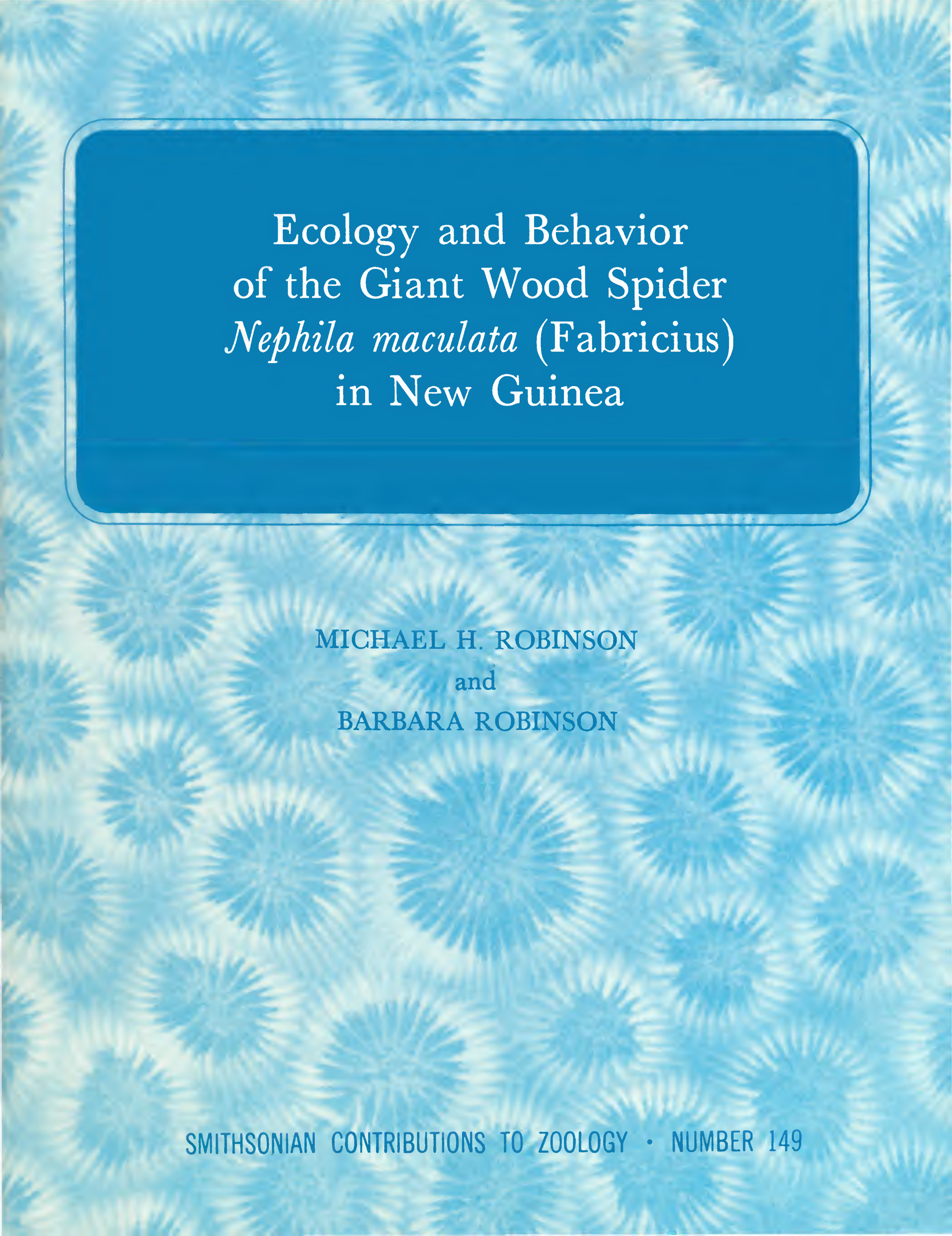

Ecology and Behavior of the Giant Wood Spider *Nephila maculata* (Fabricius) in New Guinea

MICHAEL H. ROBINSON
and
BARBARA ROBINSON

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY · NUMBER 149

SERIAL PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

The emphasis upon publications as a means of diffusing knowledge was expressed by the first Secretary of the Smithsonian Institution. In his formal plan for the Institution, Joseph Henry articulated a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This keynote of basic research has been adhered to over the years in the issuance of thousands of titles in serial publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Annals of Flight
Smithsonian Contributions to Anthropology
Smithsonian Contributions to Astrophysics
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Studies in History and Technology

In these series, the Institution publishes original articles and monographs dealing with the research and collections of its several museums and offices and of professional colleagues at other institutions of learning. These papers report newly acquired facts, synoptic interpretations of data, or original theory in specialized fields. These publications are distributed by mailing lists to libraries, laboratories, and other interested institutions and specialists throughout the world. Individual copies may be obtained from the Smithsonian Institution Press as long as stocks are available.

S. Dillon Ripley
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 149

Ecology and Behavior of the Giant Wood Spider *Nephila maculata* (Fabricius) in New Guinea

Michael H. Robinson
and Barbara Robinson

SMITHSONIAN INSTITUTION PRESS
City of Washington
1973

ABSTRACT

Robinson, Michael H., and Barbara Robinson. Ecology and Behavior of the Giant Wood Spider *Nephila maculata* (Fabricius) in New Guinea. *Smithsonian Contributions to Zoology,* number 149, 76 pages, 30 figures, 11 tables, 1973.—Investigations of the seasonal, reproductive, and population ecology of *Nephila maculata* are reported in detail. In an investigation of feeding ecology over a one-year period, the discarded remains of the prey caught by a sample population of ten adult female spiders were collected daily. These remains were identified (where possible) and the accumulated weekly discards from each spider were dried and weighed. Data from this study are analyzed, tabulated, and compared with the catches from insect traps located in the study area. The study included an investigation of web structure, frequency of web renewal, and the number of kleptoparasites associated with *Nephila maculata.*

Studies of behavior included courtship, mating, predatory behavior, and responses to predators, sunlight, and rainfall. Courtship behavior included a complex pattern of silk deposition by the male on the female, here reported for the first time for the Araneida. The predatory behavior of *N. maculata* is analyzed in terms of behavior units and behavior sequences and is compared with that of other *Nephila* species, related species, and that of other araneids studied by the authors.

The phenological aspects of the study are stressed and discussed.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year.* SI PRESS NUMBER 4779. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Robinson, Michael H.
Ecology and behavior of the giant wood spider Nephila maculata (Fabricius) in New Guinea.
(Smithsonian contributions to zoology, no. 149)
Bibliography: p.
1. Nephila maculata—Behavior. 2. Spiders—New Guinea. I. Robinson, Barbara, 1931— joint author. II. Title. III. Series: Smithsonian Institution. Smithsonian contributions to zoology, no. 149.
QL1.S54 no. 149 [QL458.A65] 591'.08s [595'.44] 73–1905

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C., 20402 · Price $1.45 (paper cover)

Contents

Page

Introduction 1
  The Species 2
  Techniques of Study 3
  The Study Area 7
Natural History and Ecology 7
  Web Studies 7
    Web Location 7
    Web Structure 8
    Web Renewal 10
    Web Strength 12
  Reproduction 12
    Males on Webs of Females 12
    Egg-laying 13
    Hatchling Behavior and Dispersion 14
    Phenology of Population Increments 15
  Prey and Prey Captures 17
    Taxonomic Range 17
    Numbers in Taxa 17
    Temporal Distribution 19
    Weights of Prey Remnants 21
    Comparison with *Argiope argentata* 23
    Comparison with Insect-Trap Catches 24
    Rejections of Trapped Insects 27
  Kleptoparasites 29
    Numbers and Nature 29
    Activities 30
    Colonization of Host Webs 32
    General Considerations 32
  Energetics 33
  Phenology 33
Behavior 34
  Terminology 34
  Sexual Behavior 34
    Finding the Female 34
    Courtship 35
    Copulation 41
    Discussion 41
  Predatory Behavior 44
    Behavior Units of *Nephila maculata* 44
    Behavior Units of Other Species 52
    Behavior Sequences 54
    Comparison with *Argiope aemula* 59
    Comparison with *Nephila clavipes* 60

Page

Categorization of Araneids by Predatory Behavior 62
Behavior of Prey in the Web 63
Responses to Environmental Factors 64
Defensive and Escape Behavior 66
Discussion 67
Phenology 67
Behavior 69
Literature Cited 70
Appendix 1: Activities of Male *Nephila maculata* during Courtship Silk-deposition 73
Appendix 2: Verbatim Notes on Selected Sequences Given to Large Acridiids 75

Ecology and Behavior of the Giant Wood Spider *Nephila maculata* (Fabricius) in New Guinea

Michael H. Robinson
and Barbara Robinson

Introduction

Araneid spiders belonging to the genus *Nephila* form a conspicuous element of the invertebrate faunas of both the Old and New World tropics. In addition, they extend into north and south temperate regions. The adult females of most species are large and build strong webs of golden silk that are often of considerable size. McKeown (1963) cites examples of *Nephila* species catching and consuming small birds and also mentions that the natives of the South Pacific use the webs for catching fish. An interesting account of the use of *Nephila* silk for fishing appears in a work of fiction by Olaf Ruhen, a New Zealander with wide experience of the Pacific region. He states (1969:64) that the web is matted into a wad the size of a human thumb and flown over the surface of the sea suspended from a kite. There it is seized by garfish which are unable to disentangle their teeth from the silk and are caught. Surprisingly there have been few studies of the biology of *Nephila* species and attention has largely centered on the taxonomy and zoogeography of this group. Fischer (1910a, b, c), Hingston (1922a, b, c; 1923), and Thakur and Tembe (1956) have published short accounts of the natural history of *Nephila maculata* (Fabricius) in India. Bonnet (1929), Coleman (1948), Gerhardt (1930), Jager (1960), and McKeown (1963) have written on various aspects of the behavior or ecology of other *Nephila* species. Peters (1954, 1955) studied the web construction of *Nephila clavipes* (L.).

Studies of the predatory behavior of *Nephila clavipes* in Panama (Robinson and Mirick, 1971) led to the conclusion that this species was primitive (Robinson, Mirick, and Turner, 1969). At this stage we thought that a more comprehensive study of a *Nephila* species would be worthwhile and rewarding. We were able to make some observations on *Nephila* and related *Nephilengys* species in West Africa during February and March 1970, and further observations on *Nephila* and *Nephilengys* in Madagascar and on *Nephila* and *Herennia* in India (March/April 1970). In New Guinea we found that *Nephila maculata* was abundant in the Wau valley (Morobe District) where we were to spend one year at the Wau Ecology Institute. The spiders living in the arboretum of this institute were protected from disturbance and we decided to make a long-term field and laboratory study of this species.

This paper is based on our studies in New Guinea but also includes comparative data from

---

Michael H. Robinson and Barbara Robinson, Smithsonian Tropical Research Institute, Post Office Box 2072, Balboa, Canal Zone, Panama.

the observations carried out in West Africa, Madagascar, and India, and unpublished data from the study carried out by Robinson and Mirick in Panama. The New Guinea studies were basically ecological and behavioral. Ecological studies included observations on web structure and habitat, sampling of potential and actual prey, phenological studies of reproduction and predation, investigation of population numbers of kleptoparasites, and recording population fluctuations of adult and immature *Nephila*. The behavioral studies were mainly concentrated on predatory behavior but also included studies of mating behavior and responses to sunlight and rainfall. Some effects of behavior are dealt with in the ecological section of this paper because the underlying behavior patterns were not directly studied. This was the case with respect to prey-rejection, web-renewal and egg-laying. Some studies that are referred to in this paper, e.g., those on web adhesiveness and population fluctuations in Wau araneids, were carried out in conjunction with our colleague Dr. Y. D. Lubin and are to be published separately. The study of five species of *Argiope* that we carried out in New Guinea is referred to in the comparative section on predatory behavior, but it is to be published in detail elsewhere.

ACKNOWLEDGMENTS.—We thank Dr. Y. D. Lubin for her assistance during this study. She provided both ideas and practical help. We are extremely grateful to the staffs of the following institutions who helped our work in Africa and India: Department of Zoology, University of Ghana, Legon; O.R.S.T.O.M. and the Institute de Rechêrche Tropicale in Ivory Coast; O.R.S.T.O.M. in Madagascar; Bombay Natural History Society; University of Delhi; Hindu University of Varanasi; Forestry Department of Assam; and, particularly, Dr. T. N. Ananthakrishnan in Madras.

In New Guinea we received much help from the staff of the Forestry School at Bulolo, The Lae Botanic Gardens, and the entomologists of the Division of Entomology laboratories at Bulolo. Our native helpers, Rennie, Lik-lik Boy, and Polino were superb naturalists and cheerful assistants throughout the study.

Our colleagues at the Smithsonian Tropical Research Institute, have, as always, contributed much to the development of the ideas presented in this paper. In particular we are grateful to Dr. A. S. Rand and Dr. H. Wolda for advice and help with the analysis of data.

THE SPECIES

Fr. Chrysanthus identified the Wau material as *Nephila maculata*. The species has reportedly a wide distribution in the Old World tropics and subtropics (Roewer, 1942; Bonnet, 1958). Roewer (1942:929) gives the distribution as "Ceylon, Indien bis China u. Australien," while Bonnet (1958: 3077) adds "Afrique occidentale et Afrique australe" and "?Mexique." The records of the species from New Guinea have been detailed by Chrysanthus (1959, 1960, 1971). The species occurs in all parts of the Wau valley where trees or bushes persist and we have recorded its presence to a height of approximately 2000 meters on the slopes of Mount Kaindi. Densities are often high in coffee plantations, where the species builds its webs in the flight paths of insects between the rows of plants.

Some details of the appearance of adult males and females are evident from the photographs illustrating this paper (Figures 17, 18, 19). The adult female varies in size from just below 40 mm in body length to over 50 mm; most of this variation is due to variations in the length of the opisthosoma. Legs I are the longest, legs IV are usually longer than legs II and legs III are the shortest at around half the length of legs I. See Table 1 for specimen measurements, note that there is often asymmetry in leg lengths. We have records of the weights of adult females ranging from 2–4.25 grams and think that the variations in adult weight probably extend above and below this range (taken from a sample of 10). The adult female is dull and dark in coloration contrasting markedly with some other common *Nephila* species in this respect. Yaginuma (1969, pl. 29) gives a color illustration of the Japanese form. The Wau specimens differ from this in that the opisthosoma is completely unmarked dorsally. The Japanese form evidently has pale yellow lines and spots on this region. Dorsal markings of the opisthosoma are present on immatures at Wau. They are not present on the penultimate instar. Hingston's (1922a) description of *Nephila maculata* in India refers to striking coloration of the dorsal surface of the abdomen.

TABLE 1.—*Sizes of adult female* Nephila maculata
(– = leg missing.)

Spider	*Wet weight (gm)*	*Length (mm)*	*Prosoma (mm)*	*Opisthosoma (mm)*	*Leg lengths (mm)*							
					I		*II*		*III*		*IV*	
					R	*L*	*R*	*L*	*R*	*L*	*R*	*L*
1	4.25	41	11	30	82	80	68	66	41	39	69	68
2	2.725	40	12	28	85	86	72	71	40	–	71	74
3	2.055	37	10	27	83	81	67	68	42	40	68	69
4	4.134	40	11	29	–	85	70	69	40	39	70	56
5	3.575	48	12	36	84	83	67	68	41	37	68	69
6	3.387	46	13	33	80	82	71	–	39	40	69	71
7	3.80	47	12	35	81	82	70	69	41	38	70	–
8	2.93	40	10	30	79	82	67	58	38	42	69	68
9	3.20	44	11	33	85	87	71	72	40	39	–	74
10	3.75	50	13	37	86	84	68	70	41	40	69	71
Average	3.38	43.3	11.5	31.8	82.78	83.2	69.1	67.9	40.3	39.3	69.2	68.9

Juveniles up to at least half the adult size (Figure 1) possess the dense hairy "gaiters" on the distal portions of the tibiae of legs I, II, and IV that are characteristic of all stages of *Nephila clavipes* and several other *Nephila* species. The females of later stages lose the gaiters as Thakur and Tembe (1956) have also noted. These authors include a figure of an adult female showing dorsal lineation and spotting on the opisthosoma (1956, fig. 1). The opisthosoma of Wau adults is a dark slatey color (almost black) with an overlying "bloom," or "patina," of gold; the latter appears to wear off with time. We found a number of adult females in the Wau area, which had conspicuous pale yellowish brown legs in marked contrast to the black legs of the "normal" form. One of these is illustrated in Figure 2, and a specimen is deposited with Fr. Chrysanthus. This form is a distinct one, and not merely a product of slow deposition of the appropriate pigmentation.

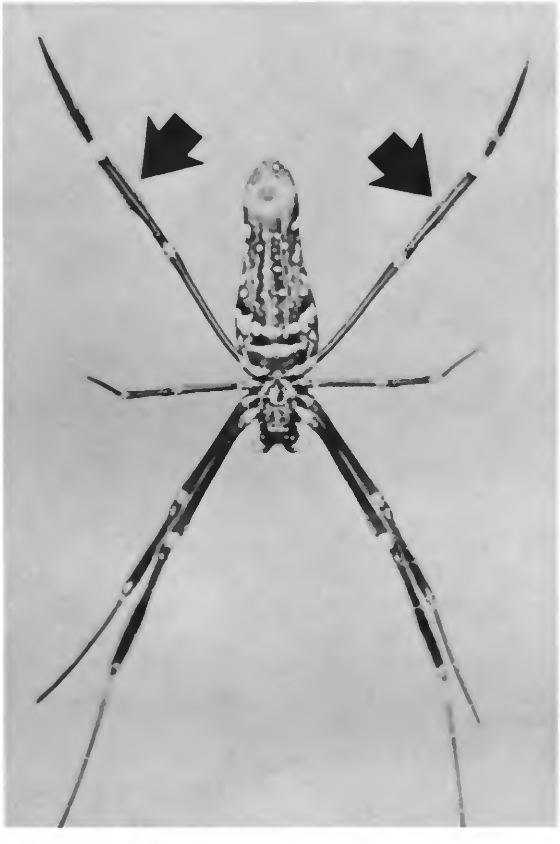

FIGURE 1.—Juvenile *Nephila maculata* showing "gaiters" on legs (arrowed) that are lost in later stages. Length ca 25 mm.

Adult males are very small, ca. 4–6 mm in body length and transluscent red to reddish orange in coloration, often with black markings on the tarsi.

TECHNIQUES OF STUDY

During the period May 1970 to May 1971 we carried out daily observations on a sample population of adult female spiders present in the study area (described later); and from June 1970–April 1971 we carried out the sampling of flying insects in the same area. During daily observations we noted the state of the web and its position; the presence or absence of males and kleptoparasites, the presence or absence of prey, and evidence of egg-laying as reflected in sudden reductions in the grossness of the female opisthosoma and/or the

FIGURE 2.—Reverse color form of adult *Nephila maculata* in typical predatory position at hub.

presence of nearby egg-sacs. This recording involved visiting ten marked adult spiders daily. Prey traps were placed under the webs of these spiders and discarded or rejected prey were collected daily for further examination and analysis. In addition to this daily routine we carried out (with Dr. Y. D. Lubin) weekly counts of all the visible araneids in three 100×2 meter transects, one of which bordered the study area. These counts included counts of adult and immature *Nephila maculata*. We also censused the kleptoparasites present in *Nephila* webs outside the study area but within a 500 meter range of its center.

Behavioral observations were carried out on adult spiders living in the study area but not forming part of our sample population. The investigations on predatory behavior utilized similar techniques to those employed by the senior author and coworkers in earlier studies and will not be described in detail here. New techniques used for the first time in this study are described in the appropriate section of the main text. Extensive use was made of filming and film analysis, particularly in the study of mating behavior. We used Super 8 mm movie film for this purpose. This allowed us to use considerably more portable equipment than was possible in previous studies where we used 16 mm film. For filming behavior sequences we used a Canon 518 camera equipped with the manufacturer's close-up lens. This enabled us to fill the frame with a portion of the body of the adult *Nephila* female, and, incidentally to use the viewing system of the camera to watch events that were not clearly visible to the unaided eye. Using zoom optics for this purpose provides an admirable technique for studying the behavior of small animals from a convenient distance (Robinson and Robinson, 1972a). All the black and white photographs were taken with a 6 cm square single-lens reflex camera equipped with close-up attachments. The photography of spider's webs is difficult (see Langer and Eberhard, 1969) but can be facilitated by spraying the web with matt-white aerosol paint and then interposing a black background between the web and surrounding vegetation. All the accompanying photographs of web structure were taken by utilizing this technique.

The rainfall data that we include in the phenological analyses are derived from the records of the Wau Ecology Institute and New Guinea Goldfields Company.

PREY TRAPS.—Our observations on the prey of *Argiope argentata* (Fabricius) in Panama were carried out by visiting ten webs at two-hourly intervals throughout the day and recording details of the prey present in the web. This method is extremely tedious and time-consuming and does not permit a determination of weights of prey except by extrapolation from weighed samples. Spiders are suctorial feeders and discard "trash packages" of prey remains after feeding. We decided to collect these packages for weighing and identification. To do this we placed meter square pieces of fine nylon netting under the webs of the ten "sample" spiders and collected the remains each morning. To prevent ants from removing prey debris we coated the prey trap attachment strings (one at each corner) with tanglefoot. The method proved entirely satisfactory. The traps caught the remains of quite small prey (as small as 5 mm insects), the conspicuous remains of large prey, and the dead bodies of rejected prey items. The latter was a "bonus" item resulting from the fact that *N. maculata* rejects many items of obnoxious prey after a preliminary bite. (If heavy rain occurred during the 24-hour interval between emptying the traps, it may have washed some very small fragments of prey through the mesh, but we think that this factor was a very small source of error in our results.)

The material from each trap was placed in a separate vial each day, dried in a drying oven, and the seven samples from each spider were examined under a binocular dissecting microscope at the end of each week. This process allowed us to make a record of prey caught, on each day of the week. We also obtained a weekly total for the dry weight of prey remains discarded by each spider. (We decided that weighing the wet remains would not give any useful information because of wide variations in water content due to climatic conditions.) Sorting the material under a binocular microscope was not easy since the masticatory process results in the extreme comminution of those insects that have thin cuticles. It proved possible, however, to identify most trash bundles to order and often to lower taxonomic divisions. The jaws and jumping legs of orthopterans served to identify the fragmented remains of those insects and the color of the cuticular fragments was a further guide to separation. Lepidopteran remains were characterized by the presence of wing scales. The elytra of even the smallest coleopterans survived the comminution of other parts. Compound trash parcels could often be separated into their multiple constituents by counting elytra, jaws, and other hard parts, and the number of prey items thereby calculated. Occasional forceps marked the presence of dermapterans and we were able to sort out some dipterans and hymenopterans on the basis of their membranous wings. Catches from the nearby insect traps were useful in giving an indication of the potential presence of some groups of flying insects that were periodically in abundance. These data helped in the determination of dubious prey remains. Larger insects that were not caught by the prey traps (e.g., melolonthids and sphingids) were seen at our Mercury vapor (Mv.) insect light and very abundant flights were noted for comparison with the prey trap data.

The spiders were marked with Humbrol model-makers enamel paint using a color/position code to identify individuals. The paint peeled off the surface of the opisthosoma after about one month so it was necessary to re-mark the spiders every three weeks. We usually had twenty marked spiders in the study area; the ten sample spiders and ten "reserves." The latter were used when one of the sample spiders died, disappeared or moved into an inaccessible position. Movement to an inaccessible position occurred very rarely since we were able to arrange the prey traps at most web sites (even when this involved some removal of surrounding vegetation.) The fact that the spider builds its web across gaps in vegetation, in flight paths, normally ensured that there was a fairly clear space beneath the web in which to erect the prey trap.

We recovered the dead bodies of some spiders from the prey traps but lost most of our sample specimens by "disappearance." Our very skilled and sharp-eyed New Guinean assistants usually found spiders that had merely moved long distances from the original web sites but many spiders disappeared without trace at some stage in the prey census. We discovered at an early stage in the study that very fat spiders would disappear for one or two days and then return, much depleted in size, to the same web location. These had produced egg-masses. As a consequence of this observation we decided not to replace missing sample spiders until they had been absent for three morning censuses. In time we noticed that egg-laying absences were often preceded by nonrenewal of the web and a fall off in catches for the days immediately prior to the absence, and this factor helped in the interpretation of disappearances. Spider movements largely occurred at night, and were noted the following morning, when the trap could be relocated. Thus there was very little disturbance of the data collection by movements from web site to web site. Individuals remained under observation for several months and provided data on *minimum* periods of adult longevity.

Insect Traps.—To sample the availability of potential prey we used two techniques. We placed three window-pane traps at sites in the study area that were typical of web locations and collected the insects from these, each morning, over most of the study period. We also used two sticky traps for a shorter period (necessitated by the late arrival of our supplies of tangle-foot); these traps were also serviced daily.

We chose window-pane traps as a sampling device since we considered these to be less conspicuous to flying insects than the opaque mass of a sticky trap. They, in fact, trapped insects not caught by sticky traps but failed to catch some insects known to be in flight (from our observations of the spider's prey and Mv. light catches.) These insects, including large beetles and moths, were not caught by the sticky traps either. We have discussed elsewhere (Robinson and Robinson, 1970a:356) the problems involved in sampling the prey available to large orb-weavers and do not consider that these have yet been solved.

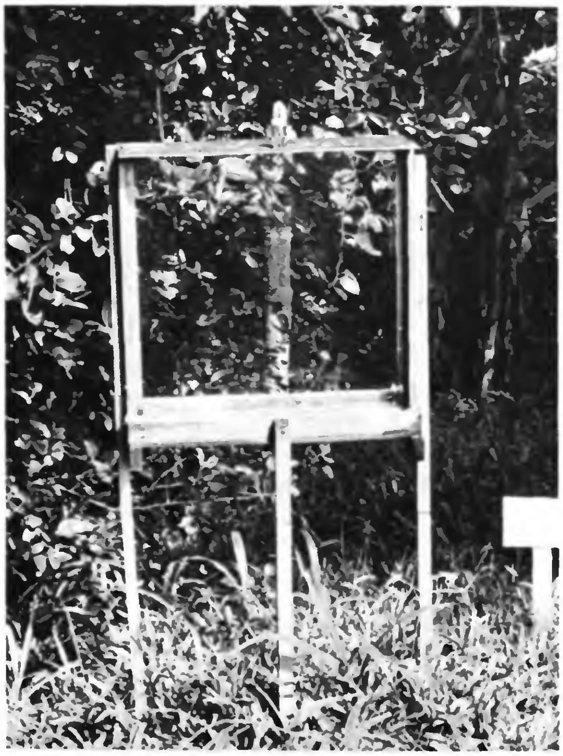

FIGURE 3.—Window-pane trap in study area.

The window-pane traps were constructed of pieces of 24-ounce clear sheet grass 24 × 24 inches in size (about 61 × 61 cm). This was mounted in a light wooden frame and its lower edge dipped into a 3 cm deep trough of water. The water contained a wetting agent and a small quantity of phenol. Figure 3 shows a trap in situ. We mounted the traps on wooden legs with their centers about 1 meter above ground level.

The sticky traps were made by smearing both sides of a meter square of nylon mosquito netting with tanglefoot (I.C.I. Osticon) and mounting the net on a light wooden frame. The traps were erected with their bottom edges about 75 cm above ground level.

Insects from the window-pane traps were preserved in 70 percent ethanol and those from the sticky traps were collected in gasoline and transferred to alcohol after the tanglefoot had been dissolved. The daily catches were examined monthly, sorted taxonomically, and graded into size ranges.

The Study Area

The approximate boundaries of the study area are shown on Figure 4. The area was originally a coffee plantation but, over a period of years, has been converted into an arboretum by the activities of the Wau Ecology Institute (formerly Bishop Museum Field Station). Trees from Mount Kaindi and other areas in the Wau-Bulolo region have been planted and have reached a considerable height above the remaining rows of coffee. The latter is picked periodically but was not pruned during our study year. Some of the tree and shrub species occurring in the area are as follows:

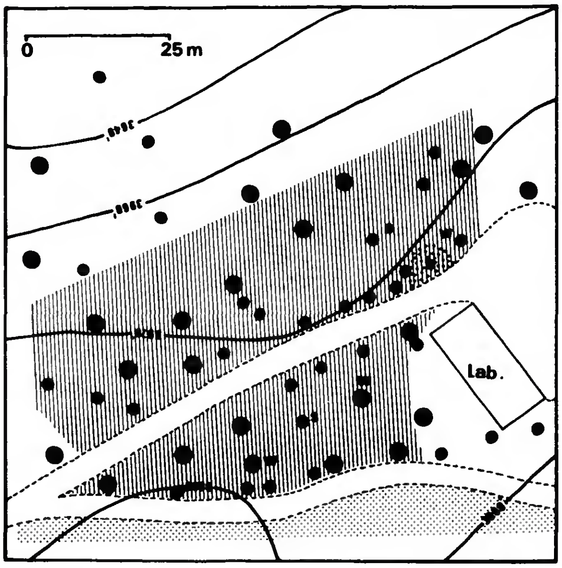

Figure 4.—Plan of study area (hatched). (Black circles=large trees, b=bamboo thicket, s=sticky trap, w=window-pane trap. Stipled area is transect 1.)

Rubiaceae: *Gardenia* species, *Neoxandia* species, *Psychotria* species, *Pavetta* species
Euphorbiaceae: *Phyllanthus* species, *Euphorbia pulcherrima*, *Macaranga* species
Meliaceae: *Disoxylon* species, *Toona sureni*
Moraceae: *Ficus calopilina*, *Ficus dammaropsis*
Sapindaceae: *Dyctioneura* species, *Allophyllus* species
Elaeocarpaceae: *Elaeocarpus sphericus*, *Elaeocarpus dolichostylus*
Anonaceae: *Anona muricata*
Solanaceae: *Datura candida*
Araucariaceae: *Araucaria klinkii*
Sterculiaceae: *Sterculia* species
Myrtaceae: *Eugenia* species
Lauraceae: *Litsia* species
Melostomaceae: *Astronia* species
Rhamnaceae: *Alphitonia incava*
Verbenaceae: *Callicarpa longifolia*

Some idea of the height of the background vegetation can be gained from Figure 3. The area supports a diverse fauna including numerous arthropods that are predators of arthropods. Among these are trap-building spiders of the families Uloboridae, Amaurobiidae, Pholcidae, Araneidae, Tetragnathidae, Agelinidae, Linyphiidae, and Theridiidae. Araneids included three species of *Gasteracantha*, two of *Argiope*, two of *Leucauge*, one of *Cyrtophora*, one of *Arachnura*, several araneus-like nocturnal forms, *Herennia ornatissima*, *Cyclosa insulana*, and the, as yet, unidentified "New Guinea ladder-web spider" (Robinson and Robinson, 1972b). The theridiids include solitary, colonial, and kleptoparasitic forms. The trap-building spiders exist alongside a large hunting spider population and some sedentary raptors (dinopids). In addition there is a diverse assemblage of predatory insects including mantids and reduviids.

Natural History and Ecology

Web Studies

Web Location

Webs of adult female spiders are almost always located with the bottom edge (lower foundation thread) above the herb layer, even when this attains a height of more than 1 meter. A proportion of webs may be built with the prey capture area partially overlapped by nearby vegetation but in most cases webs span natural gaps in woody vegetation. Hingston (1922a:643) notes that Indian *N. maculata* often builds its web where "it finds a tunnel in the tangled growth where the insects pass to and fro." We found webs located in trees at heights of more than 5 meters above the ground and even sited on telephone and overhead power cables. Webs of males and immatures were discovered closer to ground level and sometimes within the herb layer. Back-to-back web building, as noted in the case of *N. clavipes* (Shear, 1970), was uncommon in the Wau area.

Web Structure

In common with the webs of those other *Nephila* species that we have seen, the webs of *N. maculata* are markedly assymmetric in that the hub is always located in the upper third of the web. Peters (1954, 1955) has given details of the structure of the *N. clavipes* adult web, which is frequently incomplete above the hub (see also Kaston and Kaston, 1953). The web of *N. maculata* differs in being almost always complete above the hub, i.e., with the prey capture area intact in this region. Some sample dimensions of webs made by adult females (N=10) convey the structural aspects of the web of *N. maculata*:

	Range	*Average*
Viscid spirals above hub	0–10	5.7
Viscid spirals below hub	55–90	72.5
Radii (counted halfway between hub and periphery)	69–110	86.9

Compared with webs of adult males (N=5), the females' webs are appreciably larger (measurements in cm):

	Female		*Male*	
	Range	*Average*	*Range*	*Average*
Width	62–100	84.1	7.8–11	9.4
Height	79–116	96.2	10.4–13.1	11.7

In our sample of 3237 webs, those with barrier constructions occurred in 640 instances (19.8% of total sample), of which 625 had dorsal barriers only, and 15 had both dorsal and ventral barriers, but none had only ventral barriers. We note, therefore, that barrier webs occur with maximum frequency below the orb, i.e., dorsal to the spider. The structural spiral is left in during construction of the viscid spiral but since four or five viscid elements are not interspersed between successive elements of the temporary spiral, it does not present the "music-ruled" effect of the *N. clavipes* web. The above web dimensions show that the webs are often more nearly circular than those of *N. clavipes* (i.e., with their greatest width not differing greatly from their greatest height).

