THE PREDATORY BEHAVIOR OF *CYRTOPHORA*
(ARANEAE: ARANEIDAE)

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ABSTRACT

Units of predatory behavior, described in four species of *Cyrtophora*, include resting positions, jerking and tensing of the web, web shaking, prey immobilization, cutting and pulling out, transportation to the hub and manipulation of the prey at the hub. With the exception of web-shaking behavior, all units of behavior are of the "advanced" type that occurs also in spiders of the genera *Argiope, Araneus* and *Eriophora*. Four different attack sequences are given to different prey types. Two of these involve immobilization by biting and two immobilization by wrapping. Prey are transported to the hub either on a silk thread or in the chelicerae. The predatory behavior of *Cyrtophora* differs from that of *Argiope* and *Eriophora* in the following respects: (a) the spider does not maintain dragline connection with the hub, (b) immobilization wrapping is generally restricted to beetles, pentatomid bugs, and large insects, (c) prey are never left in the web after immobilization, but always carried immediately to the hub, and (d) "Rundgang" behavior, involving multiple attachments of wrapped prey to the hub, was not observed. I suggest that *Cyrtophora* has evolved from an *Argiope*-like araneid in which prey immobilization by wrapping already existed. The modifications of this advanced-type predatory behavior can be related to the specialized web of *Cyrtophora*.

INTRODUCTION

Spiders of the genus *Cyrtophora* (Araneidae) have a specialized orb web (Kullmann 1958, 1959, Lubin 1972, 1973, Blanke 1972) which consists of a nonsticky horizontal sheet with an irregular barrier web above and below, also made of nonsticky silk (see Lubin 1973: Fig. 1). The sheet is a fine-meshed orb web, composed of radii and a nonadhesive structural spiral, but lacking the typical araneid viscid spiral. Directly below the sheet is a "free space" with few thread attachments to the sheet's undersurface. The "hub" of the orb is open, of irregular shape and variable in size. I have argued that because *Cyrtophora* webs are strong, durable and infrequently renewed, they are therefore well adapted to open habitats where they are exposed to heavy rains and/or strong winds (Lubin 1973).

It seemed probable that the specialized web of *Cyrtophora* would be associated with some interesting modifications of the spider's prey-capture behavior since an effective attack through a close-meshed sheet presents different mechanical problems compared to attacks in ordinary orbs. On the other hand, it has been shown that prey-capture

behaviors of araneids are relatively conservative within genera and similar patterns often occur in closely related genera (Robinson 1975). Since the taxonomic affinities of *Cyrtophora* within the Araneidae are obscure (Kaston 1964, Kullmann 1958, Blanke 1972), I felt that a study of predatory behavior might shed some light on the relationship of this genus to other araneids.

The study concentrated mainly on the functions and variability of predatory behavior patterns within the genus *Cyrtophora*. Mechanisms, or causation, and adaptive values of these behaviors were not tested in most cases and are, therefore, largely speculative. General knowledge of the biology of these spiders (Lubin 1972, 1973, 1974) and detailed studies of the prey of *C. moluccensis* in nature (Lubin, unpublished) have aided in interpreting the functions of the predatory behavior patterns.

Robinson and Olazarri (1971) divided the prey-capture behavior of araneid spiders into five functional stages: (1) detection and location of prey, (2) discrimination of prey type, (3) prey immobilization, (4) transportation of prey to the feeding site, and (5) manipulation of prey and feeding. I have emphasized the patterns of prey immobilization and transport to the hub, as a great deal of variation occurs in these behaviors. The behaviors associated with prey detection and location and discrimination of prey type are not easily discerned; these aspects are treated less thoroughly.

MATERIALS AND METHODS

Four species of *Cyrtophora* were studied during 1970-71: *C. citricola, C. moluccensis, C. cylindroides* and *C. monulfi.* Details of size, habitat and study locations of these species are given in Table 1 and Lubin 1973, 1974. All species concerned have similar web structure. *Cyrtophora monulfi* has, in addition to the web, a conical, silken retreat above the hub, where it rests during the day (Lubin 1974: Plate 3). *Cyrtophora citricola* occasionally builds a retreat of dead leaves in the upper barrier web above the hub (Kullmann 1958, Blanke 1972). All investigations on *C. citricola, C. monulfi* and *C. moluccensis* were performed on field populations. *Cyrtophora cylindroides* were collected in the field and tested in the laboratory.

Live insects of various types were presented individually to adult female spiders. Insects tested were blowflies (Calliphoridae), fruitflies (*Drosophila* sp.), stratiomyid flies, moths and butterflies, katydids (Tettigoniidae), grasshoppers (Acrididae and Tetrigidae), dragonflies, pentatomid bugs, large scarab beetles (Melolonthinae), and weevils (Curculionidae). In most cases, with the exception of moths, butterflies and grasshoppers, insects within a category were of the same species. A weight range was established for each category of prey (Table 2). All insects tested on *C. moluccensis, C. cylindroides* and *C. citricola* came from habitats in which the spiders themselves were found. The natural prey of *C. moluccensis* included insects from all the above categories (Lubin, unpublished). The insects tested on *C. monulfi* were probably less representative of its natural prey, which may be restricted to small grassland insects.

In testing spiders with various insects, I alternated the different types of prey, and in no case was a spider tested with more than one prey per day. However, with the exception of the caged *C. cylindroides*, I had no record of the previous prey of the experimental animals. Some of the variation observed in predatory responses may have been due to differences in levels of hunger or previous experiences of these spiders.

Table 1.–Study sites, habitats, and sizes of four species of *Cyrtophora*.

Species	Length (mm)	Weight (mg) ± SD	Study Sites	Habitat	Habits
C. citricola (Forskal)	15 (Levi and Levi, 1968)	No data	Near Legon, Ghana ORSTOM Botanical Garden, Tananarive, Malagasy Republic Lamto, Ivory Coast	Roadside and wooded savanna Cacti and ornamental shrubs, fences,	Colonies, occasionally solitary. Same
C. moluccensis (Doleschall)	20-28 (Chrysanthus, 1959)	1163±415 n = 33	Wau and Bulolo, Morobe Province, Papua New Guinea	Wooded savanna Clearings and areas of human habitation: fences, electricity wires, ornamental trees and shrubs; roadside vegetation, forest edge.	Same Colonies, occasionally solitary.
C. cylindroides (Walckenaer)	15 (Chrysanthus, 1959)	326±14 n = 27	Lae, Bulolo, Morobe Province, Papua New Guinea	*Araucaria* plantations, lowland rainforest to 1000m elev.	Solitary
C. monulfi (Chrysanthus)	8-10	58±15 n = 10	Wau, Lae, Morobe Province, Papua New Guinea	"Kunai" (*Imperata* spp.) grassland, roadside vegetation, fences and ornamental shrubs.	Solitary or aggregations

Prey-capture behaviors were analyzed in terms of functional units. Commonly occurring sequences of these behavior units were established for each of the four species. Prey-capture sequences and durations of behavior units within a sequence were recorded for each prey-capture incident. Super-8 mm films were made of predatory sequences of *C. moluccensis, C. cylindroides,* and *C. monulfi* with a variety of prey. Descriptions of behavior units are based partly on analyses of these films, and partly on direct observation. The terminology and methods of description and analysis of behavior sequences are similar to those used by Robinson and Olazarri (1971). Whenever possible, I have compared behavior units and sequences of prey-capture behaviors of *Cyrtophora* with those of other orb weavers.

CYRTOPHORA PREDATORY BEHAVIOR

The general description of the prey-capture behavior of *Cyrtophora* given below is based mainly on the behavior of the three larger species: *C. moluccensis, C. citricola* and *C. cylindroides.* Differences in behavior between the four species studied are detailed later.

The spider rests at the hub or in the retreat (*C. monulfi*). An airborne insect striking the upper barrier web either drops onto the horizontal net or remains entangled in the upper barrier web. The prey produces vibrations in the web upon impact and/or during struggling (Suter 1978), and these are transmitted via web elements to the hub (Walcott 1963). Some discrimination of prey characteristics on the basis of vibration frequencies may occur at this stage (Walcott and Van der Kloot 1959, Robinson and Olazarri 1977), although accurate discrimination of prey type is unlikely (Suter 1978). Location of prey in the web often involves pulling and jerking the net or threads of the upper barrier web with legs I (the spider's four pairs of legs are numbered here I-IV from front to rear).

If the prey falls on the net, the spider runs out to it along the undersurface and, in many instances, touches it with legs I and/or with the palps before attacking. Chemoreceptors and tactile receptors abound on the tarsi and palps of araneid spiders (Foelix 1970a, 1970b), suggesting that discrimination of prey type may occur at this stage as well. Peters (1933) and Robinson (1969) obtained evidence for tactile discrimination at this stage by showing that both *Araneus diadematus* and *Argiope argentata* could distinguish between lepidopterans and other insects after touching them with the legs and palps.

Insects are immobilized by biting or by wrapping in silk, or by a combination of the two methods. If an insect remains caught in the upper barrier web, the spider runs out under the sheet and shakes it violently until the prey falls on the sheet. Insects that cannot be dislodged in this manner are attacked and immobilized in the upper barrier web. The barrier web may be reached by climbing through the open hub, climbing over the outer edge of the sheet, or by cutting a hole in the sheet and climbing through it. Insects are rarely attacked in the lower barrier web.

