
Micrathena sagittata												+	0	+	<1	+	0	+			+

TABLE 2. Continued.

SPECIES	Multiple insertion	Juddering	Walk to epigyne	Opportunistic mating	Courtship at hub	Suitor phenomenon	TR walkabout	TR contact	Hub mating thread	Insertion twist	Postcopulation attack on web	Acceptance posture	TR vibratory courtship	Postcopulation courtship	Copulation duration**	Outside thread	Jerk or twang	AWing	Copulation at hub	Postcopulation attack on mating thread	Leap apart
Micrathena clypeata												+	?	?	?	+	?	?			?
Micrathena duodecimspinosa												+	?	?	?	+	?	?			?
Araneinae																					
Cyrtophora nympha												+	+	+	<1	0	+				+
††*Mecynogea lemniscata*	+											+	0	0	28–43	0	0	+			0
Zilla sp. Wau no. 1												+	+	+	<0.5	+	+				++
Zilla sp. Wau no. 2												+	+	+	<0.5	+	+				++
Eriophora fuliginea												+	+	+	<0.5	+	+	+			++
Cyclosa insulana												+	+	+	<0.5	+	+				++
Cyclosa sp. Mt Kaindi no. 1												+	+	+	<0.5	+	+				++
Cyclosa sp. alpine grassland no. 1												+	+	+	<0.5	+	+				++
Cyclosa bifida												+	+	+	?	+	+				?
Cyclosa sp. Wau no. 5												+	+	+	<0.5–80 sec	+	+				+
Cyclosa caroli												+	+	+	<0.5	+	+				+
Mangora bimaculata												?	+	?	?	0	?				?

BEHAVIORS*

* + = yes, ++ = behavior particularly well developed, 0 = no, ? = not known, ⊕ = partial, R = rare.

** Times in minutes unless otherwise designated.

*** For explanation of parentheses, see text.

† = died in copula.

†† Subfamily Argiopinae according to Roewer (1942), but belonging here by our classification.

turns he folds up the long legs I, II and IV so that they present a very low profile and do not project beyond the edge of the female's abdomen. (Compare this leg posture with that adopted by males of *N. pilipes* shown in FIG. 10).

The female almost always responds to the start of copulation by flexing her body at the waist (pedicel) so that the apex of the abdomen is directed more ventrally and the cephalothorax forms an oblique angle with the abdomen. The male is slightly posterior to the inflexion point between the 2 parts of the female's body. Several things happen coincident with this bending. The female reaches back with her pedipalps and repeatedly touches the male with them; during this touching they move independently. At the same time, the female brings the tarsi of both 3rd legs onto the dorsal surface of the male and may also fold the anterior tarsi over him. The total length of the male's body is less than 5 mm and only the tips of the tarsi contact him. The leg movement is reminiscent of the movements made by spiders to groom their undersurface when apparently irritated by the movements of unwanted males (and also theridiid kleptoparasites). It starts off as such a brush-off movement and then, instead of developing, the tarsi simply remain in contact with the male rather than scraping forwards. It could be a scraping movement inhibited by sensory input from the epigyne or pedipalps (see Discussion). Certainly at the termination of copulation the tarsi of legs III are used to move the male forwards toward the chelicerae. On the other hand, the movement also looks as though the female is clasping the male against her. After the first 10 s or so, legs I and II are lifted off the male (if they were initially involved) and the tarsi of legs III may also be intermittently lifted.

In one copulation the female turned at the hub so that she eventually hung beneath the web plane with her ventral surface uppermost and the anterior body facing away from the web. We have no explanation of this posture. The male was in copula for a longer than average time and was apparently dead when removed by the female.

Most copulations average less than a minute (TABLE 2) and are most frequently terminated by the female. Usually the male is pushed forwards by the 3rd legs and lightly held in the jaws while he is wrapped. During the pushing forwards he may escape by jumping away from the female and dropping out of harm's way. At this stage the male may lose one or more legs and the female will proceed to wrap these tiny remnants of the male. The probability of being caught on the 2nd copulation is much higher than on the 1st. After a successful copulation and escape, the male will court the same female again and insert the 2nd pedipalp (the one not used in the 1st copulation). We have a record of a male that had lost all his left legs, but for leg I, in his 1st copulation, and successfully completed a 2nd one with only 5 legs to use for the approach, insertion attempts and copulation twist.

We saw one copulation terminated by the male. This occurred when the female rushed out on a predatory excursion when the male was in copula. He jumped off and resumed courtship after the female returned to the hub with her prey.

Interactions between males. None observed.

Argiope reinwardti (Doleschall) FIG. 22–24

This large species superficially resembles *A. aetheria.* Notes on its natural history are given by Robinson et al. (1974) and B. Robinson & M. H. Robinson (1974). It is widely distributed in the Wau Valley and is locally common on the slopes of Mt Kaindi. We have extensive notes on the courtship behavior of this species but only saw 3 successful copulations. We cannot explain the low success rate (3 out of 34 long courtships ending successfully). Size polymorphism is quite conspicuous in males of this species.

On 2 occasions in the field, we came across females that had attracted unusually large numbers of males. Both of these were newly ecdysed adults. One had 2 males at the hub of the web and 2 resting in X positions on the web frame. The other was feeding on a male, had an additional male at the hub and 2 on the web frame, with a 5th male resting beneath a grassblade to which the upper foundation thread was attached. Both the females were in clumps of adult females; the 1st had 5 females within a 2 m radius, the second had 8. None of the nearby females had males present.

Approach behavior. Males of this species move onto female's webs and may remain there, resting in X postures and occasionally building skeleton webs within the web frame (as described for males of *A. aemula*). We had one marked male remain on the same female's web for 7 days, after which it disappeared. We did not, of course, keep it under continuous observation during this period, but did not notice it at the hub of the female's web at any stage. It could have made such a visit and we would certainly have missed it if it had remained there for less than an hour.

We have data on 18 approaches that resulted in males establishing themselves at the hub of the female's web. Only one of these was made across the upper surface of the web. All but one were accompanied by jerking movements and all the males arriving at the underside of the hub shuttled to the upper surface on arrival. Fourteen approaches were slow and hesitant and 4 were rapid (one involved the male running down the 11 o'clock radius). Multiple approaches occurred in 6 cases; in these, the male made a number of false starts down radii, into the viscid spiral zone, and then returned to the web frame without penetrating very far. Several times when we placed males on the web, the female reacted by orienting towards the male and shaking vigorously. Males subjected to this treatment either froze or dropped off the frame threads. We never saw a male arrive naturally and receive this treatment (but only 9 encounters were not contrived by us and we only saw 4 of these males arrive and approach). It seems possible that in contrived introductions we may have dropped the male on the web frame in such a way that it caused an impact vibration that was more strongly alerting to the female than merely walking onto the web. Certainly one of the males that dropped off when shaken-at fortuitously drifted onto the hub of the web, on its dragline, and there walked unmolested for over an hour of preliminary courtship.

Many male approaches must occur in the early morning because we found males

ARGIOPE REINWARDTI

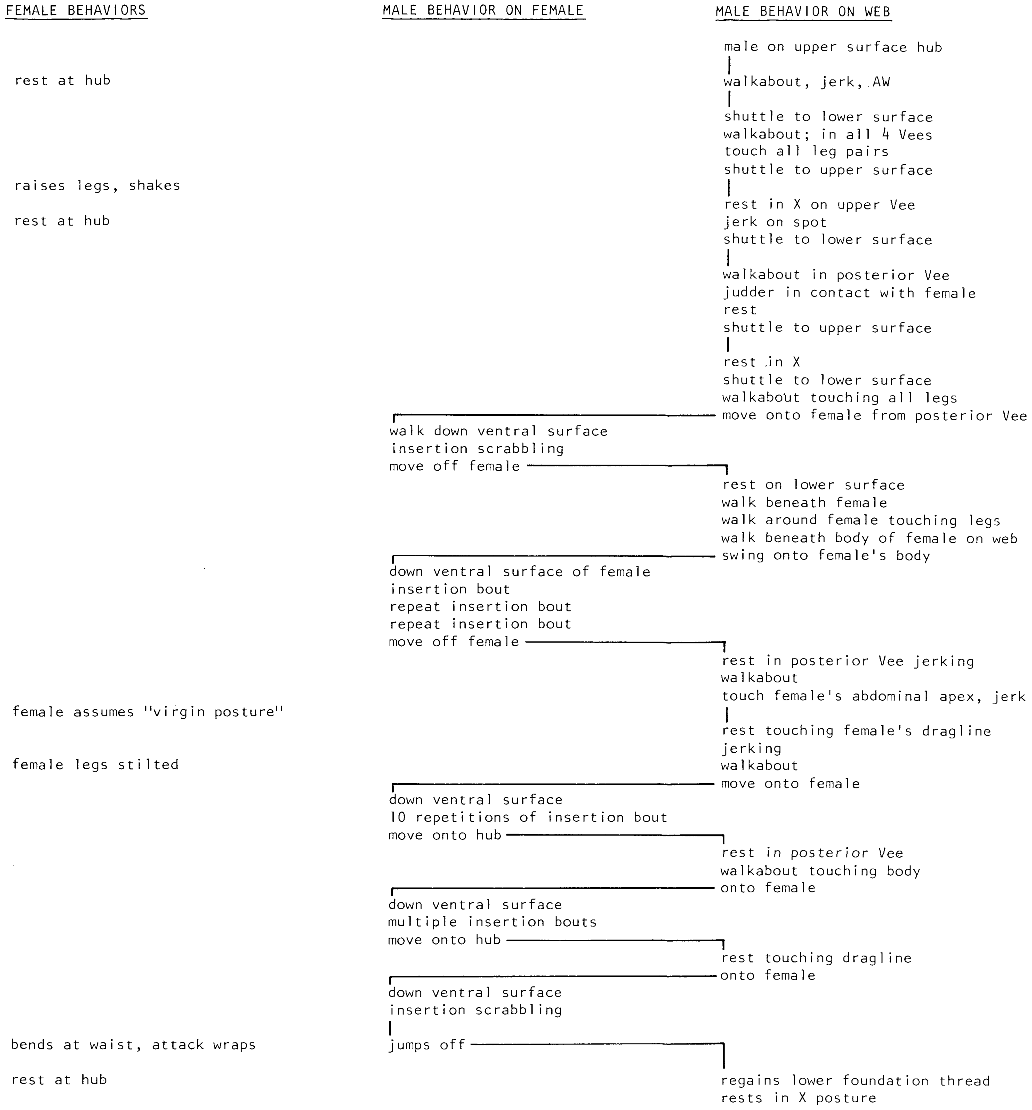


FIG. 22. Conventional summary diagram of courtship in *Argiope reinwardti*.

that we left on frame threads overnight had reached the hub before we started observations (1–2 h after sunrise). Like the males of *A. aemula,* the males of *A. reinwardti* plainly make mistakes and move onto webs of females of other species. We collected a large male that we suspected to be *A. reinwardti* from the hub of an *A. picta* web, and it went through typical *A. reinwardti* courtship when placed on the web of a female of the right species.

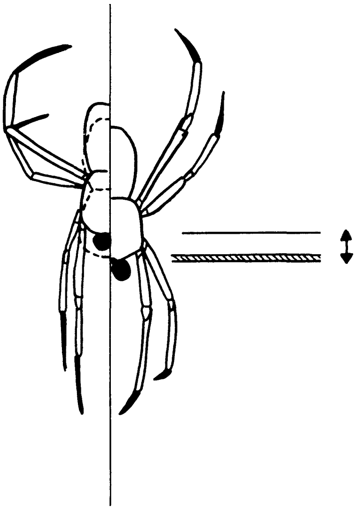


FIG. 23. *Argiope reinwardti.* Diagram of ♂ jerking movements; right side of midline shows the extreme forward position, left side shows small jerk (dotted) and powerful jerk (continuous lines); distances of movement indicated by lines on right side of diagram.

Courtship. Courtship in this species is relatively simple. It consists of 2 or possibly 3 phases. As in the case of *A. aemula,* the 1st phase consists of extensive walkabouts at the hub, first on the upper surface, then on the lower surface. This is followed by a phase of movement onto the ventral surface of the female abdomen, accompanied by insertion attempts. This 2nd phase could be arbitrarily divided into 2 parts: an initial phase when movements are largely into contact with the apex of the female's abdomen and insertion attempts are intermittent and few, and a later phase when insertion attempts predominate.

The walkabout phase of courtship involves silk deposition at the hub. Presumably the male attaches its dragline whenever it pauses, for the hub silk soon becomes carpeted with a maze of silk lines that are much finer than the structural silk of the female's web. Abdomen wagging occurs prominently throughout the walkabout phase and continual dragline attachment would allow AWing to transmit vibrations to the hub silk. The male walks almost entirely in the area contained by a line drawn to connect the tips of the female's tarsi and tends to be concentrated in the V of the posterior legs. Between walkabout bouts, the male may rest in an X posture in this V. As the walkabouts extend onto the lower surface of the hub, the male touches the legs of the female and from time to time scrabbles at them with legs I and II. Throughout the walkabout phase the male indulges in jerking on the spot. In our notes we characterize these jerkings as consisting of both high- and low-intensity components, for instance, expressed as "da da di di di"; movie analysis to some extent confirms this observation as shown in FIG. 23. We also expressed this tendency for high-amplitude movements to be followed by a train of low-amplitude ones as

— — · · · ·, — · · ·, — — — · · · · · ·, and so on. The largest number of high-amplitude movements preceding a train of dots was 3, the train of low-amplitude movements varied from ca 4–8. As courtship proceeds, the female stands in a more and more stilted position (Fig. 24) and may raise the tarsi of legs III completely off the web. We regard this as an acceptance posture. Prior to the movement of these legs, the male may approach the female in the lateral V's on the lower surface of the web and scrabble against and/or stroke the sides of the abdomen.

From time to time during walkabouts and approaches, males rub the pedipalps together and groom the first 2 pairs of legs (that have contacted the female). After careful examination of our notes and the appropriate movie sequences, we think that these movements are not ritualized signal movements but straightforward grooming. This species does not therefore have TRs in its courtship repertory.

Excursions onto the dorsal surface of the female abdomen are rare and confined to the apical ⅓ of that region. Unlike *A. aemula* males, those of *A. reinwardti* do not pass from side to side or end to end across the dorsal surface of the female. Approaches from perpendicularly above the female (i.e., from within the posterior V) frequently resulted in the male walking partway on the dorsal surface of the female so that legs I and II touch her body but legs IV, at least, remain on the web or dragline. These approaches occur frequently during the early stages of phase 2, but we have never seen a male standing entirely on the dorsal surface of the female. After a variable period of exclusively dorsal contacts, the male starts edging beneath the female's abdomen, following initial dorsal contacts with only the 1st legs and pedipalps. He frequently swings around an axis formed by the female's dragline to end up venter to venter with her abdomen. The male may then approach the epigyne, making insertion attempts but keeping one or both legs IV on her dragline. At this stage, the male may also walk down the web beneath the female and swing over onto her ventral surface. This is accomplished by seizing a foothold on the female with the legs of one side and then swinging through 180° to finish up venter to venter with the female. We have also seen a male lean away from a position standing on the web beneath the female to touch her ventral surface with his first 2 pairs of legs, while standing on the web with his other 4 legs. Approaches to the epigyne, accompanied by insertion attempts, occurred so frequently in the sequences that they must constitute a major stimulatory element of courtship in this species.

A female that is in the stilted acceptance posture may ultimately respond to persistent but unsuccessful males in 2 ways. She may adopt what, at the time of first observation, we called the "virgin pose." In this the 3rd legs are folded under the female's abdomen with their tarsi approximately over the epigyne region, apparently barring access to it. The 2nd behavior is more vigorous; the female simply lowers her body down to a position of contact with the hub silk, sandwiching the male against the web if he is on the ventral abdomen at the time. One male in these circumstances leaped off the female and dropped a considerable distance below the web.

We have one record of a male breaking off copulation attempts to move down

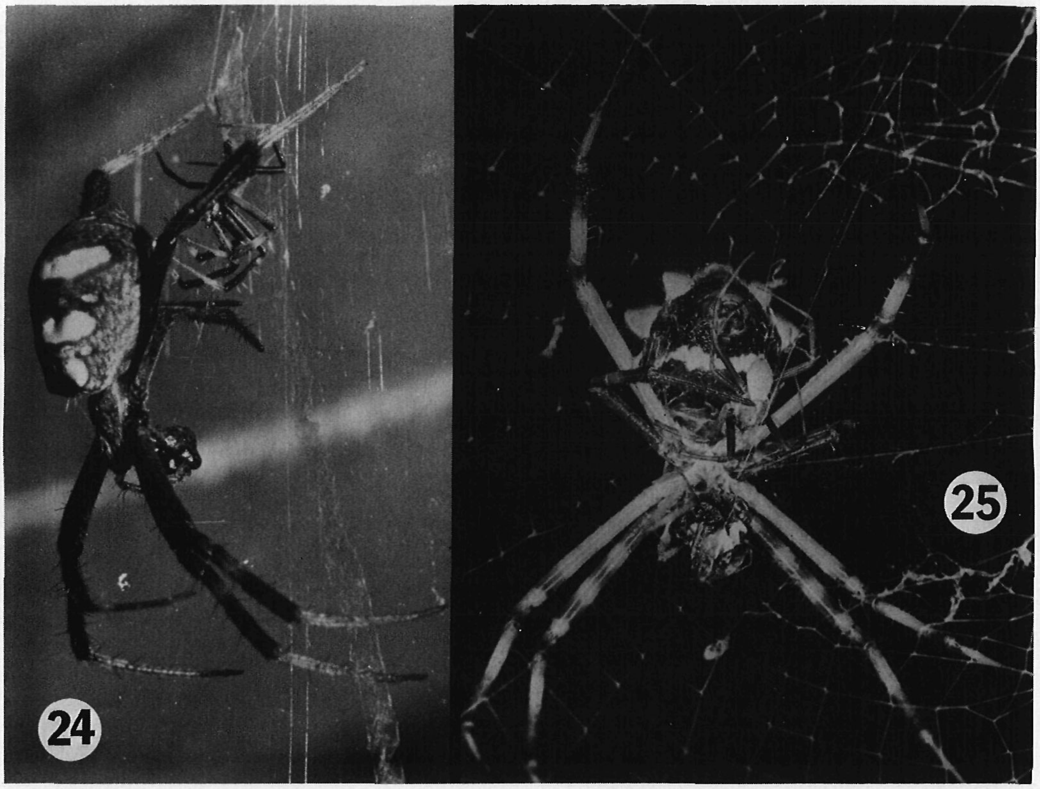


FIG. 24–25. **24.** Female of *Argiope reinwardti* at the hub of her web in a stilted posture. The ♂ is moving down her dragline, vibrating. **25.** Male *Argiope argentata* making type A courtship approach down the ventral surface of the ♀'s abdomen; she is fending him off with her left leg III.

across the ventral surface of the female's cephalothorax and feed on a prey item that the female was consuming at the time.

Insertion attempts in this species are similar to those of males of *A. aemula* in that they involve marked to-and-fro movements of the entire body. They differ in that the bulb of the pedipalp is held above the surface of the female's abdomen, perhaps the height above it of the erect epigyne. Our notes refer to rapping movements of the pedipalps, but subsequent movie analysis fails to confirm the existence of pedipalpal rapping. Its existence must be regarded as dubious pending further investigation.

Copulation. With the unaided eye, we saw 2 copulations and could not decide whether the male twisted to one side or not. The one copulation that we have, in its entirety, on film clearly did not involve twisting. The male inserted and immediately went into a prone position flattened against the female's abdomen with all his legs folded, but with the body parallel to the long axis of her abdomen. The male maintained this copulatory position while the female tried to wrap him, swinging her abdomen away from the web as in normal at-the-hub prey wrapping. She wrapped for more than 30 s but missed the male and merely enswathed some prey remnants on which she had been feeding. He eventually jumped off after 50+ s in copula and escaped with the loss of 2 legs. We saw 2 males caught and wrapped during insertion attempts. The female found feeding on a wrapped male in the field (see above) had this male stolen by another male while she was on a predatory excursion. He fed upon it for over 15 min.

Interactions between males. We saw no male interactions at the web frame but several at the hub when more than one male was present. Males courted simultaneously on 2 separate occasions (separate males, different females). Eventually they interacted and one chased the other from the hub. In one case, the males were on the hub and intermittently active for 33 min. without overt aggression; in a 2nd case, they coexisted for only 8 min. We saw males meet and touch, tapping each other, and part without fighting. After such contacts, chases usually developed. In one case, a male already at the hub, performing walkabouts, leaped off during the approach (across the web) of another male.

Argiope argentata (Fabricius) FIG. 25–27

This large, predominantly silver species has a wide distribution throughout Central and South America (Levi 1968). Over much of its range it is sympatric only with the apparently much rarer *A. savignyi* Levi and the pantropical but occasional *A. trifasciata* (Levi, ibid.). (We have never seen *A. trifasciata* in Panama during 13 years of field studies.) These species distributions may be critically important in evaluating the enigmatic aspects of *A. argentata* courtship behavior. The behavior and ecology of the species have been extensively studied (Robinson 1969; Robinson & Robinson 1970a, 1976b, 1978b). The species is highly dimorphic and there is intrasexual polymorphism in size (B. Robinson & M. H. Robinson 1978).

We have devoted more time to studies of the courtship behavior of this species than to any other and still have a major problem unsolved. [Our studies continue but we felt that we could not delay publication of this comparative study (started in 1970) any longer.] Of the species that we have studied, *A. argentata* alone is strikingly polyethic in courtship behavior. Both males and females can exhibit behaviors typical of all 3 groups into which we have divided courtship behavior. Group A behavior occurs more than 2× as frequently as the other 2 types combined. Group C behavior occurs more frequently than group B, but both, when they occur, are complete and functional in so far as they can lead to copulation. In addition, the species indulges in occasional forms of courtship that are intermediate between groups A and B, or abnormal and novel in comparison to the courtship behavior of the other *Argiope* species that we have studied.

Approach behavior. Approach across the web occurs principally on the underside. The male walks down the radius clearly belaying his dragline behind him and walking mainly with the 1st and 2nd leg pairs. One movie sequence shows that the 1st leg on the side of the spider away from the radius may tap and feel in a forward direction while the other leg I is walking. (This could be the case with the approach behavior of the species described above. It is a detail that is very difficult to determine.) As the male moves, he makes jerking movements. The approach may be direct and quite rapid, or characterized by a number of false starts. On arriving at the hub, the male almost always shuttles to the upper surface of the web. We have seen more than one male present on the hub for longer than 1 h.

Courtship behavior

Type A courtship. Courtship is in at least 2 phases. First there is a walkabout stage that occurs originally on the upper surface of the hub. This then proceeds to excursions onto the lower surface of the hub and merges into the next stage characterized by regular contacts and insertion attempts. The walkabouts differ from those of *A. reinwardti* described above in that AWing is either absent or extremely rare. Silk deposition occurs, but its effects are much less conspicuous than in the other *Argiope* spp. so far described. Walkabouts above the hub include jerking, touching the female's tarsi and pedipalps, and some genuine TRing. Males of this species cut holes in the hub silk through which they shuttle onto the lower surface. Walkabouts on the lower surface include touching and stroking the female's tarsi and frequent excursions beneath the arch of the female's body and legs. As the contact phase of courtship develops out of the walkabout phase, males pay less attention to the legs and repeatedly visit the apex of the female's abdomen. They usually descend the dragline to the spinneret region and stand on this, holding the dragline behind themselves with both legs III and IV while flailing at the surface of the female with both of legs I and II. Movement of the first 2 pairs of legs is almost exclusively against the undersurface of the abdomen and concentrated in the region immediately above and around the spinnerets. The males do not seem to judder or jerk on the spot during movements towards and onto the female's dragline. TRing against the abdominal apex, and on the dragline, occurs in conjunction with leg-flailing bouts. In the course of repeated movements up and down the female's dragline, we think it probable that this structure becomes coated with numerous elements of the male's dragline, and we would emphasize the similarity between the posture and movements of the male on this thread with its behavior on a mating thread (see below).

Males descend from the dragline to make insertion attempts (FIG. 25) and frequently make such attempts while clinging to the base of the female's dragline with the tarsi of legs IV. They also make excursions onto the female's abdomen by reaching up from below the female and swinging onto her body. We saw one copulation following insertion attempts that were made from a position in which the male stood on the hub and reached up with his pedipalps. Insertion attempts in this species are made with the entire body rather than by independent movements of the pedipalps. Compared with *A. aemula,* these movements are conspicuously dorsoventral. It is as though the male were performing press-ups at the downward limit of which the pedipalps, side by side, contact the body surface of the female. The aiming of the insertion attempts was sometimes very bad indeed. Some males deviated markedly to the right and others deviated to the left. Deviators of both types eventually managed to copulate successfully, but the existence of a tendency to run off the centerline and finish up on the crenulated abdominal edge is suggestive. Presumably whatever guides the male to the target is relatively inefficient. Males also had a tendency to move transversely across the abdomen, making insertion attempts, whenever they encountered the broad yellow band that in this species crosses the abdomen about 3 mm above the epigyne area. Deflection of insertion attempts along this mark is difficult to explain as other than a visual response (however improbable that may seem).

The nearest thing to an acceptance posture on the part of the female is a stilting of the legs that occurs following repeated male contact with the tarsi or at a very early stage in walkabouts. (The time of appearance of this posture may depend on the motivational state of the female.) This posture was sometimes accompanied by the raising of the 3rd legs off the web; however, these were not folded against the abdomen, but simply held apposed to the highly flexed 4th legs. The 3rd legs were used to brush at males moving on the ventral face of the abdomen when the female became apparently intolerant of male insertion attempts. We also saw females suddenly press their ventral surfaces against the hub silk in similar circumstances.

Type B courtship. After a period of walkabouts and contact with the legs, males indulging in type B courtship proceeded to cut a hole in the web close to the hub but beyond the attachment zone. This hole cutting was accomplished by cutting the inner end of a radius, then the outer end, and subsequently clearing away the collapsed portion of viscid spiral zone. Because of the tension on the web members, a large hole, more or less trapezoidal in form, is produced in a very short time (e.g., less than 30 s). The male bridges the gap from the cut end of the radius to the hub by moving backwards and forwards across his dragline several times. Since he laid down dragline when walking along the radius during the cutting operation, the gap is bridged from the moment of inception.

This multistrand thread is the mating thread of the male and on it he performs vibratory courtship, facing the female. If she does not respond after a courtship bout, the male may move to the insertion of the mating thread at the hub and go backwards and forwards over it, several times, laying down more silk. If the female is responsive she usually bounces on the spot at the hub and then turns towards the mating thread, bouncing. Bouncing by the female, prior to and during the turn to the mating thread, is very characteristic of all females responding to type B courtship. The female walks onto, or partly onto, the mating thread and drops into an acceptance posture, holding the mating thread with the tarsi of her short legs III and with one or both legs IV. The weight of the female is thus distributed at 2 points on the mating thread and this puts a compound flexure into the thread. The critical flexure is the one that is nearest to the male, that is, the one caused by the tarsi of legs III. After watching very large numbers of insertion approaches along mating threads in type B courtships, we are convinced that the relative position of the female's 3rd legs control the

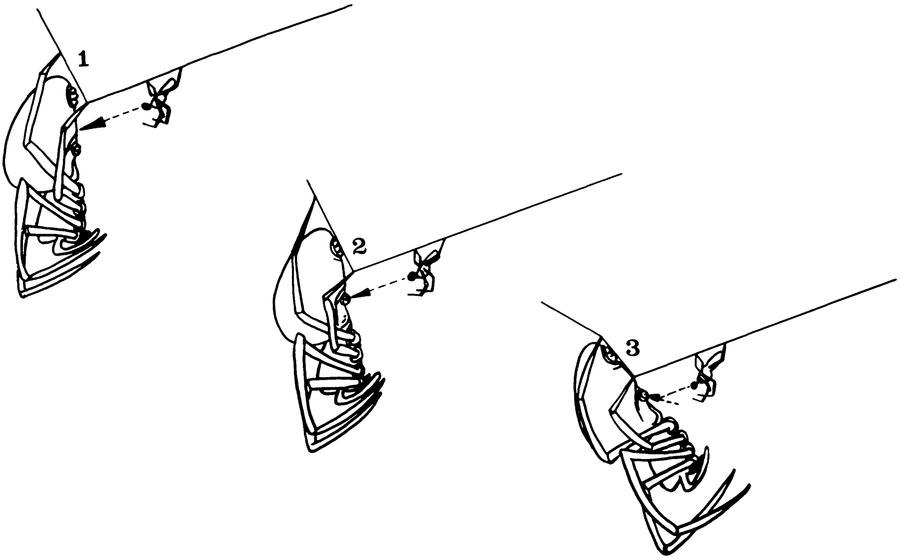


FIG. 26. *Argiope argentata.* Diagram to show how the positioning of the ♀ legs III and IV in the acceptance posture affects the relationship of the mating thread to the epigyne: 1, posture wrong, thread too high; 2, posture right for normal insertion; 3, posture right for upthrust insertion.

approach path of the male in an absolutely critical manner. If the dip point in the line caused by the tarsi of the 3rd legs is too far above the female's body, or too far back, the male running down towards the female's ventral abdomen does not arrive within contact distance of his target, the epigyne. This is shown diagrammatically in FIG. 26. Males do swing part of their bodies off mating threads at the critical point but they seldom, if ever, leave their mating thread altogether until after a successful insertion. It is worth noting at this point that the male approach to the epigyne in this type of courtship is directed by the mechanics of the mating thread, which are determined by the orientation imposed on it by the female, whereas in type A courtship the male's approach path is (or may be) self-determined.

As implied above, once the female has assumed an acceptance posture on the mating thread, the male starts to make insertion approaches. He is faced with a line sloping down to a large female that is exposing her ventral surface to him while hanging on his mating thread. He often runs down the thread towards her, but may stop within contact distance, turn back and make several aborted attempts before inserting and going into copula. Between such runs he may give further bouts of vibratory courtship and the female may scrabble at the mating thread or bounce on it.

In other species with this type of courtship, males can and do leap off the mating thread if the female approaches brusquely. We have also seen them cut the mating thread and thereby effectively isolate the female. We saw none of these behaviors in the case of *A. argentata.*

The vibratory courtship of the male *A. argentata* on the mating thread, as already noted, contains some of the elements seen in bouts of courtship given on the female's dragline in type A courtship. The main difference may lie in the effect of these movements when they are performed on the much longer mating thread. The male usually starts its vibratory courtship by TRing and follows this by bursts of bouncing that build up in intensity as they progress. The movements of the body and legs that are involved in bouncing on a mating thread are complex and varied. Not only is the nature of the movements varied, but so is the number of legs touching (or holding) the line and the position of the body relative to the line. [Analysis of the movements involved is made difficult by their speed and the small size of the males. The simple equipment we used was not capable of filming at speeds faster than 54 fps and, because of lighting problems, we were seldom able to use even this speed. We were restricted to 24 fps in all but the best conditions. When the male is less than 5 mm long (as was the case for nearly all the *Argiope* species) using sufficient magnification to produce a large image also restricts depth of field prohibitively. Thus the lateral oscillations produced by courtship movements easily take the subject in and out of focus and blur vital details. In the field, the movement of the web caused by wind-induced movements of the web itself and its supports greatly exacerbated this problem. Laboratory studies, in ideal conditions, using high-speed cameras, should eventually produce material for precise analysis. As explained earlier, neither our equipment nor our aims allowed for this.]

The male spider hanging below the mating thread could hang from tarsal holds provided by all 8 legs, or from complex combinations of these. Across a wide range of genera and species there appears to be a common tendency for legs III to be a point of suspension, with legs I, II and IV much more variably involved. The tarsi of legs III are placed on the line more or less opposite each other and the line of the legs forms a perpendicular to the mating thread. Legs I and II stretch forward and legs IV stretch back. TRing is done mainly with legs I and II and is usually unilateral. For instance, the left legs I and II are lifted off the line and the male appears to lean sideways as these legs TR. The spider may have only one leg IV on the line at any one time and frequently has both pairs of anterior legs off the line at once. Bouncing in *A. argentata* involves a movement in which legs IV slap the line and one or more of legs I and II strum on it. Discernable clearly on film is a vigorous extension and flexion of legs III against the line, which seems coupled with movements of legs IV to produce high-amplitude bounces. In a movie sequence of these movements, one tarsus IV is certainly not on the line and appears to the side of and above it. Another movement clearly involves the 3rd legs in an action that pushes the mating thread up above the level at which it is held by the anterior and posterior tarsi. Functionally similar behaviors are described below. The act must stretch the mating thread and cause resonance vibrations when the tension is released. Our film shows that in the course of high-amplitude bouncing the body of the male swings sideways to a point level with the mating thread; in some frames the dorsal surface of the male is visible in a side view of the thread.

An indication of the probable redundancy of some of the elements in vibratory courtship comes from our observation that a male that had lost both 1st legs succeeded in courtship to the point that the female came out into an acceptance posture on his mating thread. Similarly, a male with only the 3rd leg intact on his right side succeeded to the same point despite the fact that he could make no TR movements. In these cases, the vibrations produced by the specialized movements of the 3rd legs and those produced by TRing could apparently be omitted without the "message" being lost.

In only 2 of the instances of this type of courtship was the male alone at the hub before commencing courtship; in all the others at least one other male was present and sporadically active. In one of the latter cases, the male at the hub was conducting type A courtship, while the other male was on his mating thread conducting vibratory courtship. (The male conducting type A courtship successfully copulated; the male conducting type B courtship never succeeded in getting the female onto his mating thread.) One male conducted type B courtship the day after conducting type A courtship. A male arriving at the hub of a web that contained a fresh mating thread, inserted by a male that had copulated and been eaten, paused during its type A courtship and walked forwards and backwards across this mating thread 3 times. It did not then commence vibratory courtship, but resumed type A courtship on the female. We feel that this observation may mean that the mating thread silk is "labelled" in some way.

Type C courtship. We saw 10 examples of this kind of courtship. In 2 cases the mating thread was relatively short and placed inside the web frame between the latter and the start of the viscid spiral zone (see FIG. 55 for details). All the other mating threads were long and originated outside the web. They were inserted either at the junction of a radius and a frame thread or part way down a radius. One mating thread was more or less at right angles to the web; all the others lay roughly within the web plane.

On the mating threads the male conducted vibratory courtship using the components described above. In 2 instances this courtship started with the males facing away from the web. In 2 cases the female did not move out from the hub at all. In the other instances the female went out onto the mating thread and moved into an acceptance posture and males made typical insertion approaches as described above. One male had only 3 legs and, after abortive courtship on the mating thread, moved to the hub where he carried out type A courtship unsuccessfully.

All except one of the males that inserted mating threads at the periphery of the web did so in situations where there was at least one other male active on the web and where male/male interactions had occurred. In only 2 cases were there no males already at the hub of the web when the males inserted the mating threads. Only 2 of the males had been at the hub of the web and in contact with the female before inserting a mating thread at the web's periphery. One of these was the exception to the situation where male/male interactions had preceded insertion of type C mating threads. This male was established at the hub of the web with the female when, after accidental disturbance by us, she moved to the upper web margin and remained there for over 30 min. The male followed her to her new resting site and inserted a mating thread there, and he successfully courted her. When the female returned to the hub the male returned to type A courtship.

Anomalous courtship behavior. As mentioned above, we saw a number of aberrant forms of courtship that can be regarded as intermediate between the categories that we have designated. One of these was carried out after a period of walkabouts and contact courtship by a male established at the hub. This male constructed a thread, ca 8 cm long, more or less perpendicularly above the resting female at the hub. The thread was constructed beneath the web plane and not in a hole. We noted this behavior as follows: "male walks down above female 3″, he repeats this 2 or 3 times, he is possibly laying down a mating thread vertically, using the slope of the web to avoid the line's contact with the web and thus not cutting a hole in the web. Turn and TR, L, L, TR, R, bounce, bounce, ..." This assessment of what the male was doing proved correct, since the female eventually turned at the hub, moved upwards slightly and then turned sideways to assume an acceptance posture behind the hub. The female faced left for one series of insertion approaches and then turned at the hub and faced right for a further unsuccessful series of insertion approaches. The male was killed shortly afterwards as he moved about the hub. We have the entire sequence on film and suspect that this mating thread was attached to the female's dragline or somewhere beneath the arch of her body. The male entered that area immediately before we noted his construction movements. When the female climbed onto the thread she must have distinguished it from the radiating lines of her own construction on which it lay. The process of mating thread construction beneath an intact web plane is mechanically possible because of the slope of the web and as soon as the female moved onto it her weight would tend to stretch it so that she came to lie "slung" below the web plane with sufficient clearance. This could represent an extension of courting on the female's dragline (see above).

We also saw an instance of the male running out to a female that had wrapped a prey and was at the stage of biting it prior to removing it. This male made insertion attempts while the female was motionless. She was in a posture beneath the prey that had some of the elements of an acceptance posture, i.e., she was turned sideways with ventral surface uppermost. We have seen type A courtship apparently stimulated by a female returning to the hub bearing prey, but this is the only case where we have seen a male follow the female to a prey capture site. He was unsuccessful.

In one case of type C courtship, the male climbed over the female after an unsuccessful insertion attempt and left a strand of dragline extending from her leg II-L to leg IV-L. This dragline was above and to the left of the mating thread, but the male moved back along it and TRed, bounced and, in fact, conducted vibratory courtship on the "wrong" thread.

Copulation. The male turns sideways after insertion, pivoting about the inserted

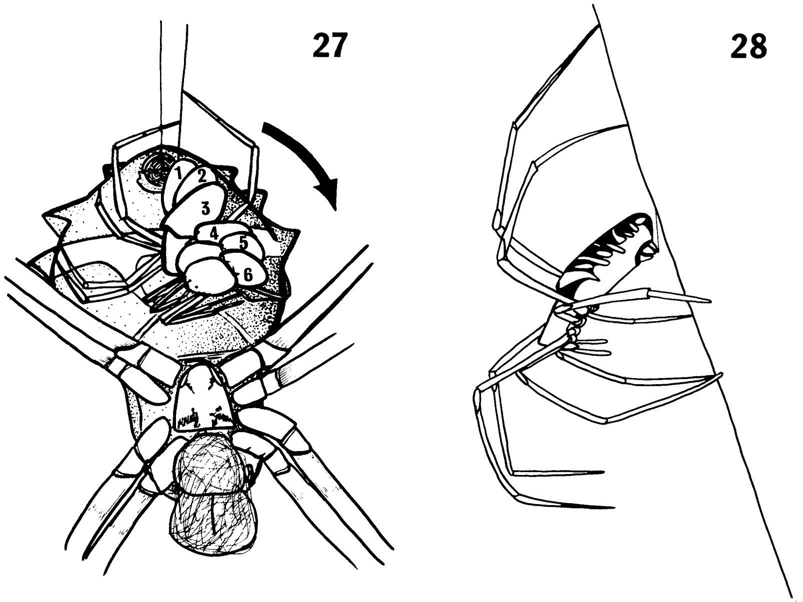


Fig. 27–28. **27.** Stages in the 90° twist that follows insertion in *Argiope argentata.* At stage 3, legs are extended in insertion stance as shown; at final stage 6, they are folded (based on movie film). **28.** Acceptance posture of ♀ *Argiope aurantia* (based on movie film, see text).

pedipalp and simultaneously folding up the legs from their splayed insertion-movement posture to the crouching "protective" posture. One sequence of such movements that we filmed took place more slowly than usual and we were able to diagram some of the position changes involved (Fig. 27). Males that survive the 1st insertion invariably turn in the opposite direction at the 2nd insertion. After a period of copulation, some males unfolded the legs I and II and these could be seen projecting beyond the side of the female's abdomen. Males that did this were in copula (or at least in position on the female's abdomen) for unusually long periods. They always appeared inert when brushed off the abdomen and wrapped or bitten by the female. We suspect that such males died in copula but cannot be certain of this. We pried one male off the female after such a copulation and found him to be dead. We saw 47 bouts of type A courtship, of which 27 led to copulation; 3 out of 7 type B courtships led to copulation, and 4 out of 10 bouts of type C courtship were successful.

During copulation, both at the hub and on mating threads, the female responds to the initial insertion by doubling from the waist and bringing the tarsi of one or more legs onto the surface of the male. The pedipalps of the female reach back and touch the male. The very long courtships were characterized by the abandonment of these female behaviors; she simply behaved as though the male were not present.

One male lost the right embolus after being pushed off the female and escaping by jumping. We found a eunuch at the hub of a captive female but have not found eunuchs on naturally occurring webs. (See Levi 1969 for comments on embolus breakages in araneids.)

Interactions between males. Males interact as they move around the foundation threads and also at the hub. On the foundation threads, males pluck and vibrate while oriented towards each other. The outcome of these duels is usually a chase in which the subordinate runs up onto vegetation or drops on his dragline. Subordinates are often persistent, regain the web and start further activities. Males at the hub respond to other males approaching across the web by plucking in an oriented manner. At the hub, 2 or more males may coexist for lengthy periods and interact only when one approaches the other closely. We have seen males drop off the hub during such encounters.

Kleptoparasitism by males. We have records of males repeatedly approaching food items being consumed by the female and feeding on these. During some of these incidents the female rewrapped the prey item, apparently in response to the male's activities.

Argiope aurantia (Lucas) FIG. 28–29

This species is the largest of the New World species and is in many ways *Nephila*-like. McCook (1890) published an early note on the mating behavior as did Peckham & Peckham (1889). These general descriptions are confirmed and extended by our own observations. The species belongs to the group of *Argiope* spp. that produces a perpendicular ribbon stabilimentum as adults and have characteristically ovate abdomens. As McCook (1890: 18) noted, several males may take up residence on a female's web. They also build small webs in the barrier webs of females. In Florida, we found males associated with the webs of females that later molted to maturity. This anticipation of maturation by males is characteristic of *Nephila* spp., as noted above. Such males were often at the hub and presumably subsisting as commensals. We saw males indulge in opportunistic mating attempts while a newly molted female was hanging from her cast cuticle in the typical, legs outstretched, immediate postmolt posture.

Approach behavior. Even the smallest males are relatively large. They approach the hub along the undersurface of radii, tapping ahead with one leg I as they proceed. The walk is usually slow and hesitant, and we did not note any bouncing during approaches. Peckham & Peckham (ibid.: 55) describe the approach as follows: "when advancing toward the female, the male seems to pause and pull at the strands of the web, as though to notify her of his approach." This sounds more like plucking than tapping. We may have missed it.

Courtship behavior. The courtship behavior of this species differs from that of all the other group A species that we have studied in the extreme vigor and speed of the male's actions when in contact with the female. Frenetic, frenzied and frantic are the adjectives that immediately spring to mind after watching this courtship. Males at the hub assume X postures when not active (as do all males of all the *Argiope* sp.

that we have seen). Once they commence activity they very rapidly move into direct contact with the female after, at the most, a short walkabout on the upper surface of the hub. Shuttling from the upper surface is accomplished through a hole cut at the hub silk by the male. Webs where several males have been involved in courtship bouts over several hours often have more than one hole cut into the hub silk; we think that each male may cut his own access hole. (The behavior of cutting access holes close to the hub could constitute a step towards the evolution of type B courtship behavior; see Discussion.)

Once on the lower surface, the male walks rapidly, or runs, around the periphery of the female, touching the tips of her tarsi where they rest on the web. The movements involved in this are rapid scrabblings involving all 4 anterior legs. The males seem to pay most attention to the female's legs I and II. Intermingled with scrabblings at the tarsi are rapid scrabblings at the abdominal margins and excursions to the anterior to flail at the female's pedipalps. In the course of these perambulations the male frequently runs from side to side over the surface of the female's body. Approaches may be made from the sides or from above the female. Examination of movie sequences of descents from above the female show that when the male is scrabbling rapidly at the dorsal surface of the female body, thorax and abdomen, the first 2 pairs of legs are frequently the only parts of the male in contact with the female. His legs III and IV are neither on her body nor on the web. The male seems to be "walking on air." We think that this phenomenon is due to the fact that the male is hanging, pendulum fashion, on his dragline above the female's back and can do this because his dragline is attached at a point on the sloping web that is perpendicularly above a point beyond the surface of the female's body. This presents no mechanical problems, since the male could attach his dragline several centimetres above the apex of the female's abdomen, but still belay it as he walked down the sloping web to climb onto the female from the web surface. It is possible that repeated excursions onto the female from above, and from the sides, may build up a scaffolding of male dragline on the female (we cannot actually see this, either on still photographs or the cinefilm).

After an intensive bout of this high-intensity courtship, the female moves into a characteristic acceptance posture (FIG. 28). This closely resembles the thermoregulatory postures that *Argiope* species assume when subjected to solar radiation from behind the web (through the hub). In such postures the spider orients the apex of the abdomen against the hub silk and directs the body at an angle to the web plane, often lifting the first 4 legs off the web (Robinson & Robinson 1978b). Gerhardt (1924c: 523) follows Emerton (1878) in assuming that there is no specialized female posture in this species. All females that we saw being courted assumed this posture during courtship, even those that subsequently attacked and caught the courting males before copulation could occur.

As courtship proceeds, following the adoption by the female of this acceptance posture, the male makes excursions onto the ventral surface of the female. He may

FIG. 29. Opportunistic mating in *Argiope aurantia*. Newly ecdysed ♀ hanging from old cuticle is being mated by ♂ standing on her ventral surface. Note large size of ♂ and the shield at the hub between arms of ribbon stabilimentum.

approach by girdling the female from above or swinging up onto her body from the side (compare with *A. aemula* above). The male does not enter from beneath the posterior abdomen of the female, presumably because this avenue of approach is more or less closed as a result of the acceptance posture (FIG. 28). As the male moves about the ventral surface of the female's abdomen, his legs IV may contact the web plane rather than rest on the female. We saw males apparently make dragline attachments on the surface of the female's abdomen during insertion approaches. We also noted that the male's legs I and II frequently reach far forwards onto the ventral cephalothorax of the female. Insertion attempts are made with the body of the male conspicuously arched dorsally and the pedipalps reaching down towards the female. In this reaching posture, the bulbus is under the anterior cephalothorax of the male. Since the segmented part of the male pedipalp is quite long, the pedipalps can reach ca ⅓ of the length of the male cephalothorax ahead of the spider when they are held extended anteriorly. We assume that they can reach approximately this distance backwards when they are moved beneath the male's cephalothorax during insertion attempts. The male moves to-and-fro beneath the female when making insertion attempts, at the same time raising and lowering the body in relation to the female's body surface. This movement may be made along a large expanse of irrelevant surface and not just around the epigyne. We have seen insertion movements made along the ventral cephalothorax of the female and even on prey packages. The epigyne of this species is visible as a posteriorly projecting finger-like process that appears to enlarge during courtship. Gerhardt (1924c: 524) illustrates a similar epigynal profile in *A. bruennichi* (Scopoli).

During courtship, the female of *A. aurantia* makes movements of the pedipalps and abdominal apex similar to those that we described as occurring in *N. malabarensis*. The pedipalps move up and down, independently, as though one was being rubbed against the other. We were alert to the possibility that this could be a stridulatory movement, but cannot be sure that contact was made between the pedipalps. We cannot correlate the occurrence of any male behavior with this movement on the part of the female.

The males that attempted opportunistic matings with freshly molted females (FIG. 29), descended the dragline onto the females without preliminary walkabouts. They did not make any courtship movements directed at the exuvia despite the fact that this was "standing" attached to the hub silk in the posture of a normal female at the hub. However, once a male was on the newly ecdysed female it behaved with all the frantic effort of a male courting a normal female. The male scrabbles vigorously at the 8 legs of the female as they hang in a plume beneath her body, then pauses, makes insertion attempts with the body bowed, scrabbles again, and so on. All the while, the female is swinging about her long axis as she dangles on her dragline. In movie sequences of this behavior, we again got the impression that the scrabbling movements that are made with quite strongly flexed legs I and II (left and right together) may involve compound tarsal rubbing. In these sequences the epigyne of the female seems to be enlarged.

Copulation. We saw 1 certain copulation and 2 probable copulations. We are unsure about the latter because, although the male remained motionless above the epigyne and appeared to have one pedipalp inserted, he remained standing erect on the female's abdomen. In the certain copulation, the male inserted and then moved down to a prone position with his body appressed to the ventral surface of the female and his legs partly encircling her abdomen. This posture is essentially similar to that adopted by male *N. pilipes,* except that the long axis of the male appears to be parallel to that of the female. [Gerhardt's (1924c, Fig. 3) illustration of the posture of copulating *A. aurantia* is accurate if one ignores the attitudes of the female's legs and her position relative to the web plane.] The female tried to wrap the male in all 3 cases.

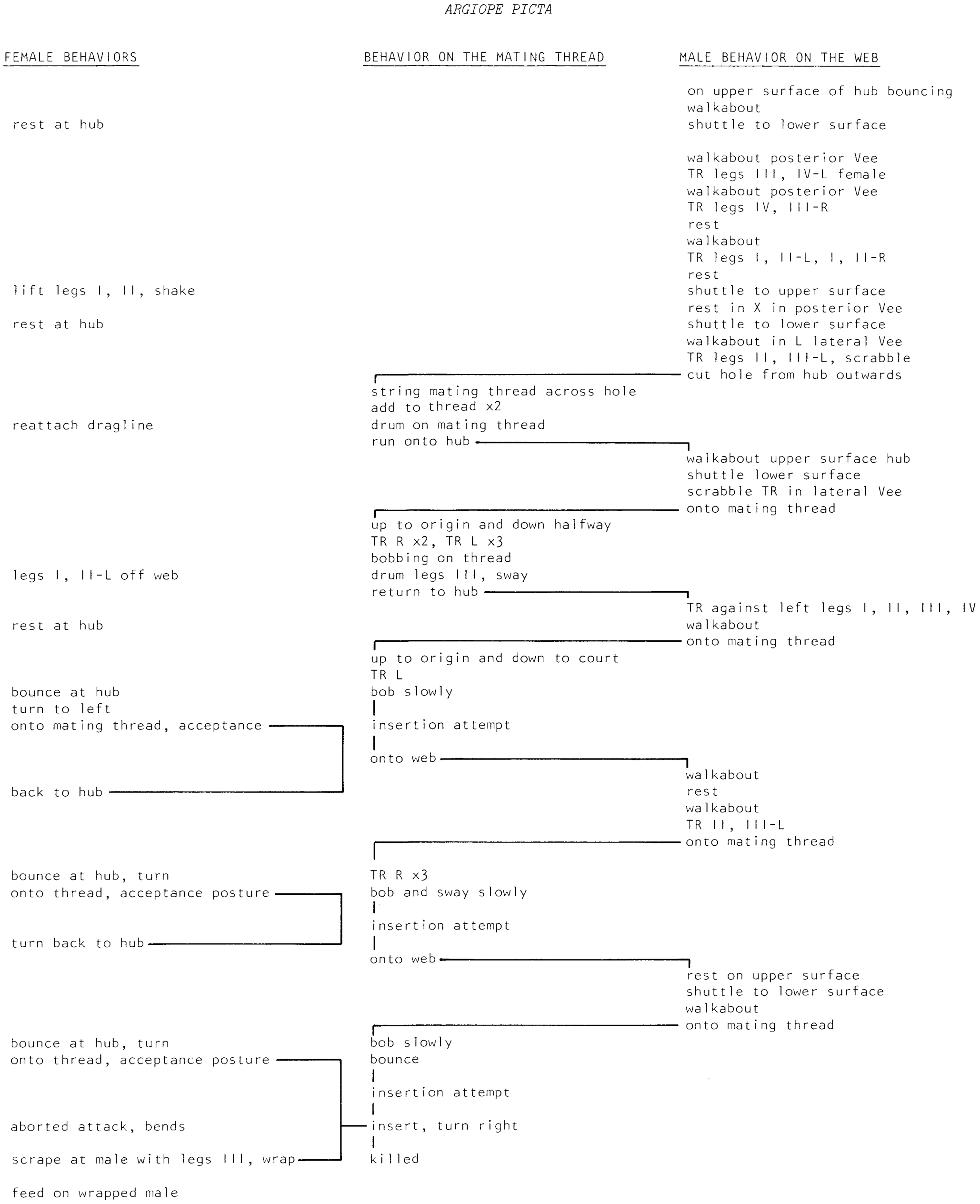
Interactions between males. Males interact with considerable vigor. We saw one fight that lasted over 40 s before the 2 males separated. The fight (filmed) is impossible to resolve into components. The 2 spiders seem to be mutually scrabbling at each other with all 4 anterior legs. We saw duelling involving males oriented towards each other and plucking vigorously at the web. Such duels lead to chases in which one contender may retreat onto the barrier web, foundation threads, or drop off belayed on a dragline. On the other hand, we have seen males coexist at the hub for long periods. During this coexistence, one male may court vigorously while another is nearby resting in an X posture.

Kleptoparasitism by males. We have records of males stopping courtship activities to feed briefly on the food being consumed by the female and one record of a male feeding on an insect stored at the capture site, i.e., in the viscid spiral zone of the web.

COURTSHIP AND MATING BEHAVIOR: GROUP B

The species that we have encountered with this type of courtship all belong to the genus *Argiope. Cyrtophora* species may be regarded as possessing some elements of group B courtship and some elements of group C, but we place them in group C for descriptive purposes (see Discussion for further elaboration). In only one species, *A. picta,* did we see any anomalous forms of courtship similar to those described in the case of *A. argentata* (see above). Interestingly enough, we found that a spider that we thought to be an *Argiope* species (*Argiope* "F" of Robinson et al. 1974) had only type C courtship. This would have been unique, as far as we know, for the genus. The spider turned out to be a species of *Gea* (see below). All species in this group insert one pedipalp at a time and court again before the next insertion attempt.

