

The Ecology and Behavior of
Nephila maculata: A Supplement

MICHAEL H. ROBINSON
and
BARBARA ROBINSON

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 218

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Michael H. Robinson
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ISSUED

MAR 25 1976



SMITHSONIAN INSTITUTION PRESS

City of Washington

1976

ABSTRACT

Robinson, Michael H., and Barbara Robinson. Ecology and Behavior of *Nephila maculata*: A Supplement. *Smithsonian Contributions to Zoology*, number 218, 22 pages, 9 figures, 1 table, 1976.—Further studies of the subject of *Smithsonian Contributions to Zoology*, number 149, have filled in gaps in that study and are reported herein. Analysis of data on the web-site constancy of *Nephila maculata* shows that this spider may, as an adult, spend considerable periods at one site. It almost invariably moves after egg-laying, possibly as an antipredator device. The spider may also move its web site when catching above-average quantities of prey. Such apparently purposeless moves reduce the numbers of theridiid kleptoparasites associated with the *Nephila* web and this may be their functional significance. It is here reported that *N. maculata* builds stabilimenta into its molting webs (that lack a viscid element). The egg cocoons of the species are described, numbers and weights of eggs are given, and it is suggested that the structure of araneid egg cocoons may be a useful character for elucidating relationships within the family. Instances of mammalian predation of araneid eggs are described and a full account is given of size and color changes in the developmental history of *N. maculata*. Males of this spider need only 7 molts to reach maturity whereas females need 13. Mature males and females from the same batch of eggs probably do not overlap in time. Details of the association between a moth and *Nephila* webs are reported and the relationship is discussed; the moth probably gains protection from association with an aversive structure. Observations show that birds may learn to avoid contact with large araneid webs.

New observations on courtship and thermoregulatory behavior are detailed. Courtship includes a preliminary approach stage in which males may react aggressively and displace one another. Copulation times may be much longer than previously reported. The thermoregulatory repertoire of *N. maculata* is at least as large as that of the other *Nephila* species studied so far.

Adult female *N. maculata* are used as food in several parts of New Guinea. Methods of cooking and the general flavor are described.

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 6138. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data
Robinson, Michael H.

The ecology and behavior of *Nephila maculata*.
(Smithsonian contributions to zoology ; no. 218)

Supt. of Doc. no.: SI 1.27:218

I. *Nephila maculata*. I. Robinson, Barbara, 1931— joint author. II. Title. III. Series: Smithsonian Institution. Smithsonian contributions to zoology ; no. 218.

QL1.S54 no. 218 [QL458.42.A7] 591'.08s [595'.44] 75-619271

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The Ecology and Behavior of *Nephila maculata*: A Supplement

Michael H. Robinson
and *Barbara Robinson*

Introduction

In 1970–1971 we carried out an investigation into the ecology and behavior of the giant wood spider, *Nephila maculata*, at Wau, Morobe District, Papua New Guinea (Robinson and Robinson 1973a).¹ We subsequently made related studies on the golden web spider, *N. clavipes*, in Panama (Robinson and Robinson 1973b, 1974). These studies of *Nephila* species, taken together, represent a very considerable accumulation of information on the natural history, ecology, and behavior of this conspicuous, ubiquitous, and ecologically important group of tropical spiders. When we returned to Papua New Guinea in 1974 we were again confronted by *N. maculata* in great abundance and were stimulated into making further studies of the biology of this magnificent species. This new work extends and amplifies our previous studies. In addition to reporting on the new investigations, we here also examine the phenomenon of web-site constancy (and its relationship to both predatory success and levels of kleptoparasite infestation) using data that we collected in 1970–1971. The most important of

the new investigations was a largely biometrical study of the life history of the species, a neglected aspect of araneid biology. This revealed marked differences in the developmental histories of the two sexes. Although the new data are from diverse aspects of the biology of the giant wood spider, we feel it is better to present them together, disconnected as they may be, rather than in a number of separate reports. The subjects covered are listed in the "Contents."

Materials and Methods

The spiders were studied in the Wau Valley, Morobe District, New Guinea, at a number of localities but principally in the grounds of the Wau Ecology Institute. Descriptions of the principal study area and of the spider are given in Robinson and Robinson (1973a). The data on web-site constancy are extracted from data gathered during the day-by-day census of the prey caught by a sample population of 10 adult female *N. maculata* that was carried out during 1970–1971. Details of this census and the broad climatic conditions that obtained at the time are given as cited above. All the other new data presented in this paper, except for the life history studies, result from observation and experimentation involving techniques similar to those used in the main study. The methods used in the life history studies are described separately in the appropriate section below.

¹Since we refer to this work throughout the paper, we have avoided conventional circumlocutions and simply cite it as "(1973a)" unless indicated otherwise.

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

Natural History and Ecology

WEB-SITE CONSTANCY

Over the years of our spider studies we have formed the impression that spiders may move from sites where they are catching an abundance of food (Robinson and Olazarri, 1971). To test whether this was true we decided to analyze the ancillary data that we collected during our studies of the prey of *N. maculata*, when we also noted the frequency of web-site changes (and distance moved, when known), the frequency of absences associated with egg-laying, and whether or not the spider returned from these absences to the same web (or moved). Additionally we counted the number of kleptoparasites associated with each sample spider *once a week, not daily as erroneously stated in Robinson and Robinson (1973a:29)*. (This error arose during transcription of field notes when one of us assumed that the other had recorded weekly totals, whereas the figures for kleptoparasites were the result of a one day per week census. Thus the figure for the average number of kleptoparasites is really 5.7 and not 0.92 as stated on page 29 of our 1973 paper. The latter figure was obtained by dividing the census total of 2978 kleptoparasites by the total number of spider days during the census—3237. This incorrect calculation seriously underestimates the average. The total should have been divided by 520—representing 10 webs on 52 census occasions. The statement on page 30 of our 1973 paper that the maximum number of kleptoparasites present on any web on one day was 15 is incorrect and an error arising from the same process of confounding. It was, in fact, 30.)

Returning to the original data, we have examined this to determine whether there are any correlations between moving from a web site and previous levels of prey capture, egg-laying, and numbers of associated kleptoparasites. We have also been able to categorize all the moves for the distance involved. Finally we have been able to compare the number of kleptoparasites present on the web before and after a move. The latter analysis is of particular interest since Robinson and Olazarri (1971:35) suggested that the orb-web spider *Argiope argentata* (Fabricius) could possibly reduce the burden of kleptoparasites by moving its web from time to time.

Several points emerge immediately from this analysis. Adult female *N. maculata* operate their webs at the same site for quite long periods. On average they stay in one place for at least 12 days and may stay for very much longer. In Figure 1 we have plotted the time distribution of intervals between one move and the next. This illustrates two things. Once having moved, the spider may make a number of moves before settling down and will then remain in one place for a considerable period. This is what one would predict if the spider were moving so as to find a good prey capture site.

Despite this tendency, there is also a tendency for the spider to move after an egg-laying excursion. Forty-three percent of all the moves that we recorded occurred after the spider had quit the web to lay eggs, and these spiders did not return to the old web but relocated their webs. This type of move is probably not occasioned by lack of predatory success at the old site since in these cases we saw the spider get fatter and fatter until it was able to lay eggs (after which it was always dramatically thinner). Furthermore, when we analyze the weight of food captured in the two clear weeks before egg-laying, we find that this is well above the weekly average for the year (see below). If a postovipositional move is not a response to low predatory success it needs explanation. There are at least two possibilities. The spider could move simply because it was unable to find its old web after moving some distance away to spin its egg cocoon. The fact that the female *does* return to her web after 16.8 percent of known egg-laying excursions (15 out of 89) is not conclusive one way or the other since the difficulty of finding the web again may vary according to the distance she travels away from it before she lays her eggs. A further possibility is that the spider moves away from her egg-laying site as an antipredator or antiparasite response. The presence of a large web close to an egg mass could be a useful clue to both predators and parasites. Certainly a large mass of nutrient-rich eggs is attractive to some predators (see later) and we have found dipteran larvae in *N. maculata* egg cocoons. If the move were a defensive response the spider should, perhaps, take down its web before the egg-laying excursion. It does not, thereby leaving at least 200 calories of valuable silk behind (calculated from Lubin, 1973:353) in addition to a possible egg-site marker for predators and parasites.

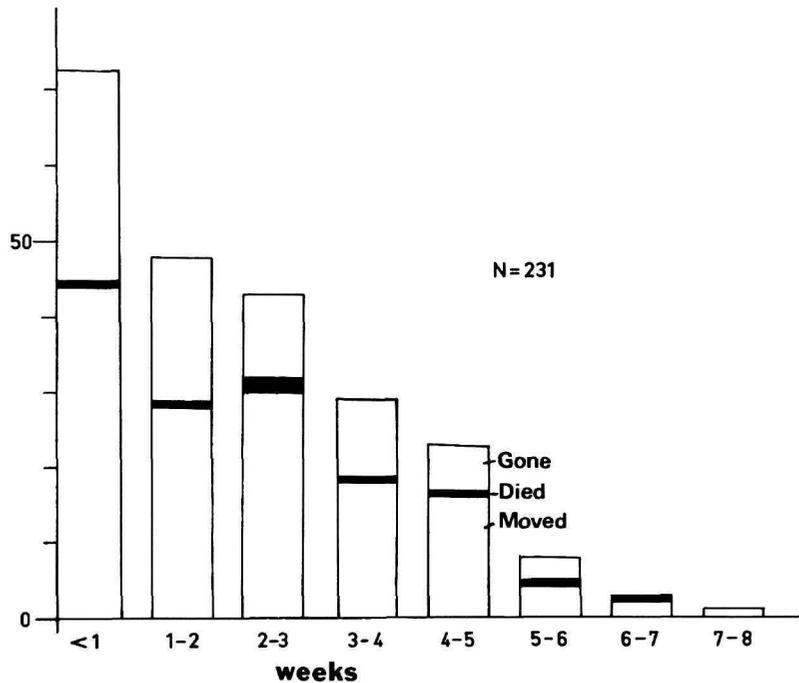


FIGURE 1.—Time intervals between one move and the next. Note that in this diagram we have included deaths and disappearances since these terminate a stay at one site. In the case of disappearance (“gone” in the graphs), we either failed to find the spider or found it in an inaccessible location.

