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THE PREDATORY BEHAVIOR OF
THE GOLDEN-WEB SPIDER *NEPHILA CLAVIPES*
(ARANEAE: ARANEIDAE)

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INTRODUCTION

Details of the role of wrapping behavior in the predatory activities of *Nephila clavipes* (Linnaeus) were given by Robinson, Mirick & Turner (1969). Their account also gave broad details of the total behavior of this species. At that time, the publication of an exhaustive account of the predatory behavior of *N. clavipes* was intended and anticipated. Since then, however, the senior author has carried out studies of the behavior of other species of *Nephila* in Africa and Asia, and with co-workers is currently engaged in a study of the behavior and ecology of *Nephila maculata* (Fabricius) in New Guinea. It now seems appropriate for us to leave details of part of our work on *N. clavipes* for inclusion in a broad comparative paper and publish here those aspects which relate most directly to the main points cited in outline by Robinson, Mirick & Turner (1969).

This paper therefore presents a summary model of the predatory behavior of *Nephila clavipes*, based on the investigations of the present authors in the summer of 1968 and further experiments carried out by the senior author in 1969. We give emphasis to the investigations and experiments that led to establishing some of the major aspects of the model and leave detailed descriptions of behavior units and behavior sequences for inclusion in the projected comparative paper. We have also left consideration of the temporal aspects of the behavior sequences for inclusion in the later paper.

Materials and Methods

Our basic observations and some of our experiments were carried out with captive adult female spiders. The spiders were not confined to cages but were released in a large screened insectary at

the Barro Colorado Island research station of the Smithsonian Tropical Research Institute. We maintained a minimum of fifteen spiders in captivity during the period of study in 1968. The experiments carried out in 1969 required a larger number of spiders and we used free-living spiders in the Barro Colorado forest as well as a number of captive spiders. Even with access to twenty or more non-captive spiders it was necessary to use some spiders more than once in an experimental series; details of how these were manipulated to obviate the possible effects of experience is given below in the appropriate section. Captive spiders were collected from the same areas as the non-captives and all were of unknown age and previous experience.

We made repeated presentations of a number of different prey items in order to establish the basic patterns of the spider's behavior. This involved fifty presentations of each of seven prey types. These were chosen for their relevance to the natural diet of the spider (see later) and because they presented large differences in size, weight and type of activity after striking the web. We used the data obtained from these observations to prepare ethograms of the type used by Robinson & Olazarri (1971) and then used these ethograms as a basis for the integrated model. Fifty presentations of each prey item meant that a proportion of the spiders received the same type of prey more than once. In general we presented but one prey per spider each day. In an attempt to avoid any possible effects of experience we avoided successive presentations of the same type of prey. In all cases at least two days (usually more) intervened between one presentation and the next presentation of the same type. Usually another type of prey, or several other types of prey, would be presented between presentations of the same type. In addition we made presentations of all the prey types to a large number of free-living spiders as a check on the behavior of our captive spiders.

In the course of our initial observational work we presented the following prey items: moths (living & dead), grasshoppers (living), crickets (living & dead), *Tenebrio* beetles (living), dragonflies (living), *Trigona* sp. (living), pentatomids (living), and blowflies (living). Later when we attempted to elucidate the stimuli which the spiders were capable of detecting at various stages in the process of predation we used a number of experimental techniques involving modified insects in the form of 'dummies'. These techniques are detailed in the appropriate section below.

All the insects that we used were weighed and measured before being presented to the spiders. Where insects were presented dead

they were killed by freezing to avoid contamination by chemical killing agents. Behavioral observations were supplemented by cinematography and the duration of behavior units was recorded on a Rustrak multi-channel chart recorder.