As in all the *Nephila* webs that we know of, the lower radii are often branched (see Kaston, 1964, for comments on evolutionary significance). The hub is entire and surrounded by a spiral strengthening zone. The hub region often appears to be braced by a thread leading from the hub silk to some nearby piece of vegetation. The viscid spiral is characteristically golden in color. Hingston (1922a:648, 1922b:912, 1922c:918) gives details of the structure and process of construction of the *Nephila maculata* web. He notes that the radii are branched and numerous (more than 100), that the temporary spiral is left permanently in place and that a barrier web is built above the main sheet. He also observed a marked asymmetry in the placement of the hub and quotes an example (1922c:918) where a web had 130 turns of the viscid spiral below the hub and only 3 above.

The webs of males were found sporadically in the study area and we have seen mature males with a web. They were all small and more like the normal, almost symmetrical orbs of *Araneus diadematus*.

The webs of immature females proved to be of great interest for two reasons. First, a proportion were found that had linear stabilimenta (Figure 5). These structures consist of a ribbon of silk placed above and below the hub and consist of multistrand silk, laid down between adjacent radii in a zig-zag line. We never saw any stabilimenta in the webs of mature females. As far as we are aware this is the first and only record of stabilimentum building by a *Nephila* species. We saw 14 such structures in the course of examining hundreds of webs over a one-year period. Although we never saw the spider construct a stabilimentum it is obvious that it is not an accidental structure resulting from some anomalous aspect of web-building, but is added after the completion of the viscid spiral. It is tempting to regard this aspect of *N. maculata*'s web building behavior as vestigial. Elsewhere (Robinson

FIGURE 5.—Juvenile *Nephila maculata* with stabilimentum.

and Robinson, 1970b) we have reviewed the various theories about the function of stabilimenta and concluded that in some cases, at least, a camouflage sensu lato function, is improbable. This would certainly seem to be the case with the rarely built stabilimentum of *N. maculata.* (*Nephila* species do apparently construct some camouflage devices; both *N. maculata* and *N. clavipes* deliberately hang plant material and discarded prey debris in their barrier webs above the hub. *Nephila plumipes* (Latreille) often hangs the corpses of prey in a line above the hub.)

The second interesting feature of some juvenile webs is the form of the barrier webs. Note in Figure 6 that the spider is standing on the main orb and that there is a netlike large barrier web dorsal to the spider and a smaller, incomplete, similar barrier web below the main orb. The structure of these barrier webs, an orb web structure with radii and a structural spiral, has not been previously described. The hub of the barrier orb is drawn away from the functional orb by an attachment line so that the effect is one of a conical dome above and below the web proper. This highly organized pair of structures is replaced at later stages by the apparently disorganized maze of lines that make up the barrier web (s) of the mature spider. As in the case of the stabilimentum we were not fortunate enough to see such barrier webs actually being built. It is, however, clear that they are not adventitious structures built by other spiders. The greater development of the structure dorsal to the spider supports the suggestion that the barrier web may protect the spider against its predators, in this case it would clearly prevent, or delay, attacks by spider-hunting wasps and parasitic dipterans. (A number of explanations of the function of barrier webs are current among arachnologists but few have been published. Hingston (1922c) suggests that it prevents the escape of large prey from the main orb. He reasons that large insects may tear themselves free of the viscid spiral but that they are then likely to strike the barrier web and be driven back into the main orb. This theory accounts for some features of the structure of barrier webs but not their preponderance below the orb, i.e., above the spider's back.)

The plane of the *N. maculata* orb web seldom appears to be perpendicular but is usually inclined to a greater or lesser extent. We did not attempt to measure angles of inclination but believe that the majority of webs fell within the range of 5°–30° deviation from the perpendicular. The spider assumes its predatory position on the undersurface of the web. The slope must facilitate transportation of prey on silk (the spider walks on the undersurface with the prey hanging away from the web, in the lower and larger portion).

Web Renewal

Our morning census revealed that webs are renewed, entirely or in part, with greater frequency than we anticipated. It was easy to distinguish renewed parts because the edges of the renewed area are conspicuous. In addition, the new viscid element in the renewed area looks fresh by contrast with the old element, in which the viscous droplets are often irregular and patches of adhering detritus are usually present.

Web renewal data from the daily census of 10 adult female *Nephila maculata* are as follows:

Days female absent or on scaffold only: 413
Total possible number of web days (3650−413) :3237
A total of 2388 webs were renewed or repaired during the 3237 days (each web averaging 1.4 days duration)

Number of webs renewed or repaired	*After*	*Percentage of webs renewed or repaired*	
1794	24 hours	daily	75.1
435	48 hours	every 2 days:	18.2
105	3 days	every 3 days:	4.3
31	4 days	within 3 days:	97.6
13	5 days		
5	6 days		
3	7 days		
2	9 days		
Total: 2388			

Nephila maculata cuts away areas of web during heavy rainfall and renews them later, without completely rebuilding the web. The spider cuts through the radii, close to the hub, on one side of the orb and an area of web collapses. (This behavior can be induced by spraying a web with water and may be a means of preventing the collapse of the entire web under the effect of a heavy load of water droplets.) When heavy rainfall occurs at the stage when the spider would be completing a new

FIGURE 6.—Web of juvenile *Nephila maculata* showing highly organized barrier webs, spider is visible on main orb (left center), barrier web below spider (extreme left) is much smaller than that above spider (center to right, conical).

web, by laying down the viscid spiral, this stage may be deferred until rainfall ceases. Other stages up to the addition of the viscid spiral appear to be carried out during rainfall. Viscid spirals added after long periods of intermittent rainfall are often untidy and incomplete.

As mentioned above we carried out, in collaboration with Dr. Y. D. Lubin, a number of experiments on variations in web adhesiveness with time. We used a modification of the technique used by Eisner, Alsop, and Ettershank (1964) and tested the adhesiveness of standard sized lengths of *N. maculata* viscid spiral, at intervals, over a period of several days. The viscid spiral, when protected from rain, maintained a high level of adhesiveness for more than two days after it had been produced (Robinson, Robinson, and Lubin, in prep.). This suggests that chemical deterioration of the adhesive is not the factor necessitating the recorded frequency of web renewal.

Web Strength

Dr. Y. D. Lubin (in litt.) has compared the strengths of elements from the webs of *N. maculata* with those of *Cyrtophora moluccensis*. The results give no absolute values but show that the *Cyrtophora* silk is much stronger than the *Nephila* silk. The latter, however, is strong enough to retain insects in excess of 2 grams (large scarabaeoid beetles) until the spider can subdue them.

REPRODUCTION

Males on Webs of Females

Figure 7 shows graphically the number of males recorded on the ten study webs during the year and also, for the second half of the study period, the number of males recorded actually on the body of the female during the morning census. We have also plotted the numbers of males recorded on the weekly census of transect 1 (p. 4) during the same period. Males are present on the webs of females throughout the year and the number increases markedly from week 36 (commencing 20 January 1971) and remains high until the end of the study period. The peaks in the number of males seen on the body of the female coincide with the peaks in the totals of males recorded on a female's web, during the period of high numbers. The greatest number of males recorded on transect

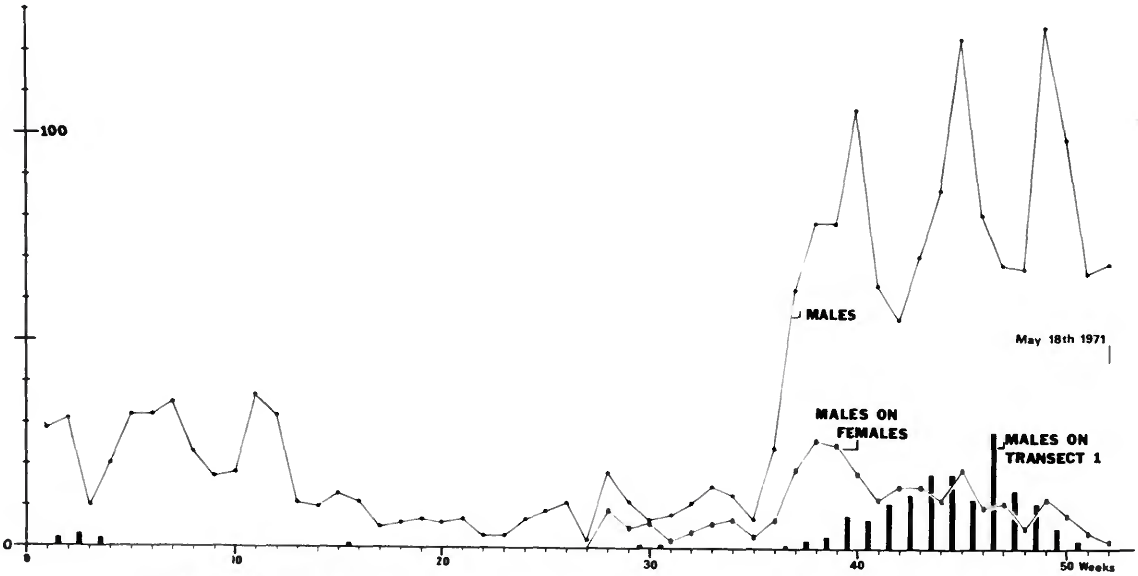

FIGURE 7.—Weekly distribution of number of males found on webs of females in study area and number of males seen on females themselves. Histograms show numbers of males censused in nearby transect.

1 also occurs during the period from week 36 to 52. Figure 8 shows the numbers of adult female and immature *N. maculata* recorded on transect 1, and it is interesting to note that the large population of males on the study area occurs during a period when the number of immature spiders is high on the nearby transect (Figure 4).

Several males may attend a female at any one time. Although we did not mark individuals we have observed conspicuous individuals (naturally marked by the loss of legs, or distinctive coloration) to be present on the same web for several days. When not actually on the body of the female the males take up positions on bridge and frame threads, on elements of the barrier web (s), within the upper part of the prey capture area, and at the hub. Males were also observed on the webs of immature females, often when these must have been at least two or more molts away from maturity. We have one record of a male mating with a female shortly after she had ecdysed, at a stage, in fact, when she was still hanging from her cast exoskeleton.

Egg-laying

Periodicity.—During the year of study, the 10 adult female *Nephila maculata* produced an estimated total of 89 egg-sacs, which on a monthly basis were counted as follows: May, 4; June, 9; July, 7; August, 8; September, 9; October, 9; November, 8; December, 6; January, 7; February, 9; March, 6; April, 7. These figures are only for cases of what we regard as *certain* instances of egg-laying. (We scored egg-laying when we found a new egg-sac near to a marked female that had been absent from a web site for 1 to 2 days *or* when a female had been absent for this period and returned considerably reduced in bulk although no egg-sac was located. Because of their camouflage, egg sacs are not always easy to locate.) Spiders that simply disappeared from our sample may have laid eggs but are not scored. The estimate must, therefore, be regarded as conservative.

There was a strong tendency for female spiders to stop web replacement and repair some days prior to egg-laying. There was also a tendency for them to stop feeding in these circumstances. Although these behaviors are not invariable they are apparent in the majority of cases as Figure 9 shows.

The old webs occupied by females on the point of egg-laying were often functional, and the fall-off in prey capture was, therefore, in many cases,

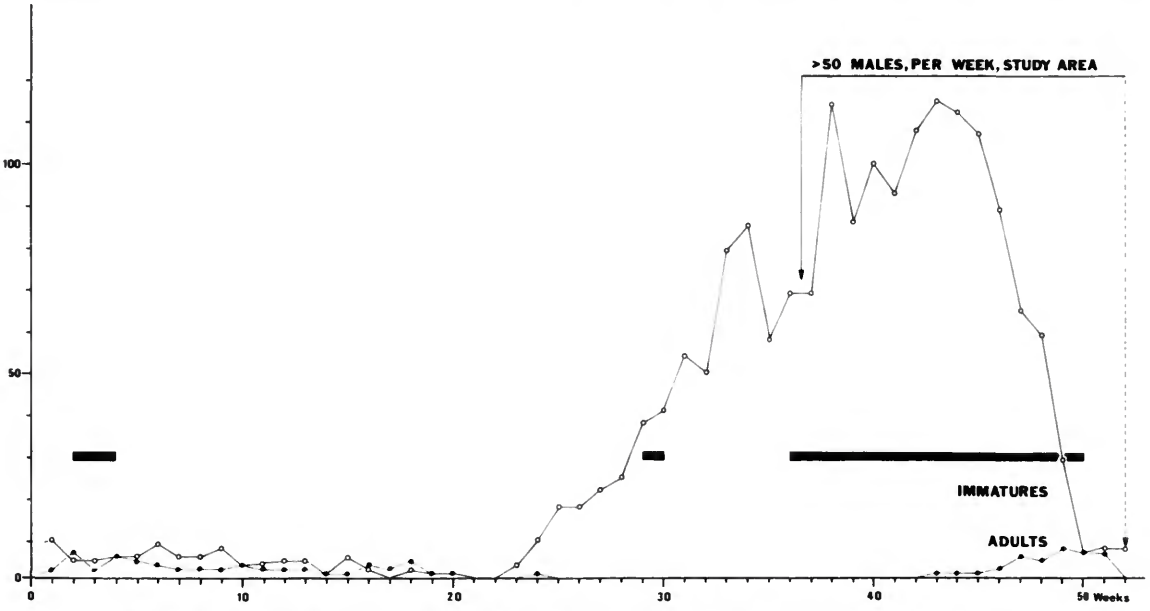

FIGURE 8.—Weekly distribution of numbers of adult and immature *Nephila maculata* on transect 1. Horizontal black bar shows weeks when males were present.

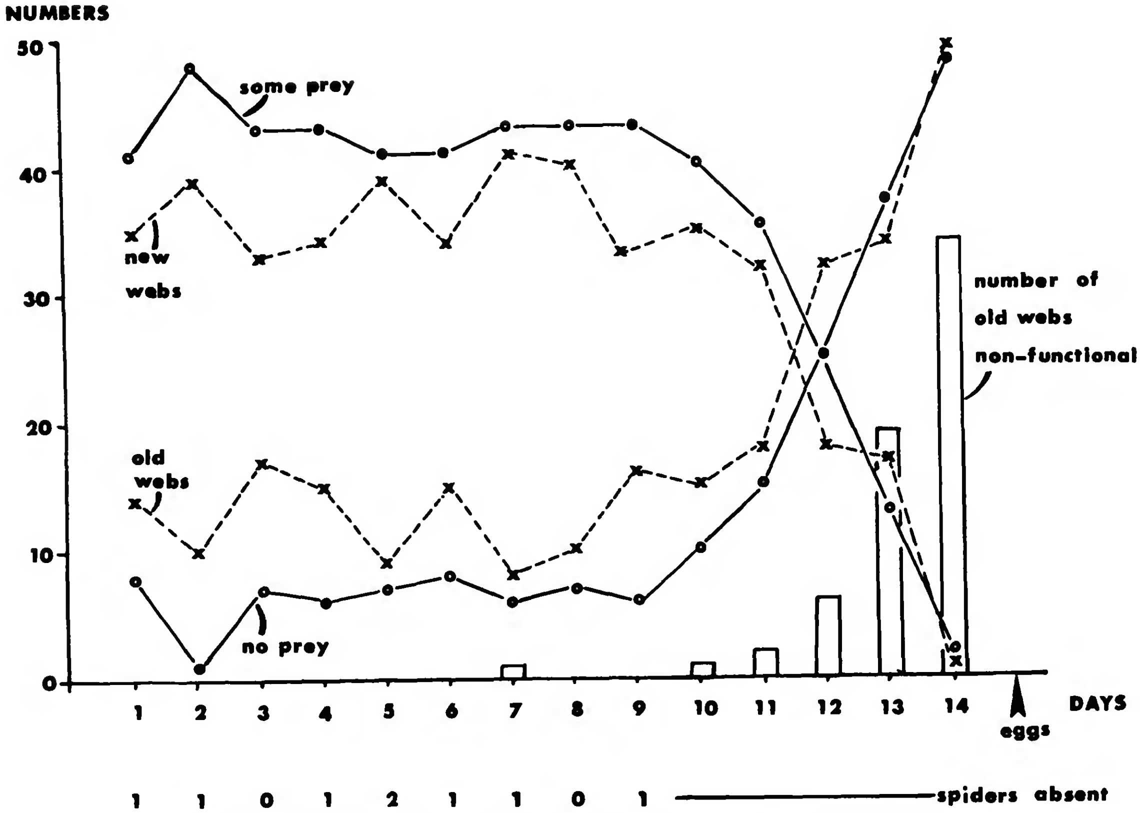

FIGURE 9.—Number of prey caught per day and numbers of new webs per day during the two weeks prior to an egg-laying excursion. Based on data from 50 periods prior to egg-laying.

due to the spider not responding to potential prey that struck the web at this time.

All the egg-sacs that were found were similar in structure and golden green in color. Most of the egg-sacs were constructed under the shelter of leaves in the upper branches of trees and shrubs near to the parent female's web site. There, because of their coloration, they are quite well camouflaged.

DEVELOPMENT PERIOD.—Unfortunately we failed to obtain data on the development period of eggs in situ, and eggs that we brought to Europe to study under laboratory conditions failed to hatch.

Hatchling Behavior and Dispersion

After hatching the spiderlings remain in roughly spherical aggregations around the egg-sac for up to nine days. During this time they respond to air currents by dropping on silk lines, but climb back into the aggregation after the disturbance has ceased. Figure 10 shows an aggregation of spiderlings two days after emergence from the egg-sac. Presence of exuviae in some masses suggests that the spiders may molt at least once before dispersing. Lowry (in McKeown, 1963:150–151) described hatching and the subsequent behavior of the hatchlings in the case of *N. plumipes,* reporting that the spiderlings could remain within the egg-sac for a considerable period before emerging to form a loose cluster around it. She concludes that emergence may be conditional on climatic conditions. Thakur and Tembe (1956:331–332) give data on the shape of the egg-sacs of *N. maculata* near Bombay, India, and speak of the cocoon being placed in "a well-concealed place." Fischer (1910a) never found the egg-sacs of this species.

We did not see the process of dispersion but on a number of occasions noted the overnight disap-

FIGURE 10.—An aggregation of newly emerged *Nephila maculata* spiderlings beneath a leaf.

pearance of clusters of spiderlings. Although we think it probable that they may disperse by ballooning on silk threads, we have not seen aerial dispersals of young in the tropics. Bristowe (1939:187) has commented that "it is probable that the young of most species disperse themselves by aerial methods in all countries where a sudden change in ground temperature occurs in the morning, but more observations are needed in the tropics before we can be certain that this means of dispersal is as important there as in temperate regions." Our observations at Wau and in Panama suggest that eggs are hatching at intervals over most of the year and this fact probably explains the absence of conspicuous massed migrations of ballooning spiderlings in these regions. Such migrations are typically autumnal in the temperate zones (Bristowe, 1939:182–201, for discussion and bibliography). We have certainly recorded the presence of very young *N. maculata,* with webs, at distances of over 50 meters from the nearest known egg-cluster. It seems a logical assumption that these spiderlings arrived at such sites by aerial dispersion.

The group of freshly emerged spiderings of *N. maculata* shown in Figure 10 has produced a clearly visible complex maze of threads. Such clumps may contain more than 1000 spiderlings. Mortality in the early stages of development must be high.

Phenology of Population Increments

Although we did not monitor the presence of early stage spiderlings in the study area—an extraordinarily difficult habitat in which to count animals less than 3 mm long—we did census the adjacent line transect (see page 4 and Figure 4). Here we recorded the presence of all trap-building spiders, scoring adult and immature spiders separately. It was not possible to measure the spiders during the census so that records of immatures, refer to obviously immature spiderlings and include several instars. All large increments of immatures were found to be due to early-stage spiderlings. Figure 8 plots the outbreaks of immature *N. maculata* at this transect. There is a fairly regular increment of spiderlings during most weeks of the census until week 25 (8 November 1970) when the number exceeds 15 for the first time. Thereafter it exceeds 15 until week 50 (2 May 1971). During the period of this higher density of immatures the number occurring at the weekly census exceeded 50 on 18 occasions. We think that *Nephila* spiderlings are probably emerging over most of the year in the study area and that the increments in the marginal transect area support this view. The larger increments in the wetter months suggest that conditions may then be favorable for either hatching, or the survival of the spiderlings, or both. The occurrence of peak populations of mature males during this period supports the view that survival rates may be higher at this time, at least for spiderlings up to the size of adult males. This matter is discussed later in an overall consideration of the phenology of the species at Wau. The data on egg-laying, on the presence of males in female's webs, and on the occurrence of immatures at the transect all suggest that reproduction in *N. maculata* at Wau, occurs throughout the year. Near Bombay, India, where Thakūr and Tembe (1956) carried out their study the climate is much more markedly seasonal than at Wau. Figure 11 gives climographs for Bombay, and for Bulolo, New Guinea, and monthly rainfall data for Wau. Bulolo is the nearest locality from which we have reliable temperature data. Near Bombay the *N. maculata* population is markedly seasonal. Thakur and Tembe (1956:330) report that the young appear at the "end of August and early in September. Their bodies then measure 1 cm." These are obviously *not* newly emerged spiderlings which are smaller than 3 mm in length. Thakur and Tembe (1956:331) also state that the females become gravid "during October and November" after which eggs are laid. The spiders become very rare by the end of December, almost absent in January and "no specimens at all were observed near Bombay during other months of the year" (Thakur and Tembe, 1956:330).

Allowing an extra month for the stages occurring prior to the 1 cm young seen in August, it would appear from this report that the spider is present for, at the maximum, seven months of the year and that five months, at least, are spent as eggs or in the egg-sacs. Reference to the climographs shows

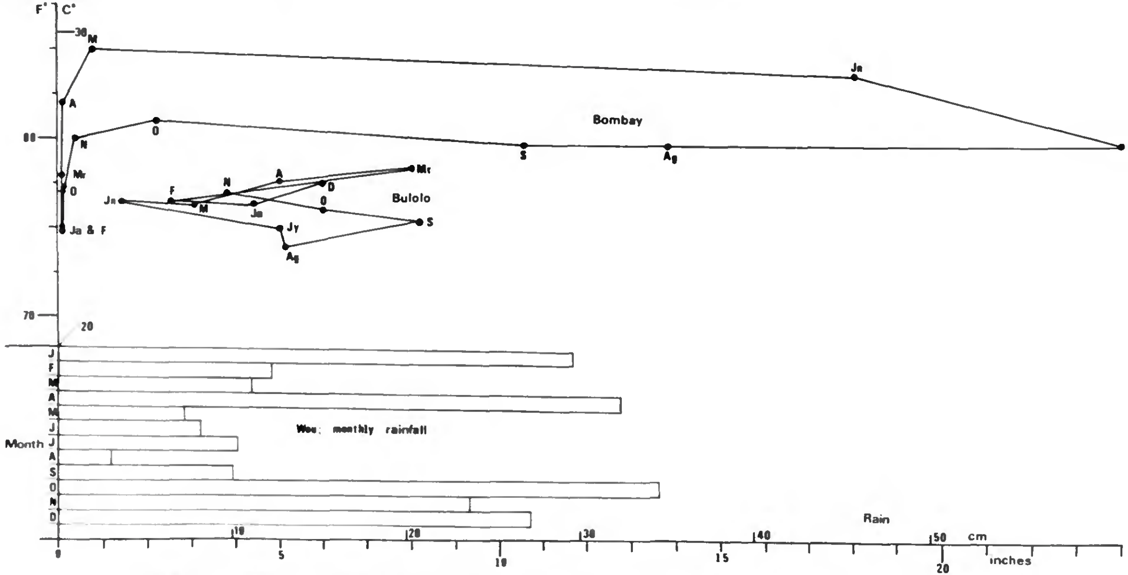

FIGURE 11.—*Above*: Climograph for Bombay, India, and Bulolo, New Guinea; *below*: histograms showing rainfall at study site during the study period.

that the spiders reappear about a month after the return of warm wet conditions (June) and become rare during onset of dry colder conditions (December/January).

PREY AND PREY CAPTURES

Taxonomic Range

Little is known of the taxonomic range of prey caught by *Nephila* species. Osorio and Moreno (1943) list 28 species of five orders of insects caught by *N. clavipes* in Cuba.

Thakur and Tembe (1956:332) state that near Bombay the food of *N. maculata* "consists almost entirely of butterflies, moths, dragonflies and grasshoppers." Hingston (1922c:918) suggests that the main prey are nocturnal "moths and flies."

Analysis of the data from prey traps and our observations over the whole of the Wau area confirm that, as Turnbull (1960) reported for *Linyphia triangularis* (Clerck), and we have reported for *Argiope argentata* (Fabricius) (Robinson and Robinson, 1970a), the spider is essentially opportunistic. Whatever is trapped at a particular web site and proves edible is prey. To illustrate: one observed spider included several winged phasmids, of two species, in its diet for a period of about three weeks. This is the only spider that we know of as taking phasmids in any quantity. Since we were also studying phasmids in this area we know that the web of this spider was built next to the one tree in the study area that was a food plant used by the two species. Thus the spider was in a position that provided it with a resource not practically available to the others. Similarly one of the sample had, for some time, a web site close to a colony of large social wasps. For several weeks this spider caught wasps of this species, which were not available to others in the sample.

In general the taxonomic range of prey caught by *N. maculata* at Wau was considerable. Analysis of the prey trap data did not permit division into taxa lower than the ordinal level in most cases, since we were dealing with fragments and were not prepared to devote a major portion of time to their determination of lower taxonomic categories. Nevertheless, some simple clues were usable; in determining orthopterans we assumed that debris of a particular green coloration represented tettigonioids rather than acridoids, since the latter were characteristically brownish in coloration in the study area. We also knew the coloration of the predominant butterfly species and were able to separate these from moth debris when wing fragments were large enough. This background must be borne in mind when considering our data on the taxonomic range of prey. (The dried prey fragments are available to any entomologist interested in working with them, either as a whole or in a particular order.)

Subsequent tables and figures show the data grouped into seven orders and the categories "others" and "unidentified." The range of organisms included in the "others" category are as follows—Araneidae: *Gasteracantha* species (1), *Nephila maculata* (3 males and 2 females); Salticidae (1); Lycosidae (1); Isoptera (2); Dictyoptera: Mantodea (2); Phasmatodea: *Eurycnema* species (1); Lepidoptera larva (1); and Dermaptera (1). Some of the easily identifiable subtaxa within the orders are as follows—Odonata: Anisoptera; Hemiptera: Heteroptera, Pentatomidae and Homoptera, Cicadidae; Diptera: Tipulidae; Lepidoptera: Sphingidae; Coleoptera: Scarabaeoidea, Staphylinoidea, Elateroidea, Cantharoidea, and Curculionoidea; and Dictyoptera: Blattaria and Mantodea.

Numbers in Taxa

Table 2 shows the total numbers of prey in each taxonomic category for the whole year. We cannot reasonably allocate the unidentified remains to orders by using the proportions obtained in the case of the identifiable remains because two groups, the Lepidoptera and Coleoptera, have features that survive maceration. Insects of these orders are thus less likely to become "unidentifiable" than are insects that are fragile and soft-bodied.

Odonates contribute only a small number to the total identified catch (12). Orthopterans are fairly low in numbers (199) of which tettigonioids constitute a major proportion (ca. 75%). Grilloids (11) and Acridioids (30) contribute relatively small numbers but are probably useful food sources because of their size when able to fly (i.e., when trappable by the spider's aerial web).

Hemipterans (273) are numerically ahead of orthopterans and the cicadas (139) are at least in

TABLE 2.—*Prey caught by a sample population of adult female* Nephila maculata *(N=10) during 52 weeks* *

Prey	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Odonata	2	–	–	1	2	–	–	–	–	1	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	1	–	–
Orthoptera	2	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	1
Grylloidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	3	3	–	–	1	1
Tettigonioidea	2	–	4	2	1	3	4	2	7	7	6	6	5	8	12	6	4	12	5	5	4	4	–	1	3	8	4	5
Acridoidea	–	–	1	–	–	–	–	1	2	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	3	4	2	1
Hemiptera	3	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–	4	–	1	3	1	–	2	1	–	–	–	2
Heteroptera	–	–	–	1	–	–	–	–	–	2	3	–	–	–	1	1	–	1	–	–	–	–	1	1	2	1	1	3
Homoptera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	4	2
Cicadoidea	1	–	1	–	2	1	–	–	–	1	–	1	–	1	–	–	–	–	1	–	–	–	–	3	9	11	5	7
Lepidoptera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Moths	55	41	39	29	42	46	29	39	29	27	34	26	25	20	24	40	23	15	10	25	12	23	27	25	24	18	13	12
Butterflies	1	–	–	–	–	–	1	–	1	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Diptera	5	8	24	2	16	20	22	9	15	6	18	25	14	21	12	16	8	7	5	2	2	4	1	–	–	2	2	4
Nematocera	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	–	–	–	–	–
Brachycera and Cyclorrhapha	–	2	–	–	–	–	–	7	1	6	5	4	4	1	2	–	2	–	–	1	2	3	–	1	–	1	–	–
Hymenoptera	10	5	1	–	–	–	–	2	–	2	–	–	–	2	–	–	6	–	–	–	–	1	1	5	–	3	–	–
Ants	5	6	2	–	–	–	3	–	1	–	4	1	–	1	6	–	1	1	5	–	–	–	–	–	–	–	–	–
Wasps	3	1	1	–	1	–	–	–	1	–	–	–	–	1	4	2	2	–	–	–	–	–	1	1	2	–	–	–
Bees	3	–	1	–	–	1	–	–	2	–	1	–	1	1	–	1	3	3	–	2	7	–	3	1	–	1	–	–
Coleoptera	32	37	22	22	42	37	29	28	28	37	27	41	23	20	32	25	16	11	12	19	15	28	28	12	18	21	20	21
Scarabaeoidea	–	–	1	1	1	–	–	–	–	1	–	–	–	–	–	–	5	17	14	19	20	11	10	15	13	2	3	3
Elateroidea	–	–	–	–	2	–	–	–	–	–	–	1	–	1	–	–	–	1	1	–	–	1	–	–	1	–	–	–
Cantharoidea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
Dictyoptera	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	1	2	–	1	–	–	–	1	–
Other orders	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–
Unidentified	43	55	61	27	49	32	31	31	34	50	73	73	35	49	41	36	33	39	47	46	32	33	32	38	32	28	28	28
Total numbers	168	157	162	87	159	140	119	119	121	141	173	180	108	128	135	129	108	107	102	123	97	109	113	109	107	107	85	90
Total grams	1.825	1.65	2.145	1.327	2.403	2.453	1.595	1.448	1.845	2.584	3.254	2.665	1.595	1.618	2.233	2.605	2.375	3.265	4.145	3.91	4.195	3.703	4.61	4.67	4.33	2.433	1.95	2.695

Prey	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	Total
Odonata	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	1	12
Orthoptera	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
Grylloidea	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11
Tettigonioidea	1	1	–	3	1	–	–	–	1	–	–	–	–	3	3	1	1	–	–	–	1	–	1	–	147
Acridoidea	2	2	–	–	1	–	–	–	–	–	–	–	–	5	2	1	1	–	–	–	–	–	–	–	30
Hemiptera	–	–	4	2	1	–	3	1	–	–	1	–	3	–	1	–	1	1	–	5	11	7	–	–	62
Heteroptera	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	4	8	35
Homoptera	1	–	–	–	1	–	1	1	–	1	–	2	–	1	1	–	1	4	1	3	2	1	2	3	37
Cicadoidea	12	18	15	2	6	5	7	2	3	8	3	–	3	5	1	1	1	–	–	–	2	1	–	–	139
Lepidoptera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1**	–	–	–	–	1
Moths	9	9	16	25	19	16	23	24	14	38	39	39	20	16	25	19	21	31	25	19	40	62	62	45	1428
Butterflies	–	–	–	–	–	–	–	–	1	–	1	–	–	2	–	–	–	–	1	1	–	–	–	–	13
Diptera	–	2	4	5	16	7	10	9	5	5	9	14	7	7	10	9	17	7	7	5	30	18	32	15	520
Nematocera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	1	1	1	11
Brachycera and Cyclorrhapha	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	44
Hymenoptera	–	–	–	–	–	1	–	–	–	1	–	–	–	2	–	–	–	–	–	2	2	2	3	2	53
Ants	1	–	2	–	2	–	3	1	4	4	–	1	–	–	3	3	3	1	–	2	5	1	1	1	74
Wasps	–	–	–	2	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	25
Bees	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32
Coleoptera	9	12	23	26	70	20	28	34	19	29	23	40	39	55	36	38	28	24	20	22	24	24	20	33	1399
Scarabaeoidea	–	1	3	5	6	1	3	2	4	3	3	4	2	2	–	1	–	–	–	–	–	2	–	1	179
Elateroidea	–	–	–	1	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	11
Cantharoidea	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	4	6	5	2	21
Dictyoptera	–	–	–	–	–	1	3	–	–	–	1	–	2	1	1	–	–	–	–	–	–	–	–	–	17
Other orders	–	–	–	–	–	–	–	4	–	–	1	1	–	–	–	–	1	–	–	1	–	1	–	1	15
Unidentified	14	13	24	15	22	13	18	20	33	51	29	33	21	27	43	31	29	16	17	13	23	34	17	20	1712
Total numbers	57	59	91	87	146	64	100	99	84	141	111	134	99	126	126	104	104	86	72	75	149	160	148	134	6039
Total grams	1.655	1.585	2.403	2.31	3.305	1.111	2.505	2.192	1.986	2.24	2.029	1.981	1.523	2.937	2.357	2.053	1.905	1.31	1.457	.985	2.027	2.223	1.464	2.473	123.544

* Average wt. per prey item, .0205 gm. Number of web-days, 3237. Average daily catch per web, .0382 gm. Numbers on row opposite ordinal name are of prey not identifiable to lower taxonomic levels.