(Certainly the web deteriorates quite rapidly and may become an insignificant remnant of silk long before the eggs hatch, but it is not possible to assess whether it might then still serve as a clue to the presence of the adjacent eggs.)

Those moves not associated with egg-laying are of considerable interest since in a sense they are “pure” moves. Egg-laying moves as discussed above could be the fortuitous result of the spider being unable to find its web after an absence. This cannot be the case with this second category of moves. These could be a simple response to poor prey capture at a given site, or a means of getting rid of kleptoparasites, or function to reduce the possibility of predation (the longer the spider remains at one site, the greater the risk of some predator finding it?), or they could be multifunctional. The lack of predatory success hypothesis can be tested if we can make an assessment of what constitutes a sufficient input of food for an adult female *N. maculata*. Since our data are for dry weight of prey remains, we need a figure for baseline predatory

success based in these terms (Robinson and Robinson, 1973a:32, convert from dry weight of prey remains to the weight of the original prey by assuming that the remains represent around 20 percent of the original wet weight). We have two bases for such an estimate. The first is to use the average weekly catch calculated from the year’s total catch for the 10 sample spiders. This works out at 0.267 grams, as follows:

Total dry weight of prey remains for year	123.544 grams
Number of spider days	3237
Average dry wt. prey remains/per day/per spider =	
	$\frac{123.544}{3237} = 0.0382$
Average dry wt. prey remains/per week/per spider =	0.0382
× 7 =	0.267

Basic data from Robinson and Robinson, 1973a.

How useful such an average is cannot really be judged at our present state of knowledge; 8 of the 10 spiders sampled have averaged weekly catches that are lower than this bulk average.

As a second basis for estimating a baseline for predatory success, we have taken the prey captures for the two weeks preceding egg-laying wherever no move occurred during these two weeks. (In making this estimate we exclude the week in which the egg-laying actually occurred.) This procedure results in a calculated average of 0.306 grams, arrived at as follows:

Total dry wt. prey remains for wks. preceding egg-laying as defined above	43.432 grams
Number of weeks involved	142
Average dry wt./per week/per spider = $\frac{43.432}{142} = 0.306$	

Matching the weight of prey caught in the week prior to the "pure" moves against these two baseline estimates, we get the following results:

Total number of moves not associated with egg-laying but preceded by an uninterrupted week at web site*	49
Number preceded by a week of 0.267 grams prey remains = 20 = 40.8%	
Number preceded by a week of 0.306 grams prey remains = 13 = 26.5%	

* Moves were only scored if they were preceded by an uninterrupted week since we were using one week's score as a criterion of success.

We feel that these results are a good basis for assuming that spiders will move from web sites that are good for prey captures and that such moves do not function to enhance prey capture efficiency, but have another function. (It can be objected that our criterion of a good week is wrong, or that it is unrealistic, since the spider almost certainly does not use the weight of prey caught in a week to determine whether or not it is doing well at a particular site. At the present we can only guess at the possible mechanisms involved but would doubt whether, if the spider *does* assess its predatory success, it does so on a day-to-day basis. To do so would mean that a spider might respond to a period of poor prey captures occasioned by bad weather as though it were due to an unsatisfactory web site.)

Returning to our original hypothesis, that moving periodically may reduce the kleptoparasitic load on the spider, we can test this by seeing whether this is actually the case. Out of the 20 moves made by spiders obtaining 0.267 grams of prey or more:

15 resulted in a reduction of kleptoparasites;

4 occurred when the spider had no kleptoparasites to start with and none immediately following the move;
1 resulted in an increase of kleptoparasites (but we noted that this spider moved into a web site that had been vacated by another spider two days before).

Of the 15 moves that resulted in a reduction of kleptoparasites, most resulted in a substantial reduction, as the following before-and-after couplets show: 7-4, 4-0, 10-1, 11-2, 5-2, 9-0, 22-0, 8-5, 9-0, 12-4, 4-0, 16-0, 15-3, 9-2, 3-0.

The fact that the spider moves its web site even when it has no kleptoparasites associated with it does not mean that the function of moving is not related to kleptoparasite reduction. The simplest mechanism for ridding a web of kleptoparasites might simply be to move from time to time irrespective of the actual numbers present. The possibility that moving from a good prey capture site is an antipredator or antiparasite strategy cannot be ignored, but even if this is the correct functional explanation we must conclude that moving *incidentally* reduces kleptoparasite numbers.

The distance the spider moves is of interest. In Figure 2 we have plotted distances moved for all the cases where we have reasonably accurate data. In some of the long moves we may have missed intermediate web sites, i.e., when the spider was found after two or three days it could have moved in stages to a new site, but, if so, it probably did not build webs en route or we would have found these. Note that a considerable number of moves are over 1.5 meters and many are over 3 meters.

Enders (1974) reported that araneid spiders will interfere with the use of space by competitors by moving onto one another's webs. This "invasion" sometimes results in supplanting a resident spider but most of Ender's data (1974:320) refer to cases where the owner of the web was absent (due to the observer's interference). In one of the cases of supplanting (out of 8 observed?, the data are not clear), the supplanting spider left a good web site to move into a poor one. At the abandoned web site the spider had taken 29 prey in 13 days, whereas it moved to a site where only one prey was taken in the same period. Although the occupation of a vacant web site or web cannot be regarded as competition, the behavior of invading any web site could result in competitive interference if it caused abandonment of an occupied web or web site. In our 5487 observations on marked *N. maculata* fe-

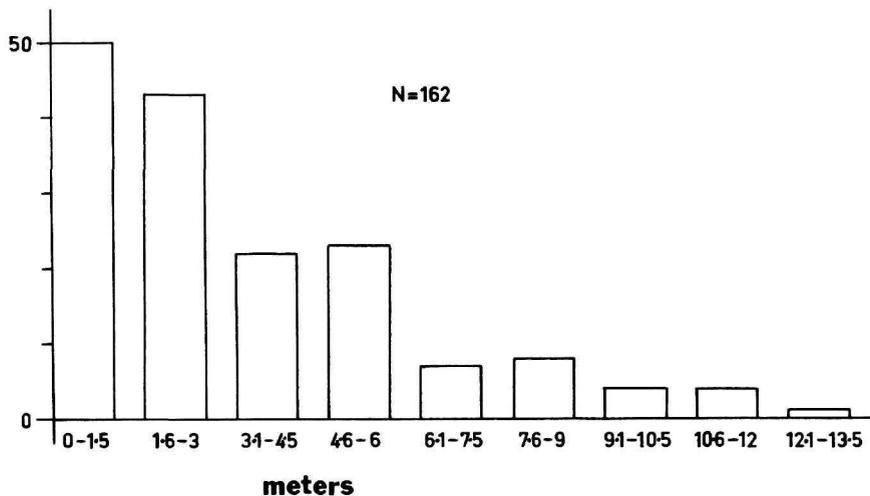


FIGURE 2.—Distances moved from one web site to the next. (The data for this graph are smaller than those presented in Figure 1 because we only recorded distances moved when we found the spider within a day or two after a move.)

males (we had 10 “reserves” marked as well as the 10 sample spiders), we never recorded supplanting. We have two records of adult female *N. maculata* feeding on subadult female *N. maculata* which clearly could have resulted from unsuccessful “invasions” on the part of the latter. We have, additionally, one record of a spider moving into a web site shortly after it was vacated, but no record of a successful supplanting of an occupying female (this would have been very evident if it had occurred). We conclude that if competitive interference occurs in *N. maculata* it does not occur sufficiently often (amongst adults) to account for moves that are not occasioned by poor prey capture results or egg-laying. Ender’s (1974) account does not make it clear whether “invasions” occur mainly between members of the same age class or whether they occur at restricted periods in the spider’s seasonal cycle. This makes assessment of the possible significance of this phenomenon difficult.

