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A STUDY OF DISTURBANCE BEHAVIORS IN Uloborus glomosus
(ARANEAE; ULOBORIDAE) AS POSSIBLE PREDATOR AVOIDANCE
STRATEGIES

by

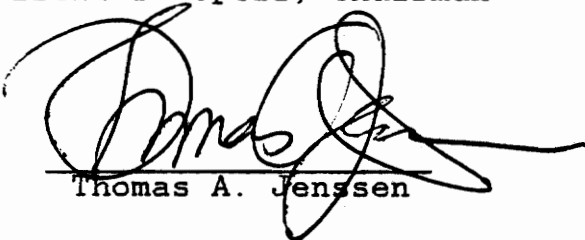
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Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE
in
Zoology

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March, 1988

Blacksburg, Virginia

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(ABSTRACT)

When touched with a contact stimulus, 50% of adult Uloborus glomosus jumped from the web; 33% remained motionless; 13% moved to the edge of the web; and 4% shook the web. In a population of juveniles, 45% moved to the edge of the web; 27% jumped from the web; 24% shook the web; and 4% remained motionless.

Adults with either stabilimenta or eggsac chains in their webs showed a tendency to shake their webs in the morning and move to the edge in the evening. Those without web structures jumped from their webs throughout the day. Juveniles with stabilimenta shook their webs in the afternoon; those without stabilimenta shook their webs in the evening. Adults aligned with web structures remained motionless when disturbed.

Marked adults observed over the course of 4 weeks moved to the edge of the web or remained motionless when contacted in the mornings and jumped in the afternoons and evenings. During this time, the frequency of the

jumping behavior increased.

An adult U. glomosus jumped from its web in response to contact by a spider-hunting wasp. Other spiders tested with a contact stimulus and the combined visual and vibratory stimuli produced by a tethered wasp responded only to contact.

Females tending their eggsac chains exhibited two types of defensive behaviors when either the parasitoid Arachnopteromalus dasys or spiderlings were placed on their eggsacs. They jerked their webs and swept the eggsacs with their long front legs.

ACKNOWLEDGEMENTS

There are many people whose help and support I would like to acknowledge, but I would first like to thank my mentor and friend Dr. Brent D. Opell who helped me in many ways during my undergraduate and graduate years at Virginia Tech. Dr. Opell taught me photography and histological techniques; showed me how to be brave when working with computers; taught me the best ways to humanely collect and fix spiders; gave me good advice on teaching; and taught me, through his example, much about patience and humility.

I extend sincere thanks to my other committee members, Drs. Fell, Jenssen, and West whose advice was good, clear, and much appreciated. They were always ready to help me throughout my study, lending me equipment and references, even supplying me with backyard work space.

I would like to extend a special thanks to Johnny Randall for helping me in countless ways including allowing me the use of his front porch for my filming study, monitoring my film when I could not, helping me build an enclosure, and especially for advising me on the best ways to spend my time when not doing research.

A special thanks also goes to Gabrielle Roth for her work as an undergraduate research assistant during

the Eggsac Defense Study.

Thanks also goes to the Virginia Tech Statistics Consulting Center for their help with my analyses.

This study was supported by two Sigma Xi grants along with matching funds from the Virginia Tech Department of Biology.

Lastly, but most importantly, I would like to dedicate this study to my family, especially to my parents, Joseph Cushing (deceased) and Paula M. Cushing who built a home of books and knowledge and free thinking; who encouraged all their children to be the best they could be in whatever path they chose; and who were always proud of our endeavors.

TABLE OF CONTENTS

General Introduction	1
Objectives	10
 Chapter 1: Surveys and Filming	
Introduction	18
Methods and Materials	20
Adult Survey	20
Juvenile Survey	22
Filming	24
Results	25
Adult Survey	26
Juvenile Survey	30
Filming	34
Discussion	38
 Chapter 2: Consistency Study	
Introduction	43
Methods and Materials	44
Results	48
Consistency Over Time	48
Consistency Between Time Periods	50
Discussion	51
Consistency Over Time	51
Consistency Between Time Periods	52