** Caterpillar.

the same size range. Lepidopterans make up the second largest group of identified remains (1442) and constitute 33.3 percent of these (23.9% of all prey caught, including unidentified packages). Of the Lepidopterans, moths (1428) constituted the largest number; this remains true even if we admit the possibility of some misclassification in this category. The preponderance of moths can be accounted for by a number of factors, one of which may be a differential potential for web-avoidance between diurnal and nocturnal insects of this order. (There are undoubtedly differences in the numbers of diurnal and nocturnal lepidopterans in the study area and this point is discussed later). Dipterans rank third in total numbers (575) and could be heavily implicated in the unidentified category. Their importance in the prey-economy of the adult spider may be less than is suggested by their numbers since very few of those caught in the study area exceeded 50 mg in weight. Hymenopterans totaled 184 and again may be well represented in the unidentified remains. Ants (74) were principally alates and catches probably coincided with nuptial flights. Wasps (25) and bees (32) are low in numbers. The Coleoptera constituted 37.2 percent of identified prey and are the insects present in the largest total number (1610). Of these beetles, those definitely identified as scarabioids (179) were probably the heaviest insects caught by the spiders during this study. Seventeen Dictyopterans were identified among the remains. Since small adult roaches were frequently observed at night and represented 12.6 percent of the total number of insects caught on the sticky traps, they may be an important element in the unidentified category. In Table 2 they are listed as "Other orders."

It is very noteworthy that the relative proportions of the major taxonomic groups that constitute the spider's prey vary very little between the ten individuals that constituted our sample. (This relative constancy is even more remarkable when it is considered that spiders nos. 1–10 were not the same individuals over the year.) Table 3 gives the proportions of the total catch that were made up by insects of the orders Lepidoptera, Coleoptera, Diptera, Orthoptera, Hymenoptera, Hemiptera, and Odonata plus unidentified and "others." The greatest range of variation is in the "unidentified" category.

Temporal Distribution

Figure 12 shows the distribution of the proportions of prey numbers, by the same categories used in Table 2, divided between the six driest and six wettest months of the year.

The overall total for the six wettest months (October, November, December, January, February, April) is less than that for the six driest months (March, May, June, July, August, September) but not markedly so (2586 against 3453).

Numbers of orthopterans, dipterans, lepidopterans, hymenopterans, and coleopterans are all higher in the dry months than in the wet months. Hemipterans are higher in numbers in the wet season. The total weight of prey caught in the wettest months exceeds that caught in the driest months—at least on the basis of the weight of prey residues: 58.674 grams (47.5%) against 64.87 (52.5%) for the wet months.

The fluctuation in weekly total catches for the major (ordinal) categories can be seen from Figure

TABLE 3.—*Percentage composition of prey per spider plus composition of insects caught by window-pane and sticky traps* (total prey sample=6039)

Prey	*Spider*												
	1 (N=585)	*2 (N=596)*	*3 (N=562)*	*4 (N=639)*	*5 (N=588)*	*6 (N=601)*	*7 (N=485)*	*8 (N=658)*	*9 (N=632)*	*10 (N=693)*	*Mean percentage*	*W. P. trap*	*Sticky trap*
Odonata	0.2	–	0.4	–	0.2	0.2	0.2	0.4	–	0.4	0.2	0.01	–
Orthoptera	3.6	2.3	3.9	2.2	2.0	4.0	4.7	3.8	4.6	2.5	3.3	0.8	1.0
Hemiptera	4.4	4.8	3.7	3.7	4.6	5.7	3.6	3.9	7.6	4.2	4.5	7.5	8.1
Lepidoptera	24.5	25.9	20.1	23.9	23.0	23.2	21.2	21.2	22.9	30.5	23.9	23.1	1.7
Diptera	9.5	9.3	8.2	10.1	10.0	9.3	7.7	8.9	12.8	7.4	9.5	26.6	11.2
Hymenoptera	2.4	3.0	2.7	2.9	3.3	2.9	3.8	4.4	2.8	2.9	3.0	9.6	5.0
Coleoptera	28.6	25.5	30.6	23.6	24.8	23.0	29.7	32.9	25.4	19.6	26.7	26.5	55.6
Other orders	0.3	1.4	0.7	–	0.8	0.8	0.2	0.7	–	0.6	0.54	5.8	17.2
Unidentified	26.4	27.7	29.7	33.3	31.1	30.7	28.8	23.7	23.8	31.9	28.3	–	0.2

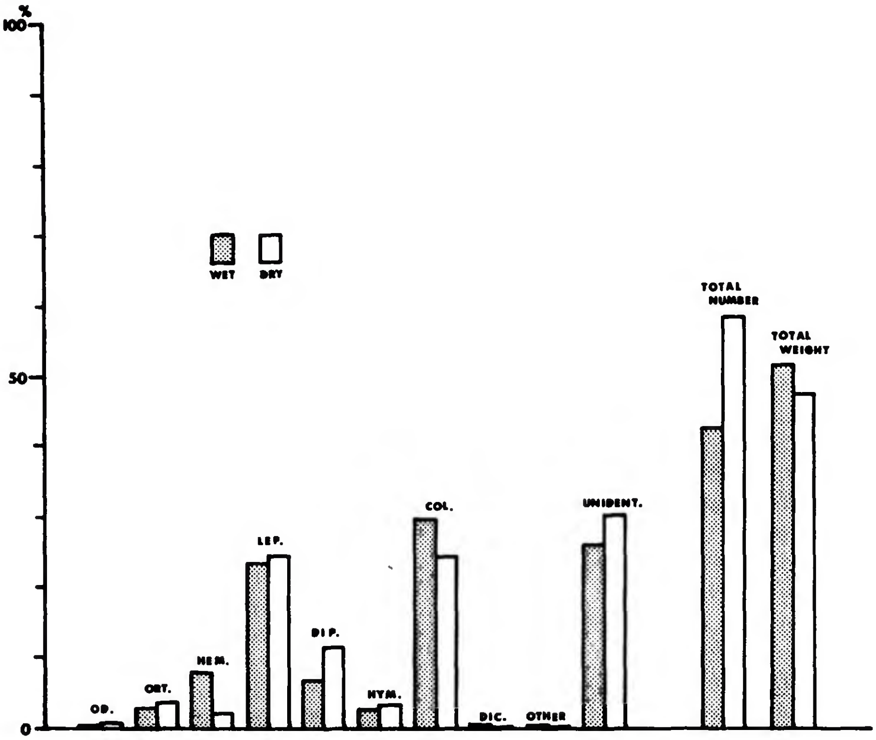

FIGURE 12.—Percentage composition of prey, by orders, divided between the six driest months and the six wettest months.

13. Note that the Odonata, Orthoptera, Diptera, Hemiptera, and Hymenoptera are absent from some weekly catches, whereas Lepidoptera and Coleoptera are always present. Table 4 gives monthly totals for the entire year and is comparable with Table 2 of Robinson and Robinson (1970a: 350). From this it will be seen that two orders, represented by low total numbers, are absent from identified catches in some months. Thus odonates are absent in January, March, April, October, and December. Dictyopterans are absent in April, June, July, and December.

Within some of the more numerous orders there are absences of subgroups in certain months. Thus within the Orthoptera identifiable gryllids were present only in September, October, November, December, with more than half the total being caught in October (a wet month). Tettigonioids were caught in all months, but three months (July, August, and September) account for more than half the total catch. The acridoids were absent in identifiable remains for the months of February, April, May, August and October, and two months (March and November) account for more than half the yearly total. Some hemipterans were present in all months, but the large and conspicuous cicadas (suborder Homoptera) were caught in all but one (October) of the six wettest months and only two (March and May) of the six driest months. More than half the total yearly catch of cicadas occurred in two months: April and November.

Lepidopterans were caught in all months but of the positively identified butterflies (13) eight were caught in four of the driest months (March, May, July and August) and five in four of the wettest months (November, January, February and April). More than half the yearly catch of moths was caught in five successive months (April, May, June, July, August).

Monthly totals of dipterans vary between 11 (December) and 95 (August) and similar totals for Hymenoptera between 7 (February) and 32 (May).

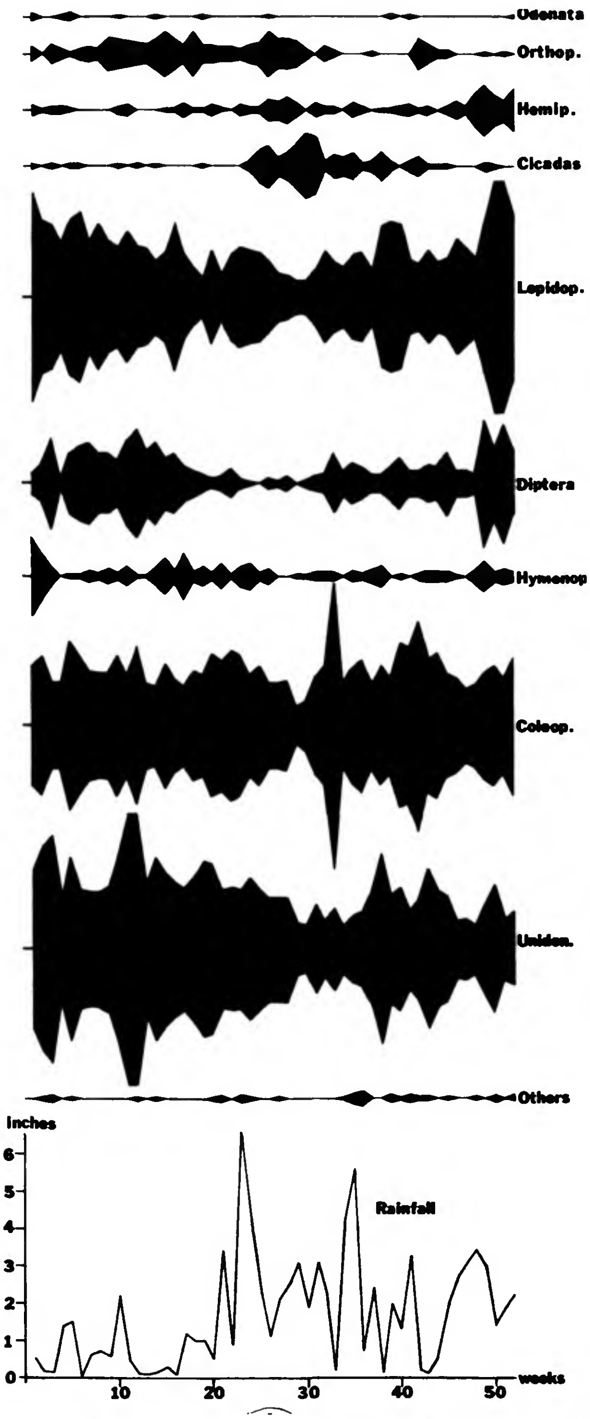

FIGURE 13.—Weekly distribution at study site of numbers of prey, by order, against rainfall.

Total catches for coleopterans range from 99 in April to 164 in January. The large scarabaeoid beetles appear in large numbers in September, and 172 out of the year's total of 179 are caught in this and the succeeding six months. This period includes the weeks of highest average weight of unit prey remains.

Numbers of unidentified prey remnants vary throughout the year and constitute 28.3 percent of the yearly total. In the six driest months the total is 1040 against 672 for the six wettest months. The difference, 368, is approximately 21 percent of the total. The highest number of unidentified remains, 237, occurs in August and the lowest, 71, in December.

Weights of Prey Remnants

The total weight of the prey remnants collected in the prey traps was 123.544 grams. The weekly distribution of the weights that make up this total are given in Table 2 alongside the average weight per unit prey (obtained by dividing the weight by the total number of prey items, identified and unidentified). What this figure may represent in terms of live weight is discussed in the section on energetics (page 33). It is more than half of the estimated live (wet) weight of prey caught by a sample population of *Argiope argentata* in one year (Robinson and Robinson, 1970a:349).

Of this total weight 64.87 grams (52.5%) were the contribution of the six wettest months and 58.674 grams (47.5%) were collected in the six driest months. The highest weekly totals occur in October when, in two successive weeks (23 and 24), the totals exceeded 4.6 grams. Totals of over 4 grams occurred in one week (19) in September and one week (25) in November. In fact in the 7 weeks commencing 23 September and ending 10 November, the prey remnants totaled 29.563 grams, 23.9 percent of the yearly total! This was also a period of high average weights of prey remnants (all averaging over .03 grams per unit). This suggests that some large prey item is seasonally available to the spiders. This is borne out by the fact that scarabaeoid beetles feature prominently in the catches for these weeks. Melolonthids, in particular, were recorded in enormous numbers at light during this period and featured heavily in prey-trap re-

TABLE 4.—*Monthly totals of insects caught by mature* Nephila maculata *sample (N=10)**

Prey	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Total*	*Percent*
Odonata	–	2	–	–	3	3	1	1	1	–	1	–	12	.2
Orthoptera	–	–	–	–	2	1	1	–	–	–	3	4	11	.18
Grylloidea	–	–	–	–	–	–	–	–	2	6	2	1	11	.18
Tettigonioidea	1	1	8	1	3	10	23	33	31	11	20	5	147	2.43
Acridoidea	1	–	9	–	–	1	4	–	1	–	10	4	30	.5
Subtotal	2	1	17	1	5	12	28	33	34	17	35	14	199	3.3
Hemiptera	5	3	3	19	9	3	–	–	5	6	3	6	62	1.03
Heteroptera	–	–	–	2	12	1	2	4	2	1	8	3	35	.58
Homoptera	3	1	5	11	5	–	–	–	–	–	11	1	37	.61
Cicadidae	19	16	8	2	3	3	1	2	1	1	32	51	139	2.3
Subtotal	27	20	16	34	29	7	3	6	8	8	54	61	273	4.52
Lepidoptera														
Moths	84	136	92	129	229	172	140	109	94	98	79	66	1428	23.65
Butterflies	1	1	2	2	1	–	2	3	–	–	1	–	13	.22
Larvae	–	–	–	1	–	–	–	–	–	–	–	–	1	.02
Subtotal	85	137	94	132	230	172	142	112	94	98	80	66	1442	23.88
Diptera	46	31	52	56	67	62	58	82	39	8	8	11	520	8.16
Nematocera	1	–	–	3	4	–	–	–	–	2	1	–	11	.18
Brachycera & Cyclorrhapha	–	–	–	–	2	–	17	13	2	6	4	–	44	.73
Subtotal	47	31	52	59	73	62	75	95	41	16	13	11	575	9.52
Hymenoptera	1	1	2	6	15	6	4	2	6	4	6	–	53	.88
Ants	1	1	–	1	4	2	1	5	4	2	2	2	25	.41
Wasps	8	5	10	8	10	5	8	2	13	–	–	5	74	1.23
Bees	–	–	–	–	3	2	2	3	7	12	2	1	32	.53
Subtotal	10	7	12	15	32	15	15	12	30	18	10	8	184	3.05
Coleoptera	147	123	173	92	119	141	136	125	69	97	80	93	1395	23.1
Scarabaeoidea	15	11	4	–	3	3	1	–	41	60	30	11	179	2.96
Elateroidea	1	–	1	–	–	2	–	2	2	1	1	1	11	.18
Cantharoidea	–	–	–	7	12	–	–	–	1	–	–	1	21	.35
Curculionidea	1	–	–	–	2	–	–	–	–	–	1	–	4	.07
Subtotal	164	134	178	99	136	146	137	127	113	158	112	106	1610	26.66
Dictyoptera Blattaria	4	3	2	–	1	–	–	2	1	3	1	–	17	.28
Other orders	4	2	1	2	1	3	–	–	–	2	–	–	15	.25
Unidentified	97	142	133	77	151	177	174	237	168	167	118	71	1712	28.35
Grand total	440	479	505	419	661	597	575	625	490	487	424	337	6039	
Percent caught per month	7.29	7.93	8.36	6.94	10.95	9.88	9.52	10.35	8.11	8.06	7.02	5.58		

*Numbers on row opposite ordinal name are of prey not identifiable to lower taxonomic levels.

mains. Their emergence is known to be facilitated by wetting of the ground where they pupate, and the rainfall in September followed a dry spell (Figure 13). The catch for the week commencing 23 September (week 19) included 14 cockchafers which also figure prominently in the following weeks 20–25 (15, 14, 11, 10, 11 and 5). The catch for October also included five other scarabaeoids of more than 20 mm in length. Other contributors to the heavy average weight during this period were very large gryllids (page 20).

In all there was one week (week 48) with a total of less than one gram of prey remnants (April 1971), six weeks with between 1.0 and 1.5 grams, thirteen weeks with between 1.5 and 2.0 grams, 22 weeks with between 2.0 and 3.0 grams, five weeks with over 3.0 and less than 4.0, and five weeks with over 4.0 and less than 5.0 grams.

We cannot assign weights to the numbers of prey in each taxonomic division since we were dealing with prey remnants and it would have been far too time-consuming to weigh each of the 6039 trash packages separately. Similarly we were not able to record size ranges of the prey items (as did Robinson and Robinson, 1970a, when recording prey in the webs of *Argiope argentata*). Thus there is no method of weighing samples and assigning approximation of weights to the numbers of prey in each taxon. We can make, however, some very crude guesses about the effect of considering weight, on the relative importance of the various categories of prey. Thus, in the case of the orthopterans, it would be reasonable to assume that most of those that were caught would be alate adults that could fly and therefore be more likely to move into webs sited well above the ground than would juveniles, which can only jump. We would assume, therefore, that the relative importance of orthopterans as prey (3.3% of the total catch) is not likely to be diminished because of below average weight. On the other hand few dipterans exceed 0.05 grams in live weight and we would predict that if the weight of the 575 dipterans caught by *Nephila* was known their contribution to the total catch would be less than the 9.5 percent calculated from their numbers. Because the catch of hemipterans includes 139 weighty cicadas (average weight probably above 0.2 grams) we would expect the prey in this category to be more important than their 4.5 percent by numbers suggests. The two orders providing the predominant numbers, Coleoptera and Lepidoptera, are, we feel, likely to contribute numbers of weighty prey and their predominant position is likely to be reinforced if we considered their contribution to the calories available to the spider. These considerations suggest that a ranking of taxonomic categories in terms of "energy bundles" would read, in descending order: Coleoptera, Lepidoptera, Orthoptera, Hemiptera, Diptera, Hymenoptera, Odonata, and Dictyoptera.

Comparison of the monthly distributions of the weight of prey with the numbers of prey gives rise to some interesting observations. The weights of prey start to rise in August whereas prey numbers fall from this point until December. The weights reach a peak in October and then fall through November to December but the December total is still higher than all the other months of relatively low weights, except March. The December low point in prey numbers is the lowest of the year. The rise in prey weights during this period corresponds to an increase in rainfall to the year's peak in October (which was also the month with the largest number of days of rain). As stated earlier, the period of high weights and relatively low numbers was one when heavy scarabaeoid beetles were abundantly represented in the catches and these probably account for the differences cited above.

Comparison with Argiope argentata

As far as we are aware the only study of a spider's prey over a one year period is that on *Argiope argentata* (Robinson and Robinson, 1970a). There have been a number of excellent studies of the prey of temperate orb-weavers (see Kajack, 1965, for an extensive bibliography), but the subjects have all been spiders with a seasonal activity covering only part of a year. *Argiope argentata* differs from *Nephila maculata* in being largely diurnal, choosing open areas for its web sites, having an advanced pattern of predatory behavior (Robinson, Mirick, and Turner, 1969), and being considerably smaller and lighter than *N. maculata*.

The area where studies of *A. argentata* were carried out has a much more seasonal climatic pattern than Wau. At Barro Colorado Island in Panama there is a pronounced dry season of 3 to 4 months (total rainfall average 8.2", three months with less than 3" rain) and a distinct wet season of 8 to 9 months, total rainfall average 98.9". This is not true of Wau where in only one month (August) did the total rainfall drop below 3", and this was exceptional.

There are major differences between the catches of the two spiders in taxonomic content and in temporal distribution. In terms of numbers, hymenopterans constitute the most important prey item for *Argiope* with a total of 3304 out of 4672 prey items. This compares with 184 out of 4327 identified prey items in the case of *Nephila*. This is 70.6 percent of the total prey caught by *Argiope* and 3.0 percent of the total caught by *Nephila*. In terms of weight these hymenopterans constitute an estimated 18.1 percent of the total caught by *Argi-*

ope and are most unlikely to increase their relative importance to *Nephila* if weight is considered. Orthopterans were the second most important prey item, in numbers, to *Argiope* (11.4%) and constituted only 3.3 percent, by numbers, of the *Nephila* catch. In weight, orthopterans rise to the predominantly important prey item for *Argiope* (55.2%) and are most unlikely to assume this importance for *Nephila*. Of the orthopterans caught by *Argiope*, tettigonioids account for 57.4 percent, acridioids for 41.4 percent, and grylloids for 1.5 percent. The equivalent percentages for *Nephila* are 73.9, 15.1, and 5.5, with 5.5 percent not assigned to superfamily.

Coleopterans are the most important prey, numerically, for *Nephila* (26.6%) and are probably the most important prey item in terms of weight. For *Argiope* they account for 5.8 percent of the catch by numbers and an estimated 6.6 percent by weight. We have not seen *Argiope* feeding on large beetles. Similarly, lepidopterans account for 23.9 percent of the *Nephila* catch and only 2.9 percent of the *Argiope* catch, by numbers, and 5.4 percent by estimated weight. Of the lepidopterans caught by *Nephila* 99 percent were classified as moths, 0.9 percent as butterflies and 0.1 percent as larvae. In the case of *Argiope* 89.8 percent were butterflies and 10.1 percent moths.

Of the other orders odonates were caught in small numbers by both species of spider, *Nephila* catching 12 (0.2%) and *Argiope* 48 (1.03%, *not* 0.14% as given in Robinson and Robinson, 1970a:349). Hemipterans occur in relatively small numbers in both cases, *Nephila* catching 273 (4.5%) and *Argiope* 207 (4.4%). As stated earlier the relative importance of hemipterans to *Nephila* should perhaps be increased if we consider that the cicadas are heavy, and therefore an important source of food that is belied by their relatively small numbers (139 or 2.3% of the total catch by numbers), *Argiope* did not catch large cicadas.

Dipterans account for 9.5 percent of the total catch of *Nephila* and 2.4 percent of the catch of *Argiope*. Their importance to *Nephila* is probably less than their numbers suggest because of their small size.

Many of the differences between the taxonomic composition of the prey of the two spiders probably result from differences in habitat, web siting, and web structure. Of these the first two are probably the most important. The two spiders are undoubtedly catching insects that preponderate in different proportions in the two habitats, and the two zones within the two habitats. Robinson and Robinson (1970a:355–356) discuss the factors that may influence the catch of *Argiope argentata* at Barro Colorado Island. The influences acting to determine the scope of the *Nephila maculata* catch, at Wau, are discussed above.

Differences in the seasonal patterns of the catches of the two spiders are grossly relatable to differences in the climatic pattern at the two localities. The effect of the lowland monsoon climate at Barro Colorado is not entirely clear but there are suggestive data (Robinson and Robinson, 1970a:352–353). The dry season in Panama is clearly more inimical to spider activity than the short dry intervals at Wau.

Comparison with Insect-Trap Catches

Kajack's (1965, 1967) studies of the food relationships between spiders and their prey were based on intensive studies of three species of small araneids. Prey caught by the spiders was sampled by removing prey items from the webs and the abundance of mobile insects was evaluated by using sticky traps. Kajack found (1967:814) that "the fauna captured on these traps coincided with those caught in the webs so that it was possible to regard the number of insects on sticky traps as an index of abundance of the potential food of the spiders." The three species that Kajack studied, *Araneus quadratus* Clerk, *A. cornutus* Clerk, and *Singa hamata* (Clerk) are all smallish spiders (Locket and Millidge, 1953), considerably smaller than *Argiope argentata*, and very much smaller than *Nephila maculata*. Kajack states (1967:813) that "very small insects which weigh hundredths or tenths of mg (from 0.05 to 0.1 mg) constitute the vast majority of prey caught in spiders' webs." Thus the spiders Kajack studied caught very much smaller prey than either *Argiope argentata* (Robinson and Robinson, 1970a) or *Nephila maculata*. This point is relevant to a consideration of how insect sampling techniques can be used to assess the prey available to the larger tropical orb-web spiders.

Pilot studies that we carried out in Panama suggested that sticky traps would not adequately sample the availability of prey to the larger orb-weavers. Many insects seemed capable of detecting the presence of such hazards and avoiding them. This view was confirmed by some studies that we carried out (in conjunction with W. Graney) to investigate the possibility that insects might detect the presence of apparently much less conspicuous traps such as spider's webs. After various trials we eventually decided to watch the behavior of insects flying in the vicinity of a 10 × 5 foot length of double nylon mist netting that was erected in the laboratory clearing at Barro Colorado Island. This was large enough, unlike a spider's web, to provide a reasonable number of interceptions by insects in an 8-hour observation period (divided into half-hour shifts). The net was presumably more conspicuous than a web but much less conspicuous than a sticky trap. Some insects proved quite capable of detecting its presence and made avoidance maneuvers. Thus an insect would fly towards the net and then, when nearby, rise almost vertically, fly over the top, and proceed on its flight path. Other insects blundered straight through the net striking its threads, while others changed direction after striking the net. It was interesting to find that the same species of insect would in one set of circumstances avoid the net while in the course of another behavior it would hit it. Thus large wasps flying on a "beeline" would hit the net, but when flying erratically from flower to flower they would miss it and take very obvious avoiding action. This suggested to us that some insects might be able to avoid webs. We tried to test this further in New Guinea by mounting a *Nephila maculata* web on the glass of a window-pane trap and operating this next to a normal window-pane trap. Each day we moved the traps around and tried thereby to eliminate any position effect. There were interesting differences between the catches of these two traps over a 14-day period. Catches of insects belonging to the orders Diptera, Hymenoptera, Coleoptera, Lepidoptera, and Hemiptera were all lower in the case of the trap with the web mounted on the glass. The total number of insects involved (462 caught by the experimental trap, 505 by the control) is unfortunately too small to enable us to determine whether there are any groups *within* orders that are less sensitive to spider's webs than others. We are continuing this experimentation in other localities.

Our doubts about sticky traps led us to consider the possibility that window-pane traps might give a better index of the food available to large spiders such as *Nephila maculata*. To test our Panama-based conclusions about the inadequacy of sticky traps we also used these at Wau. Data from the traps are of interest in two respects Firstly they enable a comparison to be made between the specificity of the web and the specificity of the traps. Secondly the trap data should reveal any cycling or periodicity of outbursts within specific groups of insects, which should be valuable as a check on fluctuations in the temporal pattern of occurrence of particular groups of prey.

In fact for the 43 weeks (3 June 1970-30 March 1971) for which we have data from the window-pane traps the three traps caught more insects than the ten spiders: 7555 compared with 4850. During the same weeks the window-pane traps caught more lepidopterans than the spiders: 1743 compared with 1064, and more beetles: 2003 compared with 1342. The weekly analysis of numbers is given in Tables 5 and 6. (All these figures deal with insects over 4 mm in length; we decided that prey less than this size would pass straight through the web of an adult *Nephila*). On the whole the majority of insects caught by the window-pane traps was small and did not include large lepidopterans and beetles of the sizes that were seen in the spider's webs. Table 7 details the size distribution of the insects caught by the window-pane traps.

In Figure 14*a* we have plotted the weekly totals of prey from the prey traps and insects caught by the window-pane and sticky traps. From this it will be seen that there is no obvious correlation, positive or negative, between fluctuations in the spider's prey numbers and the numbers of insects caught by the traps. We have worked our correlation coefficients for total numbers of prey caught per week by the spiders and insects caught by the window-pane traps. These give no basis for rejecting the hypothesis of no correlation between the two sets of results. We believe that there *is* no correlation between the two. Similar statistical results apply to comparing the weekly totals of lepidopterans and coleopterans caught by the spiders and the window-pane traps. Interestingly enough the pro-

TABLE 5.—*Weekly analysis of insects caught in 3 window-pane traps*

Prey	3*	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Odonata	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Orthoptera	2	3	1	2	-	1	1	3	1	-	-	-	2	1	-	2	-	2	1	1	1	1	2	2
Hemiptera	18	21	11	8	12	4	8	15	8	7	20	20	11	13	14	16	8	17	10	11	14	6	10	8
Cicadoidea	-	2	-	1	1	1	2	1	-	-	1	-	-	-	-	2	3	-	-	1	2	-	2	3
Lepidoptera	57	33	49	27	32	46	46	51	61	31	44	43	40	50	53	46	36	62	58	54	45	29	41	33
Diptera	65	57	75	63	100	131	91	66	60	45	63	44	26	20	33	43	31	28	45	26	19	22	24	25
Hymenoptera	17	18	18	38	18	13	18	37	25	20	21	9	10	11	18	9	16	17	14	25	14	10	20	14
Coleoptera	49	48	45	27	34	26	19	31	15	16	15	20	21	20	25	30	46	19	35	17	33	35	32	37
Scarabaeoidea ...	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Elateroidea	1	-	3	2	1	2	-	5	-	1	4	6	6	5	3	2	3	3	4	4	5	7	6	6
Cantharoidea ...	6	9	18	4	4	5	7	6	5	7	6	6	1	1	9	5	5	8	3	8	6	4	2	3
Dictyoptera	-	-	1	1	1	-	1	-	-	-	2	2	-	-	-	1	-	1	2	2	-	1	2	3
Other orders	4	3	9	2	3	7	2	9	4	3	2	3	6	2	2	2	1	4	9	4	12	5	14	19
Total	220	195	231	175	206	236	195	224	179	130	178	153	123	123	157	158	149	161	181	153	151	120	157	153

* No traps erected during weeks 1 and 2. Numbers on row opposite are of prey not identifiable to lower taxonomic levels.

TABLE 6.—*Weekly analysis of insects caught in two sticky traps* *

Prey	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	*Total*	*Ordinal* *Total*	*Per-cent*
Odonata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2	2	.06
Orthoptera ...	-	4	1	1	4	-	1	3	3	1	4	-	-	2	1	1	-	1	-	1	1	1	1	-	-	-	1	32	32	.9
Hemiptera ...	31	12	18	17	11	8	5	10	10	24	8	6	17	10	6	8	4	6	5	6	4	6	4	6	9	6	5	262	-	-
Cicadoidea ..	-	-	-	1	-	-	-	-	1	7	3	1	6	-	1	2	-	1	-	-	-	1	-	-	-	-	-	24	286	8.1
Lepidoptera ...	4	6	5	1	4	6	6	2	-	3	1	9	4	-	-	-	1	-	3	1	-	2	1	-	1	-	-	60	60	1.7
Diptera	18	15	19	20	18	12	13	23	10	18	12	16	17	8	18	14	11	16	21	13	10	9	8	17	11	17	12	396	396	11.21
Hymenoptera ..	11	12	20	10	4	9	7	10	3	11	5	2	15	5	6	3	1	5	5	3	4	3	6	5	7	3	3	178	178	5.04
Coleoptera	75	72	44	64	44	47	52	47	35	62	58	35	40	68	74	99	56	99	87	59	31	42	27	54	37	49	45	1502	-	-
Scarabaeoidea .	-	-	-	-	-	-	-	-	-	1	1	-	2	-	-	3	1	2	1	-	-	1	-	-	-	1	-	13	-	-
Elateroidea ..	14	17	10	15	14	2	4	9	19	11	10	3	11	8	9	11	4	9	10	9	13	6	14	8	6	10	13	269	-	-
Cantharoidea .	7	6	5	6	3	7	8	13	11	8	6	9	5	9	11	7	5	8	7	6	1	3	3	7	4	5	9	179	1963	55.56
Dictyoptera	9	9	7**	7	12	11	9	15	9	18	16	3	9	20	19	35	18	14	35	19	22	17	30	29	18	21	15	446	446	12.6
Other orders ..	10	7	14	2	17	8	11	6	10	12	1	6	5	1	7	13	4	5	5	-	1	3	4	6	6	3	3	170	170	4.8
Total ..	179	160	143	144	131	110	116	138	111	176	125	90	131	131	152	198	105	166	179	117	87	94	98	132	99	115	106	3533		

* Weeks 1–18 no sticky traps erected. Numbers on row opposite name are of prey not identifiable to lower taxonomic levels.
** Includes 1 Mantodea.