STABILIMENTUM CONSTRUCTION

In our previous report we noted that *N. maculata* occasionally builds a more or less perpendicular linear stabilimentum. This was the first record of stabilimentum building by species of the genus *Nephila*, and we noted that such stabilimenta were

built by immature individuals and that we had not recorded them from the webs of adults (Robinson and Robinson, 1973a:8). We subsequently discovered that *N. clavipes* builds similar stabilimenta and that these too are confined to juveniles (Robinson and Robinson, 1973b). In addition, it turned out that these stabilimenta were almost entirely confined to molting webs (i.e., those consisting of frame, radii, and no viscid spiral). In our observations on *N. maculata* webs with stabilimenta we failed to note whether these were entire functional webs or molting webs. We can now state that *N. maculata* builds stabilimenta in molting webs in the same way as *N. clavipes* and although we have no quantified data we would guess that a stabilimentum is found in molting webs of individuals (females) from about the eighth instar onward (see later for instar sizes). We believe that the spider molts in its web because this places it above ground, isolated from surrounding vegetation, and out of reach of some predators. It also is protected by the barrier web (s) when molting, but needs a very secure platform where it can harden after emergence from its old cuticle. Omitting the viscid spiral from a molting platform makes sense since the process of molting might otherwise be interrupted by prey becoming entangled in the web and shaking the spider at a vital moment. (Molting in

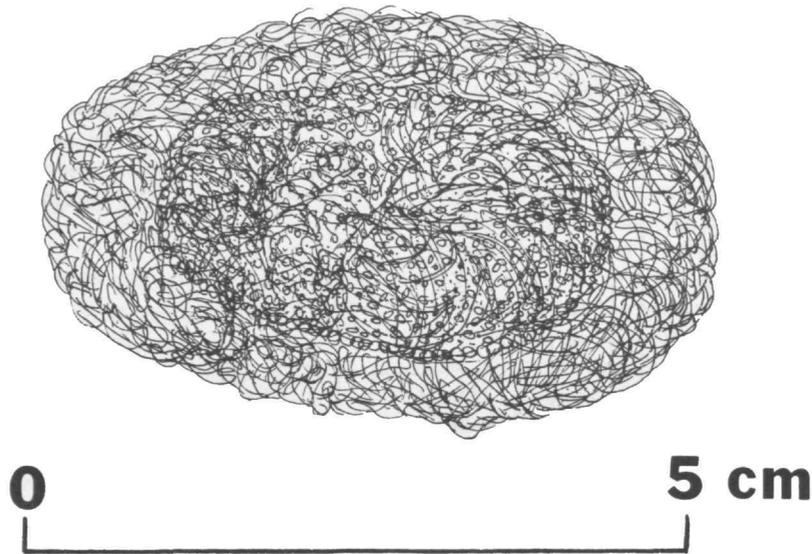


FIGURE 3.—The egg sac (also called cocoon) of *Nephila maculata*. The outer basketwork of silk strands is sufficiently transparent to allow the egg mass to be seen within.

N. madagascariensis is beautifully described and illustrated in Bonnet, 1929; our observations on molting in *N. maculata*, *N. clavipes*, and *N. fenestrata* accord fully with his.) We have speculated elsewhere (Robinson and Robinson, 1973b) on the function of these rarely built stabilimenta. We can add that we have also seen stabilimenta in the molting webs of *N. fenestrata* in Nigeria and Natal (Republic of South Africa).

EGG COCOONS

In our previous paper we did not describe the egg cocoons of *N. maculata* nor give data on the number and weight of their contents. We here rectify this omission. Figure 3 shows a typical egg sac of *N. maculata*. (Note that these are concealed beneath vegetation and less well camouflaged by color than those of most *Argiope* species which are often attached, in the open, to the frame members of the web.) Bonnet (1930a:70–72, fig. 11) describes the cocoon of *N. madagascariensis* and also the process of egg-laying and cocoon construction. We have not seen *N. maculata* build an egg sac, but, allowing for the crudity of Bonnet's illustration, we assume that the egg sacs of the two species are essentially similar. (The cocoons of *N. clavipes* that we

have examined in Panama certainly have the same general structure.) We believe that the structure of araneid egg sacs may give some clues to the relationships within the family and are currently gathering data on this subject. *Nephila* egg sacs are more closely similar to those of *Gasteracantha* species than they are to those of *Argiope*. They differ from those of the latter genus in having the eggs surrounded by an open, semitransparent "basketwork" layer of silk rather than a dense, opaque, multilayered "fabric" of silk that is typical of *Argiope* species.

The *Nephila* cocoons that we have examined contain considerably more eggs than those of other araneids that we have so far dissected and those of *N. maculata* are also considerably heavier.

Sample of 10 cocoons (judged to be within one week of laying):

Average number of eggs	2469
Range	2080–2900
Average weight of eggs	1.219 grams
Range	0.980–1.450
Average weight of silk in cocoon	0.091 grams
Range	0.070–0.110

Bonnet (1930a:74) gives details of the number of eggs in successive cocoons of two female *N. madagascariensis*. The largest numbers were 1351 and

1023 respectively; he gives no weights. The number of eggs in the egg sacs of *N. maculata* is much higher than we have found in any of the other araneid species that we have studied so far. The weight of eggs is very considerable and may amount to anything from a quarter upward of the weight of an adult spider. The eggs are presumably the main constituent contributing to the tastiness of *N. maculata* as a food item for humans. The loss of this much body weight and bulk explains why adult females are so conspicuously thin when they return from egg-laying (Robinson and Robinson, 1973a:13).

PREDATION ON SPIDER EGGS

During our recent stay at Wau we kept a number of araneids in large screened cages to obtain egg cases of known age and origin (the three large *Argiope* species at Wau have similar egg cocoons). After the spiders laid we marked the egg cases and left them in situ, examining them daily to determine development times. On two occasions holes appeared in the nylon screen walls of the insectaries and several egg cocoons that we had tacked to the frame of the cages disappeared. We assumed that the holes had been made by rodents that had eaten the egg cases. Livetrapping within the cages yielded two specimens of an arboreal rat *Melomys rufescens*. This rat climbs well and is sometimes caught in traps baited with commercial dogfood (Robinson and Robinson, in preparation). A *Nephila* egg cocoon must constitute a good energy package for this animal. In their normal site the egg sacs would be accessible to a light, climbing rodent.

DEVELOPMENT OF THE YOUNG SPIDERS: CHANGES IN SIZE AND COLOR

There have been few studies of the life histories of spiders. Levy (1970) reviewed the then available literature and published a list of 31 species (from 18 families) for which some details of the life history were known. In most cases, the minimum details known were the number of molts in the development of the two sexes. Only two araneids seem to have been studied. Of these, one is *N. madagascariensis* (Bonnet, 1929, 1930a) and the other *Araneus diadematus* (Bonnet, 1930b). In his study of *N. madagascariensis*, Bonnet raised the

spider in captivity at Toulouse, France, starting with eggs received from Madagascar (Malagasy Republic). He measured the size of each instar and recorded the time spent at each developmental stage. We felt that a life history study of the larger *N. maculata* would be of interest, but could not afford the time to raise the spider from egg to adult, in captivity. However, during April and May 1974, we noticed that immature specimens of *N. maculata* were extremely abundant at several sites in the Wau valley and decided to try to work out the stages and sizes in the life history by using a large collection as a basis for biometry. We collected a starting sample of immature spiders that seemed to cover a wide range of sizes and measured these after they had been killed in alcohol and then transferred to water. We assume that shrinkage due to dehydration was much less than it would have been if we had used specimens preserved in alcohol. Specimens large enough to be measured without the microscope were measured against a steel ruler. Smaller specimens were measured in water under a stereobinocular microscope using a millimeter scale graticule. Early sampling measurements permitted us to segregate the spiderlings into discrete classes and we then measured individuals until we had 10 in each size class. By this method we were eventually able to construct a schematic life history.

We measured the length and width of the cephalothorax, the length and width of the abdomen, and the total length of legs I and IV. In measuring legs we always measured the longest one of the pair, assuming that the shorter one may have been regenerated after being autotomized at a previous stage (hence short). Abdomen measurements yield the most variable results as this is the most elastic part of the spider's body and even in the middle instars is capable of becoming considerably enlarged during the period between the molts. In addition to measuring the spiderlings and immatures, we also noted the dorsal color pattern of the cephalothorax and abdomen and any conspicuous markings on the legs. We chose to monitor changes in dorsal coloration, rather than ventral, since this seemed to change most radically during development and is usually more visible in the field. We were able to distinguish males from females at least three instars before they became adult by using pedipalpal characteristics.