After immobilization, prey are pulled out or cut out of the sheet or barrier web with the chelicerae. Post-immobilization wrapping at the capture site, and/or biting and manipulation of prey in the chelicerae may occur at this stage. In some instances, the spider rests under or near the prey and cleans its palps, chelicerae and legs prior to transporting the prey to the hub. Prey are carried to the hub on the undersurface of the net in the spider's chelicerae, or dangling from the spinnerets on a silk thread.

Prey carried to the hub on silk are generally suspended at the hub by a thread, or wrapped (post-immboilization wrap at the feeding site) and suspended. Insects that are carried in the jaws are retained in the jaws, or wrapped and suspended at the hub. Pre-feeding manipulation of prey and actual feeding occur at the hub.

As noted previously by Kullmann (1958), *Cyrtophora* species do not leave a dragline behind them while moving under the sheet. This is unlike all other araneids, which maintain dragline connection with the hub during prey capture.

DESCRIPTION OF BEHAVIOR UNITS

Resting Positions

Several resting positions occur in the species studied.

Rest under hub.—The spider rests under the hub, with all legs in contact with the horizontal net. *Cyrtophora cylindroides* always rests in this position, as do *C. moluccensis* and *C. citricola* individuals that lack egg sacs. *Cyrtophora citricola* and *C. moluccensis* females with recent egg sacs assume a modified rest-under-hub posture, in which legs IV touch the egg sacs (Figure 1). This position is assumed at night and during part of the
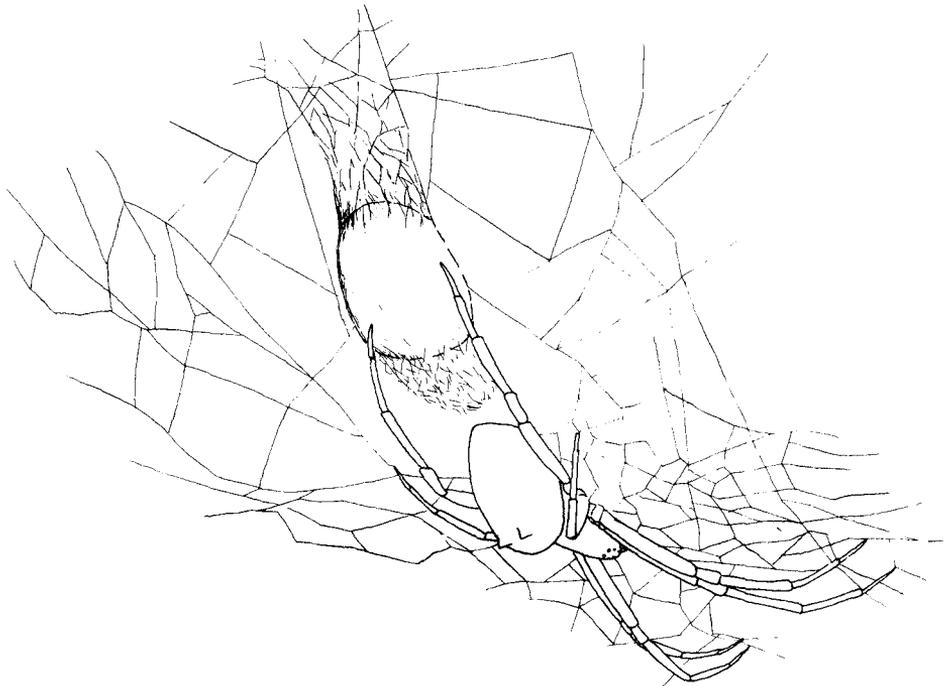

Fig. 1.–*Cyrtophora moluccensis* adult female with egg sac in rest-under-hub position. Note that legs IV are holding onto the egg sac while legs I and II are under the web in a position to monitor vibrations from the net.

day. When resting under the hub, the spider is in maximum contact with the horizontal net and is probably in the best position for receiving web vibrations.

When disturbed, *C. citricola* assumes a cryptic position which involves pulling all the legs inward toward the body, thereby obscuring the typical spider-like outline. Another small, unidentified species of *Cyrtophora* in New Guinea (sp. "D"), has a similar cryptic resting posture.

Cyrtophora monulfi leaves its retreat and rests under the hub at night, presumably when its predatory activity is most intense and/or when the danger from visually orienting predators is least.

Rest under egg sac.—*Cyrtophora citricola* and *C. moluccensis* females with egg sacs assume a resting posture under the egg sac throughout most of the day (Lubin 1974: Figure 2). In this position, the last two or three pairs of legs rest on the egg sac, while legs I or legs I and II touch the horizontal net or threads of the barrier web above the hub. Defense of egg sacs against diurnal parasites is important in *C. moluccensis* colonies (Lubin 1974) and contact with the egg sac is maximal in this position. The spider may, however, be less capable of receiving stimuli from prey in the web. *Cyrtophora cylindroides* females with egg sacs were never observed in this posture.

Rest in retreat.—Of the species studied, only *C. monulfi* consistently builds a retreat and rests in it during the day. The retreat is conical, with the open end facing downward toward the horizontal net, and is made entirely of silk. The spider can close off the open end of the retreat by pulling the lower edge inward with legs I (Figure 2). Normally, however, the retreat is open and the spider rests in it with legs I touching the threads of
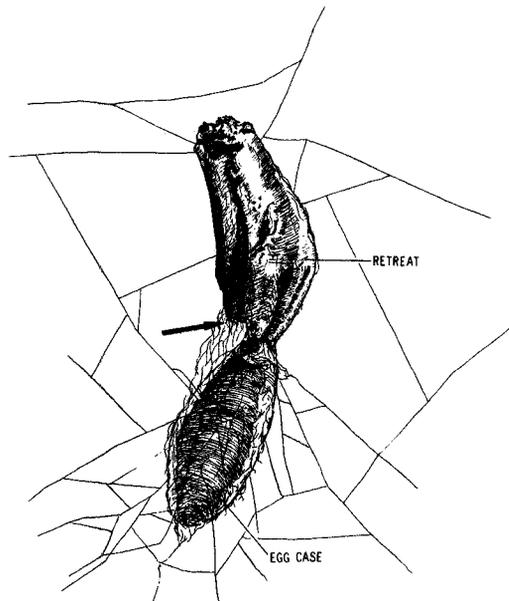

Fig. 2.—Conical silk retreat of *C. monulfi* adult female with egg sac attached to the lower edge. The spider closes off the mouth of the retreat by pulling the lower lip inward with the first pair of legs. Arrow points to lip of retreat.

Table 2.–Comparison of attack and immobilization sequences with different types of prey in 4 species of *Cyrtophora*. Frequency of occurrence, in percent, of the different sequences are shown after each sequence. n = sample size. Weight ranges of prey are, in mg: Lepidoptera 25-150 (*C. moluccensis*), 50-150 (*C. cylindroides*), 15-100 (*C. monulfi*); fruitflies c. 15; blowflies 50-60; stratiomyid flies 100-120; orthopterans 100-175 (*C. moluccensis*, *C. cylindroides*), 12-15 (*C. monulfi*); dragonflies c. 150; scarab beetles 500-1000; weevils c. 35; pentatomid bugs c. 35. Prey given to *C. citricola* were not weighed, but were similar in size to prey given to *C. cylindroides*. (A = modified sequence, see text.)

Attack sequences

Prey type	C. moluccensis		C. citricola		C. cylindroides		C. monulfi	
Lepidoptera	bite/wrap	83	bite/wrap	81	bite/wrap	90	bite/wrap	100
	bite	8	bite	9	bite	5		
	wrap/bite	8	wrap/bite	5	wrap/bite	5		
			wrap	5				
	n = 24		n = 21		n = 20		n = 25	
Blowflies	bite/wrap	76	bite/wrap	91	bite/wrap	77	bite/wrap	100
	bite	20	bite	5	bite	14		
	wrap	4	wrap/bite	5	wrap/bite	9		
	n = 25		n = 22		n = 22		n = 25	
Stratiomyid flies	wrap/bite	37						
	wrap	30						
	bite/wrap	30						
	other	3						
	n = 30							
Fruitflies			bite	100				
			n = 20					
Orthopterans	wrap	45	bite/wrap	42	bite/wrap	68	bite/wrap	59
	bite/wrap	31	wrap/bite	37	wrap/bite	16	wrap/bite	41
	wrap/bite	21	wrap	21	wrap	16		
	bite	3						
	n = 29		n = 19		n = 25		n = 22	
Dragonflies	bite/wrap	58						
	wrap/bite	27						
	wrap	15						
	n = 26							
Scarab beetles	wrap/bite	92[A]						
	wrap	8						
	n = 13							
Weevils	wrap	63						
	wrap/bite	32						
	other	5						
	n = 19							
Pentatomid bugs					wrap	85		
					bite/wrap	10		
					wrap/bite	5		
					n = 20			

the barrier web above the hub. The spider responds to vibrations in the web even when in its retreat. The egg sacs are suspended from the edge of the inner wall of the retreat and are well camouflaged (Figure 2).

Hang at hub.–During midday, when the sun is high individuals of *C. moluccensis* hang from the hub by legs IV, or III and IV (Figure 3). Spiders position themselves so that the dorsoposterior side receives the maximum insolation, while the rest of the body is shaded.