NATURAL HISTORY

In Panama, and wherever we have encountered *Nephila clavipes* in South America (Colombia & Venezuela), the spider is most frequently found at the edges of forest clearings, alongside forest trails and across forest streams and watercourses. It thus apparently exploits areas within the forest that are in all probability flightpaths of insects. The structure, size, and siting of *N. clavipes* webs is consistent with the view that the spider specialises on prey that are in flight above the herb layer rather than moving about in it. Although the web may be sited with part of the prey capture area within the herb layer it is most frequently above this or stretched across gaps in the vegetation. The structure of the web has been described by Gertsch (1948) and Peters (1954, 1955). For its area, which is large, the web has a very fine mesh which is far less penetrable by small insects than the much smaller but coarse-meshed web of *Argiope argentata* (Fabricius), as was shown by Robinson, Mirick & Turner (1969). The web of the adult spider is not a complete orb but is U-shaped with the hub very close to the upper bridge thread. Kaston & Kaston (1953, p. 176) give an excellent figure of the *N. clavipes* web. Webs of several adult spiders are often built in close proximity and fairly large aggregations of the spider may occur in apparently favourable areas (Shear 1970, has commented briefly on this phenomenon).

The adult web is frequently equipped with a barrier web consisting of a complex of strong lines arranged in a non-symmetrical manner above and/or below the main plane of the orb. There is considerable variation in the structure of barrier webs. Robinson & Robinson (1970) have suggested that they may function as early warning devices enabling the spider to detect the approach of possible predators. Certainly the spider often responds to manipulation of the barrier web by escape or other forms of defensive behavior. Web renewal is not a daily occurrence, and in captivity the spider may only renew part of the web at a time. (This is also certainly the case with free-living *N. maculata* but we have not made extensive observations on web renewal by free-living *N. clavipes*).

Our observations on the natural prey of *N. clavipes*, although limited in scope, confirm the deductions based on web structure and siting i.e. that flying prey of small to medium size may be the

PREDATORY BEHAVIOR

1. The basic pattern

Figure 1 is a summary diagram of the complex of possible sequences of predatory behavior that we have observed to be given by adult female *N. clavipes* to a variety of prey presented in several ways. It has the same summary function that Figure 2 of Robinson (1969) had in relation to the behavior of *Argiope argentata* and is not meant to be a flow diagram or relate to any cybernetic conventions. It does, however, illustrate the temporal sequence and relationships between behavior units, their degree of association, and the effects of some stimuli on the course of the sequence. Like most models it is certainly much more simple than reality.

In the predatory behavior of *N. clavipes* alternative behavior units are available at several functional stages and the 'decision' to employ one or other of these is shown, on the diagram, to be the result of a discrimination. We recognise that in some cases our assumption of the basis (or bases) for the discrimination may be an oversimplification; this matter is discussed at the appropriate place in the text.

The diagram employs simple conventions. The behavior units are shown as circles connected by lines. The arrows on the lines show the direction of change from one behavior unit to the next. In the upper half of the diagram two conventions are used to denote 'choice' points. Some of the circles are divided into two halves by vertical lines so that two behaviors may follow the behavior shown by the circle. In addition, here and throughout the diagram, small square boxes on the lines connecting behavior circles represent places where behavior may be switched from one course to another. Dotted lines from oblong boxes suggest inputs to the system that are dependent on stimulus properties of the prey.

Behavior occurring up to first contact with the prey is shown in a much simplified form. The activity *spider on hub* (which could be amplified as 'spider at hub in predatory position waiting for prey') is represented as an ongoing activity by a vertical line beneath the behavior circle. If a prey item, or in fact any item above a certain weight, strikes the web the spider is alerted (the square box has an input from *prey strikes web* and an output to *spider alert*, this represents a diversion from the ongoing activity spider at hub). The overt behavioral change following impact may be a momentary increase in the flexion of the spider's legs prior to an almost immediate movement towards the prey or a more sustained adoption of this alert position.

After the spider has been alerted two things may occur. If the prey is in a state of sustained vibration the spider almost always makes an immediate approach to it. If on the other hand, the prey is immobile or merely making spasmodic movements the spider usually *plucks* the web. If the prey has remained in the web until the spider plucks, this behavior is likely to be followed by an approach to the prey (during which the plucking movement may be repeated). When the prey escapes after the initial alerting impact, the spider usually returns to its pre-alerted state *after* plucking.

As examples of the simplification involved in our model we can cite the following examples that occur in the fairly complex section that we have traced so far. Thus a further alternative behavior that can occur on the impact of prey is not shown. Instead of the spider being alerted it may show an immediate escape response. This usually takes the form of the spider running upwards from the hub, out of the web and onto the support lines (or even onto nearby vegetation). Similarly, if it did not result in an illegibly complex diagram, we could show at least three distinct approach-to-prey behaviors. There is a rapid, unhesitant, approach that is made to rapidly vibrating insects and a hesitant, much interrupted by plucking, approach to non-vibrating insects. In addition very large or very heavy insects are approached in a slow 'deliberate' manner, in which legs I & II are flexed far back over the prosoma in a very characteristic 'cautious' gait.