TABLE 7.—*Size distribution of insects caught in window-pane traps**

Insects	<10mm	10–19mm	20–29mm	> 30mm	Total
Odonata	-	-	-	1	1
Orthoptera	29	31	7	-	67
Hemiptera					
Heteroptera	208	56	-	-	264
Homoptera	175	14	27	-	216
Cicadoidea	-	58	30	-	88
Lepidoptera	1245	451	47	-	1743
Diptera	1899	108	3	-	2010
Hymenoptera	586	122	14	-	722
Coleoptera	1659	326	17	1	2003
Other orders	368	72	-	1	441
Total numbers	6169	1238	145	3	7555
Total percent	81.65	16.40	1.92	.04	

*Numbers on row opposite name are of prey not identifiable to lower taxonomic levels.

portions of the total catches that were constituted by lepidopterans and coleopterans are similar when we compare the spider's prey with the window-pane traps. The histograms in Figure 14*b* show the percentage of the total numbers constituted by nine orders of insects in the catches of the spiders, window-pane traps, and sticky traps. The differences between the catches of lepidopterans and coleopterans mentioned above are less than 1 percent. The sticky traps, on the other hand, caught proportionally less lepidopterans (less than 1.7%) and proportionally more coleopterans (over 55.6%). These results indicate that very few of the unidentified prey packages obtained from the spiders are likely to be from lepidopterans or coleopterans; the proportions of these two orders are thus probably more truely comparable with the trap data than with those for other orders, which might be altered if the unidentified prey could be assigned to orders. Since we know that the spiders are catching larger insects of several orders than are the window-pane traps, and catching them at different times, the

TABLE 5.—(Continued)

Prey	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	*Total*	*Ordinal*	
																					total	*Percent*
Odonata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		1	1	.01
Orthoptera	6	4	3	-	2	1	-	-	-	2	15	2	-	1	-	-	1	1	-	67	67	.89
Hemiptera	14	13	12	9	21	7	5	5	8	6	6	5	15	11	8	14	12	11	8	480		
Cicadoidea	3	3	5	22	7	3	3	-	1	3	-	1	3	1	1	4	4	1	1	88	568	7.52
Lepidoptera	47	23	32	45	58	53	25	23	25	49	33	26	68	41	28	29	17	21	33	1743	1743	23.07
Diptera	19	35	13	50	78	82	53	46	46	72	47	48	45	34	32	36	25	25	22	2010	2010	26.6
Hymenoptera	12	18	12	23	30	19	22	12	15	16	12	16	18	15	13	10	7	13	9	722	722	9.56
Coleoptera	41	41	42	58	69	61	40	51	31	53	33	52	55	38	31	25	17	36	22	1491		
Scarabaeoidea	-	-	1	-	1	-	-	-	1	1	-	1	1	1	2	-	1	-	-	14		
Elateroidea	3	13	8	6	6	2	5	6	2	3	5	6	7	6	9	4	4	4	12	190		
Cantharoidea	5	2	10	13	13	8	13	15	7	7	8	11	5	7	11	12	13	5	5	308	2003	26.51
Dictyoptera	5	8	5	8	6	6	6	6	8	3	7	5	6	6	4	5	3	2	2	121	121	1.6
Other orders	7	13	11	4	5	4	1	7	7	8	1	4	7	24	13	14	28	11	20	320	320	4.24
Total	162	173	154	238	296	246	173	171	151	223	167	177	230	185	152	153	132	130	134	7555		

similarity in proportions of lepidopterans and coleopterans is in all probability merely a strange coincidence.

The difference between the sticky traps and the window-pane traps in the proportions of these two groups of insects is probably significant in terms of trap specificity. The low catch of lepidopterans by the sticky traps could be because these insects either (1) can detect the presence of the sticky trap and avoid it more readily than they avoid a window-pane trap, or (2) can escape more readily from a sticky trap than from a window-pane trap. While (1) is possible even when the vast majority of the lepidopterans involved is nocturnal moths (the level of illumination on many nights may still permit visual location or detection of traps) nonetheless (2) is an attractive hypothesis. It is attractive since both the spider's web and the sticky trap employ a similar method of initially arresting the insect in flight—an adhesive—and lepidopterans are known to have a high escape potential from spider's webs (page 64) and should have a high escape potential from sticky traps. It is tempting to think that part of the difference between the spider-prey results and the sticky-trap results is due to the active presence of the spider on *its* trap.

The differences in the proportions of beetles caught by the spiders, the sticky traps, and the window-pane traps can be explained in another way. We can assume that the spiders and the window-pane traps both lose a number of beetles that are caught by the sticky traps. The spiders lose small beetles that strike the web and are either ignored because they are too light, or which are so small that they pass through the wide mesh of the web. The window-pane traps presumably lose some beetles that are strong enough to crawl out of the water after they have been knocked down by impact with the glass. The sticky traps catch both small and fairly strong beetles. Very strong beetles escape from them.

From these results and the considerations detailed on page 25, we are convinced that neither type of insect-sampling device is adequate for the purpose of assessing the availability of prey to large orb-weaving spiders. Our light trap certainly brought in some of the types of large prey that the spiders caught, but again it is known that the responses of insects to ultraviolet light are confined to certain groups of the many nocturnally active animals (Southwood, 1966:200–201, for comments on reliability).

Rejections of Trapped Insects

Rejection of distasteful or otherwise obnoxious insects occurs, in most cases, after *Nephila* has bitten into the prey. It is then pulled out of the web and cast away from the plane of the web and falls to the ground. This treatment, in most cases, damages the insect. When a prey is detected as obnoxious *before being bitten,* it may be left for some time in situ without being bitten. It is almost always removed from the web, however, at some stage during "housekeeping" activities (when particles of plant material that blow into the web are also removed). This type of rejection also involves rough handling by the spider, and the prey is often pulled from the web in the jaws. Thus, in both cases, the rejected prey may be damaged and wholly or partly

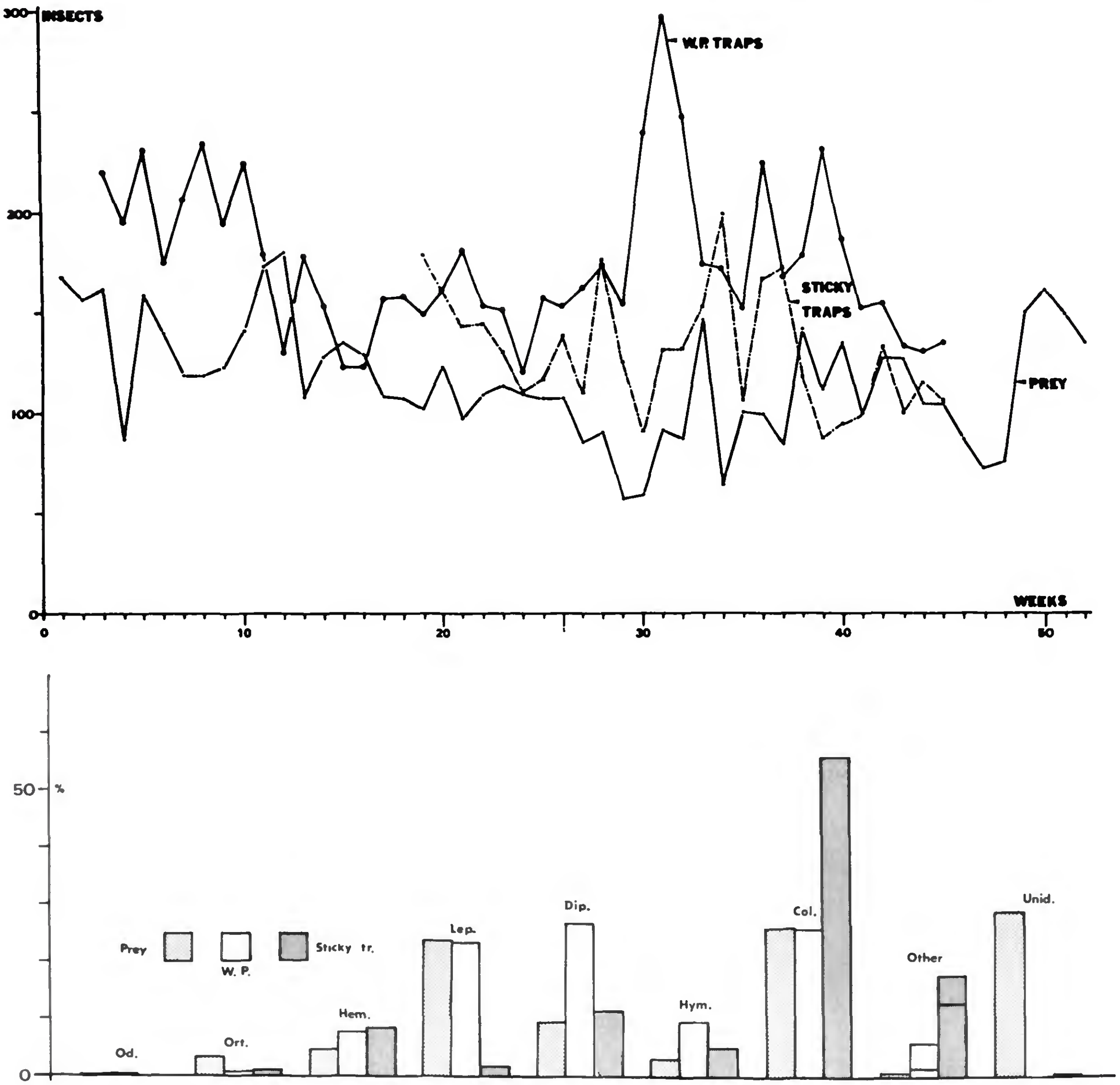

FIGURE 14.—*a*, Distribution of weekly totals of prey caught by spiders, and insects caught by window-pane traps and sticky traps; *b*, percentage composition of catches by spiders, by orders, window-pane traps, and sticky traps. Top portion of "others" category demarcates Dictyoptera from the remainder.

immobilized as a consequence. From an early stage in our sampling of the spider's prey we were aware of the presence of numbers of dead but intact insects in the prey traps. Conspicuous among these were lycid beetles, which are known to be obnoxious to a range of predators (Linsley, Eisner and Klots, 1961), and it seemed probable that these lycids had been caught and rejected by the spiders. Experiments showed that the spiders did in fact reject live lycids and we therefore decided to assume that all the intact (=undigested) insects found in the prey traps were rejects unless there were strong indications to the contrary. As it turned out the great majority of the insects so classified were aposematic and therefore, unless they were Batesian mimics, obnoxious in some degree. (We are not suggesting that the spider is responsive to the coloration of the prey but merely that this is a confirmatory piece of evidence.) Perhaps a proportion of the insects classified as rejects died in the vegetation above the prey traps and fell in, but this seems to be a very small possible source of error since corpses of known innocuous groups are extremely rare.

Of the total 371 specimens rejected during the study year, their composition was as follows: Lepidoptera, 16; Neuroptera, 18; Coleoptera: Lycidae, 198; Hemiptera: Heteroptera, 12; Homoptera, 79; Diptera, 37; *Nephila* males, 2; Phasmatodea: *Eurycnema* species, 2; Hymenoptera: Ichneumonoidea, 1; Unidentified, 6. The 371 total represents 0.3 percent of all the insects found in the traps. Of the rejects, coleopterans account for 53.3 percent, of which the lycids account for the great majority. Hemipterans rank second (24.5%) of which the majority were homopterans. These have not yet been identified but were bright blue in color. Roth and Eisner (1962) do not list any identified repugnatorial secretions from the homopterans, but many are known to produce waxy secretions which may be defensive. The heteropterans included pentatomids and reduviids, the former certainly produce defensive secretions and many of the latter have a painful bite. Neuropterans were present in small numbers (18) as were lepidopterans (16). Lacewings are known to produce odors and some forms have eversible abdominal glands (Riek, 1970:477). The "unidentified" 6 specimens include cockroaches, phasmids, and flies.

Lycids were rejected in all but six weeks of the year and their absence on these occasions seems to be quite random. This is of interest since Turnbull (1960) showed that the spider *Linyphia triangularis* (Clerck) would accept prey items at some stages in the season that were unacceptable at others. We have no data to suggest that lycids were acceptable at any stage.

Bristowe (1941:262–220) has surveyed the information available on food of spiders in great depth. He notes that coccids and aphids are either rejected or "accepted with hesitation," but that other homopterans are for the most part accepted by spiders. He also states that lacewings are rejected by most spiders. Among the Diptera he notes that sciarids, cecidomyids and empids are sometimes rejected. Flies that we identified as bibionomorphs (i.e., closely related to the above flies) were certainly among those rejected.

KLEPTOPARASITES

Numbers and Nature

Theridiid spiders of the genus *Argyroides* are frequently associated with orb-web spiders. They build their apparently unstructured complex of threads close to the plane of the host web and move about these and onto the host web. They have been generally referred to as inquilines. However this term has been used in such a variety of meanings as to be imprecise and we think that the term kleptoparasite is more appropriate.

We have conducted studies of the relationship between *Argiope argentata* and its kleptoparasites, and decided that since *Nephila maculata* seemed to have a large number of these theridiids associated with its webs further study would be worthwhile. Fr. Chrysanthus has identified at least two species from the material that we sent him and other specimens remain unidentified. Kleptoparasites of *Nephila maculata* include at least the species *Argyroides argentatus* Cambridge and *Argyroides miniaceus* (Doleschall). Of these the former was also found (by Dr. Y. D. Lubin) in the web complex of *Cyrtophora moluccensis,* which suggests that it may not be host-specific.

At the start of our study we counted the kleptoparasites present in 86 webs of adult *N. maculata* within an area of about 500 meters around the study area. We also counted the kleptoparasites on an equal number of webs belonging to immature *N. maculata* whose sizes ranged from 20 to 38 mm in length. The total kleptoparasite "load" for adults was 236, and for immatures 129. Of the adult webs 23 out of 86 had no kleptoparasites (27%). The juvenile webs contained kleptoparasites in all but 28 (32.5%) cases.

At each morning's web census we counted the number of kleptoparasites present in the ten *Nephila* samples. Figure 15 shows the fluctuation in the weekly totals. The variation is from 35–112, the average number per web per day is 0.92. This, when one considers that such tiny spiders could easily

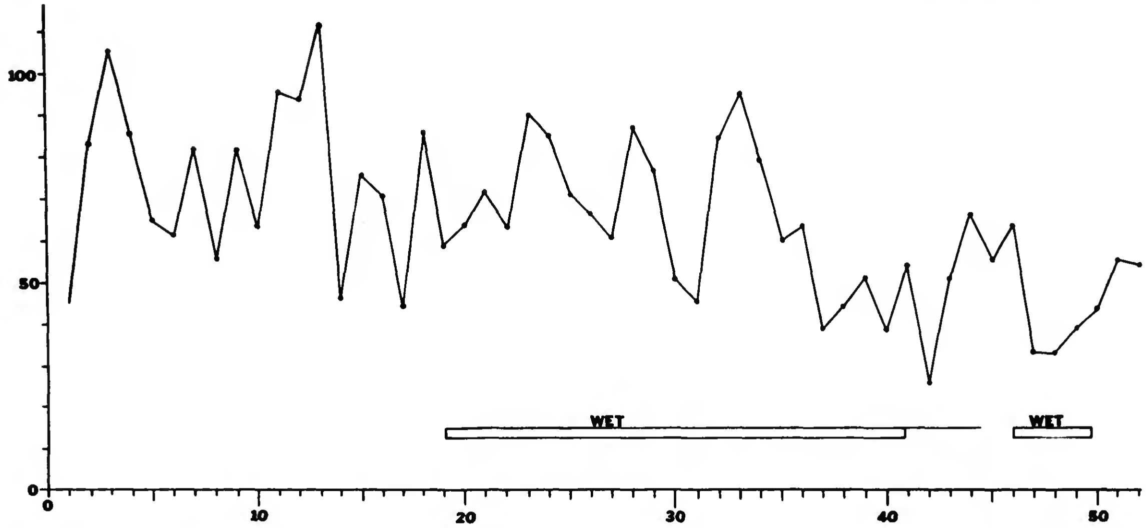

FIGURE 15.—Weekly fluctuations in numbers of kleptoparasites present on the sample *Nephila maculata* webs.

be overlooked, is suggestive of a fairly regular relationship. Fluctuations in the weekly totals of kleptoparasites do not seem to be correlated with such factors as fluctuations in rainfall, number of days of rain, weight of prey, or numbers of prey. The maximum number of kleptoparasites that we recorded on any one web, on one day, was fifteen.

Activities

Unlike *Argiope argentata* and many other araneids, *Nephila* species do not store or leave food at the capture site after it has been immobilized. All prey is carried from the capture site and stored at the hub region (Robinson and Mirick, 1971). This aspect of the predatory behavior of the host means that the kleptoparasites are not able to steal food from the capture sites as has been described for the kleptoparasites of *A. argentata* (Robinson and Olazarri, 1971:35). On the other hand the theridiids often move from their "waiting positions" around the web and down to prey as it is being attacked by the host. We have seen the theridiids moving on the surface of the prey and apparently feeding there while the host is administering the biting attack (which may last several minutes). When the host starts wrapping the prey, after the bite, the kleptoparasites move off to their complex of threads above the surface of the host web, or below it on their drag lines. This sort of feeding, during the host's attack, is not without risk and we have seen the kleptoparasites become enswathed in silk, alongside the prey, as the host wrapped the prey package. Because the maze of threads built by the kleptoparasites is in contact with the host web at various points we suspect that the theridiids may be alerted to the presence of prey in the web by vibrations produced as a result of the activities of the host and/or the struggles of the prey. Those theridiids actually standing on the host web could be expected to locate the source of the alerting vibrations more rapidly than those waiting on their own structures outside the web. We have not been able to demonstrate this.

In other cases, after the host has transported the prey to the hub and has commenced feeding, the kleptoparasites approach and move onto the prey, often climbing down the silk thread by which the prey is secured to the hub. They also behave in the same way towards prey stored at the hub. Figure 16 shows three kleptoparasites feeding on the same prey as the host and one feeding on a stored prey item. Stored prey usually become the object of stealing sensu stricto. Kleptoparasites attach lines to stored prey and then move up into their own thread complex, dragging the prey with them. We have seen prey several hundred times the weight of the theridiids stolen in this way. Once the thread

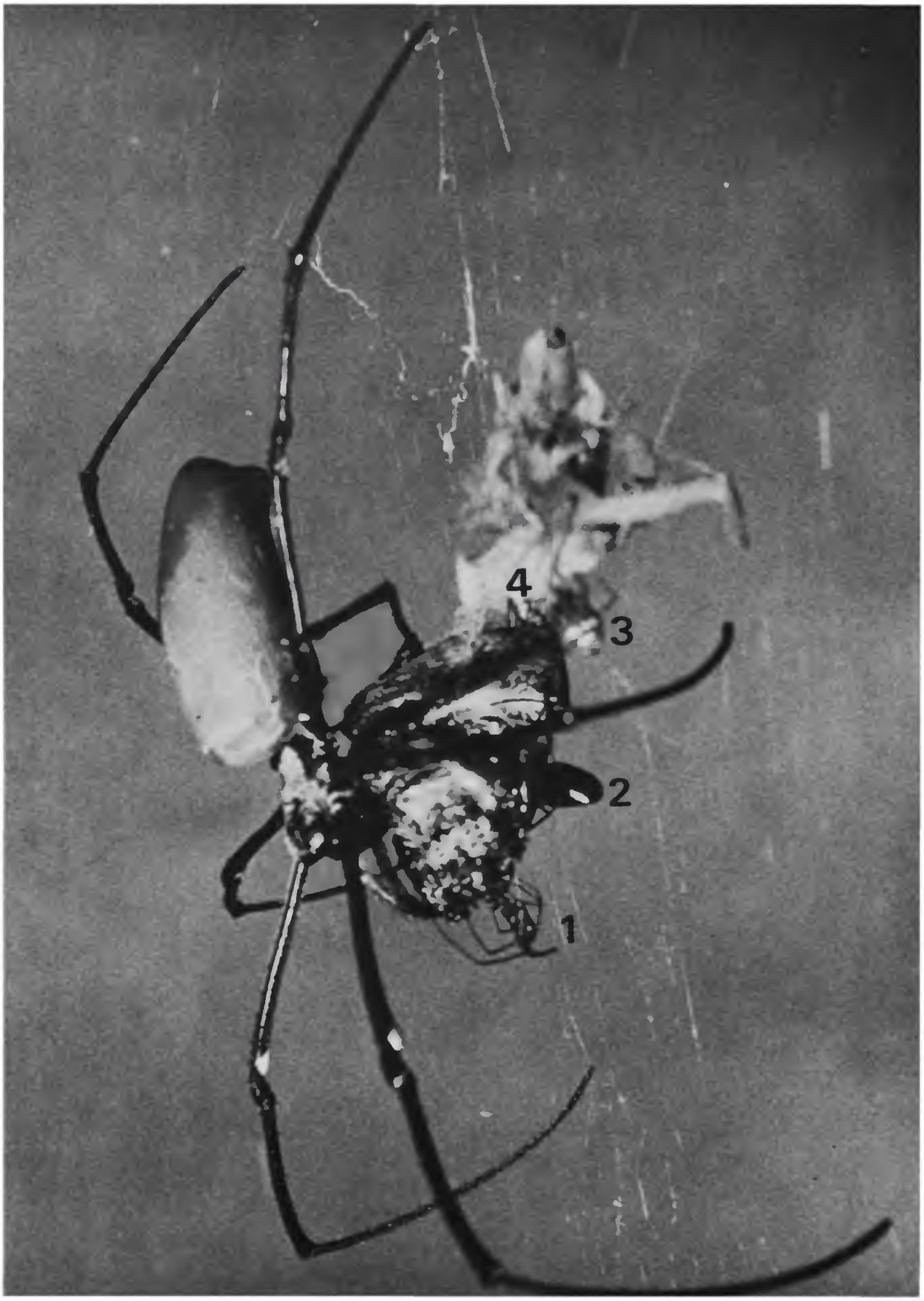

Figure 16.—Adult female, *Nephila maculata,* and four kleptoparasites (numbered) feeding on prey.

attaching the prey to the host web is severed the host appears to be incapable of detecting its location. Nor does the host appear to be alerted by the sudden loss of weight that occurs when the prey is removed from the web. On the other hand we have seen hosts apparently searching for missing prey packages hours after they have been removed. The kleptoparasites give no convincing evidence of cooperating to remove large items of prey although they are apparently tolerant of each other as they move around on the surface of large prey packages.

The host spider does not often react to the presence of kleptoparasites when they are merely moving about on its web. We have only one record, from many hours of observation, of the host leaving the hub and attacking a kleptoparasite. This was bitten and carried back to the hub where it was wrapped into the prey package on which the spider was already feeding. Robinson and Olazarri (1971: 35) observed *Argiope argentata* attack and kill theridiids that were removing prey from capture sites. Host spiders, from time to time, become aware of the kleptoparasites moving about on the prey on which they are feeding and respond by making vigorous brushing movements around the periphery of the prey with their legs. This is quite a different behavior to that ensuing from movements of the prey within the prey package. When the latter occurs the spider usually continues feeding but occasionally rewraps the prey in silk.

Colonization of Host Webs

Kleptoparasites may remain in association with a host web for up to three or four days after the host has gone. This lingering on could be adapative since our studies have shown that temporary absence of a host spider from a web site is not unusual. In fact, spiders leave their webs, lay eggs, and then return to the same site—and sometimes the same web—after one or two days absence. Also during periods of heavy rain the spiders may spend one or two days out of their webs hanging under nearby leaves. New host webs are colonized with surprising speed and we have recorded up to five kleptoparasites in the web of an adult *Nephila* 48 hours after it has moved into a web site that had been unoccupied for several weeks. This occurred even in areas where the host species had been completely absent for months. If, as we have suggested, the kleptoparasite is not strictly host-specific, it could operate by moving onto any araneid web that it detects and remaining there when conditions are satisfactory. Presumably an intermittent supply of food would constitute a reward.

General Considerations

It is difficult to assess the role of the kleptoparasites in the energy economy of the host. If we assume that a host may support four or five kleptoparasites throughout most of its adult life their combined wet weight would certainly not exceed 40 mg. Assuming that dry weight is 40 percent of wet weight this gives a dry weight of spider at 16 mg. Taking a metabolism figure of 27 calories per gram per day for spiders, based on the perhaps more active lycosids (Macfadyen, 1963:234), we get a daily intake of 0.43 calories per day by the kleptoparasites. How much of this would be available to the host, in their absence, is difficult to assess. All of the energy in food that was actually stolen would be a debit. However, a proportion of the energy taken from a source on which the host was feeding could be inaccessible to the host, since the kleptoparasites may be able, because of their small size, to extract food from prey structures such as thin legs, that the host cannot cope with because of the great size of its chelicerae. We have also observed scavenging behavior by the kleptoparasites, toward very small prey that become caught in the web and which the host ignores. This type of feeding may occur without loss to the host and could contribute to satisfying the energy requirements of the theridiids.

It is extremely difficult to assess the importance of a possible loss of 0.43 calories per day to the host, since this may vary according to the abundance, or lack, of prey from day to day.

Robinson, Mirick, and Turner (1969:492) suggest that *Nephila clavipes* does *not* store food at capture sites in order to prevent it from being stolen. If food *were* stored at these sites it might be particularly vulnerable to attack by kleptoparasites whose activities would be difficult to detect because of the large area of the web. Our studies show that *Nephila maculata* still supports a considerable number of these parasites, even though, like *N. clavipes,* it stores food only at the hub.

ENERGETICS

From the dry weight of prey residues it is possible to calculate, albeit crudely, the approximate energy input to each "average" spider. We know from our own tests that araneids can absorb up to 78 percent of the wet weight of prey, such as domestic crickets. This leaves a minimum of 22 percent to be accounted for in undigested material, unabsorbed water, and undigestible skeletal material. If we, therefore, assume that 20 percent of the wet weight of an insect is accounted for by undigestible cuticular structures, we can calculate back from our figures for the dry weight of prey-remains to the original wet weight. We believe that the degree of approximation involved is not greater than that involved in many calorific input calculations, and that an assumption of 20 percent of the total wet weight for exoskeleton errs on the generous side. If the total dry weight of prey-remains for the year, 123.544 grams, represents 20 percent of the wet weight of the insects from which they were derived (residual water having been driven off by the drying process), then the original prey weighed 617.7 grams. If we assume that 60 percent of this is water (one of the widely used crude approximations), then the dry weight of skeletal material plus food is 247.08 grams. Deduct the weight of skeletal remains and the sources of calorific input become 123.5 grams. If we assume an assimilation efficiency of 46 percent the result is 56.8 grams per year dry weight intake, or 5.68 grams per spider, yielding 0.015 grams per spider per day. Assuming that insect material averages 5000 calories per gram dry weight this gives 75 calories per spider per day, or for a 3-gram spider, 25 cal/gram. This is less than we calculated for *Argiope argentata*—40 cal/grams (Robinson and Robinson, 1970a:354). However, in view of the approximations at several stages in the calculation the differences are probably not important (Macfadyen, 1963:234, gives a metabolism figure of 27 cal/grams for Araneae).

PHENOLOGY

Spiders that have been studied from the standpoint of ecology have, so far, been highly seasonal (North Temperate studies) or present throughout the year but with a distinct period of reduced numbers and reduction of prey intake during a marked seasonal shift in climate (*Argiope argentata* at Barro Colorado Island). The Wau area is clearly one where year-round activity is possible and in the twelve months covered by our study no major variations occurred at micro- or macro-climatic levels, at least within the study area. Adult and immature female *N. maculata* were present throughout the year and so were males. Egg-laying occurred throughout the study period and at no stage did prey captures fall to a level that suggests serious shortage of food. This is in marked contrast to the situation at Barro Colorado where the spider population fell to nil at one period of the dry season and there was a very pronounced fall in prey captures preceding this.

Since the species is markedly seasonal in other parts of its range (Thakur and Tembe, 1956) it seems reasonable to assume that the ultimate factor must be climatic. It is interesting to note that in the woodland fringe habitats, represented by transects 1 and 2, adult spiders were absent for large portions of the year. On the higher altitude transect 3 (forest fringe) no adult female *Nephila maculata* were recorded during the entire year although there was a regular occurrence of spiderlings and immatures (Robinson, Lubin, and Robinson, in prep.). Since there were no major changes in the phytophysiognomy of these areas capable of affecting adult web sites during the study period, we are inclined to believe that they are susceptible to greater fluctuation in climatic conditions than the woodland and forest habitats. They are thus a fringe area for those spider species that require woodland or forest conditions. When conditions favor the survival of adult and immature *N. maculata* in the fringe areas, conditions in the adjacent forest should be optimal or nearly so. This hypothesis is borne out by the fact that the massive increase of immatures and males on transect 1, coincides with a similar increase in males, and males on females, in the study area, and furthermore overlaps the period when the spiders in the study area were just past the period of maximum prey captures (by weight). This period was one of relatively high rainfall.

Despite the overall lack of major seasonality in the biology of *N. maculata* at Wau—reflected in the presence of adults throughout the year, continual mating and egg-laying, and the results of the collection of discarded prey—there *are* temporal fluctuations in the composition of prey and the presence of males that are of interest. The fact that there is a marked seasonality in the occurrence of melolonthids in the prey traps may be associated with the fact that the immature stages of these insects probably occur in grassland soils where the variations in moisture content may be more extreme than in the woodland areas. Cicadas too seem to occur most frequently in the wetter months. Other examples of seasonality in prey composition have been noted earlier (pp. 19–21). These and the very great increase in the number of males found on females' webs during the wetter months may be fluctuations peculiar to the particular 12-month period in which we carried out our study and much more extensive studies are, of course, required to elucidate long-term trends.

In considering the relationship between the variations in the biology of *Nephila maculata* that occur over time, it became apparent that attempts to correlate them with simple climatic and/or biotic factors are fraught with complications. Some of these are detailed later in the "Discussion."

Behavior

In the section on predatory behavior we have included details of comparable behavior patterns that we have studied in other species of *Nephila* and the related genera *Nephilengys* and *Herrenia.* This inclusion of comparative material was carried out to avoid the fragmentation of an essentially synthetic approach to the predatory behavior of these species. Such a procedure has lead to some repetition, particularly since it seemed useful and necessary to include cross references to other species in both the section on behavior units and that on behavior sequences. We have included a final comprehensive section to tie together the data on predatory behavior.

TERMINOLOGY

Except in the cases of newly described behavior units, terminology follows that of Robinson (1969) as expanded by Robinson and Olazarri (1971).

The term "courtship" is here used to include all the regularly occurring interactions between the adult male and the adult female that precede the act of insemination. Morris (1956:128) has defined courtship as "the heterosexual reproductive communication system leading up to the consummatory sexual act," including in this definition precopulatory behavior between the two sexes. The term "mating" is applied to varying ranges of sexual behavior by different authors. With specific reference to spiders Alexander and Ewer (1957:311) seem to use the term to cover both sperm induction (charging the pedipalps with sperm) and insemination, although confusing matters by later referring to the "actual mating." Bristowe (1941:461–502) includes sperm induction, courtship, and copulation under the general heading of mating habits. Our inclination is to treat the term as synonymous with copulation but to use the latter term in descriptions.

SEXUAL BEHAVIOR

Finding the Female

We have no data on how males find females. It seems reasonable to assume that they could simply locate the females by locating their webs. Certainly they tend to aggregate on these webs in considerable numbers, and even spend long periods of time on the webs of subadult females. Bristowe (1941:467) concludes "most, and probably all, male spiders possess a sense which enables them to recognize the female's proximity without seeing her . . . [by touching] the web she has spun either in the form of a snare or a retreat cell."

Our observation that males will remain in the web of a subadult female after locating it (this is also true of males of *Nephila clavipes, Argiope argentata,* and other *Argiope* species) suggests that some property of the silk, rather than a specific chemical property of a female in reproductive condition, may mediate the first stage in the location of a potential mate. On the other hand it remains possible that all females produce a chemical signal of some kind, and that this is species-specific. In the course of constructing a web this substance could be transferred to it and thereby label the structure. Males will remain on a web for several days after the female has left it. This, like the similar behavior of kleptoparasites, could be adaptive since females often return to the same web after an egg-laying excursion.

Courtship

The whole subject of courtship in spiders has been the subject of considerable controversy, some of which involved hair-splitting quibbles about terminology. Bristowe and Locket (1926) proposed a theory of courtship that involved a dual function; suppression of predatory behavior in the female by "male recognition" and, stimulation of the female to the point of accepting copulatory attempts. Savory (1928) attacked this theory as being too complex and attributing powers to the spider that it probably does not possess. He proposed to regard courtship as a chain of related instinctive actions in which predatory urges become suppressed and physiological changes are induced in the participants. Crane (1949) takes an essentially similar point of view on the main issues. Platnick (1971) argues that all these authors rightly stress the role of courtship in suppressing cannibalistic tendencies, but present courtship as a one-sided activity by which the male affects the female. Actually Savory (1928:220) noted that "the male himself becomes more stimulated as courtship proceeds." Platnick (1971) applies a releaser theory derived from Tinbergen (1954) to spider courtship, suggesting that the behavior has four functions: synchronizing mating activities, orienting the individuals, suppressing nonsexual tendencies, and insuring species-specific mating. Morris (1956) in an extensive treatment of the function and causation of courtship in vertebrates (mainly fishes) suggests that the conspicuous, all-absorbing nature of many courtship ceremonies makes them dangerous to the participants and they must, therefore, have a strong selective advantage. He suggests four functions: finding a mate, finding a mate of the right species, stimulating the mate, and synchronizing reproductive arousal.

These categories differ from those of Platnick in including mate attraction (finding a mate) and not including the suppression of nonsexual tendencies (although that is implied in Morris's category of arousing the mate). Bastock's (1967) survey of courtship suggests that there is no single answer to the question of function and that this varies with the circumstances. It is clear from Morris' (1956) description that attracting a mate may be accomplished by using signals effective in one or several sensory modalities. One of the most valuable ideas to come out of the reaction chain views of courtship is that these, by the number of steps that they involve, are fail-safe systems of insuring that mating occurs between members of the same species (Morris, 1956:130).

Descriptions of the courtship of *Nephila* species are limited. As far as we are aware they include studies of *Nephila madagascariensis* by Bonnet (1930), Gerhardt (1933), Charezieux (1961), and some observations on *Nephila maculata* by Fischer (1910a,c), Hingston (1923), and Thakur and Tembe (1956). There are also some notes on the courtship of *Nephila plumipes* published by McKeown (1963).

Fischer (1910a:527) describes the insertion of the embolus after the male had struck the genital aperture "by alternate, rapid pecks of the palps, much as the fingers strike the keys of a typing machine," a graphic and accurate description. He did not see the process of sperm induction or any courtship. He notes that in one case there were five males on a web and that a male climbed stealthily onto the abdomen of a female only to be brushed off by the female as he approached the "vulva." Hingston (1923:74) describes the males, the position they adopt on the female web, their dependence on food caught by the female, and their tactics in escaping from females that chase them. He also describes a highly specialized position that the female adopts during copulation. In this the female leans away from the hub of the web by releasing all the legs on one side "the object being to lay herself open so as to receive without obstruction the advances of her mate."