In this position the spider may be exposing a minimal surface area to the sun. When mirrors and shades were used to change the direction and angle of insolation, the spider reoriented to maintain its original position with regard to the "new" sun. These observations strongly suggest the presence of behavioral regulation of body temperature. Blanke (1972) observed this posture ("Hitzestellung II") in *C. citricola* when the spider was in direct sunlight at ambient temperatures above 31°C. Behavioral thermoregulation has been described in other web-building spiders, such as *Nephila clavipes* in Florida and Panama (Krakauer 1972, Robinson and Robinson 1974, 1978), *N. maculata* in New Guinea (Robinson and Robinson 1973), the linyphiid *Frontinella communis* (Pointing 1965), and a number of other araneid species (Robinson and Robinson 1978). Mechanisms for increasing heat loss or reducing heat gain by behavioral means occur commonly in terrestrial invertebrates that face repeated, high radiant heat loads. *Cyrtophora moluccensis*, with its typically exposed web, is most certainly included in this category.

   Cyrtophora monulfi and *C. cylindroides* were not seen to hang from the hub. The white silk retreat of *C. monulfi* protects it from direct insolation, and may be an adaptation to the grassland habitat. *Cyrtophora cylindroides* is a shade-dwelling forest species and its webs never receive prolonged direct sunlight. The average midday temperature in a stand of 35-year-old *Araucaria cunninghamii* where *C. cylindroides* webs were found was considerably lower than in the surrounding open fields or at the plantation edge where *C. moluccensis* webs were located (R. Wiley, personal communication).

   Cyrtophora moluccensis also assumes a hang-at-hub position during heavy rainfall. Unlike *N. maculata* (Robinson and Robinson 1973), *C. moluccensis* does not cut out
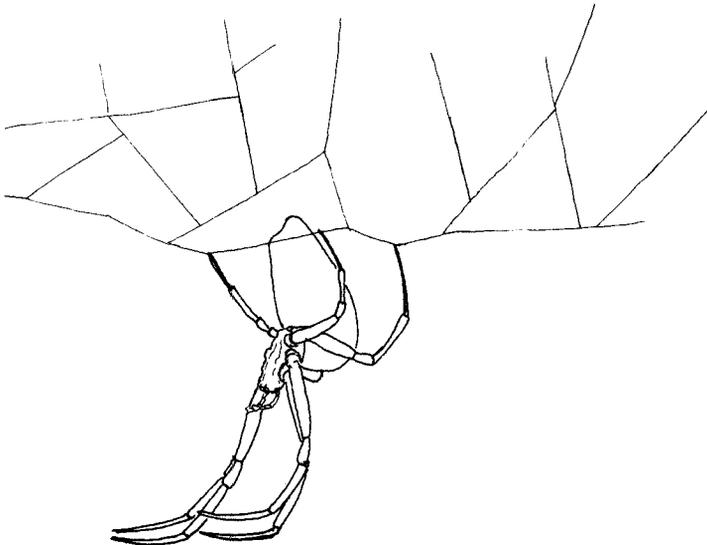

Fig. 3.—*Cyrtophora moluccensis* female hanging at the hub with legs III and IV in a sun-avoidance posture.

sections of its web during rain or move into the nearby vegetation. Presumably, by hanging at the hub, the spider presents a minimal surface to the rain, thereby reducing its impact. *Argiope argentata* was also observed to hang from the hub during heavy rain (Robinson and Robinson 1973) and it was suggested that the outstretched legs I and II act in the manner of a leaf drip-tip, enabling the water to flow off the spider's body. *Cyrtophora monulfi* does not hang at the hub in response to rain; data on *C. citricola* and *C. cylindroides* are unavailable.

Jerking

Jerking has been observed in all species studied (though not necessarily in all predatory sequences) and consists of a rapid pulling of the radii with legs I. [This was previously referred to as "plucking" (e.g., Robinson and Olazarri 1971) but Eberhard (pers. comm.) has pointed out that jerking more aptly describes the actual leg movements, since the force exerted on the radius is longitudinal to it rather than perpendicular.] The spider may jerk the web in response to movement in the web, or upon returning to the hub after a prey-capture sequence. In the latter case, the spider may turn in a circle at the hub, jerking the net at intervals as it turns. It may jerk threads of the upper barrier web as well. I also saw a low-intensity tensing of the web, in response to prey in the web. This involves slow pulling in the radii towards the body with legs I and II.

Jerking and web tensing may be a means of precise location of objects in the web. Due to the large number of radii and spiral connections in a *Cyrtophora* web, signal transmission may be somewhat diffuse. Jerking would put greater tension on the radii, and may also induce struggling in motionless prey, thereby enabling the spider at the hub to locate prey on the sheet. Robinson and Olazarri (1971) observed that *Argiope argentata* jerked the web move often when prey did not struggle and suggested that this is a method of accurately locating nonvibrating prey in the web. Earlier, Barrows (1915) proposed that radii in contact with prey would vibrate at a different frequency and that the spider could spatially compare the echo vibrations after jerking from unloaded and loaded radii. The mechanism of prey location by jerking deserves further investigation.

Like other araneids, *Cyrtophora* may also jerk the web as it approaches the prey. This probably allows for corrections in the spider's orientation toward nonvibrating prey. I have never observed *Cyrtophora* to "err" in the directional location of prey in the web. Occasionally, however, mistakes are made in distance location and the spider "overshoots the mark." This seems to occur most often with small, rapidly vibrating prey, such as buzzing blowflies, which elicit a very rapid attack [also observed in *Nephila maculata* (Robinson and Robinson 1973), and in the psechrid, *Fecenia* sp. (Robinson and Lubin, in press)].

A great deal of jerking takes place with prey trapped in the upper barrier web. Possibly signal transmission through the irregular barrier web is less accurate than through the net, making prey location more difficult.

Web Shaking

This involves sudden and large amplitude shaking of the horizontal net with legs I or legs I and II. Web shaking is quite distinct from jerking, involving a downward motion of the legs rather than the horizontal pull and release characteristic of jerking and tensing. Web shaking occurs in the context of both predatory and defensive behaviors:

a. If an insect is caught in the upper barrier web, the spider runs out under the net until it is beneath the prey and shakes the net. This may be repeated many times until the prey is dislodged from the barrier web and drops onto the net.

b. Web shaking occurs during intraspecific aggression (for example, during prey capture or web building) in *C. moluccensis* and *C. monulfi* (Lubin 1974).

c. Theridiid kleptoparasites often approach a spider feeding at the hub, apparently in an attempt to steal prey. In such instances, the spider may shake the net at or near the hub, thereby chasing away the intruders.

d. *Cyrtophora moluccensis* egg sacs are parasitized by a sarcophagid fly whose approach by flying through the barrier web elicits web shaking in adult *C. moluccensis* females (Lubin 1974). Parasite attacks have not been observed in other species of *Cyrtophora*.

Web shaking of the sort that I saw in *Cyrtophora* species does not seem to occur in other araneids, but does occur in *Pschrus argentatus* (Psechridae) which has a sheet-and-barrier web that acts as a knockdown trap like that of *Cyrtophora* (Robinson and Lubin, in press). *Nephila clavipes*, juvenile *N. maculata*, and *Argiope* and *Araneus* species vibrate their webs when disturbed by a large object, but these appear to be higher frequency vibrations whose functions may be to obscure the spider's outline (Tolbert 1975). *Metabus gravidus*, a colony-dwelling araneid from Costa Rica "bounces" on the web in response to an intruder (Buskirk 1975). It is possible that web shaking in *Cyrtophora* is derived from such antipredator web-vibrating or web-bouncing behavior.

Prey Immobilization

Biting.—Immobilization by biting occurs commonly in all species of *Cyrtophora* studied. The prey is initially grasped with legs I, II, and III, and the spider appears to bite the nearest or most readily accessible part of the insect's body. If this is a wing or a leg, the spider then moves down to a more "substantial" part of the insect's body, e.g., the base of an appendage, thorax or abdomen. Similar behavior occurs in other spiders, including *A. argentata* (Robinson and Olazarri 1971) and *Fecenia* sp. (Psechridae) (Robinson and Lubin, in press). Most prey are held in legs III, or II and III, during the bite. The duration of the bite varies: small insects are seized in the jaws and pulled out immediately, while larger prey may be bitten for several minutes (see below).

Prey that are immoblizied by wrapping may be bitten after the wrap (post-immobilization bite at the capture site). The post-immobilization bite is generally directed toward the anterior portion of the insect's body, as is the case in *A. argentata* (Robinson and Olazarri 1971).

Prey with hard exoskeletons, such as most beetles, may be given a number of short bites during immobilization wrapping. These are probably exploratory bites, rather than actual penetration through the cuticle and injection of venom. The nocturnal araneid *Eriophora fuliginea* (Robinson et al. 1972) and *N. maculata* (Robinson and Robinson 1973) also repeatedly attempt to bite coleopterans. In both instances, the authors noted that penetration through the hard exoskeleton was unlikely and one could actually hear the clicking of the chelicerae as they glanced off the smooth elytra. *Cyrtophora* may also give short, exploratory bites to prey after removing it from the net, prior to transport to the hub. Rapid "bite and back off" sequences were not observed in *Cyrtophora*, though they are common in other araneids such as *Gasteracantha, Nephila,* and *Micrathena* (Robinson and Lubin, unpublished; Robinson and Robinson 1973).