Note on terminology. All the species in this section conduct vibratory courtship from a position hanging below a mating thread. They are ventral surface uppermost and anything hanging (topographically) below their courtship position is in fact hanging below their dorsal surface, i.e., above their body. This situation can clearly produce



ARGIOPE PICTA

FEMALE BEHAVIORS	BEHAVIOR ON THE MATING THREAD	MALE BEHAVIOR ON THE WEB
		on upper surface of hub bouncing
		walkabout
rest at hub		shuttle to lower surface
		walkabout posterior Vee
		TR legs III, IV-L female
		walkabout posterior Vee
		TR legs IV, III-R
		rest
		walkabout
		TR legs I, II-L, I, II-R
		rest
lift legs I, II, shake		shuttle to upper surface
		rest in X in posterior Vee
rest at hub		shuttle to lower surface
		walkabout in L lateral Vee
		TR legs II, III-L, scrabble
		cut hole from hub outwards
	string mating thread across hole	
	add to thread x2	
reattach dragline	drum on mating thread	
	run onto hub	
		walkabout upper surface hub
		shuttle lower surface
		scrabble TR in lateral Vee
		onto mating thread
	up to origin and down halfway	
	TR R x2, TR L x3	
	bobbing on thread	
legs I, II-L off web	drum legs III, sway	
	return to hub	
		TR against left legs I, II, III, IV
rest at hub		walkabout
		onto mating thread
	up to origin and down to court	
	TR L	
bounce at hub	bob slowly	
turn to left		
onto mating thread, acceptance	insertion attempt	
	onto web	
		walkabout
back to hub		rest
		walkabout
		TR II, III-L
		onto mating thread
bounce at hub, turn	TR R x3	
onto thread, acceptance posture	bob and sway slowly	
	insertion attempt	
turn back to hub		
	onto web	
		rest on upper surface
		shuttle to lower surface
		walkabout
		onto mating thread
bounce at hub, turn	bob slowly	
onto thread, acceptance posture	bounce	
	insertion attempt	
aborted attack, bends	insert, turn right	
scrape at male with legs III, wrap	killed	
feed on wrapped male		

FIG. 30. Conventional summary diagram of courtship in *Argiope picta*. For explanation of abbreviations, see FIG. 5.

some confusion, since it is natural to use descriptive terms like above and below that relate to the position of the observer rather than the observed. We have accepted this tendency and simply refer to below the male when we mean below his position on the mating thread (or dorsal to his body). We hope that this explanation will prevent any confusion.

Argiope picta Koch L. FIG. 30–33

This yellow and black spider is common throughout the Wau Valley and coexists with *A. aemula* at many sites. In Wau there are 2 distinct color forms. This was the 3rd spider whose mating behavior we studied, and we were fortunate that it differed so strikingly from *A. aemula. Argiope picta* indulges in prolonged tactile courtship before inserting a mating thread near the hub and also reverts to contact courtship between bouts of vibratory courtship. This meant that the 1st species with group B courtship that we studied had many courtship behaviors in common with group A species, allowing us to see a possible link between the two. Many other type B species have fewer transitional features.

Approach behavior. Males accumulate on the webs of females, and we frequently found at least 2 males at the hub of a female's web, resting in X postures. The approach is most frequently along the undersurface of a radius and is similar to the general pattern of approach behavior of *Argiope* males described above. The males jerk intermittently as they walk and may remain on the undersurface of the hub after reaching that region.

Courtship. Courtship is basically in 2 stages, a contact stage and a vibratory courtship stage. Interestingly enough the male may repeatedly revert to contact courtship after the onset of vibratory courtship. The male may enter into contact courtship immediately on arrival at the hub, or may perform a short walkabout above the hub. This latter is perfunctory compared with the walkabouts of the previously described *Argiope* species. The contact courtship, performed on the lower surface of the hub, is almost always vigorous and looks highly stimulatory. The male moves to the tarsi of the apposed legs of the female and repeatedly scrabbles and TRs against them. There is a distinct tendency for initial attention to be concentrated on the posterior leg pairs. The male moves from left to right, right to left, over and over, TRing at pauses in the movements from one side to the other. The approach to the leg pairs can be lateral, from within the V, but is often a movement to a position facing the tarsal "foothold." The male then moves astride the leg pair, partway along the tarsus and scrabbles, TRs and scrabbles. At this stage the female responds by raising the affected leg pair slightly off the web and shaking the legs. Silk attachment can be seen across the V from one leg pair to the other, and we have the impression that there may be some slight restraint resulting from this. The anterior leg pairs are treated to TRing and scrabbling and the male also contacts the side of the abdomen and, rarely, the pedipalps. We did not see an *A. picta* male climb onto the body of the female while she was at the hub.

TRing and scrabbling at the apical parts of the female's tarsi is a complex process. Our movie sequences show that a variety of movements are involved. The male may move legs I, II, and III of one side against each other and against the side of the female's tarsus. Additionally, he may make what appears to be the same movement but this time performed with the female's tarsus between the moving legs. The male can move legs I, II and III right, for example, and I and II left in the typical "sawing" TR movement, with the female's tarsus somewhere in the midst of a confusing jumble of movement. The male can merely touch the female's tarsus with the anterior legs of one side, while TRing with the laterally opposite pair that are out of contact with the female. We have also seen the male stand astride the female's tarsus and stroke it with simultaneous movements of his 3rd legs. The leg flickings and kickings of the female do not seem to deter the male from further courtship. He may be lifted off the web astride her leg only to persist in TRing and scrabbling. (We have records of successful copulations resulting from courtships of females that were particularly "irritable" at this contact courtship stage.)

After a period of contact courtship, the male cuts a hole in the web and inserts a mating thread. We could detect no change in the behavior of the female that allowed us to predict when the male would do this. It is possible that she adopts a more stilted posture after a period of contact courtship, but the change, when it occurs, is not striking. Hole cutting is exactly as described for the group B courtship of *A. argentata* (see above). The male makes the cuts at the inner end of the radii and moves out, tearing back the collapsing sections of radii (bearing viscid spiral elements) as he goes. It looks as though the outer edge of the hole is simply determined by the male allowing a margin of untouched viscid spiral to remain intact. The mating thread is then laid down to bridge the hole. At the hub end, the male almost invariably attaches the end of his dragline as part of a movement during which he climbs onto the upper surface of the hub, walking on from this for some distance from the edge of the hole before turning to go back up the thread to its origin. This movement onto the hub must anchor the mating thread to several points on the hub silk rather than merely to the edge of the hole. At the origin end, the mating thread is attached to one of the cut radii. The male goes beyond the cut end to attach each outward element of the mating thread so that the origin is also, presumably, anchored at several points to a strong structural member of the web. As is implied above, the mating thread is a multistrand structure produced by the male passing backwards and forwards several times along the same line. To the naked eye, it appears as a single thread but in enlarged photographs is clearly a compound structure. When laying down the thread the male appears to use the first 2 pairs of legs to effect the movement, while 1 or both legs IV hold the dragline behind the spider, laying it out under tension.

After a bout of vibratory courtship, the male may repeat the elements of contact courtship before resuming vibratory courtship. Such renewed vibratory courtship is always preceded by the male going up to the origin of the mating thread and turning to move towards the female. Thus a further strand (at least) is added to the mating

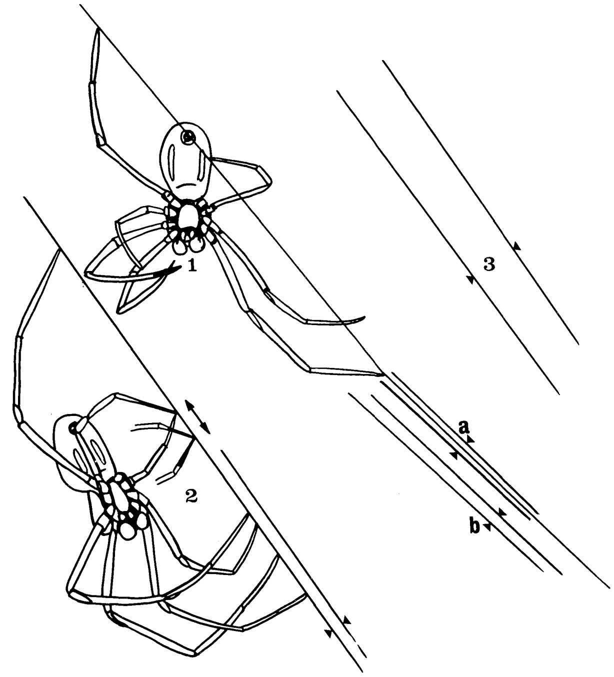
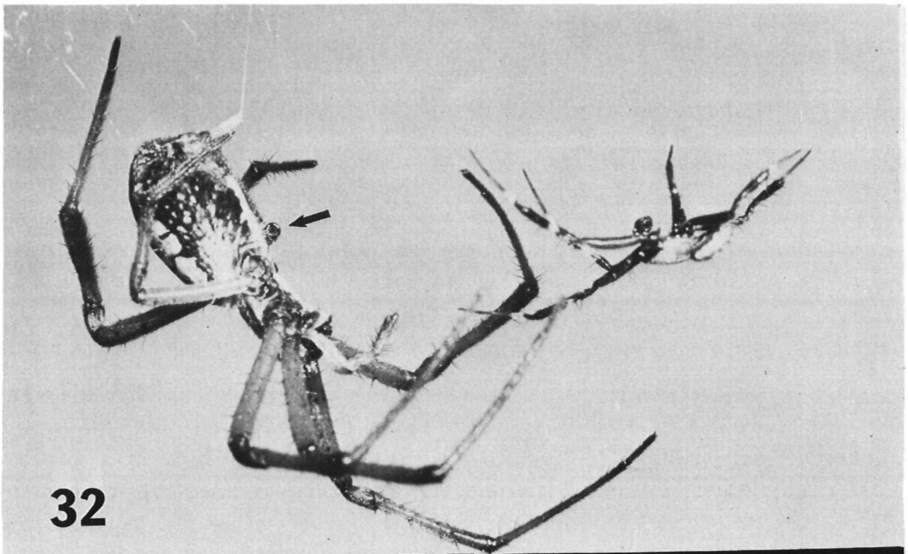


FIG. 31. *Argiope picta.* 1. TRing by ♂; a and b show deflections of mating thread that this produces (same scale). 2. Tugging with legs III; arrows show deflection produced. 3. Deflection produced by bouncing.

thread before each bout of vibratory courtship. The male may interrupt vibratory courtship to further reinforce or add to the mating thread. In time the male may add mating thread elements at the insertion in such a way that the insertion is moved vis-à-vis the female. We have also seen the male enlarge the hole containing the mating thread, after a period of courtship, by cutting radii on either side of the originally severed elements. This process may eventually produce a very large hole indeed and if 2 males are concurrently active, the female may become virtually isolated on a small island of hub silk bounded by male-produced holes.

Vibratory courtship has a number of elements that can be characterized as present in the species repertory but do not necessarily occur in all the bouts, or sequences of bouts, performed by any one male. TRing seems to belong to the initial stages of vibratory courtship. The male leans to one side, below the mating thread, removes legs I, II and III, or I and II from the line and vigorously TRs. The process is then repeated with the legs of the other side and so on. Bouncing on the line follows TRing and may increase in amplitude to a crescendo. This is usually followed by a pause during which the 3rd legs may tap the line like drumsticks (from above) and the spider makes rhythmic pulling movements. At any stage during a train of these behaviors, the female may turn at the hub, bouncing, and move into an acceptance



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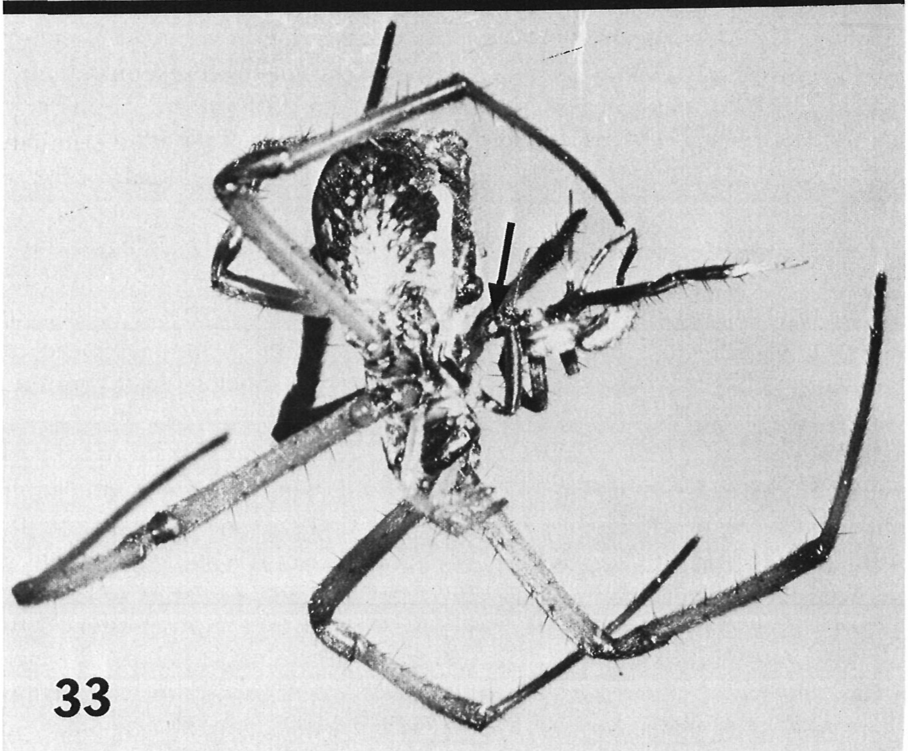

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FIG. 32–33. **32.** Female acceptance posture of *Argiope picta*; ♂ in typical courtship posture on mating thread. Note protruding epigyne (arrow). **33.** Male *Argiope picta* immediately prior to insertion. He is at the point of inflexion in the mating thread, and the right pedipalp is thrust forwards (arrow).

posture on the mating thread. If this does not occur the male eventually moves off the mating thread and again indulges in contact courtship. Such courtship is usually oriented at the tarsi facing the hole containing the mating thread. Examples of some of the movements performed on the mating thread and the degree of displacement of the thread that they produce are shown in FIG. 31. A male that had only 2 left legs, namely I and IV, TRed with these 2 legs.

The acceptance posture of the female is shown in FIG. 32 and 33. She is barely clear of the hub silk and one leg IV grips the hub behind her while she grasps the mating thread with one or both legs III and at least 1 of the first 4 legs. To assume the posture, the female turns sideways at the hub and walks herself partly out onto the thread by movements of the first 2 leg pairs. She then releases this walking hold and drops into a partly head-down posture, supported as described above. The positioning of her legs causes a sharp inflexion in the mating thread and it is to this point that the male descends to make insertion attempts (see FIG. 33).

Once the female has assumed the full acceptance posture and stopped moving, the male moves rapidly down the line towards her ventral surface, ideally arriving close to but below her protruding epigyne. He does not always make insertion attempts on arrival at the appropriate place, but may jump off, belayed on his dragline and regain the mating thread out of reach of the female. If he makes insertion attempts and does not succeed, he frequently turns and goes back up the thread, returning again to renew the insertion attempts until he either succeeds or gives up. Termination of approaches by the male occurs when he goes on past (over) the female onto the hub, or simply stops approaching her after a retreat from the inflexion point of the thread. In the latter case, the female often plucks at the mating thread with legs I and II and ultimately turns back to resume her predatory position at the hub. After such a return on the part of the female, the male either resumes contact courtship or goes into an X posture at the hub. (In this species, once the female has achieved her acceptance posture the male stops vibratory courtship; in others, see below, males continue for some time before switching to insertion attempts.)

The positioning of the female on the mating thread may not be the only factor that is critical to the success of insertion attempts, although it is important (see above). We have the strong suspicion that the epigyne is everted during courtship and that the degree of eversion may be critical to successful copulation (FIG. 33 shows the epigyne protruding more prominently than it does during noncourtship conditions). The return to contact courtship at intervals after the inception of vibratory courtship could be a means of enhancing the "receptivity" of the epigyne.

Anomalous behavior. We have a record of a male whose vibratory courtship consisted of a total of 4 TRs, after which the female turned into an acceptance posture and he immediately went into copula. This is the most abbreviated vibratory courtship we have seen in this species. Two other males that were on the same web left when this male moved onto the hub, and it is possible that the female had been vigorously courted before his arrival (and the commencement of our observations). Certainly she had been courted and mated the previous day.

More interesting is the case of a male that inserted a mating thread on the outside of an *A. picta* web and courted on that; we could not see the details of courtship (the web was in a tree 2 m off the ground), but the female turned in the direction of the male and went into an acceptance posture at the hub. She maintained this for about 40 s and then moved to the margin of the web where she again went into an acceptance posture. The male went down to make one insertion attempt, missed and the female went back to the hub. The male inserted a new mating thread and signalled again. The female again went out and into an acceptance posture. The male made 3 insertion approaches but was unsuccessful. The female attempted to wrap him and missed. This was followed by 3 further approaches. After the last of these, the male retreated down the female's web towards the hub. The female turned towards the hub and assumed an acceptance posture on a radius. The male once again approached and was wrapped, bitten and carried to the hub as prey. This female had another male at the hub when this anomalous courtship started and he courted her on a conventional mating thread and successfully mated with her 15 min. after the end of the anomalous courtship.

Copulation. On insertion the male turns sideways into a prone position with the legs folded. The female places tarsi III over the male and may then place, successively, tarsi II and I over him. At this moment, she drops into a more pendant position below the mating thread. As the female drops she may evert the spinnerets and start secreting multistrand wrapping silk as though about to wrap the male. Sometimes wrapping follows immediately after insertion but is usually suppressed and all that takes place is the production of a visible amount of multistrand silk. At some stage during the copulation, the female uses the 3rd legs to start pushing the male towards her chelicerae. This movement often starts shortly after insertion but is then suppressed for 20–30 s before it is restarted. Males of this species often respond to tarsal pushing by leaping off the female. There is a nonsignificant tendency for males copulating the 1st time to jump more readily than males jumping the 2nd time. As in all *Argiope* spp., only one pedipalp is inserted at a time and further courtship precedes the insertion of the "virgin" pedipalp. During this time, the female returns to the hub and often grooms her legs and pedipalps. Males that are caught and wrapped are eaten by the female.

Interactions between males. Males interact at all stages, but several males may coexist at the hub indulging in plucking duels and occasional chases that seem largely to result in spacing out. We have 2 records of males producing mating threads at the hub during the same period of courtship activity and then overlapping in their periods of vibratory courtship. This is a directly competitive situation. The 2 females in question each caught and killed the 1st male she allowed to copulate and then moved into an acceptance posture on the mating thread of the other male. We were

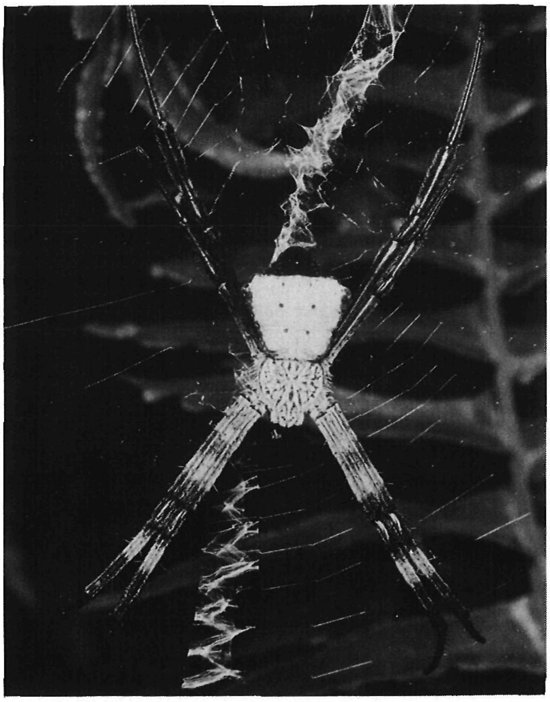


FIG. 34. Unstriped yellow form of *Argiope aetheria,* showing pentagonal abdomen and diagonal (incomplete) stabilimentum.

thus faced with the question of whether the females would otherwise have shown a continued preference for the first male over the second.

Argiope aetheria (Walckenaer) FIG. 34–36

This spider is known in Australia as the St Andrew's Cross spider because of its white cruciform stabilimentum. We never found it in the Wau Valley, but it is relatively abundant in lowland areas throughout Papua New Guinea. All of our males were collected in the Port Moresby area, as were all but one of the females. One female was collected at Madang on the north coast and was successfully mated with the Port Moresby males from 500 km away. This female was of the beautiful yellow (unstriped) form that occurs sporadically in New Guinea populations (FIG. 34). McKeown (1963) gives some details about the natural history of this species in Australia and both Clyne (1969) and Mascord (1970) have fine color plates of both sexes.

In May 1977, MHR filmed courtship and mating of an *A. aetheria* that he found near Cairns, Queensland, Australia. The basic patterns of behavior were essentially similar to those described below for the New Guinea specimens. In particular, males on the mating thread dropped legs I below the line of their body (dorsal to it in their inverted position) in the manner described below.

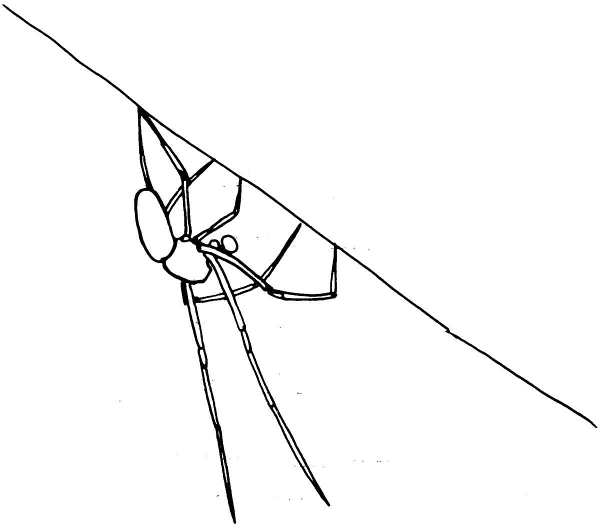


FIG. 35. Male *Argiope aetheria* on mating thread with legs I in outstretched downwards-pointing attitude (see text).

Approach behavior. Typical for *Argiope* spp.

Courtship. Courtship follows the same general pattern as that described for *A. picta,* differing only in detail. After an initial walkabout above the hub, the male moves onto the lower surface for a period of contact courtship. A hole is cut in the web across which the male inserts a mating thread and on which he performs vibratory courtship. The female, if responsive, moves onto the mating thread into an acceptance posture and the male makes insertion approaches. If these are not successful he reverts to contact courtship as the female returns to the hub. After such renewed contact courtship, the male resumes vibratory courtship and the female moves out into an acceptance posture. On insertion, the male turns sideways and the female adopts a pendant posture.

Detailed differences between this species and *A. picta* occur in all stages in courtship. The walkabout above the hub is usually prolonged and includes TRing and bouncing. The phase of contact courtship includes extensive tapping of the female's legs and body surfaces, but little scrabbling. The tapping is performed by the male when he is standing on the web. From the posterior V, he may reach forward as far as the anterior margin of the female's abdomen. Unlike *A. picta* the male seldom stands astride the female's legs when touching them but is almost always alongside the legs standing in a V. TRing occurs during contact, but most TRs are performed by the legs on the side away from those actually contacting the female. We saw males tapping the female thorax from the lateral V's and reaching right across the width of the female during this act. At the stage of vibratory courtship, there are a number of important differences from the similar behavior of *A. picta.* When the female has assumed an acceptance posture on the mating thread, the male continues to court for some time before moving down towards her and resumes vibratory courtship after unsuccessful or aborted approaches. Furthermore, he TRs extensively not only at the start of vibration bouts but at intervals throughout such bouts. The male's stance on the mating thread is very distinctive, because at intervals throughout courtship he removes both legs I off the line and stands with them held downwards at an angle to the thread and with all the elements held in a straight line (see FIG. 35). We have no idea whether this has any effect on the nature of the vibratory signal, but the posture is distinct. Tapping of the mating thread with tarsi II occurs during vibration bouts, as does a high amplitude tugging in which the body moves posteriorly while tarsi II, III and IV appear to grip the mating thread.

Insertion movements appear to be closely similar to those of *A. picta* and are performed by the male when standing on the mating thread in the posture shown in FIG. 36. The female bounces as she turns to assume an acceptance posture, and may move her 3rd legs periodically after assuming the posture (as though adjusting her position).

Copulation. Copulation occurs in the typical *Argiope* manner, i.e., the male turns sideways after insertion. The female places tarsi III over the male and may add those of the anterior legs as well. Legs III eventually brush the male forwards at the end of copulation, at which stage he may escape by jumping.

Anomalous behavior. On 2 occasions, separate males that were courting females that had food at the hub attached mating threads to the prey package and conducted vibratory courtship on these. One male evoked a rapid, violent response from the female and went back to this already-used conventional mating thread. The other male produced a fully representative train of vibratory units, and the female went into an acceptance posture on this strange mating thread. The male made 3 separate insertion attempts and was then chased by the female; he retreated to the upper foundation thread. (He eventually returned to the hub and resumed contact courtship, installing a new mating thread before we ceased observations.)

We have a record of a male that reached the vibratory courtship stage being displaced by an intruding male and dropping to the lower foundation thread of the web where he installed a long oblique mating thread and conducted vibratory courtship. In the meanwhile, the intruding male cut a new hole, inserted a thread and successfully courted the female, achieving 1 copulation. At this stage, the first male returned to the hub. The female did not respond to the male with the "outside" mating thread.

An *A. picta* male moved to the hub of an *A. aetheria* female and courted vigorously up to the contact stage without molestation. He then walked off the web and moved to a nearby *A. picta* web.

We twice saw female *A. aetheria* add ribbon silk to stabilimentum arms after extensive holes had been cut in the web, close to the hub, by courting males. We have never seen *Argiope* spp. repair a stabilimentum after its initial installation.

Interactions between males. Shaking duels and fighting occurred commonly. We had

FIG. 36. Female *Argiope aetheria* in acceptance posture on mating thread. Male in insertion posture on heavily flexed mating thread. Note open jaws of ♀.

2 instances of simultaneous courtship by males with mating threads to the left and right of a female. In one such, the female assumed acceptance postures alternately to right, left, and then right without success. Courting males that were on their mating threads moved onto the web to orient towards intruders if such intrusions occurred before the start of vibratory courtship.

Argiope sp. Wau no. 5 FIG. 37–38

We found this spider in among populations of *A. aemula* in cowpastures and on roadside vegetation near Binatang Creek in the Wau Valley. The species is the same size and has roughly the same dorsal coloration as *A. aemula,* but 2 of the anterior transverse silver stripes on the abdomen are inconspicuously broader than they are in *A. aemula.* Only when we found that the ventral markings on a preserved specimen that we had put among a collection of *A. aemula* females were different did we set out in search of further specimens. Our feeling that this was a different species was eventually confirmed by Prof. H. W. Levi after examination of the female genitalia. The species is undetermined. In August 1974, shortly before we were to leave New Guinea, we found 3 females and 2 males. Two females were adult and both were

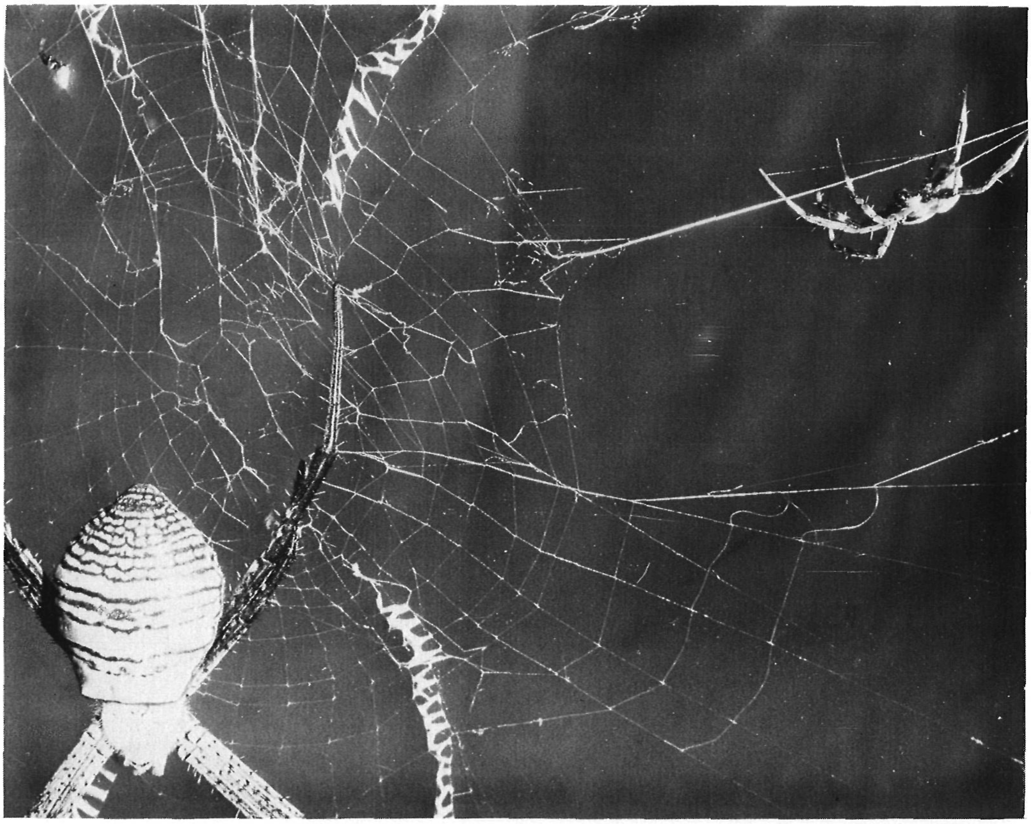


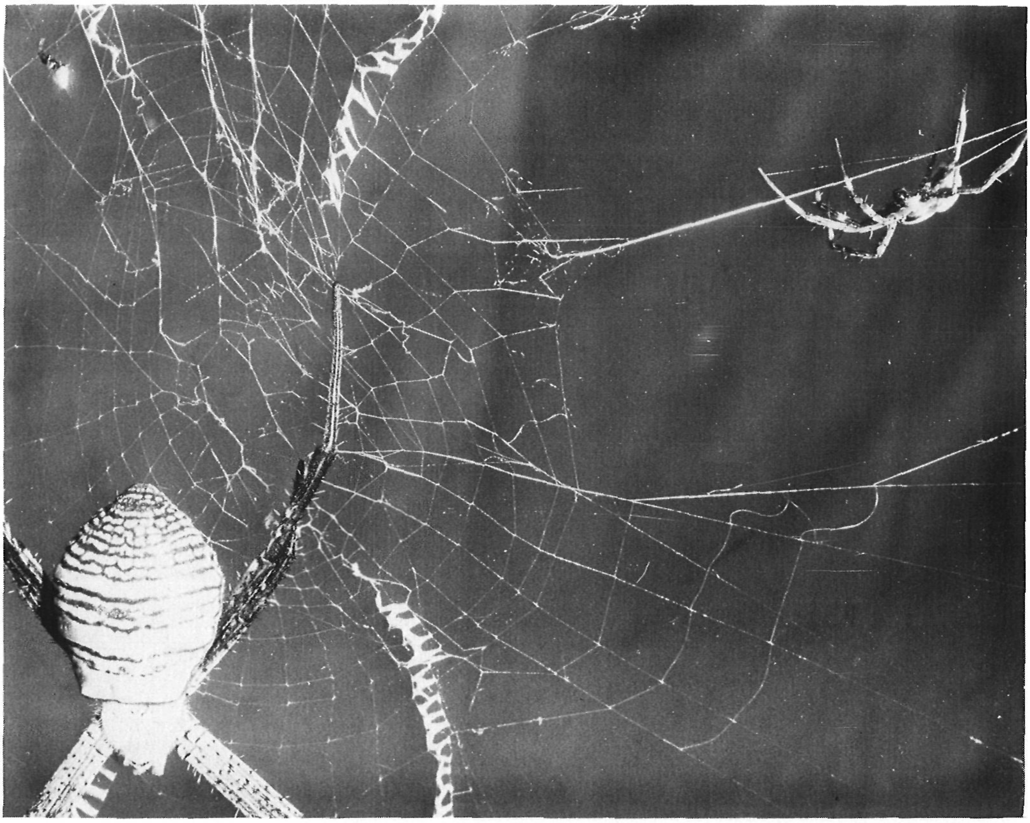
FIG. 37. *Argiope* sp. Wau no. 5 ♀ at hub [compare shape of abdomen with *A. aemula* (FIG. 19)]. Note that mating thread in hole at right of hub (♀ left) has multiple connections to hub.

courted. We were lucky to see courtship from its inception and one copulation. The courtship turned out to be quite different from that of *A. aemula.*

Approach behavior. As far as the small sample permits us to say, the approach behavior of this species is typical of *Argiope* spp. in general.

Courtship. Courtship proceeds from walkabout above the hub to contact on the lower surface of the web. After a period of contact, the male cuts a hole in the web near the hub, and then builds a more or less horizontal mating thread on which he conducts vibratory courtship.

Contact courtship consists almost entirely of tapping movements made against the legs of the female and her abdominal apex; we have no record of TRs occurring in this context nor does our film show any TRing at this stage. Since we studied this species shortly after studying *A. aetheria,* we don't think we would have missed on-the-web TRing. Contacts of the male's front legs with the female's abdomen resembled those that would have occurred prior to a male of *A. aemula* moving onto the



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Hole cutting proceeded from the hub outwards. The male walked along one edge of the developing hole as he laid down the 1st element of the mating thread that eventually bisected it. In this species, we were able to confirm an impression that we had gained from watching the construction of other *Argiope* spp. mating threads. We thought that we had seen the insertion of the compound thread being guyed by several sidestrands along its length, leaving the main thread at an acute angle. In one movie sequence of the vibratory courtship stage, 3 such threads are intermittently visible as the movement of the main thread causes them to catch the light and glisten (FIG. 37). Such branched insertions must not only strengthen the attachment of the thread but also complicate its vibration transmission properties.

The vibratory phase of courtship contains units of AWing, TRing, plucking, bouncing, and tapping. Both of legs I, II and III are involved in thread tapping. Legs I and II tap the mating thread from below (perhaps the movement should be called stomping), whereas legs III tap the line from above. The movements of the pairs of legs appear to be nonsynchronous. Bouncing characteristically increases in intensity towards the end of a bout. It appears to be produced by contractions of all the legs that are, at the time, in contact with the line. This always includes one leg IV, legs III and at least one of legs I and II. We filmed some of this bouncing at 54 fps against an artificial background. The sequence quite clearly shows the thread dimpled upwards, between the points formed by the anterior and posterior tarsi, by an upthrust of one or both legs III. TRing only involves the ipsolateral legs I and II in the sequences that we have on record.

The female bounces at the hub before turning onto the mating thread to move into an acceptance posture. If the insertion approach is unsatisfactory, the male may jump off the line or turn and walk back to his starting point. After a series of unsuccessful approaches he may pause and let the female go back to her predatory position at the hub. Alternatively he may walk across her and rest on the upper surface of the hub. Once the female has resumed her posture at the hub, the male renews contact courtship before going onto the mating thread for a further bout of vibratory courtship.

Each time the male renews vibratory courtship (after an intervening bout of contact courtship) he goes from origin to insertion of mating thread at least once and often several times. This means that the mating thread grows by accretion until it becomes substantially thicker than the structural elements of the female's web (see FIG. 38).

Copulation. The male turns sideways after insertion and the female covers him with, at least, the tarsi III. As previously described for other group B *Argiope* spp., the female almost always drops, at the moment of insertion, to hang well below her acceptance posture location. At this stage the female can be seen to have everted her spinnerets and a wisp of multistrand wrapping silk may be visible.

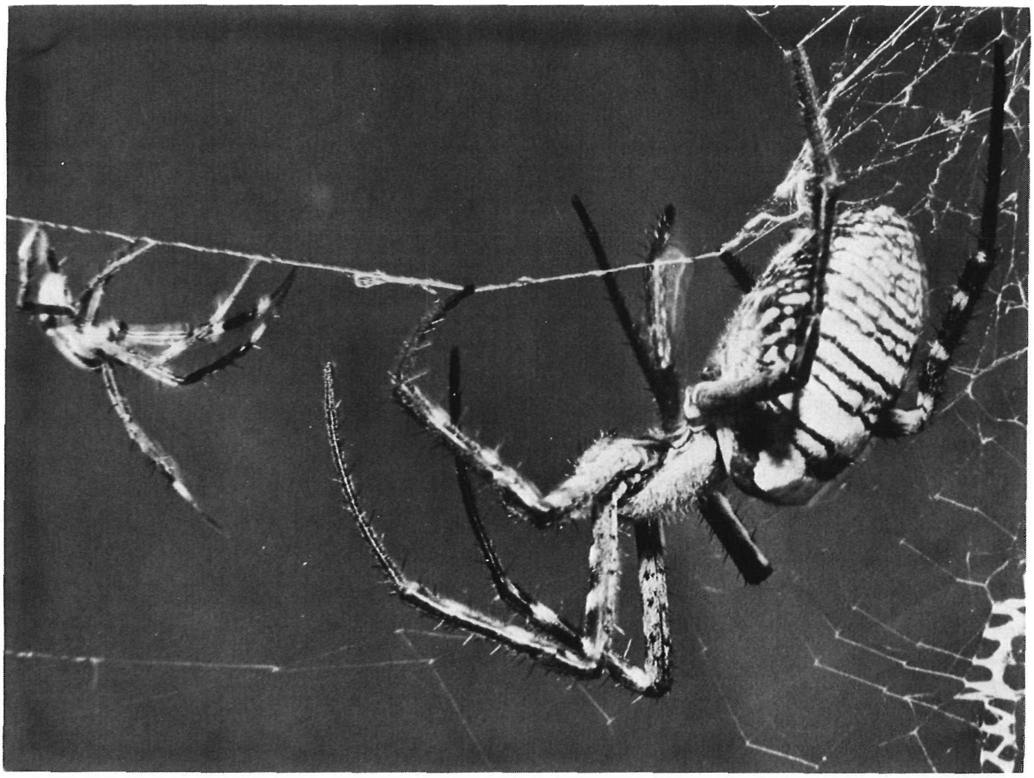


FIG. 38. Female *Argiope* sp. Wau no. 5 in acceptance posture on mating thread. Note the multistrand nature of mating thread (see text).

Interactions between males. Only one of our males entered the hub region at a time and we saw no interactions on the web margins.

Argiope sp. N.T. riverine FIG. 39–41

Near Darwin, in September 1974, we found *A. picta, A. aemula,* and *A. aetheria* in small numbers and, then, this large and impressive species at 2 locations: Robin Falls, on the Adelaide River, and later at Berry Springs, a local Nature Reserve. We worked with the Robin Falls population and sent specimens to Mike Gray, Australian Museum, Sydney, N.S.W. The species is still (1979) undetermined. The Robin Falls population consisted of around 50 adult females that were building their webs over a 100 m stretch of river. The river at this time was nowhere (at this site) more than 5 m wide and in most places less than this, and the spiders had strong foundation threads spanning the narrower reaches from riverbank tree to riverbank tree. The webs were aggregated and sharing structural lines in the manner of *N. clavipes* (Shear 1970). At the time this was the largest *Argiope* species that we had seen and

ARGIOPE sp. N. T. riverine

FEMALE BEHAVIORS	BEHAVIOR ON THE MATING THREAD	MALE BEHAVIOR ON THE WEB
rest at hub		male on upper surface of hub
		walkabout, TRing through web
		rest in posterior Vee
		TR through web legs III-R, IV-L
		walkabout
		shuttle to lower surface
		TR at legs II, III-R
		walkabout
		shuttle to upper surface
		rest in posterior Vee
		TR through hub at legs IV-R & L
		walkabout
		shuttle to lower surface
		touch and TR in lateral Vee L
		walkabout
		TR against sides of body L
		shuttle to upper surface
		rest in X in posterior Vee
		walkabout
		shuttle to lower surface
		TR in lateral Vee L
		cut hole left of hub
stilted posture		
	install mating thread x3	
	TR L, R, L, R	
	bounce	
	TR, R, L	
	drum with legs III	
	rest on thread	
	TR L, R, L, L, R, L	
bounce and turn	bounce	
into acceptance posture	bouncing to crescendo	
	insertion attempts, scrabbling	
	scrabble at epigyne	
place legs III over male	insert, turn sideways	
reach back seize in jaws, wrap	killed	
feed on male		

FIG. 39. Conventional summary of diagram of courtship in *Argiope* sp. N.T. riverine. For explanation of abbreviations, see FIG. 5.

somewhat "nephiloid" in size and shape. It is, in fact, comparable in size to *A. aurantia,* which it also resembles in having a 2-element ribbon stabilimentum (FIG. 40). Stabilimenta were rare but we counted 3 in 32 webs that we censused for prey. The webs are large (estimated ca 100 × 75 cm) and wide-meshed with eccentric hubs in the upper ½. We found largish *Tetragnatha* sp. moving on the edge of the *Argiope* webs and assume these were merely resting there before constructing their own more ephemeral webs. The resemblance to the *A. aurantia* and *A. bruenicchi* morphotype ends with the size/stabilimentum pattern. The abdomen is not striped dorsally and is what we think of as the facies of *Argiope* spp. with pentagon-shaped abdomens (*A. aetheria, A. reinwardti,* etc.). The males are not like miniature attenuated females in shape and coloration (as are *A. aurantia* males) but, on the contrary, are robust and stocky. In addition to these somewhat subjective differences, the species has a well-developed group B courtship pattern (unlike *A. aurantia* and *A. bruennichi*). We include these details in the hope that when the Australian *Argiope* species are revised, they may be of some value.

Approach behavior. Males approach the hub vibrating and plucking at intervals.

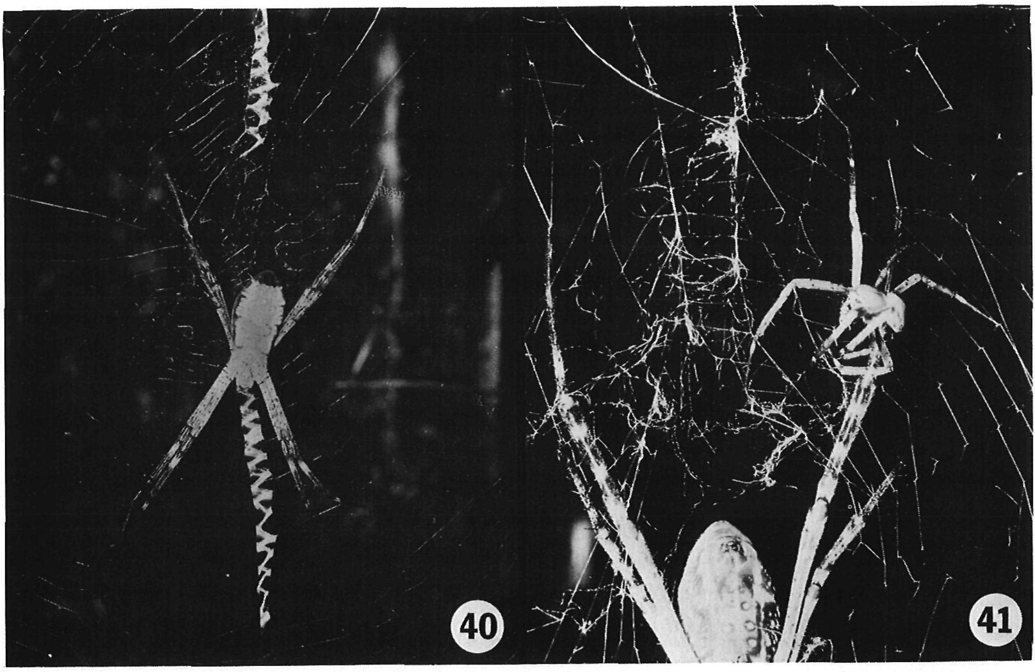


FIG. 40–41. *Argiope* sp. N.T. riverine: **40,** ♀ at hub of web showing typical shape and perpendicular ribbon stabilimentum with gap at hub; **41,** ♂ TRing at leg IV-R of ♀ through the web; note ♂ dragline silk deposited on hub.

They move on the undersurface of radii and shuttle to the upper surface at the hub. We found webs with males in X positions both on the margins and also at the hub.

Courtship. Courtship starts with a walkabout on the upper surface of the hub, during which the male touches the female's legs through the hub silk, and TRs intermittently during locomotion. This is followed by contact courtship on the lower surface of the hub which is, in turn, followed by the male preparing for vibratory courtship. The male cuts a hole to the side of the hub and there he installs a mating thread. Relative to the size of both male and female, this hole is small and the mating thread is short. On the mating thread, the male conducts vibratory courtship, and there the female assumes an acceptance posture and mating occurs.

The walkabout above the hub includes at least 3 kinds of TRing. The male may touch the female's legs through the hub silk with one or both tarsi of legs I and II on one side while TRing with the other legs I and II. He may also TR through the web against the sides of the female's legs (FIG. 41). In addition, the male may pause briefly during the walkabout and TR on the spot. Some dragline deposition occurs during these walkabouts but we did not see any AWing. On the lower surface the spider repeats these units during a much less intensive walkabout. After the spider has cut a hole at the hub, it may continue visits to the hub silk between sessions of vibratory courtship, both before and after the female responds by adopting acceptance postures on the mating thread.

All 9 mating threads that we saw were no longer than 4× the length of the male (from the tip of extended leg IV to the tip of extended leg I). We saw one clear instance where the threads laid down on the upper surface of the hub, during walkabouts following mating thread insertion, converged on the insertion of the mating thread. We saw this because of fortuitous lighting conditions and guess that it might be a regular condition. Courtship frequently started at the outer end of the mating thread and the male moved gradually inwards as it proceeded. TRs occurred regularly at the start of courtship and frequently involved legs I, II and III. One male that we filmed had only legs I, III and IV right, and legs I–III left. It consistently TRed with all 3 legs on each side despite the fact that leg IV is never involved in normal TRing. After the TRs, high-intensity bobbing occurs and further TRs may be interspersed. In bobbing, the male assumes a markedly head-down posture with the body arched ventrally so that the apex of the abdomen is very close to the thread and touches it during the bobbing movements. Legs I are held off the thread in line with the sloping body. Contrasting with this is high-intensity jerking in which legs I and II flex and extend rapidly and legs III tap the line from the sides and/or above. During this jerking, one or both of the legs II can be seen passing the line so that the tip of the tarsus appears well above it. This could be either a sawing or fiddling of the leg laterally against the line, or this leg could be held unmoving and move relative to the thread as a result of the dorsoventral body movements that result from the flexions of the other legs. We have tried to resolve this problem by movie analysis, but cannot decide between the alternatives. When the female turns and assumes a typical group B acceptance posture, the male immediately makes insertion movements. These are made, as in all the species in this section, from a stance close to the inflexion of the mating thread. We saw one immediate insertion: apart from this example, courtships were prolonged and involved numerous interpolated contact courtships as the female moved off the thread unmated and was lured back again and again. One male moved its mating thread within the hole 3 times.

Copulation. After insertion, the male turns to one side and folds his legs. The female behaves as described for *A. picta.*

Interactions between males. Males indulge in duels of plucking at a distance, and also fight and chase. We saw supplanting at mating threads. One male was driven off his mating thread by a male that was newly arrived at the hub; the supplanting male took up a vibratory courtship position on the thread only to be driven off by the original male who then successfully used his own thread.

Argiope sp. Singapore no. 1 FIG. 42

We found this spider on Singapore I and later in Malaysia at Bukit Fraser, north of Kuala Lumpur, Malaysia. We have not been able to obtain a taxonomic determination. Specimens are deposited with the Museum of Comparative Zoology, Harvard

University. This large *Argiope* belongs to what we think of as the *A. aemula* facies, i.e., spiders that have bluntly ovate abdomens that are conspicuously striped in black, yellow, and silver, and which build webs that contain cruciform stabilimenta. The species closely resembles the above-described *Argiope* Wau no. 5, but its courtship behavior differs fundamentally in the fine details. It also differs in having the legs strikingly barred. The males are relatively small with predominantly coal-black bodies; the abdomen has a conspicuous white stripe at its base and 4 white spots occur on the ventral abdomen.

Approach behavior. As for the other species of *Argiope* described above. In this species we again noted that the male lays down dragline parallel to the radius along which it approaches the hub.

Courtship. Walkabout on the upper surface of the web includes TRing and some contacts. It is followed by an extensive walkabout on the lower surface of the hub that is the main phase of contact courtship. The male then cuts a hole near the hub, lateral to the female, where the mating thread is installed. Vibratory courtship takes place with the male at or close to the inner edge of the hole, so that his legs I and II may touch the hub silk and/or legs III and IV of the female (if the mating thread is at that level).

Very distinctive TRing distinguishes the courtship of this species from those so far described. TRs on the web, against the female's body and on the mating thread all may involve simultaneous movements of all 4 legs I and II. One or both legs III may also be intermittently involved in this. Analysis of movie sequences shows that, when all 4 legs are not involved, sometimes the ipsilateral legs are rubbing against each other and sometimes the TRs include a leg from the contralateral pair (group). TRs against the female may include both lateral and "astride" contacts with the legs. During the walkabout on the lower surface the male may appear to force his way beneath the ventral surface of the female's abdomen, and as this contact courtship proceeds the female may stand more and more erect, with legs stilted. Much of the contact courtship closely resembles that of *A. picta* (see above), with the male returning again and again to touch the tips of the female's tarsi and the female reacting by "picking up her feet" and occasionally flailing her legs at the male. We also caught glimpses of sunglints on threads that lay over and between the female's legs. Apparently, dragline silk is laid down throughout this contact courtship.

When the hole has been cut and the mating thread installed, the male may return to contact courtship and will also do so, intermittently, throughout the period where vibratory courtship predominates. Vibratory courtship consists of TRing, bouncing and plucking (FIG. 42). In keeping with the 4-footed TRing, the male shows a noticeable tendency to keep all 4 anterior tarsi on the mating thread during bouncing. The body is held parallel to the thread and, at the most, one leg I may hang out of contact with the thread. The male's extreme proximity to the inner edge of the hole puts his anterior tarsi very close to the hub silk and the deltalike end of the thread. In 2 sequences on film involving 2 separate males, subsidiary threads leading off

FIG. 42. Male *Argiope* species from Singapore bouncing on mating thread. Note multistrand mating thread is very short and there are numerous dragline elements on the hub.

from near the insertion of the mating thread provide footholds for some of the anterior tarsi. One mating thread at the level of the abdominal apex of the female brought the male into contact with the 3rd leg of the female. His vibratory movements were in part directly transmitted to that leg by contact. At the height of a burst of bouncing, the male's body may be a blur of movement, but slow-motion analysis of film footage shows that it is swaying from side to side about the axis of the mating thread. We noticed AWing movements when the male was otherwise at rest on the thread.

The female bounces shortly before and during the turn into an acceptance posture. The acceptance postures that we saw were assumed very close to the hub, with the female's 3rd legs gripping the mating thread only a short distance from the insertion at the hub.

Copulation. We saw only one copulation; the male turned sideways on insertion and the female responded by dropping and placing legs III over him while simultaneously moving the pedipalps against the edge of his body. The copulation was a long one and the male escaped.

Interactions between males. We saw plucking duels, chases and expulsions, but no fights.

Argiope savignyi Levi Fig. 43–44

This species was described by Levi in 1968 and is sympatric with *A. argentata* over a considerable part of the latter's range (Levi 1968). The species is very similar to *A. argentata* and was undoubtedly confused with that species for many years. Rau (1933: Fig. 86) has a photograph of a female on a typical disc stabilimentum mislabelled as *A. argentata* (and printed upside down). *A. savignyi* is distinguishable from *A. argentata* by the greater extent of the silver coloration dorsally and by the ventral coloration. Robinson & Robinson (1978b), arguing from a presumed thermoregulatory function of the dorsal coloration, have suggested that it could be a canopy species and its apparent rarity results from only a few individuals surviving close to the ground. In courtship behavior, it belongs unequivocally to type B.

Approach behavior. We have an unusually fine film sequence showing that the approach behavior of this species involves walking movements, along the underside of the radius, of all 4 legs I and II, while legs III make intermittent movements against the radius and one leg IV pays out dragline held stiffly extended behind the male. This is the leg IV on the side of the radius; the contralateral leg IV is largely dragged behind through successive elements of viscid spiral. The basic approach behavior of this species is, therefore, exactly similar to that of all the *Argiope* species for which we have good film records. An interesting detailed difference between this species and the others (described above) lies in the fact that during pauses in approach locomotion, AWing occurs. The males also bounce and pluck during approach. The AWing in this context is of interest, particularly because AWing is an almost continuous accompaniment of the vibratory courtship of the species.

Courtship. Both the walkabout phase and the following period of contact courtship may be highly abbreviated. TRing does not occur at this stage but is an important constituent of later vibratory courtship. Holes are cut for the insertion of mating threads, and we found that they are almost always cut above a horizontal line drawn through the middle of the hub. In consequence, mating threads are usually at an angle and not horizontal. Angles measured from films and still photographs suggest that most mating threads lie between ca 30°–60° from the horizontal. Mating threads are comparatively long; all were at least 10× the length of the male (as measured from tip of posterior tarsus to tip of anterior tarsus in the legs-extended position).