After arrival at the prey the spider may immediately attack without a perceptible pause, or may touch (with the tarsi) and palpate (with the pedipalps) the prey, before attacking. We have not shown these 'investigative' stages in our diagram.

There are three basic attack behaviors, all of which involve the use of the chelicerae. In no case have we ever seen *Nephila clavipes* (or any other species of *Nephila*, for that matter) use the strategy of attack wrapping. This matter is extensively discussed by Robinson, Mirick & Turner (1969). The three basic forms of biting attack are as follows:

1. An attack similar to the seize and pull out behavior of *Argiope argentata* (see Robinson & Olazarri, 1971). This is given to very small or light prey.
2. A long bite in which the bite is not immediately followed by pulling out movements but is sustained *in situ*. This long bite may be accompanied by a special posture in which legs I & II are raised off the web and the opisthosoma is raised at its apex so that the body presents a concave dorsal aspect.

3. The third attack strategy we call *bite & back off*. It consists of a rapid forward lunge, a short-duration bite and a rapid withdrawal to a distance at which the prosoma is well away from the prey. We have shown this behavior as a repeatable unit since the lunge, bite, retreat sequence may be repeated a large number of times (we have records of over 12 repetitions) before a sustained long bite ensues. In many cases, when this form of attack is employed, the spider can be seen to open the chelicerae until they are almost held horizontally, before making the rapid forward lunge that terminates in the bite.

The type of attack strategy that the spider employs seems to be largely determined by parameters of weight and/or size of prey; our experimental analysis of these factors is described later. We have not been able to determine what factor or factors mediate the decision to cease repetitions of bite & back-off and commence sustained biting. This process is not dependent on reduction of activity by the prey (that might be consequent on a series of bites) since it occurs in the spider's behavior towards large dead prey.

Behavior following the initial attack phase is somewhat more complex than is the case with araneids that are efficient at enswathing their prey in silk. Attack is almost always terminated by *pull-out* movements. The body of the spider is lowered, on flexed legs, during the biting attack and pulling out consists of strong extensions of the leg pairs. These result in the spider pushing down on the web and pulling up on the prey. Very small prey, adhering to a small area of viscid spiral, are quickly freed, as are lepidopterans which do not adhere strongly because of their loose wing scales (see Eisner et al 1964). Other prey may be subjected to repeated pull out movements before being freed. Prey that are not readily freed by pulling movements are wrapped in the web and then cut out by the spider. Robinson, Mirick & Turner (1969) called this *wrapping at the capture site, Type 1*. We have been able to show that the spider can be induced to wrap prey (in this way) if its pulling out attempts are blocked experimentally (see later). It seems possible that the pull out movements enable the spider to gauge the degree of adhesion of the prey to the web and that the 'decision' to continue pulling, or to wrap *in situ* and then cut out, is influenced by this information. A further complication arises from the fact that the spider may wrap, at the capture site, prey that have already been freed from the web by pulling (*Post-immobilization wrapping at the capture site, Type 2*, of Robinson, Mirick & Turner 1969).

(The functional interpretation of these behaviors is that pulling prey from the web results in less web damage than wrapping *in situ* and subsequent cutting out. This can easily be substantiated by comparing the web damage resulting from the two techniques of prey-removal. Wrapping after removal from the web has a trussing effect which reduces the bulk of the prey and may facilitate its transportation to the feeding site.)

After the prey is freed from the web, and trussed in some cases, it is transported to the hub of the web. Here the spider employs one of two techniques. It may either carry the prey held in the chelicerae, perhaps supported by one or both of the first legs, or it can carry the prey package on a silk thread hanging from the spinnerets and supported by one or both of the fourth legs. Prey carried to the hub in the jaws are wrapped on arrival at the hub and then suspended from the hub silk as the spider turns to assume its predatory posture. Prey that are carried suspended on silk are not wrapped on arrival at the hub but are suspended. *Nephila clavipes* does not store prey at the capture site but carries all prey to the hub where it is hung until previously caught prey are consumed. Very small prey, carried to the hub in the jaws, may not be wrapped on arrival (but prey as small as stingless bees — 10-30mg in weight — are regularly wrapped on arrival at the hub).