Wrapping.–Prey are wrapped at several stages of the predatory sequence (Eberhard 1967, Robinson et al. 1969):

    a. Immobilization wrapping. Insects are attacked and partly or completely immobilized by wrapping in silk.

    b. Post-immobilization wrapping at the capture site. Prey that were immobilized by biting or by wrapping, are wrapped prior to transporation to the hub.

    c. Post-immobilization wrapping at the feeding site. Prey are wrapped at the hub prior to feeding.

In the wrap immobilization, *Cyrtophora* throws silk out under the sheet in broad swathes with legs IV. Often the spider approaches the prey and, turning 90° to 180°, faces away from the prey and begins throwing swathes of silk in an upward and slightly backward direction. Facing away and throwing behavior was observed most frequently in attack sequences on pentatomid bugs and large orthopterans presented to *C. moluccensis* and *C. cylindroides*. Similar behavior was observed in all species of *Argiope* studied, in *Araneus* spp. and, to a much greater extent in the nocturnal *Eriophora fuliginea* (see summary in Robinson 1975). In all wrap restraints, silk is initially thrown upwards from a distance. There is no actual bodily contact with the prey.

In *Cyrtophora*, initial throwing of silk does not always immobilize actively struggling prey. Silk swathes thrown upward onto the net may temporarily restrain prey by catching appendanges protruding through the net. The spider may then rapidly bite a hole in the net and resume throwing silk onto the prey as it drops through the hole. When the prey is thus partly immobilized, wrapping behavior changes gradually from throwing to the application of swathes of silk directly to the surface of the prey. Close contact wrapping is typical of wrapping after the initial restraint (post-immobilization wrapping).

Two phases of post-immobilization wrapping may be distinguished: wrapping of prey still caught on the net, and wrapping of prey hanging in the free zone beneath the net (free-wrapping). During the initial phase, the spider sits below the prey, holding it with legs II and III, while legs IV alternate in pulling out and applying swathes of silk directly onto the prey. In the case of insects restrained by biting, or wrapping and then biting, post-immboilization wrapping usually begins while the prey is still in the spider's jaws.

As the prey is freed from the net by pulling out or by cutting out, the first phase of wrapping merges into the second. The spider retains its hold on the net with one leg I (or with legs I and II) while grasping the prey with the remaining legs I, II, and III. The prey is suspended from the net by one or two threads. The spider is thus oriented perpendicular to the long axis of the prey and beings to rotate the prey with legs I, II and III and with the palps, while applying silk over the prey in a foreward motion with legs IV. Legs I, II and III pull the anterior edge of the prey toward the spider's body, while legs IV push the posterior edge away from the body (see Robinson and Olazarri 1971:9). The prey is thus rotated toward the spider and silk is wound onto the prey. Free-wrapping also occurs in *A. argentata* (Robinson and Olazarri 1971) and in *E. fuliginea* (Robinson et al. 1972). The prey of *Argiope* and *Eriophora*, however, is supported on a radius of the orb web, while that of *Cyrtophora* hangs beneath the net. Like *Argiope*, *Cyrtophora* moves its abdomen in an arc from side to side as silk is pulled out with legs IV. In this manner, it covers the entire insect evenly with silk.

Large, bulky prey are wrapped in a manner that reduces their bulk. When wrapping dragonflies, for example, the wings and long abdomen of the dragonfly are pulled inward and wrapped together. The resulting prey package is of more manageable size and may be carried with less risk of entanglement in the web.

Post-immobilization wrapping may also occur at the hub, and during transport to the hub. Wrapping during transport occurs mainly when an insect becomes caught in the sheet or in the lower barrier web. Occasionally, insects that are transported in the jaws are wrapped partway to the hub and transferred to the spinnerets.

Insects that are restrained in the upper barrier web may be wrapped in the same manner as those immobilized on the net. A second wrapping generally occurs under the sheet (free-wrap), prior to transport to the hub.

Pulling Out and Cutting Out

Small prey may be pulled out of the sheet with the chelicerae. The spider pulls the prey down with the jaws and legs III, while legs I and II push up against the sheet. *Cyrtophora* attempts to pull out most prey that are bitten at the capture site (either immobilization or post-immobilization bite), including large prey that are subsequently cut out of the web. Pulling out seems to follow biting in the normal sequence of prey capture behavior, but is successful only with small, compact prey such as fruitflies and occasionally blowflies. Difficulty in pulling prey out of a *Cyrtophora* web is due to the strength and fineness of the mesh, rather than web adhesiveness, as in the case of typical orb weaver.

Pulling out in the jaws may also allow the spider to test the condition of an insect that has been immobilized by biting, without loosening the grip on it. Since insects do not actually adhere to the sheet, the possibility of escape from a *Cyrtophora* web due to incomplete immobilization is greater than from webs of other araneids (Lubin 1973). There would be an advantage, therefore, to testing prey immobility prior to releasing it for wrapping.

Most prey, other than very small insects, are removed from the sheet by a combination of alternately cutting out and pulling down with the legs and jaws. In cutting out, threads of the sheet or upper barrier web in immediate contact with the prey are cut, while the prey is pulled down with legs II and III, or I, II, and III. The functional distinction between cutting out and pulling out is less clear in *Cyrtophora* species than in *A. argentata* (Robinson and Olazarri 1971). Nor is there a definite temporal sequence of cutting spiral and radial web elements, as in *Argiope*. This is understandable, as there is no difference in physical properties between these elements in a *Cyrtophora* web. In all likelihood, the combination of cutting and pulling is simply a method of freeing prey with the minimum amount of damage to the sheet. Pulling out results in the least damage; cutting and pulling out results in a small hole, approximately the diameter of the insect as it is pulled through the sheet head first.

With insects that are immobilized entirely by wrapping, cutting out occurs as part of the wrap sequence, during the transition from restraint wrapping to free wrapping under the sheet.

Transportation to the Hub

Carry in jaws.—Small prey are often carried to the hub in the chelicerae. An insect may be wrapped at the capture site and transferred to the jaws for transport, retaining a swathe of silk connecting it to the spider's spinnerets. Small prey that are seized and pulled out with the jaws are generally carried to the hub in the jaws without prior wrapping.

Carry on silk.—Most prey are carried to the hub dangling on a thread from the spinnerets held by one or both legs IV. The spider's abdomen is oriented horizontally

under the net, and the wrapped prey package hangs down over the posterior edge of the abdomen. Holding with legs IV may prevent the insect from swinging from side to side and becoming entangled in the lower barrier web. *Araneus diadematus, Argiope argentata,* and *Nephila clavipes* also support either the prey package or the thread from which it is suspended, with legs IV (Peters 1931, Robinson and Olazarri 1971, Robinson and Mirick 1971), although *A. argentata* sometimes carries prey without support.

All prey, whether carried on silk or in the jaws, are transported to the hub on the undersurface of the sheet. *Cyrtophora* carries all prey to the hub and does not leave wrapped insects in the web at the capture site.

Manipulation and Feeding at the Hub

Prey carried on silk are suspended at the hub. Upon reaching the hub, the spider pulls down on the thread from which the prey is suspended with one leg IV, thus pulling out a length of thread, and then dabs the spinnerets onto the net. The spider then turns 180° and pulls the prey up to the chelicerae with legs I and II. The silk line is severed in the act of dabbing the spinnerets to the sheet, though the mechanism for this is not understood. As yet, no evidence of a cut-off valve has been found in araneid spinnerets (Wilson 1969).

Prey are manipulated with the palps, chelicerae, and legs I and II prior to feeding. Feeding generally occurs at the anterior end of the prey. During feeding, most prey are held in the jaws alone, and the spider resumes a resting position with all legs under the web. Large prey may be held with legs III; occasionally, *Cyrtophora* feeds in a hanging position with legs I, II, and III grasping the prey and legs IV holding onto the hub. The latter position undoubtedly reduces the spider's ability to receive web vibrations.

DESCRIPTION AND ANALYSIS OF BEHAVIOR SEQUENCES

Attack Sequences

Attack sequence is used here to denote prey immobilization and subsequent behavior up to transportation of the prey to the feeding site. Analysis of *Cyrtophora* prey capture sequences with various types of insect prey revealed four basic attack sequences: (1) wrap/bite/pull out or cut out/free-wrap, (2) wrap/cut out/free-wrap, (3) bite/wrap/cut out/free-wrap, and (4) bite/pull out (or cut out). Two of these sequences involve immobilization by wrapping, and two immobilization by biting. Table 2 shows the frequency of occurrence of each attack strategy in four species of *Cyrtophora* with different insect prey. Tables 3-5 give the durations of behavior units within sequences for *C. moluccensis, C. cylindroides* and *C. monulfi.* Durations are given only for the most commonly occurring sequences with each prey type.

Post-Attack Sequences

Post-attack sequences involve transportation of prey to the hub and manipulation at the hub prior to feeding. The two basic methods of transportation, carry in jaws and carry on silk, have already been described. Frequencies of occurrence of these two methods in behavior sequences with different prey types are shown in Fig. 4. Durations of post-attack sequences and total sequence durations are shown in Tables 3 to 5.

The following discussion will concentrate on the variation in sequences of attack and transportation that occur with different prey and their possible adaptive values.