Initial walkabouts include bouncing movements at intervals and are principally confined to the posterior V. The males touched the lower elements of the female's legs III and IV through the hub silk and from time to time groomed themselves vigorously. As mentioned earlier, grooming in the context of walkabouts is difficult to distinguish from TRing. In this case, the movement of one leg against another was slow and deliberate, and we feel convinced that it was genuine grooming. In several sessions, a wave of slow grooming passed back from legs I and II, until it involved

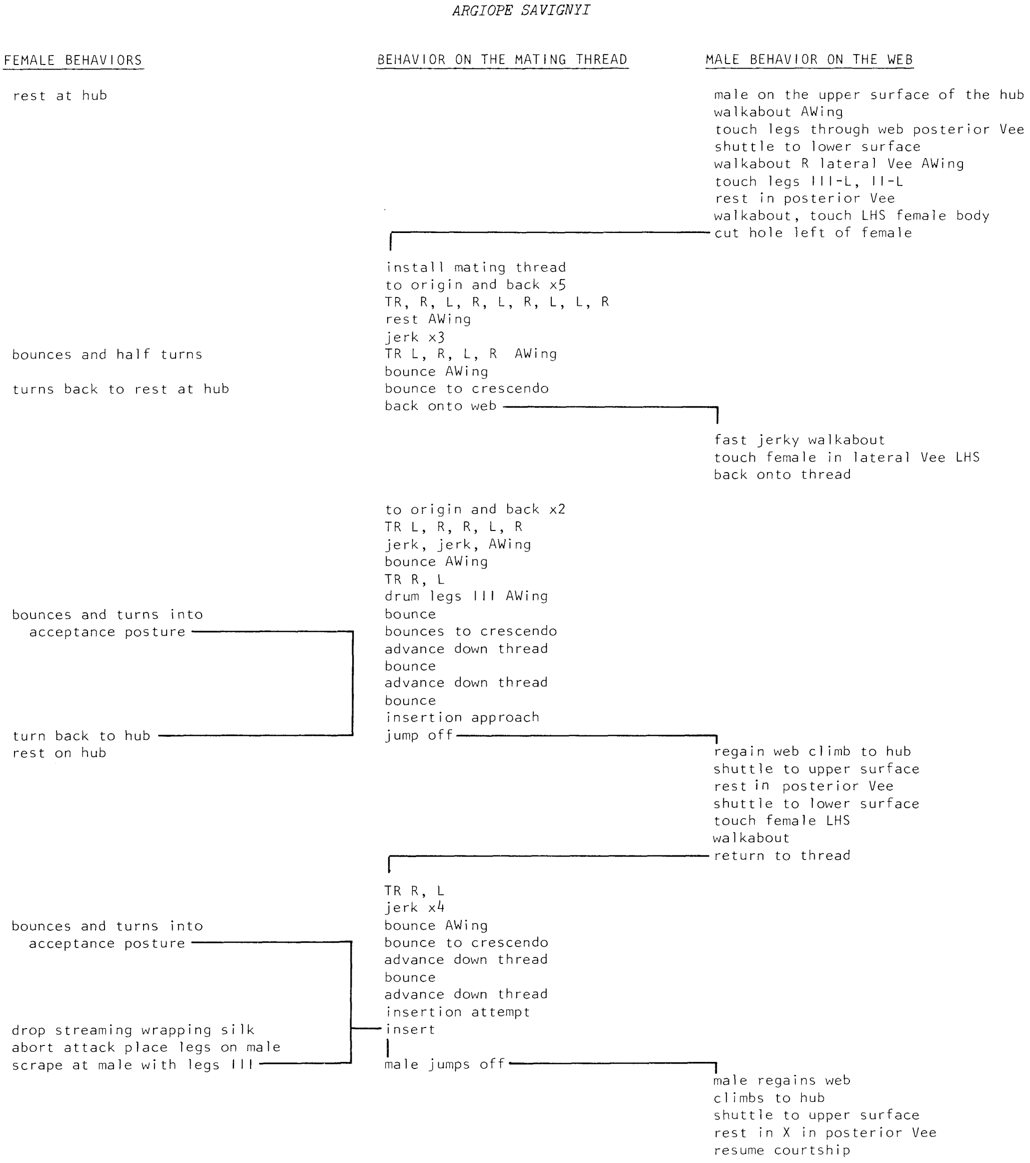


FIG. 43. Conventional summary diagram of courtship in *Argiope savignyi*. For explanation of abbreviations, see FIG. 5.

legs III and IV on one side to be followed by a similar progression on the other side. During the walkabout, the male lays down dragline silk on the hub and AWs periodically. When the male shuttles to the lower surface of the hub, more leg touching occurs, but we never saw vigorous scrabbling or TRing.

Once the mating thread has been installed, the male becomes increasingly active

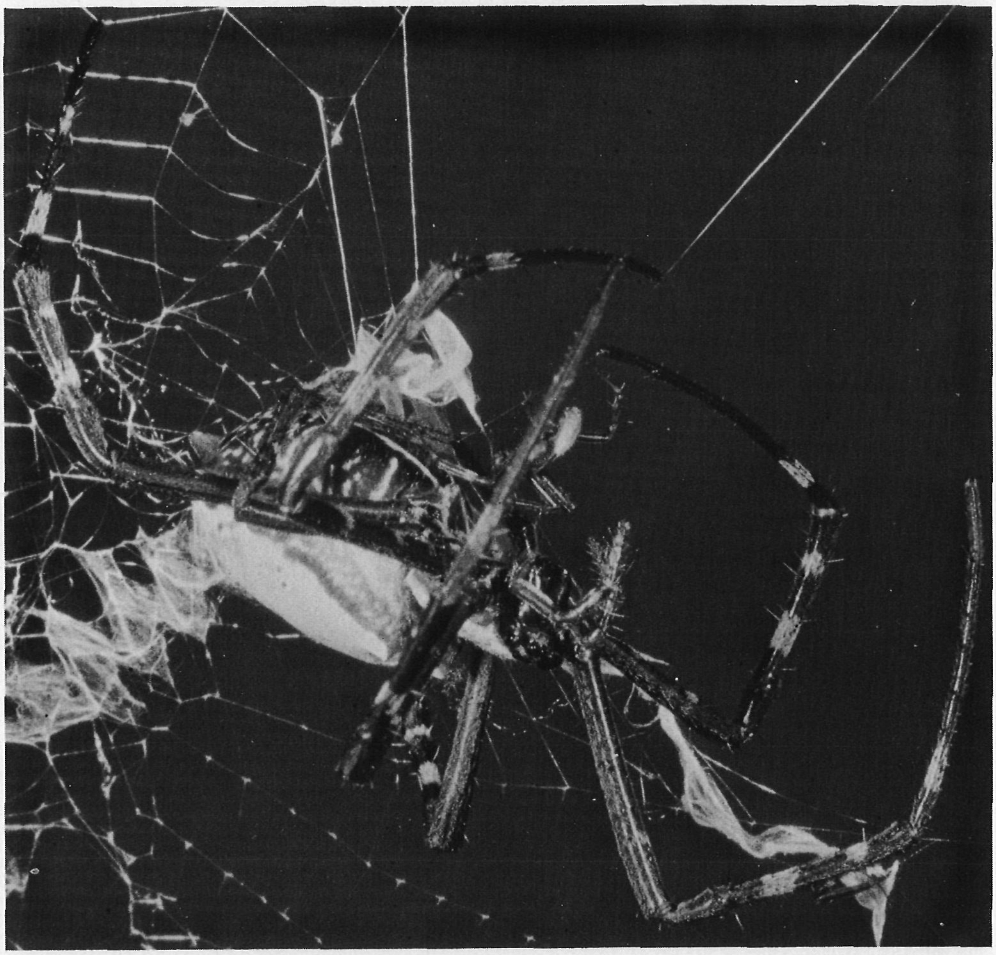


FIG. 44. Male *Argiope savignyi* at moment of insertion. Note steep angle of mating thread and that ♀ acceptance posture is partly on the hub, but both her legs III hold mating thread at a point slightly above the epigyne.

and intercalary walkabouts are fast and jerky. Vibratory courtship is distinguished by a number of characteristic behaviors. The male TRs alternately with left and right legs I and II at the start of bouts and often inserts TRs in between other units. This species AWs almost continuously throughout vibratory courtship. During AWs, the male could be pulling down on the mating thread, more or less rhythmically, or could be tapping it with his abdominal apex. The frequency of induced vibrations would be the same with either mechanism. Superimposed on this background of (presumably) low-amplitude vibrations is another rhythm produced by leg movements. We have watched sequences of the resulting body movement repeatedly and believe that we know what is happening. The male appears to be making numerous small judders out of synchrony with the AWing, and for every 5–7 small judders he makes a large anteroposterior twitch. Legs I and II are strongly flexed when the male is hanging supported by legs I, II, III and IV. They are so strongly flexed that the tarsus points posteriorly. Legs IV project behind the spider and are more or less extended; legs III are looped over the mating thread. The slight judderings may be produced by small changes in the flexion of legs I and II that rock the body back and forth very slightly. The large movements seem to be produced by a straightening of legs I and II that displaces the body backwards by up to ½ its length. Legs IV flex as this occurs. Clearly the spider could push itself backwards by straightening the anterior legs or pull itself backwards by flexing the posterior legs, or the 2 sets could work together. It looks as though the movement derives from the anterior legs and the flexure of the posterior legs is effect rather than cause. Certainly after the backwards jerk, the spider moves its legs III off the line and up towards legs IV. High-intensity bouncing may merely be a more vigorous form of this movement; it is outline blurring. When the female has assumed an acceptance posture at the hub end of the long mating thread, the male moves downwards towards her, courting, little by little, until suddenly he drops rapidly down to an insertion position (FIG. 44). This last sudden approach is made on the mating thread, but could involve slipping down the sloping line, aided by gravity. At the moment when the rapidly descending male gets into an insertion posture, he spreads his pedipalps laterally; this may prevent the pedipalp that is not intended for insertion from interfering with the one that is.

Copulation. The male turns sideways after insertion and the female reacts as described for other *Argiope* spp. We found one male with only one bulbus and assume that in addition to losing the embolus at the violent termination of copulation, males may lose other pedipalpal elements.

Interactions between males. We saw chases, plucking duels, and supplantings, but no overt fighting.

Argiope florida Chamberlain & Ivie FIG. 45–46

This species has the most restricted distribution of any *Argiope* species that we know; details are given by Levi (1968). It has some similarities with *A. argentata* in overall appearance, and the markings of the abdomen dorsally, in adult females, resemble those of immature *A. argentata* females. The webs have cruciform stabilimenta when these are present in the perfect form. In the open Palmetto Scrub where we studied this species in Florida, most webs had quite well-developed barrier webs dorsal to the spider. The adult females dropped or jumped from the hub at our approach and were, in general, extremely "nervous" spiders to study. In late August 1975, males were present on over ⅓ of the webs that we censused, either in X postures on foundation lines, at the hub, or on the barrier web.

Males of this species resemble those of *A. aurantia* in being thin and long-legged. The dorsal surface of the abdomen is patterned in a manner closely resembling that of the adult female. There is considerable intrasexual polymorphism in size.

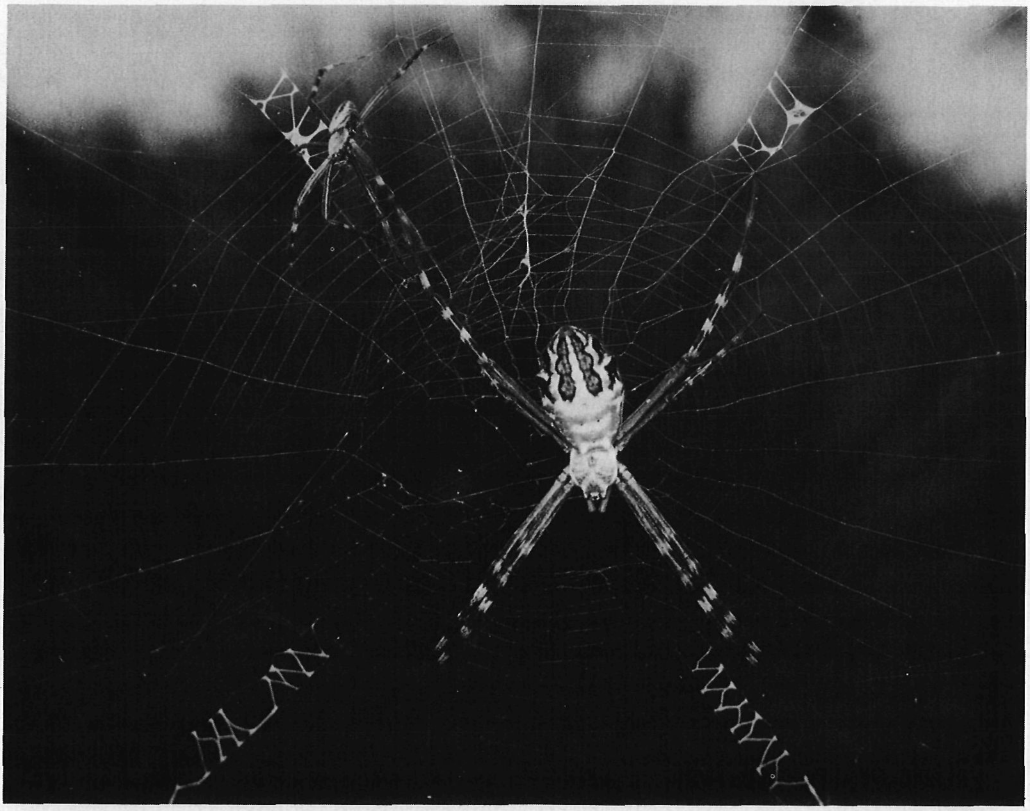


FIG. 45. *Argiope florida* ♂ at walkabout stage of courtship, touching legs IV-R of ♀. Note the relative size of the ♂, numerous ♂ dragline strands on the hub and 2 ♂-produced access holes in the hub (at 9 o'clock and 6 o'clock).

All the courtship sequences that we saw in this species took place in a high wind. The webs of the females were constantly moving with deflections of several centimeters. We were amazed that vibratory courtship could successfully take place in such conditions.

Approach behavior. Typical of *Argiope* spp. in general.

Courtship. After a walkabout (FIG. 45) on the upper surface of the hub and a usually perfunctory period of contact courtship, the male cuts a hole at the hub and conducts vibratory courtship.

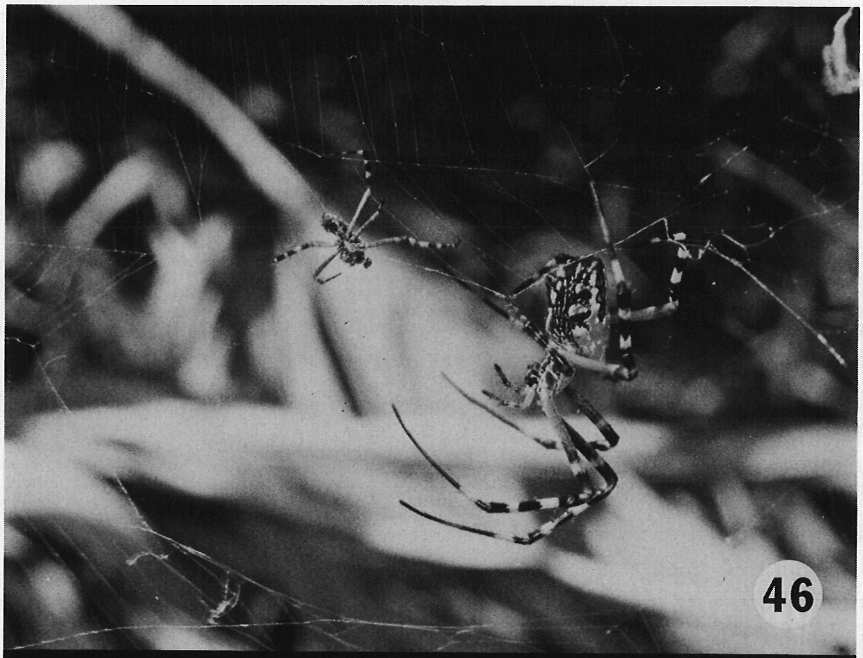
The walkabout above the hub is characterized by a bouncing gait, occasional touching of the female's legs through the web and infrequent TRing. Silk is deposited throughout the wide-ranging movements and the hub of the web of a well-courted female becomes covered with a complex of fine lines. At intervals in the walkabout, the male assumes an X posture, usually in the posterior V. When in this posture he repeatedly gives quite high-intensity bursts of bouncing on the spot. In film sequences these clearly involve trains of alternating flexions and extensions of the legs and some AWing. The effect is one of rapid press-ups. We could not decide whether these movements were part of courtship or signals to encroaching males. (More than one male was present at the hub region on many of the webs that we censused.)

To move from one surface of the web to the other, the male often cuts a hole in the hub silk; normal shuttling may be difficult for such long-legged males. We noted such hole cutting in other species with long-legged males. Activity on the lower surface of the web was perfunctory in all the courtships that we saw. It consisted of an abbreviated walkabout in which the tarsi of (at the most) 2 leg pairs would be touched.

Mating-thread hole cutting followed the usual *Argiope* pattern (but see below, Anomalous behavior). Mating threads varied from the horizontal to some angled at up to ca 60°. The longest seen was about 5 cm long. Males rapidly passed into vibratory courtship, adopting a stance about halfway along the threads. Behavior units involved in this phase included TRs, jerking and high-intensity bouncing. Due to high winds and the resulting web movements, our film of vibratory courtship is generally unsatisfactory. TRing involved legs I and II and the jerking appeared similar to that described for *A. savignyi,* but we cannot be sure that the high-intensity movements occurred against a background of minor movements. High-intensity bouncing clearly involved tapping from above the line with tarsi III, but increased in crescendo until the male was a mere blur. One male with only 5 legs succeeded in bringing the female into an acceptance posture on his line and eventually mated with her (Fig. 46). He neither TRed nor jerked, but seemed to merely sway from side to side for long periods.

After the female has moved into an acceptance posture, the male continues to court and eventually makes a rapid insertion approach. He turns and resumes courtship from further up the thread if the approach is unsatisfactory. We noted that during the duration of the acceptance posture, the female's pedipalps point towards the male (roughly at right angles to her long axis), not back under her cephalothorax (Fig. 46).

Anomalous behavior. We saw one male enlarge an outer corner of a previously cut hole so that his mating thread spanned not to the hub silk but to part of the upper edge of the hole. In this situation, when courting he was almost touching the web above his ventral surface and the thread was at some distance from the hub. Even this thread was successful; the female adopted an acceptance posture at its cramped inner end and the male successfully mated. Another male built a long mating thread from the barrier web to a radius in the main orb. This mating thread was over 10 cm long and not located in the web plane. The point of attachment on the 1 o'clock radius was well above the hub. Despite the presence of a courting male at the hub, the female eventually went out onto this horizontal thread and into an acceptance posture. She caught and wrapped the male during an insertion approach. Courtship by this male, which had only 5 legs, occurred intermittently for over 40 min. before the female moved from the hub.



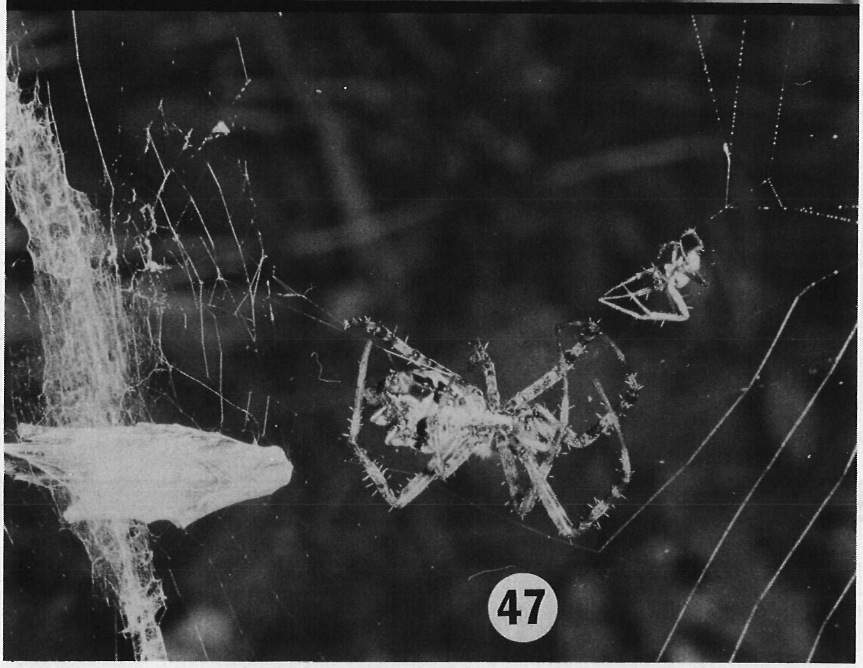


FIG. 46–47. **46.** *Argiope florida*: ♀ in access posture on anomalous mating thread built on upper edge of a hole; ♂ has successfully brought ♀ into acceptance posture with only 5 legs. Note that he has only 1 intact pedipalp. **47.** Female of *Argiope flavipalpis* in almost horizontal acceptance posture on mating thread. Note that her legs II are touching the thread that has multiple attachments to the hub; the ♀ has sharp crenulations on the edge of the abdomen.

Copulation. Males turn sideways after insertion. Females respond by dropping below the mating thread and placing the tarsi III over the male. In at least one instance, the female dropped down before the male contacted her ventral surface, i.e., during his approach.

Interactions between males. We saw many chases and plucking duels. Males occasionally fight. Fighting seems to occur when males run into each other. They then become a blurred moving mass of entangled legs. Our field notes state "males get into a melée after plucking bouts. After one fight a male dropped to the ground and was motionless for over 30 s—assumed dead—but returned to the web, trailing leg I R which seems incapable of movement." Despite fights and chases, we frequently saw up to 3 males on the hub at once. Furthermore, in at least one instance, the courting activities of a newly arrived male seemed to trigger a previously inactive resident male into courtship.

Argiope flavipalpis (Lucas) FIG. 47

This species is another form with a lobed abdomen (as in *A. argentata, A. savignyi* and *A. florida*). It has a cruciform stabilimentum but frequently the hub is covered with a dense sheet of opaque silk that we would prefer to distinguish as a shield (following McCook 1889). Ewer (1972) has described developmental changes in the stabilimentum of *A. flavipalpis,* and its ecology has been studied by J. Edmunds (in prep.). We found some adult females with disc stabilimenta. The females are conspicuously marked with large areas of whitish yellow ventrally and the lobes are pointed in comparison to those of the New World *Argiope* spp. Several individuals that we saw were markedly melanic; we do not know whether this is a temporary condition due to a short-term color change or is genetically determined. Males are relatively small (FIG. 47) and there is intrasexual polymorphism in size.

Approach behavior. This is typical of *Argiope* spp. We saw a single example of a male TRing (once) during an approach; we think this behavior is aberrant and may have been indicative of hypermotivation. One male approached down a radius in the normal manner, but ran back over the viscid spirals when chased.

Courtship. This follows the pattern: walkabout, cut hole in web, insert mating thread, conduct vibratory courtship. In our notes, we find the term "perfunctory" used over and over again to describe the walkabout phase in this species. It involves no contact with the female, as far as we can tell, and little other than walking with a jerky gait, with some AWing and silk deposition. All the walkabouts that we saw were conducted on the upper surface of the hub. We saw no touching through the hub silk.

Hole cutting proceeded in the usual way and we saw a variety of mating threads ranging from ca 10°–60° in inclination. All were short, averaging around 5–6× the body length of the male (legs extended). In the initial stages of laying down a mating thread, the male interspersed walkabouts on the upper surface of the hub between movements on the thread itself. Once vibratory courtship was started, the males became extremely persistent and remained on the mating thread for several minutes at a time, courting intermittently (unless the female responded quickly). Vibratory courtship consisted of at least 3 major components. TRing occurred at the start of courtship bouts and was then interpolated between other behaviors. TRs were vigorous and started with legs I and II. Legs III started to move in TRing fashion towards the end of a vigorous bout but seldom appeared to connect with legs I and II. As he TRed, the male leaned sideways so that the legs involved were well below the mating thread. After TRs, the spider usually made a long series of slow dorsoventral bobbing movements (press-ups) that waxed and waned in frequency. At no stage did the legs not in contact with the thread hang below the body axis, rather they remained quite strongly flexed towards the thread. As the spider moved up and down, the tarsi of these legs moved above the thread and then down again. This bobbing had none of the backward-jerk components described in the courtship of *A. savignyi* and *A. florida* (above). During the bobbing, the cephalothorax was held parallel to the thread but the abdomen was curved towards the line. Out-of-phase AWing occurred throughout bouts of slow bobbing. Bobbing increased in amplitude to give rise to a fast blurring movement in which the spider's body swayed from side to side, sometimes appearing entirely above the line for a brief instant. During this crescendo of movement, the male may have been tugging rhythmically on the line. J. Edmunds saw a similar behavior in *A. flavipalpis* in Ghana; she writes, "male . . . hauling threads, mainly vibrating for two minutes becoming more and more jerky and rapid, female vibrated a little and turned towards male" (in litt.). This is an interesting observation because the TRing movements of male spiders have a strong superficial resemblance to the movements spiders make when they are "hauling in" dragline that they have paid out when trying to establish a bridge line from one place to another, more distant one.

The female may respond by bouncing at the hub and turning into an acceptance posture. If she does not respond, the male may rest on the mating thread or move onto the hub and rest in an X posture. Frequently the male does neither, but moves to the hub and then lays down yet another strand on top of the mating thread. If the female moves into an acceptance posture, the male may make an immediate rapid insertion approach or continue courting for some time before making such an approach. If the female is not at the right stage of receptivity when the male gets in close proximity to her ventral surface, he may leap off the mating thread, turn and go back to his starting point (approximately), or continue on across the ventral surface of the female and onto the hub silk. We saw the latter happen on 3 separate occasions.

One instance of a female being attacked by a spider-hunting wasp while a male was in courtship on a mating thread provides an interesting insight into the dependence of male behavior on female responsiveness. After the female had been carried off, the male continued courting intermittently for over 30 min. There was still a male on the empty web the next morning. One web that we found had 3 holes at the hub, each containing a mating thread; these were (approximately) on the 11, 7, and 2 o'clock radii.

Copulation. Males turn sideways after insertion. The female drops below the thread and places her tarsi over the male.

Interactions between males. We saw numerous chases, plucking duels and one case of supplanting at a mating thread, but no overt fighting.

Kleptoparasitism by males. We have 2 records of males feeding on prey stored in the web at a capture site.

Argiope aurocincta Pocock FIG. 48

This rather striking species was the first one that we encountered in Natal in January/February 1975. On the coast at Umdoni Park, gasteracanthids were numerous as adults of both sexes, but *Argiope* spp. were rare. We found only 8 adult females of this species in an intensive search over some 10 acres (4 ha) of parkland. We found one adult male; all the following observations are based on the behavior of this individual. The species builds a cruciform stabilimentum and this may completely occlude the hub of the web. In open grassy areas, it is easily provoked into jumping out of the web as a defensive response. The male that we found was relatively large (FIG. 48) and strikingly orange-red in color.

Approach behavior. The male was at the hub of the web, on the upper surface, when found.

Courtship. After a walkabout period, the male cut a hole at the hub, inserted a mating thread and conducted vibratory courtship. Walkabouts were almost entirely above the hub, within the area circumscribed by the legs of the female. Silk deposition occurred, together with periodic bursts of AWing. Bouncing on the spot and tapping the web above the female's tarsi seemed to be the only stylized signal elements involved.

The hole was cut close to the hub through one arm of a cruciform stabilimentum. The mating thread, inserted at about 40°, was short, about 5× the male's length. As with most of the species described above, the male moved backwards and forwards across the thread several times before commencing courtship. Courtship started with TRs and these were followed by bouncing on the line, during which the main body movement was dorsoventral. This bouncing involved strumming movements of the tarsi of those anterior legs that were not actually gripping the mating thread. In film sequences, these strumming movements closely resemble the high-speed scrabbling movements that we described in the case of *A. aurantia.* Out-of-phase AWs occur throughout the bouncing bouts. TRs were interspersed with bouncing and, as the female started to turn at the hub, the bouncing reached a high intensity and the male appeared to be pulling rhythmically on the mating thread. This impression of pulling results from the fact that the flexed anterior legs straighten somewhat at the same time that the body moves backwards. After a brief pull, the legs flex more strongly

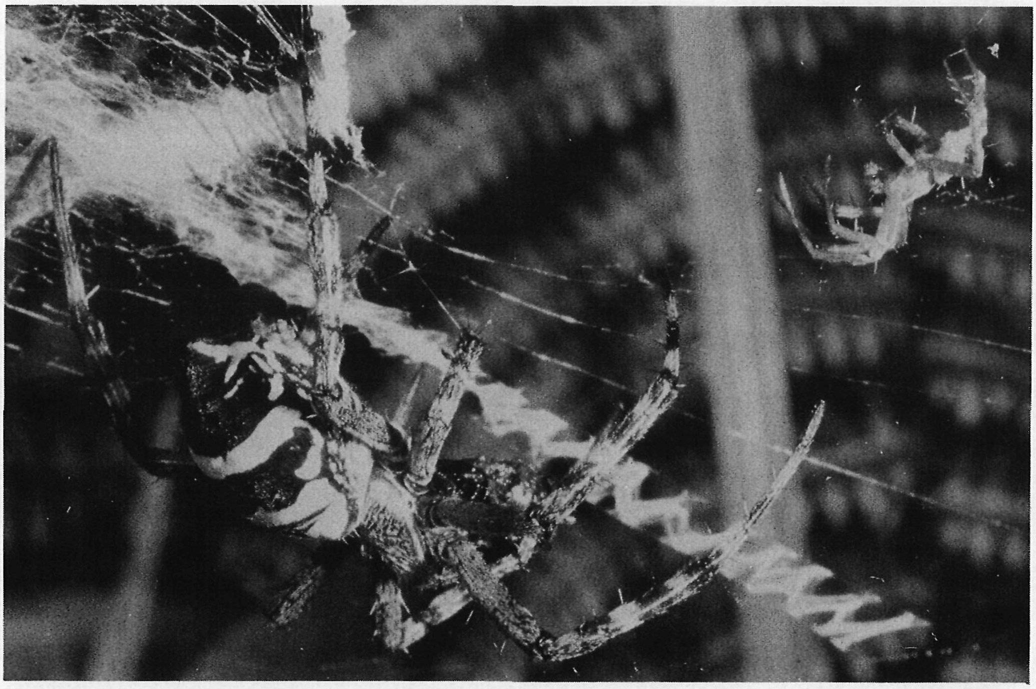


FIG. 48. *Argiope aurocincta.* Female in acceptance posture, holding prey package in jaws. Both of the ♀ legs IV are on the hub.

and the body swings forward again. The whole impression is of the male tensing the mating thread away from the hub and then allowing the stretched (elastic) thread to move back. At times throughout high-intensity bouncing, the male had one or both legs I off the line and hanging below the line of its body. The female assumed an acceptance posture close to the hub and for much of the several bouts of vibratory courtship the male was standing less than a body length away from the point where her legs III gripped the thread. This put his legs I and II very close to the female's 2nd pair of legs; in fact, he stood courting within the arch that they formed and may have touched their tarsi from time to time. While the female was in the acceptance posture, she strummed the mating thread with her legs III from time to time. The male moved down very rapidly to make insertion attempts but jumped off or retreated the first 8 times. After turning to retreat, he ran up to the intact web and circled around onto the hub surface on 2 occasions. After the female had resumed her predatory posture at the hub, the male made a walkabout and then added new elements to his mating thread before resuming vibratory courtship. He also moved onto the hub for a brief walkabout after regaining the web following a last-minute jump-off. The female had prey at the hub and fed on it whenever she returned from an acceptance posture. She actually carried the prey with her (attached by a line to

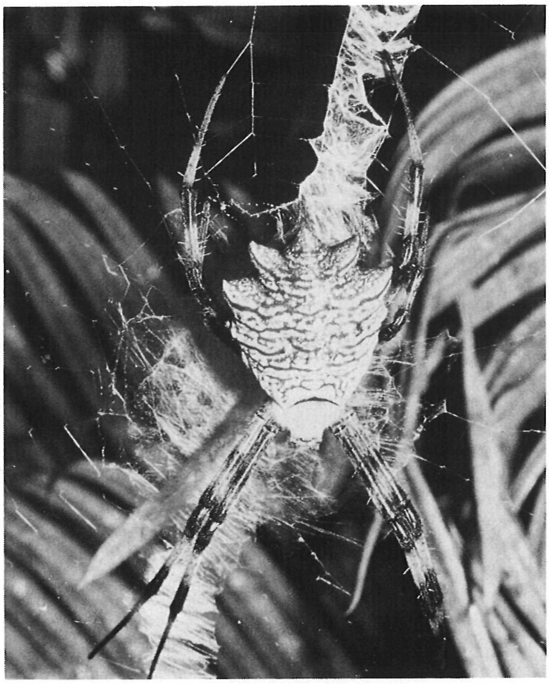


FIG. 49. Dorsal view of ♀ *Argiope cuspidata.* Note the shield at the hub of the web between the ribbon arms of the stabilimentum.

the hub) on 4 of her visits to the mating thread (FIG. 48). When copulation finally occurred, the female had left the prey at the hub.

Copulation. The male turned to the left after insertion and was touched by the female, using her 3rd legs, throughout the period. He was pushed forwards and wrapped at the end of copulation.

Interactions between males. Only one male was seen.

Argiope cuspidata Thorell FIG. 49–50

This species was closely similar in appearance, web structure and habitat preference to *A. flavipalpis* (seen by us in Nigeria, see above, compare FIG. 47 and FIG. 49), and there seems to be some confusion over the status of the 2 species (J. Edmunds, pers. commun.). We only found 6 adult females but were fortunate to find 3 males on one web and saw long courtship sessions and 3 copulations. Our field notes state that the species in Natal can vary in the dorsal coloration of the abdomen from predominantly yellow to predominantly blackish and that color change in individuals can occur quite rapidly. Unfortunately, we did not note how rapidly or in what circumstances. Males are comparatively small. The stabilimentum, in its perfect form, is cruciform and dense, and the hub region may have a shield (FIG. 49). We found all the adult females inside forest in heavy shade.

Approach behavior. Inactive males rest on the foundation threads of the web in X postures, or on the upper surface of the hub in X postures. We saw 2 approaches from the outside of the web to the hub. Both were along the underside of radii; males jerked at pauses during the movement and shuttled to the upper surface of the hub on arrival.

Courtship. Following a walkabout on the upper surface of the hub, males cut holes very close to the hub and inserted short mating threads from which they conducted vibratory courtship.

The walkabouts involved a jerky gait and silk deposition. The males showed some tendency to move up and down the arms of the stabilimentum. We recorded 2 instances of males touching the legs of the female through the web. TRs on the hub, not directed against the female appendages, also occurred, but rarely. (This may be a genuine difference between this species and *A. flavipalpis* or we may have missed seeing the behavior in *A. flavipalpis,* since the walkabouts are short in both cases.) Holes cut for mating threads were very close to the hub, and mating threads (5 examples) varied from around 35° to over 60° above the horizontal. The length varied from 4× to 7× the male's body length; the one shown in FIG. 50 is extremely short.

Vibratory courtship involved TRing, followed by bouncing that had a primarily dorsoventral component. After bouts of vibratory courtship that left the female apparently unaffected, the male would return to the upper surface of the hub for further walkabout sessions. After each interpolated excursion onto the hub, the male would add at least 2½ strands to the thread, i.e., would move from insertion to origin to insertion and then to a courtship location about halfway along the thread. When the female moved into an acceptance posture she hardly left the hub but merely turned to one side and gripped the mating thread very close to the end with her 3rd legs (FIG. 50). This may result in the very upright acceptance posture. When a male moves down to make an insertion attempt his body is inevitably in a parallel posture. Insertion excursions were made in stages with courtship being repeated as the male moved closer until his rapid final descent into contact. At the crescendo stage of vibratory courtship, when the male outline begins to blur, our film sequences show that there is a rhythmic backward tugging on the line (we thought that the final crescendo courtship of *A. flavipalpis* might have included such a movement; there is no doubt in this case). We did not note any AWing during the bouncing phase of courtship, but the angle of our film shots is such that it would minimize such movements. It could have occurred and we could have missed it. Apart from this detail, and the presence of TRing in walkabouts, we can detect no difference between the courtship behavior of *A. cuspidata* and *A. flavipalpis,* but find numerous striking similarities. Of course, any minor differences could be due to variation, since the distance between Ibadan, Nigeria, and the Natal coast is considerable.

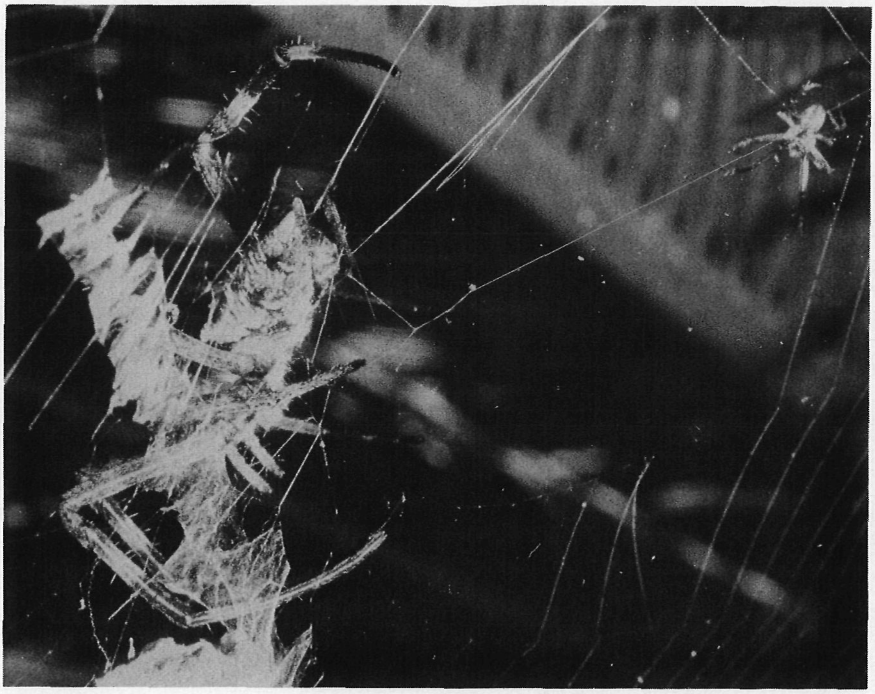


FIG. 50. Almost perpendicular acceptance posture of ♀ *Argiope cuspidata.* Note the short mating thread, which has been intensified for clarity.

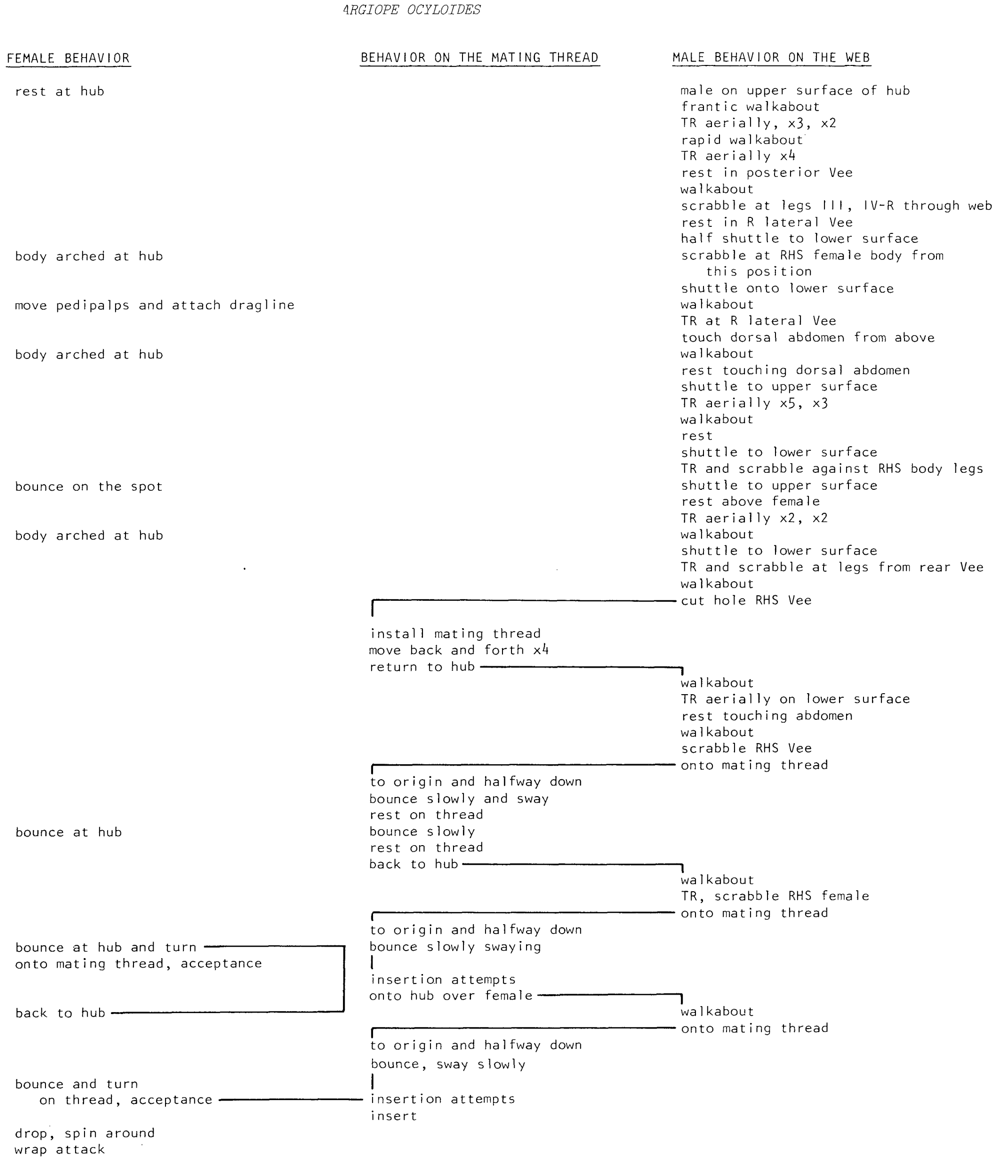
Copulation. We saw only one copulation. It followed the typical pattern for *Argiope* spp. with type B courtship behavior: the male turned sideways on insertion and the female placed tarsi III over him. He was eventually pushed forwards to the chelicerae, wrapped and eaten.

Interactions between males. Males interact on the foundation lines and at the hub. We saw plucking duels and chases.

Predation during courtship. While one female was being actively courted we saw a blue-winged spider-hunting wasp attack a nearby *Gasteracantha versicolor.* This dropped close to the *Argiope* web and the female *Argiope* dropped out of her web. She was attacked and captured by the wasp as she clambered up the web from below. The male remained at the hub of the empty web for 2 days.

Argiope ocyaloides Koch L. FIG. 51–53

Robinson & Lubin (1979) give details of the biology and behavior of this species and describe it as arborphilic. We found it at Wau exclusively on the trunks of tall trees with rough bark. Of all the *Argiope* species that we have seen, this exhibits the least sexual dimorphism in size. Males are only slightly smaller than adult females and closely similar in shape and coloration. Camouflage may be useful to males mov-



ARGIOPE OCYLOIDES

FEMALE BEHAVIOR	BEHAVIOR ON THE MATING THREAD	MALE BEHAVIOR ON THE WEB
rest at hub		male on upper surface of hub
		frantic walkabout
		TR aerially, x3, x2
		rapid walkabout
		TR aerially x4
		rest in posterior Vee
		walkabout
		scrabble at legs III, IV-R through web
		rest in R lateral Vee
		half shuttle to lower surface
body arched at hub		scrabble at RHS female body from this position
		shuttle onto lower surface
move pedipalps and attach dragline		walkabout
		TR at R lateral Vee
		touch dorsal abdomen from above
body arched at hub		walkabout
		rest touching dorsal abdomen
		shuttle to upper surface
		TR aerially x5, x3
		walkabout
		rest
		shuttle to lower surface
		TR and scrabble against RHS body legs
bounce on the spot		shuttle to upper surface
		rest above female
		TR aerially x2, x2
body arched at hub		walkabout
		shuttle to lower surface
		TR and scrabble at legs from rear Vee
		walkabout
		cut hole RHS Vee
	install mating thread	
	move back and forth x4	
	return to hub	
		walkabout
		TR aerially on lower surface
		rest touching abdomen
		walkabout
		scrabble RHS Vee
		onto mating thread
	to origin and halfway down	
	bounce slowly and sway	
	rest on thread	
bounce at hub	bounce slowly	
	rest on thread	
	back to hub	
		walkabout
		TR, scrabble RHS female
		onto mating thread
	to origin and halfway down	
bounce at hub and turn	bounce slowly swaying	
onto mating thread, acceptance		
	insertion attempts	
	onto hub over female	
back to hub		walkabout
		onto mating thread
	to origin and halfway down	
	bounce, sway slowly	
bounce and turn on thread, acceptance	insertion attempts	
	insert	
drop, spin around		
wrap attack		

FIG. 51. Conventional summary diagram of courtship in *Argiope ocyaloides.* For explanation of abbreviations, see FIG. 5.

ing on the surface of trees. We discovered this somewhat cryptic species towards the end of our stay in Wau and carried out all our observations on courtship and mating behavior with caged specimens and males raised in captivity. During a brief visit to Wau in 1977, MHR saw courtship in the field. We only saw one copulation.

Although both sexes are unusually (for *Argiope* spp.) somberly colored on the dorsal surface, they are conspicuously marked below. Both sexes have very large yellow to white patches running down both sides of the abdomen. This very conspicuous marking is, of course, only visible from below or when the spiders are oriented with their ventral surfaces uppermost. It is interesting to note that 2 other araneids that build webs on trees have conspicuous ventral abdominal markings (see *Herennia ornatissima, Nephilengys malabarensis,* above). All our close-up films of courting males show that they have long conspicuous bristles (trichobothria?) on the dorsal and inner surfaces of tibiae I.

Approach behavior. Males approach down the lower surface of the web plucking sporadically. One male reached the hub and then ascended the radius to move along the upper foundation thread and descend another radius before gaining the hub. On 2 occasions males that were commencing approaches elicited vigorous responses from the female. The female turned at the hub to orient towards the male and shook the web violently in his direction. Web shaking was accomplished by plucking movements similar to those used in predatory sequences (Robinson & Olazarri 1971); these were of higher intensity than used in predatory behavior. As the female shook the web, the male froze into immobility, and then after a pause of several seconds moved back onto the foundation thread and assumed an X posture. One of the males thus affected moved unmolested to the hub an hour later, the second approached the hub nearly 3 h later.

Courtship. The courtship of this species is characterized by a walkabout phase that is as complex and vigorous as any we have seen from group B courtship species. It is followed by hole cutting, the construction of a mating thread and subsequent vibratory courtship. With each new species of *Argiope* that we studied, we tried to predict, during the walkabout phase, whether the species would finally exhibit group A or group B courtship. Right up to the moment when *A. ocyaloides* started cutting a hole at the hub, we confidently expected it to make direct approaches to the epigyne. Perhaps the male is too large for this kind of approach and we should have guessed otherwise.

The walkabout range in this species is very restricted and the term is not very descriptive for a case like this where much of the early courtship takes place as male and female stand facing each other on opposite sides of the web. Although the male is somewhat smaller than the female, his legs are proportionally longer and the courting pair stand toe to toe (or, more correctly, tarsus to tarsus) (FIG. 52). The male's perambulations at the hub seldom take him with all his legs outside a circle circumscribing the female's tarsi; he is seldom more than a body length outside this range. The exception is made on the side of the female where he will eventually cut the hole for the mating thread. Opposite that lateral V, the male strays up into the viscid spiral zone.

Males indulge in a variety of movements at the hub. Starting at the opposite side to the female, they tap the web surface as though aiming at the points where the female is standing, make extensive and vigorous TRing and touch the female through

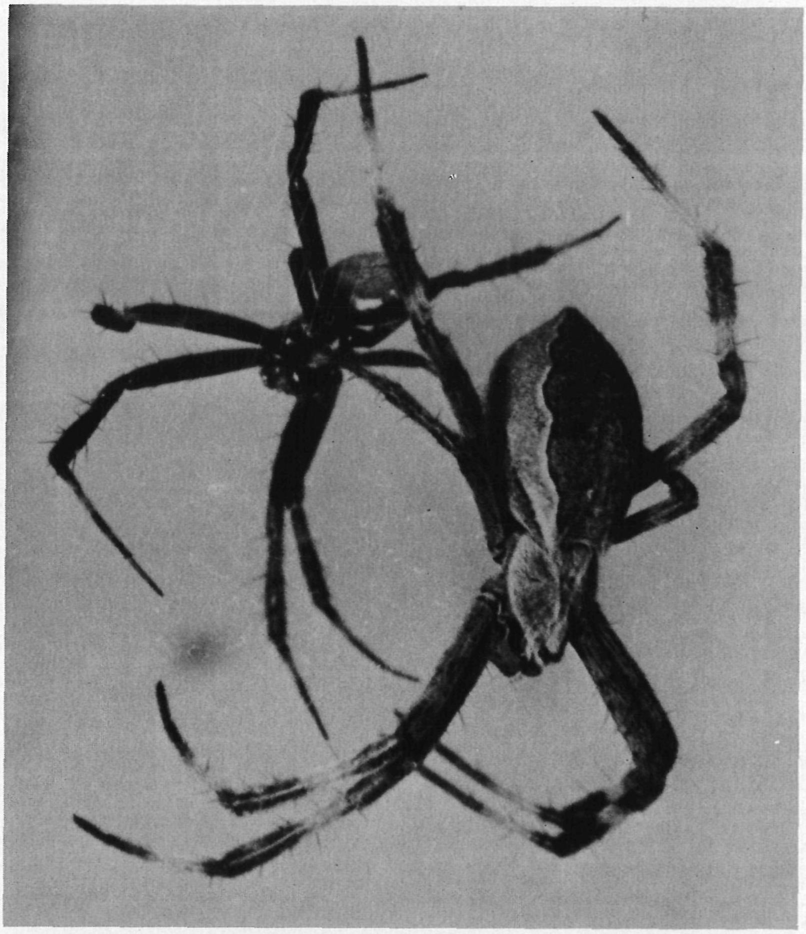


FIG. 52. Male and ♀ *Argiope ocyaloides* standing on opposite sides of the hub of the web. Note the camouflage coloration of the ♀ and that the ♂ leg span is almost as great as the ♀.

the hub silk. The TRs are not made against the female or even against the hub silk, but are made aerially as the male hangs slightly away from the hub. They are very distinctive in that they almost always involve the anterior legs of more than one side. Thus a session may start off involving legs I and II-L, and then I-R will start to move, and eventually both legs I and both legs II are moving and perhaps one or both legs III come into action. Touching the female through the hub silk is comprehensive; since the male is almost as big as the female and has long legs, these can reach through the loosely woven hub to touch the female, not only on her tarsi but also on her tibiae, femora, abdomen, and even her pedipalps. Even more interesting is the movement by which the male edges his body sideways through the hub silk (perhaps through the free zone) so that, with ventral surface facing the side of the female, he can touch her dorsal surface with the legs of the side of his body that is on the lower (female's) side of the hub. In our film sequences, males clearly touch the dorsal surface of the female's abdomen and cephalothorax from such positions.

Of course, the male may also shuttle completely onto the lower surface of the web and walkabout there, TRing and touching the female. The edging through and touching with the legs of one side, described above, may in fact be derived from shuttling. Males sometimes rest on the same side of the web as the female, with their legs I and II touching the dorsal surface of the female's abdomen from the posterior V.

Some of the TRs on the lower surface of the hub are directed at the female's legs, and we saw an interesting variant of this behavior that we have not seen in other *Argiope* species. The male placed his anterior legs on the female's legs and then TRed; during the TRs, his short legs III were off the web. From time to time during walkabouts on both sides of the hub, males make silk-attachment movements and AW, but they do not seem to be depositing silk over the female's legs.

All this male activity occurs in quite vigorous bursts to which the female is by no means unresponsive. At the least, she appears fidgety. As the male touches the female's legs, she lifts these off the web and shakes them. Eventually the female adopts a more and more stilted posture and her anterior legs, in particular, may receive concentrated male attention and become strongly flexed. The female thus comes to adopt a stance that puts her body well clear of the web. We saw one female make what we assumed to be a series of rejection responses. She started a series of high-intensity pumping movements that really shook the male backwards and forwards as he stood on the opposite side of the hub. These movements are part of the antipredator defenses of most *Argiope* species (Robinson & Robinson 1970b, Tolbert 1975). At the height of the pumping, the female's abdomen was moving out of phase with the dorsoventral press-ups of the body and seemed to be hammering against the hub silk. (This response did not deter the male for very long since he eventually installed a mating thread and courted the female from it.) The same female followed these pumping bouts by circling at the hub and making silk-attachment movements with her spinnerets. We assume that she was adding silk to the hub structure.

Hole cutting proceeds from the hub outwards and the mating thread is quite long relative to the size of the web, but no more than 5–6× the length of the male (with legs extended). At the start of vibratory courtship, the male goes out along the thread to the origin, moves up and down it several times, pauses for a very brief courtship and then moves onto the hub for a walkabout (TRing and touching), repeating this sequence several times before settling down to a more sustained vibratory courtship. Vibratory courtship in this species is both relatively simple and relatively perfunctory. Most bouts that led to the assumption of acceptance postures by females consisted simply of side-to-side swaying bouts in which the movements did not accelerate in pace nor reach a blurred crescendo. During this swaying which seemed slow and deliberate, tarsi III were moved "like drumsticks" against the mating thread and legs I and II strummed from time to time. Only 2 out of 10 such sessions started with a burst of TRing. It seems possible that the major functions of courtship in this species are subserved by the complex walkabout phase. When the females assumed acceptance postures, the males moved down in 2 or 3 stages, swaying at each stopping point, before making the final insertion-attempt approach. A male that leaped off the mating thread at the "last minute" walked up the web from the lower foundation thread and, on reaching the female's anterior legs, flailed at them, vigorously, for nearly a minute before resuming a walkabout.