The possibility of a confusing overlap in dimen-

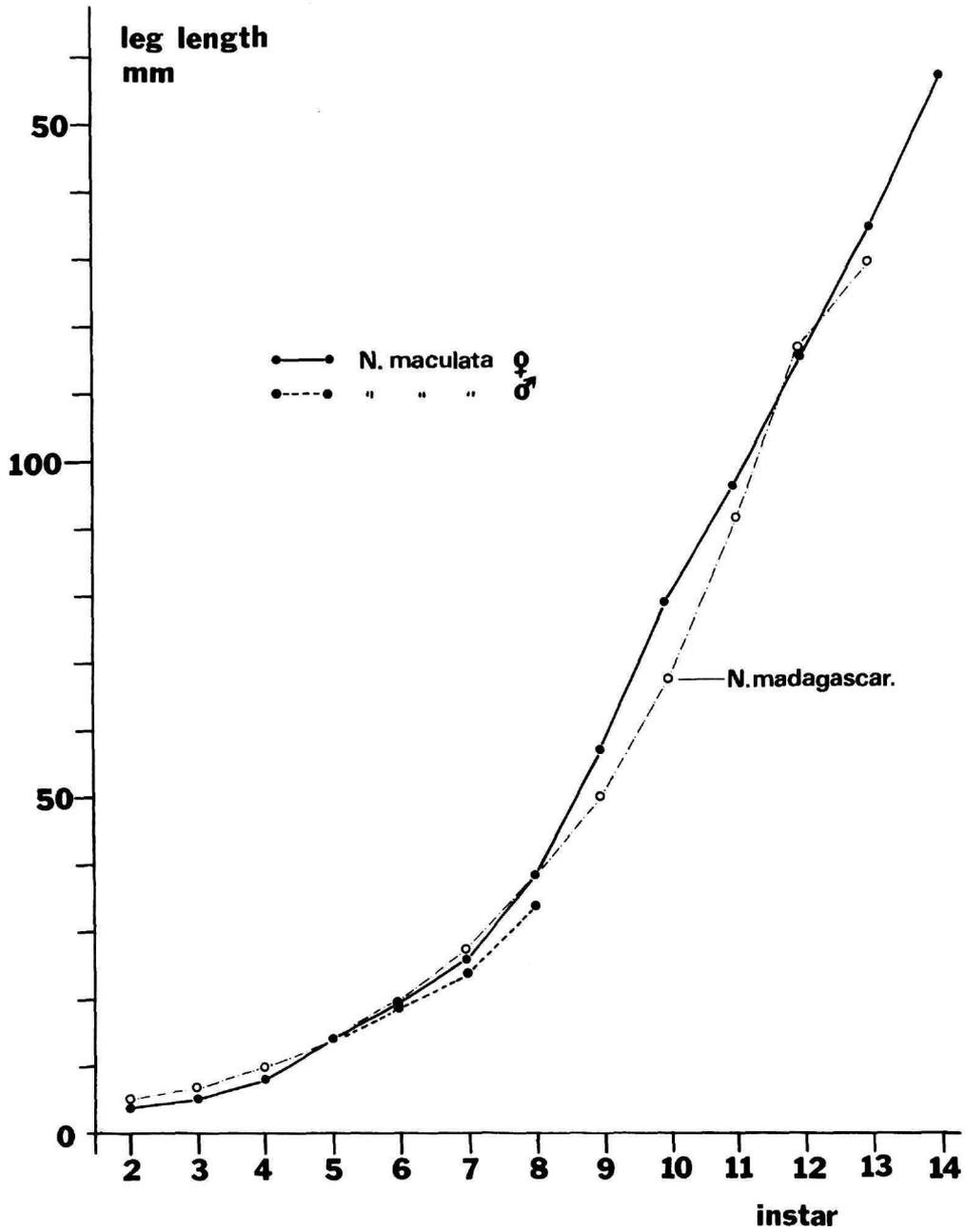


FIGURE 4.—Increase in lengths of legs I + IV for *Nephila maculata* and *N. madagascariensis* (see text). (Solid circles = *N. maculata* females, rings = males; open circles = *N. madagascariensis* both sexes.)

sions occurred only in the very smallest instars and here the leg measurements were critical since they provided an unequivocal means of separating instars. We could not decide whether some very large specimens were adult females or whether they were penultimate instars. To determine this, we kept some in large cages and were able to observe molting. In this way we confirmed the existence of instars 12, 13, and 14, about which there could have been some doubt (see later).

Allowing for an instar and molt in the egg case, after eclosion but before the rupture of the egg sac wall (see Valerio, 1974, for the basis for this designation), there are a possible 13 molts and 14 instars in the development of the adult female. Males, on the other hand, undergo at the most seven molts and adults represent an eighth instar. The comparisons with Bonnet's (1929) results with cage-raised *N. madagascariensis* are most interesting. He found that females of that species reached maturity after the 11th molt. (30.5%), or the 12th molt (56.5%) or some even after the 13th molt. 13%). We did not dissect the large specimens categorized as 12th, 13th, and adult instars, but as mentioned above, captive 12th and 13th instars were seen to molt. This does not mean that some individuals do not reach sexual maturity at their 11th and 12th molts. They may, but we are not able to detect any external evidence of this.

Males reached maturity at the 8th instar and we found no 7th instar-sized males that had adult pedipalps. Interestingly, the molt from pre-adult male to adult is accompanied by a conspicuous reduction in body length. This does not seem to have been noted by Bonnet (1929) in the case of *N. madagascariensis*. We have noted a similar phenomenon in males of several *Argiope* species.

The sizes of the various instars are given in Table 1, alongside the available measurements for *N. madagascariensis* from Bonnet (1929:317, 318 and pl. 1, where we were able to measure off dimensions not given in the text). It is remarkable that there is considerable correspondence between the measurements we obtained from wild-caught specimens and those that Bonnet obtained from cage-reared specimens of a different species. This correspondence is the more remarkable because the measurements were made in two different ways. We measured the length of the first and fourth legs separately, unaware that Bonnet had used the

length from the extremity of the first leg on the left side to the extremity of the fourth leg on the right side. The combined lengths shown in the table for *N. maculata* were obtained by simply adding the mean lengths of the two legs. Bonnet's system of measurement should produce slightly larger figures because it would include a section of cephalothorax, since he measured from left appendage to right appendage. We have graphed (Figure 4) the increase in leg I + IV length with developmental stage for the two species.

Apart from the increase in size shown on the graph, there are changes in the coloration of the body and the legs and changes in the "gaiter" on the distal portions of the tibiae of legs I, II, and IV. These gaiters of dense stiff hairs first appear at the sixth instar and become prominent at the seventh (fig. 1, p. 3, of Robinson and Robinson, 1973a, shows a seventh instar female *N. maculata*). The adult female has no gaiters.

The changes in general coloration are shown in Figure 5. The second instar spiderling is largely unpigmented and the patterning of the dorsal surfaces first appears after the second molt. Then the dorsal surface of the abdomen becomes striped and the dark stripes on a light ground persist until the ninth molt when the abdomen becomes slatey in color and ultimately is almost black. The patterning on the ninth instar represents a clear transition between the striped juvenile coloration and the adult coloration: the stripes are much reduced and a large area of the surface is slatey bronze. As we noted in our previous study (Robinson and Robinson, 1973a:2-3), the species retains some striping as an adult in other parts of its range. The striped Japanese form (Yaginuma, 1968, pl. 29: fig. 162) has a pattern closely corresponding to that of an eighth instar New Guinea *N. maculata*, i.e., compared to the spiders in New Guinea it retains a juvenile color pattern. (We have seen the species in small numbers in Northern Territories, Australia, near Darwin, where its color form as an adult is similar to the New Guinea specimens. The specimen that we saw in Singapore was also all dark. However, in India (Borivili near Bombay) and Sri Lanka (various localities), all adults were striped.) The coloration of the spider's legs changes from a translucent gray in instars three to six to a banded pattern in at least some individuals of instars seven and eight and is then replaced by the

TABLE 1.—Biometrical details of the development of *N. maculata* compared with *N. madagascariensis*

Body part (measured in mm)	Instar number ^a					
	2	3	4	5	6	7
Cephalothorax length	0.5	0.5	0.8	1.2	1.6	2.0
	0.4-0.6 ^b	0.4-0.6	0.7-0.9	1.0-1.3	1.5-1.9	1.9-2.3
Cephalothorax width	0.4	0.5	0.6	1.0	1.3	1.6
	0.3-0.45	0.4-0.6	0.5-0.8	0.8-1.1	1.0-1.4	1.4-1.8
Abdomen length	0.8	1.0	1.2	2.2	3.2	4.0
	0.7-0.85	0.9-1.1	1.0-1.7	1.5-3.0	2.5-3.6	3.4-4.8
Abdomen width	0.5	0.6	0.8	1.0	1.2	1.5
	0.4-0.7	0.5-0.8	0.7-0.9	0.8-1.1	1.0-1.4	1.3-1.6
Leg I	2.1	3.0	4.7	8.0	10.8	15.0
	2.0-2.2	2.8-3.1	4.2-5.5	7.0-9.0	10.0-11.7	13.9-18.0
Leg IV	1.8	2.3	3.7	6.2	8.2	10.9
	1.6-1.9	2.1-2.4	3.1-4.3	5.0-7.0	7.3-9.0	10.0-13.5
Σ I + IV	3.9	5.3	8.4	14.2	19.0	25.9
Body length	1.3	1.5	2.0	3.4	4.8	6.0
<i>N. madagascariensis</i> (from Bonnet 1929; see text)						
Σ I + IV	5.0	7.0	10.0	13.8 ^c	19.5 ^c	27.5 ^c
Body length	<1.0	2.0	2.4	3.2	4.7	7.0
<i>N. maculata</i>						
Σ I + IV	3.9	5.3	8.4	14.2	19.0	25.9
					(18.8) ^e	(24.0) ^e
Body length	1.3	1.5	2.0	3.4	4.8	6.0
					(5.4) ^e	(7.6) ^e

Body part (measured in mm)	Instar number ^a						Adult
	8	9	10	11	12	13	14
Cephalothorax length	2.8	4.1	5.7	7.6	9.0	10.2	14.1
	2.5-3.0	3.3-4.8	5.0-6.8	6.7-8.8	7.5-10.0	9.7-11.0	12.0-15.1
Cephalothorax width	2.1	3.1	4.4	5.8	7.6	7.8	10.1
	2.0-2.3	2.5-3.8	4.1-5.1	5.0-6.2	6.0-7.9	7.2-8.0	10.0-10.2
Abdomen length	6.8	9.7	12.5	16.6	18.8	20.8	28.0
	6.0-7.5	7.0-13.0	11.0-15.0	12.0-20.0	15.5-23.0	18.0-24.0	26.0-35.0
Abdomen width	2.0	3.0	4.0	5.5	6.9	7.5	10.2
	1.9-2.2	2.1-3.8	3.0-5.0	4.0-7.5	5.0-8.0	6.1-9.0	9.0-15.0
Leg I	21.0	31.2	43.2	52.0	62.4	72.8	86.0
	18.0-26.1	28.2-36.0	39.0-47.8	50.2-55.0	59.0-65.5	68.0-80.0	79.0-92.0
Leg IV	17.1	25.9	35.8	44.0	52.4	61.1	70.5
	16.0-20.0	22.0-31.0	30.4-39.0	41.0-46.0	46.0-55.0	51.6-65.0	68.0-74.0
Σ I + IV	38.1	57.1	79.0	96.0	114.8	133.9	156.5
Body length	9.6	13.8	18.2	24.2	27.8	31.0	42.1
<i>N. madagascariensis</i> (from Bonnet 1929; see text)							
Σ I + IV	38.0	50.6	67.4	91.7 ^d	116.8 ^d	129.0 ^d	
Body length	10.0	13.0	19.0	26.0	34.0	34.0	
<i>N. maculata</i>							
Σ I + IV	38.1	57.1	79.0	96.0	114.8	133.9	156.5
	(34.0) ^e						
Body length	9.6	13.8	18.2	24.2	27.8	31.0	42.1
	(6.3) ^e						

^a No measurements made in instar I (egg cocoon).^b Range in mm.^c Some adult males.^d Some adult females.^e Males in parentheses.