The return to the hub from the capture site is carried out in a forwards direction after the spider has turned to face the hub at the capture site. (*Nephila maculata* frequently backs slowly up the web, without turning, when carrying prey in its jaws.) When the spider has assumed its normal head-down predatory position it may undertake more or less extensive grooming activities before taking up the prey in its jaws and anterior legs. These are very similar to those that Robinson & Olazarri (1971) described for *Argiope argentata*. Prior to the commencement of feeding the spider often carries out extensive manipulations of the prey during the course of which small bites are given to region after region of the prey body.

We have a few records of prey being wrapped after removal from the web and then being transported in the jaws. Most prey that are trussed in this way are then carried suspended on silk behind the spider. Heavy prey are also carried in this way, but as in the case of *Argiope argentata*, the weight threshold for the changeover from carry in jaws to carry on silk varies from individual to individual, and from time to time within individuals (see Robinson 1969, p. 170-1).

2. Experimental investigations

To investigate the possibility that certain aspects of the predatory pattern are responses to relatively simple stimuli we carried out a number of investigations using 'modified' insects as dummies. We manipulated the size and weight of some insects and also modified such parameters as the strength of their adhesion to the web. We were able to compare the responses of the spiders, at various stages in the predatory process, to such dummies, using adequate controls or using their response to unmodified insects as a baseline.

(a) *The bite & back-off attack behavior*

Our observations on the responses of *N. clavipes* to a range of prey items (see page 123, above) showed that the bite & back-off attack behavior was only given to large and heavy prey. Since all of these that were presented to the spiders were alive there was a possibility that the response could be to size, weight or specific activity of large heavy prey, or a combination of any of these factors. Preliminary tests showed that the response was given to dead (immobile) prey so that although it remained possible that activity could enhance the response it was not the important stimulus. We then decided to manipulate the parameters of size and weight. Using small acridiids (25-30mm, 400-550mg) as prey, we added lead shot to some to double the weight (approximately) increased the length of others by inserting a wooden tooth pick in line with the long axis, and with the third group we increased both the length and the weight. The dead dummies were presented at right angles to the radii of the web. This ensured that the weight of prey was distributed over as wide an area of web as was covered by the length of the insect (or the insect + toothpick). In fact it meant that the maximum dimension of the prey was at right angles to the spider as it approached across the web. The insects were vibrated electrically at 250 cps until the spider left the hub on its predatory excursion. At that stage the vibrator was switched off so that the prey was motionless when the spider came in contact with it. The results of this experiment are shown in Table 1. In addition to the form of biting attack we noted whether the spider raised legs I & II off the web during the attack (see page 127, above) and whether the prey was wrapped *in situ*, or *free wrapped*, after the attack. There was a significant increase in leg raising during the attack in the case of the weighted insects. There was a slight numerical, but not a statistically significant, increase in the number of attacks on the long dummies that involved leg raising. There were three attacks out of ten, on heavy insects, that involved the bite and back off behavior.

Table 1. Acridiids weighted and unweighted, lengthened and normal.

Behaviors.		Prey A	Prey B	Prey C
1. Bite and back off.	yes	4	1	1
	no	6	9	9
2. Bite, legs raised.	yes	9	4	2
	no	1	6	8
3. Wrap in web.	yes	7	7	2
	no	3	3	8

Ten spiders chosen at random from wild population receive A, ten captive spiders B ten wild spiders C. A is acridiid with weight added and lengthened (total weight ca. 1000 mg length 70 mm). B is acridiid lengthened to 70 mm weight 400-550 mg. C is unmodified length 25-30 mm weight 400-550 mg.

Statistical analysis—Fisher's exact probability: differences between A & B, A & C, B & C for Bite and back off are not significant; difference between A & B significance level 0.05, difference between A & C significance level 0.005, no significant difference between B & C, all for Bite, legs raised; for wrap in web difference between A & B and B & C level of significance 0.05.