Thakur and Tembe (1956:331) note that the males aggregate on the webs of females, and remain there until the female is "ready for copulation." These authors give no details of the approach behavior nor do they describe the act of copulation but they do note that "the male does construct a web on the back of the female, but this is not used for the transference of seminal fluid from the genital organs to the *receptaculum seminis* situated in the palpus." This paragraph shows that these authors saw, but largely ignored, a behavior that constitutes a phase of courtship that is of long duration in most of the cases that we have seen.

Charezieux (1961:375) refers to a long period spent by the male in tentative, hesitant, approach behavior. This the *"travaux d'approche"* may last 30–36 hours. During this time the male repeatedly approaches the female across the web, touches the apex of the female's abdomen and retreats, eventually climbing onto the abdomen of the female, moving along its ventral face and copulating. In the approach phase the male was seen to vibrate the female's web "as if to check the responses of the female from a distance" ("comme s'il voulait se rendre compte a distance des reactions de la femelle.") Charezieux (1961:378) also states that the female eventually becomes torpid.

Mrs. Lowry's notes (in McKeown, 1963:147–148) on *Nephila plumipes* include the following points: the male may live on the female's web for weeks at a time; the male moves to the hub when the female vacates it and moves away when she returns; and he approaches the female along her drag line when she is feeding. The male eventually climbs onto the ventral face of the abdomen but retreats if the female shows signs of activity. Lowry eventually saw copulation occur when the female was torpid and after the male had tapped her body in several places.

Our observations on the courtship of *Nephila maculata* show that it contains elements of the patterns described by these authors. Confusion over descriptions of *Nephila* courtship may arise, not only because of observational problems but also because, as we discovered, some stages of courtship may be omitted by some males which behave in an "opportunistic" manner. The significance of "incomplete" courtship is discussed later. The best case of this that we have documented is the one where the male approached a female that was in the process of molting to the adult stage, and mated with her while she was still "drying out" and hanging from her cast skin. Approach in this case was accomplished in less than one minute and insemination was over shortly afterwards. We have the entire sequence recorded on film. Crane (1949:176) records a similar case in salticids; the female later produced fertile eggs.

Other examples of opportunism include behavior sequences where the male climbs onto the female and copulates while she is feeding, and omits the typical precopulatory behavior. We have two records of this type of mating and the absence of silk on the body of the female confirmed that the "normal" precopulatory behavior had been omitted. Figure 17 shows a male in the process of copulation while the female is feeding, but in this case the male had carried out the lengthy normal precopulatory behavior.

In all the other cases of courtship that we saw the procedure was essentially the same, although there were some differences of detail. We have never seen the entire process from start to finish, but have seen all the stages and filmed them on many occasions. Essentially there are three fairly distinct stages: approach and movement onto the female, complex silk deposition on the female, and movement toward the epigyne leading to copulation.

The approach stage may occur when the female is at the hub, where she may or may not be feeding, or it may occur at a prey capture site when the female is attack-biting the prey. The male approaches the female on either side of the web, i.e., either from the upper surface "facing" the female or along the lower surface on which she is standing. If the male arrives at the female on the upper surface he shuttles through the web to the side on which she is located. Then follows a period of touching which may vary in interval from a few seconds to several minutes. At this time the male may touch the tarsi of any of the female's legs and/or her mouthparts and pedipalps. This phase ends when the male climbs onto the female or retreats. Once on the female the second stage commences.

The second stage of laying down silk threads on the female may occur intermittently for very long periods and the male may spend the greater part of several days standing on the female. During this time he periodically indulges in complex "weaving" or thread deposition activities. We have one record of two hours continual activity at this stage, which was the longest period of uninterrupted observation that we carried out. To observe the details we watched the pair through the lens system of a cine camera equipped with a telephoto zoom lens, to which we attached a supplementary close-up lens. This allowed us to watch the pair from a distance, and, at the same time, vary the field of vision from

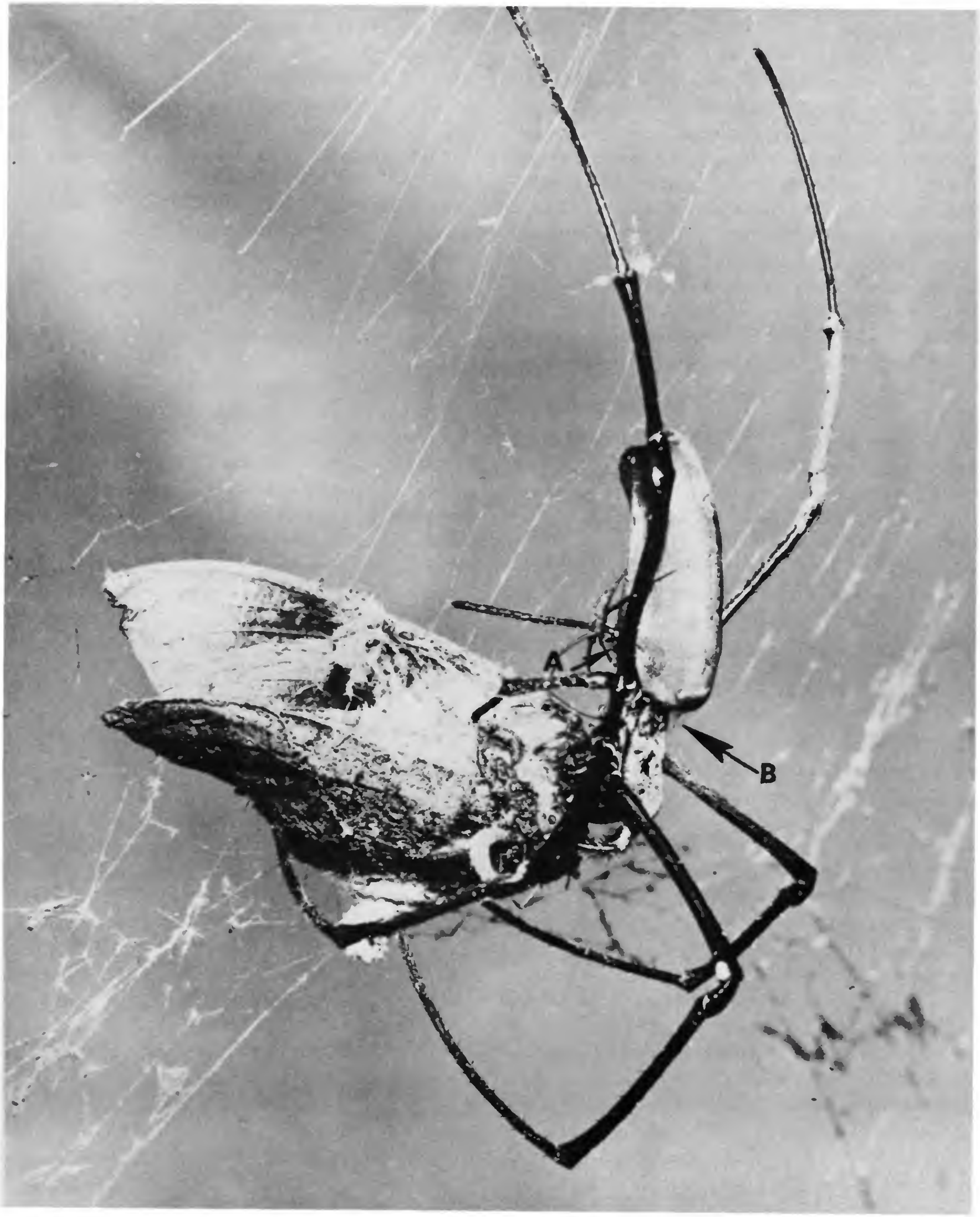

FIGURE 17.—Profile view of copulation in *Nephila maculata*. One embolus of the male is inserted (A). The gusset of silk that the male has attached from the abdomen of the female to her thorax is clearly visible (B). Silk can also be seen on the leg bases.

one occupied by the entire female to a narrow view of only part of her body. Such observation is very tiring and two hours was really beyond the limit. The notes on this session are given in Appendix 1. Essentially the male lays down silk threads between the bases of the female's legs and between the prosoma and the dorsal basal edge of the opisthosoma. Nearly all of the bouts of silk deposition, observed during the 2-hour session, were initiated by the male moving down from dorsal surface of the female's abdomen, where he had been standing motionless. Before moving onto the thorax the male attached silk to the raised fronto-dorsal edge of the abdomen. The distinct dabbing movements of the male spinnerets against the female marked the start of a deposition bout. The male attached silk lines between the abdominal edge and positions on the dorsal surface of the prosoma. He returned frequently to the abdomen to repeat the process. Threads were placed on the opisthosoma at various distances from the raised anterior edge of the structure and then stretched to points on the prosoma at varying distances from the waist. They were stretched parallel to the long axis of the spider and also at angles such as left opisthosoma to right prosoma. Mixed in between these movements were those involving the leg bases. In these the male moved either from the opisthosoma, or, more frequently, from the prosoma, onto the coxa-trochanter region of one or other of the eight legs. He then attached lines to the leg base immediately beneath it. Attachments were made to the upper and lower surfaces of the basal joints and from these to leg bases on both adjacent and opposite outsides of the prosoma. In the latter case the lines traversed the dorsal surface of the prosoma.

The most interesting postures adopted during this lashing process occurred when the male, from above, passed lines onto the lower (ventral) surfaces of the legs. To do this the male would arch his body and twist it sideways between the legs so that it moved like a shuttle. On occasion the male moved entirely beneath the leg bases while attaching threads. The results of this silk deposition can be seen in Figures 17 and 18, which are of two different adult females. The view in Figure 17 shows the lateral profile of the two spiders (male + female) and, on the female, a sheet of silk threads can be seen curving from the anterior edge of the opisthosoma to the posterio-dorsal region of the prosoma. Also visible in this photograph is a complex of threads extending well up onto the femur of left leg II and other threads connecting the base of right leg I to the basal region of the right chelicera. Figure 18 is a dorsal view of a pair of *Nephila* and shows silk lines between all the leg bases and also the complex of threads on the dorsal surface of the prosoma. Figure 19 shows another pair of spiders with the male in the act of attaching silk to the left lateral aspect of the female's opisthosoma. Some lines are attached from the leg bases to the ventro-lateral margins of the prosoma, but the male spends very little time beneath the female during the process of silk deposition.

During the process of intermittent silk deposition the male rests fairly frequently. The rest attitude is almost always assumed on the dorsal surface of the female's abdomen and usually above the raised anterior edge (where there is a fairly conspicuous pale line). While they are resting males may tap at the bases of the female's legs, or hold onto these with the feet of legs I and II. Contact in these cases may possibly be with the silk between the leg bases of the female. We have records of males assuming special postures when the female moves about in a precipitate manner (as she may do during a predatory excursion). One male consistently responded to the movement of the female by flattening himself against the steeply sloping anterior declivity of the abdomen and in this position could be seen clinging to the silk "shrouds" on the thorax. Such a position was also adopted by other males for which we have a less complete record. We are inclined to believe that this is the most secure and sheltered position that the male can adopt and that it may help to secure him against disturbance by the female.

We saw few instances in which the female appeared to respond to the activity of the male. These rare responses only occurred when the male was on the ventral surface of the legs. In this situation several females made brushing movements directed at the males (by bringing the tibia of a third leg along the underside of their prosoma). These movements were similar to those made in apparent response to the activities of kleptoparasites. Copulation follows the stage of silk deposition, and approaches to the female genital orifice may occur intermittently during silk deposition

FIGURE 18.—Male on dorsal surface of the abdomen of a female *Nephila maculata*. Silk lines are visible on the thorax of the female leading to the leg bases and abdomen.

FIGURE 19.—Male *Nephila maculata* in the act of attaching silk to the right fourth leg of the female. Silk produced by previous deposition activities is clearly visible on all leg bases. Note that at least five kleptoparasites are visible on this photograph.

bouts. We have film records of three successful copulations and a still photograph of another (Figure 17).

Approaches to the region of the epigyne are made by two basic routes. The male most frequently moves on the dorsal surface to the apex of the opisthosoma and then walks forward down the ventral surface, halting just behind the margin of the epigyne. There is a tuft of longish stiff hairs immediately anterior to this furrow and these may act as a marker for locating the appropriate region. The male can also circle around the anterior region of the opisthosoma to reach the same point, and frequently *retreats* from the ventral surface by a rapid circling move. When descending the ventral face of the female opisthosoma he is clearly belayed on the drag line which is attached somewhere near the abdominal apex. Presumably the drag line is also used when circling, but it is not then clearly visible.

Copulation

A typical copulatory position is shown in Figure 17. From this it is obvious that only one embolus is inserted at a time and the other is simultaneously raised above the long axis of the male's body. The swollen distal portion of the pedipalps are, at this stage, black and shiny, the emboli are long and extremely narrow in their distal region. The embolus of the left palpus is clearly visible in its inserted position in the photograph. Insertion may be very brief and is often a matter of seconds. Such brief insertions may represent unsuccessful attempts. At other times they may last for over a minute. The removal movements are conspicuous. The structures sometime appear to stick so that there is a distinct recoil upon the embolus being freed. Insertion is preceded by the spider beating upon the female genital region with very rapid alternating movements of the pedipalps. Analysis of film suggests that this beating is done with the emboli reflexed backwards.

The palps are used alternately, several times, with pauses between bouts of insertion. Bristowe (1941:491) suggests that this technique is used by the majority of spiders.

Charezieux (1961:377) shows a pair of *Nephila madagascariensis* in a copulatory position exactly comparable to that adopted by *N. maculata*. He notes (1961:378) that the male beats on the epigyne with his palps ("Il frappe alors de ses bulbes copulateurs l'epigyne, les actionne rapidement tous les deux"). He does not state whether one or two palps are involved at the same time, although this may be implied. Charezieux also refers to the brevity of copulation and also to the fact that it may be repeated several times.

The female makes no attempt to attack the male during or after copulation (in marked contrast to the behavior of several New Guinea *Argiope* species; Robinson and Robinson, in prep.). Thakur and Tembe (1956:331) state that copulation occurs at irregular intervals for a day or two, and that the female does not attack the male, but that "he just dies a natural death, apparently due to exhaustion." They do not describe the act of copulation.

Discussion

The most interesting aspect of the courtship behavior of *Nephila maculata* is the complex thread deposition, which the male normally undertakes. This behavior was not described by Fischer (1910a, b,c) Hingston (1922a,b,c, 1923) or Thakur and Tembe (1956), although the latter authors presumably are referring to the results of this process when they state that the male builds a web on the back of the female (1956:331). Preliminary studies that we have carried out on *Nephila clavipes* suggest that silk binding is absent from the mating behavior of that species.

It is not described for *N. madagascariensis,* and presumably would not have been missed by the authors that studied this species. As far as we are aware there are no published accounts of other araneids indulging in such complex silk deposition during courtship. Bristowe (1929:320–321), however, records that during the courtship of *Meta segmentata* the male may begin to wrap the female as though she were prey. The female tears herself free and Bristowe assumes that the behavior is the result of multiple motivation and that although the female is not restrained by the silk she may be stimulated by the male's actions. Bristowe (1929) and others following his generalizations based on a limited number of observations on a limited number of species (e.g., Platnick 1971:40–41), state that courtship in araneids involves the building of mating threads onto which the female is coaxed during mating. Descriptions of the construction of mating threads, e.g., by *Meta segmentata* (Bristowe, 1929:320–321), mention that the male walks backwards and forwards over the female trailing a series of threads that are eventually to become a single composite copulation thread (=mating thread) on which copulation occurs. It is not clear from the description exactly how the copulation thread is oriented in relation to the female, whether it is dorsal or ventral. If it is laid down by the male walking across the dorsal surface of the spider then there is some similarity between this and the behavior that we have detailed for *Nephila maculata*. Our own observations on the mating behavior of *Argiope aemula* show that the male moved very extensively over the dorso-lateral surfaces of the female prior to copulation (Robinson and Robinson, in prep.). These movements had some of the character of the *Nephila maculata* binding movements but did not include discernible silk attachment movements. The existence of such wandering may be of interest in considering the evolution of courtship behavior in araneids. In passing it is worth noting that in Thomisids the male may, as in the case of *Xysticus lanio* C. L. Koch, tie the female to the ground with silk. This process, described by Bristowe (1931:1406) is presumably not entirely to restrain the female since she frees herself after copulation has occurred.

Perhaps the most interesting question about the binding behavior is: what is its function? At first sight it would seem logical to assume that it functions in some way to restrain the female so that the male can safely copulate. This is suggested, albeit indirectly, by the fact that the behavior is omitted on occasions when the male can catch a female at the molting stage or while she is feeding. Despite the fact, however, that the leg bases are the subject of a great deal of binding activity, the female is well able to rush off on predatory excursions from the hub *after* the silk has been heavily deposited. Her running ability does not, therefore, seem to be impaired. It may be that the binding, particularly the deposition of threads from the opithosoma to the prosoma, *on the dorsal surface only,* prevents the female from bending at the waist. The male would then be able to copulate without the danger of being picked off by the female. This explanation of the binding behavior only occurred to us after we had seen *Argiope aemula* mate, and in the process pick off the male from her ventral surface. This observation was made at the end of our stay in New Guinea and we were not then able to carry out any experiments on the efficacy of the binding in preventing the *Nephila* female from moving at the waist. However, we have since carried out experiments with the females of *Nephila clavipes* and gluing threads on dead females effectively prevents backward ventrally directed movements of the prosoma. This evidence is certainly not critical but is suggestive. The unrestrained spider is able to bend at the waist to an angle of over 90 degrees when not in contact with a substrate (presumably by contracting muscles associated with the waist joint) and further than this when it can use the legs to pull the thorax towards the abdomen. It can also achieve a more than 90 degree flexure by allowing the abdomen to drop toward the thorax in a ventral direction, a situation in which the action of internal muscles is presumably supplemented by gravity. This degree of bending could be sufficient to enable the female to pick off the male in certain circumstances, i.e., by seizing one of the legs projecting beyond the waist joint onto the prosoma of the female. This can be visualized by examining Figure 17.

If the act of mating were to be accomplished rapidly, once the male had assumed a copulatory position, there would not seem to be any adaptive advantage in insuring his postcopulatory survival by an elaborate precopulatory behavior pattern. If, however, a binding function of silk deposition insures that the male can safely achieve repeated insemination bouts it could be of survival value.

The immunity of the male to attack by the female, a point that we have observed in all the matings that we have seen, could be a direct consequence of the binding behavior as suggested above or it could be that the female is not restrained by the silk but by some change in her internal state consequent on the males' behavior. There are a large number of cases of complex courtship patterns which have the effect (among others) of lowering hostility between the sexes or reducing predatory drives that might otherwise be directed against the male. In this particular case the restraint is not exercised during the approach stage, which may also be one during which the male is at risk, but actually during the process of copulation. Signaling systems may exist that enable the male to identify himself as nonprey to the female during the approach stage. The web-strumming that the male of *Nephila madagascariensis* performs during his approach (Charezieux, 1961) would seem to belong to this category. We did not observe such behavior in the case of *Nephila maculata.* (We suspect that the males of *N. maculata* may be light enough not to trigger a predatory response as they move across the web.)

There are still other possible explanations, in terms of function, of the complex binding behavior. The structure could be a sperm web. We consider this unlikely because it is constructed in a manner which suggests unnecessary complexity for such a function. A sperm web would presumably not need to encompass the leg bases in such a thorough way, nor would the complex diagonal members laid down from opisthosoma to prosoma seem to be necessary. However, since we did not observe sperm induction we cannot entirely exclude this possibility. A further possibility is that the structure provides a foothold for the male so that he can cling securely to the female until the moment for copulation arrives. This too seems a fairly remote possibility since the male could, presumably, achieve a secure position on the female by attaching his drag line to some part of her body and gripping its far from smooth surface with his tarsal claws. At the most he could achieve a very secure foothold with a modest skeleton structure of silk lines rather than the complex structure that he does build.

The foothold theory gains no direct support from our observations on *Nephila clavipes.* These show that the male is able to move about the surface of the female with facility for long periods, and remain there during fairly violent activity (during prey wrapping) without a silken foothold structure. A primary foothold function for the silk could thus be justified only by assuming that the surface of *Nephila maculata* afforded considerably less foothold than that of *Nephila clavipes.*

There is no reason to assume that the silk structure has only one function. Therefore, it could function as a restraining "harness," a platform of footholds, and a sperm web.

All the authors who have described *Nephila* mating refer to the passivity of the female during copulation. It seems worth reiterating that courtship activities may function principally to induce such a state, which may be due to internal rather than external restraint.

The proportion of matings that we observed in which the stage of silk deposition was omitted do not raise major problems in explanation. Behavioral investigation of courtship patterns over a wide range of organisms has shown that stages in a species-specific courtship pattern may be omitted in a proportion of instances, while at the same time successful mating ensues. Such exceptions are often explained in terms of variations in individual readiness to mate or reproductive drive, etc. Ethologists argue about the validity of drive concepts (Hinde 1966:139–147), but accept the fact that animals do not always respond to the same stimulus situation in the same way. Morris (1956) shows how courtship patterns that can be idealized into reaction chains do, in reality, have a degree of variability in both the presence of, and ordering within, their component units of behavior. Thus one explanation for the opportunistic males of *Nephila maculata* (which copulate without first going through the normal prior phase of silk deposition on the female) would be that they are highly motivated to copulate and that this internal state in some way suppresses the preliminary elements of behavior. Alternatively males could be regarded as capable of recognizing situations in which certain stages of mating can be omitted as unnecessary. Our observations do not provide any basis for deciding between these and other possible alternatives.

A further general problem remains. Alexander and Ewer (1957:312) in their discussion on the origin of mating behavior in spiders argue that the "double process" of spider mating (stages of sperm induction *and* sperm transfer) confers a selective advantage in that "it permits the male to prepare for the mating beforehand, and, when in the proximity of the female, to be as quick as possible with the actual insemination." They postulate that sperm induction may have evolved through an intermediate stage of spermatophore production, as in pseudoscorpions and scorpions, and that the protospiders may have produced spermatophores that became redundant when web-spinning arose. To our view, however probable this may be, it does not bear on the problem raised by the mating behavior of *Nephila maculata,* where although the male may be prepared to insemination beforehand he nevertheless spends a great deal of time actually in contact with the female before copulation occurs.

PREDATORY BEHAVIOR

Behavior Units of Nephila maculata

In this section we describe the behavior units in order, from those involved at the initiation of a predatory excursion to those preceding the onset of feeding at its successful conclusion.

BEHAVIOR PRIOR TO CONTACT WITH THE PREY.—*Predatory Position at the Hub*: The normal waiting position at the hub is shown in Figure 2. Note that all the leg pairs are separate (compare with the predatory position of *Argiope argentata* described by Robinson and Olazarri, 1971:2) and extended in a more or less bilaterally symmetrical pattern. Normally all the tarsi are in contact with web members, but under the influence of strong incident sunlight this position may be considerably modified (p. 64). The spider rests on the underside of the web, at the hub, with the body more-or-less parallel to the plane of the web. The drag line is attached to the web just above the hub. The waiting stance of all the species of *Nephila* that we have seen is fundamentally similar, even to the disposition of the legs and the angle that they form to the body.

Plucking: After there has been an impact of some object with the web the spider orients towards the general direction of the prey (or other object) and then may either approach directly or make plucking movements. These are usually carried out with both legs I, which may be extended almost parallel to each other in the direction of the prey (Figure 20). In effect the spider jerks the web members on which the tarsi of legs I are placed, without breaking tarsal contact with the web. Such plucking movements may be repeated as the spider approaches the prey across the web. As in the case of *Argiope argentata,* plucking movements occur most commonly if the prey is immobile after it strikes the web. Approach plucking may be abandoned and the spider accelerate towards the prey if the latter becomes active after a plucking bout. Radii lying within a fairly wide sector around the prey may be plucked before the spider leaves the hub on a predatory excursion. When this happens the spider eventually approaches along the radial direction leading to the prey. We have never seen the spider have to make directional corrections to the left or right after it has set out on an approach pathway initiated by plucking. We have seen such corrections made when the spider has run towards the prey without prior plucking. A full discussion of the possible function(s) of plucking is given in Robinson and Olazarri (1971:5–6) and their conclusions are supported by our observations on *Nephila maculata.* This species often carries out wide-sector plucking after returning to the hub following a predatory excursion. It will also perform plucking movements from a prey capture site if other prey become entangled nearby. Such prey may then be approached without the spider first returning to the hub. We have not seen *Argiope* species behave in this way.

Approaches to the Prey: Approaches to prey may be rapid or slow and deliberate. Rapid approaches are made by the spider running across the undersurface of the web and occur most frequently when the prey is active. In such cases the spider may even overshoot the position of the prey along the radial pathway by several inches (this occurred in 3 out of 20 presentations of live dragonflies to adult female spiders). After overshooting, the spider either turns or backs up to the prey. Approaches may start slowly and accelerate if the prey becomes active during the approach. Slow approaches may be punctuated by pauses during which the spider stops and plucks, or may be continuous, when plucking with one leg I may form part of a stride forwards.

Very large prey may be approached slowly even when they are active. When the spider nears such prey it may raise legs I and one or both legs II off the web and flex them dorso-posteriorly. The resultant stance looks very defensive. It may also involve a dorsally directed concave curvature of the entire body brought about by flexion at the waist. A similar posture was noted by Robinson and Mirick (1971:128) in the case of *Nephila clavipes.* A very similar posture is adopted if the spider is touched lightly from above when it is at the hub.

FIGURE 20.—Female *Nephila maculata* plucking as she advances toward prey (not shown).

All approaches to prey involve the production of a dragline by which the spider remains attached to the web at some point. The spider at the hub has a dragline attachment to the web at the hub region, but it frequently reattaches the dragline before making a predatory excursion. It seldom attaches the dragline at other points on the approach pathway. Exceptions to this occur when the prey is particularly heavy, then the spider can be seen to make the characteristic dabbing movements of the spinnerets against the web, as it closes with the prey.

Not all objects striking the web are approached and particularly heavy objects may elicit an escape response. In the escape response the spider runs up from the hub to the upper frame members, towards nearby vegetation. Escape responses are described in detail later.

Behavior on Contact with Prey.—*Touching and Palpation*: In most cases when the spider contacts the prey it touches the prey with one, or both, legs I and continues its approach until it is standing with the anterior prosoma above part of the prey body. The tarsi of the leading legs touch the prey and the approach gait is unbroken until the spider assumes the attack stance. However, in some cases, when the prey is touched with the tarsi of the outstretched leading leg(s) the spider halts so that it is approximately a leg I length away from the prey (8–9 cm). It may then back up the web until it is more than this distance from the prey, and wait out of contact, or even retreat to the hub. We saw such behavior only in the case of very heavy prey (over 1.5 grams) and then only in a proportion of cases. When halted the spider may raise legs I and II off the web and assume the peculiarly curved attitude described above. Eventually the spider either retreats to the hub (infrequently) or advances slightly and taps the surface of the prey with the tarsi of legs I. The *tapping* movements, are slow, deliberate, and often repeated. Verbatim notes of attacks on large acridiids in which bouts of tapping occurred are reproduced in Appendix 2.

Tapping is often followed by prolonged tarsal touching and then most frequently by the bite and back-off attack behavior described below. However, in a proportion of cases, touching is followed by a slow advance to the assumption of an attack stance over the prey and in this case, as the spider moves forward, the pedipalps may be extended and contact the prey during the advance. In some cases they may be lowered onto the surface of the prey only when the spider assumes its attack stance. This pedipalpal contact (=palpation) is almost certainly made during the normal touching approach but is not then conspicuous because the advance to an attack posture merges without pause into attack itself and a separate palpation stage cannot be distinguished. Exceptions to this have been observed in attacks on pentatomids and reduviids when there is sometimes a pause between the assumption of an attack stance and attack. We presume that the odors produced by these insects may affect the spider and contribute to the abnormal pause that allows palpation to be seen as a distinct stage. Robinson (1969) found that *Argiope argentata* palpated prey that were covered in spider silk in a very distinct way and assumed that they did this because they received an unusual stimulus from such prey.

Attack Behavior.—*Nephila maculata* attacks all prey with the jaws and does not use silk as an attack weapon. Three types of attack are discernible.

Long Bite: The greater proportion of prey is dealt with by a sustained or long bite. The spider opens the chelicerae (by lateral movement), stoops and inserts the fangs into the prey. The bite is then sustained at its initial point of entry for a long period. If the spider is dealing with a prey that is vibrating or kicking, the point of insertion of the fangs may be the point of initial contact and therefore apparently random in location. Sometimes this bite may be ineffectual, as for instance when the spider bites into the wing of a moth and the fangs simply pass through the structure. Such bites are corrected and the spider moves the point of insertion, in steps, until it contacts more substantial tissues. Stepwise movements of the point of insertion of the fangs may occur in bites that are initially delivered to the body of the prey, and these are more difficult to account for in terms of function and causation. Thus in 12 out of 25 encounters with live dragonflies the bite was eventually sustained at a point on the thorax just behind the head. Since bites were moved to this position from other locations in 6 of the 12 cases there could be some element of choice in the exact location of the bite on the body of the prey. (This region of the prey plus the thorax in general may be a particularly conspicuous target in contrast to the abdomen which is long and very narrow.)

The spider could presumably determine the location of this target at the touching stage. In addition, the wings are attached to the bulbous thorax and vibrations of the web produced by wing movements could lead the spider to this region. (Four bites were initially aimed at the wing bases). Hingston (1922c:920) states that *N. maculata* always bites the thorax of the prey first; thus, "she behaves as though she knew the anatomy of her prey." Bites at some heavily sclerotised insects may not penetrate at first attempt and the spider may move along the prey, attempting an insertion, until a vulnerable region is found. In presentations of melolonthid beetles we found that the spiders appeared to be unable to penetrate the smooth and curved elytra. Sustained bites at these beetles were often made at the lateral or apical margins of the elytra where the soft ventral surface of the abdomen apparently offered a more easily penetrable bite site. Attempts to bite into the elytra *were* made and the impact of the fangs as they repeatedly glanced off the cuticle could be heard distinctly.

Bite and Back-off: As described earlier, and by Robinson and Mirick (1971) in the case of *Nephila clavipes,* attacks that are preceded by slow approaches and made after leg raising and preliminary tapping of the prey are often carried out by the bite and back-off behavior. This entails a rapid lunge at the prey followed by a short bite and subsequent retreat. After the first bite the spider retreats to a position usually within about 10 cm of the prey. Lunges, bites, and retreats may be repeated a number of times. We have a record of 9 cycles of attack over a period of 80 seconds when the prey was a large melolonthid beetle and one of 13 such attacks, in 2 bouts, for an attack on a 5 cm acridiid. The bites are rarely sustained for more than a few seconds. We suspect that they seldom exceed 5 seconds, and most of them are considerably less. They are usually carried out with legs I and II raised back over the prosoma of the body of the spider and the spider's body arched. Prior to the attack there are often intention movements, during which the spider spreads the jaws to a pincer-like extent while swaying forwards and then backwards on the spot where it is standing.

After a series of attacks the spider moves close to the prey and delivers a sustained bite. This may be preceded by tapping and palpation. We have seen a series of short bites followed by wrapping behavior without the occurrence of a sustained bite. Even a sustained bite may be interrupted by the prey struggling vigorously.

Seize and Pull-out: Very small and light prey are simply seized in the jaws and pulled from the web. Thus in the presentation of 50 live blowflies (25–50 mg) the bite time was one second or less in 4 cases and this was followed by a pull-out time of similar duration. On a purely arbitrary basis we can separate this behavior from the other attacks on these flies where bite times of up to 18 seconds were recorded (average for all 50 attacks 5.16 seconds). The distinction between a short bite and seizure in the jaws is thus somewhat arbitrary. A less arbitrary criterion for distinguishing between the categories "seize in jaws" and "bite" would be possible if it could be determined whether venom was used when the prey was simply seized in the jaws and pulled from the web. The distinction between seizure in the jaws and biting in *Argiope* and other advanced araneids is made operationally and is simple, since prey that are bitten are always wrapped at the capture site. This is not the case with *Nephila* species since prey that are given sustained bites of several minutes may subsequently be removed from the web by being pulled out (Robinson, Mirick, and Turner, 1969; Robinson and Mirick, 1971).

REMOVAL OF PREY FROM CAPTURE SITE.—*Pulling Out*: At the termination of a biting attack the spider almost always attempts to pull the prey from the web. This behavior occurs in all the *Nephila* species that we have observed and Robinson and Mirick (1971;129) have described it in the case of *Nephila clavipes.* Hingston (1922c:920) describes this behavior as tearing the prey from the viscid attachments. Without releasing its cheliceral hold (i.e., bite) the spider pulls outwards on the prey, often repeatedly flexing and extending its legs in the process. If the prey becomes freed it is then carried back from the capture site to the hub. Sometimes if it becomes only partly freed, the spider may hang away from the web wholly or partially suspended on its drag line and pass its legs between the prey and the web. This motion frees the prey of the remaining attachments essentially by stripping the viscid element away from the prey in a "teasing" movement. Damage to the web resulting from the process is surprisingly slight. In most cases, a few viscid spiral elements may be broken and the golden droplets of adhesive stripped off others, but large holes are rarely produced. This contrasts sharply with the results of the cutting-out behavior carried out on prey that are wrapped at the capture site.

(Records of prey capture sequences given in the next major section of the description of predatory behavior show that the pull-out technique succeeds with certain types of prey. With other types of prey it is either replaced, after failure, or, omitted altogether.)