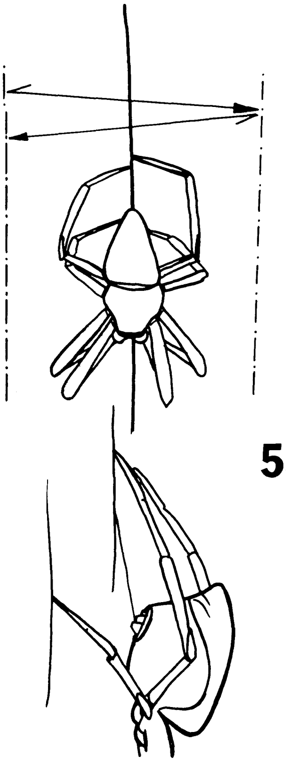
One male that started off with a mating thread at ca 60° on the right-hand side of the female brought her out onto it 4 times, but did not achieve a successful mating. He then constructed a mirror-image mating thread on the left of the hub. He courted twice on this before moving back to his original construction. In this instance, the female's web was built from front to back of the cage and we were able to film the courtship sessions from a point just slightly above the web plane. We can therefore measure the lateral displacement of the mating thread/male's body during the swaying part of courtship. This is shown in FIG. 53.

Copulation. We saw one copulation. After insertion occurred, the female jerked and dropped, spinning around suspended on her dragline. Even on film we cannot resolve the details of the male's copulatory posture from the blurred, spinning couple. We think that he is more or less parallel to the female's long axis and certainly tightly appressed to her. This means that the copulatory posture of this species is similar to that of *A. aurantia* and *A. reinwardti.* Further study is needed. The male was wrapped and eaten.

Interactions between males. We never saw more than one male at the hub at a time in noncaptive examples. In captivity, we introduced as many as 3 males to a single female. They interacted at the web margins with plucking duels, but we never had 2 males at the hub at the same time.

COURTSHIP AND MATING BEHAVIOR: GROUP C

The arrangement of species in this section presented us with a major problem. If we try to group the genera from the primitive to the advanced vis-à-vis our interpretation of their courtship behavior, there are a number of criteria that can be used, and these are by no means easy to weight for importance. We have opted for a relatively simple, but perhaps meaningful solution in this section and can thereby leave consideration of the contentious points until later. We have chosen to first describe courtship in genera with a high degree of sexual dimorphism in size and have left the genera where the sexes are little different in size until last. We make an exception to this arrangement only in the case of *Gea* sp. (Wau, Papua New Guinea) because this genus is widely regarded as very close to *Argiope* on morphological grounds (Levi 1968). This scheme puts spiders of the subfamily Gasteracanthinae before the other genera in this section. This subfamily is not only characterized by having minute to small males, but is also distinct because the female starts by accepting the male out on his mating thread but then returns to the hub of her web carrying



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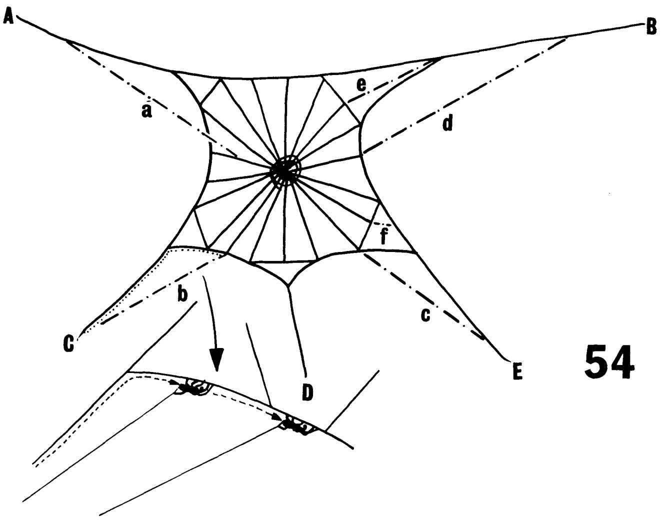

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FIG. 53–54. **53.** Mating thread of *Argiope ocyaloides* seen in profile during the swaying movement. The broken lines indicate the extent of the lateral displacement of the thread. **54.** Diagram to illustrate the various possible placements of mating threads in type C courtship. AB, upper bridge thread, E and C, extensions of lateral foundation threads; D, extension of lower foundation thread; a–d, mating threads constructed on the outside of the web frame (a is attached partway down a radius; b, c, and d are inserted at the junction of a radius with a frame thread); e and f, mating threads built within the web frame in the triangles formed between frame threads and a 2nd-order foundation thread. The detail at b shows how the ♂ carries the mating thread out to its insertion.

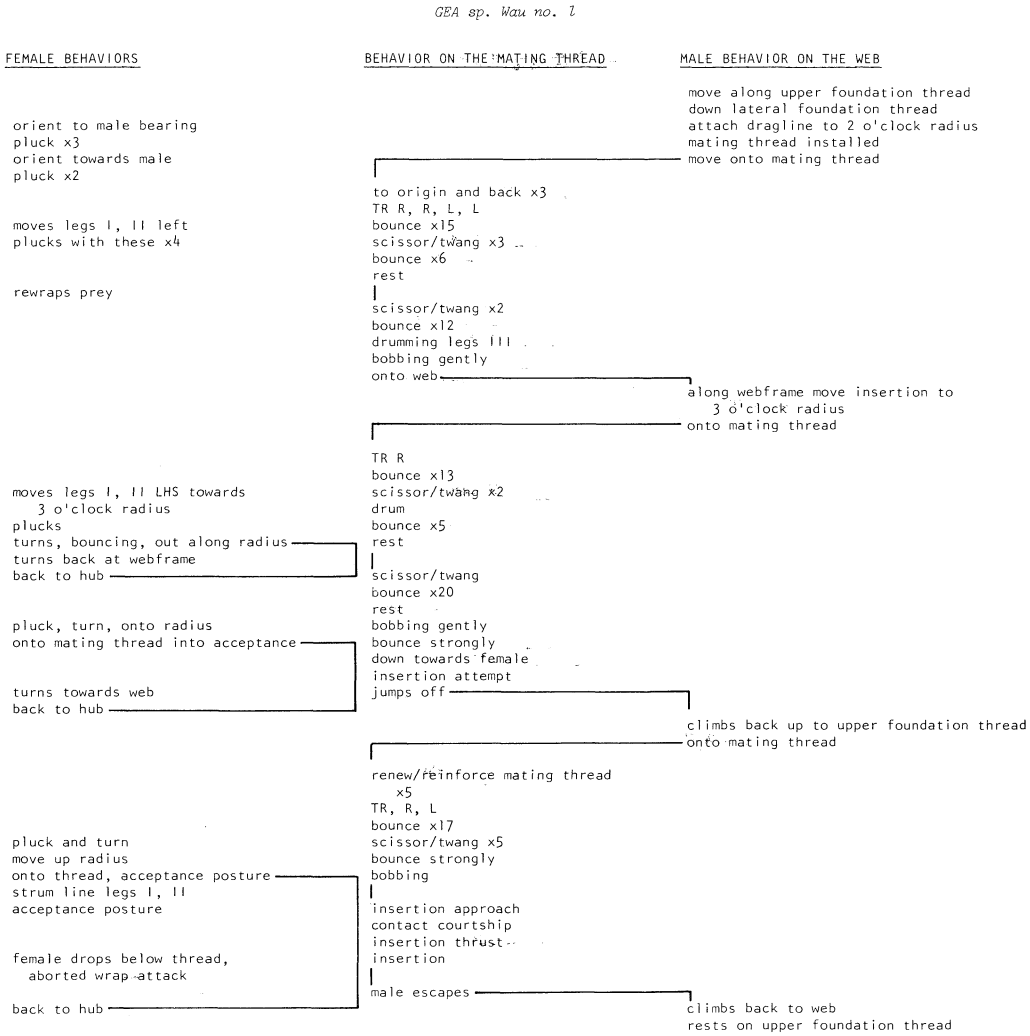
the in copula male. In terms of the duration of copulation there is no doubt that the substantial proportion takes place on the female's web and not on the mating thread; this could be regarded as a distinct subgroup within group C courtship. Placing genera with small males first conveniently separates the genus *Cyrtophora* from *Mecynogea.* Species belonging to these genera share a characteristic and highly specialized web structure that is completely distinct from that of all other araneids. The domed, horizontally oriented webs of these spiders are fine-meshed, but have no sticky elements whatsoever. There is some disputation about whether they are primitive or derived (Kullmann 1958, Lubin 1973). The courtship behaviors are sufficiently distinct (apart from the difference in size of the males in proportion to the females) for us to feel that the possession of a similar web may be no evidence of close relationship.

Spiders with group C courtship do not move onto the female's web to perform contact courtship at the hub. Instead they may move, at the most, onto the prey-capture area to attach mating threads. We therefore designate this under the subheading "attachment of mating thread" rather than "approach behavior." We have also separated vibratory courtship into 2 phases, demarcated by subheadings in the descriptive sections below. We define long-distance courtship as the behaviors taking place on the mating thread while the female is still on her own web, and short-distance courtship as the behaviors taking place after the female has moved off her web onto the male's mating thread. This usage roughly corresponds to that formulated by Blanke (1973). It is partly arbitrary, as will be seen, but we feel that it is useful in reducing the formal (descriptive) complexity of an otherwise confusing process. We continue to refer to the spider's (male and female) positions on the mating thread from the observer's point of view rather than from the anatomical directions of the observed. Below thus means below the hanging spider even though such a location is above the spider in the sense of "dorsal to the spider." FIG. 54 shows the variety of locations at which mating threads can be inserted around an orb web.

Gea sp. Wau no. 1 FIG. 55–57

When we first encountered this spider at Wau we decided that it was an *Argiope* sp. It built a small web among grass blades that frequently had a cruciform ribbon stabilimentum. The spider, in shape and dorsal markings, looked like a miniature *A. aemula.* It even assumed a cruciform, *Argiope*-like, resting posture at the hub of its web (FIG. 56). Specimens labelled *Argiope*? and sent to Fr. Chrysanthus were not identified by him as *Gea* spp. but given an "*Argiope* sp. to be determined" label. Accordingly, we assumed that this was indeed an *Argiope* species and were pleased when it turned out to have an unambiguous type C courtship behavior. Here, we thought, was a link between *Argiope* and the other genera. During our studies of *A. aurantia* and *A. florida* in Florida we saw *Gea heptagon* for the first time, living in an exactly similar habitat to "our" *Argiope* sp. "F" (see Robinson et al. 1974 for natural history notes under this designation). Not only did *Gea heptagon* look like our "*Argiope*" but it had a similar web and characteristic stabilimentum. We therefore sent specimens of our spider to Prof. H. W. Levi, asking if it was indeed a *Gea.* This was confirmed (Levi, in litt.). It has not been determined to species, but there are at least 3 species recorded from New Guinea (Roewer 1942).

As noted earlier, we never found adult males of this species in the field. We raised adults from penultimate-instar males in captivity and then introduced them to free-living and captive females. All the males were thus naive sexually. *Gea* males look extraordinarily like *Argiope* males but are much larger relative to the female than those of all *Argiope* spp. (except *A. ocyaloides*). They are at least ½ the body length of the female. We do not know whether there is any intrasexual size polymorphism in this species.



GEA sp. Wau no. 1

FEMALE BEHAVIORS	BEHAVIOR ON THE MATING THREAD	MALE BEHAVIOR ON THE WEB
		move along upper foundation thread
		down lateral foundation thread
orient to male bearing		attach dragline to 2 o'clock radius
pluck x3		mating thread installed
orient towards male		move onto mating thread
pluck x2		
	to origin and back x3	
	TR R, R, L, L	
moves legs I, II left	bounce x15	
plucks with these x4	scissor/twang x3	
	bounce x6	
	rest	
rewraps prey		
	scissor/twang x2	
	bounce x12	
	drumming legs III	
	bobbing gently	
	onto web	
		along webframe move insertion to 3 o'clock radius
		onto mating thread
	TR R	
	bounce x13	
moves legs I, II LHS towards 3 o'clock radius	scissor/twang x2	
	drum	
plucks	bounce x5	
turns, bouncing, out along radius	rest	
turns back at webframe		
back to hub	scissor/twang	
	bounce x20	
	rest	
pluck, turn, onto radius	bobbing gently	
onto mating thread into acceptance	bounce strongly	
	down towards female	
	insertion attempt	
turns towards web	jumps off	
back to hub		
		climbs back up to upper foundation thread
		onto mating thread
	renew/reinforce mating thread x5	
	TR, R, L	
	bounce x17	
pluck and turn	scissor/twang x5	
move up radius	bounce strongly	
onto thread, acceptance posture	bobbing	
strum line legs I, II		
acceptance posture	insertion approach	
	contact courtship	
	insertion thrust	
female drops below thread, aborted wrap-attack	insertion	
	male escapes	
back to hub		climbs back to web
		rests on upper foundation thread

FIG. 55. Conventional summary diagram of courtship in *Gea* sp. Wau no. 1. For explanation of abbreviations, see FIG. 5.

Attachment of mating thread. Males move onto the foundation threads of the web from surrounding vegetation and may adopt X postures, hanging from upper foundation threads, spending several hours in inactivity before proceeding to courtship. The webs are built in among grass blades and males move onto females' webs either directly off the web supports or by streaming silk bridge threads from nearby vegetation.

Movement on the female's web seems to involve no specialized gait; the male moves slowly and waves legs I antennalike ahead of him. Mating threads are inserted either

FIG. 56. Female *Gea* sp. Wau no. 1, showing dorsal patterning, resting posture and the cruciform ribbon stabilimentum.

from the web margins to nearby vegetation or the male may move partway down a radius to install the thread at an insertion within the viscid spiral zone. Threads may thus lie in the web plane, if attached to foundation threads, or at an angle to the web plane if attached within the viscid spiral zone. We saw some mating threads installed almost at right angles to the web but most were approximately in the same plane as the web. All were long. Even the shortest was at least 20× the length of the male in his outstretched posture. It is noteworthy that these long, external mating threads are not traversed many times by the males so they must be much less accretionary in structure than the mating threads typical of group B courtship. Typically, courtship started on the 1st return journey from the origin of the mating thread.

Long-distance courtship. The male adopts a courtship stance about halfway along the mating thread. His posture is one that differs somewhat from that of the *Argiope* species described above. Legs I and II point forwards, but are strongly flexed, whereas legs IV are extended backwards; the major difference is in the positioning of legs III, which are frequently directed forwards towards legs I and II and may touch the thread much nearer to these legs than to the point vertically beneath coxae III. Courtship involves a number of vibratory behaviors. TRing is present in the repertory of this species; TRs often commence a bout of long-distance courtship and may occur

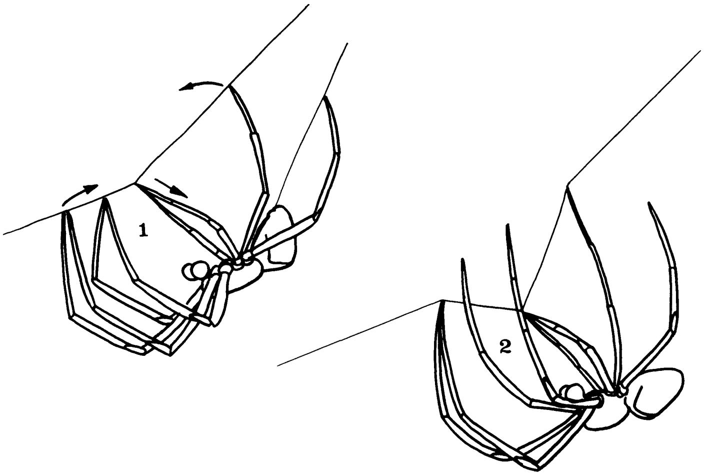


FIG. 57. Male *Gea* sp. Wau no. 1. Scissoring movement on mating thread: 1, start of movement; 2, maximum stretching of mating thread before release.

at intervals throughout it. Bouncing is the predominant component of this phase of courtship. It involves drumming movements of legs III, which are brought down from above the mating thread into contact with it. The movements of these legs are independent, i.e., nonsynchronous. AWing is virtually absent during the low-intensity bouncing or bobbing. This seems to be the result of movements of legs I, II and IV. At intervals in the bouncing, legs I may be removed from the thread and then hang below the male's body, more or less extended. Bouncing certainly involves a side-to-side component in addition to its principal dorsoventral movement. The most conspicuous new component of vibratory courtship not seen in the preceding *Argiope* species is a high-intensity bouncing and jerking movement. This is produced by the maximum extension of legs I, IV and III against the mating thread. Since they maintain their tarsal hold on the line, there is a scissoring effect (FIG. 57) and tarsi IV swing anteriorly towards the footholds of legs I and II, and the entire body-plus-leg outline of the male looks bowed and semicircular in outline. We think that this movement puts a considerable downward kink in the mating thread, as shown in FIG. 57. This must pull vigorously on the radius where the mating thread is inserted and there must be a strong twanging effect when the stretched line is suddenly released by the spider again flexing its legs.

The responses of the female at the distant hub are fairly conspicuous and allowed us to predict her further behavior. She stands in an *Argiope*-like X and one of the early indications that she is attending to, or aware of, the male's courtship is a restless movement of both her legs III. This movement is slight but obvious. She picks the tarsi off the web by raising the leg slightly and then puts it down back into contact. The 2 legs move independently but both sides are involved. This can be followed by

1 of 2 alternative movements. One of these leads to an approach to the mating thread and is an orientation of legs I and II towards the radius on which the mating thread is inserted. The movement usually starts with the appropriate leg II separating from its apposed position against leg I and "feeling" in the direction of the incoming vibrations. This "feeling" involves a lifting of the tarsus off the web and inching it towards the radius that bears the insertion of the mating thread. This movement of leg II is usually followed by a similar movement of leg I. If the appropriate mating thread is above the line of the 3 o'clock to 9 o'clock "equator" of the web, the female eventually turns at the hub to face with her legs I and II, left and right, at either side of the appropriate radius. She may then pluck gently in the direction of the male and start moving across the web towards his mating thread. Alternatively she may move back to her normal predatory posture and repeat the performance one or more times before moving out to the male.

The alternative to this gentle feeling and turning is for the female to turn vigorously at the hub and shake the web in the direction of the male. Such shaking may be followed by a cessation of courtship and ultimately by the male leaving the web, whereon the female turns back to her normal hub posture. However, the female may shake and then run vigorously towards the mating thread. This response looks like a predatory excursion and the male either stops courtship and leaps off the mating thread or simply runs back to the origin of his mating thread. While the gentle response leads predictably to the assumption of an acceptance posture by the female (but not necessarily to successful copulation), the "violent" response does not always end courtship. Males that have jumped off the mating thread may persist and resume long-distance courtship after some time has elapsed. We have not a big enough sample to estimate success rates with any degree of confidence, but one male that was subjected to this treatment eventually reached the stage of short-distance courtship, although he did not achieve a copulation.

During a gentle approach, the male continues courtship on his mating thread as the female moves up her web and onto her thread. We have the impression that the high-intensity jerkings may increase at this stage, but have insufficient evidence to prove this.

Short-distance courtship. The female seems to have no problem in finding the end of the mating thread and moving onto it. In all the cases that we saw, with a variety of mating thread orientations, we never saw a female move more than a short distance onto the long mating thread. Frequently she moved only 1 or 2 cm from the insertion, i.e., just over her body length from the web. As the female moves up the web and onto the thread, the male slides, courting, along the thread so that he is almost in contact distance with the female when she halts on his line. The female drops into a head-down posture but almost always holds the line not only with legs IV and III, but also with strongly flexed legs II. In this attitude, she is not in the full acceptance posture. She strums on the thread with her 3rd legs and taps the line with tarsi I and II. The male bobs and sways on the line, tapping it with legs III and moves the short distance towards the female. At contact distance, i.e., when the male can touch the anterior legs of the female with his legs I, he halts and further vibratory courtship intervenes. This is variable in duration and is terminated by an insertion approach. The male TRs and also taps the female and the line with tentative movements of his 1st legs. The male may also make bouncing movements at this stage. Approaches for insertion attempts look very much like the forward lunges that araneids make when attacking dangerous prey. The legs I and II are flexed back, partly over the dorsal surface of the cephalothorax as the spider darts forward. The lunge may be aborted before the male contacts the ventral surface of the female. When this happens, the male jumps off the mating thread and regains it somewhere near his preapproach starting point. Courtship is then repeated; the male moves down to contact distance, and so on. The male may break off this contact courtship without making an insertion attempt by simply turning on the thread and walking back up to his starting point before repeating the sequence of approach to contact location. This phase is thus frequently characterized by repetitions of: court at short distance/approach/court in contact/retreat, and so on. As this proceeds, the female may inch forward and come to adopt a more pendant full acceptance posture. In this attitude, her leg movements cease, only to be renewed (apparently) if the male does not attempt insertion. When the female adopts the full acceptance posture she frequently starts to produce a small quantity of multistrand silk and we have one instance where the female's slow progression along the mating thread, as she adopted successive unsuccessful acceptance postures, was clearly marked by a series of tufts of white silk superimposed on the mating thread a few millimetres apart.

Copulation. In the insertion movement the male swings forward and upward from his hanging posture. This movement presumably drives the embolus of the pedipalp into the epigyne from below. At the movement of insertion, the female drops below the mating thread and the male goes into a prone posture in which he is perhaps slightly twisted sideways. All the copulations that we saw were brief and the details were difficult to decipher. The female starts to wrap the male after insertion, but this seems to be suppressed for a few seconds before the male is pushed away with legs III and wrapping restarts. Only 1 of the 5 males that successfully achieved copulation escaped this wrapping attack. He courted the female again but did not succeed a 2nd time.

Interactions between males. We saw no fights, chasing or plucking duels between males. Competition, if it occurs, probably takes place between males that are conducting long-distance courtship concurrently.

Subfamily GASTERACANTHINAE

This subfamily of araneids is rich in tropical species and has received relatively little attention from ethologists and ecologists. Details of courtship behavior are, as far as we know, restricted to the accounts of Emerit (1967), Muma (1971) and Mascord (1967). Robinson & Lubin (1979) studied the ecology and behavior of 2 species of *Gasteracantha* in the Wau Valley where we made our first studies of the courtship and mating behavior of this genus. Although Roewer (1942) places the spiders of the genus *Micrathena* in this subfamily, their mating behavior differs fundamentally from that of *Gasteracantha*-group spiders in that the female does not retire to the hub of her web during copulation.

(Added July 1979: Using a 20-power binocular microscope to watch copulations of *Gasteracantha taeniata* and *G. theisi* in the field, we now know that haematodochal pulsations occur throughout the entire period when the 2 sexes are paired. Movement of the male's legs to an outstretched posture coincides with haematodochal expansion. The male copulates with one pedipalp and separates from the female and courts again before using the other pedipalp.)

Dr M. Emerit, University of Montpelier, identified our African gasteracanthids. These species are designated with a letter/number code with the prefix EM.

Gasteracantha taeniata (Walckenaer) FIG. 58

This large, yellow and black species is wider than it is long. It is common throughout the Wau Valley, and particularly in coffee plantations. The webs are built high off the ground between trees and bushes. It coexists with *G. theisi* almost everywhere at Wau. Males are proportionally and actually small (FIG. 58). They are easily distinguishable from those of *G. theisi* because they lack the red marking on the ventral apical margin of the abdomen found in *G. theisi* males.

Attachment of mating thread. The very long mating threads of this species are attached to the junction of radii with the web frame or to radii themselves. The latter type of attachment is seldom more than 1 or 2 turns of the viscid spiral down the web. The extreme length of the mating threads (often they are several hundred millimetres long) is in part due to the fact that the female's webs are slung across broad gaps between vegetation and have extremely long support threads. This means that the nearest substrate (other than a web element) is a long distance from the end of a radius. Many mating threads that we observed were set at an angle from the outer ends of the bridge thread down to an insertion on the lateral foundation thread. We saw males moving onto the web frame along the bridge thread from its attachment points on vegetation. The tiny male could walk several metres along these threads before coming to the female's web. The dragline that forms the basis for the mating thread is paid out behind the male as it walks. The movement of the male along web-frame elements almost always alerted the female at the hub and she would turn at the hub and pluck vigorously, sometimes running up the web towards the male. Males responded to such runs by freezing or dropping off the web. Such treatment does not necessarily deter the male, who may persist in courtship and be ultimately successful.

Mating threads that were inserted within the viscid spiral zone were produced by the male walking back to the origin across a series of discrete dragline elements. He would, for example, lay down one dragline as far as the web frame and there attach

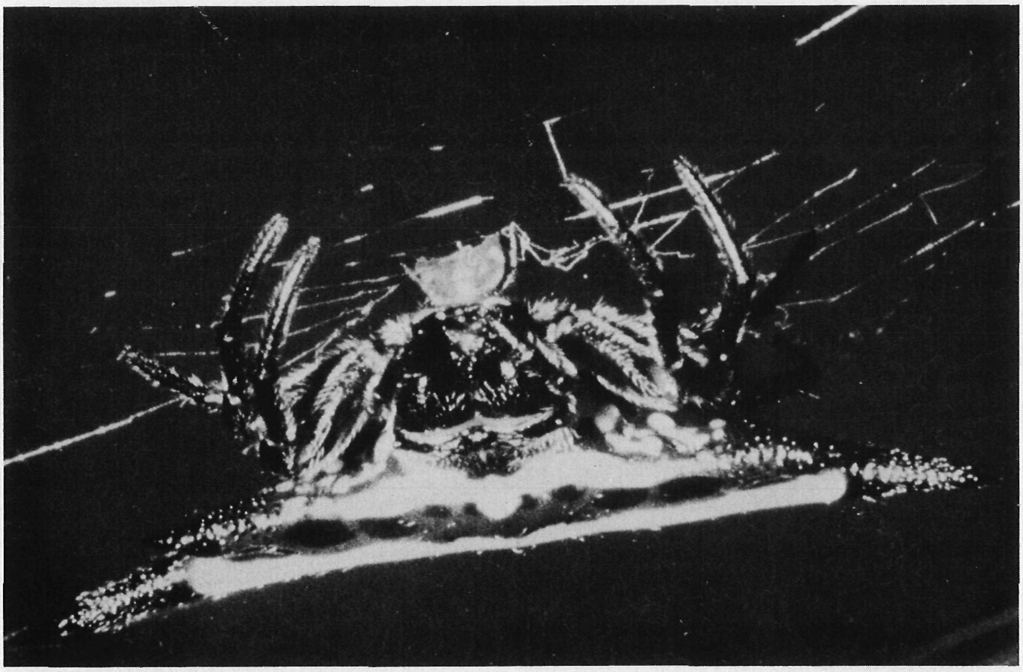


FIG. 58. View of ♀ *Gasteracantha taeniata* from anterior with profile view of in copula ♂.

it before proceeding on down a radius and producing a 2nd dragline element. On the return journey the male payed out dragline behind him but did not attach it when he came to the junctions of his previous separate draglines. Thus the new dragline (to become the mating thread) formed a continuous line from origin to insertion. This behavior clearly shows that the male has no difficulty in "recognizing" his own dragline; at the junction of 2 separate dragline elements and a web frame, there was never any hesitation: the male moved on steadily across his own previous constructions.

Long-distance courtship. Some of the difficulties involved in interpreting the details of vibratory courtship in *Gasteracantha* species are outlined in the general introduction of this paper. Added to the small size of the males and the consequent necessity of using high magnifications when filming them is the further problem of the exaggeration of movement that is consequent on the length and elasticity of the mating thread. Not only does one start with little depth of field because of the high magnification needed to see detail, but further distortion occurs because the thread is likely to move out of the plane of focus, since the movement produced by the tiny male is amplified by the basic nature of the thread. Additionally, the slightest air current moves the thread.

As the male moves along the mating thread to his courtship location, he belays dragline behind him and this thread is visible as separate from the mating thread, i.e., it does not add to an accretionary thread. His courtship stance is assumed at some distance from the web, frequently ca 10–20 cm away from the insertion. That he does not court close to the inner end of the thread could be because he is using a critical level of resonance of the thread.

Vibratory courtship is conducted from a basic stance that differs somewhat from that of the *Argiope* species described in section B. Legs I and II reach ahead of the male's body and are commonly flexed, whereas legs III and IV are held conspicuously apart from the 2 pairs of anterior legs and roughly parallel to each other. They do not point in an extreme posterior direction; the tarsal stance of legs IV, at the most, is opposite the apex of the abdomen. *Gasteracantha* males have legs that are closer to being uniform in length than those of most araneid species and legs III, in particular, are almost equal in length to legs IV (in most araneids they are conspicuously shorter).

The movements involved in courtship involve all 8 legs, the pedipalps, and the dorsoventral movement of the body about its long axis. Legs I and II either TR or are rubbed independently against the courtship thread in violin-bowing movements (or both). Certainly during low-amplitude bobbing movements, rubbinglike movement of legs I and II can be seen. We have examined movie footage of these movements repeatedly and are sure that in some cases the legs are being rubbed against each other, but this cannot be said with certainty for all cases. In high-amplitude bouncing, the flexure of legs I and II is increased momentarily and then just as quickly relaxed. Since the leg is aligned anteroposteriorly, increasing the flexion must pull back on the mating thread, and the whole cycle of flex/relax, flex/relax, etc., must introduce a fairly powerful tugging component into the bouncing. All the male's legs are stout and relatively short; we assume that the retractor muscles are quite well developed. The legs III and IV are involved in movements that seem to extend them straight against the mating thread and then they flex at right angles to the long axis. This see-saws the body and alternately pushes up on the thread and pulls down on it. Such a movement must produce compound vibrations of the thread. In a bout of high-intensity bouncing the line is oscillating up and down over a range of several centimetres. During low-intensity bouncing (bobbing) we can detect a movement of the male pedipalps in some film footage; this could be asynchronous, superimposing a rhythm on top of that of the bobbing movements, just as we think AWing functions in the vibratory courtship of other araneids. We also detected scissoring movements in blurred high-amplitude sequences. We think that these include movements of the unit legs III + IV towards the anterior legs.

The female responds (at the hub of her web) by turning towards the radius to which the mating thread is attached. She may pluck that radius and then turn back to her predatory position, or walk slowly out to the mating thread. The pluck/turn-back sequence may be repeated several times before the female eventually moves to the mating thread. On the mating thread the female assumes an acceptance posture but does not strum or pluck the line.

Short-distance courtship. The female acceptance posture is simple; she hangs down from the mating thread supported by legs III and IV. The assumption of the acceptance posture is undramatic; the female simply seems to hinge down from a position parallel to the thread to one more or less at right angles to it. The weight of the female causes the thread to sag considerably and there is a distinct angle at the point where it is gripped by her legs III. The male courts right up to the point when the female assumes an acceptance posture, then seems to flow smoothly down the line "as though on wheels" to make an insertion attempt. At this stage there is no extensive leg contact or tapping between the 2 sexes. The male either inserts or jumps off. Analysis of film sequences shows that, as the male reaches the female, he stops at the moment his anterior legs touch her abdomen, then extends his pedipalps (or pedipalp, we can't tell) and makes a vigorous thrust towards the epigyne. The smooth glide forwards, towards the female, is accomplished in an interesting manner. One of the pairs of anterior legs (probably legs II) is off the line and hanging below the male, pointing towards the female. Legs III and IV grasp the line, but do not make walking movements while the spider pulls itself forward with the one pair of anterior legs that is still on the line. As these legs make a "hand-over-hand" movement the line must slip through the tarsal hold of the posterior legs, pulley fashion. The hanging anterior legs must contact the female ahead of the others and could act as sensors to detect the appropriate range for the commencement of the thrusting of the pedipalp.

The male may reach contact distance and, instead of making insertion attempts, jump off the line. We have not seen males turn and retreat. If the male jumps off the mating thread, he regains it at the point of attachment of the dragline and approaches again. Again there is not any contact courtship. A series of unsuccessful insertion approaches is usually completed by the female simply turning and going back to the hub.

Copulation. The male inserts from a ventral surface uppermost position beneath the gently sloping mating thread. He carries out his copulation standing almost at right angles to the female's body (FIG. 58), clinging to the genital tubercle of the female (terminology of Emerit 1969). The change from the approach orientation to the copulation posture is sudden: it is as though the male flipped partly over, turning from the point of insertion so that his ventral surface becomes pressed down against the anterior face of the upstanding genital tubercle.

We don't know how this sudden movement is accomplished. At first we thought that the female flipped him up with a deft movement of one of her anterior legs, but we later noted that "the feet do not seem to be used to flip him into position but he is lifted up by her body movements." Movie analysis shows that the male is reaching forwards with all his legs I and II at the moment of insertion, supported on the thread with legs III and IV. At insertion the female suddenly reaches upwards with her anterior legs to regain her foothold on the thread prior to turning and walking back to the hub. If the movement caused the male to swing because of its vigor and rapidity, he would swing back against the genital tubercle unless trapped by the mating thread. This kind of flipping would be crudely analogous to the effect involved in tossing a pancake (English style). The explanation is plausible, but we have evidence that males can assume a normal copulatory posture without the upward movement of the female.

The female moves back to the hub, carrying the male in copula. At the hub she assumes a predatory posture and may catch prey and feed without interrupting the copulation. We have also seen a female move out onto the mating thread of a 2nd courting male and there adopt a perfect acceptance posture with the 1st male in copula on her epigyne. At intervals throughout the long copulation the male shifts his position slightly, rocking from a position tilting to one side to tilting to the other. Additional to these slight positional changes, males periodically extend all the legs laterally, presumably releasing their hold on the genital tubercle for a moment or 2. This extreme extension effect could be an accompaniment to blood pressure changes that occur when the spider is pumping sperm. According to Rovner (1975), lycosid spiders show rhythmic erection of trichobothria during copulation. (See note p. 117.)

All the copulations that we were watching at the moment of termination were ended by the male who seemed to disengage his pedipalp and then jump off the female, belayed on a dragline. We missed the ending of many copulations, but found the male nearby shortly after we noticed that the pair were no longer in copula.

Interactions between males. Several males may be active and have mating threads at the same time. This may result from more or less synchronous maturation in a particular area. Emerit (1969) noted a tendency for the courtship activities of one male to trigger activity in the others that were associated with the same web. This would explain our observation of finding several (up to 3) males courting simultaneously from different positions around the web. We have one record of a male walking along a mating thread that was already in use by the constructor. When the female came out to this thread, the invading male jumped off.

Gasteracantha theisi Guérin FIG. 59

This species is also common at Wau. It resembles *G. taeniata* in that it builds similar-sized webs in similar sites. The dorsal coloration of the abdomen varies from almost white to yellow. Males are proportionally larger than those of *G. taeniata.* We could detect no major differences between the courtship behavior of this species and that of *G. taeniata.*

Attachment of the mating thread. Mating threads were long and attached at the junction of radii with frame threads or on radii within the outer part of the viscid spiral zone. The process of attachment was similar to that described for *G. taeniata.* We have notes of mating threads attached to radii in the lower ½ of the web and ending on lower frame threads. One male built a mating thread onto a web that the female had constructed to the stage of installing the temporary spiral, i.e., it had a complete frame and complement of radii but no viscid spiral. This male courted successfully and mated with the female when she interrupted further web building to move onto his mating thread. We make frequent reference in our field notes to males plucking as they move about the web frame installing mating threads. None of our films shows this.

Long-distance courtship. Long-distance courtship is carried out from a position on the mating thread several centimetres from the insertion. The male adopts a posture that is basically similar to that described for *G. taeniata.*

Vibratory courtship consists principally of bursts of bobbing followed by bursts of high-intensity bouncing. The behavioral components that produce these vibrations seem indistinguishable from those described for *G. taeniata.* However, we did note that bouts of high-intensity bouncing were preceded by the male reaching forward with a leg I and then pulling back on the mating thread. It looked as though the release of tension from this twanging movement formed the starting point of a bouncing session that was then produced by extensions and flexions of legs III and IV. If the female is responsive she turns at the hub to orient towards the radius to which the mating thread is connected.[5] Both during courtship and during the insertion of the mating thread, the female may tap, pluck and TR in the direction of the male. Tapping involves lifting the tarsi of legs I and II off the web and bringing them sharply down on the radius; perhaps we should call it rapping. The female may then move out along the radius and proceed onto the mating thread or she may turn back to a predatory position. Females may also move as far as the insertion of the mating thread and turn back to the hub without going into an acceptance posture. Thus, in this and other *Gasteracantha* species, there are a number of stages at which the female can make a negative response to male courtship. She may show an initially negative response by shaking the web violently in the direction of the male, or may apparently ignore him and not even turn at the hub. Males may quit the web after courting unresponsive females, females that shake, or even females that move into acceptance postures. We have not studied a sufficiently large sample of males with known case histories to be able to characterize the situations that lead to the abandonment of courtship. In general, such males move off onto the webs of other females to continue courtship elsewhere.

Short-distance courtship. As in the case of *G. taeniata,* this is an abbreviated stage. The female moves onto the mating thread and drops into an acceptance posture with few or no preliminaries, and the male moves down to either insert or jump off. The female may tap the thread with her anterior legs 2 or 3× before dropping to an acceptance posture, but this perfunctory movement is all we have seen in the way of short-distance courtship on her part. The male continues courting as the female moves out, but then simply glides down the intervening distance to make an insertion attempt. The behavior of jumping off the mating thread at the conclusion of an aborted insertion approach occurs so frequently that it must be an important element of male behavior. It looks like an escape movement but we have never seen the male

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[5] We have discovered (November 1979) that intense bouncing in this species and *G. taeniata* starts with a leg-stretch posture similar to that shown in FIG. 60.

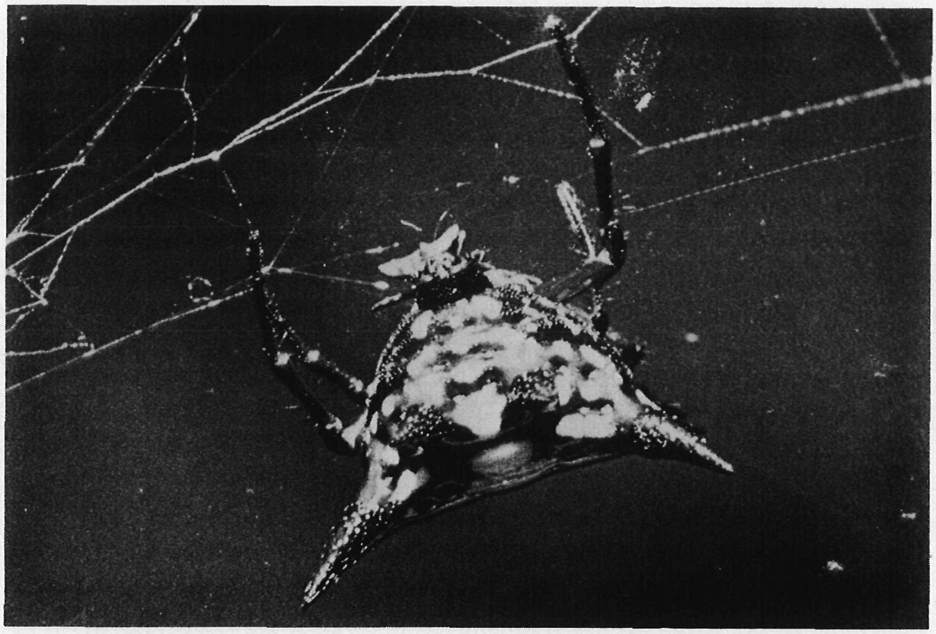


FIG. 59. Posterior view of ♀ *Gasteracantha theisi.* Legs of in copula ♂ are extended laterally.

attacked by the female at this stage. Possibly it could be of survival value if the spider courts the wrong species of female (we have collected a male *G. theisi* that was courting a *G. brevispina*).

Copulation. The male inserts and changes orientation to stand against the genital tubercle, as described for *G. taeniata.* During copulation, the male moves about and periodically extends the legs (FIG. 59). Because the 2 posterior spines are quite close together and the genital tubercle is on the midline of the abdomen, it is possible to estimate the midline in photographs and film sequences by drawing a line from the tubercle to bisect the abdominal margin between the 2 spines. Doing this shows that the male is always in a copulatory position that is substantially asymmetrical. We suspect that if he inserts the left pedipalp, the left margin of his body lies close to the midline and the right margin to the female's left of the midline, and vice versa. Such wobbling movements as occur during copulation do not affect this original asymmetry. (This interpretation agrees with Chrysanthus 1959, Fig. 21–22.)

Interaction between males. None were seen other than the tendency for simultaneous courtship, as noted for *G. taeniata.*

Gasteracantha brevispina (Doleschall) FIG. 60–61

At Wau this species builds high up in shade trees in coffee estates, on telephone wires and electricity cables, and is markedly gregarious. Assemblages of adult and juvenile females with numerous males and kleptoparasites may fill quite large areas with loose aggregations of webs that share very long bridge threads and foundation lines. The adult females are very variable in color (Robinson & Lubin, in prep.) and smaller than either of the previously described species. Males are proportionally larger than those of *G. theisi.* Chrysanthus (1959, 1971) gives somewhat misleading illustrations. The webs of this species were too high off the ground for us to conduct in situ studies of courtship. Since the spiders show a tendency to build on telephone wires, we constructed a complex "cat's cradle" of strings about 2 m above ground level and introduced 20 adult females to this. They settled well and we conducted all of our observations at this more convenient height.

Attachment of the mating thread. In the aerial aggregations of webs that this species builds, males must move almost exclusively along the silk lines that span the considerable distances between the trees or other supports. Males that move by constructing bridge threads must run a considerable risk of being borne away by strong air currents at that height above the ground. Our artificial colony probably constituted a simplified situation; in it, the males walked exclusively on silk or on the support strings of our frame. Nineteen out of 27 mating threads that we saw constructed were built within the web frame. The most frequent site was within the crudely triangular area bounded by the upper foundation thread, the lateral foundation thread and the 2nd order foundation thread (see FIG. 54). As can be seen in the figure, this area can be sufficient to enclose a mating thread that is many times the length of the male. We again noted that males jerked as they walked about the web frame. However, the jerking could have been caused by the female responding to the male's presence by plucking (one very real problem about making observations on this situation is that it is difficult to observe both the male and the female simultaneously).

One frequently observed behavior, which occurs also in other *Gasteracantha* species, was for the male to insert a mating thread, walk along it and then move the insertion up or down the web element so that the angle of the thread was changed. This behavior occurred both before and after the onset of courtship. When it occurred after a bout of courtship, it was almost always after one that did not result in the female assuming an acceptance posture on the thread. To move the insertion like this, the male must cut the thread as he reaches its junction with the web and simultaneously attach his dragline near the cut end. Such behavior contains most of the elements necessary for the highly specialized "treadmill" behavior of *Isoxya* (see below).

Long-distance courtship. The male assumes a courtship stance more or less midway along the mating thread. The posture is similar to that of the males of the other *Gasteracantha* species described above. However, this species adopts a curious posture, involving the 2nd pair of legs, that is absolutely characteristic. This posture may be adopted at the beginning of courtship and at intervals throughout. Legs II are held back over the posterior dorsal surface where they form 2 forward-projecting C-shaped prongs (FIG. 60).

Vibratory courtship in this species involves bobbing and high-intensity bouncing.

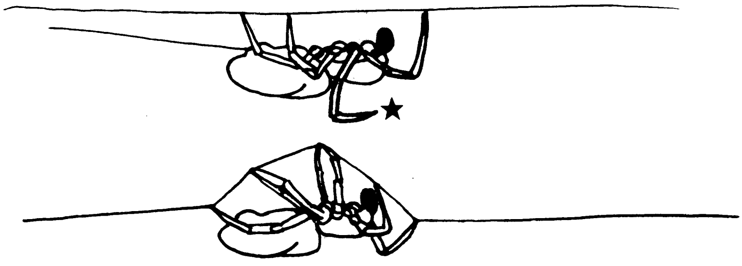


FIG. 60. Courtship movements of ♂ *Gasteracantha brevispina.* Above: insertion approach with legs II (starred) in C-shaped attitudes. Below: posture used to stretch mating thread prior to high-intensity bouncing.

During bobbing the anterior legs tap the line from below and those of one side and then the other seem to brush against it sideways. When high-intensity bouncing starts, the legs II are extended against the mating thread (FIG. 60), causing an upward deflection. When the tension thus created is released, the whole line vibrates up and down over a vertical displacement of up to 3 cm. Legs I flex and twang the line at the start of bouncing.

The female response to vibratory courtship is to turn at the hub of her web and orient towards the point of attachment of the mating thread. She may pluck vigorously in the direction of the male, and we have noted that this plucking is indistinguishable from plucking in predatory sequences. Again in this species we have notes of males jumping from the mating thread in apparent response to such plucking early in courtship sequences. It is not, however, a signal that predicts unsuccessful courtship (or an ultimately unreceptive female), since females that plucked at this stage frequently moved into acceptance postures and often, finally, mated. Females sometimes move forwards as far as the edge of the web and then move back; others do not even leave the hub but turn back to a predatory posture. During unproductive courtship sessions, the males tend to edge towards the insertion of the mating thread, little by little, until they reach the web. As noted earlier, they may then move the insertion, or simply turn and go back along the thread to a new starting point. Such edging along is punctuated by tapping and bouncing.

Short-distance courtship. When the female assumes an acceptance posture on the mating thread, she hangs supported by legs III and IV. Both pairs of legs are held close to the undersurface of the abdomen. After the female has assumed the acceptance posture the male may continue to court for a short time, but then glides down for an insertion attempt. He may abort this at the last minute and jump off the thread. We saw a female lunge forward at this point but are not convinced that this was a predatory movement; it could have been an anticipation of insertion.

Copulation. When the male has inserted, he assumes a more or less upright posture on the female's abdomen and she turns, after some leg waving, and goes back to the hub. We have a particularly good film sequence of this insertion-and-turn phase and

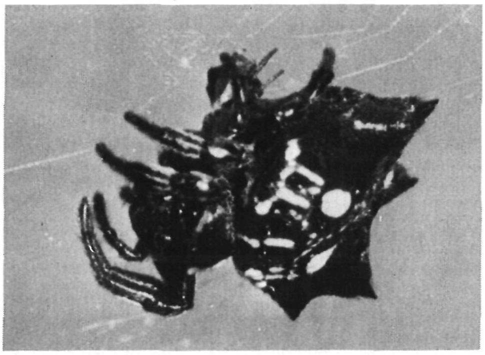


FIG. 61. Female *Gasteracantha brevispina* with in copula ♂ above; note that ♂ legs IV are extended.

it is clear that, after the turn back towards her web, the female attaches dragline to the mating thread. The period of 2 or 3 s of leg waving (by the female) before she turns involves rapid movements of her legs I and II. We consider that it is possible that she may cut the mating thread at this stage and hold it until she attaches her own dragline to the cut end after turning. This action would prevent the male being fouled on the old mating thread. Muma (1971) stated that the female of *G. cancriformis* secured the male to her abdomen with a few strands of silk. This is not what happens during this phase unless the female is using the mating thread silk or her anterior legs to pick up silk from her own spinnerets. We consider both possibilities highly unlikely. We think that if the female were using her own silk to fix the male onto her body, such movements would certainly involve her 4th pair of legs, since these are involved in all other forms of silk manipulation. We never saw such movements in any *Gasteracantha* species.

The male has bouts of movement and leg extension (FIG. 61) and bouts of quiescence throughout the long period of copulation.

Interactions between males. We saw one male cut away a mating thread that was being used by another male. The male was moving along the web frame, apparently in the course of constructing his own mating thread when he arrived at the insertion of the rival male's thread. We think that he arrived at the point by chance, but the cutting was clearly deliberate since he had not previously interfered with any web elements.

Gasteracantha sp. Wau white FIG. 62

We found this form on the slopes of Mt Kaindi, Wau. It is strikingly different from specimens of *G. taeniata* found throughout the Wau Valley and on the slope of Mt Kaindi below Namie Creek. We found this form only above Namie Creek and most frequently on the abandoned stretch of the Wau/Edie Creek road at the approach to Blue Point. Forms with a white dorsal surface to the abdomen predominate, although

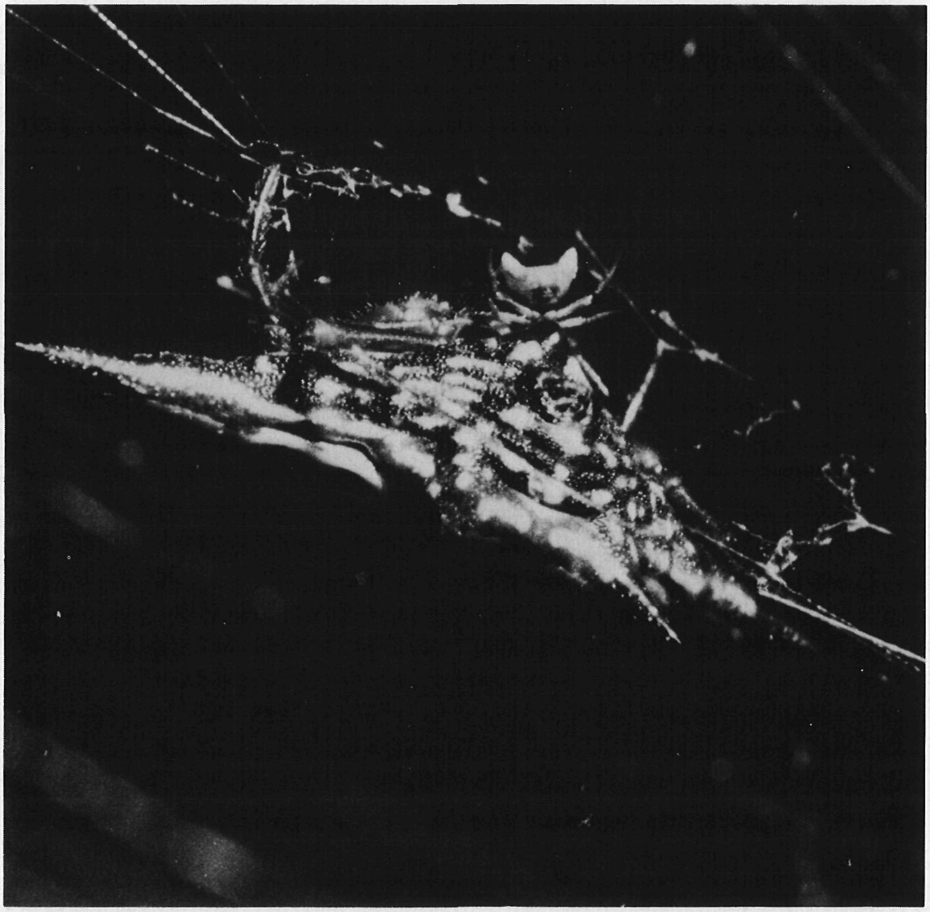


FIG. 62. Posterior view of ♀ *Gasteracantha* sp. Wau white. Male in copula photographed at the movement of swinging from side to side with legs extended (see text).

some individuals are a pale yellow. Neither color form has the broad black transverse bar on the abdomen seen in *G. taeniata.* The shape of *Gasteracantha* sp. white differs from that of *G. taeniata* in that the posterior lateral spine is not thick and robust, but fine-pointed. We assumed that this was a distinct species with a higher (altitudinal) distribution than *G. taeniata.* However, Chrysanthus (1971: 50, 52, FIG. 114, 115) describes a form of *G. taeniata* from Mt Missim, Wau, that is closer to our white form than it is to typical *G. taeniata.* He states (1971: 52): "A specimen from Mt Missim, East New Guinea, strongly differs from the typical form; there are no dark stripes, the sigilla are yellow, the remaining part of the dorsal side is greenish yellow . . . I could not detect any difference between the epigyne of this specimen and that of the typical form." It is possible that our form is another deviant *G. taeniata*; we think not. We sent Fr. Chrysanthus specimens in 1971, along with specimens of *G. taeniata* and

G. theisi; his letter to us of February 1971 gave his determinations of the 2 latter species, but merely designated our white species as sp. 7. When we received the Papua New Guinea specimens back, after Fr. Chrysanthus' death, the specimens of the white *Gasteracantha* were still unlabelled other than as sp. 7. (Note added to ms in press: Herbert W. Levi, July 1979, in litt., thinks that this is probably *G. signifera* Pocock.)

The species builds aerial webs with extremely long bridge threads and has fairly robust, straw-colored males; the males have a distinctly different abdominal outline from those of *G. taeniata* (compare FIG. 62 and 58).

Attachment of the mating thread. As described for *G. taeniata* and *G. theisi.* We have a single record of a male removing a 5-cm section of the lateral foundation thread from the web and replacing it by a strand of his own dragline on which he then carried out vibratory courtship.

Long-distance courtship. The long-distance courtship of this species consists of bobbing and bouncing. During bobbing the male makes alternate movements of the left and right legs I and II. The anterior legs that are on the line stamp (or tap) down on it, while the legs taken off the line may rub against each other in a movement that could be TRing. During high-amplitude bouncing, the motive force seems to be derived from flexions and extensions of legs III and IV. Legs II are held off the line and may be flexed, but not so strikingly as the legs II of *G. brevispina,* as described above.

Short-distance courtship. Males make the final approach to an insertion attempt in stages. We saw no specialized female behaviors that were performed prior to the assumption of an acceptance posture.

Copulation. Copulations followed the pattern described above for other *Gasteracantha* species.