All levels one-tailed

Although this number is not statistically significant we regarded the occurrence of this behavior in attacks on the weighted insects as being highly suggestive. We then carried out a further series of experiments, using similar sized acridiids, in which we quadrupled their weight.

We found that very heavy dummies of small size often dropped out of the webs before the spider reached them. We therefore increased the length of both experimental (very heavy) dummies and controls (normal weight) by adding the toothpick to the insect. This worked in a perfectly satisfactory way to distribute the weight over a greater number of web members. As before, we vibrated the dummies until the spider commenced its predatory excursion. The results are given in Table 2. There is a statistically significant effect of weight on the occurrence of the bite & back-off attack behavior. Note that we did not induce this attack behavior in all the presentations; we consider that with large, heavy active insects there may be some heterogeneous summation. We attempted to test for the possible additive effect of activity, at the moment of contact

Table 2. Acridiids weighted and unweighted all lengthened to 70 mm.

Behaviors.		Prey A	Prey B
1. Bite and back off	yes	8	2
	no	4	10
2. Bite, legs raised	yes	11	4
	no	1	8
3. Wrap in web	yes	12	11
	no	0	1
4. Quit the web	yes	4	8
	no	8	4

Prey A weights 1700-1800 mg.

Prey B weights 400-550 mg.

Statistical analysis — Fisher's exact probability: Difference between A & B for bite and back off, level of probability 0.025; difference between A & B for bite, legs raised, level of probability 0.01; difference between A & B for wrap in web not significant; difference between A & B for quit the web not significant.

All levels one-tailed

with the prey, by tapping weighted and control dummies from behind the web. (We did this when the spider was in tarsal contact with the prey and before it had attacked). This led to a numerical, but non statistically significant, increase in the number of bite & back off attacks. It is very difficult to standardize simulated prey movements.

A by-product of these experiments was the suggestion that the wrapping of prey *in situ* might be a response to the failure of the spider to *pull out* the prey. The number of wrap *in situ* responses was significantly greater in the case of the artificially lengthened prey used in the first experiment. These were, to the observer, obviously a much greater problem to the spider at the pull out stage. We therefore decided to carry out some experiments to see if increasing the adhesion of the prey to the web, or its 'apparent' adhesion, would affect the spider's behavior at this stage in the predatory process.

(b) *Pulling out and wrapping behavior*

As a first simple experiment we used domestic crickets as prey. We simply presented 20 dead unmodified crickets and scored the

Table 3. Wrap *in situ* behavior (i). Experiment with 'winged' and normal crickets.

	Wrap in web	Pull out alone	No result
Winged crickets	18	1	1*
Normal crickets	1	19	—

* Spider disappeared before completion of pair.

Behavior to live dragonflies matched in weight with crickets.

	Wrap in web	Pull out alone
Time of persistent pull out attempts (before inception of wrap <i>in situ</i>) averages.	20	0
	Winged crickets	Dragonflies
	194.5 secs	68.7 secs

number of them that were wrapped *in situ* and the number that pulled out and subsequently wrapped at the hub. We then matched the sizes and weights of these crickets to a second set to which we attached thin paper 'wings' at right angles to the long axis of the body. These dummies were presented in such a way that the 'wings' greatly increased the surface adhering to the web. We then scored the number of wrap *in situ* and wrap at hub responses. The results are shown in Table 3. The increased adhesion resulted in a highly significant increase in the number of prey that were subjected to being wrapped and then cut out rather than being pulled out. The spiders made very persistent attempts to pull out the winged crickets, two succeeded and the remainder averaged 194.5 seconds of abortive pulling-out attempts. This is very interesting since the spiders started wrapping dragonflies (of lower weight) after only 69.7 seconds of pulling out attempts. (Testing these two sets of data—pull out times for dragonflies and winged crickets, with the Mann-Whitney U test, shows that the difference is significant; p is less than 0.001).

We also carried out a further experiment on this aspect of the predatory process. In this case we passed a thread through the thorax of the crickets and presented twenty crickets with the thread hanging below the insect and twenty in which we passed the thread through the web and then held it from behind. In the second case we were able to prevent the spider from pulling the cricket from the web by exerting a force in the opposite direction. The results are shown in Table 4. Again the spiders that were unable to pull the prey from the web wrapped it at the capture site and then cut

Table 4. Wrap *in situ* behavior (ii). Experiment with stringed crickets.