Chapter 3: Eggsac Defense Study

Introduction 56
Methods and Materials 58
Results 60
Discussion 63

Chapter 4: Stimulus Study

Introduction 65
Methods and Materials 67
Results 69
Discussion 71

Summary 73

Literature Cited 79

Figures 85

Figure 1. Postures involved in the jumping
behavior 86

Figure 2. Adult survey: TIME * ALIGNMENT 87

Figure 3. Adult survey: TIME * RESPONSE 88

Figure 4. Adult survey: RESPONSE * STAB/SAC 89

Figure 5. Adult survey: RESPONSE * ALIGNMENT 90

Figure 6. Adult survey: STAB/SAC * ALIGNMENT 91

Figure 7. Growth plots 92

Figure 8. Juvenile survey: TIME * RESPONSE 93

Figure 9.	Juvenile survey: TIME * ALIGNMENT . . .	94
Figure 10.	Juvenile survey: TIME * STABILIMENTA .	95
Figure 11.	Juvenile survey: STABILIMENTA * ALIGNMENT	96
Figure 12.	Juvenile survey: TIME * RESPONSE . .	97
Figure 13.	Predator-prey interaction sequence . .	98
Figure 14.	Arachnothrombus	99
Figure 15.	Consistency study. TIME * BLOCK for blocks 1 - 5	100
Figure 16.	Consistency study. TIME * BLOCK for blocks 6 - 9	101
Figure 17.	Consistency study. TIME * RESPONSE .	102
Tables	103
Table 1.	Response variables for adults with neither linear stabilimenta nor eggsac chains	104
Table 2.	Summary of filming	105
Table 3.	Consistency study sampling procedure . .	106
Table 4.	Summary of eggsac defense behaviors by 12 females	107
Table 5.	Summary of responses to a contact stimulus and a tethered wasp	108
Appendices	109
Appendix 1.	Adult survey data table	110
Appendix 2.	Juvenile survey data table	111
Appendix 3.	Consistency study data tables . . .	112

VITA 113

GENERAL INTRODUCTION

Most predator prey studies of spiders view spiders as predators rather than prey. Although spiders are important prey items of some wasps, birds, and other spiders, few studies investigate the defensive mechanisms spiders use to avoid predation. Crane (1952) defined seven distinct defensive mechanisms in invertebrates: crypsis; active escape; startle response; attack; withdrawl into protected position; unpalatability; and chemical concealment (a "smoke screen"). The first five of these mechanisms are expressed by different spiders. No spiders are known to be unpalatable nor do spiders have the ability (as do some cephalopods) to release a chemical smoke screen. Therefore, these last two defensive mechanisms will not be discussed.

Crypsis, as described by Robinson (1969a), includes background coloration (homochromy); countershading; disruptive coloration; and mimicry of inedible objects. For example, members of the genus Gasteracantha (Araneidae) have a bizarre body form that resembles a thorny twig (Robinson 1969a). Some spiders in the families Clubionidae and Salticidae mimic distasteful ant species (Reiskind, 1977). Miagrammopes (Uloboridae) species have long, slender legs and abdomens that confer a twig-like appearance (Lubin et al. 1978, Lubin 1986,

Opell 1984, 1986), as do many members of the family Tetragnathidae (Robinson and Robinson 1970), while Wagneria (Araneidae) resembles debris (Robinson and Robinson 1970).

Several genera in both the ecribellate orb-weaving family Araneidae and the cribellate orb-weaving Uloboridae enhance their morphological crypsis by adding denser silk structures called stabilimenta to their webs. These stabilimentum builders include five araneid genera: Argiope, Cyclosa, Gasteracantha, Gea, and Nephila (Tolbert 1975) and six uloborid genera: Uloborus, Zosis, Octonoba, Conifaber, Philoponella, and Lubinella (Lubin 1986). Marples (1969) describes stabilimenta as consisting:

". . . of straight or zigzag ribbons of silk radiating from, or surrounding, the hub [of the orb web]. Sometimes the hub is transformed into a central platform of varying degrees of complexity, and this may be combined with the peripheral decoration. Sometimes foreign bodies, such as the pellets formed from the remains of prey wrapped in silk, pieces of vegetable matter or even the egg cocoons of the spider itself, play a part in the decoration."

Marples chose to use the word "decoration" in place of "stabilimentum" since he believed the latter term to be a misnomer implying a stabilizing, rather than a cryptic, function. In describing the cruciate zigzag stabilimentum in the webs of the genus Argiope (Araneidae) Hingston (1927) says "the structure is

therefore a confusion device. Through its presence the outline of the spider is lost. The spider looks part of the complicated zigzag and is no longer a living thing."

Although the stabilimentum's cryptic function is supported by many authors, (Hingston 1927, Bristowe 1941, Marson 1947 a, b, Marples 1969, Ewer 1972, Eberhard 1973, Tolbert 1975, Lubin 1980), it is only one of three postulated functions. Horton (1980) and Eisner and Nowicki (1983) suggest that stabilimentum is aposematic, serving to warn avian predators (such as blue jays) of the web's presence. The blue jays (Horton 1980) associated the stabilimentum with the web's adhesive capture threads that stuck to their feathers and, therefore, chose not to feed on the spider.