Table 3.–Duration of attack and transportation to hub and total durations of commonly occuring prey capture sequences in *C. moluccensis*. Total sequence durations represent the time from initiation of an attack to suspending the prey at the hub; manipulation of prey at the hub and feeding are not included. Not all behavior units were timed in each sequence; thus, sample sizes vary for each behavior category.

n = number of prey for which behavior was timed; M = mean duration, in seconds; SD = 1 standard deviation.

(A = Durations of wrap and cut out/free wrap were lumped together; B = wrap attacks that were too short to measure accurately are designated as 1 second duration; C = test-bites and manipulation of prey with legs and jaws; D = sequence repeated several times).

Prey and attack sequence		Attack		Transport		Total sequence
		Wrap	Bite	Cut out/ free wrap	Carry to hub	
Moths	n		16	15	12	16
(bite/wrap)	M		75.1	47.5	20.3	109.6
	SD		85.1	21.3	30.5	111.9
	Range		6–265	21–90	5–116	50–340
Blowflies	n		18	16	14	18
(bite/wrap)	M		36.1	22.7	7.6	112.5
	SD		31.5	8.3	3.0	101.2
	Range		5–130	12–39	3–13	32–377
Stratiomyids	n	10	10	9	7	10
(wrap/bite)	M	8.6	109.9	52.2	11.6	185.0
	SD	5.8	61.6	14.5	10.95	104.5
	Range	2–17	3–219	7–55	5–36	77–412
Stratiomyids	n	9[A]			6	9
(wrap)	M	56.1			9.5	96.4
	SD	44.5			8.5	62.2
	Range	15–136			3–25	22–201
Stratiomyids	n		9	9	5	9
(bite/wrap)	M		76.2	21.9	9.6	117.1
	SD		49.7	7.0	4.3	58.6
	Range		8–156	12–36	4–15	46–218
Grasshoppers	n	6[B]	6	4	2	3
and katydids	M	13.5	54.2	37.0	6.5	195.3
(wrap/bite)	SD	16.8	76.6	10.4	2.1	115.3
	Range	1–38	2–207	24–49	5–8	69–295
Grasshoppers	n	10[A]			6	10
and katydids	M	40.0			28.3	101.1
(wrap)	SD	14.95			28.8	88.7
	Range	22–58			9–75	53–323
Grasshoppers	n		5	5	5	5
and katydids	M		27.0	35.0	5.0	128.2
(bite/wrap)	SD		19.3	7.1	1.9	54.8
	Range		7–55	28–44	3–8	72–191
Dragonflies	n	7[B]	7	7	7	7
(wrap/bite)	M	10.7	106.6	57.6	12.4	282.4
	SD	13.1	152.4	10.5	6.1	217.1
	Range	1–37	1 –448	50–78	4–23	128–765
Dragonflies	n		14	14	12	14
(bite/wrap)	M		135.0	51.8	14.9	330.1
	SD		138.0	35.0	12.4	149.8
	Range		12–334	16–138	4–40	119–600

Table 3.–continued.

Weevils (wrap/bites)[C]	n	6	6	3	2	6
	M	16.8	56.5	16.3	4.5	117.2
	SD	7.6	70.0	14.4		53.7
	Range	9–28	1–184	8–33	3–6	60–202
Weevils (Wrap)	n	12[A]			6	12
	M	12.45			12.3	56.6
	SD	3.1			13.5	34.6
	Range	8–19			2–36	20–123
Scarabs (wrap/bites/ wrap)[D]	n		12			12
	M		529.1			661.0
	SD		374.0			357.2
	Range		57–1395			120–1400

Comparisons are made with the prey capture behaviors of *C. citricola* in Spain (Blanke 1972) and of other araneids.

Sequences With Moths.–Lepidoptera are nearly always immobilized by biting, by all four species of *Cyrtophora*. The third attack sequence, bite/wrap/cut out/free wrap, is the predominant one used with moths and butterflies. Robinson (1969) showed that *A. argentata* immobilizes moths by a long bite, while most other prey are restrained by wrapping. He suggested that since moths can escape readily from sticky webs by shedding the loose scales in contact with the web (Eisner *et al.* 1964), a rapid restraint by biting would be most advantageous. As the *Cyrtophora* web is nonsticky, scales can be of little advantage in freeing a moth from the web. It is more likely that a moth can slip out of the silk thrown on it during a wrapping attack and, therefore, the bite immobilization and immediate injection of venom is more effective. Robinson (1969) showed that Lepidoptera are recognized by the spider, at least in part, by their surface texture. Other araneids (e.g., *Eriophora fuliginea* and other *Argiope* spp.) which have sticky orbs and both wrap and bite immobilization behaviors, also use the biting restraint for Lepidoptera (Robinson 1975).

A small proportion of "mistakes"–moths attacked by a wrap immobilization sequence–was made by *C. citricola*, *C. cylindroides*, and *C. moluccensis*. This was found to be the case with *A. argentata* as well (Robinson 1969). Most of these mistakes were made with moths attacked in the upper barrier web. These moths were wrapped only a few times (2- to 3-seconds duration) and immediately bitten. It is possible that discrimination of prey type is more difficult in the barrier web, due to its diffuseness, than under the sheet. As moths make up a large fraction of the prey of *C. moluccensis* in the area studied (and possibly of the other species as well; Lubin, unpublished data), one might expect mistakes in the method of attack to be minimized. This appears to be the case: *C. moluccensis* made 8.3% mistakes with live moths, while *A. argentata* (which does not feed on lepidopterans to any large extent) made 17.2% mistakes with live moths and 16% mistakes with live butterflies (Robinson and Olazarri 1971). *Eriophora fuliginea*, a nocturnal araneid which may specialize on moths, attack-wrapped only 6% of the live moths (Robinson et al. 1972). These differences, while suggestive, are not statistically significant.

Most moths are wrapped at the capture site and carried to the hub on silk. The larger species, *C. moluccensis* and *C. citricola*, carry a small percentage in their jaws after a bite/pull out in jaws attack sequence. Some of these however, are wrapped part way to the hub and transferred to the spinnerets.
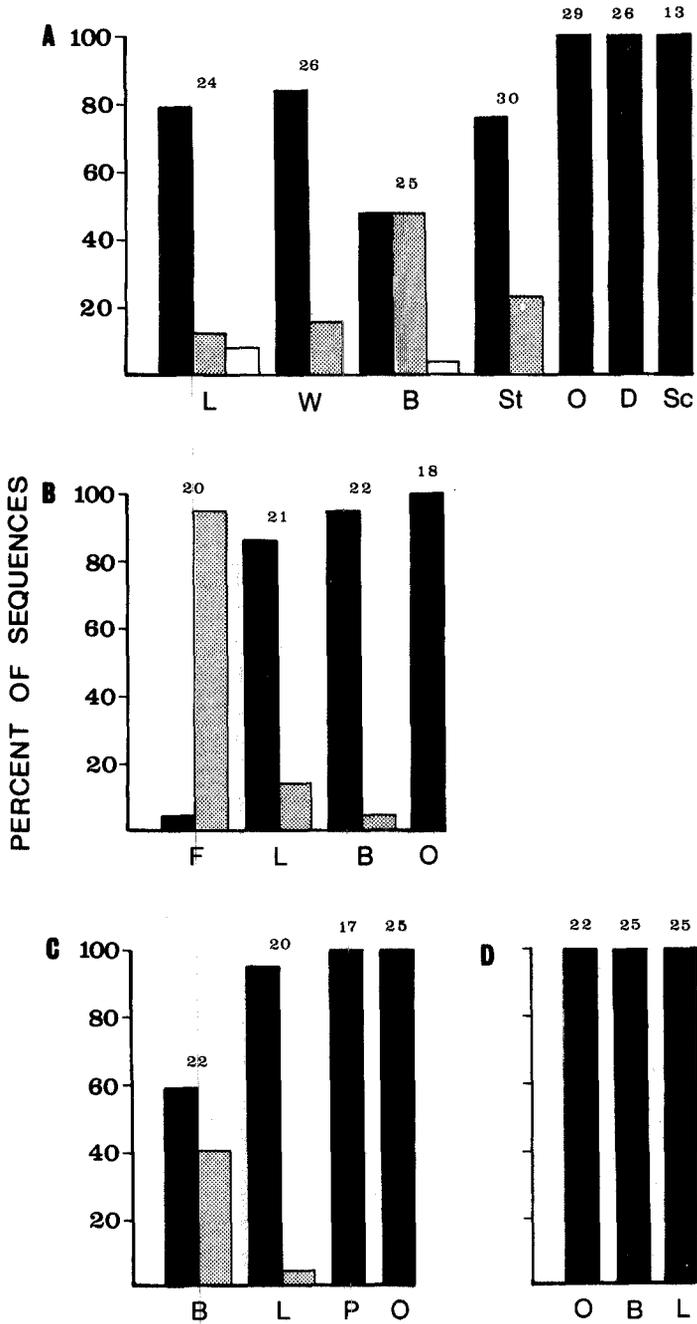
Fig. 4.—Frequency of occurrence, in percent, of transport to hub sequences in *C. moluccensis, C. citricola, C. cylindroides*, and *C. monulfi*. Transport sequences are: black bars = carry on silk, shaded bars = carry in jaws, white bars = carry in jaws and transfer to carry on silk.