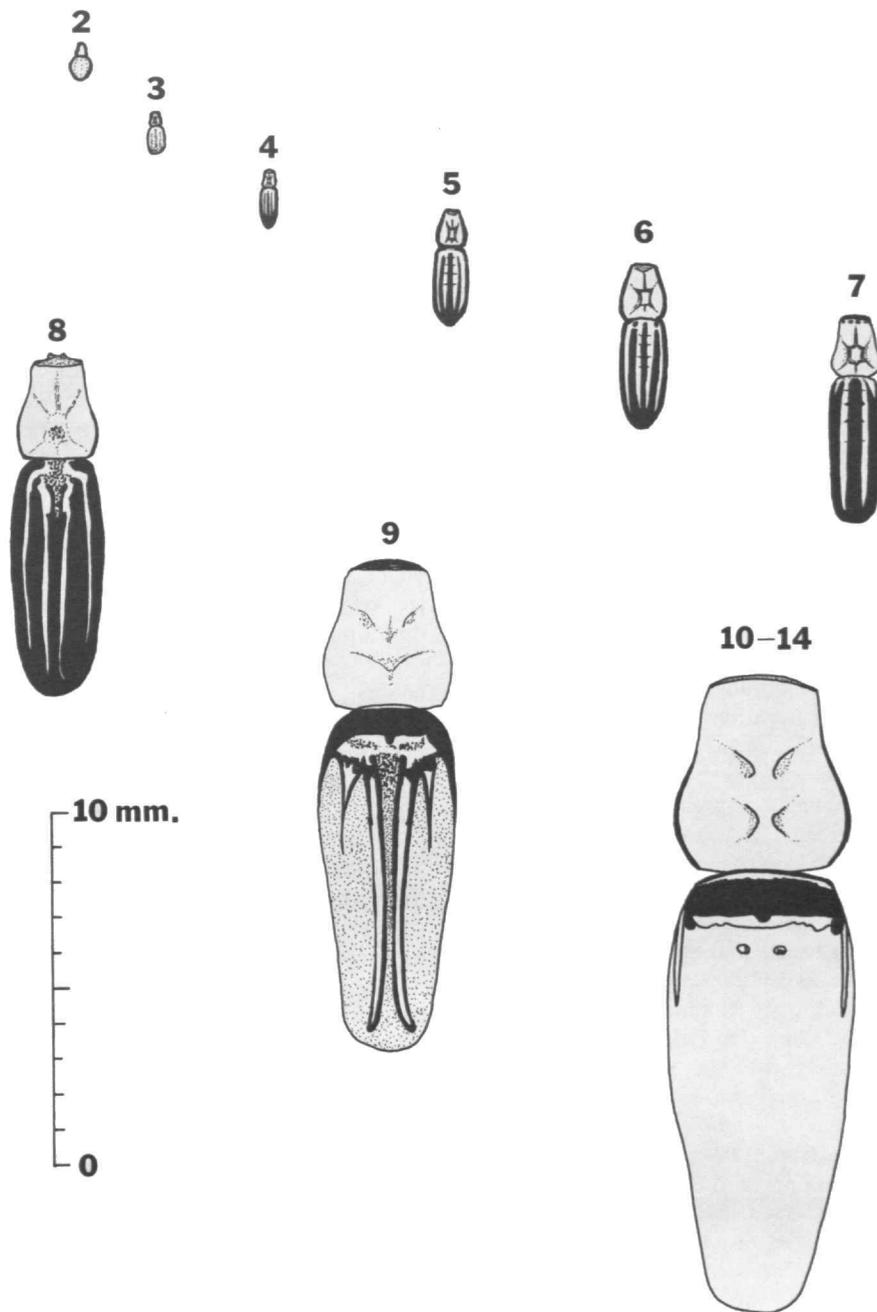


FIGURE 5.—The dorsal coloration of immature stages of *N. maculata*. (Black = black or dark brown coloration, white = pale grey on abdomen and silvery color on thorax except for instars 10-14, which includes adult, where the bulk of the abdomen is shown white but is dark slate gray to almost black. The coloration of the adult male is not shown. Instar 8 = an immature female.)

adult color pattern of black legs with bright yellow areas on the underside of the femora at their apices.

The significance of the color changes is by no means clear nor is there any obvious functional explanation for the differences in adult coloration between the New Guinea forms and those in Japan, India, and Sri Lanka. Striping may be good obliterative (disruptive) camouflage for the early stages in development since many of the early stage spiderlings build their small webs down in the herb layer where there is a background patterning of vertical lines. As the web becomes larger and more prominent, camouflage—or any form of concealment—may become impossible and camouflage patterning valueless. It is interesting to note that *N. madagascariensis* retains a complex patterning of the dorsal surface into the adult stage (Bonnet, 1929, pl. 2).

We did not record the details of changes in the ventral patterning of the abdomen during development, but from the study of photographs (that were taken for other reasons but incidentally record the color patterns of the ventral abdomen) can state that they are minor compared with the changes in dorsal coloration. The general yellow spotting of the juvenile forms remains on the adult but is less prominent. The broad yellow bar associated with the epigyne region (Robinson and Robinson, 1973a, fig. 1) is also prominent in the adult (see Figure 6).

Levy (1970) has discussed the life cycles of spiders in relation to the development rates of the two sexes and has concluded that spider life cycles fall into two basic classes. There are spiders (the majority?) in which the developmental rates of the two sexes are the same (and they mature at the same time) and others in which males mature long before females. Although we have no data on the time it takes male *N. maculata* to mature, we now know that they mature after a maximum of seven molts at a tiny fraction of the weight of an adult female. Unless they have some means of delaying the final molt and remaining at the web-building seventh instar stage for long periods, they must become mature around about the time females of the same generation are also in their eighth instar (given roughly equivalent growth rates and assuming an average rate of predatory success). Once adult, the males cease building webs and presumably subsist on food reserves and occasional com-

mensalism with females. We think that it is extremely improbable that male *N. maculata* are, in these circumstances, substantially more long-lived than males of *N. madagascariensis*. Bonnet (1929:509) states that the life of the male in the adult state is very short (“La vie des ♂ [sic] a l'etat adulte est fort courte”) from 1 to 2 months. If this is so there seems little chance of siblings mating.

Deevey (1949) reported a very strong influence of food supply on the number of molts that *Latrodectus mactans* underwent before reaching maturity. Clearly we have no means of assessing the possible influence of this factor on our results. However, we would guess that the presence of large numbers of immature spiderlings, at any time, is likely to reflect favorable conditions for survival and development. For this reason, and because our larger species has only one molt more than *N. madagascariensis*, we suspect that our data reflect the results of reasonably “normal” conditions of development.

INSECT ASSOCIATES OF *Nephila maculata*

During the year of our earlier study (April 1970–April 1971) we recorded the presence of a pyralid moth resting on the webs of the sample population of adult female *N. maculata* on over 30 occasions. The moth was *Hurculanea* sp.² (Pyralidae: Pyralinea). Figure 7 shows it resting on a web element in a typical head-down posture. The moths assumed such resting postures, by day, only on the upper structural members of the web or the associated barrier web (frame threads, foundation threads, mooring threads, and barrier web threads, see Robinson and Olazarri (1971) for comparison of U.S. and British terminology). The threads on which the moths rested were nonviscid and always horizontal or near horizontal; we did not find them on sharply inclined threads. At rest the moth assumed a delta-shaped attitude with the forewings completely covering the body outline and the antennae apposed to the body and concealed. The moth hangs from the spider's silk supported by the hind legs whose tarsal claws grip the line. These

² Identified by D. Ferguson, National Museum of Natural History, Smithsonian Institution, Washington, D.C., to whom we are most grateful.