A third hypothesized function of the stabilimentum is that it strengthens a web. Robinson and Robinson (1970, 1973, 1978) found, for example, that, despite common belief, most webs of Argiope and Nephila (Araneidae) are devoid of stabilimenta, and spiders which do incorporate stabilimenta into their webs often have incomplete or skeleton webs that would be reinforced by these thickened bands of silk. Their data also indicated that Argiope rarely builds the complete cruciform stabilimentum so evident in photographs of this spider. Single or multiple arms of stabilimentum silk are more common and are usually built below the hub in the larger

portion of the web. Based on this evidence, they suggest that the stabilimentum is strengthening and adjusting the mechanical state of the web. The Robinsons themselves admit that "this view is . . . somewhat nebulous" (Robinson and Robinson 1970).

In the same study they also provide evidence against the hypothesis (Horton 1980, Eisner and Nowicki 1983) of the aposematic function of stabilimenta. They determined that some birds (flycatchers, antshrikes, and kingbirds) could use the stabilimentum patterns as cues for locating the resident spider. However, they suggest that with juvenile araneids, which often construct a solid circular stabilimenta platform, the stabilimenta may have an anti-predator function (Robinson and Robinson 1970).

Araneid and uloborid orb-weaving spiders that include stabilimenta in the hubs of their webs are all diurnal and typically rest at the web's center (Eberhard, 1973). In this position they are particularly vulnerable to visually hunting predators. When disturbed, many of these spiders show distinct avoidance, or escape behaviors (Crane's second predator avoidance mechanism) including jumping or dropping from the web, moving to the edge of the web, and moving through the web to the other side. Although these behaviors have been described, little quantitative evidence has been gathered to support

the hypothesis that these are effective predator avoidance mechanisms.

Incidents of jumping (or dropping) from the web, which Edmunds (1974) calls an escape response, have been reported in the araneid genera Araneus (=Epeira) (Pekham and Pekham 1887, Eberhard 1970); Cyclosa (Hoffmaster 1982 a, Levi 1977, Eberhard 1973); and in Argiope (Hoffmaster 1982 a, Robinson and Robinson 1970, 1978, Ewer 1972, Eberhard 1973, Tolbert 1975). The jumping response has also been observed in the uloborid genus Uloborus (Hoffmaster 1982 a, Marples 1969, Eberhard 1970). I have observed this response in non-orb-web-weavers of the families Linyphiidae and Theridiidae.

Many orb-weavers move to the edge of the web when disturbed. This response has been reported in the araneid web-weaver genera Nephila (Hoffmaster 1982a); Cyclosa (Hoffmaster 1982 a); and Argiope (Ewer 1972, Tolbert 1975, Hoffmaster 1982 a). The uloborid genus Uloborus also exhibits this response (Hoffmaster 1982 a, Eberhard 1973).

Some large orb-weavers complete their webs by biting out the hub to leave a hole. When disturbed, they move through this hole to the other side of the web placing the web between the spider and the stimulus. This has been reported only for spiders of the genus Argiope (Tolbert 1975, Robinson and Robinson 1970).

Crane's third predator avoidance mechanism is the startle response. This is also commonly shown by orb-weaving spiders that vibrate or shake their webs when disturbed. Edmunds (1974) considers this shaking response a startle display because "the animal becomes blurred in appearance, possibly with an apparent increase in size, and it must be very difficult for a predator to launch a successful attack on such a target." Shaking has been noted in the araneid genera Cyclosa (Levi 1977, Eberhard 1973, Hoffmaster 1982 a); Argiope (Robinson and Robinson 1970, 1978, Ewer 1972, Eberhard 1973, Tolbert 1975, Hoffmaster 1982 a); and Nephila (Hoffmaster 1982 a). It has also been noted in the uloborid genus Uloborus (Eberhard 1973) and the cobweb genus Pholcus (Pholcidae) (Edmunds 1974).

The fourth predator avoidance mechanism described by Crane (1952) is an attack response. Visually oriented spiders such as thomisids, salticids, and lycosids often rear up and lunge at a stimulus. A rearing, or attack, response against disturbance is also occasionally seen in orb-web spiders of the genus Argiope (Ewer 1972, Tolbert 1975, Hoffmaster 1982 a). However, this is not a common response to disturbance by these orb-weavers.

Much more common among orb-weavers is the fifth predator avoidance mechanism mentioned by Crane (1952): withdrawal into a protected position. Many orb-weavers

of the genus Araneus build a retreat made of leaves bound together by silk (Levi 1968, Eberhard 1970, Edmunds 1974). The spider remains in this retreat most of the day and often returns to it when disturbed. Members of the genus Tetragnatha (Tetragnathidae), if disturbed while on the web, run to surrounding vegetation where they assume a twig-like cryptic posture (Eberhard 1973). Some Philoponella (Uloboridae) species use a silk retreat (Lubin 1986). Cobweb spiders of the family Theridiidae commonly run to a silken retreat at the edge of their webs when disturbed (Eberhard 1973).