	Wrap in web	Pull out alone	Reject
Experimentals	19	0	1
Controls	2	18	0

Experimentals were held by string from behind the web.

it free. In this experiment the spiders made extended and persistent efforts to pull the prey before initiating the wrapping behavior.

The process of *free wrap* proved to be much more difficult to elicit under experimental conditions. We had observed that this behavior occurred most frequently in the treatment of butterflies and moths. These could be freed from the web by pulling but were, nonetheless, bulky and cumbersome insects. Other cumbersome insects such as dragonflies adhered strongly to the web, were wrapped and then cut free of the web, and were thus largely trussed and packaged at this stage. They were not therefore suitable for experiments on free wrap behavior. We reasoned that free wrapping was a response to insects that could be removed from the web by pulling but were too bulky to be transported without becoming entangled in the web. The spider makes movements during the pulling out process that could enable it to gauge the bulk of the prey as it is removed from the web. These movements involve legs I & II. The tarsi are passed along the adhering margins of the prey and ease them away from the viscid elements of the web. Our observations on the removal of butterflies and moths from the web suggested that the cumbersomeness of detached prey was, to a large extent, a function of apparently chance factors. Thus it was partially dependent on the point on the prey body at which the spider exerted the pull out movements (i.e. the point at which the prey was held in the jaws), and partially a result of the orientation of the wing and body surfaces in relation to the sticky elements of the web. (Some idea of the complexity of these factors can be gained by visualizing the process of picking up a randomly cast down book, by the spine, from a sticky surface. A winged insect, like the book, may open in a variety of ways, depending on where it is seized and where it is stuck down.)

Starting from this point we tried to present a series of moths to the spiders with the entire dorsal surface of their wings adhering to the web but at differing orientations to the radii (and therefore the hub and the spider). We hoped that these would be seized at different points on the body and that our sole experimental variable

would be the 'apparent' bulk of the prey beneath the spider during the prey-removal process. Our aims proved to be extraordinarily difficult to achieve and the results, although suggestive, are not convincing. In an attempt to manipulate the bulkiness of a series of presentations of butterflies (*Anartia* sp.) we trimmed the wings of half of them down to small (5mm long) stubs. We then matched the weights of pairs of intact and mutilated specimens and presented the pairs, successively, in random order to the spiders. Only the intact insects elicited any free wrap behavior, and only 24% of these were so treated. This result is not statistically significant. If the number of free wrap occurrences is compared not with the total number of presentations of intact butterflies, but with that number less the number wrapped *in situ* or subjectively scored as presenting below average bulk on removal from the web, the result is significant. However this depends on our subjective assessment of the bulk and is unsatisfactory.

These results do not enable us either to accept or reject, with confidence, the hypothesis that the free wrap response is related to the bulkiness of the prey after its removal from the web. We have yet to design an adequate test for this.

DISCUSSION

A number of features of the predatory behavior of *Nephila clavipes* are of interest from the comparative standpoint. The most important of these, in our view, are the total reliance of the species on biting, as an attack strategy, and the fact that the spider does not store prey in the web at the capture site. Both these features represent marked differences from the behavior of araneids belonging to the genera *Argiope*, *Araneus* and *Eriophora*. Reliance on attack (immobilization) wrapping, as the principal means of attack, probably extends to a much greater number of araneid genera.

These aspects of the predatory behavior of *N. clavipes* have been discussed in some detail by Robinson, Mirick & Turner (1969). These authors suggested that "advanced" spiders would obtain at least two advantages from the addition of immobilization wrapping to their behavioral repertoire. They would be enabled to attack large and/or dangerous prey without closing to the potentially dangerous contact distance involved in biting, and also could achieve a considerable economy in time spent at the capture site in subduing the prey. The bite & back off attack behavior, that we have described for *N. clavipes*, immediately suggests to the observer that it is a danger-avoiding device. Our experiments on the stimuli that