Interactions between males. We again noted that activity bouts by one male on a mating thread tended to stimulate other males into activity. Males that were inactive on mating threads assumed a "cryptic" posture with all the legs folded tightly against the body and the ventral surface tightly appressed to the thread. Males in this position extended their legs and started bobbing apparently in response to courtship vibrations from active males.

Gasteracantha sp. Singapore FIG. 63

We found this bright yellow species building webs in the herb layer at Bukit Timah, Singapore. It is roughly similar in shape to *G. theisi,* but has much longer spines. We saw 2 courtships, both of which led to successful copulations.

Attachment of the mating thread. We saw the construction of 2 mating threads. One was attached to the end of the 1 o'clock radius and led to an origin along the upper bridge thread about 40 cm outside the edge of the web; it was thus very long and almost horizontal. The other was attached to the 11 o'clock radius and was oblique to the web plane, being attached at its origin to a leaf.

Long-distance courtship. One male courted on the mating thread for less than 60 s before the female came out and copulation started. The other courted in 3 successive bouts of a total duration of less than 2 min. The courtship of both males included similar components, but differed markedly in intensity. Courtship consists almost entirely of bobbing and high-intensity bouncing. During these movements, particularly during bobbing, legs I may be held off the mating thread and pointed anteriorly, like small LLs below the body. During bobbing and bouncing, legs II, III, and IV extend and flex in complex patterns to produce movements that vary in intensity. Once bouncing starts, the body outline becomes blurred (in movies shot at 24 fps) and the displacement of the mating thread in the vertical plane becomes considerable (more than 4–5 body thicknesses). We have the impression that a single high-amplitude twanging movement may start a train of bouncing, but we cannot see this clearly on the film (it certainly occurs in *G. curvispina,* see below). The leg pairs that provide most of the movement lie in the same transverse plane so that legs II point anteriorly and legs III and IV point posteriorly, with the gap between legs II and III greater than the gap between III and IV when viewed from the side. In frontal view, each pair of legs forms a diamond shape, with one point at the mating thread and the shape varying from a long thin diamond when the legs are extended to a short squat diamond when they are strongly flexed outwards. Since legs II may be flexed when legs III are fully extended and legs IV partly extended, the spider is capable of producing complex deformations of the thread, and its body see-saws during the process.

During courtship, the female may orient, at the hub, towards the male and move up a radius towards his mating thread. We saw no evidence of TRing by the female at this stage (see above), but our sample was small. Both females plucked the radius several times before moving towards the male. One female made 2 partial excursions, but turned back before reaching the thread; the 3rd time she went all the way.

Short-distance courtship. Before assuming an acceptance posture the female strums the mating thread once or twice. This is the only evidence of a short-distance courtship behavior that we saw in this species, although, as in all the *Gasteracantha* species, the male continues to court during the movement of the female towards and onto the mating thread. Once the female has assumed an acceptance posture, hanging down from legs III and IV, the male makes a staged approach, but does not stop for more than a moment at each stage. The final insertion approach is a typical "glide" down the line from a distance up to 5 cm away. During this glide, legs I are off the line in their reversed L posture until the very last moment. The approach may be aborted at the stage when the male assumes his insertion posture. In aborting the approach, the male simply jumps (or drops) off the mating thread. Analysis of these drops shows that the pauses in the staged approach mark attachment points of the male dragline, since it is at one or other of these points that the male regains the mating thread. (It is not always the point from which he started the "insertion glide" so we assume that such dragline anchor points may sometimes disconnect during the drop, failing to hold the male so that the line strips back to the previous attachment.)

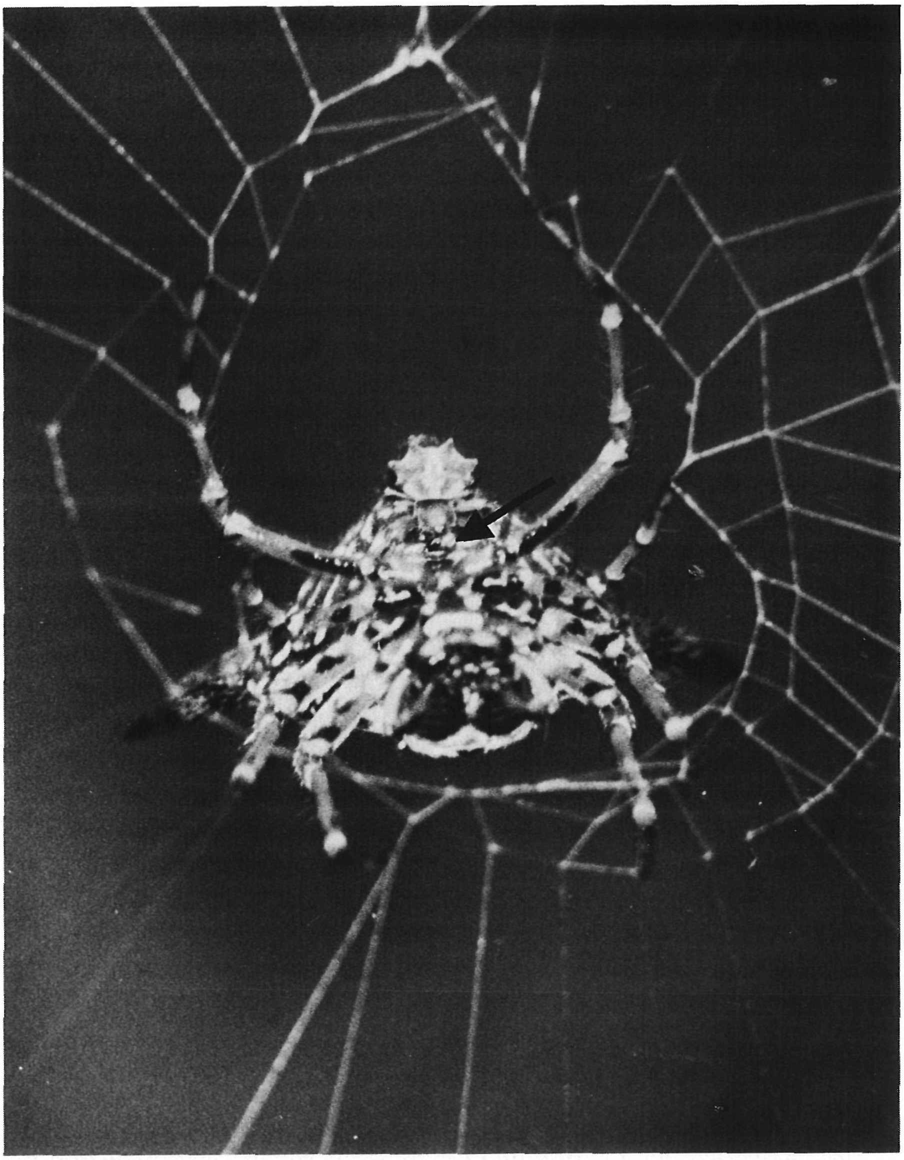


FIG. 63. *Gasteracantha* sp. Singapore; ♀ seen through the open hub of her web with ♂ in copula, his left pedipalp (arrow) is inserted.

The final insertion posture, assumed at very close quarters, is very clearly visible in one of our movie sequences. The male pauses, momentarily, some 2–3 mm away from the female and folds both legs I and II back over the dorsal surface of the cephalothorax, leaving only the pedipalps stiffly (apparently) extended in front of his body.

Copulation. This follows the pattern described for other *Gasteracantha* species (FIG. 63). The female returns to the hub and there behaves as if the male were not present.

Interactions between males. None were seen.

Gasteracantha falcicornis Butler FIG. 64

We studied this species in Nairobi, Kenya, where we found it abundant in the gardens of the Kenya National Museum and the Nairobi City Park. We saw and filmed many courtship sessions, but unfortunately were attacked and robbed while working on this species in the Nairobi City Park. The armed robbers stole all our exposed film that was in a bag with other valuables. We were left with only our notes on this magnificent species.

Gasteracantha spp. are frequently striking and beautiful spiders, but this is among the most impressive. The adult female is large, glossy and brightly colored with very large posterior lateral spines. These curve upwards and may partly recurve over the dorsal surface of the cephalothorax. They are very much like the horns of a Texas steer in shape. Due to the two-dimensionality of photographs and drawings, illustrations of this species frequently give the impression that the spines curve backwards rather than upwards (see, for instance, the otherwise excellent illustration of this species in Levi & Levi 1968: 66). We found the webs of adult females slung on very long bridge threads between trees and bushes and in large gaps in hedges. Most of the webs were at least 2 m above the ground, and the bridge threads were frequently several metres long. The web frames were often triangular, with an attachment point at the lower angle formed by the junction of the 2 lateral foundation threads. Most of the courtship activities that we saw were in high winds that caused very considerable movements of the webs. Once again we were impressed by the fact that the females were so responsive to the movements of the tiny males about the webs and to their vibratory courtship, in view of the noise in the system that must have resulted from the effects of the wind on the web and mating thread.

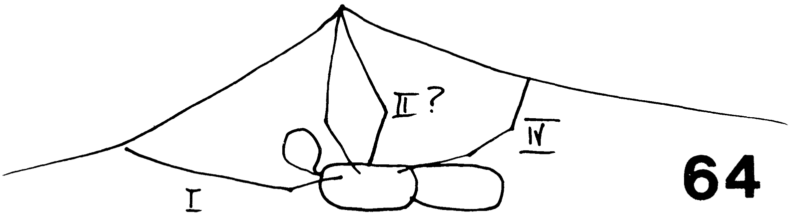
Attachment of the mating thread. Since these webs were often separated from web supports by very considerable distances (hundreds of times the length of the adult male) it is not surprising that most of the mating threads that we saw were built from silk web supports to the web rather than from vegetation to the web. We have one note of a mating thread that was over 60 cm long. During the insertion of mating threads, the females frequently oriented towards the tiny, moving male and plucked vigorously. Males reacted to such plucking in a variety of ways. Some retreated to their starting point and assumed motionless postures; others went boldly on with their activities, and yet others paused for a short time and then carried on with their activities. We could see no obvious relationship between the form or intensity of the female's plucking and the male response.

Long-distance courtship. The absence of any film records means that our descriptions of the movements involved in long-distance courtship cannot be checked against frame-by-frame analysis. This is particularly unfortunate in this case because we noted 2 courtship movements that clearly require detailed elucidation. First, we noted that at the start of long vibratory courtship bouts, the male TRs several times. We now think that this movement may have been the unilateral movement of legs I and II against the mating thread that we have already described above for other species of *Gasteracantha,* since this looks like TRing. It differs in that the legs are not distinctly rubbed against each other as they are when lifted off the line during TRing sensu stricto. Nonetheless, we can be sure that movements of the legs I and II alone occur as part of the courtship repertory of this species.

We also saw clearly, for the first time, movements of the legs that stretch and then suddenly release the mating thread. In our notes we then described these as flicking movements. They should be called high-intensity twanging. They result in the line being jerked very strongly. Essentially, the line is sharply deformed between legs I and IV by being pushed upwards. The sudden release of the tension exerted by this leg pressure between the "footholds" of legs I and IV causes a very distinct twang to occur (as judged by the violent movement that it transmits to the male's body). We sketched the posture occurring before the twang and attribute the upward kink in the mating thread to the pressure exerted by leg II of the male. We reproduce our notebook sketch in FIG. 64. The legs producing the kink had to be either legs II or legs III. Without the possibility of film analysis we cannot decide which, but suspect that our original interpretation may have been correct. Certainly we were able to analyze a similar movement in *G. curvispina* with greater exactitude (see below). Twangings occurred intermittently in groups of 1–3 throughout high-intensity courtship. Thus, courtship in this species consisted of the basic *Gasteracantha* pattern of bobbing and bouncing, with movements of legs I and II preceding bobbing and twanging bouts interspersed throughout the bouncing. A systematic detailed study of this species might reveal that twangings were particularly numerous when the background noise produced by wind-induced web movements was high. Certainly twanging would seem to be an attention-eliciting courtship component. Males that courted for long periods without success often moved the insertion point of the mating thread between bouts of courtship.

We have a record of a female moving from the hub to an acceptance posture after only 22 s of courtship by a male that we had introduced to the web. At the other extreme, males courted sporadically over a period of several hours without the female ever leaving the hub. Female responses to courtship included violent plucking, mere orientation toward the male, no overt response and both partial and complete excursions toward the mating thread.

Acceptance postures were always assumed very close to the insertion of the mating thread and often the female body was touching part of her web. Male approaches were staged, but females could turn and return to the hub before the male started his insertion approaches. We suspect that at least some of these retreats were correlated with the occurrence of violent disturbances of the web that occurred in high winds. Otherwise insertion approaches were typical of *Gasteracantha* species.



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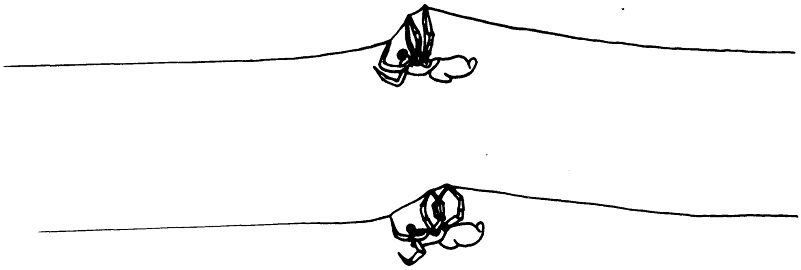

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FIG. 64–65. **64.** Notebook sketch of twanging posture of ♂ *Gasteracantha falcicornis.* **65.** Male *Gasteracantha curvispina* pretwanging posture. The ♂ makes an upward deflection of the mating thread by upthrusting legs III and IV. Two variants of the posture are shown.

Copulation. We have one record of a female placing her legs III over the male following insertion and remaining thus for over 40 s before turning to return to the hub. Otherwise the behavior of this species was typical of that we have described for other *Gasteracantha* species. Males stood erect on the female's abdomen, against the genital tubercle. In this location the male moved from time to time and extended his legs laterally.

Interactions between males. We found several females with more than one male courting simultaneously. One female had 3 such males, all with extremely long mating threads. These were attached to the 1, 11 and 7 o'clock radii, respectively. The males were still on this web when we returned 4 h later. We then made observations for an hour, during which the female successively oriented towards 2 of the males, from the hub, but did not approach either of them.

Gasteracantha curvispina (Guérin), EM 4195 FIG. 65–66

We studied this species at the experimental station of the International Institute for Tropical Agriculture, Ibadan, Nigeria, under ideal conditions (see Acknowledgments). The species was common at the edge of the forest and on agriculture plots, where it built its web high off the ground in gaps between forest fringe trees. We were able to work at these heights from the roof of a field vehicle generously provided by IITA. This made both an observation and a filming platform. The species is nongregarious but otherwise resembles *G. brevispina* in the disposition of its aerial webs.

Attachment of the mating thread. This proceeds as described for other *Gasteracantha* species.

Long-distance courtship. This consists of TRing, bobbing, twanging and bouncing. TRs precede the more vigorous forms of vibratory courtship. We saw long trains of TRs in which the male swivelled from side to side on the mating thread as he TRed with the legs I and II that were then off the silk and hanging slightly below the body. TRs were usually followed by low-amplitude bobbing. High-amplitude bouncing was carried out with the spider supported on the "looped" pairs of legs II, III and IV. Bursts of bouncing commenced with a single twang and twanging at intervals throughout the bouncing. Twangs were produced, as previously suspected, largely by the perpendicular extension of paired legs against the thread, in this case by legs III. Legs IV were simultaneously extended directly upwards while the partly extended legs II also appeared to be holding the thread into a wave form. This is illustrated in FIG. 65. We have sharp movie sequences of several of these twangs and there is no doubt that the above description fits all cases. The leg stretch position is achieved quite slowly and held for several frames of film, perhaps for up to a second or so, before being suddenly released. Following the release the male immediately becomes a blurred bouncing object, while the line moves up and down over a considerable distance.

As before, females responded to courtship in a variety of ways from apparent indifference to rapid predatory excursions. We have notes of one female undertaking an extensive repair of the side of her web at which a male had been both courting and moving his mating thread for over 3 h. She installed 7 threads between the web frames, and we concluded that his cutting of web elements as he moved the insertion of the mating thread had caused a loss of web tension.

Short-distance courtship. One female went out onto the male's thread 6 times, but although she stopped at the end of it for long periods she never dropped into a full acceptance posture and the male never made a full insertion approach. Insertion approaches were staged (FIG. 66) and could be aborted by the male jumping off at the last minute. We have 2 notes in which the male is described as cutting the mating thread when a female approached very vigorously. This cutting is certainly an element in the behavior of some *Isoxya* species.

Copulation. Copulation was initiated on the mating thread; after insertion the female turned and returned to the hub where most of the long copulation occurred.

Interactions between males. We saw males that were moving along the same web element indulge in bouncing duels and one case of a chase that ended on nearby vegetation. One male followed another onto its mating thread and at some stage the owner swung down well below the line of the thread, which was apparently cut by the invader.

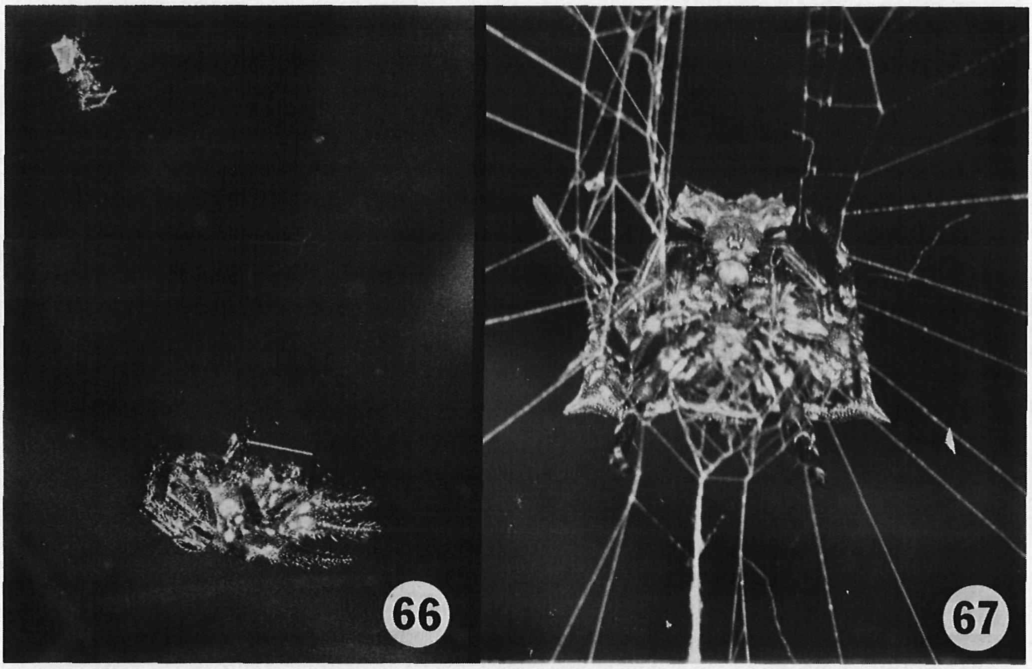

FIG. 66–67. **66.** Female *Gasteracantha curvispina* at upper edge of web, in acceptance posture. The ♂ is TRing prior to approach. **67.** *Isoxya tabulata* seen in copula. Note that the ♂ (above) is roughly parallel to the ♀ (facing the camera).

Gasteracantha versicolor (Walckenaer), EM 4192

The courtship and mating behavior of this species was studied by Emerit (1967) with specimens raised from eggs obtained in the Malagasy Republic. His study was the first observation of courtship in a *Gasteracantha* species. The description gives excellent details of copulation but relatively sparse details of the courtship on the mating thread. Emerit (1967: 900) saw TRing: "Il fait dans le vide, des moulinets alternatifs vifs avec sa deuxième paire de pattes, comme s'il boxait . . ." but apparently did not realize how widespread this movement is in the courtship behavior of araneids. Emerit's (1969) study of the ecology, behavior and general biology of this species is a model of meticulous research.

We studied this species at Umdoni Park on the coast of Natal, Republic of South Africa. It was there extremely abundant in midsummer (January/February). The large aerial webs were built seldom more than a metre off the ground and spanned gaps between bushes in the understorey of the parkland.

Attachment of mating thread. This was as described for the other species of *Gasteracantha.* We saw one mating thread nearly 100 cm long, attached to the end of a radius that was at least 20 cm long from frame to hub.

Long-distance courtship. This was very similar to that described for *G. curvispina,* consisting of bouncing, TRing, twanging and bobbing. We could detect no major differences in the courtship of these 2 species. Twanging was a conspicuous element of courtship that occurred after the initial TRing and bobbing phase. It was achieved by conspicuous press-up extensions of legs II, III and IV; bouncing followed twanging and produced considerable deformations of the long mating thread. This twanging is a movement that has many analogues in other species of araneids that have type C courtship (e.g., see *Eriophora fuliginea* or *Cyclosa insulana,* below). It is essentially a stretch-and-release movement. (The stretch is achieved in a remarkable diversity of ways in different genera and species.) The female often responds to courtship by extending one or more legs on the side facing the radius to which the mating thread is attached, and plucking in the direction of the male (contra Emerit 1967: 900). We have a film sequence showing the female at the hub, oriented towards the male (who is on the mating thread) and strumming slowly with all 4 legs I and II.

Short-distance courtship. The female assumes an acceptance posture in the normal way and the male then makes a staged approach. We saw no evidence of any complex behaviors by either sex at this stage. If the male aborts an insertion approach, he merely makes another staged approach after regaining the mating thread. He does not recourt the female that is in the acceptance posture. One female lunged at an approaching male as if to attack him. Insertion approaches include the adoption of a distinct insertion posture when the male is almost in contact with the female. To do this, he lifts both anterior legs out of the line of advance and holds them back over the dorsal surface of the cephalothorax.

Copulation. This follows the general *Gasteracantha* pattern. We found one female in copula at the hub of her web who was being courted by 2 other males stationed on mating threads at opposite sides of the web. She responded repeatedly to both males by moving out into acceptance postures on their mating threads.

Interactions between males. Males that encountered each other when moving about the web (inserting mating threads) bounced at each other and sometimes touched each other with extended legs I. After such touching, one male usually dropped off the web.

Gasteracantha cancriformis (L.)

This is probably the only *Gasteracantha* species in the New World; the other species recorded by Roewer (1942) are dubious, to say the least. The species is relatively common in Panama in certain localities and does surprisingly well in coastal areas. We studied specimens from the Gamboa Pipeline Road and ultimately built up a large insectary culture entirely supported by drosophiloid flies. Muma (1971) has described courtship and mating in this species. His males apparently courted on the radius of the female's web and copulation was initiated there. He describes no special posture adopted by the female in response to courtship that could correspond to what we have called an acceptance posture. Our observations on this species differ from his in that we saw a perfectly normal *Gasteracantha*-type courtship in which males attach mating threads to the outside of the female's web and there conduct vibratory courtship. The female goes out onto the mating thread and assumes a typical acceptance posture.

Attachment of the mating thread. We saw relatively short mating threads inserted within the web frame (i.e., in the triangle formed by upper foundation thread, lateral foundation thread, and second-order thread) and also on the outside of the web. The latter were up to 30 cm long and the most frequent site was below the bridge thread with an insertion on the upper radii (10, 11, 1 and 2 o'clock).

Long-distance courtship. This consisted of TRing, bobbing and bouncing. The TRing was marked by a side-to-side swinging. Bobbing was hardly distinct from bouncing, which we think entirely lacks a twanging component. We have reviewed our footage of high-amplitude bouncing many times and find that, though it is carried out with the male hanging below the mating thread on "looped" legs II, III and IV, there is no sign of push-ups occurring (that would indicate twanging). During bouncing, the pairs of legs are merely flexed and extended in complex rhythms. Legs I are off the thread and flexed back over the dorsal surface of the cephalothorax. As in most *Gasteracantha* species, courtship is conducted some distance from the edge of the web.

The female responded to male movements around the web with plucking and web shaking, and sometimes responded in this way to courtship. Such courtships were not necessarily unsuccessful.

Short-distance courtship. Males continued courtship as the female moved out onto the mating thread; some females paused at the edge of their webs before inching out onto the mating thread, and we noticed that in these cases the male continued courtship until the female was actually on the thread. However, once the female was on the thread, courtship ceased and insertion attempts started irrespective of whether the female assumed a full acceptance posture or not. Males aborted their approaches in a variety of circumstances that we were not able to categorize exactly. The fact that some females then returned to the hub perhaps indicates that such a female was not sufficiently receptive at that time.

Copulation. This followed the normal *Gasteracantha* pattern. Muma (1971) observed a female that strapped the male in place against the genital tubercle "with 3 or 4 strands of non-viscid silk." We did not see this behavior. The in copula male moved from side to side and regularly extended his legs during copulation. We collected one male after copulation and replaced him on the same (previously virgin) female's web some 2 h after the end of the 1st copulation. After a very brief courtship from a mating thread on the opposite side of the web to the original one, the female moved out and the pair immediately went into copulation for a 2nd time.

Interactions between males. We saw nothing further than simultaneous courtships from opposite sides of the web.

Isoxya tabulata (Thorell), EM 4192, EM 4196 FIG. 67

We studied this species at Umdoni Park on the coast of Natal, Republic of South Africa, where it was extremely common during the period when we were studying *G. versicolor.* This spider has a roughly quadrangular abdomen and a somewhat variable dorsal coloration. The males are proportionally much larger than most *Gasteracantha* species males (FIG. 67). The aerial webs are built in shade; inside forest, or on the shaded edges of roads, trails and pathways. We saw numerous courtships and in the majority of cases the female moved out onto the mating thread. However, we saw only one copulation. This is the species in which we discovered the *treadmill effect.* The realization of what was happening and the rejection of the other interpretations of the phenomenon constitutes an interesting study in the effect of repeated observation. The movies confirm the final interpretation that we arrived at before any of the movies were available for viewing (see below).

Attachment of the mating thread. This section of courtship is indistinguishable from that of *Gasteracantha* species. Males move about the foundation lines of the web, eliciting plucking, web shaking, and some chases from the resident female. Eventually they insert a mating thread at the junction of a radius with a foundation line or some way down into the viscid spiral zone, on a radius. In the process they may do some cutting of web elements. The mating thread usually has its origin on the bridge thread or some nearby web attachment. After a period of unsuccessful courtship the male may go down to the insertion of the mating thread, release it and move it some distance. The new attachment is usually on an adjacent radius, and the male merely changes the angle of the mating thread (and, of course, the female now receives the direct vibrations down a different radius).

Long-distance courtship. The comparatively large males are squarish in outline. They may reach a location on the mating thread from which they will conduct courtship and then simply hang there for long periods, motionless, close to the line and apparently resting. The first sign that vibratory courtship is about to commence is that the male hangs well below the silk on looped legs III and IV, and with legs I and II of one side on the line. The other anterior legs are held close together in a typical unilateral TRing posture. From such a position the male courts by bobbing, bouncing and twanging. In all the sequences that we observed, a regular bobbing movement predominated and bouncing was mainly confined to the period during which the female is approaching across her web and onto the mating thread. The movements involved in bobbing are relatively simple. For long periods the only legs that moved regularly were the 3rd legs that moved anteroposteriorly over a short distance (0.5 cm?) as though tugging on the line. At other stages, legs IV moved anteriorly at the same time that legs III moved posteriorly. This produced a scissoring movement; both legs reversed the direction of movement in an apparently synchronized way. At times a beckoning movement of one leg I was superimposed on these other components. While this leg I was moving, the other leg I and both legs II were off the web and hanging slightly below the male's body. The use of left and right legs I was alternated so that the spider swivelled from side to side.

Bouncing was produced by flexions and extensions of the looped leg pairs, as in *Gasteracantha* species. However, the occasional twangings were produced by extreme extensions of legs IV in a direction perpendicular to the cephalothorax. This is very different from the "push-up" posture of *Gasteracantha* species, which principally involved legs II and III.

Females at the hub behaved in much the same way as *Gasteracantha* females. They oriented towards the radius to which the mating thread was attached, turning and plucking. They also made partial excursions towards the origin of the mating thread. Some females simply sat tight and did nothing.

Short-distance courtship. Females responding to long-distance courtship often ran towards the mating thread. Early in our observation we noted that the males responded to female approaches by turning to face away from the web and when the female actually moved onto the thread, the male would suddenly swing away from her as though belayed on his dragline, while the female dropped in an arc in the opposite direction. The male swung further because he was a long distance from the origin of the mating thread, whereas the female was usually only on a very short length of thread, close to the origin. Over and over we interpreted this swinging apart of the 2 sexes as being due to the male cutting the mating thread and effectively isolating himself from the female. The first time we saw this, we noted: "Female approaches by running up the radius towards him but never reaches the male along the mating thread, the line appears to break; the female scrabbles at it." Repeated observation showed that there were 3 constant features of this situation: the male turned away from the female as she reached his thread, the pair swung apart in opposite directions and the female continued to scrabble at the line. We saw one incident where the male turned away but the female missed the mating thread's origin and he continued courting without the thread breaking or being cut. Eventually we made an observation where everything happened more slowly than usual and we got the final clue as to what was really happening. This time when the male turned, the pair did not swing apart, but the mating thread dropped and the female, though running towards the male, got no nearer to him. During this running, she accumulated a conspicuous white ball of silk beneath her cephalothorax. We believe that at some stage immediately before the pair swing apart (or drop below the original level of the thread), the male attaches the section of the mating thread bearing the female to the spinnerets and holds onto the other section while paying out silk in the direction of the female. He could cut the line before turning and, holding the cut end of the section bearing the female, attach his dragline to it as he turns. We are inclined to believe that he attaches the line first and then turns to face away from the female before cutting the line beneath his feet, while holding onto the part on which he eventually comes to stand. Either way, he has put the female on a practically endless track. As she moves towards him, he can simply pay out silk from his spinnerets. Then, though she may run rapidly, she gets no closer. This aspect of the phenomenon justifies our calling it the treadmill effect.[6] (This could provide a mechanism for controlling, if not exhausting, the female's predatory drive.) We were never able to determine at what stage the line was cut; movies shot at slow motion are of no help; the subject is too small, definition is insufficient and the action is too fast.

As in most *Gasteracantha* species, the male may continue to court as the female moves across the web. We saw one male turn away and produce the treadmill as another male approached along his mating thread from the web end. This suggests that the behavior may not be entirely dependent on the male being approached brusquely by a conspicuously heavier spider. In one revealing incident, a female stopped her scrabbling approach on the treadmill and dropped into an acceptance posture. The male turned and approached her only to be seized, wrapped and carried back to the hub as prey. Clearly the treadmill does not always exhaust the predatory drive. When the female assumes an acceptance posture the male turns and makes insertion approaches. At this stage he must attach the line bearing the female to the cut end of the line on which he is standing, thus restoring the mating thread. The only successful courtship that we saw involved about 40 s of treadmilling, during which the female accumulated an obvious bundle of silk against her body. She then settled down, with one leg IV holding the edge of her web and legs III holding the mating thread, in an incomplete acceptance posture. The male turned and approached her slowly, inching forwards and strumming gently with his legs III at pauses during the approach. The female dropped into a hanging acceptance posture, but her legs I-L and II-L were also gently strumming. The male approached to contact distance and then jumped off. He started the whole approach procedure again from about 30 cm away, aborted that approach at contact distance, and made 5 further approaches before inserting. The approach phase lasted slightly over 3 min.

Copulation. There was no post-insertion flip by the female; the male assumed his copulatory stance while the female was hanging from the mating thread, swinging from side to side. The pair remained at the edge of the web for over 7 min. before the female, still in copula, went back to the hub. After a total of 75 min. the female attempted to remove the male with her legs IV, while leaning away from the hub. At that stage, he dropped on his dragline and was collected.

The copulation posture in this species differs from that of *Gasteracantha* species in that the male stands, venter to venter, more or less parallel to the female and not perpendicular to her abdomen (FIG. 67). Presumably this is associated with the absence of a genital tubercle. This male had only one pedipalp discharged.

Interactions between males. We frequently found several males resting or courting on one web. We saw several encounters in which males met on web frame elements and flailed legs at each other before one retreated. We saw no cases where one male

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[6] See also Stowe (1978: 144).

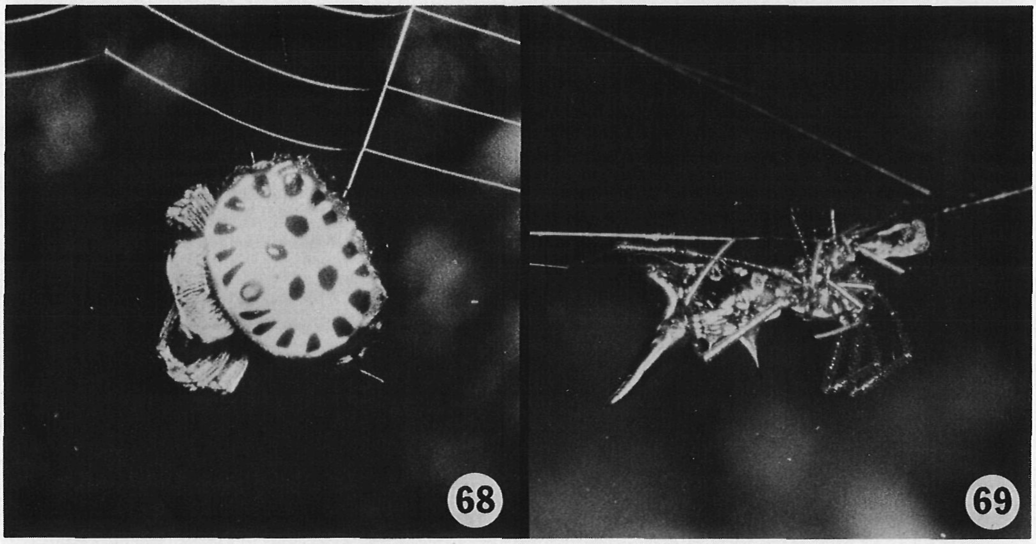


FIG. 68–69. **68.** Female *Aetrocantha falkensteini* at edge of web in acceptance posture. **69.** *Micrathena sexspinosa*: ♀ on mating thread that is a cleared radius; ♂ is inserting pedipalp by pushing it above his dorsal surface (both ♂ and ♀ are ventral surface uppermost).

cut another's mating thread attachment, and one case (details above) where a male formed a treadmill for a male moving onto his mating thread.

Isoxya cicatrosa C. L. Koch

We found this species in coastal scrub near Mombasa, Kenya. We saw 2 incomplete courtships performed by 2 separate males. These establish the fact that vibratory courtship is conducted on a long mating thread that is attached to a radius from an origin some distance from the web. In view of the strange courtship described by Mascord (1967) for *Isoxya* (=*Gasteracantha*) *minax,* we feel that even scant details are worth recording.

Our single reel of movie footage shows the male bobbing and bouncing on looped legs III and IV.

Aetrocantha falkensteini Karsch., EM 4193 FIG. 68

This pretty little gasteracanthid (FIG. 68) was present at our IITA study site at Ibadan, Nigeria. We found only 2 males and have details of incomplete courtships. These at least establish that males attach mating threads to radii, often within the viscid spiral zone, and court by strumming with legs I and II while hanging from looped legs III and IV. This strumming was later replaced by bouncing. One female came onto the mating thread and into an acceptance posture. The male descended to stand on her abdomen for 30 s. The female then returned to the hub, leaving the male behind. We collected the male and examined his pedipalps; there was no suggestion that they had been inserted. Males walked jerkily around the web and certainly moved the insertion of the mating thread after unsuccessful courtship bouts.

We suspect that a genuine copulation would take place at the hub after an initiation on a mating thread.

Micrathena species

Chickering (1961) lists 40 species of *Micrathena* that occur in Central America. Many of these are small, rare or widely dispersed. We studied 2 species that are often numerous in Panama and have brief notes on courtship in 2 other species. We also found *M. sagittata* occurring commonly in the Lake Placid region of Florida and were able to study it there. Although the Panama species, *M. schreibersi* and *M. sexspinosa,* have type C courtships, both had interesting aspects to their courtships and mating behavior that would suggest that the study of other species in the genus could prove rewarding. Certainly the 3 species that we studied in detail were less uniform in behavior than any 3 of the several *Gasteracantha* species described above.

Little has been published about the basic biology of spiders of this genus. They typically build aerial webs with an open hub and perpendicular ribbon stabilimenta (when present). A wide range of species are spiny and brightly colored. It is tempting to think that the colors are aposematic, since the spines are heavily sclerotized and sharp. In contrast to these species, others are cryptic and one in particular, *M. horrida,* seems to be a detritus mimic. Limited studies of a small number of species suggest that attack wrapping may be missing from the predatory repertory of this genus (Robinson, unpubl.; Lubin, pers. commun.). The entire copulation of *Micrathena* species is brief and carried out on the mating thread rather than the hub of the web (compare with *Gasteracantha* and *Isoxya*).

Micrathena sexspinosa (Hahn) FIG. 69

Chickering (1961: 459) notes that this species is one of the 2 most abundant species on Barro Colorado I (the other being *M. schreibersi,* see below); it is large, ca 15–16 mm long, and brightly colored with a yellow abdomen and 2 large red posteriorly projecting spines. The males are small, ca 6 mm long, narrow-bodied and reddish brown overall. The species occurs in light to heavy shade on forest edges and within forest. Its courtship behavior is distinguished by the fact that males convert a radius within the female's web into a mating thread. This characteristic is shared with some *Mangora* species (see below). It has a copulatory position in which the male faces the posterior of the female with his dorsal surface to her ventral surface (see also *M. sagittata*).

Attachment of the mating thread. The male moves onto the web frame and then starts to make excursions down one or more radii before choosing the radius that he will eventually convert into a mating thread. The movements about the web frame are characterized by more or less rhythmic AWing that is quite conspicuous due to the fact that the abdomen is long and fingerlike. These AWs are fairly regular and may occur at the rate of 1–2 per s; hence, we came to refer to them as *ticking* movements. They are made both as the male moves about and also when he pauses in one place.

Excursions down the radii are usually made from the upper part of the web, and we saw no radii below the 3 o'clock to 9 o'clock line used for mating threads.

To prepare the radius the male inches down it, little by little. He may move down past 2 or 3 turns of viscid spiral and then turn back to his starting point before returning to penetrate a little further down the radius and so on. As the male passes turns of viscid spiral, he flails at these with legs I and II of one side, eventually breaking the threads and clearing a small portion of one side of the radius. He returns to the starting point and comes back along the radius, removing viscid spirals from the other side by flailing legs I and II on the opposite side. This clearing away of viscid spiral elements is done first to one side of the radius and then the other. The male seldom advances one cleared side more than 2 or 3 viscid spiral turns ahead of the other. Since the male lays down dragline each time he returns from the limit of his advance to his starting point, male silk is continually laid down on top of the radius. The male can make as many as 30 round-trip journeys in clearing 16 turns of viscid spiral from both sides of a radius. The freed radius becomes thickened and conspicuously white, and the thickest part is that closest to the origin. As the male works at this preparation of the mating thread the ticking AWing continues and the male also taps the radius, flails and scrabbles at the viscid spiral elements and sways from side to side. All this activity clearly sets up vibrations that are transmitted down the radius to the female and can be legitimately regarded as part of long-distance courtship. Certainly the female will orient towards the male and make approaches up the radius during this phase. We have seen the female approach, and mating occur, even when the male had only cut 2 turns of viscid spiral.

Long-distance courtship. Males stop clearing activities and stand conducting vibratory courtship at the very edge of the cleared area. This can be described as pure courtship, since it is unconnected with mating thread construction. Such courtship consists of bobbing, TRing and AWing. The bobbing has a strong swivelling component as the male moves from side to side about the axis formed by the radius. (The radius, unlike a mating thread, is oriented so that the male does not naturally hang below it.) The female at the hub may extend one leg II in the direction of the male and then turn towards him. At this stage she may pluck vigorously or start out towards the male, only to turn back and resume a head-down posture at the hub.

Short-distance courtship. The male continues to court as the female approaches. When she reaches the start of the free radius/mating thread, the female halts and may take one or more of her legs I and II off the web, but she does not assume a very distinctive acceptance posture since she stands more or less parallel to the radius, usually with one of her legs IV gripping her dragline behind her abdomen and the other holding the radius/mating thread. Whatever the other legs are doing, the legs III grip the line and probably support the female throughout the approach of the male and copulation. During the close approach of the female, i.e., before she halts, the male may flatten himself against the mating thread momentarily, interrupting both AWing and bobbing.

We saw 2 versions of the female response to male insertion approaches. Usually, as the female halted, the male moved straight down with no apparent preliminaries and passed beneath the relatively shallow arch roofed by the female's ventral cephalothorax and flanked by legs I and II. As the male passes the female's pedipalps, these scrape along his dorsal surface and he flexes his body strongly from the pedicel (waist) so that it curves towards the female at both extremities and appears to be concave dorsally. This posture brings the anterior of the cephalothorax closer to the ventral surface of the female and at this stage the female takes her legs I and II off the thread and brings one or more tarsi of these legs sharply in to touch the male on his dorsal surface. Alternatively, the female may start this leg movement when the male has not yet reached her and then she appears to pull the male towards her with her legs I and II. We saw no evidence of strumming by the female at this stage. Females of *M. sagittata* adopt an essentially similar acceptance posture but do so on a long and elastic mating thread located outside the web. They also make a number of courtship movements when in acceptance postures (see below). The "grasping" movements of the female do not always result in the smooth passage of the male into a copulatory approach. It is at this stage that the male may abort his approach and drop off the thread. We saw one male seized and wrapped at this stage. Like males wrapped after copulation (see below), he was cut free of the web and dropped; we removed him from the silk package and he recovered completely. We assume that he was not envenomated.

Copulation. As the male moves beneath the female he reaches forward and upwards (over his dorsal surface) with a pedipalp. When an insertion is achieved the female drops slightly below the thread and may place legs I and II on the male. Copulation takes place with male and female in the positions shown in FIG. 69. We are almost certain that only one pedipalp is inserted on each separate copulation, but this is extremely difficult to see. Examination of males after copulation shows a deformation of only one pedipalp. We are positive that only one insertion is made per copulation in the case of *M. schreibersi* (see below). The only existing description of a *Micrathena* copulation is that of Montgomery (1903: 120). His female *M. gracilis* (Walckenaer) made no web and copulated without any courtship. The male inserted the left palpus and turned to the right side of the female. After separation, during which the male moved completely free of the female, he returned to insert the right pedipalp. None of our males succeeded in copulating twice. All 5 copulations that we saw ended in the male being loosely wrapped by the female; in one case, the package was left in the web and the male struggled free unmolested while another male in a dropped package did likewise. We intervened to release the others although they might well have escaped unaided.

Our movie sequences suggest that the male may move slightly to one side of the female's midline during copulation, but this is extremely difficult to judge. In any case there is nothing comparable to the 90° twist that occurs after insertion in *M. schreibersi* (see below) and *M. gracilis* (Montgomery, ibid.).

Interactions between males. We saw none.

Micrathena schreibersi (Perty) FIG. 70–71

This is the most frequently encountered medium-sized *Micrathena* species in lowland central Panama and the female is strikingly aposematic in coloration. Males are less than ½ the length of the females and extremely thin. Chickering (1961: 453) notes that the male abdomen is "constricted near the middle" but his figure 161 does not really show this feature adequately. We think that this construction allows the male to bend his abdomen around that of the female when he is in copula (see below).

Attachment of the mating thread. This species builds mating threads that are similar to those of many *Gasteracantha* species in being long and inserted at the junction of radii and frame threads, or on radii partway down into the viscid spiral zone. The latter kind were inserted by males that walked around the web frame AWing and then made excursions down the radii. Such excursions were seldom more than 1–2 cm in length, taking the male past, at the most, 2 or 3 turns of viscid spiral. However, we have a single record of a male building a short mating thread entirely attached to a radius. The origin was close to the attachment of the 2 o'clock radius to a 2nd-order frame thread and the insertion 6 viscid spiral turns down the radius. The male did not clear the viscid spiral away from the radius and the thread hung below the web in a shallow arc. This kind of thread is intermediate between those of *M. sexspinosa* and the long typical mating threads of this species. Some mating threads were oblique to the web plane and attached to nearby vegetation, while others were simply attached to bridge threads and lay within the web plane. Females often reacted vigorously to males installing their mating threads. They turned at the hub and plucked or shook the web. Males were seldom deterred by such behavior, which forms no basis for predicting the outcome of a courtship. It is perhaps significant that in this species, as in the previous one, some of the behaviors associated with long-distance courtship are present as the male moves about the web frame attaching the mating thread. These include the rhythmic AWing that we described above as ticking, and also tapping movements of legs I against the web frame that are similar to the movements by which *M. sexspinosa* clears away viscid spiral elements.

Long-distance courtship. This is relatively simple and may be repeated at intervals, over long periods, if the female is unresponsive. The male starts courtship after rapidly gliding down the mating thread from its origin to a point about ½ to ⅔ of the way towards the insertion. There does not appear to be any genuine TRing in the courtship repertory. The principal component appears to be irregular bouncing interspersed with fairly regular bobbing. The bouncing appears to be caused by scissoring contractions of legs I and IV towards each other. The male hangs below the mating thread with legs I and II extended well forwards and legs IV extended well behind the body. Legs III form a simple loop almost perpendicular to the ventral thorax. During high-intensity bounces legs I and II of one side may hang down, while legs I and II of the other side do the tugging with both legs IV counterposed.

Bobbing is more or less in synchrony with AWing and legs I may tap the line during this low-intensity movement. We counted, for instance, over 200 bobbing movements during the first 5 min. of a 40-min. period spent on a mating thread by one male (during which time the female remained entirely at the hub). Long pauses may intervene between such bursts of activity; during these the male rests closely apposed to the thread. New bursts of courtship frequently start with the male going back to the origin of the mating thread and then returning to a courtship stance. In one 95-s courtship session, the male went back to the origin of the thread more than 20 times! During long courtships that draw no favorable response from the female, the male may shift the insertion of the mating thread from radius to radius.

Short-distance courtship. In this species, courtship activities conducted by the male after the female has moved onto the mating thread may occupy a considerable amount of time. They are clearly important and the movements involved are highly characteristic and distinctive. The female moves to the mating thread along a radius and may pause en route. She usually assumes her 1st acceptance posture close to the web and may hold the radius, rather than the mating thread, with her 4th legs at this stage (FIG. 70). What follows is that both sexes touch the line as they move towards each other. The male may be as much as 10 cm away at this time. He continues courting, but now folds his legs II away from the extended 1st legs so that they are acutely flexed and close to the anterior face of the cephalothorax. Legs III form the typical nearly perpendicular suspension loop and both legs IV are extended behind the body, holding the mating thread. All the subsequent courtship movements by the male are made with legs I. These tap the line rapidly and alternately in a movement that is difficult to describe. It is as if the 2 tarsal segments are drumsticks that are drummed against the mating thread from above and the sides. They hit the thread slightly apart—in both time and space. The movement is from the joint between the tibia and the metatarsus (the tarsus and metatarsus work as a unit) and only the very tip of the tarsus touches the line. The effect on movie sequences is one of flickering tarsi. During this movement the female may touch the line with her legs I and II in "beckoning" movements and move forwards, towards the male. Her full acceptance posture is one in which the mating thread is gripped between her legs III and IV. Legs III are held against her abdomen while legs IV extend backwards; legs I and II reach forwards off the thread. The male also inches forwards, but pauses during the process to continue the drumming with legs I. When he is within 3–4 cm he starts to make insertion approaches, but these may be aborted over and over again. The male simply jumps off the mating thread and regains it at the location of his last pause (where he presumably attached his dragline). We have several records in which this phase of courtship far exceeded, in duration, the phase of long-distance courtship. Eventually, the male glides down the line to make a complete insertion attempt. Our movie sequences of this do not show the attitude of the pedipalps, but do show the long 1st legs streaming back, like whiplashes, over the dorsal surface of his cephalothorax.

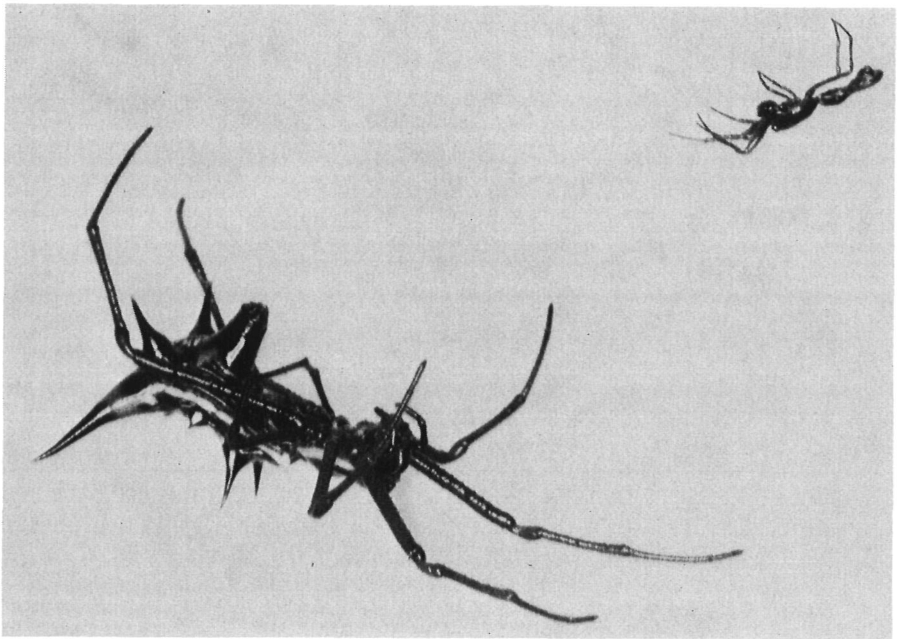


FIG. 70. Female *Micrathena schreibersi* (left) on mating thread in acceptance posture; ♂ (right) is courting.

Copulation. Immediately after insertion, the male turns sideways through 90° and comes to lie across the ventral surface of the female's abdomen, posterior to the junction between cephalothorax and abdomen. His long abdomen appears to bend at the constriction noted above so that it follows the transverse sectional curvature of the female's body. It is thus presenting the minimum profile. The female reaches back and touches the male with her 1st and 2nd legs and also places tarsi III over him. Since the female partly releases her hold on the mating thread in order to touch the male, she drops well below it, suspended on legs IV, and rotates to and fro before regaining the thread with one or more legs I and II and releasing her hold on the male. We do not feel absolutely certain about the relationship between the direction of turn and the sidedness of the pedipalp inserted. We think that FIG. 71 shows an insertion of the right pedipalp followed by a turn to the left side of the female. This agrees with Montgomery's (1903) evaluation of a similar movement in *M. gracilis.*

Interactions between males. We saw 2 males move onto the same mating thread. They carried out a bouncing duel before one male cut the thread.

Micrathena sagittata (Walckenaer)

This species is similar in general appearance to *M. sexspinosa,* although the adult female is about ½ the length of that species. The male is proportionally larger and has a wedge-shaped abdomen. We have never found *M. sagittata* to be abundant in

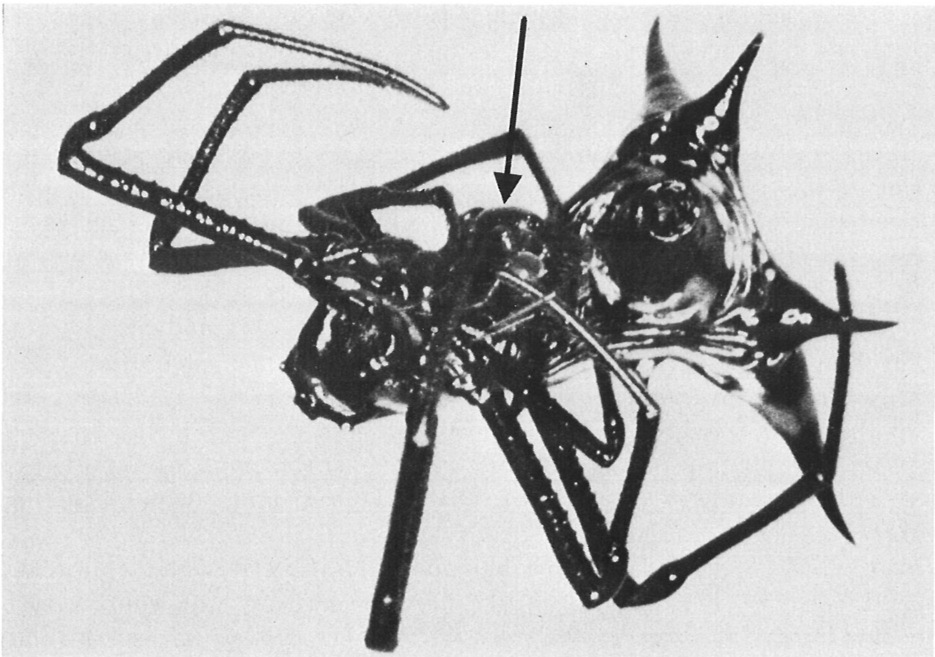


FIG. 71. *Micrathena schreibersi* ♂ (arrow) in copula twisted around side of ♀ abdomen. His right pedipalp is swollen.

Panama, but it was extremely abundant in 1965 in the Lake Placid region of Florida. The species resembles *M. schreibersi* in building a long mating thread and resembles *M. sexspinosa* in having a head-to-tail copulatory posture.

Attachment of the mating thread. Males attach mating threads to the ends of radii where they join frame threads. We did not see any male go down a radius into the viscid spiral zone while inserting mating threads. Some of the threads that were attached from webs strung between bushes exceeded 50 cm in length.