It is appropriate to consider these five behavioral responses as predator avoidance mechanisms only if predators exert selection pressure to maintain the behaviors in the population. The three most important groups of predators on orb-weaving spiders are other spiders, wasps, and birds (Bristowe, 1941).

Most spiders are opportunists and readily attack conspecifics and other spiders. Wandering spiders of the families Lycosidae (wolf spiders) and Salticidae (jumping spiders) attack and eat orb-weavers (Bristowe 1941, Hoffmaster 1982 a). When one web-spinner enters another's web, it is often captured (Bristowe 1941). In the Araneidae orb-weaving species Argiope argentata (Fabricius), Nephila clavipes (Linne), Cyclosa caroli (Hentz), and the uloborid species Philoponella

(=Uloborus) republicana (Simon), moving to the edge of the web, dropping or jumping from the web, and shaking the web were effective defensive behaviors against the visually oriented salticid predator Phiale guttata (Koch) (Hoffmaster 1982 a). The shaking response was particularly effective in dislodging the salticid from the orb-spider and propelling it either off the web entirely or into the sticky spiral where the orb-spider could subdue it.

Birds are also important spider predators, especially hummingbirds and other small nesting birds such as starlings, wrens, tits, and robins (Bristowe 1941). Birds tend to be generalist spider feeders, hunting primarily conspicuous, diurnal spiders (Bristowe 1941). When Hoffmaster (1982 a) exposed the four aforementioned orb-weavers and the araneid species, Leucauge venusta (Wakkenaer), to the hummingbird Phaethornis superciliosus (Linne) (family Trochilidae), all the spiders except P. republicana shook the web. Argiope argentata and L. venusta also moved to the edge of the web; and all the spiders except A. argentata and Cyclosa caroli dropped or jumped from the web. Each behavior was in direct response to hummingbird attacks. Hoffmaster's quantitative evidence supports the hypothesis that these disturbance behaviors are responses to attacks by visually oriented predators.

Bristowe (1941) says that "fossorial wasps [primarily those in the families Sphecidae and Pompilidae] are commonly regarded as being one of the most, if not the most important enemies of spiders." Because pompilids store only one prey item per cell (burrow) upon which they lay their egg (Krombein 1967), they hunt only large spiders, usually wandering spiders rather than orb-weavers. In contrast, sphecid mud-dauber wasps store many spiders per mud cell and are much less selective about the size class of their prey. They collect a wide range of spider taxa-- wanderers and web-builders alike-- including immature individuals (Krombein 1967). Sphecid wasps include the genera Chalybion, Trypoxylon, Sceliphron, and Trypargilum. The last three genera build mud cells on buildings, rocks, and trees, whereas Chalybion uses the mud cells built by other wasps (Evans and Eberhard 1970). A female wasp hunts a spider, paralyzes it with her sting, and then carries it back to an existing mud cell. Before closing off the cell, she lays an egg on the abdomen of one of the paralyzed spiders (Rau 1915).

Predation pressure from these mud-daubers may be an important factor that serves to maintain the previously described predator avoidance mechanisms in the orb-weaving spiders. Some orb-spiders jump from their webs in response to sphecid or pompilid wasps (Richards

and Hamm 1939, Eberhard 1970, Coville 1976). Of the sphecid genus Trypargilum, Krombein (1967) notes that these wasps, when hunting web spiders, "probably snatch the spiders directly from the web. Species . . . that use snare builders almost entirely, probably dash at the spider in its web and frighten it into dropping off the web to the ground where the wasp picks it up." Richards and Hamm (1939) cites several examples of this behavior by pompilid wasps. It appears that most wasps find it difficult to capture a spider hanging from its dragline in midair.

There is no record of the effectiveness of the shaking response against hymenopteran predators. However, Hoffmaster's (1982 a) work suggests that this behavior may effectively dislodge non-flying predators such as other spiders.

Objectives:

The purpose of this study was to examine predator avoidance behaviors in the Uloboridae orb-weaver Uloborus glomosus (Walckenaer). This spider exhibits three of the five putative predator avoidance mechanisms discussed above: crypsis, active escape, and a startle response. These horizontal orb-weaving cribellate spiders are common throughout the eastern U.S. and are abundant on the shrubbery of the Virginia Tech campus.

Uloborus glomosus remains in what is thought to be

a cryptic posture at the hub of its horizontal web most of the time except when attack wrapping a prey and sometimes when feeding at the web's hub. This cryptic posture involves appressing the first pair of long front legs and extending them directly ahead of the spider, with the tibia-metatarsus joint bent at 90 degrees (Opell and Eberhard 1984). When assuming this posture, the spider resembles a small twig --none of the spider's extremities are distinguishable. Dense setal tufts on the tibiae of the long first legs further enhance this resemblance. According to Opell and Eberhard (1984), these tufts hide the tips of the second legs which rest next to the tibiae of the first legs and obscure the outline of the legs. The legs of these spiders also display disruptive coloration.