Wrap in situ: Very large prey, as well as prey that for other reasons cannot be freed by pulling, are wrapped at the capture site while still enmeshed in the web. Such prey are cut from the web, partly during the wrapping process and partly when it is complete. *Nephila* species wrap relatively slowly (when compared with species of the genera *Argiope, Araneus, Eriophora,* and others). The spider stands on the prey and casts skeins of silk onto it by alternate movements of the hind limbs. These movements are easily counted, unlike the very rapid movements of *Argiope* species. The prey becomes covered with a complex of silk skeins but not completely enswathed in a layer of silk (another contrast with the advanced spiders). The prey is not normally rotated about an axis while silk is laid down directly from the spinnerets, a behavior frequently performed by *Argiope argentata.*

The wrapping bout is interrupted frequently as the spider cuts entangling web elements that resist the passage of the wrapping silk over its surface. Cutting is done by bringing the chelicerae down to the strand or by pulling the silk up to the jaws on the tarsus of a leg, and also by apparently snapping it with a foot. Towards the end of a wrapping bout the spider may have turned through 180 degrees and be hanging with its dorsal surface partly oriented towards the web, while the prey is suspended below the web on just one point of attachment. Figure 21 shows this remarkable wrapping stance. The consequence of this style of wrapping is that the resultant prey package invariably hangs below the web. Attack wrapping by many other species of araneid, on the contrary, often results in a prey package that lies securely in the web plane and has to be cut *out* of the web before transportation (Robinson and Olazarri, 1971, figs. 3, 7).

Free-wrapping: As in the case of *Nephila clavipes* (Robinson and Mirick, 1971:135–136) some prey that are freed from the web by pulling are wrapped before transportation. This form of wrapping results in the prey being trussed into a large fairly compact prey package and is applied to bulky prey that can nevertheless be freed from the web without being wrapped in situ. The freed prey may be held in the jaws until the first skeins of silk are passed over it by movements of legs IV; it is then held with legs III until it is trussed in silk. The spider is normally hanging below the web plane while it performs the free-wrapping, in the manner shown in Figure 21.

TRANSPORTATION TO THE HUB.—*Carrying in Jaws*: Light prey are carried to the hub in the jaws, as is the case with most araneids. *Nephila maculata* commonly exhibits a behavior that we have only seen occasionally in other *Nephila* species, and have not noted in other araneids. Prey from the large area beneath the hub of the web are carried in the jaws as the spider backs up the web hanging head downwards. This backing movement is illustrated in Figure 22. In effect the spider fends itself off the web surface with walking movements of legs I, II, and III while climbing "hand over hand" up the drag line with the tarsi of legs IV. In cases where we were able to watch the process at close range, it became obvious that the spider was in fact gathering up quite considerable lengths of the drag line into a loose hank as it made its ascent backwards. The process is fairly slow compared with merely turning and walking forwards to the hub. This latter behavior does occur in the spider's repertoire and ensures a more speedy resumption of its predatory position at the hub. Thus in 50 presentations of live moths 42 spiders backed up the web, and 7 turned and walked or ran back to the hub. These seven averaged 4.4 seconds for the return journey, whereas the average time for those that backed up the web was 34.8 seconds (detailed analysis in section on behavior sequences). What are the possible adaptive advantages of this behavior? A spider

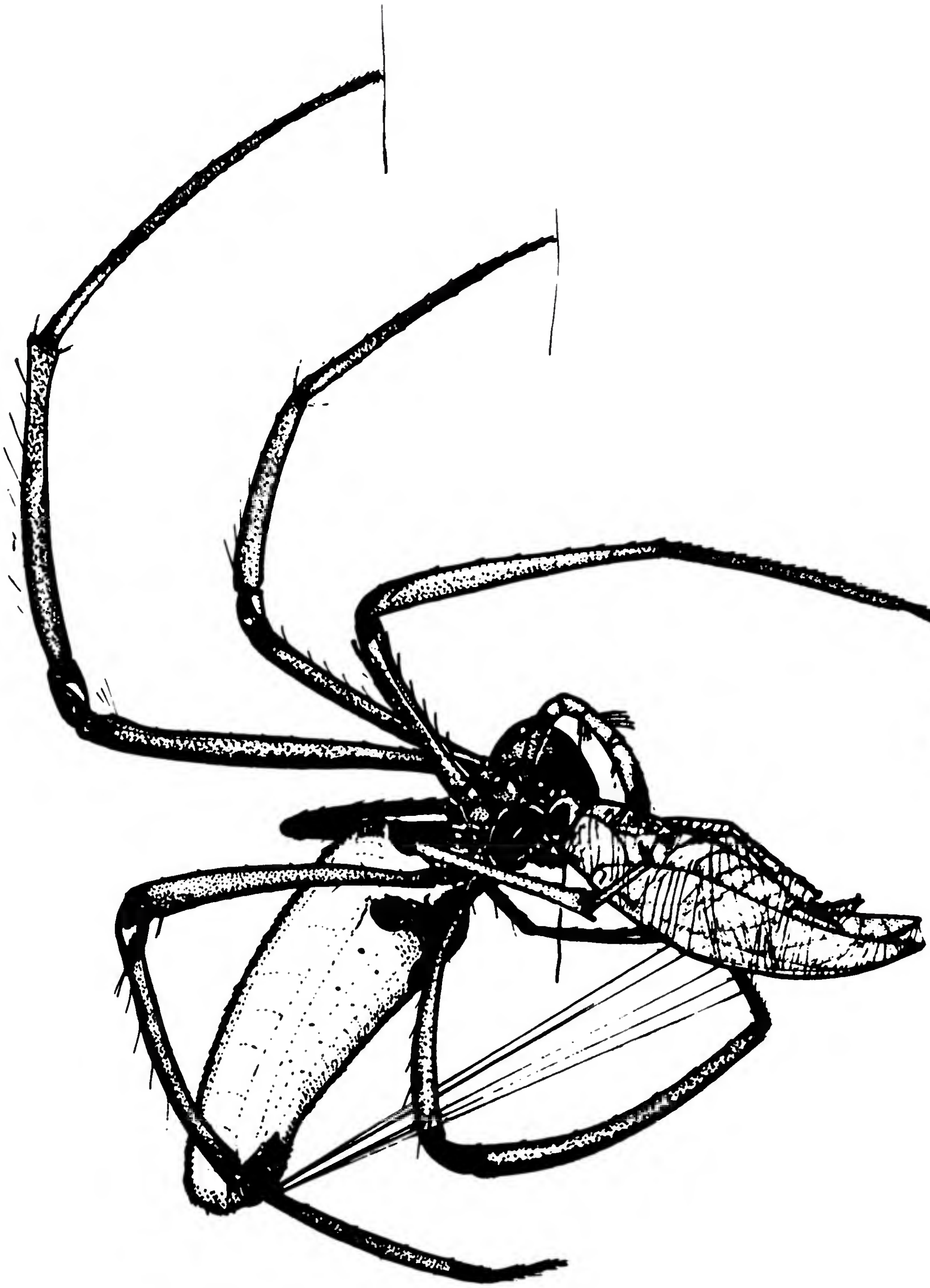

FIGURE 21.—Wrapping posture of *Nephila maculata* (based on film records).

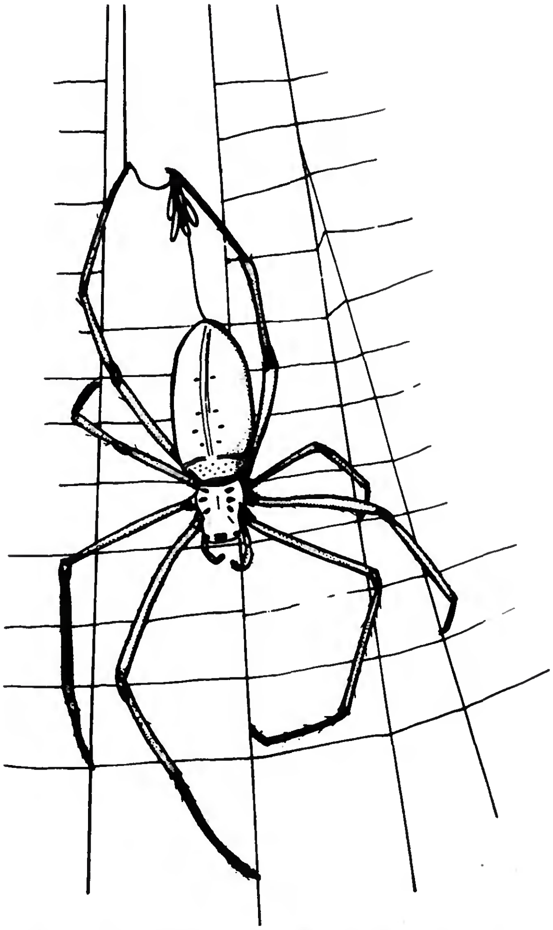

FIGURE 22.—*Nephila maculata* backing up the web to hub. Prey (carried in jaws) omitted for clarity. Note that the dragline is being ascended backwards and collected in the tarsus of the left fourth leg. (Based on successive frames of film records).

carrying a load in its jaws and ascending the undersurface of an inclined web has the center of gravity in a position that is more favorable to a trouble-free ascent than a spider walking forwards with prey in its jaws. The question of why *N. maculata* ascends backwards and *N. clavipes* (for instance) does not is difficult to resolve.

Carrying on Silk: The other basic method of carrying prey back to the hub is on a silk thread suspended from the spinnerets. The suspensory thread may be suported by being held by one or both legs IV, or may, less commonly, be without secondary support. Large prey are carried back to the hub in this way. Because of the slope of the web, prey carried on silk hang away from the web plane and seldom become entangled in the web during transportation.

Wrapping in Transit: Prey, particularly those carried forwards in the jaws, occasionally become entangled in the web during transportation. When this happens the spider makes pulling movements, and, if these fail, briefly wraps the prey and then proceeds to carry on silk as described above.

BEHAVIOR AT THE HUB WITH PREY.—*Carried in Jaws*: Prey carried in jaws are almost always wrapped in silk on arrival at the hub. The spider usually wraps in a head-up position comparable to that shown in Figure 21, and turns to achieve this position if it arrives at the hub in a different orientation. Before wrapping. the spider usually attaches its drag line to the hub silk. Wrapping at the hub is carried out in the slow manner that it characteristic of the genus. Small prey, carried from the upper region of the web, are often wrapped when the spider is in a head-down position (as it will be when arriving from above the hub). Wrapping in this case is achieved by the spider swinging the abdomen into an almost horizontal position with the anterior prosoma close to the web and the apex of the opisthosoma well away from the web. In this position the long legs IV can make wrapping movements without fouling the web.

Carried on Silk: When the spider arrives at the hub with prey suspended behind it on a silk thread a process of attaching this thread to the hub region is carried out. The spider dabs the spinnerets against the hub silk at the point of arrival, thereby making the first attachment of the prey to the hub. It then turns until it assumes the head-down position normally adopted when the spider is at the hub. As it circles to the left or right it attaches its drag line, at intervals, to the hub. As it does this the leg IV on the side opposite the direction of turning is used to stretch the drag line between the points of attachment (Figure 23). The stretching movement is essentially similar to the one that most araneids use when laying down the viscid spiral between the radii during web building. We recorded the direction of turns made by spiders during this *rundgang* and the number of attachment points made with different types of prey.

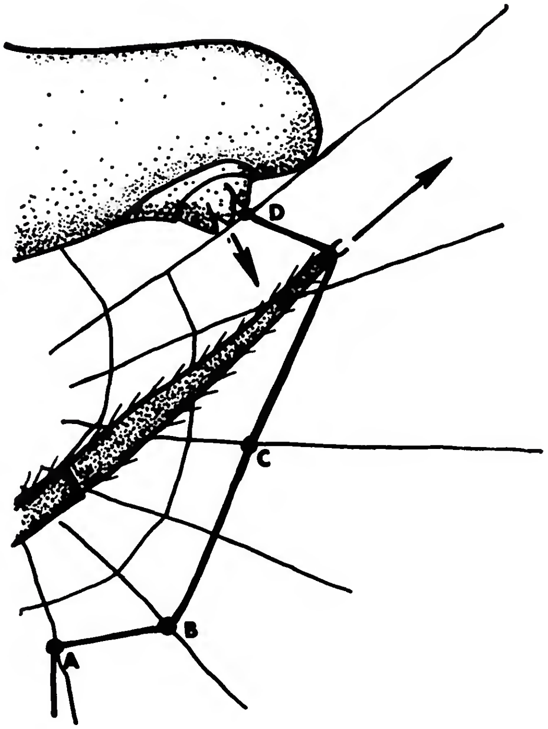

FIGURE 23.—Silk attachment during the *rundgang*. The silk line leading from the prey package has been attached at A, B, C. Between attachments, as between C and D, the spider stretches the silk with movements of the appropriate leg IV, as shown.

These data are given in the section on behavior sequences.

Prey at the Hub: If the spider was feeding at the hub before catching the prey with which it is returning there is some modification of the behaviors described above. If the previous prey was large the new prey will almost always be attached at some distance from the old, often above it, and the spider will resume feeding on the old prey after the process of attachment. If the previous prey was small, and/or partially consumed, the new prey and the old prey are frequently wrapped together into one bundle and the spider then feeds on the compound package.

Assumption of a Feeding Posture: After the spider has suspended the prey package from the hub it frequently backs a few centimeters up the web and reattaches its drag line before moving back to the central region of the hub. Before commencing feeding the spider may undertake grooming activities in which the legs are rubbed together and particular attention given to the tarsal regions. The tarsi of legs I and II are almost always drawn through the chelicerae, one by one, after a predatory sequence, and the other tarsi may also be treated in this way. After such grooming, and sometimes a variable period of inactivity, the spider often plucks the radii over a wide sector and then reaches out with one of the first legs until it contacts the thread on which the prey is suspended. It hauls on this thread until it can grasp the prey package and manipulate it. The period of prey package manipulation varies considerably in duration and involves some or all of the first three pairs of legs. The short third legs are used for manipulation *beneath* the spider while the flexed legs I and II operate in front of the prosoma. During the manipulation the prey package is moved backwards and forwards, rolled over and twisted from side to side. The spider makes short bites at the prey as it is manipulated. Eventually the spider sustains a cheliceral insertion at one point and places legs I and II back on the web in their normal extended positions; one or both legs III may still hold the prey, but this is unusual. At this stage we assume that the spider is feeding.

Feeding Behavior: We have not watched the entire process of feeding, but examination of discarded prey remains allow certain deductions to be made about the processes involved. The remains of heavily sclerotized prey items, such as beetles, consist of entire exoskeletal shells. These suggest straightforward suctorial feeding; however, the elytra and membranous wings of beetles are often found separately. We believe that these may be nipped off and discarded during the feeding process. The discarded remains of orthopterans are frequently in a highly comminuted state suggesting that at some stage in the feeding process the spider chews up the prey into smaller portions. This process may facilitate the digestion of prey material that is otherwise not readily accessible to enzymes that are simply pumped into the interior of a perforated but entire insect. Very soft insects, such as flies, can be seen to be kneeded between the chelicerae during feeding, and are highly compressed when dropped as trash parcels.

Behavior Units of Other Species

In Ghana, mainly in the Legon area, we encountered two species of *Nephila*: *Nephila constricta* and *Nephila turneri* (the latter a large and striking spider), as well as *Nephilengys cruentata*. We presented a variety of prey items to the *Nephila* species, and also to *Nephilengys cruentata*. We concentrated attention on the latter species since the spider is in many ways similar in appearance to an *Argiope* and builds a cocoon-like retreat that is continuous with the web. We encountered *Nephilengys* again in Madagascar, at a forest site near Perinet and carried out further observations there. We first encountered *Herrenia* species at Manaas in Assam and later encountered the genus at Periyar in Kerala, South India. The spider builds elongate webs close to large tree boles and from this habit and its appearance we decided that it must be a *Nephilengys*. We eventually found very similar spiders building webs in similar situations at Wau. Specimens of these were identified by Fr. Chrysanthus as *Herrenia ornatissima*. Since this genus is in the *Nephila* group we carried out studies of its predatory behavior.

All the *Nephila* group spiders that we studied en route to New Guinea possessed broadly similar behavior units. All attacked a wide range of prey by biting. All except *Herrenia ornatissima* made pull-out attempts after biting and all tapped large prey from a distance before biting. The *Nephila* and *Nephilengys* species showed the type of bite and back-off attack on large prey that we have described above for *Nephila maculata*. We were unable to induce *Herrenia ornatissima* to attack very large prey and did not see bite-and-back-off behavior in this case. None of the spiders could be induced to attack prey by wrapping, although we presented types of prey (acridiids, beetles, dragonflies etc.) that *Argiope* species consistently attack in that way. We observed wrapping at the capture site (after biting) in all the species, and this was performed with slow alternate movements of legs IV as in *Nephila maculata*. All the species, except *Herrenia ornatissima* wrapped prey, on occasion, that had been freed from the web by pulling. All the species hung prey at the hub and did not store it at the capture site. *Nephilengys cruentata* assumed an extraordinary position in its retreat (Figure 24) facing outwards towards the web, but with its dorsal surface towards the web that lies above the retreat. Spiders returning to the retreat with prey enter the retreat head first and turn over and towards the entrance when they are inside or at the entrance. This considerably complicates the behavior of wrapping prey at the feeding site (hub or retreat) and also complicates the process of hanging prey at the retreat entrance (equivalent to hanging it at the hub in the other species).

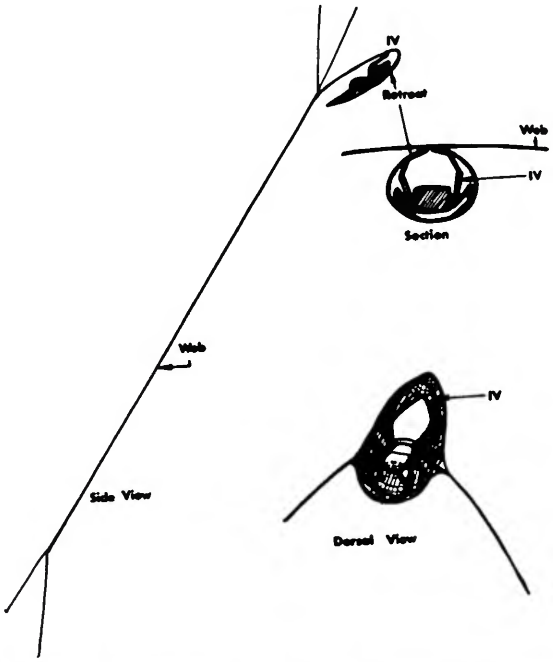

FIGURE 24.—Relationship of the retreat of *Nephilengys cruentata* to the main orb and the position of legs IV in relation to the retreat. Note that these legs contact the dorsal surface of the retreat which is continuous with the web surface.

Herrenia ornatissima builds its elongate webs close to tree boles, often less than 2 cm away from the bark, and rests in a cuplike silken depression at the top of the web, close to or touching the bark. This again poses problems since at this place the spider only has access to the upper surface of the web. It is interesting to note that the dorsal surface of this spider is beautifully camouflaged and that it is very difficult to pick out against a background of bark (Figure 25). The specific name may

FIGURE 25.—Male (above) and female (feeding) *Herrenia ornatissima* on surface of web. The web is built very close to the surface of a tree and is elongate. The female has a camouflaged dorsal surface.

be derived from the very bright orange-red spot on the ventral surface that is not visible when the spider moves about the upper surface of the web, as it normally does.

We did not observe, in the other species of *Nephila,* the process of backing up the web with prey in the jaws that is so characteristic of the carry-in-jaws technique of *Nephila maculata.*

Table 8 summarizes the main features of the behavior units of these species.

TABLE 8.—*Units of predatory behavior*
(+ present, - absent, ? not known)

Behavior unit	*N. maculata*[1]	*N. clavipes*[2]	*N. turneri*[3]	*N. constricta*[3]	*Nephilengys cruentata*[4]	*Herrenia ornatissima*[5]
Legs reflexed approach	+	+	+	+	+	+
Tapping	+	+	+	+	+	+
Bite and back off	+	+	+	+	+	?
Attack bite	+	+	+	+	+	+
Attack bite with leg raising	+	+	+	+	+	-
Pull out	+	+	+	+	+	?
Wrap in situ	+	+	+	+	+	+
Cut out	+	+	+	+	+	+
Free wrap	+	+	+	+	+	?
Attack wrap	-	-	-	-	-	-
Carry in jaws	+	+	+	+	+	+
Carry on silk	+	+	+	+	+	+
Wrap in transit	+	+	+	+	+	+
Wrap at hub	+	+	+	+	rare	?
Wrap at retreat	-	-	-	-	+	-
Leave prey in situ	-	-	-	-	?	-

[1] New Guinea. [2] Panama. [3] Ghana and Ivory Coast. [4] Ghana and Madagascar. [5] New Guinea and India.

Behavior Sequences

We follow Robinson and Olazarri (1971) in here presenting descriptions of the behavior sequences given to various types of prey. The responses given to each type of prey are outlined separately and illustrated in a standard form. Comparisons between the types of sequences given to different types of prey are largely confined to the concluding part of this section.

The prey types chosen for replicated presentations to the free-living adult spiders represent prey that figure prominently in the diet of the Wau spiders (p. 18) and others of interest for comparative purposes (Table 9).

TABLE 9.—*Behavior sequences given by* N. maculata *to four types of prey* (durations in seconds)

	Flies (N=50)	*Moths* (N=50)	*Katydids* (N=50)	*Dragonflies* (N=30)
PREY WEIGHT (mg)				
m	34.8	137.3	129.6	110.9
sd	11.2	56.3	30.3	21.2
ATTACK UNITS				
Bite				
m	5.1	15.8	16.6	44.5
sd	3.8	9.5	10.0	31.6
Pull out				
m	2.5	16.4	16.2	52.2
sd	2.1	13.9	17.2	24.2
Wrap and cut out				
m	none	none •	none	(N=21) 101.2
sd				38.6
TRANSPORT UNITS				
Carry in jaws				
Forward	(N=7)	(N=8)	(N=3)	On silk (N=23)
m	10.2	4.4	4.0	23.6
sd	9.3	1.9	-	11.5
Back-up	(N=43)	(N=42)	(N=47)	(N=7)
m	58.7	34.8	42.8	30.7
sd	20.3	22.7	18.4	17.5
Wrap at hub	(N=6)	(N=35)		(N=7)
m	26.3	44.0	61.2	61.5
sd	10.1	15.0	19.7	11.6
Total				
m	65.0	105.3	166.6	238.8
sd	29.1	43.9	45.2	61.5

• One free wrap, one wrap in transit.
m=mean, sd=standard deviation.

Sequences with Live Flies: Fifty blowflies were presented to 30 spiders. Where the same spider was used for two observations at least one day intervened between presentations. The results are summarized in Figure 26. All the flies were bitten for short periods, pulled from the web and carried in the jaws to the hub. On 7 out of 50 occasions the spider turned at the capture site and ran or walked back to the hub facing the direction of movement. In all the other cases the spider backed up the web in the manner described earlier. Only 6 of the 50 captured flies were wrapped immediately on arrival at the hub. Only four spiders plucked the web before rushing down to attack the prey—a reflection of the fact that the majority of flies vibrated in a sustained manner after striking the web.

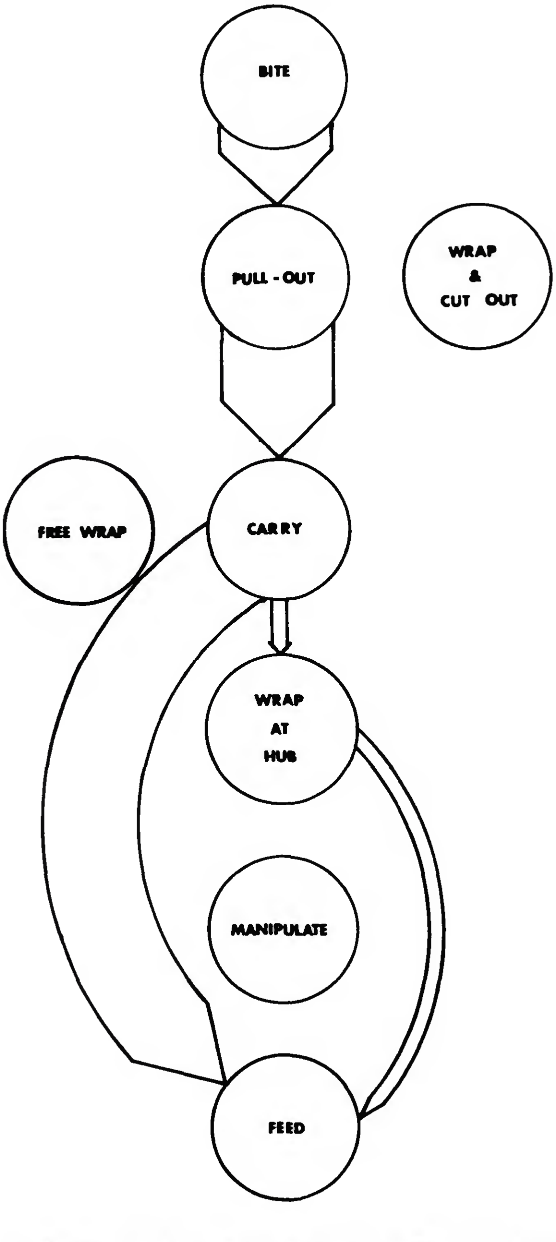

FIGURE 26.—Predatory sequences upon live flies. The width of the arrows is proportional to the number of responses in the direction indicated.

Five spiders overshot the mark, running beyond the prey, as they made their attack. This led to some delay in biting. The sequences are simple and rapid; run to prey, bite, pull out, carry in jaws backing up the web, feed.

Temporal Aspects: The attack and removal from the web stages of the sequence are of short duration (bite average 5.1 seconds, range 1–18 seconds; pull-out average 2.5 seconds, range 1–13 seconds). The total durations are long, due to the slow nature of the backing-up process when the prey is carried in the jaws. The average back-up time was 58.7 seconds, range 21–106 seconds, while the average turn-and-run time was 7 seconds, range 3–13 (or 10.2 seconds if the one spider that turned and walked to the hub is considered in addition).

The total sequence durations for those sequences in which the spider turned before returning to the hub are all less than two-thirds of a minute, the others average well over one minute.

Sequences with Live Moths: Fifty live moths were presented to 28 spiders. The moths were of different species but fairly similar in size and weight. All were bitten at the capture site and then pulled from the web, without capture-site wrapping. Eighteen spiders plucked the web from the hub before making a predatory excursion. Four spiders had distinct stages of touching or palpating the prey before biting. Transportation was predominantly effected by backing up the web with the prey in the jaws (42 out of 50), seven spiders turned and ran back to the hub with the prey in their jaws. One spider wrapped the prey after it stuck in the web during in-jaws transportation.

Fifteen prey items were not wrapped at the hub after transportation, two of these had been wrapped prior to or during transportation (1 free-wrap).

The form of the behavior sequences given to live moths is summarized in Figure 27.

Temporal Aspects: The attack and pull-out phases are of longer duration than in the equivalent stages of the attack on flies. Bites averaged 15.8 seconds; range 6–58 seconds, and pull-out units averaged 16.4 seconds, range 1–70 seconds. Transportation times were again high in the case of spiders that carried the prey in their jaws while backing up the web (average 34.8 seconds, range 3–118). Those that turned and ran back to the hub averaged 4.4 seconds; range 2–8. After wrapping,

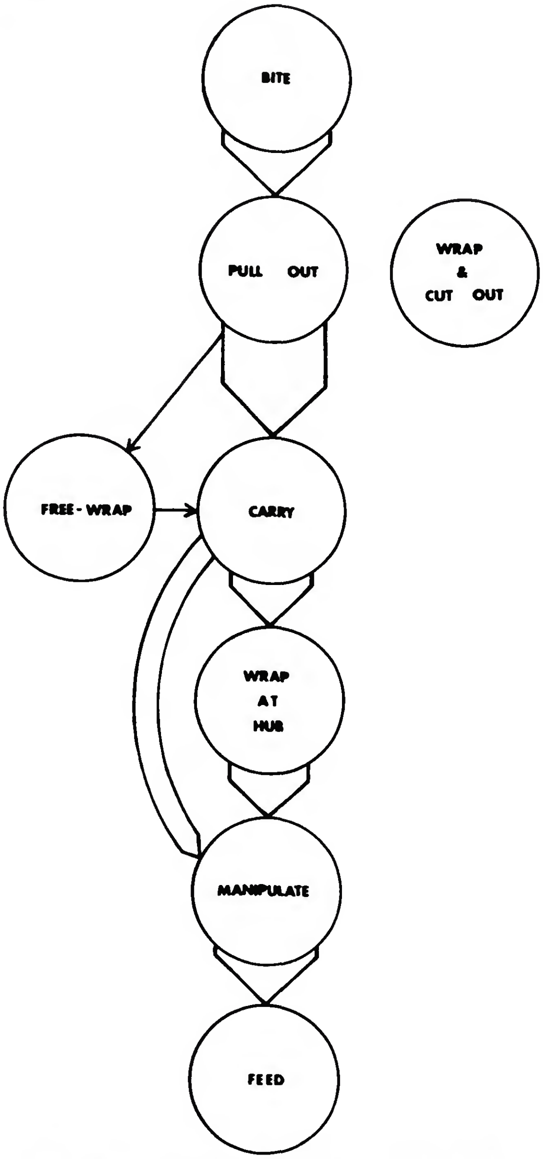

FIGURE 27.—Predatory sequences upon live moths.

15 spiders turned right at the hub and 20 turned left. Wrap at hub averaged 26 leg movements per spider and 2.1 silk attachments in the *rundgang*.

Wrapping at the hub after transportation (70% of all cases) accounted for an average of 44.0 seconds.

Sequences with Live Katydids: Fifty live katydids were presented to 32 adult spiders. These were bitten and pulled out in all cases. All except three of the katydids were subjected to being carried in the jaws as the spider backed up the web to the hub. Three katydids were carried by the spider in the jaws as it ran to the hub after turning at the capture site. All the spiders wrapped the prey at the hub after transportation. The sequence for small katydids was thus very simple, as shown in Figure 28. Plucking occurred in 11 cases out of 50. It is interesting to note that free-wrapping did not occur in any of these sequences and that prey were not wrapped at the capture site.

Temporal Aspects: Bite durations were slightly longer than those given to moths, averaging 16.6 seconds. This difference is not significant (statistical analysis in Table 9). The pull-out time averaged 16.2 seconds, slightly less than that given to moths. Transportation times were high—mean 42.8 seconds—for those spiders that backed up the web with prey in their jaws. The three spiders that turned and ran back to the hub averaged 4 seconds for transportation. All the prey were wrapped at the hub after transportation and this behavior unit accounted for a mean time of 61.2 seconds. Total sequence durations averaged 166.6 seconds; this is higher than in the case of moths. Thirty-three spiders turned left at the hub and 17 turned right. Silk attachments during the *rundgang* averaged 3.3 and leg movements during wrap at hub averaged 43.8 per spider.

Sequences with Live Dragonflies: The sequences given to live dragonflies were characterized by the high proportion of wrap and cut-out units that occurred. Dragonflies are much more bulky than katydids in the sense that a greater area of insect structure become enmeshed and adherent to the web, because of the body length and the extended wings. At the same time the insects do not pull easily from the web. This contrasts with moths which have a large wing area in contact with the viscid spiral. We therefore interpret the high proportion of wrapping at the capture site, which occurs after extensive pulling-out attempts, as a response to the problem of prey removal (Robinson and Mirick, 1971). Twenty-one out of 30 dragonflies were wrapped at the capture site after pulling-out attempts. Pulling-out attempts were successful in removing prey from the web in only nine cases. Free-wrapping behavior occurred after successful

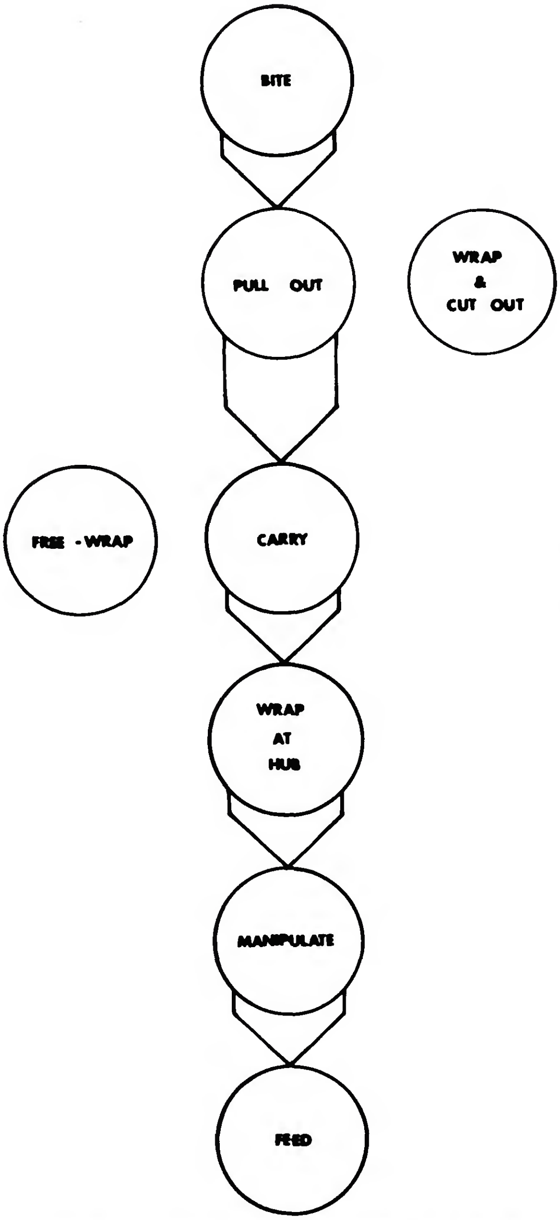

FIGURE 28.—Predatory sequences upon live katydids.

pull-out attempts in one case and after cutting out in two cases. Pulling-out movements resulted in the spider severing the head of the dragonfly in one case. The head was then transported to the hub as though it were the entire prey. The spider removed and transported the remainder of the dragonfly several hours later. Wrapping occurred during transportation in one case. There were thus four cases of wrapping not obviously associated with the removal of the prey from the web or its storage at the hub (three cases of wrapping at the capture site after removal from the web and one wrap in transit). Wrapping at the hub occurred in every case where the spider freed the prey by pulling, i.e., in all those cases where the prey was carried to the hub without having undergone wrapping behavior. Transportation was predominantly carried out by the spider suspending the prey on silk behind its body and walking forwards back to the hub. Twenty-three spiders carried prey in this way although one of these started by backing up the web with the prey in its jaws. The prey in this case became entangled in the web, was wrapped in situ, cut out, and then carried on silk. Figure 29 summarizes the results.