Long-distance courtship. This was basically similar to the long-distance courtship of *M. schreibersi,* conducted at some distance from the insertion of the mating thread and consisting of line tapping, bobbing, and intermittent bouncing. The courtship posture differed from that of the other *Micrathena* species in that the 3rd legs were directed forwards and therefore grouped with legs I and II rather than gripping the thread halfway between legs I and II and legs IV. AWing did not occur very frequently during this stage of courtship, but sometimes the male curved the body from end to end so that it was concave ventrally and then made slow AWs, as though tapping the abdominal apex against the thread. Line tapping that occurred sporadically during bobbing appeared brusque and peremptory. The flexed legs I and/or II were moved from their base to bring the tarsus against the thread like a hammerhead (see below). Only one set of legs I and II were on the line during bouncing; the other, e.g., the right-hand set, could be seen moving beyond the thread.

Short-distance courtship. The female came out onto the mating thread to assume a very shallow acceptance posture close to the web, i.e., she was at a very shallow angle to the thread with little more clearance at her hanging anterior than at the supported posterior. In the full acceptance posture, legs I and II were off the thread and flexed dorsolaterally side by side in a "crab-cheliped" attitude. This was rather similar to the position adopted by *M. sexspinosa* shown in FIG. 69. The male quickly moves into a position quite close (2 or 3 body lengths) to the female. Both during her approach to the mating thread and as he inches forward, the male drums on the mating thread. This behavior is analogous to that of *M. schreibersi* in similar circumstances, but is distinctly different in form. In *M. schreibersi* only the left and right legs I were involved and the movement was almost entirely movement from the tibio-metatarsal joint. In *M. sagittata,* all 4 anterior legs are involved and the movements are from the base of the leg. These tappings of the line look very different from the tarsal flickerings of *M. schreibersi.*

When the male starts to make insertion approaches there are a number of further striking differences. The male aborts the insertion attempt after contact with the female, and instead of jumping off the line he merely steps backwards to his starting point, backing up the line. This action is a form of contact courtship in which the male actually touches the ventral surface of the female over and over again. Some of the approaches are made with legs I and II flexed back over the dorsal surface of the male's cephalothorax and these are probably true insertion attempts. However, other approaches are made with legs I and II flexed, but projecting ahead of the male; these seem to be part of short-distance courtship since the legs scrabble vigorously at the undersurface of the female before the male backs off. Approaches are made repeatedly until an insertion is made or one or both participants cease activity. The female hangs passively most of the time but may make occasional beckoning movements with her anterior legs. We noticed that the male attached his dragline to the mating thread before commencing these approaches-to-contact. However, we only saw one male jump off the mating thread at this stage of courtship. Males sometimes turn around and walk back to their starting point, but simply backing up is by far the most frequent behavior.

Copulation. Males insert the pedipalp with their dorsal surface towards the ventral surface of the female and copulate facing her posterior. They do not turn 90° after insertion. The body is not parallel to the body of the female but forms an angle of perhaps 20°–30° to her ventral surface. During copulation the female may bring legs II over the body of the male but does not release her hold on the mating thread with legs III to drop beneath the thread.

Interactions between males. We saw bouncing duels, chases that finished up on nearby vegetation, and one protracted fight. In the fight, 2 males met head-on on a mating thread and interlocked legs. One was eventually driven off. During the fight the female moved out into an acceptance posture and the victor (probably the male that was the original constructor of the mating thread) made insertion approaches.

Micrathena clypeata (Walckenaer)

This strange, roughly heart-shaped, flattened species is dull brown in color and cryptic rather than aposematic. It is, in our experience, nowhere common, but we have seen more specimens from Barro Colorado I than elsewhere. The male is flattened and ticklike. We found a male already courting a female on the Navy Pipeline Road, Gamboa, and the following notes are based on this incident, which did not lead to copulation. We collected both the male and the female, but unfortunately the female did not build a web in captivity until after (5 days) the male had died.

The female had her web in forest. It was located about 0.5 m above ground and suspended on a long bridge thread (ca 2 m) between 2 understory bushes. The male had built a mating thread from the junction of the 2 o'clock radius to the bridge thread and was courting vigorously when found. His courtship consisted of bobbing, bouncing and line tapping. We had no cameras, nor even a hand lens, so were unable to see the details of the leg movements (the male is about 4 mm long). The courtship was repeated in bursts over a period of 15 min. without the female leaving the hub. At this stage we collected the pair.

Micrathena duodecimspinosa (O.P.-Cambridge)

Females of this species are generally distributed in the Canal Zone and fairly common on Barro Colorado I. We have only seen one male and he was inactive on a long mating thread attached to the 10 o'clock radius and ending in nearby vegetation. He did nothing over a 30-min. period of observation. We collected him, but he died before we could introduce him to a female. This, like the above, is thus a species that produces a true mating thread.

Cyrtophora nympha Simon FIG. 72

Both *C. nympha* and *C. sellata* occur in Panama. They build webs of brownish silk that remain at one site for long periods and become littered with leaves and plant debris. The webs are difficult to locate and when found look abandoned, since the spider rests outside the orb concealed in a retreat of dead leaves or other plant debris. *Cyrtophora nympha* builds a fine-meshed nonadhesive orb that is arranged more or less horizontally but may curl up slightly at the edges. Above the orb is a dense snare of more or less vertical threads; below it the snare is much less dense. Typically the spider builds its webs in small trees and bushes, with the orb itself near a layer of leaves and the snare occupying the free space between the sheet and the branch above it. The orb is often elongate rather than circular and fits the shape of the leafy basin that it occupies. The spider usually has its retreat at the inner end (i.e., the end closest to the tree or bush). The lower boundary, or "floor," of the space occupied by the spider is formed by a layer of leaves or sometimes by a single large leaf. The spider may bridge living leaves with silk to form this floor or may take advantage of naturally occurring conjunctions of horizontally oriented leaves. Colonies of *Uloborus republicanus* often occur in the upper snare and we have found symbiotic lepidopteran larvae living in the web complex and feeding on prey remains (Robinson 1977).

The adult female is dull brown with stocky legs. Her egg-cocoons, shaped like inverted straw beehives, are stacked one on top of the other in perpendicular columns. We hand raised males of this species from the egg and carried out all our studies with captive specimens.

The courtship and mating behavior of this species should yield insights into the possible effects of web architecture on the courtship behavior of araneids. The female operates a heavily braced horizontal sheet of extremely fine mesh and operates it from a distant retreat at that. Gerhardt (1928a: 644–49), in the first study of *C. cicatrosa* Forskal, was concerned with the question of whether the species would have a courtship similar to that of other araneids or whether it might resemble other sheet-web builders. His account and that of Blanke (1972) emphasize the typically araneid form of the courtship and mating. Our concern was more specific: would *C. nympha* fall into group A, B, or C of our courtship classification? In fact, the species inserts the mating thread beneath the main orb, entirely attached to it, and there conducts vibratory courtship. The behavior involved in the insertion of the mating thread involves extensive perambulation on the female's web and very close approaches to her. These stop short of contact. To insert the thread, the male cuts away extensive parts of the lower snare. This type C courtship thus has at least some elements of type B courtship, but this may be attributable to adaptation to courtship on this peculiar web type (some insight into this can also be gained from our studies of *Mecynogea,* which we think is not directly related to *Cyrtophora*).

Our hand-raised males were polymorphic in size and we suspect that this phenomenon is likely to occur in natural conditions. Males resemble *Argiope* males in general shape but have a more globular abdomen with pronounced shoulders on the anterior edge. Blanke (1976) has described the previously unknown male of *C. sellata.* Some males of *C. nympha* have a blood-red dorsal surface to the abdomen; otherwise, they are a dark brown color with barred legs. All males, even supernormal males, are small relative to the adult female (see FIG. 72).

Attachment of the mating thread/approach behavior. Males move from the upper snare or the periphery of the sheet onto its surface. They may travel on the upper surface for some distance before cutting a hole and shuttling through to the lower surface. Once having achieved the lower surface, they concentrate their activities either on that surface or in the lower (diffuse) snare. Males of *C. nympha* may rest in the lower snare for days prior to sustained courtship, just as *Argiope* males may rest on the upper surface of the hub.

Prior to the insertion of a mating thread, the males make extensive walkabouts on the sheet, advancing towards and retreating from the direction of the female's retreat.

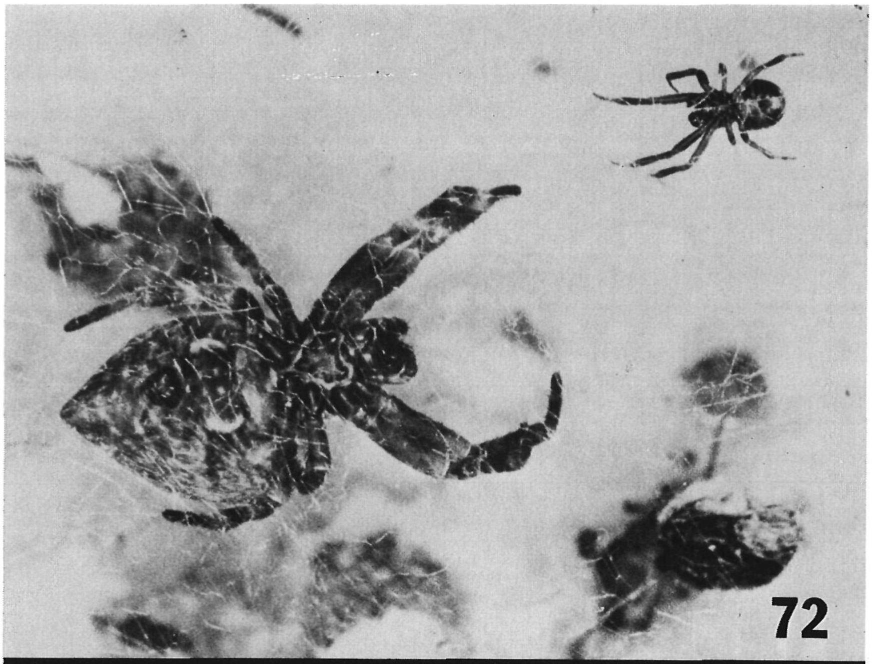
During such advances we saw males approach to within a centimetre of the female, and we suspect that contact may be made at this stage during some courtships. During the walkabout the male TRs vigorously and taps the sheet with an extended leg I. The leg is held stiffly during such tapping and seems to move from the basal joint; it is not quite straight but slightly curved. Lateral tappings with both legs I gives an impression of wingbeat movements. At pauses during the walkabout the male may adopt what we called a "salticid" posture in which the legs I are held off the web in a posture similar to that adopted by many courting salticids. When the male stops walkabouts for long periods of inactivity, he goes into a very characteristic Y-shaped resting posture. The base of the Y is formed by the body and legs III and IV, which are gripping the web close to the body while the left and right legs I and II form the 2 arms of the Y. These pairs of legs are held so close together that they appear as one unit on each side. This pose is as characteristic of the resting males of this species as the X posture of male *Argiope* species.

During the walkabouts, the male makes numerous dragline attachments and moves into and out of the lower snare where dragline attachments are also made. Eventually the male starts inserting the mating thread. This is usually inserted on the web sheet close to the entrance to the female's retreat. The origin of the mating thread may also lie on the sheet, in which case the male takes advantage of the curvature of the web to stretch the line so that it does not touch the undersurface of the sheet. Alternatively, the origin may be attached to one of the perpendicular threads in the lower snare. In either case the male does not usually succeed in producing the entire thread in one journey along the lower surface of the sheet, because he has to prune away encumbering members of the lower snare en route. He usually passes between origin and insertion several times before a single, unobstructed tight line is visible. (After this stage, the male may still pass backwards and forwards many times before the thread is completed. We have records of a male making the round trip 8 times before commencing vibratory courtship and then moving from origin to insertion to origin another 10 times after the 1st courtship bout.) During the walkabout and the thread installation the female may respond, in various ways, to the male's activities. She may emerge from her retreat and adopt a stance on the edge of the sheet facing it. This is similar to the attitude that she adopts prior to a predatory excursion. From this position she can pluck and web-shake. Web shaking in *Cyrtophora* species is used to shake prey out of the upper snare and also (in colonial species) as a response to invading conspecifics (Blanke 1972, Lubin 1973, 1974). After shaking, the female may turn to face her retreat but remain outside it, or may return to the retreat. We saw no predatory excursions at this stage of courtship. Males respond to plucking and web shaking by freezing or (very occasionally) by dropping off the sheet into the lower snare.

Long-distance courtship. Although the perambulation of the male may have a courtship function, we regard the activities on the mating thread as long-distance courtship in the strict sense. The male assumes a position on the thread facing the female and conducts vibratory courtship. This may be prolonged and punctuated by long periods of inactivity but is usually quite complex. The behavior units involved include TRing, bobbing and jerking (bouncing).

We have a particularly good movie sequence filmed with the camera in the same axis as the mating thread that shows the movement of the legs relative to the male's long axis. All 8 legs grip the line during low-amplitude bobbing that provides a background rhythm for other vibratory movements. Looking from behind the male, legs I are seen to move from time to time like a conductor's baton, in sweeping action that takes them laterally away from and below the mating thread. During some bursts of bobbing the male assumes a Y posture on the mating thread, with legs I held anteriorly at an angle to the long axis and well below the body (anatomically dorsal to the inverted male). Prior to TRing, legs I and II are extended but move back into a flexed position when TRing takes place. Our films show that not only are legs I and II involved in the TR, but the homolateral leg III frequently moves into contact with the others, and one leg I and II of the opposite side may move vigorously. The baton-like movements of legs I also occur independent of TRing, as part of low-amplitude bobbing. Most bobbing takes place with legs I and II strongly flexed ahead of the male. As bobbing increases in intensity the male sways from side to side on the thread. Bobbing is punctuated with bouncing; from the side, the jerk component of bouncing is pronounced. The male seems to pull back on the thread so that his whole body jerks back and simultaneously bounces up and down. Legs III slap the line from above throughout bobbing and bouncing. Gerhardt (1928a) noted a similar involvement of the 3rd legs in the courtship movements of *C. cicatrosa.* As already noted, the male may pause during courtship to reinforce the mating thread. Our films show that this may produce a multiple guying of the origin; that is, the 3-dimensional guying produced by exactly this kind of behavior in *Argiope* species (e.g., see FIG. 38). (In fact, we have seen all the elements of long-distance courtship in *Argiope* species with type B courtship.)

Short-distance courtship. During long-distance courtship the female may emerge from her retreat and face the mating thread. Eventually, if receptive, she moves towards it and may stop with her 1st and 2nd legs very close to the insertion. At this point she may drum rapidly on the sheet with these legs before actually moving onto the mating thread. The male continues courtship throughout these movements, but as she moves onto the thread he may turn and retreat along the thread for some distance before turning to face the female again and courting. The female assumes an acceptance posture close to the insertion of the thread. In 12 out of 15 cases that we saw, she actually had her 4th legs on the web itself while in the full acceptance posture. This posture is assumed in the manner adopted by most araneids; the female releases her hold with legs I and II and hangs downward supported by legs III and IV. She thus has her ventral surface facing the male at an angle of 70°–90° to the line of the mating thread. The positioning of the tarsal hold of legs III clearly determines the proximity between the inflexion in the mating thread and the epigyne.



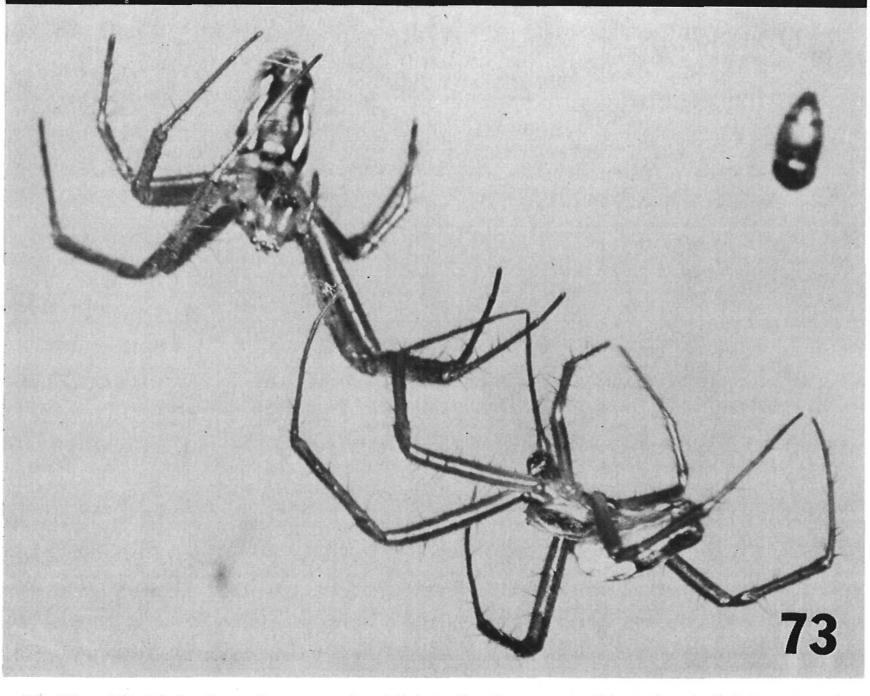


FIG. 72–73. **72.** Male *Cyrtophora nympha* (right) closely approaching the ♀ (left) across the sheet of the orb web. **73.** Male *Mecynogea lemniscata* (right) standing on mating thread. Female is at hub.

Gerhardt's (1928a: 648–49) illustrations of the acceptance posture of *C. cicatrosa* show the female suspended from the mating thread by her 4th legs and dragline attachment, so that her 3rd legs are held against the side of the abdomen. Blanke (1972), in his exhaustive and excellent review of the ecology and behavior of *C. citricola* illustrates an acceptance posture involving legs III (Fig. 26).

Male courtship at this stage consists of TRing, gentle bobbing and strumming with the 3rd legs. When the male moves very close to the female, he seems to rely entirely on this strumming. From 3 to 5 body lengths away from the female, the male makes insertion approaches from which he may back up or jump off the line.

Copulation. During the insertion approach the pedipalps are extended in front of the body and insertion of one only precedes copulation. Copulations are short and the male does not appear to twist noticeably on insertion. We think that the male stood on the abdomen of the female during copulation, but he could have retained his hold on the mating thread with legs III and IV. Such a posture is described by Gerhardt (1928a: 646–47) to be the copulatory position of *C. citricola.* Viewing the copulation through the web sheet and lower snare made such a detail difficult to decide.

Interactions between males. We saw chases around the edge of the web sheet.

Mecynogea lemniscata (Walckenaer) FIG. 73–74

As noted in the general introduction to this section (above), *Mecynogea* resembles *Cyrtophora* in having a fine-meshed horizontal orb entirely lacking a viscid spiral. The males are quite large in proportion to the females (often at least ¾ the length of the adult female) and are strongly patterned on the dorsal surface of the abdomen. The species is highly seasonal in Panama; adults appear about the beginning of July and are absent by early October.

The web of *M. lemniscata* is constructed in gaps between vegetation and the orb is strongly domed. Webs sometimes form small aggregations with shared support threads. The female rests on the underside of the hub at the apex of the dome and may pass to the upper snare, during courtship and prey capture, through a hole at the hub. Courtship in this species has many interesting features and does not fit readily into the descriptive arrangement we have used for other group C species. The mating thread is not used for mating but only for part of the vibratory courtship. Contact precedes vibratory courtship of this kind. The female assumes an acceptance posture hanging from the sheet, and copulations are long and involve multiple insertions without intervening courtship. No TRing occurs on the mating thread.

The taxonomy of spiders belonging to this genus is subject to some dispute. Both Roewer (1942) and Bonnet (1957) place this species in other (and different) genera. Roewer (ibid.) places it in the genus *Allepeira* while Bonnet (ibid.) places it in the genus *Hentzia.* Prof. H. W. Levi (pers. commun.) is currently revising the group.

Approach behavior. Males approach the female by various routes, but most of the complete approaches that we watched started from the upper snare. The male moved about for a considerable time in the upper snare, moving in and out of the threads and attaching his dragline frequently. During these movements the males AWed regularly and sometimes with great vigor. In particularly intense AW movements, the long narrow abdomen of the male looks like a flexing finger. In addition to AWing, males gently tugged at members of the upper snare with one or both legs I and tapped with one leg I. In general most females reacted brusquely to these initial movements around the snare. They oriented towards the male and plucked vigorously at the orb. This web-shaking response is one that this species shares with all the *Cyrtophora* species that we have seen (see also Lubin 1973). It is normally used to dislodge prey items from the upper snare and shake them down onto the sheet where they are attacked. Males are quite violently shaken by these tactics, but do not drop onto the sheet. They sometimes freeze for several minutes but often continue moving. On several occasions females moved into the upper snare and chased males to its outer reaches. They did this by moving through a hole at the hub. (This is also a component of predatory behavior.) Males moved down from the upper snare to touch the orb on its upper side, often very close to the footholds of the female beneath. After a period of movement in the upper snare, the male would move to the margin of the orb and start edging beneath this. His approach on the sheet was characterized by AWing and slow tugging. At this stage the male either continues moving around on the lower surface of the domed orb or quits altogether. In addition to AWing and tapping as he moves, he rubs his pedipalps together in a conspicuous manner. All these movements must transmit vibrations to the female. Since the male attaches his dragline at frequent intervals, the AWing movements probably result in a direct tugging of the orb, via the spinnerets and dragline. The female may be apparently unresponsive or orient towards the male and jerk the web slowly. If she behaves in this way, the male may slowly approach to within contact distance and touch her with his extended legs I. Frequently the male approaches the side of the female more or less at right angles. Such approaches to contact distance are interspersed with walkabouts.

On the other hand, the female may respond vigorously to the pressure of the male on the undersurface of the orb. She may orient towards him, web shake and then chase him right off the orb. Surprisingly, we found that males on contiguous webs would respond to the transmitted vibrations from such encounters by moving down onto the web of the pursuing female. In several cases these incoming males were the immediate subjects of attack by the female.

Successful approaches often resulted in the male finishing up at the hub of the domed orb and the female being displaced to the periphery. We saw this happen and also found pairs at this stage in cases where we missed the antecedent events. This situation is one that resembles the results of web invasion by another individual of the same species, but we saw no evidence that the male at the hub was operating the web as a trap. Once males have become established on the lower surface of the orb, they behave quite fearlessly and move around with apparent impunity. One of the courtship encounters that we watched occurred on the web of a female that had a wrapped female hanging from her orb. We assume that this female had invaded the web during the early morning and had been attacked and killed. After an hour of approach behavior the male was walking boldly around the web and spent nearly 20 min. feeding on the prey package containing the dead female. Eventually the female web-owner carried this prey package to the hub where she started feeding. This was fortunate for us, since it produced an unusually long period of courtship. During this, the male courted the feeding female and attempted innumerable copulations with her while she had a large prey package grasped against her ventral surface (where it effectively covered her epigyne).

Vibratory courtship. After a period of contact courtship and mutual circumambulation on the orb, the male eventually installs a mating thread. This occurs after the female has resumed her position at the hub. The mating thread is often quite short and forms a chord across the curvature of the dome. Often it is less than 1 cm below the sheet at its furthest point and the male can simply reach up from the thread in order to resume his foothold on the sheet of the orb. He can thus move from a foothold on a single thread to a stance on a surface without changing his location on the web. The courtship stance is one in which all the tarsi grasp the thread. The tarsi of the flexed legs I and II are more or less in line with the body axis but are angled quite sharply backwards (FIG. 73). On the mating thread the male performs quite short bursts of vibratory courtship and then moves forward to touch the female. The sequence of court–forwards–touch is repeated until the female moves into an acceptance posture.

Vibratory courtship is relatively simple. It consists of strumming with legs III and bouncing. Several completely successful courtships that we saw consisted entirely of strumming and never progressed to the bouncing stage. The strumming movements are made with tarsi III acting like drumsticks, moving up and down against the thread. In some sequences we counted the number of such movements before the male moved to touch the female. Bouts ranged between 10 and 34 strums. During the move into contact distance, the male may either move his legs off the thread and walk on the web or glide fowards on the thread itself. At contact the male may scrabble against the female while AWing, or simply touch her. Several times during this court/contact stage, the female may move off on a walkabout followed by the male. After such perambulations the whole process starts again. The male may also move the position of the mating thread, or simply renew it, several times. Eventually the female assumes an acceptance posture. All our views of this on movies or still photographs confirm the impression that we got from simple observation: the female assumes the acceptance posture on her web and not on the small mating thread (FIG. 74). She hangs suspended by her 4th legs, which grip the web with much more than a body's width between the tarsi. In most acceptance postures, the 3rd legs are also held wide apart; one may grip the sagging sheet above the apex of the abdomen. The 3rd legs are never held with their tarsi opposed (meeting in the midline of the body),

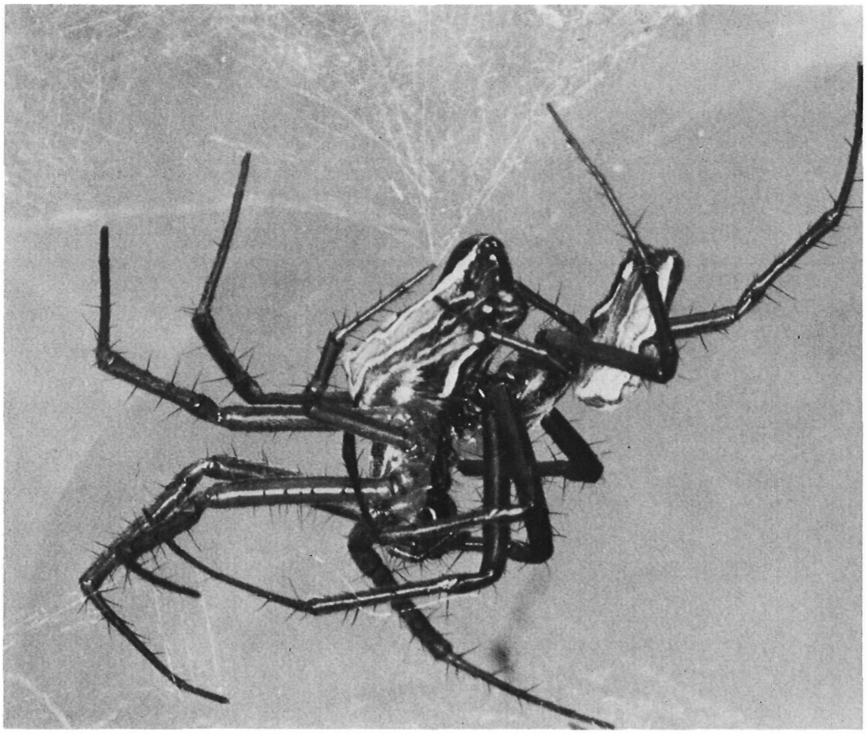


FIG. 74. Copulating posture of *Mecynogea lemniscata*; note that the ♀ is hanging from the orb, not the mating thread.

as they are in acceptance postures assumed on mating threads. (The acceptance posture is closely similar to the position that the female assumes at the hub when feeding on a prey item of her own size; she then hangs down holding the prey beneath her ventral surface and with legs I and II off the web.) When the female is in the acceptance posture the male moves into a copulatory stance. This is accomplished without the rapid forward lunge seen in some type C courtships. It is, in fact, not an insertion movement followed by a copulatory posture, but a precopulatory stance followed by an insertion series. It is thus directly analogous to the movement onto the body of the female made by males with type A courtship.

The male simply approaches the female in her acceptance posture and, while retaining a hold on the web with his legs IV, walks down the ventral face of her abdomen with his legs I, II and III, which finish up gripping the female's legs and providing most of the support for the body movements involved in copulatory attempts. At first the male may form an angle of 60° or more with the ventral surface of the female, but he eventually finishes up standing more or less parallel to her. To accomplish this he must move the foothold of legs IV, presumably after gripping the female with his other tarsi.

Copulation. Like the males of some *Nephila* species, the male may start the copulatory series with his ventral surface well above the ventral suface of the female and the extended pedipalps out of alignment with the epigyne. He then stoops and moves to bring the pedipalps in alignment with the region of the epigyne and close to the body. At this point he makes rapping movements on or around the epigyne and soon an insertion occurs. A white spherical sac (the haematodocha) swells up above the bulbus of the inserted pedipalp, remains inflated for some time and then collapses. This is followed by further rapping movements and further insertions. The rapping movements seem to be made from the base of the segmented portion of the pedipalp, with the black bulbus moving like a clenched fist in a knocking movement. Much of the time both bulbi move side by side in synchrony, but occasionally they seem to be almost alternating. In addition to the movements of the pedipalps vis-à-vis the male's body, there are the movements of the male's body in relation to that of the female. In effect the male makes both anteroposterior movements by swaying on his legs and making rapping movements with the pedipalps. It looks as though insertion may occur as a result of a downward (pedipalp intrinsic) and backward (body) movement of the pedipalps. We think that the inserted pedipalp is held in a downstroke attitude and has its bulbus very close to the epigyne. Meanwhile, the other pedipalp raps gently at the ventral surface of the female's abdomen close to the epigyne.

We noted repeatedly that the epigyne seems to enlarge as mating proceeds, and consider it highly likely that repeated rappings are stimulatory in function. Withdrawal does not result in the kind of recoil that we noted for many *Nephila* species' withdrawals. The withdrawn pedipalp is lifted up, then both pedipalps are rubbed together and touched against the chelicerae. At this stage the male may back up the body of the female to stand with the anterior part of his cephalothorax over her spinnerets. The next insertion bout is initiated by the male moving down towards the epigyne region, pulling himself down with the movements of the 1st legs. Multiple insertions involving both pedipalps, separately, occur during the long period of sustained acceptance posture. The male remains on the body of the female during the whole of this time, merely moving slightly, inserting, withdrawing, rapping, and so on. Females are extremely passive and hardly move at all for minutes on end. Males were not attacked at the end of long mating bouts.

Interactions between males. We saw plucking duels and chases, but no fights.

Zilla species Wau no. 1 FIG. 75–78

This species was extremely common on the slopes of Mt Kaindi at Wau. It builds a large symmetrical orb in between herbs and bushes in secondary growth on trails, at roadsides and on forest edge. We became interested in the species because it builds a perpendicular ribbon stabilimentum above and below the hub of its web (FIG. 75). This stabilimentum is of zigzag ribbon silk and structurally similar to the stabilimentum of *Argiope aurantia.* As far as we have been able to ascertain, stabilimentum building is not recorded for this genus [see Eberhard's (1973) review of the subject].

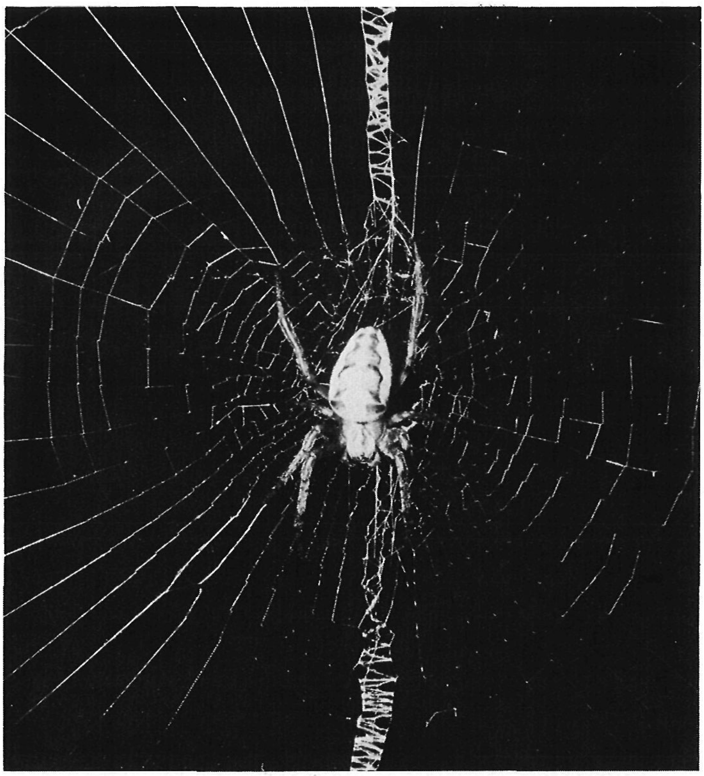


FIG. 75. Female *Zilla* sp. Wau no. 1 at hub of web showing perpendicular ribbon stabilimentum.

We had no idea what genus this spider belonged to, but Prof. H. W. Levi placed it near *Araneus* and tentatively in *Zilla* because of the presence of only one macroseta on the patella of the male (Levi, in litt. 1974). Males are quite large (more than ½ as long as the females), but lack the complex patterning seen on the dorsal surface of the female's abdomen. The species certainly has an *Araneus*-like courtship and mating behavior (see later).

Attachment of the mating thread. Males approach the web along the silk web supports. After a period of moving around the web frame, during which they may TR occasionally and make short bursts of bouncing on the spot, they start inserting mating threads. The mating threads may be attached to the ends of radii where they join the web frame or may be inserted some way down into the viscid spiral zone (at the most 2 or 3 turns of viscid spiral from the edge). We saw mating threads attached to radii in the upper part of the web and a much smaller number attached to lower radii (e.g., the 7 o'clock radius). The male moves between origin and insertion several times, thereby constructing a multistrand thread. Threads are usually long and the outer end is most frequently attached to a web support thread at a very acute angle.

ZILLA sp. Wau no. 1

FEMALE BEHAVIORS	BEHAVIOR ON THE MATING THREAD	MALE BEHAVIOR ON THE WEB
		along upper foundation thread
		down lateral foundation thread
orient towards male		attach dragline to 1 o'clock radius
pluck x2		mating thread installed
pluck		move onto mating thread
rest at hub		
	to origin and back x2	
	TR L, R	
	TR L x11	
	TR R x10	
	bounce x8	
	jerk x2	
	TR L x7, L x2, R x2, R x2	
orient towards male	rest	
pluck	TR L x2, L x2, R x2, R x8	
pluck	bounce x10	
rest on hub	jerk x2	
	drum legs III	
	TR L x3, jerk, R x12, jerk	
	walk towards web 6 cm	
orient towards male	TR R x2, L x2, L x2, R x2, L x2	
pluck	jerk, jerk, jerk	
pluck	bounce x12	
remain facing male	bobbing, jerk, bobbing	
	TR R x4, jerk, R x4, R x4	
	jerk, jerk, jerk	
move up radius onto thread	towards web 2 cm	
halt	bobbing	
	jerk, jerk	
into acceptance posture	turn away from female	
	turn back towards female	
remove leg IV-R from web	TR R, L	
swing to left	advance to contact	
	scrabble at side of female	
	step back 1.5 cm	
	TR R, L	
	advance to contact	
female restores leg IV-R on thread	scrabble at side of female	
acceptance posture correct	insertion approach	
	insertion	
drop below thread on dragline		
scrabble at male		
	male jumps off	
rest at hub		
		male regains upper foundation thread
		rest on upper thread
		down foundation thread
		install mating thread

FIG. 76. Conventional summary diagram of courtship in *Zilla* sp. Wau no. 1. For explanation of abbreviations, see FIG. 5.

Long-distance courtship. The male courts from a position hanging below the mating thread in the half nearest to the web. The courtship movements include TRing, strumming the line with legs III, bobbing, and bouncing (jerking); AWing is absent.

The TRs of this species are particularly easy to analyze, since the legs are long and the movements are exaggerated. FIG. 77 shows a representative TR bout from this species based on frame-by-frame analysis of a section of movie film. Wherever we have described TRing in the descriptions of other species throughout this paper, we expect that the basic components are similar to those shown in FIG. 77 and that the variations in TRing style merely affect the detail. (For most species, particularly those with small males, analysis of the movement is not easily accomplished.) TR bouts may involve a variable number of bowing movements of the legs of one side in uninterrupted succession and these may be repeated by the same legs before alternation of sides occurs. Thus it is possible, for example, to have a TRing session that goes TR-Right 5×, pause, TR-R 2, pause, TR-R 2, change sides, TR-Left 5, pause, TR-L 2, pause, TR-L 4, etc. In *Zilla* no. 1 we noted that TR 2, pause, TR 2, pause, TR 2, pause, was a fairly regular basis for TRing bouts. Even though up to 15 or so movements could occur in uninterrupted succession, males seemed to "get stuck in the groove" and make bursts of only 2 movements. The male may simply lift the TRing legs clear of the mating thread or lean over conspicuously to the side of the TRing legs; there seems to be no relationship between the posture adopted for TRing and the stage of courtship. Neither is it an idiosyncrasy, since the same males adopt different postures at different times.

The drumming of the 3rd legs against the mating thread is another particularly clear-cut behavior in this species. The terminal segments of the appendage move as one unit, hitting the mating thread like a drumstick (i.e., the tarsus and metatarsus move as a unit from the tibio-metatarsal joint). At the onset of courtship all 8 tarsi grip the mating thread. During TRing legs I and II of one side, and occasionally a leg III, are lifted off the thread while the process is occurring. During drumming, all the legs are on the line except the 2 drumming legs III that are beating against the thread. In bouncing, only one leg I may be on the web at some stages, while the other leg I and both legs II may be held in "mid-air." The spider is then supported on legs III and IV and a single anterior leg. At other stages in bouncing, the spider may have more than one anterior leg gripping the line.

Bouncing in this species is clearly based on the same types of leg movements that occur in bouncing in many of the other species described above. The spider also does high-intensity push-ups while pulling sharply backwards on the thread and then relaxing to move forward into its former stance. Bouts of this high-intensity bouncing are short in duration and interspersed between long periods of TRing, drumming and gentle bobbing. At the time we first saw them, we called such brief periods of intense movement "jerking." Bobbing has a strong component of side-to-side swaying or even rhythmic rocking.

Throughout all male activity, inserting the mating thread and courting, the female is highly reactive. She orients towards the male and often plucks and web shakes with extraordinary energy. These responses shake the male violently whether he is on the web frame or out on his mating thread. Males freeze when subjected to this kind of shaking, but do not necessarily abandon further courtship. Some females follow web shaking with pursuit; others change their behavior and follow-up shaking with low-amplitude strumming on the hub. This takes the form of regular relatively slow contractions of all 4 anterior legs that pull on the radii from the hub. We saw cases where the female placed the tarsi of both legs I and II on a single radius (see FIG. 78).

Short-distance courtship. Males continue courtship as the female moves up the radius and out onto the mating thread. The female drops into an acceptance posture that is much more pendant than any that we have described so far. Prior to the adoption of a full acceptance posture, the pair may meet on the mating thread, facing each other with legs I and II extended and touching. Both spiders then scrabble with the interdigitating legs before the female drops down into the acceptance posture and swings away from the male in the process. The male may TR and bob several times before moving forwards into contact with the hanging female. When the female drops into the acceptance posture, she is hanging more or less perpendicularly and frequently swings to one side, rotating about her long axis, so that one side of her body (rather than her ventral surface) is facing the male. This rotation, which occurs in the other Wau *Zilla* sp. (below) and in some of the other species described hereafter, results from the positioning of legs III and IV relative to the mating thread. At an early stage the female hangs from legs IV and the partly extended legs III. Since she was in a normal walking posture before dropping into the acceptance posture, the tarsi of legs IV grip the mating thread behind legs III. As she drops, the female takes one leg IV off the thread and holds on with leg III of the opposite side. This movement off the web of one leg IV and one leg III means that the support is asymmetric (i.e., she may hang from IV-L and III-R or vice versa); the result is a rotation to one side. Confronted with an incorrectly oriented female, the male scrabbles at her surface and particularly at her anterior legs with his legs I and II while hanging from the mating thread with his legs IV. He may even step back and repeat a small element of vibratory courtship. During this short-distance courtship, the female usually has her anterior legs folded against the anterior cephalothorax or close to it. She may unfold them to scrabble back at the male during his noninsertion approaches, but is entirely passive most of the time. The multistrand nature of the mating thread is obvious at this stage of courtship, since the strands often separate at the footholds when these are some distance apart and carrying the entire weight of the female.

Eventually the female assumes a symmetrical foothold and then hangs so that her ventral surface faces the male. He makes insertion approaches with his body parallel and close to the ventral surface of the female. As his pedipalps contact the epigyne region, his anterior tarsi drum rapidly on the anterior legs of the female. They curve around these in a complementary curve, from below (anterior to) her. Advances from a position parallel to the mating thread into this insertion posture are repeated until insertion occurs or the female retires.

Copulation. At the moment of insertion the male must release his hold on the mating thread, because the copulating pair either drops some distance below the mating thread, belayed on the female's dragline, or swings around just beneath the thread. In the latter case we have seen the male finish up with his dorsal surface on the side facing the web, i.e., the pair has rotated through 180°. At the end of copulation, the female sometimes scrabbles at the male and tries to wrap him. If he is quick enough, he jumps off on his dragline, regains the mating thread and later courts again.

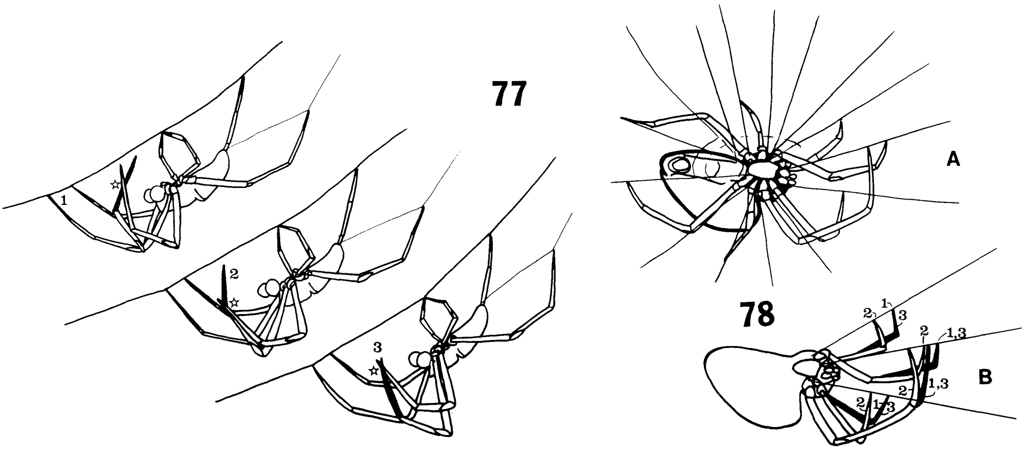


FIG. 77–78. **77.** Male *Zilla* sp. Wau no. 1, TRing with right legs I and II. 1, 2 and 3 show successive stages in this movement. The stars indicate points of contact of legs. **78. A,** ♀ *Zilla* sp. Wau no. 1 at hub of her web, oriented toward ♂ and strumming in his direction. **B,** numbers refer to successive positions of legs.

Interactions between males. We saw jerking duels between males and long chases. We have one note of an incident where a male courting on his own mating thread had the thread invaded by a 2nd male that simply walked down the thread towards him. The original owner dropped off the thread and the 2nd male immediately started courtship on it only to drop off, in turn, in response to very violent web-shaking by the female. The original owner of the thread eventually made his way back to the thread and courted there. The female approached him and went into a series of acceptance postures but copulation never occurred.

Kleptoparasitism by males. We have a note of one male going into the viscid spiral area to feed on a prey package left in situ by the female. The female jerked at him once or twice and the male then removed the prey package and carried it out onto his mating thread where he fed upon it.

Zilla sp. Wau no. 2

We found this much smaller species also on Mt Kaindi; it built a similar web with a perpendicular zigzag stabilimentum above and below the hub. Courtship and mating in this species turned out to be essentially similar to that of the other Wau *Zilla* sp.

Attachment of mating thread. Males moved onto the web supports from surrounding vegetation and down onto the web frame. Most of the long mating threads we saw were strung between the lateral extensions of the upper foundation thread and the lateral foundation threads and were inserted at the junction of a radius with the lateral foundation thread. Some males inserted mating threads on the radius itself by moving down it to the outer edge of the viscid spiral zone. Males, while perambulating the web frame, tapped ahead of themselves with an extended leg I and occasionally TRed. The females responded to this phase of male activity by orienting (at the hub) towards the male and plucking, web shaking or making predatory excursions.

Long-distance courtship. This is conducted from the half of the mating thread nearest to the web, the male hanging beneath the thread supported at the start on all 8 legs. The units involved included TRing, bobbing and bouncing (jerking), with little drumming of legs III. TRs were similar to those of *Zilla* no. 1, but seldom in bursts of more than 2 per side at a time. Bobbing accompanied TRing and jerking was apparently done almost entirely by press-up movements in which rapid flexions of legs III were conspicuous. An anteroposterior tugging was much less obvious in the jerky bouncing of this species than in the previous one.

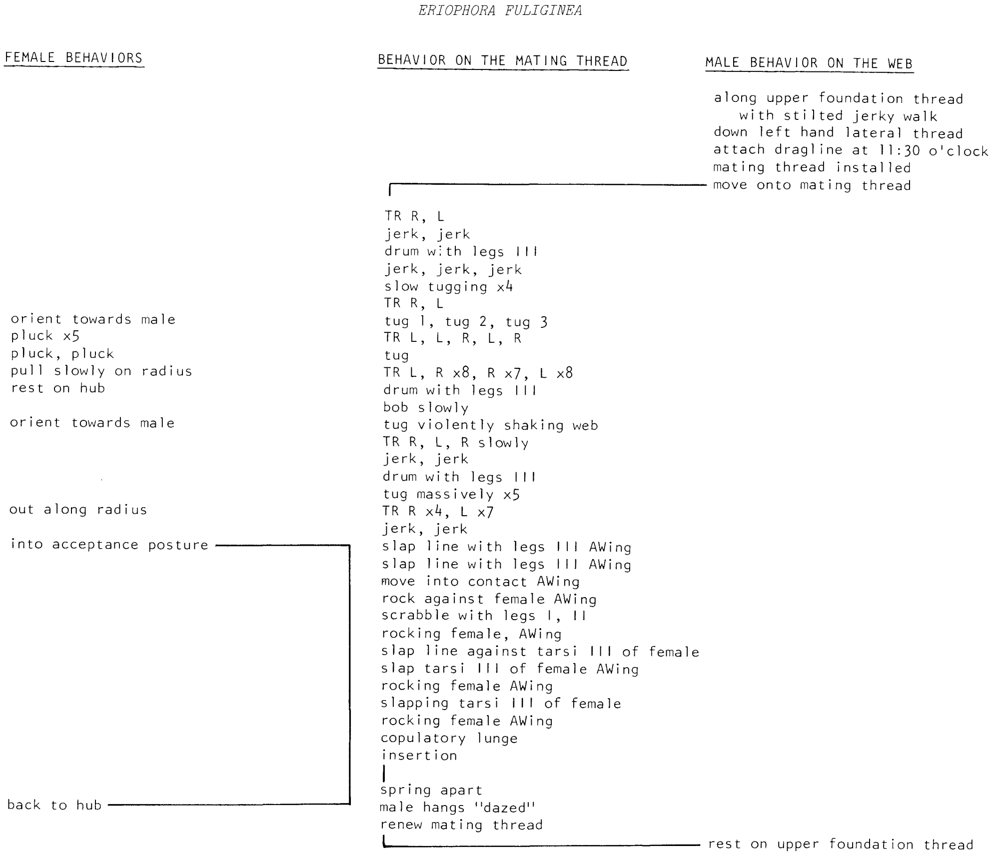
Short-distance courtship. The male continued courtship as the female moved up the web and onto the mating thread. On the mating thread the female moved into an acceptance posture after a preliminary bout of mutual contact scrabbling and (as in the previous species) often swung about to face sideways when she had dropped below the thread into a perpendicular posture. In one case the female remained facing sideways for over 2 min. of sustained contact and vibratory courtship by the male. Several females adopted acceptance postures that depended on suspension from tarsi IV only; we feel that this "narrow" foothold may have resulted in the tendency to rotate away from the male (but see Discussion for further elaboration). The contact phase of short-distance courtship in this species involves an apparently more frenetic "dancing on the female" than did this stage of courtship in *Zilla* no. 1. The male stands parallel to the female and drums on her legs I and II with his tarsi I and II, but also stamps on her ventral surface with high-stepping movements of his 3rd legs. Legs II may also move up so that they embrace the sides of the hanging female. These legs then tap and stroke the sides of the female. Eventually the female is correctly oriented and the male makes insertion approaches, still drumming on her legs and sides; the pedipalps also seem to be drumming on the epigyne region.

Copulation. The events following insertion follow exactly the same pattern as in *Zilla* no. 1. The female drops and swings around on her dragline while the pair remains tightly in a clinch or she rotates without dropping. The male usually jumps off to end copulation or occasionally may be brushed off and attacked.

Interactions between males. None were noted.

Eriophora fuliginea (C. L. Koch) FIG. 79–85

We put this large nocturnal species out of order in this section. It has the least difference in the relative size of males and females of all the species that we studied and should come after the *Cyclosa* species in that respect. However, its courtship and mating behavior is more closely similar to that of the *Zilla* species than to the *Cyclosa* species and it is convenient to describe it at this stage. *Eriophora fuliginea* is the only strictly nocturnal species that we studied. The problems of studying the courtship



ERIOPHORA FULIGINEA

FEMALE BEHAVIORS	BEHAVIOR ON THE MATING THREAD	MALE BEHAVIOR ON THE WEB
		along upper foundation thread with stilted jerky walk
		down left hand lateral thread
		attach dragline at 11:30 o'clock
		mating thread installed
		move onto mating thread
	TR R, L	
	jerk, jerk	
	drum with legs III	
	jerk, jerk, jerk	
	slow tugging x4	
	TR R, L	
orient towards male	tug 1, tug 2, tug 3	
pluck x5	TR L, L, R, L, R	
pluck, pluck	tug	
pull slowly on radius	TR L, R x8, R x7, L x8	
rest on hub	drum with legs III	
	bob slowly	
orient towards male	tug violently shaking web	
	TR R, L, R slowly	
	jerk, jerk	
	drum with legs III	
	tug massively x5	
out along radius	TR R x4, L x7	
	jerk, jerk	
into acceptance posture	slap line with legs III AWing	
	slap line with legs III AWing	
	move into contact AWing	
	rock against female AWing	
	scrabble with legs I, II	
	rocking female, AWing	
	slap line against tarsi III of female	
	slap tarsi III of female AWing	
	rocking female AWing	
	slapping tarsi III of female	
	rocking female AWing	
	copulatory lunge	
	insertion	
	spring apart	
back to hub	male hangs "dazed"	
	renew mating thread	
		rest on upper foundation thread

FIG. 79. Conventional summary diagram of courtship in *Eriophora fuliginea.* For explanation of abbreviations, see FIG. 5.

behavior of nocturnal spiders are considerable. We studied this species in a large screened insectary and found it behaved normally even under the illumination of powerful movie lights. In view of the fact that in most tropical regions the nocturnal araneid fauna is rich and abundant, we expect to extend our studies of courtship and mating in nocturnal species to make up for the present deficiency.

The predatory behavior of this species was described by Robinson et al. (1971) who also gave brief notes on web structure and ecology. The species is large and builds an aerial web that is strong enough to catch and hold some species of bats.

This species is so large that many details of the behavior of both sexes that we were unable to see in smaller species, or species with small males, were easy to see. We therefore devote a disproportionate amount of space to detailed descriptions. These may provide some insights for the interpretation of the courtship behavior of closely-related genera.

Attachment of the mating thread. Males in the insectary moved about the underside of the roof and onto the female's web by way of various silk supports connected to the upper foundation thread. Presumably in natural conditions, they can move onto the web from any of the many attachments to vegetation. Similarly, although all the mating threads had their origins on the underside of the insectary roof, we would expect that they would be strung from surrounding trees and other plants under normal circumstances. Males moved about the web frame with a slow, stilted gait, vibrating from time to time and tapping the web ahead with an extended leg I. Considering the weight of the male we have no doubt that its movements were detected by the female, but there were very few orientation or plucking responses. It seems certain that the male's movements are recognized as those of nonprey in this case; see Discussion below).

Males frequently inserted the mating thread onto an attachment far down into the viscid spiral zone on a radius. There was no clearing of connections between the viscid spiral and the radius. We saw the male make slow tugging movements on the radius before proceeding down it, on several occasions but not consistently. Once the mating thread was installed the male moved backwards and forwards, between origin and insertion, several times before commencing courtship. On these reinforcement trips the male often extended the thread by moving the insertion down the radius and the origin out across the cage roof. One thread was taken down the radius to within 6 cm of the female's leg IV. Such invasions of the viscid spiral zone suggest strongly that the male had somehow inhibited the female's predatory impulses.

Mating threads built in captive conditions ranged between ca 15–25 cm in length. These are short relative to the body length of the male. Lack of suitable supports may necessitate longer threads in nature. All the threads that we saw built (and used) were oblique to the web plane; some were almost at right angles to it.

Long-distance courtship. The long-distance courtship of this species involves units that produce low- and high-amplitude displacements of the mating thread, and we were particularly fortunate that filming by artificial light produced some film footage that allows us to correlate the extent of the vertical displacement of the mating thread with the ongoing activity of the male (below).

The male TRs, AWs, drums on the mating thread with legs III, bobs and bounces. Bouncing in this species deserves our alternative designation of jerking, since the movements of the mating thread that it produces clearly move the female at the hub of her web; when the male jerks the mating thread she is jerked or shaken passively.

TRing is as described for *Zilla* no. 1. The male makes bowing or sawing movements of one tarsus over the other. In the main it is leg II that is hardly moved, while tarsus I is moved over it in a brisk manner. However, leg II can move at the same time as leg I, giving a movement analogous to palm rubbing in humans. These movements transmit relatively low-amplitude deflections to the mating thread. TRs are always unilateral.