Numbers of trials are shown for each prey type. Prey types are: L=moths and butterflies, B=blowflies, St = stratiomyid flies, O = orthopterans (katydids, grasshoppers, pygmy grasshoppers), D = dragonflies, W = weevils, Sc = Scarab beetles, F = fruitflies.

Sequences With Flies.—Blowflies are immobilized predominantly by biting. Biting attacks were used on 96% of the blowflies tested on *C. moluccensis*, 90% of those tested on *C. citricola*, 100% of those tested on *C. monulfi*, and 95% of those tested on *C. cylindroides*. Small fruitflies tested on *C. citricola* were always immobilized by biting in a bite/pull out attack sequence (see also Blanke 1972:181). Blanke (1972) found that *C. citricola* attacked houseflies by biting.

Cyrtophora species attacked blowflies by biting even when the flies equalled or exceeded the weight of the spider (as in the case of blowflies given to *C. monulfi*). Wasp-mimicking stratiomyid flies (soldier flies), however, elicited 66.7% wrap restraints in *C. moluccensis*. *Cyrtophora* attacks most hymenopterans by wrapping (*C. citricola*: Blanke 1972; *C. moluccensis*; incidental observations). More than half of the wrap attacks on stratiomyids were of type I (wrap/bite), in which the wrap was of short duration (2 to 17 seconds), and was followed by a long bite not significantly different in duration from the bite given in a bite/wrap attack sequence. Possibly the spiders mistook the stratiomyids for wasps during the initial attack. One may postulate that the spider switches off the wrap attack as soon as it recognizes the prey to be nonhymenopteran. Recognition may occur only upon actual contact with the prey, after immobilization wrapping has begun. Since prey discrimination in orb weavers is based on tactile and chemosensory cues, the wasp mimicry of stratiomyids must extend to nonvisual characters, e.g., wingbeat frequency, for the spider to err in their recognition. Acoustical mimicry has, in fact, been described in a syrphid fly *Spilomyia hamifera* (Gaul 1952). Blanke (1972), however, found that *C. citricola* treated unidentified syrphid flies like other flies and immobilized them by biting.

Argiope argentata attacked 74% of live flies and 98% of live stingless bees (*Trigona* sp.) by wrapping (Robinson and Olazarri 1971). Peters (1931, 1933), however, found that vibrating flies were bitten by *Araneus diadematus*, and *Eriophora fuliginea* attacked most stingless bees by biting and pulling out (Robinson et al. 1972). The latter authors suggested that a biting attack is elicited by small, rapidly vibrating prey that have become trapped by only a few viscid spiral elements and may, therefore, easily escape. Since *E. fuliginea* has a coarser mesh web than *A. argentata*, stingless bees are held by fewer threads (often only one); this may explain the predominance of biting attacks in *E. fuliginea*. Because of its lack of sticky threads, the *Cyrtophora* web is relatively inefficient in restraining small, active insects (see evidence on blowfly escapes from *C. moluccensis* webs, Lubin 1973); hence, a rapid, biting attack would be most effective.

Transportation sequences with flies are variable (Fig. 4). Blowflies are carried entirely on silk by *C. monulfi* and predominantly on silk by *C. citricola* (95%) and *C. cylindroides* (59.1%). *Cyrtophora moluccensis* uses both methods with equal frequency. Stratiomyids, which are heavier than blowflies, are carried mainly on silk. Fruitflies, which are small and light, are not wrapped at the capture site and are carried in the jaws by *C. citricola*.

When fruitflies were tested in rapid succession, *C. citricola* attacked each additional fly while retaining the previous ones in the jaws, thus accumulating up to 5 fruitflies in the jaws. However, after 4-5 fruitflies had been accumulated, they were wrapped together into one prey package, and transferred to the spinnerets. Four to 5 fruitflies weigh approximately 40 to 50 mg, and are within the weight range of blowflies which are carried on silk by *C. citricola*. These observations imply that prey weight influences the mode of transportation to the hub in *Cyrtophora*. Other factors such as size and bulkiness of the prey may also be important.

Table 4.–Durations (in seconds) of attack and transportation to hub, and total durations of prey capture sequences in *C. cylindroides* (see Table 3). (A = this sequence was repeated several times.)

Prey and attack sequence		Attack		Transport		Total sequence
		Wrap	Bite	Cut out/ free wrap	Carry to hub	
Moths	n		19	18	18	19
(bite/wrap)	M		290.2	55.9	10.0	414.7
	SD		187.1	19.3	3.1	180.7
	Range		46–764	23–83	4–15	189–844
Blowflies	n		17	17	16	17
(bite/wrap)	M		212.65	26.8	10.7	258.2
	SD		202.55	16.2	4.2	211.25
	Range		36–693	5–70	5–20	55–767
Katydids	n	3	3	3	3	3
(wrap/bite)	M	26.0	25.0	32.3	8.0	164.3
	SD	19.2	39.0	26.0	6.1	69.8
	Range	4–39	1–70	7–59	1–12	88–225
Katydids	n	4		4	4	4
(wrap)	M	29.25		49.5	12.0	179.75
	SD	11.7		58.4	4.3	141.5
	Range	14–42		16–137	8–18	76–377
Katydids	n		16	16	13	16
(bite/wrap)	M		48.6	54.0	12.7	241.4
	SD		43.2	37.4	6.8	84.2
	Range		6–151	5–127	4–30	85–381
Pentatomids	n	18			9	18
(wrap/cut	M	161.7			11.1	281.2
out/rest-	SD	115.1			4.9	171.5
clean)[A]	Range	29–383			6–20	44–577

Sequences with Orthopterans.—Orthopterans are immboilized either by biting or by wrapping. Although wrap restraints (sequences 1 and 2) occur more frequently in *C. moluccensis* and *C. citricola*, no one sequence predominates in all four species. It is significant that all three attack sequences involving both wrap and bite immobilization are commonly used on a single type of prey.

Argiope argentata wraps all crickets (Robinson and Olazarri 1971). Other *Argiope* species also wrap orthopterans (Robinson, B. and M. H. Robinson 1974). These authors have suggested that wrapping enables the spider to restrain dangerous prey while maintaining a safe distance from it. Species that do not attack prey by wrapping (e.g., *Nephila* spp., *Herrenia ornatissima, Micrathena* spp.) often restrain orthopterans and other large prey with a repeated bite/back-off sequence that is considerably less efficient than a wrap immobilization (Robinson et al. 1969, Robinson and Lubin, in press).

Since immobilization wrapping does occur in *Cyrtophora* species, why is it not used more frequently with orthopteran prey? There are perhaps two explanations. First, because of the strength and density of the horizontal orb web, *Cyrtophora* may be more protected from potentially dangerous prey than is *Argiope* (or any other typical orb-web spider). The horizontal sheet is always situated between the spider and its prey. Hence, the spider can "afford" to utilize a more direct bite immobilization, rather than wrapping

Table 5.–Durations (in seconds) of attack and transporation to hub, and total durations of prey capture sequences in *C. monulfi* (see Table 3).

Prey and attack sequence		Attack		Transport		Total sequence
		Wrap	Bite	Cut out/ free wrap	Carry to hub	
Moths	n		25	25	20	25
(bite/wrap)	M		164.4	99.1	37.15	398.6
	SD		128.7	41.2	64.1	220.5
	Range		16–457	22–165	2–277	98–785
Blowflies	n		25	23	14	25
(bite/wrap)	M		118.2	56.0	14.0	245.7
	SD		108.9	23.2	8.9	124.1
	Range		28–545	14–107	3–32	111–626
Small	n	8	8	8	6	8
grasshoppers	M	5.4	30.0	27.0	5.0	155.9
(wrap/bite)	SD	4.9	18.55	7.7	3.2	110.3
	Range	1–16	1–59	11–36	2–11	94–423
Small	n		12	11	5	12
grasshoppers	M		79.75	38.9	4.2	184.7
(bite/wrap)	SD		92.5	18.0	1.9	109.5
	Range		17–333	17–73	2–7	40–437

from a distance. An analogy may be drawn between the methods of attack of *Cyrtophora* species and that of the sheetweb spider (Linyphiidae) or purse-web spider (Atypidae), both of which seize their prey in the jaws from a position of relative safety beneath a layer of silk. Second, since the horizontal sheet forms a barrier between the spider and its prey, it is difficult for *Cyrtophora* to completely immobilize prey by wrapping unless a large portion of the insect protrudes through the sheet into the thread-free zone. Katydids are often not heavy enough or strong enough to break the sheet of a *Cyrtophora* web, and in such instances direct immobilization by biting may be more effective. Orthopterans that struggle and damage the sheet are immobilized entirely by wrapping. Many of the wrap/bite sequences given to orthopteran prey consist of a short-duration wrap and long-duration bite, as already observed with stratiomyid flies. Possibily the initial wrap attack is switched off upon some sort of feedback from the prey, e.g., prey harmless, or prey body not protruding through sheet. The predominance of biting attacks on blowflies may also be explained in this manner.