evoke this behavior gave results which are entirely consistent with this view. In fact increasing the weight of the prey eventually results in the suppression of attack behavior and its supersession by escape. We obtained evidence that *N. clavipes* would lose some large prey by escapes, during the prolonged process of a bite & back off attack. Prey of similar size presented to the much smaller *Argiope argentata* were not lost during wrapping attacks in any of our presentations. (The senior author has obtained similar results in comparing the performance of *Nephila maculata* and *Argiope aemula* (Walckenaer), dealing with large acridiids and melonlonthid beetles.) We have also recorded injuries inflicted on *N. clavipes* during biting attacks on prey that had biting mouthparts and have one record of injury following the defensive kicking of an acridiid. The economy in time spent at the capture site that is a potential consequence of attack wrapping was examined in detail by Robinson, Mirick & Turner (1969), who suggested that a major factor in this economy was the ability of the spider to leave an attack-wrapped prey in situ after delivering a short bite. These authors argued that once the prey was wrapped the spider could safely leave it and not transport it to the hub until the bite had taken effect. With biting attacks, on the other hand, the bite could not be terminated until the prey had been safely subdued by its effects. The economy in time that results from this process is greatly exaggerated if one compares time spent in bite & back off attacks with time spent in wrapping attacks on similar prey by other spiders. (This comparison will be made in the projected comparative paper; it was not made by Robinson, Mirick & Turner (*ibid*) because the data for the attacks of *Argiope* species on very large prey was not then available).

It is interesting that although *N. clavipes* wraps prey at the capture site it does not store them there. Once this type of wrapping behavior has evolved it would seem but a short step to utilize it to enable the spider to interrupt the predatory process after the attack phase and defer the removal of the prey from the web, and its transportation, until later. This step, according to Robinson, Mirick & Turner (*ibid*) would be advantageous in circumstances where large numbers of prey arrived in rapid succession, or where prey left at the hub during an attack might be in danger of being stolen by kleptoparasites in the absence of the spider. At the time these authors suggested that *N. clavipes* may transport all prey to the hub because the depredations of kleptoparasites might be more difficult to detect if prey were stored at a number of capture sites in a

very large web. The arguments dependent on the effects of kleptoparasites are not easy to resolve. We have seen prey stolen from the hub, during the absence of the spider, on many occasions. We have also seen *N. clavipes* respond to, attack, and eat, kleptoparasites that were moving about near to the periphery of the web. Other hypotheses to explain the absence of capture-site food storage by *N. clavipes* include the possibility that this spider has not evolved a sufficiently efficient wrapping technique to safely allow the storage of prey *in situ*, or that the presence of prey packages in an already fine meshed web might render it more conspicuous, and hence avoidable, to flying prey.

It seems worth stressing the fact that *N. clavipes* can be induced to wrap prey *in situ* if these are made difficult to remove from the web by pulling. This simple function of post immobilization wrapping at the capture site may have been obscured by the fact that such wrapping can serve other functions in the predatory strategy of other araneids. The function of simplifying the safe removal of prey from the web seems to us, on *a priori* grounds, to be basic and probably primary. Similarly the existence of free-wrapping behavior suggests that the trussing or packaging function of wrapping is an important one in its own right, and not merely the useful by-product of a process serving another function. Both these opinions derive from our study of the behavior of *N. clavipes*, and, as far as we know, were not anticipated by earlier studies of more "advanced" araneids.

If we now consider the model shown in Figure 1 our earlier comment that this represents a very considerable simplification can now be expanded. We have detailed some of the behaviors that are not included in the model on pp. 132-134. In our account of the experimental side of our studies it is obvious that the investigation of the effect of external stimuli on the course of predatory sequences is not complete. Although we have shown that some behavior units can be brought into play in response to simple stimuli we have not shown that these are the only effective stimuli in all cases. We have made no progress at all in investigating the effect of internal factors on the behavior of the spider. In all these respects the model is inadequate, although it is already quite complex.

We have also ignored any discriminations that may be involved in the termination of acts of behavior after they are brought into play. The spider must, for instance, both start and stop the process of bite & back off, and start and stop the process of pulling out the prey. Peters (1931, 1933a, 1933b), in elegant studies of the behavior

of *Araneus diadematus*, was able to show that the change in stimulation brought about as a result of one behavior could be the trigger for the next behavior in the sequence. This approach has not yet been made in the case of *N. clavipes*. It should be productive.

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