Drumming by legs III can occur simultaneously with TRing, independently of TRing but in conjunction with bobbing, and totally independent of both TRing and

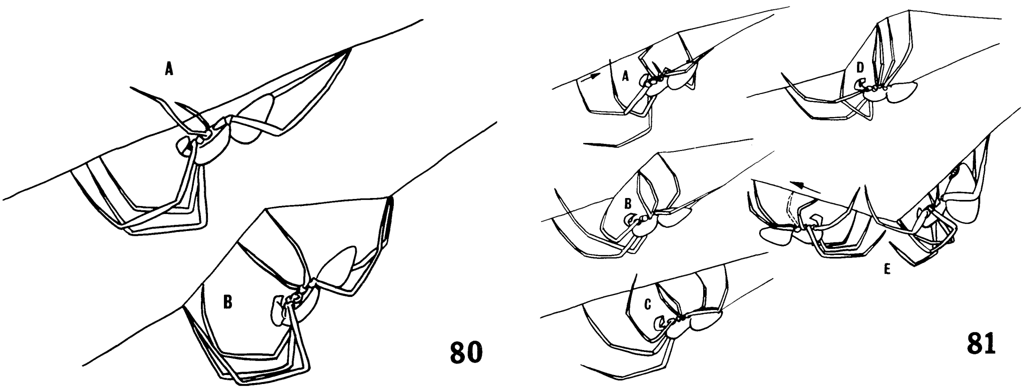


FIG. 80–81. *Eriophora fuliginea.* **80.** Jerking/tugging posture of ♂: **A,** starting posture; **B,** push-up on thread with legs III. **81.** Second form of jerking/tugging by ♂; 2 variants shown. **A, B** and **C** are successive stages of 1 variant (A, starting position; B, push-up of thread by legs III and one leg IV; C, release of tension). **D,** a variant of the push-up posture B in which both legs IV are used. **E,** slow tugging by ♂ legs III that occurs when ♀ is on mating thread (♀ left).

bobbing. This is clearly a basically similar behavior pattern over a wide range of araneids with type C courtship. We have already described the homologues in the courtship of *Gasteracantha, Micrathena, Cyrtophora* and *Zilla* species. Blanke (1972: Fig. 22) illustrates this behavior in *C. citricola.* Essentially the male flexes and extends legs III, out of phase with each other, held in such a way that the tarso-metatarsus, acting as a unit, moves against the mating thread. We call this drumming because the base of the tarsus moves against the thread like the head of a drumstick. Sometimes the tarsal claw may engage the thread and deflect it upwards or downwards, but we think that this is fortuitous and normally the line is not so deflected, i.e., the moving tarsi slap the thread but do not grip it. Drumming on the mating thread is a preliminary to tarsal tugging in short-distance courtship and precedes the action in the complex jerking of long-distance courtship.

AWing is a very minor component of long-distance courtship in this species but a very conspicuous element of short-distance courtship. When the male is courting the dragline is clearly visible, belayed behind him more or less parallel to the mating thread. The occasional AW that occurs during bobbing clearly pulls on this dragline.

The male is seldom motionless on the mating thread; when he is not indulging in the movements described above, or jerking intensively, he is usually bobbing rhythmically. This movement that produces moderate deflections of the mating thread is produced by regular flexions and extensions of the 3rd and 4th legs, in pairs, and similar movements of whichever of legs I and II are gripping the thread at the time.

Jerking (bouncing) occurs in at least 2 forms and one of these may itself occur in 2 variants. The basic operation is the same in all cases; only the means of effecting the jerk differ in detail. The basic operation is one in which the spider exerts tension on the line by leg movements and then releases this tension to cause a distinct "twanging" jerk that is transmitted down the web to the spider at the hub.

The 1st type of jerking is shown in FIG. 80. At the start the male is standing parallel to the thread with legs IV extended posteriorly and all the anterior legs on the thread (the particular male that is illustrated had II-R missing); legs III are extended above the thread as at the start of a drumming session. The male then flexes the anterior legs strongly, pulling back on the thread with all anterior tarsi. At the same time it grips the line with one or both tarsi III and extends these upwards, to their maximum extent more or less at right angles to the long axis. The male thus tenses the line by the strong backwards pull and also stretches it between the grip of the anterior legs and legs IV. This is a very similar process to that described for several *Gasteracantha* species. (This description of the process is based on observations of the spider and analysis of the movie footage. There could be undetected subtleties occurring during this kind of jerking. One possibility is that the spider could tense the line by pulling with the anterior legs and then, when it starts to exert the secondary tension with legs III, allowing the line to slip through its tarsi before gripping again.) The release of this tension produces a sudden blurring deflection of the thread and spider in the vertical plane. For several seconds it is impossible to decipher what happens; the spider may relax its legs or simply release the tarsal hold and let the line revert to its steady state.

The second type of jerking involves movements of one anterior leg and legs III and IV. In one variant, both legs IV are moved; in the other, only one is moved. We have seen both variants used interchangeably by the same spider, in long, mixed series. Both variants are shown in FIG. 81. The most striking variant of this form of plucking is undoubtedly the one where the spider pulls back along the length of the mating thread by strongly flexing a leg I and simultaneously extends both legs III and both legs IV above its ventral surface. These legs are so extended that even the coxae project perpendicular to the ventral surface. Our interpretation of this posture is that the strong upthrust of these legs takes up the slack resulting from the pulling movement of leg I and allows the spider to hold the line taut for a moment before it releases it to produce a strong jerk. At the end of several seconds of blurred bouncing, the male can be seen with its legs back into the relaxed position. It could thus release the tension by simply relaxing the posture that was exerting the tension; on the other hand, it is entirely possible that a simple relaxation of the tarsal hold, letting the thread slip through, would achieve at least part of the observed effect. We cannot be sure. The 2nd variant of this kind of jerking involves the erection of legs III perpendicular to the ventral surface of the male together with one leg IV. However, in this case, the male holds the thread behind his body by thrusting out the other leg IV in line with the long axis. This posture puts a triangular "tuck" in the thread similar to that involved in the 1st plucking posture described above. As before, the movements of the 3rd and 4th legs accompany a strong flexure of one 1st leg that pulls back strongly on the mating thread. Release of the tension produces a convulsive jerk and subsequent bouncings. The female at the hub is moved in time with the vibrations.

Our original notes on these movements emphasize that the flexing of the mating thread can be a slow tug at the start of a sequence leading to more and more massive and rapid movements as the bout progresses: "massive, massive high intensity tugging, it may be against the fixed point of legs IV, vigorous pulling, it's a magnificent slow-motion tug, TR R, TR L, tugging 1, 2, 3, TR R, TR R, tug, TR R, massive tugs more jerky than previous ones shaking the whole of the female web."

The female responds at the hub of her web by turning, orienting towards the male and plucking or web shaking. She may then go out to the mating thread and halt in a preacceptance stance or chase out at speed and cause the male to drop off the thread or retreat precipitously. Females that responded violently in this way later assumed perfectly normal acceptance postures in response to further courtship (often by the same male that had been chased off). Significantly, some females would move to the appropriate radius and move partway towards the male only to turn back and resume their predatory posture at the hub of the web. We have noted this behavior in other species and think that it marks the dawning of sexual motivation (see Discussion).

Short-distance courtship. The short-distance courtship in this species may be prolonged and is undoubtedly complex. Its complexity and frequent long duration suggests that complete sexual arousal in the female is not achieved at the time when she makes a pacific movement onto the mating thread. While the female is moving from the hub to the mating thread, the male continues to court with TRs, drumming and jerks. Eventually she moves along the mating thread so that the pair are in contact, facing each other. The weight of the female causes the thread to sag so that the spiders are on opposite slopes of a roughly V-shaped inflexion in the thread, with the female in a walking posture. They meet with their anterior legs overlapping but not necessarily touching (FIG. 81E). The male meanwhile drums with legs III and from time to time gives a series of slow tugs, using these legs to pull on the thread, so that it is tugged away from the female and released, tugged and released. The male may bob gently throughout the drumming. Tugging with the 3rd legs may be reinforced by tugging involving both the 3rd and 1st legs (as described for long-distance courtship). Eventually the female either drops into an acceptance posture or retreats back to the hub; we have seen the male simply leap off the mating thread at this stage and hereby abruptly terminate a short-distance courtship bout. (Bouts that do not lead to an acceptance posture, however they may be ended, do not usually mark the end of courtship. The male normally recommences long-distance courtship and the whole cycle is repeated.)

The female acceptance posture involves suspension of her body from 2 loops, one formed by the 4th legs that grip the mating thread behind the hanging spider (dorsal to her as she hangs) and the other formed by the 3rd legs that grip the line close to her ventral surface. She hangs more or less perpendicular to the mating thread with

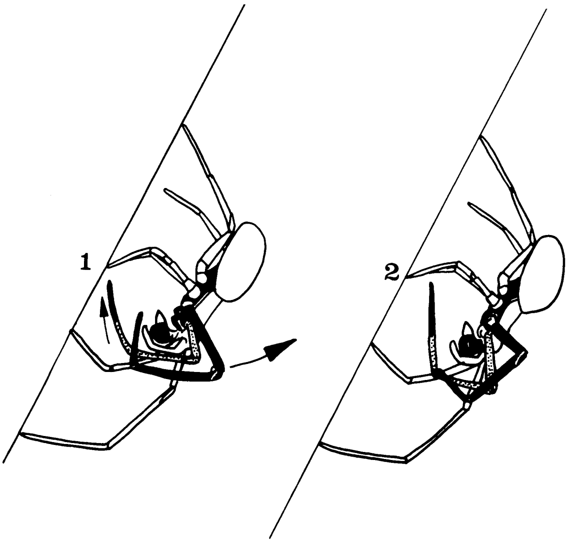
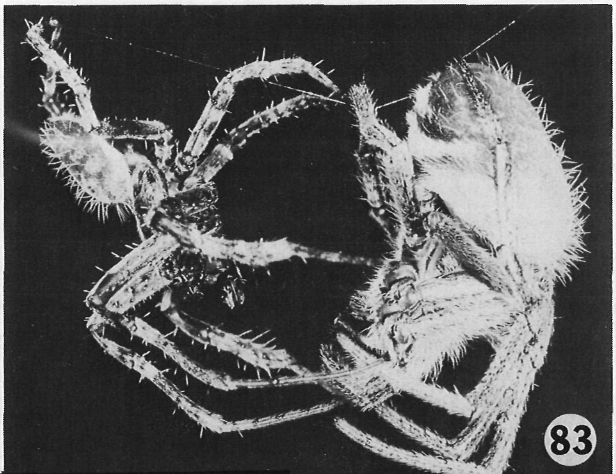


FIG. 82. Male *Eriophora fuliginea* TRing; 1 and 2 are successive stages.

the apex of her abdomen actually touching the thread. She is also belayed on her dragline that is attached to the mating thread close by where she hangs. This basic posture is shown in FIG. 83 and 84. The male is now out of contact since she has swung in an arc away from him. He advances the short distance into contact and drops alongside her, supported on the loops of his 3rd and 4th legs. While the female hangs with her abdomen touching the line and her 3rd and 4th legs fairly close to her body, the male adopts a very different stance. His 3rd legs point forwards and upwards and his 4th legs are extended behind his body so that his long axis forms an angle of ca 45° to the ventral surface of the female. The tarsi of the 3rd legs grip the mating thread either very close to, or immediately adjacent to, the point where the female also grips the thread with her 3rd legs. The male's legs I and II rest with their tarsi touching the female (either on her flexed legs I and II or on the anterior part of her cephalothorax or its other appendages). When the pair are in this loose clinch, a further stage of short-distance courtship occurs. Throughout this stage, AWing occurs with what appears to be metronome regularity. In addition the male flexes his anterior legs, while maintaining his foothold on the female, and then relaxes them. Repetitions of this movement cause a rhythmic see-sawing of the pair, backwards and forwards. Similar movements of legs III cause a side-to-side swaying.

From time to time, the male raises legs III off the thread and drums on the thread very close to where the female's legs III grip the line. The male also flails at the legs of the female with his anterior legs. These leg-flailing sessions were always followed by the female making small adjustments in her position relative to the male by shifting the foothold of one or more of the supporting legs. Eventually the male makes an



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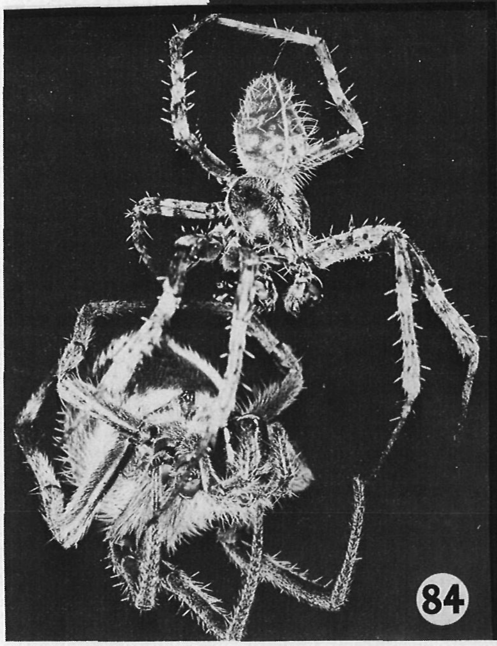

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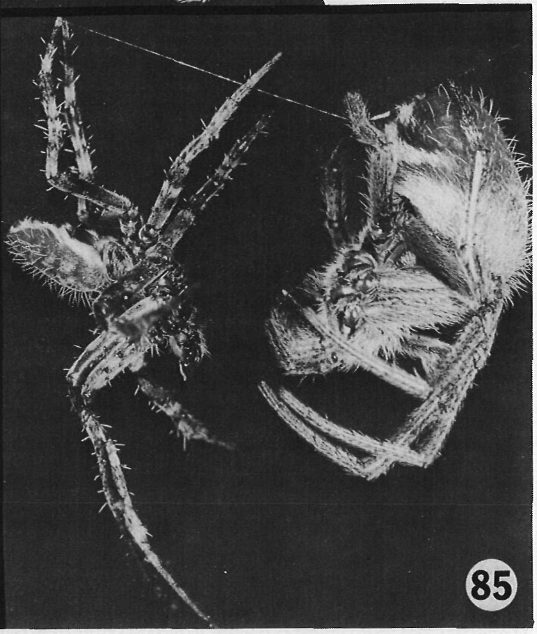

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FIG. 83–85. **83.** Female of *Eriophora fuliginea* in acceptance posture on mating thread (♂ on left). Note positions of her legs III and IV. Legs III of the ♂ rest with the tarsi touching hers on the thread, while his legs I and II touch her body and anterior legs. **84.** The same situation as in FIG. 83 from a different angle. Note that the ♀ (ventral surface facing camera) has opened her chelicerae. **85.** Start of a copulatory lunge by ♂ *Eriophora fuliginea* (right). He is swinging upwards with his legs III clear of the mating thread (see text).

insertion attempt; this takes the form of a rapid forwards and upwards lunge (FIG. 85). With the pedipalp extended and the embolus pointing ventrally, the male describes an arc with his body. The foothold of legs IV is the center about which the arc is described and the movement brings an embolus up against the anterior surface of the extruded epigyne. One film sequence that we have of an insertion lunge that missed shows that at the end of the arc the male's body was in contact with the mating thread across the entire length of its ventral surface. The motive force for the lunge appears to come from the flexion of the previously extended 4th legs. The movement is quite rapid and occurs in less than a second.

(When we originally saw this swinging insertion lunge, we were unable to decide whether it involved removing the 3rd legs from the mating thread at the height of the movement. If this were the case the movement would be powered by flexion of the 2 larger legs IV, as stated above. We decided that legs III passed at each side of the line in some lunges. The only film sequences that we have show at least one leg III passing the line.)

Copulation. Copulation is brief and in the copulatory posture the male is appressed to the female, with his abdomen projecting beyond her abdominal apex. Separation is violent; the male jumps back in a blur of movement and the female turns immediately and returns to the hub. Immediately after copulation, at least one male spent time grooming his pedipalps, rubbing them together and apparently drawing them through the chelicerae and then rubbing them with the anterior legs.

Interactions between males. None were seen.

Cyclosa sp.

Spiders of the genus *Cyclosa* are small to medium-sized araneids that build roughly symmetrical orb webs in the herb layer of secondary growth and forest. At Wau, 2 species are abundant and 3 other species not uncommon. Many *Cyclosa* species build devices of adventitious material into their webs that form strings or patches and on which they are able to achieve concealment (either by filling a gap in a broken line of material whose color they match, or resting on top of such material). Such devices have been called stabilimenta, but we feel that this term should be reserved for unadorned structures of ribbon silk. Rovner (1976) has shown that *Cyclosa turbinata* carefully conserves its detritus device by renewing the web around it. Detritus-covered devices built by *Cyclosa* species are structurally similar to the gibbets of some *Nephila* species and often contain egg sacs that are also covered in detritus and prey remains. Bristowe (1941: Fig. 60, 61, p. 431) describes or illustrates the devices found in the webs of *C. insulana* and *C. bifida* in Malaysia. We studied these 2 species (the most common) at Wau and found no devices similar to those described by Bristowe. There is little doubt that we were dealing with the same species. In the light of such variation in an antipredator device over this geographical range, it would be interesting to compare the detailed nature of courtship behavior of the Malaysian representatives of these 2 species with our Papua New Guinea results. We carried out more studies of *C. insulana* than of any other *Cyclosa* species.

As far as we can determine, the only species for which copulation has been described is *C. conica* (Pallas) on which there are notes in Gerhardt (1923b, 1926).

Cyclosa insulana (Costa) FIG. 86–89

This species is common throughout the Wau Valley as a clearing species, preferring sunny areas on forest fringes and roadsides. Robinson et al. (1974) give brief notes on its natural history and seasonality at Wau. We made more studies of this than of any other *Cyclosa* species. It is quite large and males court readily.

Attachment of the mating thread. Males move onto the silken web supports from surrounding vegetation and then move down the lines onto the web frame. On the web frame they TR sporadically and insert mating threads of variable length and orientation. Short mating threads are built in the roughly triangular corners of the web frame, where the outer foundation threads join second-order foundation threads (FIG. 54). They are also sometimes attached partway down the radius within the viscid spiral zone. Such short threads may be from ca 3–10 cm long. Longer threads are built from the bridge thread or nearby vegetation to insertions on the frame of the web, opposite radii or onto the outer ends of the radii themselves. Such threads can exceed 30 cm in length. Males tend to move backwards and forwards along the mating thread several times before starting courtship, making it a multistrand structure. As they are moving back and forth at this stage, males TR, both while facing the web and while facing away from it. Such TRs are discrete and not sustained.

Long-distance courtship. Long-distance courtship is conducted on the ⅓ of the mating thread closest to the web. The male's stance on the mating thread involves support by the looped legs III and legs IV. Legs III are oriented so that they point slightly forwards of a line perpendicular to the ventral surface of the cephalothorax; legs IV grasp the mating thread well behind the spider. Legs I and II are typically flexed and held ahead of the male more or less in line with the long axis of his body. The anterior legs may be all on the line or all off the line; they are involved in a variety of movements that produce vibrations but do not seem to be important in supporting the male beneath the mating thread.

The components of long-distance courtship include TRing, bobbing, bouncing and high-intensity jerking. AWing seems to be absent, and drumming with the 3rd legs is either rare or absent. TRing may occur with all the anterior legs off the thread, or with 1 or 2 legs on and the others off. It most frequently involves legs I and II on one side moving while the opposite legs are motionless but can involve all 4 anterior legs. Legs III occasionally join in a compound TR but more frequently the leg III on the side of the TRing legs is lifted off the thread and makes movements in midair that are similar to TRing movements. This "sympathetic" movement perhaps indicates a sparking-over from the nerve center controlling TRing in legs I and II.

CYCLOSA INSULANA

FEMALE BEHAVIORS	BEHAVIOR ON MATING THREAD	MALE BEHAVIOR ON THE WEB
		along upper foundation thread bouncing
		down lateral foundation thread
		attach dragline at 1 o'clock
		mating thread tightened
		onto mating thread
	to origin and back x5	
	TR R, L, R, L, L	
	bounce x12	
	bobbing	
	TR L, R, L x6, L x11	
orient towards male	stretch/release	
pluck x2	bounce, high intensity	
rest on hub	TR R x13, R x3, L, L	
	stretch/release, stretch/release	
	bounce, high intensity	
orient towards male	stretch/release	
pluck x2	TR R x16, L x12	
rest on hub	rest	
	TR R, L, L, L, R, L, L, R, L, L	
	stretch/release	
	bounce, high intensity	
	bobbing	
	TR R x5, L x5, L x8, L, L, L	
	stretch/release	
	TR R & L simultaneously	
	stretch/release, stretch/release	
	bouncing x21	
	bobbing	
orient towards male	stretch/release, stretch/release	
pluck x4	bobbing	
pluck, pluck	drum with legs III	
	stretch/release	
move up radius	bouncing x9, very high intensity	
pause at edge of web	TR R, L, L, L, R, L, L, L, L, R, L	
onto mating thread, halt	stretch/release	
into acceptance posture	bounce x5	
	TR R	
swing sideways	down to contact	
	jump apart	
	TR L, L, R, L	
	TR R, jerk line with legs III	
	down to contact	
	scrabble at female	
	spring apart	
	rest	
scrabble at mating thread		
good acceptance posture	TR L, L, R, jerk	
	bobbing	
	down to contact	
	scrabble at female	
	spring apart	
	TR L	
	jerk, bounce x3	
	down to contact	
	insertion approach	
	spring apart	
	TR R, jerk	
	down to contact	
	insertion approach	
	insert	
back to hub	spring apart	
	move off web towards nearby female *Cyclosa insulana* web	

FIG. 86. Conventional summary diagram of courtship in *Cyclosa insulana*. For explanation of abbreviations, see FIG. 5.

Bobbing results from movements of the 3rd and 4th legs that flex and relax synchronously, but may coincide with TRing or scrabbling movements of legs I and II. The most interesting component of the vibratory courtship of this species is the high-amplitude jerking behavior. This is undoubtedly the functional equivalent of the complex movements of *Eriophora fuliginea* that result in a shaking of the female's web. However, the movements (FIG. 87) are quite different in detail. Spiders have evolved a variety of ways of achieving high-amplitude shaking of the female web. In *Gasteracantha* species we called these movements twanging; they clearly involved press-ups against the mating thread, although rather different ones from those seen in *E. fuliginea.* The *C. insulana* movement proved to be particularly difficult to elucidate; the impression given to the observer is most misleading. We thought that the male bowed its entire body, folding at the waist to bring the anterior cephalothorax and posterior abdomen towards the thread, giving the spider a concavely-curved ventral surface. This proved to be true (FIG. 87). However, direct observation led us to believe that legs II pushed up on the line, outstretched, as the body bowed and that this tensed the thread when it was opposed to a similar movement of legs IV. Repeated movie analysis of several sequences of jerking, performed by 3 different males, showed finally that this is not the case. Legs II do thrust upwards outstretched as the body bows, but they do not thrust against the line but rather pass at each side of it. In a movement exactly opposite to that of *E. fuliginea* and the *Gasteracantha* species with twanging behavior, the 3rd legs of *C. insulana* pull down on the mating thread, flexing towards the ventral surface of the body as the body bows. At the same time, legs II and IV thrust moderately upwards. The effect is to stretch the mating thread in precisely the opposite way to the stretching achieved in all 3 jerking movements that we described for *E. fuliginea* (above, FIG. 80–81). The male builds up to the maximally bowed position in less than a second (8–17 frames of film at 24 fps). The change from this curved, legs II and IV upthrust posture to the next stage is abrupt and produces an immediate massive deflection of the mating thread in the vertical plane. Legs II are slashed downwards, side by side, from their position thrusting above the thread to a position below the thread. At the same time legs III, that have been holding the thread down, are thrust upwards to their maximum extent. This coupled movement simultaneously releases the tension on the thread and dramatically shifts the center of gravity of the spider. It is little wonder that a huge deflection of the thread occurs. Once the line is resonating, the male keeps the bounce going by further movements of legs II.

Since we later found a similar behavior in several species of *Cyclosa* and since the whole complex of actions is marked by the curving of the male's body and the upthrust of legs II, we eventually came to call the start of jerking the *Cyclosa*-stretch. However inaccurate this description may be in categorizing the effects of the behavior, it certainly draws attention to the most conspicuous aspect of the movements. We think that the term is worth retaining.

Once alerted to the possibility that movements of legs that had no grip on the mating thread could be employed in producing vibrations, we noticed that during normal bouncing the male was in fact raising and lowering legs II above and below the line, as well as TRing and tapping the line with flexed legs I and II.

During the complex of male courtship activities, the female can react in a variety of ways. She may orient towards the radius on which the mating thread is inserted, may orient and pluck or web shake, or may simply remain immobile at the hub. If she makes an excursion up the radius towards the male, she may go all the way the first time, or go partway and turn back. Eventually, however, the female goes out to the mating thread and assumes an acceptance posture.

Short-distance courtship. As the female moves up to the mating thread the male continues vibratory courtship and as she moves onto the mating thread his activities may increase in tempo. He TRs, bobs and bounces until the female is in contact distance. After she has dropped into an acceptance posture the male may remain parallel to the mating thread and continue courtship, including high-intensity jerking. The female drops into her acceptance posture after brief contact. She hangs perpendicular to the line, suspended from legs IV and III. On near-vertical mating threads, the female's acceptance posture is almost horizontal so she is not merely hanging like a pendulum on a thread, but her position must be determined by the position of the footholds and the attitudes of the legs III and IV.

The male edges forwards towards the female, moving legs III along the line by a combination of stepping and what looks like sliding (i.e., they sometimes move forwards without being lifted off the line). When legs I and II meet the body of the female, they step down her ventral surface and the male is then hanging with the ventral surface of his cephalothorax roughly parallel to the entire ventral surface of the hanging female and with his abdomen tilted backwards. He is supported by legs IV, which grip the line behind him and, presumably, by legs III, which now embrace the female. Legs I and II intermittently hold the female's anterior legs. The male is now in a position to make insertion attempts and does so by reaching forwards into a position where the pedipalps are close to the ventral surface of the female in the approximate area of the epigyne. The reaching forwards movement is characterized by an increased flexure of the male's body at the waist as he apposes his ventral cephalothorax to the surface of the female. Where there was a gap between the pair, none is now visible. At this point we have never been able to see the details of pedipalp posture or movement. Insertion could be achieved either by the movement of the pedipalp occasioned by the body movement or by an intrinsic movement occurring after the juxtaposition of the bodies. If insertion does not occur, the pair separates suddenly and the male "springs back" to a position, on the thread, facing the female but more than a body length away from her. The female bounces but does not move from her acceptance posture. In our early notes we ascribed this springing apart to the male jumping off the mating thread on his dragline. Analysis of movie sequences shows that the male does not swing away on the end of a thread, but springs away still oriented towards the female. We think that during his final approach the male

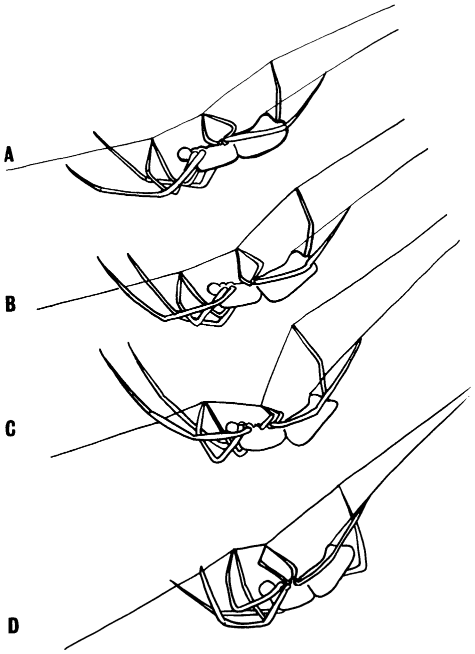

FIG. 87. The "*Cyclosa*-stretch." Male *Cyclosa insulana* at 4 stages in the production of a high-intensity jerk: **A,** start of movement; **B,** partial stretch; **C,** (the stretch posture), legs II are thrust upwards above the thread and the body is curved towards the thread, thus stretching the thread; **D,** tension is released as legs II are swung back beneath the thread.

somehow exerts a tension on the mating thread behind his legs IV, so that when he releases his hold on the female (maintained by legs III, II and I) the recoil pulls him back away from the female. This would be a device with considerable survival value, because it is precisely at this final stage of intimate approach that the male would be most vulnerable to an attack by the female. Our movie footage of the male's movements immediately prior to the insertion attempt and during the separation does not give clear views of the position of the mating thread throughout the entire sequence. Glimpses of the thread at various stages show that something peculiar is going on. We have attempted a reconstruction of this in FIG. 88. One aspect of this behavior is very striking: immediately before the rapid separation of the pair the male swings his extended legs IV forwards from their trailing position. This simultaneous movement of 2 large levers from their basal joint(s) must be a major part of the process of springing back. Interestingly enough, the position of the legs at the end of this swing is anticipated in the pre-insertion-attempt posturing of the male (FIG. 88A). Unfortunately, we cannot tell whether in the rapid forward swing legs IV are gripping the thread as they do in the earlier similar posture.

The female is usually remarkably passive throughout the entire process of short-distance vibratory courtship that is followed by contact courtship. As the male taps

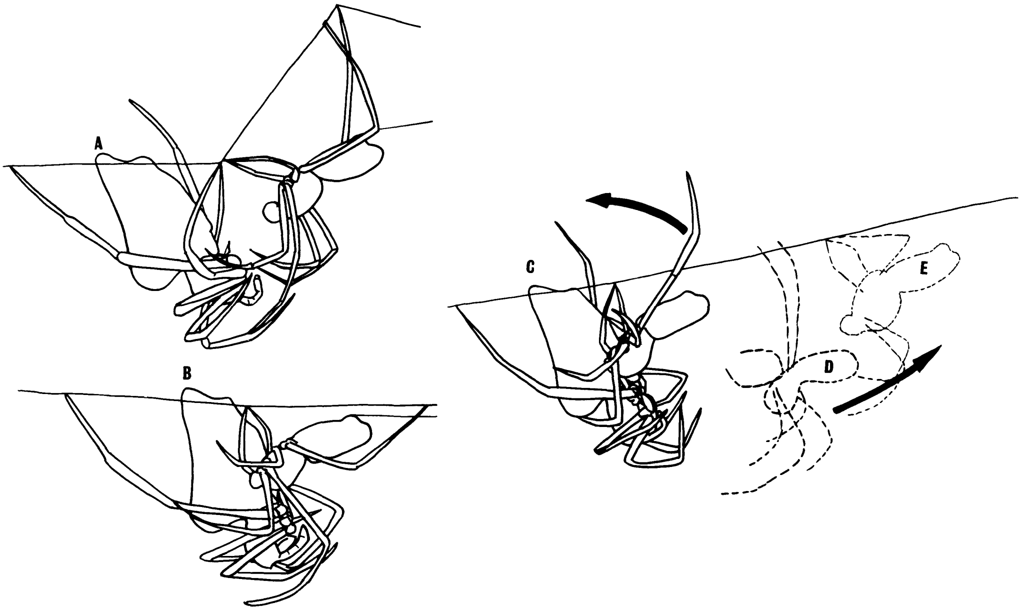

FIG. 88. Spring-apart movement by ♂ *Cyclosa insulana*: **A,** movement of legs IV prior to insertion; **B,** insertion; **C,** movement of legs IV at moment of separation; **D** and **E,** ♂ jumps back away from ♀.

and scrabbles at her anterior body and legs, she hangs in a more or less inert acceptance posture, perhaps adjusting the relative position of her legs III and IV from time to time, but not doing anything else. She may remain in an acceptance posture for several minutes while the male makes many insertion attempts and springs back over and over again.

Copulation. If the male ceases these activities the female usually turns around and walks back to the hub. When an insertion occurs, the pair remain in close contact for the duration of the copulation and then spring apart. The male seems temporarily dazed and hangs there for some time before recovering. The copulatory posture is shown in FIG. 89.

Interactions between males. We saw plucking duels and occasional chases. However, males accumulate on the silk web supports of females' webs and may be found there for several days, in numbers as high as 5 per web. Such males fold all their legs against the sides of their body and rest touching the silk threads. We call this the cryptic posture and have seen it adopted (during prolonged periods of inactivity) by males of all the *Cyclosa* species that we have studied.

Cyclosa sp. Mt Kaindi no. 1 FIG. 90

This large and highly elongate *Cyclosa* species was found only at altitudes above ca 1800 m. It builds its web under rocky overhangs or in earth caves and other sheltered

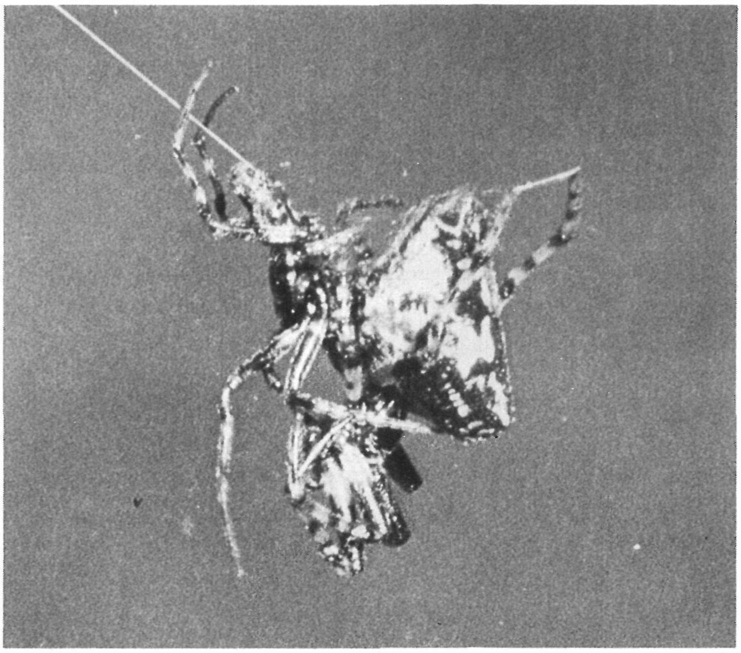

FIG. 89. *Cyclosa insulana* seen in copula. This photograph corresponds to stage B of FIG. 88. The ♂ legs IV are actually on the mating thread, which is less conspicuous than the ♂ dragline to which it is roughly parallel (dragline is immediately behind ♂).

sites. The web of the adult female contains a vertical detritus and egg sac device above the hub against the lower end of which the spider rests. Males are elongate and cryptically colored. We found this species only on Mt Kaindi and the portion of the Bulldog Road at Edie Creek. (We never found it at any height on Mt Missim on the opposite side of the Wau Valley to Mt Kaindi.) FIG. 90 shows that the species is gregarious; individual webs may share some structural elements.

Attachment of mating thread. Males moved onto the females' web supports from the root tangles of overhanging surface vegetation in earth caves. On the silk they made extensive walkabouts, jerking, but not TRing, as they moved. Mating threads were inserted both inside and outside the web frame. Inside they typically spanned the corner triangles between the primary foundation threads and the 2nd-order lines, being inserted on radii or on the points of intersection of radii and frame threads. Outside the frame, most mating threads spanned from the bridge thread to a radius/frame intersection at a low angle. Such threads were much longer than threads inside the frame. We saw one male insert a mating thread on the hub of a skeleton web (i.e., a web that was unfinished and lacking a viscid spiral). During the process of insertion, the female responded by plucking and sometimes by running out from the hub towards the male.

Long-distance courtship. All males courted on the ¼ of the mating thread nearest the web. The components of long-distance vibratory courtship include TRing, AW-

FIG. 90. Habitat of *Cyclosa* sp. Mt Kaindi no. 1. Earth cave with at least 12 webs of adult ♀ clumped in an aggregation. Devices of detritus and egg-sacs are visible.

ing, drumming with the 3rd legs, bobbing and bouncing. The species also carried out the high-amplitude jerking that we had come to call the "*Cyclosa*-stretch" (see above). AWing (not seen in *C. insulana*) occurred throughout the period after the male had assumed a courtship posture on the mating thread and was not otherwise actively courting. It also occurred in conjunction with drumming (legs III), bobbing and TRing. Drumming involved deliberate-looking movements of legs III against the thread from above. TRing was almost entirely unilateral and often alternating. We noticed that during TRing the 3rd legs held the mating thread above the line of the footholds of the anterior legs and legs IV. Such a posture could tighten the thread to enhance the transmission of the vibrations produced by TRing. Bobbing occurred in conjunction with TRing and with tapping or stomping movements of the anterior legs on the mating thread.

The stretching movement that precedes bouncing and produces high-amplitude jerking seems to be achieved in the same way as in *C. insulana.* Our movie footage shows the forward extension of legs II above the mating thread and the curvature of the body, plus a sudden downswing of legs II. It does not allow us to determine the positions of legs III relative to legs I and IV. We cannot, therefore, be certain that the totality of movements involved is similar to that illustrated for *C. insulana.* However this may be, the effect is the same. The male produces a massive jerk on the thread and then bounces rhythmically.

The female turns at the hub and plucks in the direction of the mating thread before turning to resume a predatory posture or making an excursion to the thread. Females that do not move to the male after the first such orientation often do so later, but others stop responding and the male then ultimately stops courting and leaves.

Short-distance courtship. The male continues courtship as the female approaches, TRing, bouncing and even stretching. The acceptance posture assumed by the female is one in which the apex of her long abdomen projects above the mating thread; legs IV, when fully extended to hold the thread, reach about ⅔ of the length of the abdomen. The male approaches by advancing his legs III until their foothold is close to that of the female's 3rd legs. He then touches the female with his anterior legs; these scrabble at the legs and cephalothorax of the female. Since the male of this species is quite elongate, the bent insertion posture described for *C. insulana* is exaggerated. The male bends at the waist to bring his cephalothorax parallel to the body of the female, while his abdomen forms an angle pointing back to the mating thread. We saw a large proportion of 1st-time insertions in this species (8 out of 11).

Copulation. During copulation the pair are tightly appressed and the female may swing up from her pendent position to one more or less parallel to the mating thread. We saw a number of spring-apart disruptions of insertion attempts but at the time were not alerted to the possibility that a special mechanism was involved. We do not know if the male swings the 4th legs forwards to do this as described for *C. insulana.*

Interactions between males. We saw none.

Cyclosa sp. alpine grassland no. 1

We found this species to be abundant in stunted trees in the alpine grassland habitat some 8 km beyond Kaisenek Village, roughly SE of Wau. The species is small and with a more or less spherical abdomen. It resembles in size and overall shape the *C. velata* of Chrysanthus (1961: 201–03), but has prominent tubercles on the anterior dorsal surface of the abdomen. The male has a much less globular abdomen than the female.

Attachment of the mating thread. This is carried out as described for the other *Cyclosa* species. We have one note of a male going down a radius as far as the free zone at the hub to insert a mating thread within contact distance of the female. This is equivalent to the behavior we described for one instance of mating thread insertion in the Kaindi *Cyclosa.*

Long-distance courtship. Before commencing courtship the male usually traversed the mating thread from insertion to origin and back to the courtship location. Most courtships were carried out from the ⅓ of the mating thread nearest to the web.

Vibratory courtship consists of TRing, drumming with legs III, bobbing, jerking and bouncing. TRing plays a relatively insignificant part in the total sequences. A few unilateral TRs start the first few sessions and then become less and less frequent in later sequences. The courtship consists preponderantly of bobbing and high-intensity bouncing, with interspersed pauses. We were unable to detect any AWing during this phase of courtship. TRing is unilateral, but a leg I from the opposite side may join the other legs in a 3-unit TR. Jerking starts the high-intensity bouncing bouts and is the result of a *Cyclosa*-stretch. This species is short, and the stretch is not so conspicuous as it is in elongate species that become bowed. Nevertheless the long legs II thrust forwards and upwards and the tarsi end up well above the line. Legs I are on the thread and pull the line back towards legs III. At the moment when tension is released, legs II swing down below the line into a semiflexed posture. The upthrust and pull-back are repeated regularly throughout the duration of the bouncing bout. Absolutely characteristic of bouncing in this species is the position of legs IV. After the initial stretch, both legs IV are placed so that the footholds are a very short distance away from those of legs III. Thus, instead of extending behind the body, legs IV are strongly flexed so that the tarsi reach forwards from the femorotibial joint. They appear to parallel the position of the 3rd legs, and this is a most unusual posture for a courting male.

Females at the hub respond to courtship with the repertory of behaviors that we have described for the other *Cyclosa* species. The only small variant that we noted was a tendency for the female to move a short distance out from the hub along the radius leading to the male and pluck, web shake or strum from that position. As in the other species, females would then either move out to the male or move back to the hub, there to assume a predatory posture. Excursions to the male were almost all made at the run.

Short-distance courtship. The male continues courting during the approach of the female. The female frequently pauses on the male's thread in an ambulatory position without dropping into an acceptance posture. At this stage the male advances into contact and the female may scrabble at him violently. If this happens he jumps off, belayed on his dragline, and swings beneath the mating thread while the female returns to the hub. This situation differs from the "spring-apart" behavior described for the other 2 *Cyclosa* species in that it occurs at contact before the female has dropped into an acceptance posture and before the male has started to make an insertion attempt. We saw this happen over and over again and assume that females of this species move onto the mating thread when their level of predatory motivation is still high and has to be exhausted. The number of repetitions of the approach phase to copulations was well in excess of 20:1. Despite this we never saw a male successfully attacked at this stage. We saw at least 5 instances of the mating thread being cut (or breaking) during these initial contacts; in such cases the female swung back into contact with the web and the male dropped away in the opposite direction. When the female assumes an acceptance posture, she hangs in the typical *Cyclosa* manner and the male drops, supported by his 3rd and 4th legs, to make an insertion attempt, drumming on the female with legs I and II as he does so. We saw only 4 copulations in over 90 approach/contact sequences. All of these were 1st insertion-attempt successes.

Copulation. Copulation takes place with the pair closely apposed and hanging from the mating thread. The male jumps off to end copulation and then hangs immobile for several seconds before starting efforts to regain the mating thread. The female turns immediately after the separation and returns to the hub. After a pause, the male may start courtship again. We saw no 2nd copulations between the same male and female but, since the male courts again, we assume that this does occur.

Interactions between males. We saw one male detach another male's mating thread from the outside of a web on which he was in the process of adding a thread himself. Other than this we saw no interactions between males.

Cyclosa bifida (Doleschall)

This species is present in moderately shady secondary growth throughout the Wau Valley. It is a tailed species and we frequently found males (in cryptic postures) associated with females' webs. Despite this we never succeeded in seeing a successful courtship, though we introduced many males to females. We saw one courtship that resulted in the female moving onto the mating thread, and we report this briefly.

The male inserted a mating thread between the 2 o'clock radius and the junction of the upper and lateral foundation threads; the insertion of the thread was some 40 cm down the radius, and the female oriented towards the male and shook the web violently during its insertion. On this thread the male TRed, plucked with one leg I and made rapid bouncing movements. The female came out rapidly, scrabbled at the male, and he dropped off the line. This process was repeated once. After this the male assumed a cryptic posture and no further courtship occurred. We did not see a female acceptance posture and think that the long-distance courtship is probably more complicated than the simple sequence that we saw.

Cyclosa sp. Wau no. 5

We found this species only at the MacAdam Memorial Park, Wau. A moderately elongate species with an egg-sac and detritus device, it resembles none of the species that Chrysanthus has described for New Guinea (see Literature Cited). We never found more than 8 adult females at any one time. We first found this species in 1974 and MHR found a small group of adults in the same locality in 1977. In 1974 we found only 2 adult males during 6 months of intermittent monitoring of this small population. Both courted when we introduced them to adult females and both courtships led to copulation.

Attachment of the mating thread. Both mating threads that we saw built were long and attached from vegetation to the web. They were constructed in high winds. One was attached to the 7 o'clock radius, the other to the 4 o'clock radius. The fact that both were attached to radii located in the lower ½ of the web may not be significant in view of the small sample size. When they were being attached, the deformation of the web due to high winds was great and we could not decide whether or not the males jerked as they moved around the web frame.

Long-distance courtship. This consisted of TRing, stretching and bouncing. No AWing was involved and if bobbing occurred we were unable to distinguish it from wind-induced movements of the long mating threads. TRing involved all four legs I and II for at least part of the time and 3 anterior legs for the rest of the time. Courtship sequences started with bouts of TRing with long pauses (15–20 s) in between. These TRs were followed by longer pauses of several minutes and then by stretch/release and high-amplitude bouncing. The courtship posture of this species is highly characteristic. The male hangs well clear of the mating thread because the loops formed by legs III and IV are extended maximally upwards. As the species TRs, it angles the cephalothorax away from the mating thread with a fairly obvious flexure from the waist. This puts legs I and II further away from the mating thread and the enhanced space available presumably permits the mass TRing of all anterior legs. The leg II movements involved in the post-stretch bouncing are also quite distinctive. The stretch involves a typical *Cyclosa* upthrust of these legs, but after the immediate swing-down-and-jerk they are upthrust again and then drawn backwards towards the anterior edge of the cephalothorax in a movement that we described at the time as a beckoning movement. This is still a fitting descriptive term. The beckoning is not done with simultaneous movements of the legs II, but in alternating movements; one is thrust forwards and then brought back while the other goes forwards. Perhaps the tarsi are drawn along the edge of the thread during this movement. If so it should produce a highly characteristic vibration superimposed on the bouncing.

One male carried out 6 bouts of TRing/bouncing over a period of 9 min. before the female came out onto his mating thread. The other male achieved the 1st female excursion (a different female) after 3 bouts of courtship (abbreviated TRing/bouncing). We did not see any female behaviors other than orientation at the hub. Plucking could have taken place, but we are not sure because of massive wind-induced web movements.

Short-distance courtship. This was basically similar to that desribed for *C. insulana.* The male continued vibratory courtship until the pair were in contact distance and the female dropped into an acceptance posture. At this stage the male edged forwards to hang from his 3rd and 4th legs and make insertion attempts while drumming on the anterior parts of the female with legs I and II. One male went into copula at the 1st insertion attempt. The other indulged in the spring-apart behavior on 2 insertion attempts and was successful after the 3rd female excursion onto the mating thread. The spring-apart behavior looked just like that described for *C. insulana,* but we could not see the details.

Copulation. The 2nd male was in copula for a much longer time than any males of the other *Cyclosa* species that we studied. When this male was collected his right pedipalp was visibly discharged. We lost the other male after one copulation had occurred.

Interactions between males. None were seen.

Cyclosa caroli (Hentz)

This is the common *Cyclosa* species in the Madden Forest Preserve, Canal Zone, Panama, where it occurs in low vegetation both inside the forest and on the shaded edges of roads and trails. It builds a detritus and egg-sac device in its webs. Levi (1977) gives the geographical distribution and notes on natural history.

Attachment of the mating thread. Mating threads were attached both within the web frame and outside it. Males would insert a mating thread at one angle, opposite one radius and then in the process of reinforcing it would move the insertion, or origin, to change the angle and the point of insertion. One male carried the insertion of his mating thread down the radius to a point of insertion almost at the hub. This was on a skeleton web (compare this behavior with that of the Mt Kaindi *Cyclosa* species in similar circumstances). Mating threads can lie in the web plane or outside it.

Long-distance courtship. This started after a mating thread reinforcement movement. It includes TRing, bobbing, stretching and bouncing. Drumming with legs III occurs as a component of bobbing and sometimes of bouncing.

TRing in this species is similar to that described for the *Cyclosa* species from MacAdam Park, Wau. The spider hangs well clear of the mating thread on stilted legs III, its cephalothorax flexed away from the thread thereby giving a considerable clearance for the anterior legs. From this posture all 4 anterior legs are involved in a compound TR. Bobbing occurs as the male stands parallel to the mating thread with his body straight and the anterior legs on the thread. One of the 4th legs grips the mating thread while the other hangs below it, extended backwards, gripping the dragline and holding it away from the mating thread. Legs III drum against the line from above in alternating movements. Stretching follows the pattern seen in other long-bodied *Cyclosa* species; legs II are thrust forwards and upwards so that the tips of the tarsi appear well above the line. We think legs I pull back on the thread opposed by legs III that grip the line. The recoil movement following relaxation is accompanied by a very rapid swinging down of legs II from above the line to a position well below the long axis of the male (i.e., dorsal to it in its inverted position). Further high-amplitude bouncing seems to be mainly powered by the swinging above and below the thread of the long 1st legs. These definitely pass the line rather than push up on it. (Since they bear stiff bristles they could scrape against it like a file, but that would probably produce visible deflections at the point of movement; these do not occur.) Legs I do not remain entirely stationary during this massive movement of legs II. They may be lifted off the line and brought down on it or could simply move to either side of it in miniature versions of leg II movements. We cannot be sure about this; the movements are only detectable in movie sequences and are very slight.

Short-distance courtship. The male continues to court during the approach of the female, who drops into an acceptance posture some distance (several male body lengths) from the courting male. All the females that we studied dropped straight into an acceptance posture out of contact with the male (compare with the behavior of *C. insulana*). Males approach acceptance-posturing females very rapidly and, at contact, either make a very rapid transition to an insertion attempt or drop off. We saw very little contact courtship, but presume that the male's anterior legs stroke and drum on the anterior parts of the female.

Copulation. We saw 9 copulations that occurred at the 1st excursion of the female and on the 1st insertion approach of the male. One male jumped off the line the first time and successfully copulated at the 2nd approach of the female. Separation following copulation was achieved safely in all cases. The male jumps backwards off the female, belayed on his dragline and he may pay out more dragline as he swings away from the female. One male added so much silk to his original dragline attachment that he finished up hanging nearly 50 cm beneath the lower margin of the web.

In this species the in copula pair changes its posture relative to the mating thread immediately after insertion occurs. This change must be due to the female changing her foothold. In some cases the female swings up into a position parallel to the mating thread and in others she spins around, perhaps hanging from her dragline, to face the web, carrying the copulating male through 180°. During copulation the male is not pressed tightly against the female's ventral surface for his entire length; the abdomen is sharply tilted away from her by a flexure at the waist, exactly as in the insertion approach. After separating from the female the male is inactive for several seconds before struggling up his dragline to regain the mating thread. One male died

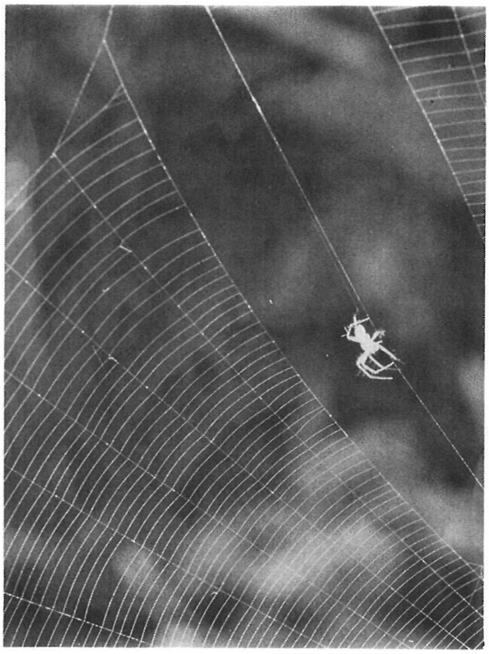

FIG. 91. Male *Mangora bimaculata* on radius of ♀ web that he has prepared as a mating thread.

in situ on the mating thread after trembling for several minutes. Prior to this 2nd session on the mating thread, this male had successfully courted and mated once with the same female. Death occurred some 15 min. after the copulation.

Interactions between males. We recorded 3 instances of simultaneous courtship of the same female by 2 separate males (6 males in total). These males had constructed mating threads at different times but when, after varying periods of inactivity, 1 of the 2 males at a web started courtship the other started within a minute of the first. We think that males may perceive the vibrations set up by courting rivals and respond by starting their own courtship. We also have a note of a male that was perambulating the web frame prior to installing a mating thread and there encountered another male that was in the cryptic posture and inactive. The active male touched the inactive one with his legs I and then moved off along the web frame.

Mangora bimaculata (Pickard-Cambridge, O.) FIG. 91

A number of *Mangora* species are locally abundant in the Canal Zone and elsewhere in Panama. All build regular orb webs of very fine mesh in grass and low herbage, both in the open and inside forest. The spider is diurnal and the female remains at the hub of her web by day. Males are about ¾ the length of females and similarly marked with reddish background coloration and green and gold patterning. We have seen courtship in this species on 3 occasions, but have not seen the preparation of the mating thread or a female response and copulation. Despite this, we feel that this species is worthy of inclusion here because of the fact that the male utilizes a prepared radius as a mating thread. In the example of this shown in FIG. 91, at least 50 turns of viscid spiral have been cleared away from the edge of the radius involved. The isolated radius does not appear to be conspicuously thickened by the constant addition of the male's dragline, as was the case when *Micrathena sexspinosa* similarly cleared a radius to make a mating thread (see above). The courting male in the figure has dragline belayed beyond him, and this is noticeably much finer than either the cleared radius or the nearby intact structures.

Our notes on other instances of courtship indicate that the radius is cleared to within 3 or 4 turns of viscid spiral from the hub. The number of elements that have to be cleared varies with the size of the orb. We have one note of a radius from which only 15 turns were cleared.

Long-distance courtship (from halfway down the radius) consists of intermittent unilateral TRing, drumming with legs III and bouncing. We have no movies of this behavior and cannot categorize the components of bouncing. Our photograph fortuitously shows drumming with the 3rd legs: the male has leg III-R raised above the surface of the radius and leg III-L on it.