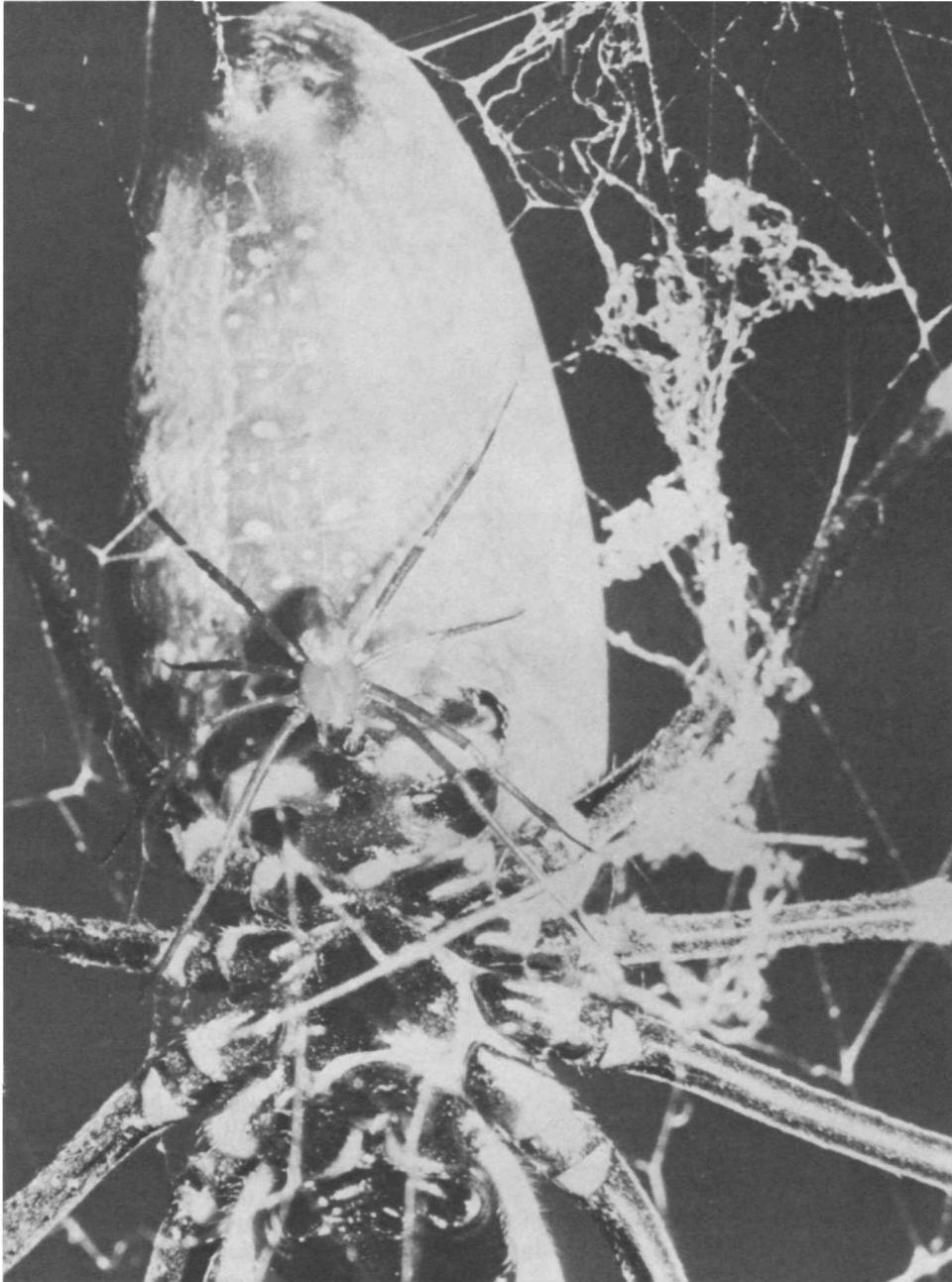


FIGURE 6.—Photograph of the ventral surface of an adult female showing the spotting and longitudinal pale lines. (This photograph also shows a male in copula with right embolus inserted and left pedipalp raised.)



FIGURE 7.—Moth of *Hurculanea* sp. resting on a web element of a *N. maculata* web, head-down and ventral surface toward the camera. (Note the position of the two legs III that are holding the silk.)

legs are extended in the plane of the wings, beneath them, and one leg may be extended asymmetrically as shown in Figure 7.

During our first visit to New Guinea we failed to find *Hurculanea* on the webs of araneids other than *Nephila*, but we have since found several specimens associated with the webs of *Argiope reinwardti* (Doleschall). We believe that the associa-

tion between this moth and araneid spiders is not fortuitous and raises interesting questions about its function, mechanism, and evolutionary origins. In its resting attitude, the moth has most of its typical insect structures concealed either by attitude (legs, antennae) or color and structure (head and wings). Both the dorsal and ventral surfaces of the body have camouflage markings. The insect is generally

similar to the irregularly shaped pieces of leaves and other plant debris that accumulate in and on *Nephila* webs within the forest. The moth is probably protected by a relatively unspecialized form of special protective resemblance (plant-part mimicry). However, adopting a resting attitude on spiders' web must involve the insect in fairly complex background selection and settling behavior (see later) and we would expect it to confer some additional advantage over resting, in a similar manner, on vegetation. It could be that resting in a position that is virtually isolated from nearby substrates protects the moth from the large numbers of predatory or omnivorous ants that constantly forage on the surface of leaves, twigs, and stems in this district. Even if ants moved along the frame threads of the web, and we have not seen them do this, the moth might well be alerted to their approach by the vibrations of the web silk. Pocock (1903) reported an instance of commensalism between a social eresid spider and a microlepidopteran, *Batracheda stegodyphobius* Walsingham. He claimed that the moths were sensitive to vibrations set up by the spiders and actively escaped predation.

Despite the possibility that resting on a spider's web is a defense against ants or other ambulant predators, we are inclined to believe that it is a defense against predation by birds. We believe that the strong webs of araneids are hazards to birds and are avoided by them where possible. If this is so, then a camouflaged insect that associated with spiders' webs would have camouflage as a primary defense and the deterrent presence of the web as a secondary defense (for discussion of the concepts of primary and secondary defense see Robinson 1968, 1969, and Edmunds, 1974). The evidence for the idea that araneid webs may constitute a hazard to birds is derived from two sources: records of bird captures by spiders and direct observations. McKeown (1936:154-173) lists a large number of Australian araneids, including *Nephila* spp., catching and consuming birds. He even quotes (page 165) a report of a bird avoiding a spider's web by drastic evasive action. Our own observations (detailed separately below) show that when a naive bird flies through a spider's web the experience can have a lasting effect in producing a strong aversive response. If this hypothesis is correct, we would predict that *Hurculanea* species will not be found associated with spiders that build ephemeral and

weak webs (e.g., the four species of *Gasteracantha* found in the same area).

The question of how the moth detects the presence of, and alights upon, the appropriate web element is an interesting one. At first sight it would seem to imply a complex discrimination and a complex maneuver. We were unable to observe this process: moths released by day in a large insectary containing *Nephila* webs settled indiscriminately. Presumably they make a background selection at dawn and, after initially settling, only exhibit escape responses. Experiments on background selection by cryptic moths have been conducted in confined quarters and the result (rather than the process of selection) has been the object of study (Sargent, 1966, 1969a, 1969b). We have observed a large nematoceran (Diptera) settling on the webs of various cribellate spiders in the Wau area. In this case the insect flew in bobbing flight, with its long legs extended forward of the almost vertically oriented body, until a web member was touched, then the insect settled instantly. The fly looked as though it was aware the web was nearby before it actually touched it. Moths, as lepidopterans, may be preadapted to alight on spiders' webs in two ways. First, we have observations that suggest that butterflies may be able to see and avoid spiders' webs in some circumstances, and the compound eyes of most nocturnal moths seem to be as relatively large as those of butterflies. Second, because of their loose wing scales, they are less likely to become stuck to spiders' webs than most other insects (Eisner, Alsop, and Ettershank, 1964). They may thus be able to see the lines of the web and alight on them and, because of the loose wing scales, the consequences of mistakes may be somewhat less than they would be to a nonlepidopteran.

An alternative to alighting directly onto the silk would be to alight on nearby vegetation and move, by walking, onto the framework of the web. Even if the moth found itself on a lower web element, it could walk upward to an upper frame member.

The moth runs some risk of being attacked by the spider if it persists in moving after settling on (or walking onto) a web member. Adult *N. maculata* will move onto frame members of the web, in apparent predatory excursions, if a vibrating insect is touched against these. However, as the spider approaches a light motionless insect, it plucks and the moth could use this as a cue to arrest movement

or escape by flight. The problem of alerting the spider to its presence is probably not a major one. A number of insects have solved this problem. Emesinids (Hemiptera) are commonly seen moving about the webs of araneids. Wygodzinsky (1966: 52-54) quotes observations on this problem and notes that the insects do not seem to become entangled in the webs. He suggests that their long-legged gait may help them to move about the web (presumably by reducing potential points of contact to the tiny area of the tarsi). The nymphs of all emesinids, and the adults of some species are apterous and they must be capable of locating webs and walking onto the webs from adjoining substrates.

Stages in the evolution of resting on the silk lines of a spider's web can be envisaged as follows:

1. A cryptic moth that is a crude leaf-mimic rests hanging from leaves and twigs supported by two legs only.

2. Because webs occur in the understory where this cryptic moth rests, it is only a small behavioral step from resting on a narrow leaf edge to resting on a narrow silk line. Moths that have this aberrant behavior are at the selective advantage over those resting on vegetation because of their association with a hazard to aerial predators.