When disturbed, some individuals jump from the hub of the web while others will run to the edge of the web. Both of these behaviors are active escape responses. The jumping behavior has several distinct elements (Fig. 1):

- 1) The spider propels itself off the web anteriorly at an approximate angle of 16 degrees to the vertical.
- 2) It releases a variable length of dragline silk attached to the web's hub and hangs at the end of this dragline in the cryptic posture described above. Both at the hub and at the end of the dragline, the spider maintains an approximately horizontal orientation, although at the hub

the long front legs are bent at the tibiae-metatarsus joint about 80 degrees whereas at the end of the dragline the legs are bent at this joint only about 25 degrees. 3) After an interval of a few seconds to 20 minutes the spider swings upward and grasps the dragline with the first two pairs of legs. It uses these legs to ascend the dragline back to the web's hub. 4) The spider stops from one to five times on its ascent. At each stop, the spider reassumes the cryptic posture; orienting itself vertically rather than horizontally with the long first legs directed toward the web and bent at the tibiae-metatarsus joint about 90 degrees.

Eberhard (1973) described a similar behavior in the uloborid Philoponella diversus (Marx). Pekham and Pekham (1887) suggest that "the habit of keeping still after dropping must not only help a spider to avoid detection, but must also make it more certain of finding its way home after the danger is over." This may also explain why uloborids rarely lower themselves onto a substrate after jumping; to do so might risk entangling their dragline or exposing themselves to predators.

Some U. glomosus show a startle response when disturbed. This shaking behavior consists of a series of rhythmic oscillations that continue for several seconds and appears to be initiated when a spider is contacted ventrally. This behavior also has distinct features:

after being contacted, the spider alternately flexes and extends the long front legs and, to a lesser extent, the second pair of legs. Sudden flexion/extension sequences result in the rhythmic movement of the spider's body and sets up web oscillations.

These apparent predator avoidance behaviors are not always effective in eluding predators. Uloborus glomosus have been found in nests of the mud dauber genera Sceliphron and Trypoxylon (Dorris 1968). Other uloborid prey (species unidentified) have been cited from Trypoxylon nests (Iwata 1976, Griswold and Coville 1986). These observations demonstrate that the horizontal cribellar web of U. glomosus does not itself entirely deter hymenopteran predators and thus makes relevant an investigation of the three postulated predator avoidance mechanisms.

This study had five objectives: 1) to determine the frequency of the postulated predator avoidance behaviors in adult and juvenile populations of U. glomosus and to determine what factors influence the expression of these behaviors, 2) to determine how consistent the disturbance behaviors expressed by individual spiders are both throughout a day and over several days, 3) to obtain direct evidence that these hypothesized predator avoidance mechanisms actually enable a spider to avoid

visually hunting predators, 4) To determine what stimuli are necessary or sufficient to trigger the active escape (jumping from the web) and the startle (shaking) responses, and 5) to investigate the influence of eggsacs upon an attending female's behavior. Each objective is discussed more fully below.

1 & 2) Several factors may influence the expression of the disturbance behaviors. I was particularly interested in the influence of time of day, the presence of silk stabilimentum, the presence of an eggsac chain, and alignment of the spider with the stabilimentum or the eggsac chain.

If the jumping behavior is a predator avoidance strategy, I expected to see differences in the expression of the jumping behavior from one time of day to another at both the population and individual levels (objectives 1 and 2). The jumping behavior is likely to be costly both energetically and strategically because, after a spider jumps, it may fall into another spider's web or lose a productive web site. Therefore, it would be to the jumper's benefit to weigh the cost of this behavior with the likelihood that the disturbance is, in fact, a predator. Since hymenopteran predators are diurnal and are active 1 - 3 hours after sunrise until 1 - 3 hours before sunset (Coville 1987), spiders which jump from the

web should do so most readily during times of the day when predators are most active.

The shaking response, on the other hand, seems, from Hoffmaster's study, to be associated with predation attempts by non-flying visually hunting predators such as other spiders. If this is the case, then I predicted no difference in the display of this disturbance behavior from morning to afternoon to evening either for the population of U. glomosus (objective 1) or for individual spiders (objective 2), as wandering spiders like salticids are active in the morning and the afternoon and others, such as lycosids, are active in the evening. If the shaking response is primarily a startle display, it would be effective against any visually hunting predator and would, therefore, also be displayed during all times of the day.

One hypothesis of the function of stabilimenta is that they enhance the spider's crypsis. Mature female U. glomosus often have a linear chain of eggsacs in their web. When such an eggsac chain is present, the female spider normally remains aligned with it. In such a position it is very difficult to distinguish spider from eggsac. Therefore, the eggsac chain may also have a cryptic function.