Predatory sequences initiated by immobilization wrapping in *A. argentata* were shorter than those initiated by biting (Robinson et al. 1969). It was suggested that another advantage to the spider of restraint wrapping was to minimize time spent away from the hub, the hub offering both protection and a central location for monitoring web vibrations. This seems particularly applicable to *Argiope* which returns to the hub after immobilization wrapping, leaving the prey in the web. *Cyrtophora* does not leave wrapped prey in the web. Furthermore, sequences in which prey are restrained by wrapping alone (sequence 2) are not significantly shorter in duration than sequences initiated by either bite/wrap or wrap/bite attacks (Tables 3 and 4), and the reduction in time spend away from the hub is not as pronounced as in *A. argentata*. Thus, the advantages of a wrapping attack may be more limited for *Cyrtophora* species.

Orthopterans were invariably carried to the hub on silk, though crickets of the same or greater weight than the orthopterans used here were carried in the jaws by *A. argentata* (Robinson 1969; *A. argentata* weighs approximately the same as *C. moluccensis*). The significance of this difference is unclear. It may be more difficult to carry heavy prey in the jaws under a horizontal orb web than under a near-vertical web.

Sequences with Dragonflies.—The dragonflies tested on *C. moluccensis* weighed approximately the same as the katydids, and the observed predatory sequences were similar to those with katydids as prey. The hypothesis proposed to explain the occurrence of all three sequences with orthopteran prey may be applied to dragonflies as well. Dragonflies were given a significantly longer bite than were katydids, whether it be an immobilization bite (t = 1.65, p = 0.05) or post-immobilization bite (t = 1.80, p < 0.05). Thus, the duration of the bite does not appear to be weight dependent, but may be related to other factors such as intensity of struggling of the prey or prey shape.

Dragonflies, like grasshoppers and katydids, were carried to the hub on silk.

Sequences with Beetles.—Small weevils (ca. 35 mg) and large scarabid beetles (500 to 1000 mg) were tested on *C. moluccensis*. All beetles were immobilized by wrapping. Attack sequence 2, wrap/cut out/free wrap, was used on most weevils. About 30%, however, were given short, exploratory bites after the initial wrapping restraint. This method of attack seems to be a variation on the typical wrap/bite sequence, where a series of short test-bites replace the long bite normally given to non-coleopteran prey. Half of the weevils that were bitten were carried to the hub in the jaws, and half were wrapped again and transferred to the spinnerets. In this instance, carrying on silk is perhaps influenced by the smooth surface of the beetle rather than by weight.

The attack sequence with large scarabs (*Melolontha* sp.) is a more complex variation of sequence 1, involving the behaviors wrap/attach thread to sheet (or hub)/test-bites/wrap, which may be repeated several times. A typical attack sequence on *Melolontha*, taken from field notes, is as follows:

Spider at hub. Moves to prey under sheet. Touch prey with palps and legs. Wrap (throw silk swathes under prey). Cut out with jaws while wrapping. Attach thread to sheet with spinnerets. Wrap (move over surface of prey). Begin rotating prey while wrapping (rotate-wrap). Test-bites. Rotate-wrap. Attach thread to sheet near hub. Test-bites. Rotate-wrap. Attach thread to sheet. Test-bites. Rotate-wrap. Cut proximal thread to sheet and attach thread closer to hub. Turn 180° at hub. Pull prey up with legs I and II. Manipulate with legs I and II, jaws and palps.

The hard and smooth exoskeleton of most coleopterans precludes rapid immobilization by biting. Small beetles, such as the weevils tested on *C. moluccensis*, would slip through the horizontal sheet unless immediately wrapped by the spider. Large *Melolontha* sp. were both active and heavy enough to break through the horizontal sheet, and escaped unless wrapped immediately. Beetles were also observed to slip through the enswathing silk. This may explain the necessity for the long, repeated wrapping bouts given to *Melolotha* sp. Both weevils and scarabs were wrapped repeatedly at the hub during manipulation and early stages of feeding.

Beetles were never attacked by a simple wrap/bite sequence. The total handling time for melolonthiid beetles was significatly longer than for any other prey type. Perhaps penetration through a beetle's armour is difficult and a large number of short, exploratory bites are necessary before the spider can select a spot through which the venom and digestive enzymes can be injected. As a result, complete immobilization of the prey is slow and bettles must be wrapped repeatedly to avoid loss.

Both *Eriophora fuliginea* and *Argiope argentata* attacked *Tenebrio* beetles (about one-fourth the size of *Melolontha* sp.) with a repeated wrap/bite sequence, similar to that used by *C. moluccensis* on scarabs (Robinson and Olazarri 1971 Robinson et al. 1972). Robinson and Robinson (1973) tested *Melolontha* sp. on *Nephila maculata* and on *Argiope aemula* in New Guinea and found that although both responded with lengthy, complex sequences, *A. aemula* dealt more efficiently (more rapidly and with fewer losses) with the beetles than did the larger *N. maculata*. The latter lacks the wrap immobilization behavior, and attacks large prey by a repeated bite-and-back-off sequence. Thus, the wrapping attack, even when prolonged, is more effective with hard-cuticled prey such as beetles.

In 6 out of 13 complete predatory sequences, *Melolontha* were carried to the hub on silk. In the remaining instances, a distinct carry stage did not occur; rather, with each wrap/attach thread sequence, the prey was moved slightly closer to the hub. This method of transporting prey to the hub occurs frequently in several species of *Gasteracantha* and *Micrathena* (which do not carry prey on silk) with prey that are too heavy (or bulky?) to be carried in the jaws (Robinson and Lubin, unpublished). Probably carry-on-silk behavior evolved from this simpler but less efficient behavior sequence of wrap/attach thread to hub.

Sequences with Pentatomids.—Pentatomids (stink-bugs) were tested on *C. cylindroides*. Ninety percent were attacked by wrapping (sequence 2). The remaining 10% were given short test-bites (too short to measure accurately), and were then wrapped.

Pentatomids are well known to discharge noxious defense secretions (Eisner and Meinwald 1966). Twelve (60%) of the twenty pentatomids tested were actually observed to discharge a defensive secretion upon being attacked by the spider. Spiders that immobilize prey by wrapping (e.g., *Argiope* spp.) can attack pentatomids and other hemipterans with greater efficiency than can species with only bite immobilization behavior (e.g., *Nephila* spp.), as they can avoid the main force of the discharge (Robinson and Olazarri 1971). Similarly, bombadier beetles can escape more readily from spiders that attack by biting rather than wrapping (Eisner and Dean 1972).

In 60% of the sequences with pentatomids, spiders interrupted the attack, stopping to rest on or near the prey and clean the palps, legs and mouth parts. Spiders gave the appearance of being stunned by the discharge, remaining immobile for durations of a few seconds to over five minutes, before initiating cleaning or resuming the attack. Many attacks on pentatomids by *C. cylindroides* were unsuccessful. Nonetheless, remains of pentatomids and of other hemipterans were found in prey traps under *C. moluccensis* webs, indicating that this species, at least, does capture pentatomids under natural conditions (Lubin, unpublished).

Pentatomids, though lighter than blowflies, were always carried on silk. This is perhaps because of the noxious secretions. It is unclear how long it takes for the secretion to dissipate or become exhausted. Pentatomids were transported in the jaws by *A. argentata* (Robinson and Olazarri 1971), however, this may have been after a period of resting at the hub, having been left in the web for sufficient time for the secretion to disperse. In most instances, *C. moluccensis* did not begin to feed immediately after suspending a pentatomid at the hub, but remained resting at the hub or began cleaning. Thirteen out of 20 sequences with pentatomids were interrupted by resting or grooming behavior. Sequences with katydids of similar size were never interrupted. In 6 instances, interruptions in the capture sequence occurred just after the discharge of noxious secretion by the prey.

Table 6.–Comparison of attacks by *Cyrtophora*, *Argiope* and *Nephila* on similar prey types. Only predominant initial attack sequences are shown.

Prey	*Cyrtophora*	*Argiope*	*Nephila*
Moths	bite/wrap	long bite/wrap	bite
Blowflies, Houseflies	bite/wrap bite/pull out	wrap/short bite bite/pull out	seize and pull out
Orthopterans	wrap/bite wrap bite/wrap	wrap/short bite	bite and back off
Dragonflies	wrap/bite wrap bite/wrap	wrap/short bite	bite and back off
Beetles	wrap wrap/short bites	wrap/short bites	bite and back off
Pentatomids	wrap	wrap/short bite	–

Sequences with Multiple Prey.–Insects given to spiders that already had prey at the hub were treated in the same way as first prey. Second or third prey were not left in the web, but were carried back to the hub in a complete predatory sequence. This was determined by presenting multiple prey (fruitflies, blowflies, and katydids) to *C. citricola*, *C. moluccensis*, *C. cylindroides* and *C. monulfi*. Many other species, including 7 *Argiope* species (Robinson 1975), *Arachnura* and *Gasteracantha* species (Robinson and Lubin, in press), leave second or third prey wrapped in the web, and return to feed on the first prey at the hub. Except in the case of very small fruitflies given to *C. citricola* in rapid succession, each successive insect is attacked and transported separately. All prey are suspended individually near the hub. The order in which they are eaten is not necessarily the same as that in which they were suspended. If the spider is already feeding on an insect at the hub, it will usually resume feeding on it after returning from another capture.