BIRDS AND *Nephila* WEBS

On our second visit to New Guinea we hand-raised a number of insectivorous birds for use in experiments on insect defensive adaptations. These birds were raised on a diet of raw eggs, bread, and milk, and confronted with a variety of insects when they were several months old. We conducted experiments in a large experimental cage into which the birds were admitted from their living cages. We tested the palatability of various araneid spiders and found that the birds—Butcher Birds (*Craticus cassicus*) and Shrikes (*Lanius schack*)—would readily eat all the large common araneids, including *N. maculata*, taking them live from the grass floor of the experimental cage where we placed them. On one occasion several *N. maculata* were left overnight in the experimental cage and one built a web from the roof of the cage close to the entrance from the living cage housing five Butcher Birds. When the birds were admitted to the experimental cage, one bird flew straight out and through the

web. The effect was dramatic: the web broke, but the bird was brought to earth fluttering as though crippled. A section of web was adhering to the upper surface of the bird's right wing, over the elbow joint. This immobilized the joint sufficiently to bring the bird down, and it spent several minutes in frantic preening activity before it finally removed the sticky web material and hopped onto a perch from which it was able to resume normal exploratory behavior. For at least three weeks after this incident the bird was reluctant to enter the experimental cage and only did so after its cage mates had done so. Since the birds were only given insects (their favorite food) inside the experimental cage we regard this aversive response as being an intense one. No other birds ever flew into *Nephila* webs in the experimental cage. This incident occurred, in all probability, because the spider had fortuitously built close to the home cage exit and the bird flew so rapidly through the door that it had no time to avoid a novel hazard with which it had had no previous experience. We think that this observation reinforces the conclusion (above) that large orb-webs may constitute a hazard to birds and we would expect birds to quickly learn to avoid webs.

Behavior

COURTSHIP AND MATING

Our previous study included details of the courtship and mating behavior of *N. maculata* and concentrated mainly on the complex behavior of the male once it had moved onto the body of the female. We did not at that stage have information on the approach of the male to the female during the initial stages of courtship, nor did we look at interactions between males. We can now add some details on these subjects. In addition, we have seen more copulations and postcopulatory behavior and must revise some of our previous descriptions.

MALE APPROACH.—There seem to be two possible categories of male movements on the web of the female:

1. Initial movement onto the web and approach to the female or to a waiting position.

2. Subsequent repeated approaches to the female from a waiting position.

We distinguish these on a post hoc basis. We have

introduced males to various locations on the outer perimeter of the female's web and watched their movements. These movements are very different from those of an "established" male that has been "in residence" for sometime. We therefore describe them separately.

Initial movements on the web are slow and the spider walks with legs I more or less constantly off the web, waving them in front of him and tapping the web lightly from time to time with one or other tarsus I (this movement across the web is very similar to that of courting males of *Leucauge papuana*, Robinson and Robinson, in prep.). At this stage the female may detect the presence of the male and pluck the radii, at which moment the male will freeze or even drop off the web in an escape movement. Figure 8 plots the approach movements of three males approximately to scale. Some idea of the hesitant slowness of this approach can be gained from the fact that it took male A 3 minutes 52 seconds to move from his starting point to point X. After 27 minutes all three of these males had assumed head-down postures above the hub and were then intermittently making approaches to the female. This pattern of hesitant initial approach occurred whenever we introduced a male onto a female's web. We assume that males arriving naturally behave in a similar way but have never seen this happen. Most frequently we find webs in which the males are "resident," having assumed waiting positions somewhere above the hub. Males in residence face down the web and make the second type of movement in direct approaches to the female. The initial movement onto the web and into a waiting site must be one that entails considerable risk. Any movements of the female are likely to result in the males making escape responses (dropping off the web on their dragline). We have seen two males that were moving up the web respond to a female predatory excursion by simultaneously dropping off the web. Once the males have reached a position above the hub they are much less "nervous." This may be because they are much less at risk in this relatively neutral³ part of the web, or could result from the fact that in their approach they have somehow gauged the

state of the web-owner. The latter explanation seems improbable since *N. maculata* males will move onto the webs of immature females that are unlikely to be sexually receptive and tolerant of males; perhaps the male's apparently cautious approach is exactly that and not a series of signals to the female. (We have one record of a male *N. maculata* moving onto the web of an adult female *Argiope aemula*, where he eventually assumed a waiting stance and subsequently visited the female at the hub before moving off. He was not attacked.)

Approaches to the female may be numerous, of short duration, and made on either surface of the web. The male may walk slowly with legs I off the web as in the initial approach, but more frequently the waving of legs I is merely intermittent. However, the approach to the female is interspersed with one or more bouts of on-the-spot jerking. In this, the spider bobs up and down with all legs in contact with the web. The effect of this must be to transmit a fairly regular group of (burst of) vibrations to the female. As he approaches, the male usually enters the V made by the two legs IV of the female and may bounce, on the spot, in that area. During this kind of approach the male may lightly touch the female's fourth legs and the apex of the abdomen. Figure 9 shows the movement of the male—lightly touching the female on the abdominal apex. He immediately retreats if she moves and often retreats after merely touching the female once or twice. Ultimately such approaches are followed by the male moving onto the body of the female and commencing the silk deposition activity that we described in detail in our previous paper (Robinson and Robinson, 1973a:36, 38, 41).

INTERACTIONS OF MALES.—Males interact at all stages of approach and courtship. When males are at the "resident" approach stage, described above, a male down at the female resting place will orient toward an approaching rival and move out to contact distance. When two males meet in this manner, they touch legs (I and II) and from this stage may go on to fight, or one may simply retreat, leaving the victor to approach the female. We have seen a number of these encounters and have the impression that size is not decisive in determining the outcome. The subject is susceptible to quantification and we think that it would repay further study (we would guess that a small, highly motivated, male could drive off a larger, less highly motivated,

³ The area above the hub is without viscid spiral in some *Nephila* species, and in *N. maculata* it has a poorly developed and small, viscid, spiral zone (Robinson and Robinson, 1973a:8).

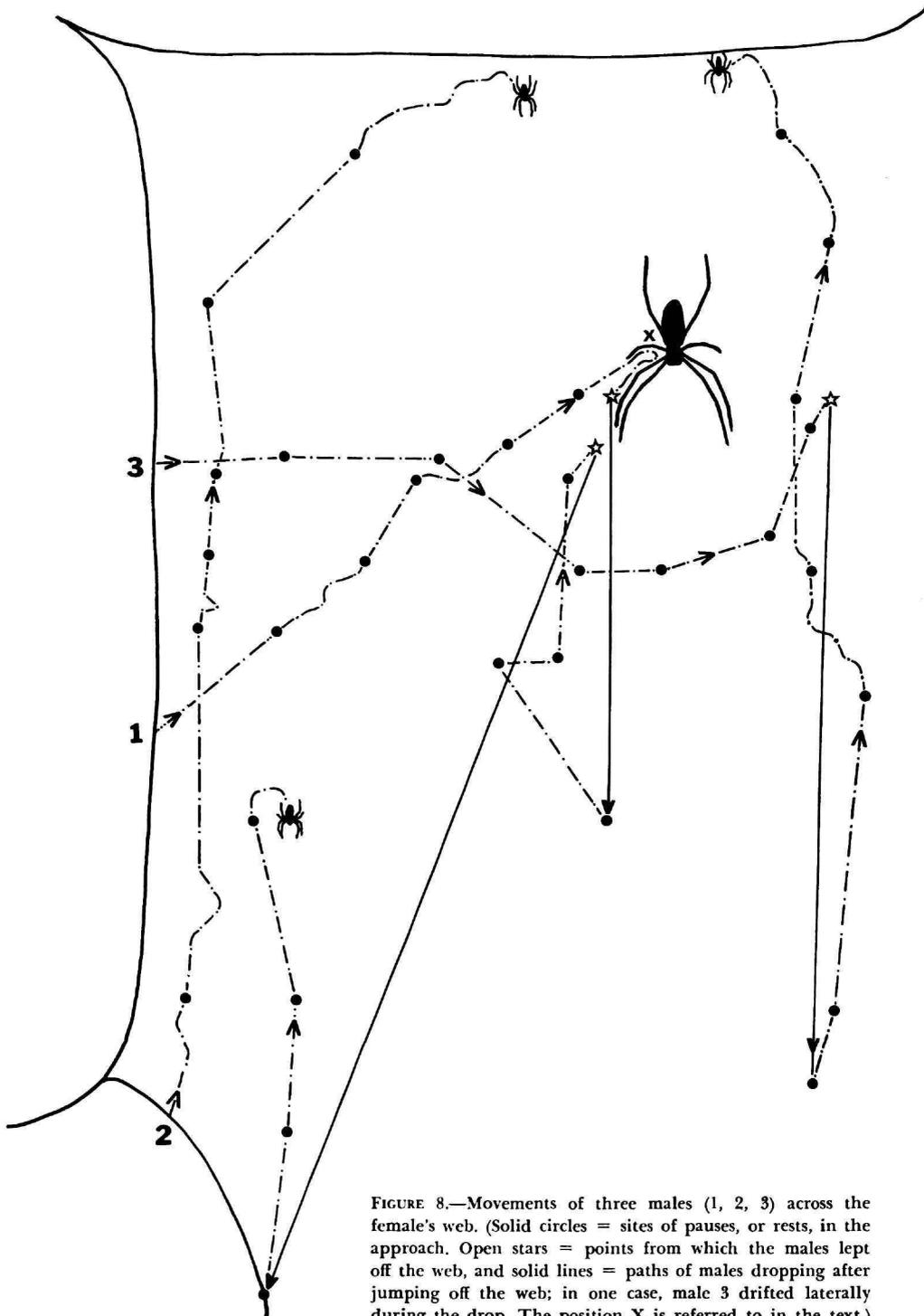


FIGURE 8.—Movements of three males (1, 2, 3) across the female's web. (Solid circles = sites of pauses, or rests, in the approach. Open stars = points from which the males left off the web, and solid lines = paths of males dropping after jumping off the web; in one case, male 3 drifted laterally during the drop. The position X is referred to in the text.)