If posture and alignment with the stabilimentum or with an eggsac chain enhance the spider's crypsis and

thus protect it from visually hunting predators, then the spider should remain in its cryptic posture aligned with the stabilimentum or with the eggsacs throughout the day. Additionally, if stabilimenta or eggsacs are particularly effective cryptic devices, then spiders which have neither stabilimenta nor eggsacs may display different disturbance behaviors than spiders with these web structures. Spiders which have these structures but are not aligned with them may also show different disturbance behaviors than spiders which utilize these devices to enhance their crypsis.

3) As previously noted, orb-weavers jump from their webs directly in response to hymenopteran and avian predators. If the jumping and shaking behaviors (in particular) are predator avoidance strategies I expected to observe instances of these behaviors in response to predators during my study.

4) As an approaching flying predator (such as a wasp) provides several potential cues, it is important to determine which stimuli trigger the disturbance behaviors. Spiders may respond to sight, air-borne vibrations, and direct contact. Pekham and Pekham (1887) noted that orb-weaving spiders jumped or dropped from their webs when a tuning fork was held near them.

Occasionally I observed U. glomosus jump from its web when gently blown on, although the behavior was elicited more readily when the spider was lightly touched. The shaking response appeared to be set off only by contact. Therefore, I predicted that either a contact stimulus or air-borne vibrations trigger the disturbance behaviors shown by U. glomosus.

5) Finally, I wished to determine the influence of eggsacs upon a female's behavior. While conducting the population studies (objective 1), I noted that mature female U. glomosus with eggsacs tended to remain with their eggsacs when disturbed and seldom showed the disturbance behaviors described above. This behavior may be adaptive either because it enhances the protective resemblance of the female or because it places the female in a better position to defend her eggsacs against predation or parasitism. Although these hypotheses are not mutually exclusive, each predicts a different female response. If the eggsacs are primarily enhancing the female's crypsis, then the female should not respond to an insect (i.e. an eggsac parasite) crawling over her eggsacs. However, if the female is protecting her eggsacs, then she should display a defensive behavior when an insect crawls over them.

INTRODUCTION: SURVEYS AND FILMING

Uloborus glomosus spiderlings emerge from eggsacs as 2nd instars and reach maturity in the 6th instar. Mature females have a cephalothorax-abdomen length of 10 to 12 mm. Uloborids build their webs at night but monitor them and capture prey during both day and night. They replace their webs at night, but only when damage is great. During the day both juvenile and adult uloborids rest at the hub of their orb webs in what appears to be a cryptic posture (Opell and Eberhard 1984).

This study had two objectives: 1) to evaluate the factors that may influence the expression of the disturbance behaviors in juvenile and adult U. glomosus, and 2) to determine if these behaviors are, in fact, predator avoidance strategies. To accomplish the first objective I was specifically interested in the following factors: time of day (morning, afternoon, or evening); presence of a stabilimentum; presence of an eggsac chain; and the alignment of the spider (or spiderling) with either of these two web structures.

If the three disturbance behaviors are the results of predation pressure, then there may be a time difference in the expression of the behaviors correlating with the times when visually hunting predators are most active. Such time differences in behavioral patterns

have been noted in both vertebrates and invertebrates. Tinbergen (1965) described the differences in habitat selection at night and during the day in Black-headed gulls as a response to predation pressure. At night the gulls roosted in exposed, open areas where mammalian predators would be visible from afar whereas during the day, the birds occupy the grassy breeding grounds where mammalian predators would be more difficult to see but where the camouflaged brood is more protected from flying predators. Robinson (1968 a, b, 1969b) described the time influenced behavioral patterns in several mantids and stick insects (Orthoptera) which he, also, said evolved in response to predation pressure. These animals are active at night and assume a cryptic resting attitude during the day unless they are disturbed. Disturbance (such as touching or pinching the insects) triggers escape behaviors such as jumping or dropping from the substrate, startle displays such as suddenly exposing brightly colored wing patterns, or defensive behaviors such as attempts to bite the stimulus.

If the disturbance behaviors shown by U. glomosus developed in response to predation pressure, particularly wasp predation, then they should be seen most frequently during the morning or afternoon when wasps are most active (Coville 1987). If, on the other hand, the shaking behavior is primarily a response to nonflying

predators as Hoffmaster (1982a) suggested, then this behavior should be as frequent in the morning as in the afternoon or evening since nonflying predatory arthropods (i.e. wandering spiders, ants, reduviid bugs) are active all day long.

If stabilimenta and eggsac chains provide cryptic protection for the spider, then spiders that incorporate these structures into their webs should capitalize on their camouflage value by remaining aligned with these structures. Thus, spiders that have either a stabilimentum or an eggsac chain in their web should exhibit the three disturbance behaviors less frequently than spiders without these web structures.