Temporal Aspects: Bite durations averaged 44.5 seconds, persistant pull-out attempts after biting averaged 52.2 seconds (only nine of these were successful). Wrapping at the capture site averaged 101.2 seconds in duration. Total sequence time for live dragonflies averaged 238.8 seconds. This mean sequence time is higher than that involved in any of the sequences reviewed so far despite the fact that the dragonflies were not heavier, on average, than the moths or katydids (Table 9). The seven spiders that wrapped at the hub averaged 61.5 seconds for this behavior, four turned left and three turned right.

Sequences with Large Acridiids: We made 25 presentations of very large acridiids to an equal number of spiders. These insects were between ca. 45 mm and 50 mm in length and between 2 and 3 grams in weight. They had large mandibles and spiny posterior legs. They thus were potentially dangerous and capable of vigorous escape and defense activities. We expected that they would present considerable problems to a spider that did not have an attack-wrapping behavior. They did. The spiders were successful in completing a predatory sequence in 13 out of the 25 cases. Twelve acridiids escaped at some stage in the spider's attack sequence or without being attacked. The successful sequences were all highly complex and the partial sequences of the unsuccessful spiders that attacked the grasshoppers were also complex. The complex

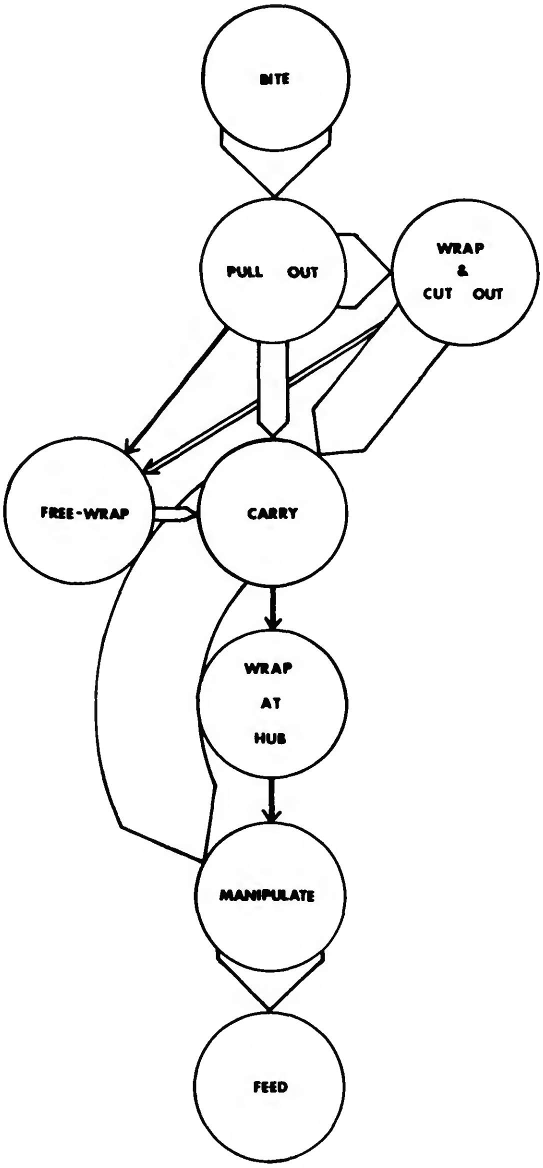

FIGURE 29.—Predatory sequences upon live dragonflies.

sequences cannot be given in diagrammatic form but a selection of verbatim field notes are given in the appendix. In general the sequences showed complexity at the approach, attack, and removal from the web stages. Approach was of the hesitant type described in the section on behavior units. In more than half the cases approach was preceded by retreat from the hub away from the point of impact of the prey. This form of defensive behavior makes adaptive sense when objects hitting the web are large and/or heavy. Attack units involved the employment of the bite-and-back-off technique with numerous repetitions of the short bite. Retreating away from the prey between bites was a fairly regular occurrence. Early bites were often directed at appendages rather than the body proper and this again indicates the temerity with which the spider approaches such large prey. Prey removal always involved extensive wrapping even when the degree of attachment to the web had been greatly reduced by the tearing consequent on the prey's struggles. A summary of the major features of the complex sequences is given below.

Temporal Aspects: Because of the repetition of major units in the attack and approach systems, as well as extensive prey-packaging operations, the duration of the total sequences is consistently high. In extreme cases the duration exceeds three-quarters of an hour. The data (below) on both structural and temporal aspects of the sequences support the analysis given above.

UNITS OCCURRING IN THE 13 SUCCESSFUL SEQUENCES

Sequential order of units	*Proportion of occurrence*
1. Retreat from hub before attack	9/13
2. Plucking before attack	7/13
3. Slow approach ± leg raising	11/13
4. Tapping prey before attack	8/13
5. Bite and back-off attack	11/13*
6. Sustained bite ± prior 5	12/13
7. Wrap in situ, interrupted by rest periods	13/13
8. Carry on silk	13/13
9. Hang on hub	13/13

* Maximum number of interrupted bites = 13 in two sessions, 3 followed by 10, more than 8 minutes later.

DURATIONS (MINIMA AND MAXIMA) FOR THE 13 SEQUENCES (in minutes and seconds)

Sequential order of units	*Range*
1. Approach (from retreat position or hub)	1:10– 7:40
2. Bite and back off	0:54–14:10
3. Sustained bite	0:40– 8:30
4. Wrap and cut out	1:14–13:40
5. Transportation	0.30– 3:10
Total Sequence Time:*	9:40–47:01

* Includes time spent retreating and rest periods, which are not included in units 1–5.

Sequences with Live Melolonthids: At certain times of the year melolonthid beetles constitute an important element of the prey captured by free-living spiders. Initial observations suggested that these bulky, comparatively heavily-armored insects, are not easily subdued by the biting attacks of *Nephila maculata.* We, therefore, presented living melolonthids to the spiders and concurrently presented a similar number to the much smaller *Argiope aemula.* The latter species builds its webs in the herb layer and is much less likely to catch the beetle in large numbers. It is, however, a spider that has attack wrapping as its major predatory strategy and a comparison of the behavior of the two species towards the beetles was of interest. For ease of comparison we include details of the *Argiope* predatory sequences in this section, under a separate heading.

Ten melolonthids were presented to both species of spider. *Nephila maculata* attacked, in all cases, by biting attacks, but these proved to be more complex than any that we had previously observed in that they did not conform to the "typical" pattern. Thus the bite-and-back-off pattern was employed in five out of ten presentations but in only one case was it followed by a sustained bite. In four out of the five cases the spider wrapped the prey after a series of bite-and-back-off units. This is most unusual. In the five other presentations the spiders made bites at the prey without withdrawing from contact between bites, but in only two cases were a series of such bites followed by a sustained bite; in the three others the spider then proceeded to wrap the beetle. Thus contrary to the pattern observed in presentations of other insects, wrapping occurred in the absence of a sustained bite in all but three of the cases. Examination of the detailed notes on the sequences shows that the spiders had extreme difficulty in penetrating the hard, smooth and rounded cuticle of the insect and biting attempts were often unsuccessful in penetrating the cuticle effectively. In this situation the spider seems to have the capacity to switch in the wrap behavior unit. Reexamination of the detailed notes on the behavior of *N. maculata* towards large acridiids shows that in one or possibly two cases the spider commenced wrapping after a long series of bite-and-back-off units had terminated in a relatively short sustained bite; at the time we missed the possible implications of this behavior.

In only one case did the spider attempt to pull the prey out of the web prior to wrapping it in situ and then cutting it from the capture site. The beetles, unlike the acridiids, did not struggle vigorously during the attacks and made no attempt to raise the elytra and beat the wings (p. 63). As a consequence they were not largely freed from the web when the spider prepared to transport them. All the prey were transported to the hub on silk lines and not carried in the jaws.

Temporal Aspects: Total sequence times were long in duration and average over 12 minutes. Operations at the capture site (approach, attack, and packaging) occupy more than half the sequence time in nearly all cases.

Comparison with Argiope aemula

Nephila maculata ranges from 2 to 4 grams in weight and is much heavier than *Argiope aemula* (0.5–0.9 grams). Despite this fact *Argiope* takes less time to attack heavy melolonthid beetles (0.5–0.8 grams in weight). Durations (in minutes and seconds) of predatory sequences are given below. Those for *Argiope* are for times spent actually in contact with the prey and include periods of rest-on-prey (ROP) (two sequences) but not periods of rest-on-hub (ROH). The latter period is omitted because the spider is at that stage capable of initiating new attacks and is not occupied with predatory behavior. *Nephila* does not have a rest-on-hub behavior. The *Nephila* attacked all the prey by biting whereas *Argiope* attacked all the prey by wrapping.

Arigiope aemula	*Nephila maculata*
4:21 ROH	7:57
6:40 ROH	10:58
4:13 ROH	8:17
5:15 ROH	31:10
9:18 ROP	28:41
8:47 ROP	12:15
4:05 ROH	9:18
3:24 ROH	13:08
6:39 ROH	11:32
11:32 ROH	10:29

Robinson, Mirick, and Turner (1969) have argued that attack wrapping gives the spider the potential of leaving the wrapped prey at the capture site without having to wait there until it is sufficiently subdued to be safely cut from the web and transported. It can thus reduce the time spent away from the hub by interrupting a predatory sequence before transportation and leaving this process until after a period at the hub monitoring the web. In the sequences given to live melolonthids the two that did not involve rest at hub stages were longer than all but one of those that did.

The wrapping units were extensive and punctuated by short bites or biting attempts. The enswathement of the prey was very extensive and produced layers of silk that were very thick in comparison to the effects of wrapping by *Nephila*. In fact the wrapping behavior of *Argiope* looks much more effective than that of *Nephila*. It involves synchronous (or nearly so) movements of the two fourth legs, which cast broad skeins of silk over the prey in rapid succession. On the other hand the leg movements of *Nephila* are slow and alternating. They carry relatively narrow skeins of silk onto the body of the prey.

All the beetles were transported on silk behind the spider; in two cases the insects were wrapped again at the hub after being hung. *Argiope* appeared to be able to bite the wrapped prey without difficulty, although its chelicerae are much smaller and less heavily sclerotized than are those of *Nephila*.

Comparison with Nephila clavipes

Table 10 summarizes the main features of the attack sequences of *Nephila maculata* and *N. clavipes* for a number of types of prey. Robinson and

TABLE 10.—*Comparisons of sequence units and durations (in seconds) of* N. maculata *and* N. clavipes *

	Lepidoptera *N. maculata* (on moths, N=50)	 *N. clavipes* (on butterflies, N=20)	Orthoptera *N. maculata* (on katydids, N=50)	 *N. clavipes* (on crickets,N=20)	Dragonflies *N. maculata* (N=30)	 *N. clavipes* (N=10)
Prey weight (mg)						
m	137.3	102.4	129.6	231.5	110.9	142.7
sd	56.3	33.0	30.3	25.8	21.2	37.1
ATTACK UNITS						
Bite						
m	15.8	29.4	16.6	29.3	44.5	63.7
sd	9.5	18.6	10.0	17.6	31.6	23.7
Pull-out						
m	16.4	47.6	16.2	12.8	52.2	61.6
sd	13.9	33.6	17.2	26.9	24.2	55.3
Wrap, & cut out						
m	none	135.7 (N=7)	none	47.0 (N=1)	101.2 (N=21) **	75.6 (N=7)
sd		25.9		–	38.6	18.4
TRANSPORT UNITS						
Carry on silk						
m	none	16.0 (N=7)	none	19.0 (N=1)	23.6 (N=23)	24.9 (N=7)
sd		3.7		–	11.5	16.1
Carry in jaws						
	Forward Backward		Forward Backward			
m	4.4 (N=8) 34.8 (N=42)	28.5	4.0 (N=3) 42.8 (N=47)	11.2	30.7 (N=7)	53.0 (N=3)
sd	1.9 22.7	16.4	– 18.4	10.5	17.5	–
Wrap at hub						
m	44.0 (N=35)	99.6 (N=13)	61.2 (N=50)	50.7	61.5 (N=7)	68.7 (N=3)
sd	15.0	38.6	19.7	19.8	11.6	22.9
Total						
m	105.3	228.9	166.6	141.3	238.8	210.0
sd	43.9	47.9	45.2	47.5	61.5	61.3

* *Trigona* (stingless bees) smallest prey of *N. clavipes* not strictly comparable with flies presented to *N. maculata* (N=50). All sequences are: Bite, Pull out, Carry in jaws, Wrap at hub. Mean total sequence time = 70, sd = 15. See Table 9 for *N. maculata* on flies.

** Two were wrapped after removal from the web (see text).

Mirick (1971) give further details of the predatory behavior of *N. clavipes,* including a summary diagram. Generally the similarities between the two spiders are more striking than the differences. Differences between sequence durations are discussed below. The other main differences lie in the form of the behavior units and have been detailed in that section.

In terms of unit and sequence *durations* comparisons are complicated by the fact that the insects presented to the two species were not similar in size (including weight), morphology, or species. In order to minimize size differences we have selected sequences of *N. clavipes* predatory behavior that were given to insects that were the closest in size to those used in presentations to *N. maculata.* This selection has considerably reduced the sample sizes for *N. clavipes,* all of which are now smaller than those for *N. maculata.* This factor may further complicate the comparison. In addition, it must be remembered that *Nephila maculata* is larger, heavier, and has longer legs than *N. clavipes.* Unlike *Nephila clavipes,* which transports prey in the jaws by walking forwards to the hub, *N. maculata* backs up the web, in most cases, when carrying prey in its jaws.

Despite these differences, and complicating factors, there are overall similarities in some sequence and unit durations—and in the composition of the sequences. Thus, with dragonflies of roughly similar weight, overall sequence times are comparable, even to range and deviation! Bite and pull-out durations are similar, but the smaller *Nephila clavipes* shows much more variance in pull-out durations. Transportation times for prey carried in the jaws are higher in the case of *N. clavipes,* moving forwards up the slope of the web, than for *N. maculata* moving backwards. This difference is not statistically significant but suggests that our inference, that backing up may be advantageous if prey is bulky, could be correct. The possibility that it could be due to the longer stride of *N. maculata* is to some extent discounted by the very close similarity of the durations of carry-on-silk transportation. Both spiders wrapped this prey in situ more frequently than they successfully pulled dragonflies from the web.

Comparison of sequences that *N. clavipes* gave to domestic crickets and *N. maculata* gave to the katydids show that these were similar in duration despite the fact that the crickets were heavier. Only one cricket was not removed from the web by pulling and no katydids were wrapped in situ. In this case the process of backing up the web with prey carried in the jaws (*N. maculata*) was a lengthy proccess compared with the process of transportation by walking forward with the prey in the jaws, carried out by the smaller *N. clavipes.*

In the case of butterflies, *Nephila maculata* was able to free these, in all cases, by pulling them from the web, whereas *N. clavipes* wrapped in situ 28 percent of the butterflies, before cutting them from the web. This fact can be related to the differences in free space, beneath the two species, that is available for the process of removing bulky prey by pulling. *N. clavipes* spent considerably more time, on average, wrapping prey at the hub after transportation and this again may be related to the problem of passing silk over bulky prey when there is a relatively small amount of free space beneath the spider. The mean total sequence duration for the treatment of butterflies by *N. clavipes* is over twice that taken by *N. maculata.* This is at least partly affected by the long duration of the pull-out, wrap-in-situ, and wrap-at-hub units, in the case of *N. clavipes.*

When dealing with small prey of less than .050 grams both spiders give similar sequences of basically similar mean durations. *Nephila clavipes* attacked stingless bees (*Trigona* species) by a simple bite, pull-out, carry-in-jaws, wrap-at-hub procedure. *Nephila maculata* attacked slightly larger *Calliphora*-like flies in this way, although it backed up the web in 86 percent of the cases. Although *N. clavipes* wrapped all the *Trigona,* on, or shortly after, arrival at the hub, *N. maculata* wrapped only 12 percent of the flies within one minute of arrival at the hub. Flies may be relatively much smaller in relation to the jaws of *N. maculata* than *Trigona* are to *N. clavipes,* and there could thus be less need to secure them by wrapping to prevent them being lost during further attacks.

Very large orthopteran prey elicited similar attack behavior from the two species (see Robinson and Mirick, 1971, and above). We did not present large beetles to *N. clavipes* but suspect that they would probably encounter the same problems in handling these prey as *N. maculata* (and probably in a more exaggerated form).

Categorization of Araneids by Predatory Behavior

Table 11 gives, in summary form a broad categorization of the predatory behavior of those araneids for which we have data. There are essentially two major groups of predatory techniques employed by araneids and the distinction between these two groups is made on the basis of the presence or absence of attack wrapping. Further distinctions or subdivisions of the predatory techniques can be made within the two major groups on the basis of the employment of other forms of wrapping behavior. Such categorization would follow that made by Robinson, Mirick, and Turner (1969) on the basis of a much smaller sample of araneid species. We have, so far, found no araneid that shows the behavior of the hypothetical "Stage 1" constructed by Robinson, Mirick and Turner (1969:499). This stage forms one of the alternative sequences found in most of the *Nephila* group spiders but does not occur as the sole predatory technique. We would predict that if it occurs as a unique technique in any species existing at present, that species would probably be a small spider within the *Nephila* group or a spider specializing on prey much smaller than itself and possibly building a close-meshed web of lightweight silk. In such a situation prey could be bitten, pulled from the web, and wrapping need only occur at the hub (where it would serve the function of allowing the spider to store prey caught during one predatory excursion while it made further attacks on subsequent prey.)

Robinson, Mirick and Turner (1969:500) noted that some spiders with a *Nephila*-type attack behavior were able, as a consequence of post-immobilization wrapping, to leave prey in the web at the capture site and return to the hub to feed on already caught prey. They thereby were able to omit the transportation of newly caught prey. This subcategory of a *Nephila*-type predatory technique was suggested by studies of one *Gasteracantha* species and two *Micrathena* species in Panama. Studies of *Gasteracantha* species in New Guinea confirm that they too store prey at the capture site (Y. D. Lubin, pers. comm.).

The occurrence of pull-out behavior in *Nephila* species as an almost invariable first approach to removing prey from the web has been remarked upon as possibly primitive behavior. We know that

TABLE 11.—*Predatory behavior of araneid spiders classified on the basis of principal attack units; subclassification based on prey storage strategies*

(US = United States, P = Panama, NG = New Guinea, A = Africa, I = India)

Attack biting used exclusively No attack wrapping		Attack wrapping a major predatory component Attack biting reserved for some prey items	
All prey stored at hub	Some prey left in situ after attack	Prey stored at hub	Some prey left in situ after attack
Nephila clavipes (P)	*Gasteracantha cancriformis* (P) ***	*Cyrtophora moluccensis* (NG) *	*Argiope argentata* (P)
N. maculata (NG)			*A. savignyi* (P)
N. turneri (A)	*G. theisi* (NG)		*A. florida* (US)
N. constricta (A)	*Micrathena schreibersi* (P)		*A. trifasciata* (US)
Herrenia ornatissima (NG)			*A. aurantia* (US)
Nephilengys cruentata (A & I) **			*A. picta* (NG)
			A. aemula (NG)
			A. reinwardti (NG)
			A. aetheria (NG)
			Araneus marmoreus (US)

* Y. D. Lubin, pers. comm.

** Site of prey storage not determined.

*** This species is now known to attack wrap very large prey (determined after manuscript at press).

it occurs also in *Nephilengys* species. The size of prey that can be removed from the web in this way may ultimately depend on the relative length of the spider's legs I, II, and IV, which determines the maximum distance between the spider's body and the web surface. This, in turn, determines the free space available for removing and manipulating prey. Other factors, presumably including the deformability of the web plane may restrict the practicability of using the pull-out technique for removing prey. *Herrenia ornatissima* may be unable to use the pull-out technique on larger prey because its legs are relatively short (compared to those of *Nephila* species) and also because deformations of the web plane could result in parts of it being pushed against the nearby tree trunk and adhering thereto. Spiders that build close-meshed webs may not be able to free prey by the pull-out technique unless they immobilize them very rapidly, i.e., before the prey's struggles enmesh it inextricably. *Nephila* species are remarkably fast in their movements across the web, this too may be a consequence of having relatively long "sprinters" legs.

The occurrence of wrapping after a series of apparently abortive biting attempts in the attacks on very large, or heavily armored, prey by *Nephila maculata* is of interest for two reasons. First, it suggests that wrapping behavior is not necessarily triggered by the stimuli that the spider receives as a consequence of a successful attack bite, as Peters (1931) claimed for *Araneus diadematus*. It could, however, still be triggered by the act of biting. In cases where the chelicerae do not penetrate there is no possibility of the spider testing the edibility of the prey by taking in materials from within the insect cuticle. In such cases the decision to proceed with the predatory act must be based on the perception of stimuli derived from the outside of the prey. Secondly, the occurrence of wrapping behavior in the absence of prior successful biting can be regarded as a possible first step in the evolution of attack wrapping. As such it is of prime interest.

Behavior of Prey in the Web

In the course of presenting a wide variety of prey to *Nephila maculata* we made a large number of incidental observations on the behavior of the prey items after they had become enmeshed. These are of some interest since they indicate different escape potentials of prey when the spider is present in the web. Since the prey were mostly thrown into the web by the experimenters their initial orientation may be unnatural and this could affect their subsequent behavior. However, if some of these prey show escape movements that are wholly or partly effective, there is good reason to assume that prey arriving in a more natural manner would be, at the very least, as likely to escape.

In general only very small prey and very large prey tend to escape if the spider is present and reacting normally. Otherwise, the approach to the prey is so rapid that the spider is attacking before they prey has had time to free itself. Lepidopterans are an exception.

Of the very large prey the acridiids kick vigorously when in the web and these movements, together with their weight, cause extensive tearing of the web so that they slip downward towards the lower margin and may then escape. In addition, our data suggest that a vigorously kicking, large acridiid is approached much more cautiously than an inert one and this may gain the insect escape time. Furthermore, even when an attack has started (and is at the protracted bite-and-back-off stage) the spider may be repelled by vigorous kicking and the prey may be able to escape. We have long suspected that orthopteran regurgitants may affect spider silk but have not investigated this matter. Most large beetles struggle when in the web and may slip to the edge and escape. Their relatively short legs have a much less dramatic tearing effect on the web, but the movements that they produce may help to loosen the attachment of the prey from the viscid element. It is noticeable that they close their wings and elytra in the web, thus presenting a compact smooth mass. In general large beetles seem to have a much smaller surface area/weight ratio than large acridiids and therefore, per unit weight, have less surface in contact with viscid droplets. They thus slip out of contact with adhesive fairly rapidly. After watching the wrapping attacks of *Argiope aemula* on beetles, we are struck by the fact that relatively smooth cuticle presents a much more difficult surface on which to deposit enswathing layers than does the cuticle of orthopterans. If viscid droplets adhere less strongly to shiny surfaces, some beetles could have a higher escape potential than others—beetles and insects.

We have no records of lepidopteran escapes from our prey-analysis studies. When throwing moths into the web during the studies on predatory sequences we found that a number did not adhere sufficiently to remain in the web until the spider arrived. In these cases vigorous fluttering movements apparently facilitated escape.

Very small prey items, e.g., nematocerans and small hemipterans were ignored by the adult female *Nephila* even when struggling. Some of these are certainly consumed by kleptoparasites, but some may escape. We suspect that when rain wets the web small insects that have not been attacked may be liberated.

Responses to Environmental Factors

SUNLIGHT.—Many tropical insects that assume more-or-less immobile resting attitudes by day change their orientation in apparent response to changes in the direction of incident sunlight. Thus many orthopterans minimize heat absorption by aligning themselves with their long axis parallel to the sun's beams. Kettlewell (1959) noted this in the case of Brazilian katydids, and Uvarov (1965) has reviewed reports of this phenomenon in acridiids. There are some reports of spiders assuming a special orientation with respect to the sun's position. Thus Pointing (1965) showed that the linyphiid *Frontinella communis* (Hentz) would orient to the sun's disc in both horizontal and vertical planes unless it was in the shade or at web temperatures below 30°C.

Krakauer (1972) has studied the thermal responses of *Nephila clavipes* and found that at temperatures of above 35°C the spider orients the tip of its abdomen towards the sun and thereby reduces the radiant heat load on its body. In addition he found that the spider may also employ evaporative cooling by extruding liquid from the chelicerae. Krakauer's experimental technique was to place heat lamps above the middorsal area of the abdomen of captive spiders, but he did not experiment with spiders in the field. He does however suggest, on the basis of field records, that *Nephila clavipes* builds its web oriented in a plane normal to the area of maximum insolation and that the tilt of the web to the vertical faciliates postural thermoregulation by reducing the angle at which the spider has to hang in order to point at the sun when this is at its zenith.

Our attention was independently drawn to the response of *Nephila maculata* to bright sunlight when we found a mature female standing with her long axis more or less at right angles to the web, facing away from the sun. This complex posture is shown in Figure 30, and is the reverse of that figured by Krakauer (1972, fig. 2). Despite the difference in position the total effect is presumably the same, i.e., the minimum surface area is exposed to radiant heat. We assume that positions such as this are not so economic of energy as those involving aiming the abdominal apex at the sun but become necessary because of web orientation.

To investigate further orientation to the sun we mounted a circular mirror on a tripod and then manipulated the apparent position of the sun by directing sunlight onto spiders that were otherwise in the shade. In this way we elicited responses to "impossible" positions of the sun. Such positions, e.g., when the sun was apparently shining upwards from below the web elicited orientations that made adaptive sense, the spider aligned itself as though it were minimizing heat absorption from this improbable heat source. We were also able to induce movements of spiders across the hub region through more than 90 degrees of arc in a few minutes and thus replicate the effects of several hours of azimuth shift.

We did not have the necessary equipment to monitor temperature at the surface of the spider but black bulb temperatures were in excess of 30°C when we made our observations. Clearly spiders have a capacity of postural thermoregulation, which includes positions that are more complex than would be necessary if the web were always simply oriented to be normal to the area of maximum insolation. In fact many of the postures may involve the spider in energy-consuming attitudes, but presumably these need not be adopted for very long periods in most tropical regions where uninterrupted sunlight (except in dry season periods) may be unusual. *Nephila maculata* seldom builds out in the open and may thus be shaded for long periods, even when there is uninterrupted sunlight in open areas. We are strongly inclined to think that web-

FIGURE 30.—*Nephila maculata* orienting to strong sunlight, which is passing through the web from the right of the picture. This spider has lost the left leg I and right leg II.

site choice is much more likely to be determined by availability of supporting structures (and predatory success) than by the necessity for economizing in energy expenditure on postural thermoregulation.

One point that emerges from our observations as worthy of further investigation is the extent to which heat and visible light interact in mediating the orientation of thermoregulating spiders. It seems entirely possible that temperature may trigger the response of postural thermoregulation (as suggested by the work of Pointing, 1965, and Krakaeur, 1972) while the actual orientation may be based on responses to visible light. We made no attempt to determine whether the spider's eyes were involved in the sunlight response, but are currently doing so in experiments with *Nephila clavipes.*

RAINFALL.—Pointing (1965:73,75) has noted that his spiders responded to heavy precipitation by moving to positions in the barrage of threads above the sheet web. There they assumed head-down positions until the rainfall ceased. However they responded to less heavy raindrops—but heavy rainfall—as they responded to sunlight, i.e., by presenting the minimum surface area to the rainfall. From our observations on *Argiope argentata* in Panama we know that some spiders may adopt special rainfall postures if they remain in their webs and do not seek shelter under nearby vegetation. Thus *Argiope argentata* hangs away from its sloping web so that the body is almost perpendicular and legs I and II, which are always directed anteriorly, are off the web. In the rainfall posture these two pairs of legs are held outstretched in line with the midlateral plane of the body and at a fairly acute angle to the long axis, i.e., they are held more anteriorly than in the normal resting attitude. This position could be interpreted as minimizing the cross-sectional area exposed to the rain—assuming that tropical rains fall more-or-less vertically—or that the spider in this position maximizes the flow of water off its body surface with the anterior appendages forming a sort of drip-tip. We have since seen this behavior in *Nephila clavipes,* and *Leucauge* species. In the latter case the spider hangs almost vertically, head down, from its horizontal web. Charezieux (1967) has described a rainfall position adopted by *Nephila madagascariensis.*

Nephilia maculata responds to heavy rain by cutting away areas of web (p. 10) and may then retire to shelter under the leaves of nearby vegetation. Continuous fairly light rain can evoke the web-cutting response, but the spider may then remain at the hub of the partially dismantled web. When it does this it assumes a position somewhat similar to that assumed by *Argiope argentata.* Figure 20 of *N. maculata* essentially shows the basic attitudes of the legs when the spider is responding to rainfall. The rainfall posture differs from the plucking only in that the spider hangs away from the inclined web, more or less in a vertical position, but with the abdominal apex tucked in against the web.

DEFENSIVE AND ESCAPE BEHAVIOR

Nephila maculata exhibits behavior that can be categorized as defensive because of its form and/or context. Touching the spider lightly on its dorsal surface (unprotected by the web) evokes a characteristic posture. In this the prosoma is raised anteriorly and the total length of the body assumes a concave dorsal orientation. The posterior margin of the prosoma thus becomes pressed against the anterior margin of the opisthosoma at the waist joint. In addition, the first two pairs of legs are flexed and raised off the web. This posture may be a defense against aerial predators or parasites. The body flexure could protect the possibly vulnerable waist and position the body so that the legs can be used to fend-off insects attacking from above. The raised legs may constitute a barrier to such attacks since they are held over the prosoma. Because these legs are not gripping the web they may be instantly available for defensive movements.

Escape movements occur in response to disturbance of the barrier web or to violent movements within the orb. The spider invariably runs upwards onto upper frame members and often into the shelter of surrounding vegetation. Whether or not the escape run terminates on a frame thread or in vegetation seems to be largely dependent on the strength of the initial disturbance and whether or not it persists. We have not been able to quantify this. The form of the escape run is often distinguishable from a predatory run because it includes dorsoventral "bouncing" of the body.

Discussion

This study spanned one year, on a day to day basis, and touched on many aspects of the biology of *Nephila maculata*. Despite its wide scope, it is only an introductory investigation into the bionomics of the species and thus we can raise in detail the more general questions that the study provokes and outline some of the principles that have emerged.

PHENOLOGY

In terms of seasonal patterns of predation exerted by large trap-building spiders we have added data from a much less climatically variable area than that where we carried out our study of the prey of *Argiope argentata* (Robinson and Robinson, 1970a). Differences between the results of the two studies are not, unfortunately, ascribable to the differences in climatic pattern alone. Two different techniques were used to determine the number, nature, and temporal distribution of the prey caught by two spiders of distinctly different ecologies. From data on population dynamics, in addition to the data from the prey-capture studies, we feel confident that *Nephila maculata* in the more equable (than Panama) climate at Wau, is able to subsist throughout the year without major perturbations. This raises a question that seems to bedevil many studies of animal phenology in the tropics. How typical was the year during which the study was carried out, or how consistent are long-term patterns of climate? Indications from Barro Colorado suggest that there may be major differences between the dry seasons in the amount of rainfall, to name only one factor. Thus the dry season after our study of *Argiope argentata* in Panama (Robinson and Robinson, 1970a) was much wetter, and the present dry season (1972) has been distinguished by an abnormally high January rainfall. At Wau there are indications of very considerable fluctuations in the annual distribution of rainfall. Thus, in May 1970 the rainfall at our study site was 2.8 inches and in the May following our study the rainfall was 7.7 inches. Brookfield and Hart (1966) give coefficients of variaton (cv) for the monthly rainfall at the Wau number 1 station, based on 28 years of complete data. All months show more than a 30 percent coefficient and four months (January, May, August, and October) show more than 50 percent. These authors also give the standard deviations for monthly rainfall at this station, which also reflect the great variability. Brookfield and Hart (1966:14) define areas of high variability for annual means as those with a coefficient of variability greater than 25 percent. Wau number 1 has an annual cv of 15 percent. The annual variation may be much less important to some organisms than the short term variations.