DISCUSSION

Similarities between predatory behavior units of *Cyrtophora* spp. and those of *Argiope* spp. and *E. fuliginea* have been noted throughout the text. Behaviors that did not occur in *Cyrtophora* but which occur in *Argiope* are maintenance of dragline connection with the hub (true of all araneids with sticky orbs), resting at the hub during a prey capture sequence, and "Rundgang" behavior (Peters 1931), involving multiple attachments of wrapped prey to the hub by dabbing the spinnerets against the hub as the spider turns in an arc of 180°. Web shaking is the only behavior observed in *Cyrtophora* that does not seem to have a functional counterpart in *Argiope* or *Eriophora*.

Attack sequences of *Cyrtophora*, *Argiope* and *Nephila* with similar prey types are compared in Table 6. *Cyrtophora* shares with *Argiope*, *Araneus*, *Eriophora* and *Arachnura* the ability to attack by wrapping and to free-wrap the prey by rotating the prey package while it is held away from the web. *Nephila*, *Herrenia*, *Micrathena* and perhaps *Gasteracantha* attack all prey by biting and do not rotate the prey while wrapping (Robinson 1975, Robinson and Lubin, in press; unpublished observations). The wrap/short bite sequence which *Argiope* uses with most prey other than moths is less

commonly used by *Cyrtophora*, and a broader spectrum of prey types may be immobilized by biting. Immobilization wrapping may have certain disadvantges for *Cyrtophora* due to peculiarities of the nonsticky knockdown web (see earlier).

It was suggested that environmental factors such as rain and wind, and prey availability in open habitats would select for the nonsticky web of *Cyrtophora* (Lubin 1973). The evolution of a new trapping method, along with drastic modification of web structure, appear to have modified the predatory behavior of *Cyrtophora* only slightly. I suggest that *Cyrtophora* is derived from an "advanced" araneid precursor in which complex predatory behavior including both wrapping and biting restraints already existed, and that only small changes in predatory behavior were necessary to comply with the new web type. These changes were:

    1. Loss of a dragline connection with the hub during prey capture activities. As the *Cyrtophora* web is persistent, and accumulation of draglines on the horizontal orb might interfere with signal transmission to the hub and reduce the trapping efficiency of the spider. The dragline, considered a primitive form of silk production (Kaston 1964, Savory 1952), is probably found in all sticky-orb araneids, although few authors have remarked specifically on its presence. *Cyrtophora* species do not produce a dragline during locomotion under the sheet. The same is true for the related New World genus *Mecynogea* (personal observations) which constructs a *Cyrtophora*-type web. The dragline is used by many orb-weavers for rapid return to the hub, either by climbing up the thread (e.g. *Nephila*, in a "hand-over-hand" motion) or by swinging out onto a dragline beneath the plane of a horizontal web (e.g. *Leucauge*); for dropping out of the web when disturbed; and when hanging from the web surface during prey capture. In all these activities *Cyrtophora* dispenses with the use of a dragline. The lower barrier web would probably interfere with the spider swinging below the sheet on a dragline, and there is no advantage to walking on a dragline under a nonsticky sheet, over walking on the web itself. Furthermore, when disturbed *Cyrtophora* does not usually drop out of the web, but climbs into the barrier web or nearby vegetation. A similar escape behavior was observed in *Mecynogea lemniscata* (Exline 1948). During prey capture, *Cyrtophora* hangs from the web or from the prey by legs I and II (during wrapping) or by legs IV (during biting and feeding). As the sheet is uniformly strong and fine-meshed, it provides more even support to the spider moving under it than would a typical orb with its weak viscid spiral (in many instances, the viscid spiral alone could not support the weight of the orb weaver; see Lubin 1973). Based on these considerations, I would argue that the loss of dragline production in *Cyrtophora* during locomotion on the web came about with the evolution of the nonadhesive knockdown web.

    2. Reduction in the use of wrapping for prey immobilization. Eberhard (1967) argued that immobilization by wrapping was an "advanced" trait, probably derived from post-immobilization wrapping at the capture site. Not all orb weavers share this trait (Robinson et al. 1969). Immobilization wrapping is an effective method of restraining large and/or dangerous insects. *Cyrtophora* does attack-wrap, but this method is reserved mainly for beetles, pentatomids, and hymenopterans (see also Blanke 1972), as well as some other large insects that can break through the horizontal sheet. As noted above, the sheet acts as a barrier

between the spider and its prey, making it safer to attack prey directly by biting and, at the same time, more difficult to restrain insects solely by wrapping.

3. *Cyrtophora* does not leave wrapped prey at the capture site. It shares this behavior with *Nephila, Herrenia, Gasteracantha* and *Micrathena*. Other araneids (e.g. *Argiope, Eriophora, Cyclosa*) often leave prey in the web after an immobilization- or post-immobilization wrap, particularly when a wrapped prey package is already present at the hub (Robinson 1975). There are two possible disadvantages to leaving prey in a *Cyrtophora*-type web. First, since *Cyrtophora* renews its web only infrequently (Lubin 1973), a dead insect in the sheet might be overlooked and thus lost or stolen by kleptoparasites. Second, in *Cyrtophora* wrapped insects hang below the sheet, attached by a single thread rather than rolled up along a radius and attached firmly at both ends, as is the case with prey left in sticky orbs. Prey packages left in *Cyrtophora* webs are probably more vulnerable to theft by kleptoparasites than prey left in sticky orbs.

4. *Cyrtophora* does not perform "Rundgang" behavior when hanging prey at the hub. As the function of this behavior is not known, it is difficult to speculate on reasons for its absence. Possibly this multiple attachment of prey to the hub serves to distribute prey weight evenly around the hub and/or to reinforce the hub. Since *Cyrtophora* has a horizontal sheet, there may be no need to distribute prey weight evenly around the hub; or *Cyrtophora* silk may be sufficiently strong so that multiple attachments to the hub are unnecessary. *Cyrtophora* webs have an open hub, but it is irregular in shape and the fine-meshed web around it lends strong, cross-braced support for suspended prey packages.

Kaston (1964) and Kullmann (1958, 1972, 1975: 373) suggested *Cyrtophora* as a link between the sheet web-building Linyphiidae and the Araneidae. Earlier, McCook (1889) suggested that the related New World genus *Mecynogea* (the "Basilica" spider) was similar to the Linyphiidae in its manner of web construction. Kaston (1964) placed *Cyrtophora* and *Mecynogea* between the linyphiids and the genus *Nephila* in his scheme of the evolution of spider webs, based on the following similarities: (1) *Cyrtophora* and some linyphiids construct a non-adhesive, 3-dimensional, knockdown web; (2) both *Cyrtophora* and *Nephila* have irregular barrier webs on either side of the orb; (3) *Cyrtophora* and *Nephila* webs have bifurcated radii toward the periphery of the orb and retain the non-adhesive, structural spiral (*Nephila* webs have a viscid spiral as well).

The linyphiid web consists of an irregular-mesh, horizontal sheet with a barrier web above and below it. The sheet, which may be domed or tent-shaped (as in the web of *Linyphia marginata*), lacks the basic elements of an orb web: radii, spiral and hub. It is difficult to imagine the complex web of *Cyrtophora* derived from the unstructured sheet-web of a linyphiid. Structural similarities between *Cyrtophora* webs and those of linyphiids are probably superficial ones, resulting from convergent evolution. Blanke too (1972) regarded the similarities between *C. citricola* and the linyphiids as convergent evolution and noted that, in all aspects of morphology and behavior, *C. citricola* was an araneid. Exline (1948) arrived at the same conclusion regarding *Mecynogea*, based both on web structure and on spider morphology.

The implied relationship between *Cyrtophora* and *Nephila* is equally tenuous. The barrier web of *Nephila* is derived from a rudimentary orb web (Robinson and Robinson 1973), while there is no evidence that this is the case in *Cyrtophora*. Forked radii occur in webs of several araneids, including *Eriophora fuliginea*, and are therefore not unique to *Cyrtophora* and *Nephila*. They may be characteristic of large orb webs where constant

mesh size is desirable. Without forked radii, mesh size would increase markedly toward the periphery of a large orb. Egg sacs of *Cyrtophora* are more similar to those of *Argiope* than of *Nephila* (Kullmann 1961; unpublished observations). The courtship behavior of *C. citricola* (Blanke 1972) and of *C. nympha* in Panama (Robinson and Robinson, in press) is of an "advanced" type, most similar to that of certain *Araneus* species. Levi (1978) noted that, based on morphological similarities, both *Cyrtophora* and *Mecynogea* are "related, but not closely, to *Araneus*" (p. 741). Finally, based on predatory behavior, I contend that *Cyrtophora* is quite removed from both the linyphiids and the nephilinids. *Cyrtophora* predatory behavior is similar to that of *Argiope, Araneus*, and *Eriophora*, and includes the advanced behaviors of immobilization wrapping, throwing bands of silk onto the prey from a distance, and rotating the prey during the post-immobilization wrap. Prey immobilization by wrapping does not occur in linyphiids (Bristowe 1941, Eberhard 1967) or in *Nephila* (Robinson et al. 1969, Robinson and Mirick 1971). On this evidence alone, it seems unlikely that *Cyrtophora* separated from the main line of araneid evolution prior to the separation of the Nephilinae from the rest of the araneid line. The differences between the predatory behaviors of *Cyrtophora* and *Argiope* are relatively minor and may represent changes in behavior associated with the evolution of a specialized web.

ACKNOWLEDGMENTS

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