Demonstrating that these factors do influence the disturbance behaviors shown by U. glomosus would only provide inferential evidence that they are predator avoidance strategies. I carried out the second objective of this study to provide direct evidence that these behaviors are effective predator avoidance strategies by observing U. glomosus in a natural setting. Their behaviors were watched continuously for many days in hopes of witnessing predator-prey interactions between the spiders and their natural enemies.

METHODS AND MATERIALS: SURVEYS AND FILMING

Adult Survey:

Spiders living in shrubbery at three sites on the Virginia Tech campus were studied during June and July, 1986. Two-hundred-twenty-two observations were made during the morning (08:00 - 10:00), 227 during the afternoon (12:00 - 14:00), and 146 during the evening (17:00 -19:00) for a total of 595 observations. Since adult male U. glomosus lack a cribellum and do not build typical capture webs (Opell 1979), I used only adult females in this study. Each day I made observations, I recorded the temperature. Temperature was recorded on only one day during the morning (25.9 °C. The mean temperature during the afternoons was 35.6 °C (s.d. = 4.81); the mean during the evening was 28.5 °C (s.d. = 0.70).

For each intact web at a site I recorded the time of day of the observation; presence of a linear stabilimentum or of an eggsac chain; alignment of the spider with the stabilimentum or with the eggsac chain (spiders had either a stabilimentum or eggsac chain, never both); and the behavior the spider exhibited when disturbed. As a stimulus I lightly touched the venter of each spider with a 13 mm diameter rubber pipette bulb on the end of a 4 mm diameter, 45 cm long dowel rod. Using the dowel rod minimized the influence of my presence. The rubber bulb was considered an approximately standardized stimulus similar in size to the rubber

pencil eraser used by Tolbert (1975) in his study of predator avoidance behaviors.

The data collected were analyzed using a log-linear analysis designed for multivariate categorical data (Fienberg 1987, Bishop et al. 1975). As spiders were not marked or removed after testing, there were compounding problems of analyzing the three time sub-surveys at each site together: some individuals' responses would have been recorded two or three times while others' only once. Since the log-linear analysis viewed each time subsurvey separately these compounding factors probably had little effect on the final model selected.

Juvenile Survey

During August and September 1987, I conducted a similar survey of juvenile (3rd and 4th instar) U. glomosus in the field. This survey differed from the adult survey in four ways: 1) Since juvenile U. glomosus males spin typical capture webs, this survey included both males and females. As male and female uloborids cannot be easily distinguished until they enter the penultimate (5th) instar, the sex of the individuals tested could not be determined. 2) Being juveniles, these spiderlings never had eggsac chains in their webs. However, some individuals had circular rather than linear silk stabilimenta. 3) The stimulus used for this

juvenile survey was a 4 mm diameter plastic sphere affixed to the end of a 4 mm diameter, 15 cm long wooden applicator stick. (Third and 4th instar spiderlings, the only stadia observed during this survey, are approximately 4 - 5 mm long.) Relative to spider size, this stimulus was approximately the same size as that used in the adult survey. The spiderlings were ventrally contacted in a similar manner. 4) The same three campus sites were used in both the adult and juvenile surveys, but in the juvenile survey, the morning, afternoon, and evening sub-surveys were conducted at different bushes within the limits of each site. This ensured that no individual would be tested more than once, thus avoiding the confounding problems of the adult survey data. Adults and juveniles from the different sites on campus were assumed to be samples from a single population, although dispersal distances for these spiders have not been documented. There were 1800 total observations in this survey: 600 during the morning, the afternoon, and the evening. I also recorded the temperature during each subsurvey. The mean temperature during the mornings was 20.7 °C (s.d. = 6.32); during the afternoons, 26.1 °C (s.d. = 4.14); and during the evenings, 23.8 °C (s.d. = 5.06).

To determine the stadium of juvenile spiders I collected every 10th individual and measured the length

of its carapace and first femur. I compared these data with the values used by Opell (1987) to assess the stadia of U. glomosus from the same population.

As in the adult survey, at each site I recorded time of day; presence of a silk stabilimentum; alignment with the stabilimentum; and disturbance behavior shown by the spiderling. These data were also analyzed using a log-linear analysis.

Filming:

I used a VHS (video home system) camera to obtain qualitative information on the adaptive value of these behaviors as predator avoidance strategies. The camera was set up on a tripod on the open porch of a farmhouse in rural Montgomery County, Virginia that supported a natural population of U. glomosus. An adult U. glomosus female was allowed to build a web within a 22 x 22 cm square horizontal frame constructed of wooden dowel rods. This frame was then hung from the rafters of the porch directly beneath an active mud dauber nest (genus Trypoxylon). When a spider disappeared or refused to build a web for several days it was replaced with another adult female. Eight females were filmed. Except for a two week period these spiders were filmed from about 08:00 to 19:00 nearly every day from late June through August 1987, for a total of about 280 hours. I used

six-hour VHS videocassette tapes to minimize disturbance during the filming episodes and reviewed them in fast forward mode.