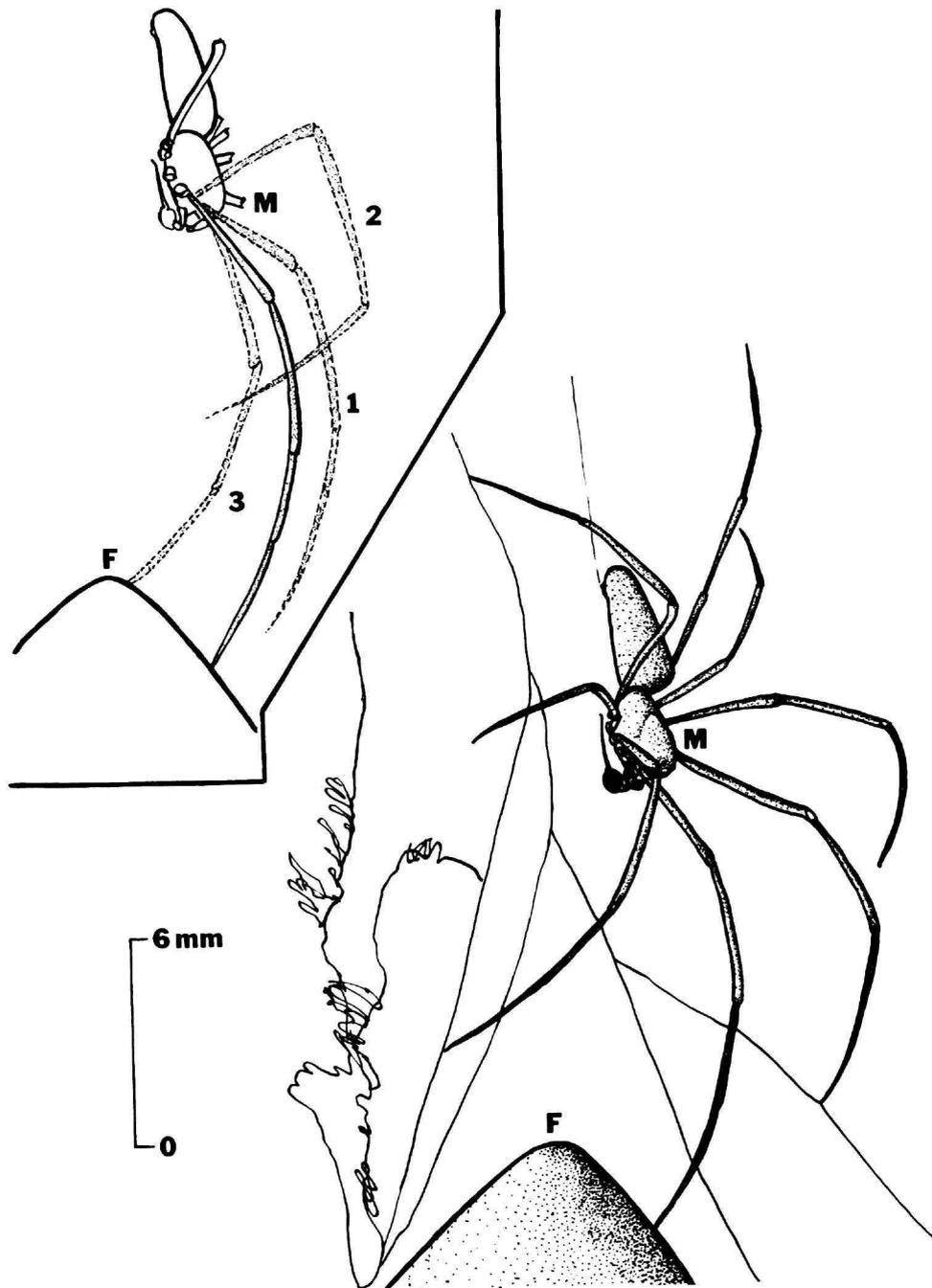


FIGURE 9.—Male *Nephila maculata* (M) gently touching the apex of the female's abdomen (F). (The inset shows the movements of the male's first left leg (1, 2, 3) during this activity (traced from frames of 8 mm film about 6 frames apart, filmed at 18 frames per second).)

rival). Males that have moved onto the female and commenced the prolonged direct stage of courtship seem to be interrupted less frequently than those at the approach stage, but such interruptions do occur and we saw one case of complete supercession. The male was displaced after at least one hour and 25 minutes on the female and one copulation (he had probably been there for a much longer period). The intruding male came down the web to the female, touched her right leg IV very briefly and then moved straight onto the abdomen; the male in possession jumped straight off the female to 20 cm below the hub. Note that a succession of males will mate with a female and aggressive interactions between them can determine, if anything, mainly the order of copulation. (There is a further possibility. We suppose that the female must eventually stop accepting males and intermale aggression may, therefore, actually prevent some males from mating.)

COURTSHIP.—Our further observations confirm the details of direct courtship given in our earlier paper and we have seen further instances of “opportunistic” mating in which the male copulated with a newly ecdysed female. Two new observations are of interest: we have found that males continue courtship into the night and have seen the female catch and kill a courting male. The males courting during the night were seen on a web (built on the side of a house) that was dimly illuminated by light from a window, so that we cannot say that the phenomenon occurs under natural conditions, but see no reason why it should not. The first and only example of the female seizing and killing a male came during a session in which the female had been courted and copulated with by a succession of males. Our observations on this female extended, with numerous breaks, from 10:30 AM to 10:40 PM (nightfall at 6:15 PM). After the second observed copulation of the day, male number 4 moved onto the female, went immediately to the epigyne, and without preliminaries attempted an insertion. The female bent at the waist, pushed the male forward to the jaws with legs I and II and bit him for 30–40 seconds. The male was then picked up in the tarsi of legs I and flicked away from the web with the typical leg movements used in discarding prey remnants after feeding or in the removal of an inedible item from the web (our field notes are somewhat less than objective—“lovely contemptuous rejection movements”). One hour and twenty minutes after

this incident another male was in copula with this female.

COPULATION.—Our recent observations on copulation in *N. maculata* make it evident that we made an erroneous assumption in our previous report and that other observers have made a similar mistake. We reported that copulations were brief and that though “such brief insertions may represent unsuccessful attempts” (Robinson and Robinson, 1973a:41) we imply that insertions of over a minute are normal. These were all we saw during our previous study. During our second study, we saw several very long insertions and have seen long insertions in three other species of *Nephila* and would guess that these are a regular feature of *Nephila* mating. We timed the following copulations: 12 minutes, 35+ minutes, 13 minutes, 21½ minutes, 12¼ minutes, 68 minutes, 48 minutes, 15 minutes. We think that short insertions may be typical of the stages leading up to long insertions and we simply missed the latter (due to confounding and impatience) during our previous study. None of the copulations that we saw ended in the female attacking the male, he simply withdrew and moved on to other activity.

TERMOREGULATORY BEHAVIOR

In our previous study we reported that *N. maculata* oriented itself in such a way as to minimize heat absorption when the sun was shining through the web (Robinson and Robinson, 1973a:64–65 and fig. 30). We subsequently discovered this and other postures in the behavioral repertory of *N. clavipes* in Panama (Robinson and Robinson, 1974). Our report of the thermoregulatory behavior of *N. clavipes* details the thermoregulatory postures that enable it to minimize heat absorption irrespective of the orientation of its web. We here report that *M. maculata* has an equally extensive repertory of thermoregulatory postures and shows no tendency to orient its webs normal to the direction of maximum insolation.

Spiders as Human Food

Bristowe (1932:392–393) reported that in Siam (?present-day Thailand) *N. maculata* is eaten as food, raw or roasted. The flavor, with salt, is said to be similar to raw potato and lettuce mixed. New

Guineans from several areas of the Central Highlands eat araneid spiders, particularly *N. maculata*, which is large and often plentiful, and *Cryptophora moluccensis*, which is fairly large and occurs in colonies (and so may be easy to collect in large numbers). *Nephila maculata* are collected alive and placed in the hollow of a bamboo stem 3"-4" in diameter and 18" long. During collecting, the open end of the bamboo is stoppered with a piece of folded banana leaf. Eventually, when sufficient fat adult females are obtained, the stoppered stem is put in the embers of a fire and left there for 10-15 minutes until the green bamboo is blackened. The spiders "split their skins" during the cooking process. They are then eaten, either entire (legs and all) or the abdomen is nipped off and the rest discarded. We ate several and found the flavor good and the texture in no way repugnant. Descriptions of food flavors always involve comparisons with familiar foods and can be misleading. Inevitably a fire-roasted food item has a smoky flavor predominant, but we both agree that *N. maculata* has also a nutty flavor (M.H.R. compares it to peanut butter without the objectionable consistency). We both ate spiders that were packed with eggs. *Nephila*

maculata (adult females) must be a good source of palatable protein in an area where protein sources are scarce. Gravid females weigh 3 grams or over and are, at times, abundant; they must be useful occasional food.

Conclusion

No synthetic summary is possible for a study that encompassed a number of disparate elements in the biology of a large invertebrate. We think that biological studies lose an essential element when they cease to be inductive and that the types of questions raised by aspects of this essentially supplemental study are worth pursuing further. For instance, the question of the ecological role of changing web sites is critical to our understanding of much of araneid biology, and the adaptive significance of various types of life history strategies are a potentially fertile area for further study. As we press further with studies of tropical spiders, we come to agree more and more with Robinson and Olazarri (1971:35) that "the problems seem limitless and the spiders remain an intellectual challenge."

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