OVERALL SYNTHESIS AND DISCUSSION

Attempting to draw together the subject matter of a study as extensive as this—to compare, contrast, synthesize and generalize—is a major task. We have tried to avoid repetition and overlapping but are aware that this may be unavoidable. Below we first recapitulate the major features of the 3 basic courtship systems and summarize the main types of behaviors that we have discovered. This leads naturally to speculation about the evolutionary origins of these behaviors. A central issue in most past treatments of spider courtship has been the question of its presumptive functions; we deal with this subject before reexamining our evolutionary scheme for araneid courtship and mating behavior. Finally, we review what to us are the exciting questions posed by our researches and suggest fields for future investigation.

BASIC PATTERNS OF COURTSHIP AND COPULATORY BEHAVIOR

In addition to the overall patterns of behavior that distinguish the 3 distinct types of courtship that we have described (above and FIG. 2a, b, c), there are simple behavior units that are shared by species with distinct types of courtship patterns, and even some units that are restricted to subgroups within the 3 major divisions of species. For instance, *tarsal rubbing* extends as an absolutely characteristic behavior from some species of group A, through group B species to the majority of group C species. Female acceptance postures involving a head-down hanging attitude are found both in group B and in all group C species. We here first summarize commonalities of behavior *within* the 3 major groups and then *between* the major groups.

Group A courtship and copulation

The males of all species within this group show the common courtship behavior of approaching the female at the hub (or its equivalent) and performing a walkabout there for a variable period of time. Most species of *Nephila* (and probably all of them) and some species of *Argiope* exhibit the *suitor phenomenon,* in which males accumulate on the webs of immature females and establish themselves there, awaiting the maturation of the web owner. Spiders of the subfamily Nephilinae share a common element of male courtship behavior, that of juddering. Juddering involves the male making rapid to-and-fro movements on the hub silk without removing the tarsi from the web. Such movements are also characteristically made when the male has placed one or more anterior legs in contact with the dorsal abdominal surface of the female from behind (see FIG. 8). Although juddering occurs in the behavior of other males from other genera, this contact juddering is probably a diagnostic element of nephilinid courtship. Also central in the courtship repertory of *Nephila, Herennia* and *Nephilengys* is the repeated contact between the pedipalp(s) (with reflexed embolus) and the region of the epigyne. This pre-insertion movement of the male organs against the epigyne region is one that involves movement within the segmented portion of the pedipalp (intrinsic movement) rather than a movement of the pedipalp that results entirely from movements in space of the body to which it is attached. In general the movements that group A *Argiope* species make against the region of the epigyne are made largely as a consequence of body movements. Thus, although their function may be similar (see below), the mechanism is distinct. With the exception of *Nephila maculata,* none of the nephilinid species that we studied has complex courtship behavior occurring prior to the approach to the epigyne. This contrasts markedly with the typical situation for those species of *Argiope* with type A courtship. TRing is completely absent from the courtship repertory of the entire nephilinid group.

The behaviors of females during courtship are simple in all the *Nephila* species that we have seen; there is no acceptance posture in any of them [despite Hingston (1923: 74), who describes an acceptance posture for *N. maculata*]. However, both *Herennia ornatissima* and *Nephilengys cruentata* adopt access postures that permit the males to approach the epigyne region; with both these species the fact that the female occupies a specialized structure on the web, rather than an open web, clearly necessitates such a posture.

The *Argiope* species with type A courtship all have a quite complex walkabout phase in their courtship repertories. This stage involves a variety of subsidiary behavior units, and TRing makes its appearance at this level. The courtship of *Argiope aemula* is the most complex of all the *Argiope* species with this type of system and has obvious parallels with that of *Nephila maculata,* thereby constituting a case of convergence since the 2 species are not closely related. Contact courtship also reaches its most complex forms with this group of *Argiope* species where TRing occurs directly against the legs and body of the female and elaborate movements are made against the ventral surface of the abdomen and the epigyne region. Fundamentally similar behavior units are found throughout this diverse assemblage of species.

The behavior of the females of some of these *Argiope* species is quite complex and acceptance postures, made at the hub of open webs, become consistent and formalized. Those of *Argiope aemula, A. aurantia* and *A. reinwardti* involve an increase in accessibility of the female's ventral abdomen to the courting male. There are also quite well-defined rejection movements in these species. Opportunistic mating is confined entirely to group A species.

In summary, there is an increase in general courtship complexity of male behavior from the *Nephila* species to the *Argiope* species, and *Argiope* species have one behavior in particular that is present over a wide range of araneid species; this is tarsal rubbing. It appears in 2 contexts, that of the walkabout and that of contact with the female. From the evolutionary viewpoint, descent of the male onto the body of the female via her dragline (seen at its maximum development in the *Argiope* species, particularly *A. argentata*) or off the web on a male dragline (some *Nephila* species, see above) could represent steps towards vibratory courtship on a mating thread. This matter is discussed in more detail below.

Copulatory postures in nephilinids are simple venter-to-venter, anterior-to-anterior stances in which the male stands erect on the female's abdomen. Several insertions involving several dilations of the haematodocha may be made without the male leaving this posture. Since Gerhardt (1933b) regards this aspect of male behavior to be of crucial evolutionary importance and there are certain semantic problems involved in defining *a* copulation, it is important to define the terms used herein. Throughout this paper we have defined the term copulation to refer to the activity of the male that occurs following insertion and continues until the pair separate. This presents no problems in the vast majority of cases in which the male inserts the embolus of one pedipalp and separates from the female when he withdraws this, renewing courtship before he inserts the 2nd pedipalp. However, in the nephilinids and also in the case of *Mecynogea lemniscata,* the male may make several insertions while in a copulatory stance or posture before separating from the female. In addition, the same male may then approach the epigyne region several more times and indulge in several sessions of multiple insertions, each terminated by movement off the female or movement away from the region of the epigyne. It is less confusing to refer to these grouped multiple insertions as copulatory bouts; by implication this means that they consist of a number of separate copulations. Since we saw haematodochal pulsations in only a small number of cases, we do not know that an insertion necessarily involved sperm transfer, so this usage is arbitrary. The position of males of *Nephila pilipes* during copulation is distinct and almost certainly precludes the possibility of multiple insertions. The *Argiope* species of group A are separable into those that turn sideways immediately after insertion and those that remain in a parallel posture. Unfortunately we have insufficient data on the 2 species that we observed to have a parallel posture to state categorically that this does not involve multiple insertions, but we think that only one insertion takes place before the pair separate and courtship intervenes between copulations. As far as we know, the 90° twist after insertion is confined to males of the genus *Argiope* and *Micrathena schreibersi.*

All the species that exhibit type A courtship have a distinct sexual dimorphism in size and all the species for which the life histories are known also have intrasexual size polymorphism.

Postcopulatory separation very rarely (almost never) leads to attacks on the male in nephilinids. On the other hand, an attempted attack almost always occurs when *Argiope* separate, in species of both group A and group B.

Group B courtship and copulation

All the species so far discovered with type B courtship belong to the genus *Argiope.* The extent and complexity of contact courtship and walkabout activities that precedes the construction of a mating thread varies considerably within the species that we have studied. (Our study of the literature suggests that this form of araneid courtship has not previously been described, but we could certainly have missed a description in the widely scattered literature.)

In terms of the duration, complexity, and our subjective evaluation of the importance of the walkabout/contact courtship phase, we would place *Argiope ocyaloides* at the top end of the scale and *A. savignyi, A. flavipalpis* and *A. cuspidata* at the bottom end. The latter species all have a perfunctory walkabout/contact phase of courtship. TRing occurred either at the walkabout/contact phase or the vibratory courtship phase of all the species belonging to this group. We did not see it occur in the walkabout/contact phase of the courtship of *Argiope* Wau no. 5, *A. savignyi* or *A. flavipalpis,* but cannot be certain that it does not occur rarely in these species. *Argiope ocyaloides* is outstanding among the species of this group for the relatively large size of the male.

Contact courtship in these species greatly resembles that found in the *Argiope* species with type A courtship (except, of course, that no species had anything like the binding behavior found in *A. aemula*). TRing was a conspicuous feature of the contact courtship of 6 of the 11 species. The *Argiope* species from Singapore had the characteristic of 4-legged TRing as the usual form of this behavior. Four species that had perfunctory contact courtship also had an abbreviated walkabout phase. Two of these 4 species (those from South Africa) are represented by very small samples, but the others certainly must be representative. Courtship on the mating thread was frequently interrupted by the recurrence of contact courtship in 9 out of the 11 species, and such recurrences followed unsuccessful vibratory courtship in all species. Vibratory courtship conducted on the mating thread was the least complicated in *Argiope ocyaloides.* In all the other species it included TRing, bobbing, bouncing and drumming with legs III. All the major elements of the vibratory courtship of species with group C mating, with the exception of high-intensity jerking or twanging/plucking, were present in the courtship repertories of these species. The exception is particularly important in the mechanical interpretation of courtship behaviors. The very proximity of the male's mating thread to the female in group B courtship, in which the insertion is always on the hub silk, must mean that the vibratory signals are little attenuated by intervening structures. In short, the male may have no need for a high-power signal (see below).

During courtship we rarely saw the female make any responses to the male that could be identified as units of predatory behavior. In fact, the only such unit was plucking and we never saw this followed by a predatory excursion. Bouncing frequently occurred prior to the female turning to move onto the mating thread. This bouncing was a low-amplitude form of the pumping movement that all *Argiope* species make in a context suggestive of an antipredator function (see Robinson & Robinson 1970b, Tolbert 1975). The acceptance posture of all these species was assumed on the mating thread in the typical araneid manner that characterizes almost all the species described in the group C section. The only deviation from a classic posture was that the female, confined to a relatively small hole containing a relatively short mating thread, sometimes placed her legs IV so that they gripped the hub silk rather than the mating thread itself. The positioning of the 3rd legs determines the spatial proximity of the inflexion in the mating thread to the epigyne region, as illustrated in FIG. 26. This factor seems to be as important in ensuring successful insertions to spiders of group B as it is to spiders of group C. The major, and perhaps in terms of survival value, most important difference between the options available to males approaching females in this acceptance posture and males approaching group A females is that of aborting the approach by instantaneous escape-jumping. Males repeatedly do this in all the species of this group that we studied.

Copulation in these species is of short duration, involves only one pedipalp for each occasion and only one insertion for each pairing. A postcopulatory attack by the female is normal. After one insertion, males court again if they have successfully survived the 1st insertion. All the males turned through 90° after insertion, to assume the tightly apposed transverse copulatory posture of most *Argiope* species males. An exception to this was *A. ocyaloides* in which some turning occurred, but the amount was slight (vestigial?). In most cases the copulation was terminated by a female brush-off and males were regularly attacked by females at this stage. We noted that the intention movement of wrapping attack was made by the female at the moment of insertion, but attack behavior was usually suppressed. The female's legs III were consistently placed over the copulating male at the start of copulation. Males of several of the group B *Argiope* species died in copula.

Group C courtship and copulation

All the species that we studied that are classified in this group have more features of courtship and copulation in common than any of them have with spiders of the other groups, but it would be possible to separate them into subgroups on the basis of consistent differences of detail. However, these subgroups would not necessarily be natural ones in all cases. The separation of the *Gasteracantha*/*Isoxya* species from the *Micrathena* species can be made on the basis of copulatory behavior. It also separates these species from all the others in group C, and could be natural (see below). Separating *Cyrtophora nympha* and *Mecynogea lemniscata* from all the other species because of the location of their mating thread creates a quite artificial group (in our opinion), as would a grouping of species that convert a radius into a mating thread (*Micrathena sexspinosa* and *Mangora bimaculata*).

None of the males of the species preface vibratory courtship with contact courtship and none of them invade the female's web to conduct extensive walkabouts at the hub prior to vibratory courtship (although males of *Mecynogea lemniscata* have a courtship phase that resembles this behavior of group A and B males). None of the males cut a hole in the female's web from the hub outwards (although the males of *Micrathena sexspinosa* and *Mangora bimaculata* do remove extensive amounts of female web structure, they do so from the outside inwards). All the species conduct complex multicomponent vibratory courtship on a mating thread, on which (with the exception of *Mecynogea lemniscata*) copulation is initiated. TRing occurs definitely in 16 of 30 species and is certainly absent in only 3 species. Six of the species for which we cannot be certain whether the behavior is present or absent have males so small that interpretation of TRing-like movements is difficult. A large proportion of the males have behaviors in their courtship repertories that produce massive deformations of the mating thread and transmit powerful vibrations to the female's web. Where we were able to analyze the mechanisms underlying these powerful behaviors, we found a considerable variety of component behaviors. Drumming on the mating thread with legs III, first seen in the courtship repertory of group B males, occurred in the repertory of all group C males without exception. Our hypostatization of vibratory courtship in these species into 2 phases, long-distance and short-distance courtship, is based on a simple operational procedure. However, the vibratory components of short-distance courtship do not differ from those of long-distance courtship as far as we were able to detect. (When it becomes possible to measure the nature of the vibrations that are actually detected by the female, we suspect that differences will be found.)

In terms of short-distance contact courtship, this has an interesting distribution that more or less follows our general ideas about subgroups within group C. Thus, while contact courtship is quite well developed in the species of *Gea, Cyclosa, Zilla, Eriophora* and *Mecynogea* that we studied, it is rudimentary or absent in *Gasteracantha/Isoxya* and *Cyrtophora nympha.* The *Micrathena* species have a variable amount of contact courtship, but it seems to be important in *M. sagittata* at least.

Females respond to male movements during the attachment of the mating thread, and long-distance courtship, by plucking and frequently by making rapid excursions towards them that had all the characteristics of predatory excursions. All the species made plucking movements and the majority made excursions towards courting males. These were particularly common in the case of *Isoxya tabulata, Mecynogea lemniscata* and *Eriophora fuliginea.* In some species, lunges at the male even occurred after the female had moved onto the mating thread. We saw this behavior most frequently in some *Cyclosa* species, particularly the *Cyclosa* sp. alpine grassland no. 1 from the Wau Valley.

Acceptance postures in group C species were broadly similar over the entire range of the species studied. The female hung below the mating thread suspended from legs IV and III. In the case of *Micrathena sexspinosa* and *M. sagittata,* the females assumed acceptance postures that were more nearly parallel to the mating thread than to the normal hanging posture. The acceptance posture of *Mecynogea lemniscata* differed from that of all other species in that it was assumed on the hub of the web rather than on the mating thread; thus the 3rd legs that are looped to grip a single thread in the normal araneid acceptance posture are spread wide to grip the web in this species.

Male insertion attempts in group C species fall into at least 3 categories: 1, insertion without scrabbling movements at the epigyne and without a rapid swing or lunge (*Gasteracantha* sp.); 2, insertion after a period of body movements made in contact with the female, during which the pedipalps rub on or scrabble at the epigyne region but in which there is no rapid swing or lunge (*Gea, Zilla, Cyclosa* sp.); and 3, a sudden forwards lunge in which the embolus is driven rapidly into the epigyne. Gerhardt (1933b: 69) refers to this last behavior as "Die insertion im Sprung" and states that it occurs in the genus *Cyclosa* (and *Zilla*) and in a modified form in the genus *Cyrtophora.* Unless we have completely misunderstood Gerhardt's (ibid.) usage we must say that none of our *Cyclosa* species jumped or leaped into copula, although they all separated from copulation with a striking, rapid, rearwards movement (see above). The insertion attempts of *Zilla* species are almost indistinguishable from those of *Cyclosa* on our movie sequences. We would place *Cyrtophora* between types 1 and 2 above.

Mecynogea lemniscata belongs in an entirely separate category in that the male assumes a posture standing on the female, from which he makes multiple insertion attempts (and insertions). If we classified this species on the basis of insertion behavior, it would be placed somewhere close to *Nephila/Herennia* (where it clearly does not belong on other grounds).

In terms of copulatory postures, all the species in this group exhibit typical venter-to-venter, anterior-to-anterior, copulatory postures except for the *Micrathena* species and the *Gasteracantha* species. The *Gasteracantha* species stand more or less at right angles to the female's abdomen, against the genital tubercle, while the closely related *Isoxya* species have a simple parallel posture. The *Gasteracantha* posture is clearly a deviation from the characteristic araneid posture that is imposed by the presence of the tubercle; the 2 sexes are venter to venter, anterior to anterior, but not with their long axes parallel.

The 3 species of *Micrathena* that we saw copulate were strikingly different from the other species in this group. *Micrathena schreibersi* parallels most *Argiope* species in copulating with its long axis at right angles to that of the female; the male indulges in a post-insertion twist. Males of this species, in contrast to *Argiope* males, are slim-bodied and long. They actually curl around the body of the female so that the apex of the in copula male's abdomen is level with the dorsal surface of the female's body. The other 2 *Micrathena* species are characterized by copulatory postures in which the dorsal surface of the male body is close to the ventral surface of the female and the male faces the female's posterior. This could be a consequence of a modified acceptance posture on the part of the female, or result from the low elasticity of the mating thread, or both (see FIG. 69). Copulation in all group C species, except *Mecynogea lemniscata,* is brief and almost certainly involves but one pedipalp per copulatory bout, with intervening courtship before the other pedipalp is inserted.

Separation after copulation is male-initiated in nearly all these species, and usually accompanied by the male's rapid leap off the body of the female or a leap apart. In the *Gasteracantha* and *Isoxya* species the male resumes courtship and has to bring the female to the mating thread again to achieve further copulations. Postcopulatory attacks are most unusual in these species, whereas they are quite common in *Micrathena* species where separation may be female-initiated (it is noteworthy that *Micrathena* species attack-bite prey but wrap males without biting or at least without injecting venom). The postcopulatory separation by leaping apart seems to be a highly specialized behavior in *Cyclosa, Zilla* and *Eriophora* (see, for instance, FIG. 88 C–E). Postcopulatory attacks in these species are quite rare (as a consequence?). Since these species separate explosively, the male passes away from the female and usually has to spend some time in resuming a courtship location. Further courtship has to take place to bring the female out into another acceptance position before another copulation can occur.

ORIGINS OF THE BEHAVIORAL UNITS INVOLVED IN COURTSHIP

It is arguable that one of the major contributions of ethologists to the biological study of animal behavior lies in their approach to the origins of signal behaviors or displays. This is an enormous, diverse and contentious field of study that we cannot review in detail here. However, the essence of the approach (that has been particularly successful in studies of threat and courtship behavior) has been to consider how behaviors that might be appropriate to systems other than those being studied could come to be modified to subserve new functions within the system under study. This approach has been enlivened by a recognition that an animal can in many situations have conflicting tendencies to behave in incompatible ways and that in these situations a variety of inappropriate, irrelevant or out of context behaviors can occur. Such behaviors can, it is argued, acquire signal function in the new context and, being subject to selection in the new situation, become specialized (or ritualized) with their new function greatly enhanced. An application of this viewpoint to the courtship situation is summarized by Hinde (1970: 393–95) in the following way:

"The threat and courtship postures of fishes and birds can be understood in terms of conflicting tendencies to behave in incompatible ways. Characteristically, threat involves tendencies to attack and to flee, while courtship involves tendencies to attack, to flee from, and to behave sexually towards a mate. *In many species, however, other tendencies are involved.* [our emphasis]

"Evidence that threat and courtship postures occur when there are conflicting tendencies comes from study of the situations in which they occur, the behaviour which accompanies the display, the behaviour which occurs before or after the display and from components of the display."

Broad reviews of the origins of courtship displays are given by Bastock (1967) and Morris (1970), while Eibl-Eiblesfeldt (1970: 91–148) gives an admirable general treatment of the origins and classification of displays. A more recent and less conventional treatment is that of W. J. Smith (1977: 312–88). N. G. Smith (1974: 689) states the general ethological viewpoint that goes beyond, but includes, the conflict origin of displays as follows: "New displays, on the other hand, generally arise by ritualization of previously existing behaviours or functions; that is, when a selective advantage accrues to those individuals who, to convey information, use certain behaviours or functions in a manner that is either partly or totally different from their original purpose."

This point of view has been applied to the courtship of invertebrates in the beautiful comparative studies by Crane of salticid spiders (1949b) and fiddler crabs (e.g., 1957). One of the problems about applying the approach to araneid spiders is that, as highly visual animals, we can have little conception of the perceptions of animals that must be principally dependent on tactile, chemotactic and vibroreceptive sense organs. However, we can apply our general knowledge of the behavior of araneids and, in particular, our broad knowledge of their predatory behavior to approach the question of the origins of courtship behavior. At present we must rely on an intuitive assessment of the types of evidence that Hinde (quoted above) regards as legitimate sources for the interpretation of the origins of display. Later, in-depth studies should allow at least some of our interpretations to be tested in a quantitative manner.

A priori one might predict that the major source of conflicts in the araneid courtship situation would be between sexually motivated approach tendencies and tendencies to flee, in the case of males, and between predatory tendencies and sexual tendencies in the case of females. Additional sources of behaviors that could become involved in courtship would be maintenance behaviors such as grooming, responses to climatic factors, and feeding. Behaviors that are normally associated with movement and direction finding (spatial orientation) on structures of silk could also be expected to be sources for conversion into courtship displays.

As well as considering the source of behavior units, we should consider the new functions for which they become transduced or translated. We feel that to make a simultaneous attempt to consider source and function would be much too confusing and, therefore, consider function separately in the next section.

Male behaviors

The bouncing on the spot and juddering movements that occur in the approach and courtship behavior of males of groups A and B look like inhibited locomotion. They certainly occur in contexts where approach/withdrawal conflicts are predictable. Juddering in particular, as seen in the nephilinids, frequently occurs when the male is partly in contact with the female and is often followed by actual movement off the web onto the body of the female. The to-and-fro nature of the movement conveys an impression of locomotory hesitancy (Smith 1977: 107) and conflict.

The walkabout behavior of male araneids at the hub in fact involves many alternations of approach towards the female and then movement away from her. It could involve alternating attraction and aversion and be based on a conflict movement.

Silk deposition on the hub, which is so conspicuous an aspect of the walkabout behavior of *Argiope* species (of groups A and B), is perhaps an intensified version of dragline production that accompanies all spider locomotion. Abdomen wagging may be an associated behavior; it resembles the movement that spiders make as they dab their spinnerets against the substrate to attach the dragline during locomotion but is made in vacuo, i.e., the spinnerets do not contact the web surface. (Note, however, that in some forms of juddering the abdominal apex does touch the substrate; see FIG. 8). In a conflict situation, silk attachment would be a component of escape behavior and could conceivably become ritualized in an abbreviated form.

Tarsal rubbing is one of the most widespread and characteristic behaviors of male araneids. It occurs as a component of the walkabout and contact courtship of *Argiope* species in group A and occurs at that phase of courtship and of vibratory courtship in *Argiope* species of group B. In group C, it is a component of long-distance courtship in a wide variety of species. We can think of 2 possible origins for this behavior. The 1st, which we think most probable, is that it arose from grooming movements. The behavior looks like a formalized version of the extensive grooming that all spiders perform, from time to time, on their legs and particularly on the distal sections where the chemoreceptors are concentrated. One condition for the translation of a grooming movement into a courtship element would be that it was likely to occur frequently in the context of primitive courtship. Our guesses at why this could be the case are based upon our conception of the direction of change in the evolution of araneid courtship systems and on further guesses about the chemotactic situation confronting the courting male. If approach to the hub of the web is primitive and if the female is producing powerful chemotactic or olfactory signals, then the male at the hub might well be constantly stimulated to groom the appropriate sense organs, particularly those that he used to "touch-taste" the female. If such a movement then acquired a signal function (see below), it is easy to see how it could become an increasingly important component of courtship behavior. Apart from the fact that we are nearly totally ignorant about the chemical environment that obtains at the hub of the web (or elsewhere), the theory has another drawback. Normal grooming of the legs is usually of 2 kinds: they are rubbed against each other as in TRing, but also they are usually drawn through the chelicerae one at a time (and washed?). We have only rarely seen the latter happen during courtship. (A prediction emerges from the hypothesis that is not at first evident. Since *Nephila* species do not TR nor groom they should lack a major chemical component of close-quarters sexual contact.)

After writing this section we found the following passage in Savory (1928: 215): "Two curious actions are often exhibited by spiders during their courtship. One is a sharp twitching of the abdomen, which is sometimes violent enough to cause a distinct tapping sound as the ground is struck . . . . The other is more difficult to understand. The spider stops its courting actions and rapidly rubs its legs together. On at least one occasion a female spider has also been seen to do this." It may be due to intense stimulation or, since the legs contain sense organs, Savory (ibid.) suggests that it "may have the effect of sharpening the senses and be the equivalent of blowing one's nose or taking off one's gloves." We take this to be a reference to what we call abdomen wagging and tarsal rubbing. If these movements occur in the courtship behavior of spiders from other families, it seems reasonable to assume that they are derived from really basic elements of spider behavior. The derivation of AWing from dragline behavior and TRing from grooming would certainly fit this hypothesis. We certainly could not better Savory's superb analogy.

The other behavior to which TRing has a superficial resemblance is that involved in gathering in silk lines that have been extruded to form bridge threads from place to place. These are hauled in by movements of legs I and II. Admittedly such movements are rarely unilateral and do not involve the rubbing of one tarsal surface over another, but they need only that further development to make them into a TR. If we read the evolutionary direction of change in reverse of our opinion, making group C courtship primitive, it is possible to think that silk-hauling movements associated with constructing and tightening a mating thread could have become ritualized with a signal function. Certainly the context is right.

The behavior of bouncing on the mating thread could be derived from the pumping movements made by most araneids as a response to intruders on the web and in other defensive contexts.

Hole cutting in type B courtship systems has analogies with the behaviors used in web management and predation where large sections of web may be collapsed by cutting radii (either in response to particularly large prey or heavy rain).

The origin of the mating thread, assuming that this is not the original condition of araneid courtship, is a particularly difficult evolutionary step to explain. We think that there are 2 suggestive clues. One is that males of some group A *Argiope* species spend part of their courtship time standing on the female's dragline (attachment to the hub), where they may conduct both contact courtship and also make a variety of movements that would transmit vibrations directly to the female. They also attach their own draglines to the female dragline. It is conceivable that the first functional mating thread could have been a compound structure consisting of male- and female-

FIG. 92. *Argiope argentata* anomalous courtship on single thread beneath the hub (see text); ♀ in acceptance posture, ♂ in copula being pushed forwards by ♀ legs III.

derived dragline elements constructed on the undersurface of the hub and spanning below a sloping section of hub silk. On such a thread, the female could have adopted a stance that placed her clear of the hub silk in an access posture. [We report one anomalous courtship of *A. argentata* conducted on a mating thread that was thus oriented (see FIG. 92).] On the other hand, a mating thread built on the outside of the web frame (as in most instances of type C courtship) would require no behaviors that are not part of normal web construction. The movements that are used to install a radius during the construction of an orb web are exactly similar to those involved in the construction of a mating thread outside the web; they differ only in their location.

In assessing the sources of male courtship behaviors, it is important to remember that male araneids construct and operate normal orb webs until they mature. They therefore have a complete repertory of web-building and predatory behavior.

Female behaviors

Plucking at the hub and web shaking are units in the predatory/defensive behavior of most araneids. Their use by the female in response to male movements, around the web and in courtship, are probably in their original context and they may have no signal function in courtship (see later). Similarly movement of the female along a radius may be a relatively unmodified part of predatory behavior that normally has the last stage (actual attack) suppressed. This interpretation could apply to movement along a small mating thread at the hub in group B courtship. Acceptance and access postures qualify as pure courtship behavior on the part of the female. Their derivation is difficult to determine. The acceptance posture found in all group B species, and with slight modification in all group C species, has the female hanging from a single thread supported on the looped legs IV and III. No posture assumed during predatory activities has analogies with this posture. In wrapping attacks, when the spider may hang below the web plane, the posture is essentially reversed; the spider hangs from legs I and II, using legs III to manipulate the prey while legs IV cast silk onto it. During feeding at the hub (or retreat), the spider may hang away from the web supported by legs IV, while it manipulates the prey with legs III. Only the thermoregulatory posture assumed when sunlight strikes the spider through the web has elements of the acceptance posture (Robinson & Robinson 1974b, 1978b). In this posture the spider hangs from the hub silk supported by legs IV and III, while the anterior legs hang free. The access posture of *Argiope aurantia* (FIG. 28) is exactly similar. A derivation of an acceptance posture from a thermoregulatory stance would be difficult to visualize.

THE SIGNAL FUNCTION OF COURTSHIP BEHAVIORS

We deal with the possible overall functions of courtship in the next major section. Here we examine the possible functions of the units of courtship behavior in terms of their immediate effect on the web, or mating thread or sense organs of the recipient. At this stage of research this section is largely speculative. We hope it is justified as a stimulant to further research.

Bouncing and juddering movements made during the approach and the walkabout at the hub transmit low-amplitude regular vibrations to the web. These may, because of their regularity, be distinct from the vibrations produced by struggling prey. This could also be a feature of the bouncing gait that is characteristic of some approach and walkabout locomotion. Since locomotion on the web constantly changes its location vis-à-vis the female, it could have been selected to be readily distinguishable from the struggles of a prey item that would emanate from a more or less constant direction.

TRing as part of the walkabout phase must produce vibrations that are transmitted to the hub silk through the legs that are on the web. It is also possible that TRing produces airborne vibrations—it looks like a stridulatory movement. TRing against the body of the female during contact courtship could provide both direct tactile stimulation and synchronous (or simultaneous) vibratory input. Even when, as described above, the male touches the female with one set of anterior legs and TRs with the others, the movements of the TRing legs could be transmitted, in a modified form, through the male's body to the contacting legs. TRing and touching could thus not only be stimulatory in at least 2 modes, but could also represent a chemotactic "tasting" of the female. Such a function is, for instance, hypothesized for the tapping of the female by the male that occurs in the courtship of *Drosophila melanogaster* (see review in Bastock 1967: 53–57). TRing as part of the long-distance courtship of group C species and the vibratory mating-thread courtship of group B species must function exclusively as a vibration-producing device, unless long-distance stridulation is involved. On mechanical grounds it would seem, a priori, to be a less efficient vibration producer than direct manipulation of the thread; this argues for it having evolved in a different context (see below).

Bouncing and bobbing movements seem to be exclusively vibration-producing in function. The variety of high-intensity bouncing movements that we have variously called tugging, twanging, jerking, and high-intensity bouncing seem by their "morphology" to be devices that produce vibrations capable of being transmitted along long mating threads and then across webs to produce powerful signals at the hub. Interestingly, they are highly developed in groups where the males are small and mating threads are long, as well as in some species that have large males and large webs.

The variety of tapping and scrabbling movements that occur in short-distance courtship, as well as the rapping and scrabbling movements that are involved in insertion attempts, clearly have a tactile function but could, conceivably, transfer chemical substances from males to females or vice versa, as could the contact movements of group A courtship. (Pheromonal involvement at this stage of araneid courtship has, to our knowledge, never been suggested, but it is a theoretical possibility.)

The variety of female responses made from the hub of the web could be read by the male as signals indicating the state of the female, whether or not they have become specialized for this purpose (which we are inclined to doubt). This applies to web shaking, plucking and strumming. It also applies to the excursion to the mating thread, where we have good inferential evidence that the male can interpret the speed and vigor of the approach and react accordingly (by continuing to court, making a treadmill, or jumping off the mating thread). This piece of behavior seems to be one of the points in the courtship sequence that is most susceptible to experimentation and investigative manipulation.

The form of the female acceptance posture and the state of the epigyne may also have signal function. If the female is not gripping the mating thread correctly, she is not oriented to receive an insertion, and this could indicate that further stimulation is necessary before the male can effect a copulation. Touching, tapping and insertion attempts may effectively monitor the information contained in the form of the acceptance posture. Information about the state of copulatory readiness may also, in some species at least, be reflected in the state of the epigyne. This could certainly be detected during precopulatory contacts.

In the descriptive section we have detailed a number of behaviors that can effectively block insertion attempts in group A courtship. These presumably have or acquire a signal function.

THE FUNCTION OF COURTSHIP

In our description of courtship in *Nephila maculata* (Robinson & Robinson 1973: 36–44), we reviewed some theories of the function of courtship in animals in general and spiders in particular. We concluded that the function of courtship in spiders had been the "subject of considerable controversy, some of which involved hair-splitting quibbles about terminology." We still think that this is a reasonable assessment. The functions ascribed to spider courtship by Bristowe & Locket (1926) were: (1) the suppression of predatory behavior in the female by a process of male recognition, and (2) the stimulation of the female to the point of accepting copulatory attempts. Savory (1928) challenged this hypothesis on the grounds that recognition of the male results from stimulation of the female and it is not, therefore, necessary to postulate a separate functional entity. The whole argument, like so many arguments in animal behavior theory, is due to definition problems and not due to any fundamental difference of approach; both parties recognize that the predatory behavior of the female towards the male is blocked during courtship. The view that the male must somehow establish his identity as nonprey can be traced back at least as far as Montgomery (1903: 145): "that male is most quickly accepted by the female who most quickly and surely announces himself, *by his rhythmic movements,* to be a male" (our italics). Crane (1949b: 203–04) reviews theories of the function of spider courtship with her customary lucidity and concludes from her studies of salticids that "courtship serves to bring to mutual attention and proximity two individuals of the same species, opposite sex and requisite physiological condition; simultaneously it inhibits their usual predator and self-protection behaviour while stimulating each sex so that copulation may take place." (This definition is more precise and careful than anything that the earlier workers said but it means essentially the same thing.) Crane (ibid.: 204), adds a list of secondary functions of courtship that brings in a number of new functional categories. Thus: "courtship display acts as an effective isolating mechanism between similar and well-evolved species" and "sexual selection operates in the sense that males of chronically mediocre drive . . . do not use sufficient energy and persistence to win acceptance by females."

It is worth relating these spider-based theories of courtship function to more general theories to see if the araneologists have missed anything that was seen by less specialized researchers. Morris (1956), generalizing from his studies of courtship in vertebrates (mainly fishes and birds), suggests 4 functions: finding a mate, finding a mate of the right species, stimulating the male and synchronizing reproductive arousal. N. G. Smith (1974: 681) emphasizes the function of courtship in reducing aggression between partners: "Courtship behaviour has many advantages and functions, not the least of which is the reduction of hostility between potential sex partners." The influence of the ornithological bias is particularly evident in W. J. Smith's definition of the function of courtship (1977: 430): "What ethologists have usually called courtship has two main functions. First it facilitates mutual awareness and recognition of two individuals of opposite sex, sometimes after a preliminary searching or advertising phase that brings them together. Second, it enables the paired individuals to cooperate to fertilize the female's eggs."

Synthesizing these variously expressed views on the functions of courtship and applying them to the araneid case, we think that as an analytical convenience the following functions can be considered separately: 1, reduction of predatory or other inimical tendencies; 2, mutual arousal to a state of reproductive readiness; and 3, elimination of interspecific mating.

1. Reduction of predatory or other inimical tendencies

This function of courtship could be achieved at 2 possible levels. One could be regarded as the tactical level of the particular behavior unit while the other is the strategic level of the basic organization of courtship activities. It could be argued that having extremely small males relative to the females is a strategy for reducing the predatory tendencies of the female, since these males would not be so stimulating as potential prey items as would larger males that were closer to the optimum prey size (if there is such a thing). Similarly, placing the action of courtship and mating on a male-derived structure located outside the female's insect trap (web) could also be an evolutionary strategy that functioned to reduce the predatory drive of the female. On the other hand, a movement that was made during courtship that was maximally distinct from the movements of prey organisms could be regarded as a tactical solution to the problem of predatory behavior suppression.

Considering the tactical means of suppressing predatory behavior first, we are still faced with the possibility that this is achieved in a complex way. The male's behavior could minimally stimulate predatory tendencies and simultaneously stimulate sexual tendencies, whose arousal could act to block predatory tendencies. There is a further possibility. The male's courtship could contain specific signals that are keyed to the female in such a way that their detection by her, blocks predatory drives and permits sexual arousal to occur. This may seem to be a hypothesis that is indistinguishable from the preceding one. It is in fact a suggestion that the male signals do not merely provide the negative labelling "nonprey" but rather the positive label "potential sexual partner." This idea accords with Bristowe & Locket's (1926) idea of a male-recognition function for courtship activities. Distinguishing operationally between these alternatives would be very difficult indeed. At present we would guess that a male-recognition signal might have to be more finely tuned than a signal that had the message "nonprey." (A signal "potential sexual partner" could also contain a species identification element; it might thus be finely tuned for this reason too.) Both these hypotheses take us into the highly controversial field of drive theory, motivational states, and explanations of the causation of behavior that depend on models of internal states of organisms. Although this is to some extent inevitable, we have tried to avoid it. We do this by examining the ways in which courtship behavior may simply reduce the risks of predatory behavior occurring.

We have already suggested that the movements involved in approach and courtship may, by their regularity or rhythmicity, be unlike the vibrations produced by prey organisms. [Although there have been studies of the sensitivity of the vibration receptors of araneids, for instance, those of Frings & Frings (1966) and Walcott (1969), we do not know what vibrations spiders actually attend to. The literature is full of examples of animals not responding to, or apparently not utilizing, sensory information for which they have a proven sensory capacity.] In addition to the possibility that the vibrations of courtship lie outside the range of those that release predatory tendencies, or at least are suboptimal in that context, it is also possible that courtship activities function to produce *habituation* of predatory responses. Habituation is defined (e.g., Thorpe 1963) as "the relatively persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement." The conditions for the habituation of a predatory response would occur if reaction to a given stimulus (a pattern of vibration) were not followed by reinforcement in terms of contact with a potential prey. Spiders in fact can habituate to vibrations (Peckham & Peckham 1887, Bays 1962). The situation with group A courtship could provide nearly ideal conditions for habituation, particularly in those species that exhibit the "suitor phenomenon." When males live on the hub of the web for long periods of time and are intermittently active, it is not inconceivable that the female habituates to their presence. (Obviously if the initial stimulation was suboptimal, habituation would be accelerated.) Even the species of groups A and B that do not live on the web for weeks prior to courtship could provide a situation leading to habituation. In practice it would be extremely difficult to distinguish between the effects of habituation and sexual arousal that could both result in the reduction of predatory responses to moving males. The species that exhibit the suitor phenomenon would be good subjects for research, since males move onto the webs of subadult females for whom sexual arousal can (perhaps) be ruled out. Indeed, these species could be invaluable subjects for a study of the mechanisms for reducing or suppressing predatory drives.

Group C species also provide conditions that could lead to habituation. Courtship on the mating thread could repeatedly evoke unsuccessful predatory tendencies until the female becomes habituated to the presence of the male. From our observations we would conclude that there is little evidence of this. Male activities do result in plucking and web shaking, and even predatory excursions, but not on the scale that would be involved if habituation were occurring (unless the initial stimulation were suboptimal). Moving the insertion of the mating thread from radius to radius could be interpreted as a device to facilitate habituation by adding an element of confusion to the situation.

Our basic assessment of the influence of predatory behavior on the courtship situation is that in no species that we have studied does the female regularly respond to the male with the vigor and intensity that she would apply to a prey item. Even the extremely large males of *Eriophora fuliginea* move about the web frame of the female without eliciting the rapid and efficient attacks that these spiders make on large prey items. Our records of males moving onto the hub of the web of nonconspecific females of group A and B and remaining there with impunity are very suggestive indeed. We think that studies of the behavior of theridiid kleptoparasites and insects such as emesinid bugs (Hemiptera: Reduviidae) might provide some insights into how intruders can move about on orb webs without eliciting attack. On the other hand, the study by Blanke (1974) of the courtship and mating behavior of *Meta segmentata* does show an interaction between predatory and sexual behavior. Our own studies of the treadmill effect on *Isoxya tabulata* show that elements of courtship behavior exist whose function may be to protect the male. Once the female has assumed an acceptance posture on a mating thread, males of many of the species that we have studied have options that minimize the risks that can result from the occurrence of predatory behavior at that stage of courtship. The insertion approaches of *Cyclosa* species, associated as they are with leap-apart escape movement, exemplify a specialized enhancement of the escape options that result from the evolution of the mating thread. There is a possibility that predatory tendencies that are suppressed/not released/habituated at the vibratory stage of courtship could be evoked by contact with the male. The repeated approach/escape movements that the mating thread permits could provide a situation in which the predatory tendencies evoked by contact are reduced or habituated.

There is a tendency to look at courtship in araneids from the standpoint of the effect of male behavior on the female, since the male is so conspicuously the more active participant. However, we have already suggested that the male may be in a conflict situation where tendencies to approach and tendencies to flee are opposed. Males making insertion approaches frequently abort these approaches and make escape movements, even when the female has made no move towards them. Such "false escapes" could serve to exhaust the escape motivation of the male. (In fact, the occurrence of "irrelevant" escapes at any stage of courtship is good evidence of the presence of a strong escape tendency that is acting against the sexual tendency to approach the female. Measuring the strength of this tendency could be accomplished by scoring the number of escape movements that were unprovoked by female behavior. Such irrelevant escape behavior is more easily identified in the courtship of groups B and C, particularly during short-distance courtship and insertion approaches. We have detailed many examples of this, e.g., turning on the mating thread to retreat, jumping off the thread belayed on a dragline, running over the female to the protection of the hub, jumping apart, and so on. (Repeatedly walking onto and then off the body of the female may serve a similar function in species of group A.) Sexual tendencies could also be opposed by tendencies to feed or attack. The binding behavior of males of *Nephila maculata* and *Argiope aemula* could be devices for reducing the predatory tendencies of the males by allowing them to perform units of predatory behavior. We think that this is highly unlikely since not only is the female too large to evoke attack behavior, but the binding behavior is totally unlike prey-wrapping in that it involves single-strand silk and this is attached to the female dragline-fashion rather than cast with legs IV, as it is in prey-wrapping. The fact that males often feed on the female's prey during courtship suggests that feeding tendencies can exist at the same time as sexual tendencies.

Returning to the strategic devices that could function to reduce the effects of predatory tendencies, there are 2 major possibilities that can be reviewed. Extreme sexual dimorphism in size could be an adaptation that functions in part to facilitate courtship of group A and became unneccessary as the mating thread evolved. Small relative size could function both to reduce the risk of the arousal of predatory tendencies and also to make it easier for the male to escape from the female should she attack. The latter function was suggested by Bristowe (1929). Males of *Gasteracantha/Isoxya* species are small and have group C courtship but extreme sexual dimorphism may be multifunctional.

The evolution of the mating thread greatly enhanced the escape options available to the male. It put the female on a single thread of male origin off her web and away from the trapping viscid spiral elements; even the group B mating threads offer most of the escape options available to the producers of group C (fully external) mating threads. These options have been detailed above and need not be repeated here. The essence of the mating thread is that it increases the male's control over the situation.

2. *Mutual arousal to a state of sexual readiness*

This is an aspect of araneid courtship that is rich in its potential for experimental studies. We think that there are a number of measurable (overt) indicators of sexual readiness in the female that could be studied as courtship proceeds if the vital question of standardizing (or controlling for) the initial state of sexual motivation can be solved. In some species the degree to which the epigyne is erected is almost certainly indicative of arousal. [This change was noted by Savory (1928) as a general consequence of courtship; see also Bristowe (1941: 488–89) and Crane (1949a: 204).] We also think that the detailed nature of the female's acceptance posture may reflect her state of arousal. Thus, the critical positioning of the female's 3rd legs on the mating thread, determining the success or failure of the male's insertion approach in some species at least (see FIG. 26), could be a reflection of the degree of arousal. The male certainly responds to incorrect acceptance posture with further courtship. In some species, females in the acceptance posture swing to one side so that their ventral surface is not facing the male; this may be another sign of incomplete arousal. Additionally, we have noted above that females may make incomplete excursions towards a mating thread, or may move onto it but not assume an acceptance posture; these behaviors and others could be used to calibrate arousal.

Male arousal is more difficult to assess and the effect of courtship on males requires much more study. Females in group C species may indulge in contact courtship when males fail to respond to the adoption of acceptance postures by making insertion attempts. Such behaviors could provide a key for assessing male arousal.

We are currently studying the effects of successive courtships by different males of the same female to determine whether there could be a cumulative or facilitating effect that would be reflected in the measurable parameters of courtships and copulations.

3. *Elimination of interspecific mating*

Our results so far are of little value in deciding how courtship could act as a filter to eliminate interspecific mating. We have noted some gross differences between the courtship behaviors of sympatric species of the same genus, but until careful study shows how much of courtship behavior is redundant, we see no way to approach this problem. In particular we think that analysis of the vibratory courtship of araneids must await study not only of the nature of the vibrations induced in the web, but their experimental manipulation to determine which of them are the effective stimuli. This is a major task fraught with technical problems. Although we think it likely that species-filtering may result from courtship behavior, it may be that the ultimate barriers differ from species to species. They could be ecological, phenological, morphological or behavioral.

THE EVOLUTION OF COURTSHIP BEHAVIOR IN ARANEID SPIDERS

We have already given a summary of our view of the direction of evolutionary change in the courtship behavior of orb-web spiders (Robinson & Robinson 1978a). As far as we are aware, this is the first attempt to do this for the araneids. Gerhardt (1933b: 68–71) summarized the results of his extensive studies of 30 species of araneids (see bibliography herein for a full list of his publications) by grouping the species according to a number of criteria, but without stressing the evolutionary implications of his research. As Crane (1949b: 171) pointed out, Gerhardt was most interested in copulation methods and "made few observations on the courtship phases of reproduction." The list of 30 species given by Gerhardt (1933b) includes only 3 from our group A; all the others are group C species. We have no reason to assume that Gerhardt was even aware of the existence of courtship behavior corresponding to our group B courtship that provides a link between groups A and B. Nor does he seem to have been aware of the copulatory posture assumed by most *Argiope* species in which the 90° twist occurs. Gerhardt based his phylogenetic speculations principally on copulatory postures, the number of insertions per copulation, whether or not the copulation "spring or jump" occurred, or the number of swellings of the haematodocha per insertion. He does state that all the genera that he studied produced a mating thread, except *Nephila* and *Argiope,* and that this structure is also produced by the uloborids (1933b: 68–69).

To interpret the results of our courtship and mating studies for an evolutionary scheme we need to use all the clues from other studies of araneid behavior that are available. This is particularly true because there is no generally accepted phylogeny of the araneids based on physical characters; the taxonomists have not committed themselves yet. In an undoubtedly oversimplified straight-line scheme, we place group A courtship as primitive, group C as advanced, and group B as intermediate and annectant. The order could be reversed (see below), and we would not claim that the species in either group A or group C are linearly related.

The reasons for placing group A at the primitive end of the scale are several. These species have the least complex male behaviors and by far the least complex female behaviors. Complexity, in general, is a nonprimitive state. We would place *Nephila/Herennia/Nephilengys* at the primitive end of the scale of predatory behavior (since they lack attack wrapping and this is unlikely to be a secondary condition; see Robinson 1975). Additionally, most treatments of the evolution of orb webs place both the nephilinids and the *Argiope* species as primitive (see Kaston 1964). As argued above, it is logical to consider that TRing and AWing both arose in the context of type A courtship and then became specialized for a signal function that was highly adaptive in the more advanced types of courtship (see above). The theory of the origin of the mating thread from a male dragline attached to the dragline of a resting female, in type A courtship, is one that we find seductive in its simplicity.

If type B and C courtship systems evolved from type A, we should at least be able to provide a tentative explanation for the selective advantages that the change could confer. We have already argued that the change should greatly enhance the male's escape options. This would directly affect his fitness if it could be shown that precopulatory cannibalism would be reduced as a consequence. A reduction of postcopulatory mortality would also affect fitness if males normally copulate more than once (as they undoubtedly can). If at this stage we had to guess, we would say that both pre- and postcopulatory mortality is no higher in group A species than it is in group B and C species. If the evolution of the mating thread allowed males to compete, permitting female choice based on characters reflecting overall fitness, it could be subject to strong positive selection pressure. The situation in *Argiope argentata,* where anomalous type C courtship sometimes allows males on the periphery of the web to lure females away from the hub where other males are already in possession, could be an indication of this possibility. (Why the female should respond to the outside male by moving out and assuming a complex acceptance posture that is not in the repertory of group A courtship is another matter altogether.)

(Competition and female choice is possible in group A courtship, but it is a situation that does not lend itself to simultaneous courtship in which there is a clear separation of the efforts of the competing males. Two simultaneous walkabouts on the same small hub are possible but their spatial separation cannot be very great. Contact courtship could only permit successive comparisons of competing males. In type B and C courtship the mating threads of different males can be oriented so that the female could, theoretically, make her choice between 2 or more simultaneous sets of vibrations from 2 or more separate directions.)

The evolution of courtship on a mating thread could have been influenced by selection pressures not intrinsic to the courtship situation per se, for instance, by ecological or phenological factors. If group A courtship could exist only if accompanied by extreme sexual dimorphism in size, then selection against such a dimorphism would affect the courtship system. We think that extreme sexual dimorphism in size is a condition that can only be sustained in the humid tropics (Robinson & Robinson, in prep.). If males take only a fraction of the time to mature that females need and do not live long as adults, they can only overlap with adult females if the climate permits several generations during each season. This may be impossible in stringent climates where selection could favor larger males that lived longer. This is, admittedly, only one of several solutions to a generation gap. With the sexes less dimorphic, selection could favor any steps toward a less dangerous system of courtship, i.e., towards type B or C courtship. Such an evolutionary pathway might first allow tropical spiders to utilize stringent habitats in the tropics and be a preadaptation to successful invasion of the temperate regions. At present the genera with group A courtship are most successful and widespread in tropical regions. (The Gasteracanthinae, with small males and a mating thread, do not accord with the predictions of this hypothesis.)

Type C courtship could have evolved several times, conferring different adaptive advantages in different cases. Convergence could be widespread.

Returning to Gerhardt's (1933b) groupings of araneids, we think that copulatory postures are an unreliable guide to relationships within the Araneidae. Twisting through 90° after insertion occurs in at least one species of *Nephila* and also in most species of *Argiope* and at least one *Micrathena* species. It seems improbable that any of these genera are directly related. The other characters that Gerhardt (see above) used to subdivide araneids seem to be less reliable than our groupings of mating behaviors. For instance, the copulation jump/spring is attributed (Gerhardt 1933b: 69) to the genera *Araneus, Singa, Cyclosa, Meta, Zilla* and *Theridiosoma.* Our movies show that it does not occur in the 6 species of *Cyclosa* that we studied. It may thus be a variable character within the genus.

THE FUTURE

In the synthetic sections above, we have raised a wide variety of questions to be answered by future research. Despite this we have ignored some really basic and/or interesting problems that could concern future researchers in this field. One of these, for example, is suggested by some of our observations on the behavior of males of *Herennia, Nephila* and *Argiope* species. The postcopulatory survival of the eunuch males of *Herennia ornatissima* raises the question of adaptive function. This may be intuitively obvious: the sterile males could live on simply to protect their parental investment by driving away other males that attempt to mate with the female that they originally mated. The intrasexual size polymorphism found in *Nephila* species could function to allow micromales to mature early and mate with females ahead of their siblings, or to give macromales an edge over smaller males in aggressive encounters, thereby insuring primacy of mating. The embolus tip of an *Argiope* male frequently breaks off at the end of copulation and remains in situ in the epigyne (Levi 1969). Such an occurrence could block the female to further copulation and protect the parental investment of the 1st male to court a female. These possibilities suggest that there may be a range of complex adaptations, behavioral, structural or developmental, that may operate to ensure that competition between males is an important aspect of araneid reproductive biology. This is surely a potentially productive field for future studies. We expect that the diversity and complexity of adaptations in this field will prove to be at least as great as that discovered by investigators of araneid predatory devices. Unfortunately the basic physiological knowledge necessary to interpret organismic studies is still lacking. For instance, it would be useful to know what happens to the sperm received by a single female *Nephila* from a series of successive matings by different males. We cannot know whether there is an advantage to being the 1st male until such basic facts are available. Understanding of the structure and functioning of the internal reproductive organs is essential. These need investigating with the ingenuity, thoroughness and analytical skill that has been brought to studies of the structure and function of araneid external genitalia by Grasshoff (1974a, 1974b), for instance.

Another largely unexplored aspect of araneid courtship is that of female-finding by males. On this subject our own studies have given us contradictory insights. We have records of *Argiope* males that we tracked over tens of metres as they moved, in numerous short stages, by constructing airborne bridge threads. The ultimate bearing of these movements was towards a web of a female of the right species. The moves seemed purposive and directional. On the other hand, we have seen similar males repeatedly approach the wrong species. The involvement of a sex-attractant pheromone in araneid courtship has long been hypothesized. Blanke (1975) was able to demonstrate the existence of such a pheromone in the extremely sedentary (web-site constant) araneid *Cyrtophora cicatrosa.* The whole subject of the role of pheromones in the reproductive biology of spiders is still an open and potentially exciting field. Jackson (1978) showed that contact with the web silk of some species of dictynid spiders was sufficient to release courtship in males of the appropriate species. The males discriminated on contact between the webs of their own species and those of other species. This result suggests that the silk is labelled in some way, perhaps by a pheromone. There are strong a priori reasons for assuming that a similar mechanism could occur in araneids. We saw a number of instances of males apparently courting or making insertion attempts on prey packages that were being consumed by females.

If an aphrodisiac pheromone were associated with the web or the female, such misdirected efforts would be easily explicable.

There have been very few studies of geographic variation in behavior patterns. Araneid spiders may present a remarkable opportunity for this kind of research because of the unusually extensive geographical distribution of some species. For example, according to Bonnet (1955: 697), *Argiope trifasciata* is widely distributed in every zoogeographic region and is even recorded from Antarctica. Few terrestrial animals, vertebrate or invertebrate, have such a widespread range. A study of geographical variation in (for example) the courtship, predatory and web-building behaviors of such a species could be of fundamental biological interest. In all probability the obstacles in the way of such an investigation would not be methodological or logistic, but would stem from the decline of support for taxonomic work. There might well be no one able to determine whether the study was really one involving the same species throughout its putative range.

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