What aspect of rainfall may most directly affect web-building spiders is presently unknown. The operation of a trap that is damaged by rainfall could be affected by the number of discrete rainfall periods per day, the intensity of the rainfall, the number of successive days of rain, and so on. We have plotted web renewal and prey-capture figures against some of these aspects of rainfall, but there are no simple correlations. Similarly we need to know much more about the effect of the various aspects of rainfall on the different developmental stages of the spider before we can assess the effects of this factor on the biology of the species. Small webs produced by immature stages may be more susceptible to damage by rain than the stronger webs of adults; but, on the other hand, they may be built in more sheltered sites. Such sites may be available to immatures with small webs whereas adults may only be able to build their webs in more exposed sites. The complexities are immense. Many biologists accept climatological data from one point in an area and use this to interpret biological data from the entire area. Perhaps this is a valid technique for some organisms and some aspects of their biology. It is interesting to note that the three Wau rainfall stations, separated by less than 1 kilometer in horizontal distance, and 150 meters in height, show very considerable differences in the temporal pattern of precipitation.

Since our data on web adhesiveness suggest a correlation between this factor and relative humidity, periods of rainfall that do not result in raindrop damage to the web may be more favorable to the spider than periods when the efficiency of the adhesive droplets could be adversely affected by low humidities. This is yet another factor to be considered as part of the complex interaction between the arachnid and climate. It is usual to delimit seasons by rainfall and temperature criteria and many of the climographs used by biologists plot these two factors (Richards, 1957). D. Leston of the University of Ghana (pers. comm.) has suggested that hours of sunlight may be crucial to many organisms and, if these are considered, some tropical areas with two grossly distinct seasons in terms of rainfall and temperature then have three seasons. Since many orb-web spiders have responses to sunlight plus radiant heat, variation in hours of sunlight may affect them directly as well as indirectly.

Web-building spiders could also be affected indirectly by the influence of climatic factors on the structure of their habitat. Web supports for the immature stages of spiders, such as *Nephila maculata,* may depend on the presence of ephemeral nonwoody vegetation (herbs and forbs). These may cycle in abundance during the year in many parts of the range of the species. This is certainly true, from our own observations, of the Bombay site where Thakur and Tembe (1956) studied the species. Even such apparently obscure factors as a period of heavy production of wind-dispersed seeds could affect the success of spiders, since their webs may trap very large numbers of them and become conspicuous and ineffective. Large-scale leaf-fall may have a similar effect and also increase the amount of sunlight reaching the area of the forest in which the spiders build their webs. Apart from increasing the drain of energy involved in thermoregulation, increased illumination could then render the webs and spiders more conspicuous to predators, prey, and parasites.

Our phenological studies were primarily concentrated on variations in the weight and nature of the prey items with time. The data are too crude to permit anything more than guesses about their significance. This is a complex field. It seems possible that there may be differences between adult female *Nephila* in the caloric input necessary to maintain a regular egg-laying routine (whatever that may turn out to be). Thus there are certainly considerable differences in the size of adult females, other than those of expandable parts such as the opisthosoma. Small females presumably have a lower caloric requirement than adults of large size. We have no baseline from which to calculate the maximum rate of egg-sac production. It seems quite possible that the minimum interval between egg masses may be fixed physiologically and that the animals can adjust to variations in food supply by altering the number of eggs in the egg sac and extending the period between layings. Certainly the increase in the size of the opisthosoma prior to egg laying is very striking and may represent a considerable increase in weight. We have no idea if there is an upper limit to food intake that could be achieved under normal conditions in the field. Questions about the relationship between food supply and egg production could, perhaps, best be answered by a laboratory study with captive specimens.

The fact that the total weights of prey remnants varied, on a weekly basis, between less than one gram to nearly five shows that there were (at least relatively) lean weeks and rich weeks. Detailed analysis of the data shows that lean weeks are lean weeks for all spiders. Thus in week 47 (commencing 14 April 1971) the total catch was .958 grams. No spider was responsible for more than 210 mg, 5 spiders caught more than 100 mg, 5 spiders caught less than 100 mg. In rich week 24 (commencing 28 November) with a total of 4.670 grams of food remains, two spiders accounted for more than 1 gram of remains each, two spiders exceeded 500 mg in rejected remains, three spiders exceeded 200 mg and the remainder fell below this. Thus the spread on the good weeks is greater than that on the lean weeks.

The spiders should, presumably, be attempting to maximize their catches and could be expected to show some evidence of smoothing the variations in the abundance of potential prey by behavioral adjustments. Thus they could attempt to compensate for low catches at one place by moving the location of their webs. In addition, they might feed on some organisms, during periods of low catches, that they would reject when food was abundant. Our data do not show a positive correlation between predatory success and stability of web site, nor, unfortunately, a negative correlation between movements of web sites and low returns of prey. The influence of other factors could mask such effects. Nor have we any evidence that the spiders accept some types of prey, during periods of relative food shortage, that are rejected at other times. Despite this, we thought that the effects of the spider's behavior might result in there being less variability in the numbers of the prey that they caught than there was in the numbers of insects caught by the window-pane traps. This proved to be the case; but since the means of the two samples are quite different this evidence is, at the most, only suggestive.

Turning to the phenology of population increments, it is obvious that it is necessary to conduct detailed studies on the developmental rates of the two sexes, under different feeding regimes, and at different times of the year, before we can begin to elucidate this problem. Collection of egg sacs leading to estimations of the fertility of the eggs, the developmental period and factors that influence it, conditions favoring eclosion and subsequent dispersion, are all necessary and practicable further steps in the study.

Studies carried out in the relatively benign climatic regimes of upland tropical areas like Wau, should provide some clues about how widely distributed species manage to cope with the more extreme climatic regimes in other parts of their range. (Tropical is here used in the sense of Richards (1957:135), i.e., it applies to the area that lies within the isotherm of 20°C mean annual temperature.) We can ask whether the adaptations which enable *N. maculata* to exist under the very different climatic regime at Bombay already exist in the Wau population. Evidence from the fringe habitats in the Wau area suggests that they may not.

Levy (1970) has suggested that the life cycles of spiders may fall into two broad categories based on the developmental rates of the two sexes. In one class are the majority of spiders studied so far (primarily temperate region), in which spiders of both sexes that derive from the same cocoon reach maturity at the same time. In the second class are those spiders in which the sexes mature at substantially different rates (siblings could not mate). Levy (1970:534–535) suggests that there are two strategies that would insure a coincidence of adult males and females in the latter case. These are that cocoons should be produced throughout "long periods of the year," or that there should be two adult phases in the year with males of one phase coincident with females of the previous phase. He suggests that, in the case of *Nephila madagascariensis*, the two phase system may operate. Bonnet's (1930) data show that males mature in approximately a quarter of the time necessary for females to mature. Our data show that there are mature males and females present throughout the year and copulation plus egg laying is occurring throughout the year. In Bombay the same species has an apparently one phase reproductive cycle (like a temperate species). This aspect of adaptive reproductive strategy on the part of *Nephila maculata* could either be a result of the direct influence of different climatic regimes or be due to genetic differences in the reproductive biology of the spiders in different parts of their range.

BEHAVIOR

Nephila maculata is the second tropical member of this genus whose courtship behavior has been studied. The discovery of the complex silk-deposition activities of the male adds a new element to the picture of araneid courtship behavior. Generalizations about araneid courtship have, so far, been almost entirely based on studies of north temperate forms. We think that further comparative studies of tropical forms are essential if the evolution of courtship behavior is to be understood. The possibility that silk deposition may be a primitive condition cannot presently be rejected. The occurrence of this or similar behavior in other species and genera may have been missed by students, because of the practical difficulties involved in seeing large numbers of courtship sessions in seasonal, and widely dispersed, temperate forms.

Our observations on the predatory behavior of *Nephila maculata*, other *Nephila* species, and *Nephilengys* and *Herrenia*, as well as the study of *Argiope* species in New Guinea, show that these species conform to the overall categorization of araneid predatory behavior provided by Robinson, Mirick, and Turner (1969).

The experiments with large melolonthids as prey show that the absence of attack wrapping in the *Nephila* group of spiders places them at a disadvantage, compared with spiders that have attack wrapping, in capturing large prey. This raises the question of why the *Nephila* species have not been out-competed by *Argiope* species (or other advanced spiders). No existing *Argiope* species appear to occupy quite the same niche as the *Nephila* species. Furthermore all the *Nephila* species that we have seen build large strong and relatively fine-meshed webs that are operated day and night. Other large spiders that build webs of comparable size (e.g., *Eriophora fuliginea*, see Robinson, Robinson, and Graney, 1972) operate them principally at night. At night, moths may constitute a large proportion of the prey and attack biting is the most effective strategy for dealing with these insects. There is probably an advantage in sheer size when operating a large web. (The immatures, probably in the same zone of the forest habitat as *Argiope* species, have at some stage, webs that are similar in size, and they may be more close to niche overlap at this stage).

The sun-orientation behavior that we have described raises some interesting questions since, as far as we know, it does not occur in *Argiope* species that build webs in positions that are more frequently exposed to direct sunlight. There are a number of possible explanations of this difference. *Argiope* species may orient their webs so that the spider does not receive radiant heat on its black, ventral surface but on its reflectant dorsal surface. What evidence we have does not support this theory. There are very considerable differences in the surface to volume ratios between the smallish, flattened, *Argiope* species and the large cylindrical *Nephila* species, which must have less surface area per unit volume than the *Argiope* species. This should lessen the heat load that they have to compensate for but increase the problem of heat dissipation once they become heated. The brain, situated in the prosoma, may be an organ that is particularly sensitive to high temperatures and it is worth noting that all the *Nephila* species that we have seen have silvery (possibly reflectant) dorsal coloration of the prosoma.

Stabilimentum building by immature *Nephila maculata*, the first records of this phenomenon for the genus, raises interesting questions. It seems unlikely that this implies any close relationship with the genera of spiders that presently build ribbon stabilimenta. If it was evolved independently and is now a vestigial character in *Nephila maculata* what was its original function? Similarly the construction of orb-like barrier webs by juvenile *N. maculata* is a newly described piece of behavior and may have important implications from the standpoint of defense against predators, suggesting that the immature stages that build such barriers may be particularly susceptible to attack by flying predators. It might also be a clue about the origins of barrier webs in general.

We have since discovered that in Panama immature *Nephila clavipes* build complex structured barrier webs that are drawn away from the main web at their centers and are conical. These are similar in gross structure to those described for *N. maculata* (p. 10), but do not have an orderly spiral. They are most complete above the dorsal surface of the spider where there may be two distinct plane structures. Above the main orb, ventral to the spider, there is usually one plane structure and a second supporting complex. The existence of a triple barrier (two plane structures and one supporting structure) above the spider suggests that this complex may be defensive. The spider must be protected from below by the main orb as well as the secondary structures. Full details of the juvenile barrier webs of *Nephila clavipes,* with photographs, are to be published separately.

We suspect that almost any long-term studies of tropical spiders would reveal suggestive, new, information about their behavior and ecology. This is part of the fascination of spiders.

Addendum

Since this study was at press, new information has become available on two subjects dealt with herein: (1) Stabilimentum building by *Nephila* species (pp. 8–19, herein). It has been discovered that, on rare occasions, *Nephila clavipes* builds linear ribbon stabilimenta. Details and comments on the possible evolutionary significance of these structures, will be given by us ("The Stabilimentum of *Nephila clavipes* and the Origins of Linear Stabilimenta in Araneids," *Psyche,* in press). (2) Postural thermoregulation by Nephila species (pp. 64–66, herein). The repertoire of thermoregulatory postures of *Nephila clavipes* is now known to include an analogous posture to that described herein and illustrated in Figure 30. A detailed analysis of the thermoregulatory behavior of *N. clavipes* is in preparation ("Adaptive Complexity: The Thermoregulatory Postures of the Golden-web Spider *Nephila clavipes* at Low Latitudes.").

Literature Cited

Alexander, A. J.. and D. W. Ewer

1957. On the Origin of Mating Behavior in Spiders. *American Naturalist,* 91:311–317.

Bastock, M.

1967. *Courtship: A Zoological Study.* London: Heinemann Educational Books Ltd.

Bonnet, P.

1929. Les Araignées exotiques en Europe, II: Elevage a Toulouse de la grande Araignée fileuse de Madagascar et considérations sur l'Aranéiculture (Première Partie). *Bulletin de la Société Zoologique de France,* 54:501–523.

1930. Les Araignées exotiques en Europe: II. Elevage a Toulouse de la grande Araignée fileuse de Madagascar et considérations sur l' Aranéiculture (Deuxième Partie) *Bulletin de la Société Zoologique de France,* 55:53–77.

1958. *Bibliographia Araneorum,* 2(N-T):4. Toulouse, France: Douladore.

Bristowe, W. S.

1929. The Mating Habits of Spiders, with Special Reference to Problems Surrounding Sex Dimorphism. *Proceedings of the Zoological Society of London,* 1929: (2):309–358.

1931. The Mating Habits of Spiders: A Second Supplement. *Proceedings of the Zoological Society of London,* 1931: (4):1401-1412.

1939. *The Comity of Spiders.* Volume 1. London: Ray Society.

1941. *The Comity of Spiders.* Volume 2. London: Ray Society.

Bristowe, W. S., and G. H. Locket

1926. The Courtship of British Lycosid Spiders and its Probable Significance. *Proceedings of the Zoological Society of London,* 1926(2):317-347.

Brookfield, H. C., and D. Hart

1966. *Rainfall in the Tropical Southwest Pacific.* Department of Geography Publication G/3, Australian National University, Canberra.

Charezieux, B.

1961 Contribution a l'étude du comportement sexuel de l'Argiopide *Nephila madagascariensis* observé dans son pays d'origine. *Bulletin de la Société Zoologique de France,* 86:372–379.

1967. Comportement de l'Araignée *Nephila madagascariensis* Vinson au moment des chutes de pluie. *Annales de la Faculté de Sciences de l'Université de Madagascar,* 5:117–120.

Chrysanthus, Fr.

1959. Spiders from South New Guinea, II. *Nova Guinea,* new series, 10:197–206.

1960. Spiders from South New Guinea, III. *Nova Guinea Zoology,* new series, 3:23–42.

1971. Further Notes on the Spiders of New Guinea, I: (Argyopidae). *Zoologische Verhandelingen,* 113:1–52.

Coleman, E.

1948. An Interesting Spider. *Victorian Naturalist* (Melbourne), 64:206.

Crane, J.

1949. Comparative Biology of Salticid Spiders at Rancho Grande, Venezuela, Part IV: An Analysis of Display. *Zoologica,* 34:159–214.

Eisner, T., R. Alsop, and G. Ettershank

1964. Adhesiveness of Spider Silk. *Science,* 146:1058–1061.

Fischer, C. E. C.

1910a. Pairing of the Spider *Nephila maculata* Fabr. *Journal of the Bombay Natural History Society,* 20:526–528.

1910b. Further Note on the Spider *Nephila maculata. Journal of the Bombay Natural History Society,* 20:528.

1910c. Further Note on the Spider *Nephila maculata* Fabr. *Journal of the Bombay Natural History Society,* 20:887–888.

Gerhardt, U.

1930. Biologische Beobachtungen an *Nephila madagascariensis* Vins. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin,* 8:358–360.

1933. Neue Untersuchungen zur Sexualbiolgie der Spinnen, insbesondere an Arten der Mittelmeerlander und Tropen. *Zeitschrift fur Morphologie und Ökologie der Tiere,* 27:1–75.

Hinde, R.

1966. *Animal Behaviour.* New York: McGraw Hill.

Hingston, R. W. G.

1922a. The Snare of the Giant Wood Spider (*Nephila maculata*), Part I. *Journal of the Bombay Natural History Society,* 28:642–649.

1922b. The Snare of the Giant Wood Spider (*Nephila maculata*), Part II: The Continuation of the Snare. *Journal of the Bombay Natural History Society,* 28: 911–917.

1922c. The Snare of the Giant Wood Spider (*Nephila maculata*), Part III: Further Lessons of the *Nephila. Journal of the Bombay Natural History Society,* 28:917–923.

1923. The Giant Wood Spider (*Nephila maculata*). *Journal of the Bombay Natural History Society,* 29:70–76.

Jager, S. de

1960. *Nephila,* a Highly Intelligent Spider. *African Wild Life,* 14:205–208.

Kajack, A.

1965. An Analysis of Food Relations Between the Spiders—*Araneus cornutus* Clerck and *Araneus quadratus* Clerck—and Their Prey in Meadows. *Ekologia Polska,* A, 13:717–768.

1967. Productivity of Some Populations of Web Spiders. Pages 807–820, in *Secondary Productivity of Terrestrial Ecosystems, II.* Warsaw: Państwowe Wydawnictwo Naukowe.

Kaston, B. J.
1964. The Evolution of Spider Webs. *American Zoologist,* 4:191–207.

Kaston, B. J., and E. Kaston
1953. *How To Know the Spiders.* Dubuque, Iowa: Wm. C. Brown, Co.

Kettlewell, H. B. D.
1959. Brazilian Insect Adaptations. *Endeavour,* 18:200–210.

Krakauer, T.
1972. Thermal Responses of the Orb-weaving Spider *Nephila clavipes* (Araneae: Argiopidae): *American Midland Naturalist,* 88:245–250.

Langer, R. M., and W. Eberhard
1969. Laboratory Photography of Spider Silk. *American Zoologist,* 9:97–101.

Levy, G.
1970. The Life Cycle of *Thomisus onustus* (Thomisidae: Araneae) and Outlines for the Classification of the Life Histories of Spiders. *Journal of Zoology* (London), 160:523–536.

Linsley E. G., T. Eisner, and A. B. Klots
1961. Mimetic Assemblages of Sibling Species of Lycid Beetles. *Evolution,* 15:15–29.

Locket, G. H., and A. F. Millidge
1953. *British Spiders.* Volume 2. London: Ray Society.

Macfadyen, A.
1963. *Animal Ecology: Aims and Methods.* London: Pitman.

McKeown, K. C.
1963. *Australian Spiders.* Sidney: Angus & Robertson.

Morris, D.
1956. The Function and Causation of Courtship Ceremonies. *Fondation Singer-Polignac, Colloque International sur l'Instinct* (Paris), 261–266.

Osorio, J. M., and A. Moreno
1943. Contribuciones de Zoológica Económica, I: "La Araña Gran Tejedora" *Nephila clavipes* (L). *Memorias de la Sociedad Cubana de Historia Natural,* 17:53–57.

Peters, H. M.
1931. Die Fandhanglung der Kreuzspinne (*Epeira diadema* L.) Experimentelle Analysen des Verhaltens. *Zeitschrift fur Vergleichende Physiologie,* 15:693–748.
1954. Estudios adicionales sobre la estructura de la red concéntrica de las arañas. *Communicaciones del Instituto Tropical de la Universidad de El Salvador,* 1:1–18.
1955. Contribuciones sobre la etología y ecología comparada de las arañas tejedoras tropicales. *Comunicaciones del Instituto Tropical de la Universidad de El Salvador,* 1-2:37–46.

Platnick, N.
1971. The Evolution of Courtship Behaviour in Spiders. *Bulletin of the British Arachnological Society,* 2:40–47.

Pointing, P. J.
1965. Some Factors Influencing the Orientation of the Spider *Frontinella communis* (Hentz.) in Its Web (Araneae: Linyphiidae). *Canadian Entomologist,* 97:69–78.

Richards, P. W.
1957. *The Tropical Rain Forest.* Cambridge, England: Cambridge University Press.

Riek, E. F.
1970. Neuroptera. Pages 472–494 in *The Insects of Australia.* Melbourne: Melbourne University Press.

Robinson, M. H.
1969. Predatory Behavior of *Argiope argentata* (Fabricius). *American Zoologist,* 9:161–173.

Robinson, M. H., Y. D. Lubin, and B. Robinson
In prep. Population Studies of Web-building Spiders at Wau, New Guinea.

Robinson, M. H., and H. Mirick
1971. The Predatory Behavior of the Golden-web Spider *Nephila clavipes* (Araneae: Araneidae). *Psyche,* 78: 123–139.

Robinson, M. H., H. Mirick, and O. Turner
1969. The Predatory Behavior of Some Araneid Spiders and the Origin of Immobilization Wrapping. *Psyche,* 76:487–501.

Robinson, M. H., and J. Olazarri
1971. Units of Behavior and Complex Sequences in the Predatory Behavior of *Argiope argentata* (Fabricius): (Araneae: Araneidae). *Smithsonian Contributions to Zoology,* 65:1–36, figures 1–16.

Robinson, M. H., and B. Robinson
1970a. The Prey Caught by a Sample Population of the Spider *Argiope argentata* (Araneae: Araneidae) in Panama: A Year's Census Data. *Zoological Journal of the Linnean Society of London,* 49:345–357.
1970b. The Stabilimentum of the Orb-web Spider *Argiope argentata*: An Improbable Defence against Predators. *Canadian Entomologist,* 102:641–655.
1972a. Techniques for the Observation of Spider Behaviour. *Bulletin of the British Arachnological Society,* 2:58–59.
1972b. The Structure, Possible Function and Origin of the Remarkable Ladder-web Built by a New Guinea Orb-web Spider (Araneae: Araneidae). *Journal of Natural History* (London), 6:687–694.
In prep. Comparative Studies of the Mating Behaviour of Orb-web Spiders, 1: *Argiope* species.

Robinson, M. H., B. Robinson, and W. Graney
1972. The Predatory Behaviour of the Nocturnal Orb-web Spider *Eriophora fuliginea* (C. L. Koch) (Araneae: Araneidae). *Revista Peruana de Entomologia,* 14:304–315.

Robinson, M. H., B. Robinson, and Y. D. Lubin
In prep. Long-Term Changes in the Adhesiveness of Spiders' Webs.

Roewer, C. Fr.
1942. *Katalog der Araneae.* Bremen.

Roth, L. M., and T. Eisner
1962. Chemical Defences of Arthropods. *Annual Review of Entomology,* 7:107–136.

Ruhen, O.

1969. *Scan the Dark Coast*. London: Hodder and Stoughton.

Savory, T. H.

1928. *The Biology of Spiders*. London: Sidgwick and Jackson.

Shear, W. A.

1970. The Evolution of Social Phenomena in Spiders. *Bulletin of the British Arachnological Society,* 1: 65–76.

Southwood, T. R. E.

1966. *Ecological Methods*. London: Methuen & Co. Ltd.

Thakur, M. K., and V. B. Tembe

1956. Bionomics of the Giant Wood Spider, *Nephila maculata* Fabr. *Journal of the Bombay Natural History Society,* 53:330–334.

Tinbergen, N.

1954. The Origin and Evolution of Courtship and Threat Display. Pages 233–250 in *Evolution as a Process*. London: Allen and Unwin.

Turnbull, A. L.

1960. The Prey of the Spider *Linyphia triangularis* (Clerck) (Araneae: Linyphiidae). *Canadian Journal of Zoology,* 38:859–873.

Uvarov, B.

1965. *Grasshoppers and Locusts, I*. Cambridge, England: Cambridge University Press.

Yaginuma, T.

1969. *Spiders of Japan in Colour*. Osaka: Hoikusha Publishing Co. Ltd.

Appendix 1

Activities of Male *Nephila maculata* during Courtship Silk-deposition

(Notes on two-hour observation session; time intervals omitted, except for long rest periods; silk attachment occurs at all points listed)

Start: male moves from dorsal surface abdomen (DSA) onto base of third leg left (3L), to surface abdomen, right then left, to 4R then across thorax to 4L, 3L, back to DSA right, pause 2 min.+, DSA left, to 4L, to 4R, 3 and 2R rapidly, then 4L, 3L, 2L, back to DSA right, then 3R, 2R, 1R, DSA left, pause 1.40 min., then to 4L taps leg base, 3L taps leg base DSA right, three silk attachments, then 4L, 3L, 2L, to DSA left one attachment, 4R, 3R, 2R, 1R, then DSA left, DSA right, then 4R, 3R, 2R, 4L, 3L, 4R, 3R, 2R two attachments, DSA and pause left, then right, rest 1.20 with legs 1, 2, on bases of female leg 4R, then move to halfway up female DSA, then back to abdominal margin right, 4L, 3L, 2L then between 2–1L, DSA left, pause 2.10 on outer edge, touching legs of female, then DSA right, pause 3.15, 4L, 4R, 3R, between 3–2R, 4L, DSA center, 4L, DSA right pause 2.25, DSA left two attachments, 4L, 3L, 2–1L, 4R, 3R, 3–2R, DSA right pause 1.00+, move halfway up right DSA, pause 2.05, 4R, 3L, 4–3R, 3–2R with two attachments below leg bases, DSA right 4.00, DSA edge right taps bases of female legs 2 and 3R (apparently feeling beneath female's legs, 3.30, 3L, 3–4L, 4R, 3–2R, 4L, DSA right, then against raised anterior edge of abdomen as female attacks coccinellid beetle beetle rejected, female backs up web to hub, male remains on scarp of abdomen, female strokes the base of her legs 4, 3, 2L with tarsi of opposite legs 2, 3, as though feeling the silk deposited by the male, silk now clearly visible as a gusset at the leg bases, male inactive for 2.30 min., female plucks web in response to gust of wind, male moves to 4R, underneath 4R, 3R, 2R, 1R, 2R, then DSA median position, 4L, 3L, DSA median, DSA right, 4L, DSA right, rests 2.00+, 4R, 4L, 2L, 3L, all well-up from leg bases, DSA right in upper half abdomen, 2R, 4L, 3–2R, DSA center, 4L, 3–2L, DSA center about 8mm from edge, male feels between 2–3R, 3–4R with legs 1 and 2, DSA right 1.12 then 4R, 3R, 2R, DSA left, 4L under, 3L under, DSA right pauses 40 sec. touching 4R with legs, then 4–3L, 2L, 4R, 3R, 2R, 1R, 4L, 4R, DSA right rest 1.00+3R, 2R, 4L, 4R, 3–2R, 2–1R, DSA right 3–2L, 2L, 1L, 4R under, 3R, 2R, DSA left rest 2.32, 3–2L, 2–3R, 4L under, 3L under, 4R, 3–2R, DSA right, DSA left, rest 2.05 tapping 4R, 3R, 4–3R, 2–1R, DSA right backs up to abdominal apex and attaches line, returns to edge tapping occasionally 2.45, down to 4R, 3L, 3–2L, 4–3R, 3–2R, DSA left rest tapping 4, 3L 1.43, 2–3R, 3–4L, 3–2L, 1–2L, 4R, 3R, 2R, all under, DSA midline 1.00+, moves underneath female abdomen sideways, on top again, 4L, 4R, 1R, pedipalps!, 4L, DSA right, sidles to underside of abdomen advances down, then, on top, 1L, pedipalp L, 1R, 2R, 2–3R, 2–1L, DSA right, pauses 2.20, then sidles under abdomen and quickly back, again under approaches epigyne taps with pedipalps, taps again, alternating movements, ?insert right pedipalp momentarily, then left, left still down, standing with right legs 1, 2, on base of female legs—2 minutes insertion ???, male shuttles up onto DSA after observer accidently touches web foundation line, motionless, touches 4R, 4L, 1–2R, 4R under, 1–2R under, DSA right 1.00+, 4R, 3R, 4R under, 3–2R, 2–1R, DSA left rest less than 1.00, 4–3L, 2–1L, 3–2R, 4–3R, DSA midline then up to apex abdomen, insect strikes web female responds immediately, male stands on scarp of abdomen—is this a response to female's movement?, prey escapes rest 2.00, male moves up to DSA from scarp, female cleans pedipalps, rests 2.12, then spends 5.00+ on DSA intermittently tapping leg bases of female . . . [MHR's observation period ended, BR takes over].

Down to 3R, DSA median 1.10, 4L, 3L, 3L, DSA right, pauses 2.40, cleaning feet. 2R, 3R, 1R, 2R under, DSA center 3.10, 2L, 3L tapping, 3R–4R, 2–3L, DSA right rest 1.40, 3–4L, 3–4R, 2–3L, 3–4R, DSA left, 2–3–L, DSA right, rest 2.10, 1–2L, pedipalp L, 3–2R under, 2–3L, 4R, DSA median 2.20, 2–3R, DSA center rest 1.40, 2–3L, 3–4R, 2–3R, 3–4L, 3–2L, 3–4R, 3R, DSA center rest less than 1.0, chelicerae R, 1R, chelicerae L, 3–2L, 3R, 2L, 3R, 2L, 3R, 3R, 4R, DSA center rest less than 1.00, apex of abdomen, down ventral surface of abdomen, shuttle to DSA center, 4R, 3R, 3L, 4R, 3R, 4L, 3L, 3R, 4R, 2R, 3–4L, DSA right rest 2.18, apex of abdomen, down dorsal surface to scarp right, rest 1.10, web blows in wind, male stationary. Female cleaning and moving abdomen as if trying to remove male, swings off web so that all legs on one side can scrape at male.

End of session: 2 hours; time spent in silk attachment, approximately 49.55 minutes.

Appendix 2

Verbatim Notes on Selected Sequences Given to Large Acridiids

(See pages 57–58, for background)

Behavior	*Elapsed time (min.:sec.)*
Presentation 1: 50 mm acridid	
Pluck	0– 0:09
Slowly down to prey	0:10– 0:18
Touch	0:18– 4:15
Move down ½ in., tap with legs I, raise these back off web over thorax in defensive posture	4:15– 7:40
Lunge forward, bite, back-off	7:40– 7:42
Motionless	7:43– 9:20
Edge forward until pedipalps contact prey	9:21– 9:28
Lunge forward over prey, bite, back off	9:20– 9:32
Motionless	9:33–11:50
Lunge, bite	11:51–11:57
Sustained bite on second right leg of prey	11:58–15:05
Move bite location, in short steps to right thorax	15:05–15:10
Short biting attempts jaws edgewise to tough thorax	15:11–15:18
Return to biting prey leg 2R	15:19–17:30
Shift bite to junction of leg 1R and thorax	17:31–21:25
Small bites at thorax edge	21:26–22:20
Wrap prey (×32)	22:21–23:15
Cut out and pull	23:16–23:34
Wrap (×28)	23:35–24:12
Cut out	24:13–24:56
Wrap (×16)	24:57–25:08
Cut out	25:09–26:39
Carry on silk, supported by both legs IV then left IV	26:40–27:10
At hub	27:10
Turn right, attach carry-silk 3 times	27:11–27:38
Pause and clean, feet, chelicerae, pedipalps	27:39–28:40
Pull up prey, handle, then feed.	28:41–28:42

Total sequence time 28:42

Presentation 4: 50 mm acridiid

(The absence of a substantial bite in this sequence should be noted.)

Retreat to 18" above hub on upper foundation thread	0:01– 2:02
Edge slowly down to hub	2:03– 2:18
Slowly approach prey, legs I & II (×3) raised off web, pluck	2:19– 3:10
Halt 8" from prey	3:11– 3:17
Resume slow approach	3:18– 3:51
Touch with legs I	3:52– 3:55
Touch with legs II as well	3:56– 4:10
Palpate	4:11– 4:22
Lunge, bite, back-off	4:23– 4:25
Pause, motionless	4:26– 4:34
Lunge, bite, back-off	4:35– 4:38
Pause	4:39– 4:46
Lunge, bite, back-off	4:47– 4:50
Pause	4:51– 5:07
Lunge, bite, back-off	5:08– 5:10
Pause	5:11– 5:16
Lunge, bite, back-off	5:17– 5:25
Pause about 3" from prey touching it with 2 legs I, one leg II	5:26–12:40
Move close to prey and palpate along dorsal surface thorax to head	12:41–13:12
Turn left and wrap (×86) cutting intermittently	13:13–16:25
Cut along upper surface of prey and attach line to intact web above	16:26–16:42
Palpate down to head	16:43–17:08
Cut out below	17:09–17:27
Wrap (×16)	17:28–17:51
Cut above	17:52–17:57
Wrap (×8)	17:58–18:05
Cut final attachments	18:06–18:35
Carry on silk with support from both legs IV	18:36–19:15
At hub	19:16
Turn right at hub and attach silk 4 times	19:17–19:23
Manipulate prey	19:24–20:18
Feed	20:18

Total sequence time 20:18

☆ U. S. GOVERNMENT PRINTING OFFICE: 1973—510–224/22

Publication in Smithsonian Contributions to Zoology

Manuscripts for serial publications are accepted by the Smithsonian Institution Press, subject to substantive review, only through departments of the various Smithsonian museums. Non-Smithsonian authors should address inquiries to the appropriate department. If submission is invited, the following format requirements of the Press will govern the preparation of copy.

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½" top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 pages, including typescript and illustrations.

The *title* should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an *abstract* as an introductory part of the text. Identify the *author* on the first page of text with an unnumbered footnote that includes his professional mailing address. A *table of contents* is optional. An *index,* if required, may be supplied by the author when he returns page proof.

Two *headings* are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In *taxonomic keys,* number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporate page references in the key.

In *synonymy,* use the short form (taxon, author, date:page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within an entry, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in, or at the end of, the entry. For *references within the text,* use the author-date system: "(Jones, 1910)" and "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910:122, pl. 20: fig. 1)."

Simple *tabulations* in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal *tables* must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Use the *metric system* instead of, or in addition to, the English system.

Illustrations (line drawings, maps, photographs, shaded drawings) can be intermixed throughout the printed text. They will be termed *Figures* and should be numbered consecutively; however, if a group of figures is treated as a single figure, the components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9*b*." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed *Plates,* and individual components should be lettered (Plate 9*b*) but may be numbered (Plate 9: figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork. An instruction booklet for the preparation of illustrations is available from the Press on request.

In the *bibliography* (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." For capitalization of titles in foreign languages, follow the national practice of each language. Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures," "plates," "pages."

For *free copies* of his own paper, a Smithsonian author should indicate his requirements on "Form 36" (submitted to the Press with the manuscript). A non-Smithsonian author will receive 50 free copies; order forms for quantities above this amount with instructions for payment will be supplied when page proof is forwarded.