To more precisely define and describe the disturbance behaviors, I filmed adult females with a Super 8 mm movie camera as they jumped from and shook their webs in response to contact stimuli (the tip of a finger). As uloborids often shake their webs during prey capture, I also filmed the shaking behavior of an adult female when fruit flies were placed in her web. I then compared this shaking behavior with the shaking disturbance behavior.

RESULTS: SURVEYS AND FILMING

In the adult population, 50.2% of the spiders jumped from the web in response to contact, 12.8% moved to the edge of the web, 32.9% remained motionless (most of which were spiders with eggsac chains), and 4.0% shook the web. In the juvenile population, 26.9% of the spiderlings jumped from the web in response to disturbance, 45.4% moved to the edge of the web, 3.6% remained motionless, and 24.1% shook the web. (Data tables for these two surveys are presented in appendices 1 and 2).

Adult Survey:

Four variables were recorded during the adult survey: time of day (T); stabilimenta/eggsac, called stabsac (S); alignment of the spider with either stabilimentum or eggsac chain (A); and response of the spider to disturbance (R). Each variable had several levels, as follows: TIME: 1 = morning, 2 = afternoon, 3 = evening; STABSAC: 1 = linear silk stabilimentum, 2 = eggsac chain, 3 = neither; ALIGNMENT: 1 = aligned, 2 = not aligned, 3 = no web structure to align with; RESPONSE: 1 = jumped from the web, 2 = moved to the edge of the web, 3 = remained in position (no response), 4 = shook the web.

To evaluate the associations between these variables the data were fitted to a log-linear model (Bishop et al. 1975, Fienberg 1987). The null hypothesis for the model selection states that a given model is a good fit to the data. Therefore, a model with a p-value > 0.05 is a good fitting model. The model thus selected indicated two-way interactions between the following 5 pairs of variables: TIME and RESPONSE (TR); TIME and ALIGNMENT (TA); RESPONSE and ALIGNMENT (RA); RESPONSE and STABSAC (RS); and STABSAC and ALIGNMENT (SA). The G^2 value of this model was 30.99 with 25 degrees of freedom resulting in a p-value of 0.1892 indicating the model was a good fit to the data. Adding the two-way interactions

between TIME and STABSAC did not improve the model's fitness. No higher order (i.e. three-way) interactions were found to significantly contribute to the fitness of the model.

Figures 2 - 6 illustrate these 5 associations. In each of these graphs, the y-axes are the estimates of the log-linear parameters in the model. The x-axes are the levels of one of the two variables in the association; the lines are the levels of the second variable in the association. The greater the separation of the lines, the greater the contribution of those levels to the interaction between the two variables. These points do not summarize values of the raw data but, portray parameters estimated by the model. Appendix 1 reports the actual values from which this model was computed.

The table below each graph displays the ratios of the log-linear parameter estimates to the standard errors. The standard errors are calculated according to the "delta" method (Bishop et al. 1975, Lee 1977). As these ratios are calculated under the assumption of normality, the values in the table are treated as values in a Z-Table. Ratios greater than $/1.96/$ correspond to a p-value < 0.05 . Therefore, those ratios $> /1.96/$ indicate interactions contributing most to the significant association between the two variables. Positive ratios indicate a positive association between

those levels of the variables, and negative ratios indicate a negative association between the levels.

According to the model (Fig. 2), adult spiders tend to be aligned with their stabilimentum or eggsac chain in the morning (ratio = 2.733), but are not aligned in the evening (ratio = 2.168). There is no tendency for either alignment or non-alignment in the afternoon (ratio < /1.96/).

Figure 3 indicates that in the morning spiders tend to shake the web when disturbed (ratio = 2.432) but do not move to the edge of the web (ratio = -2.879). In the afternoon spiders show no striking preference for one disturbance behavior over another (all ratios are < /1.96/). In the evening spiders show a weak tendency to move to the edge of the web when disturbed (ratio = 1.819). Spiders that jump from the web when disturbed do not do so more during one time of the day than another. The same is true for spiders that show no response to disturbance.

Of the spiders that have either a linear silk stabilimentum or an eggsac chain in the web (Fig. 4), the former move to the edge of the web when disturbed (ratio = 4.674), show some tendency to jump from the web (ratio = 1.839), and tend not to remain in position or show no response (ratio = -7.856). Spiders with an eggsac chain in the web show no response when disturbed (ratio =

7.856). These spiders tend not to move to the edge of the web (ratio = -4.674) and show a weak tendency not to jump from the web (ratio = -1.839). The kind of web structure a spider has (stabilimentum or eggsac chain) has little effect on the occurrence of the shaking response (ratios < /1.96/).

Spiders that are aligned with either silk stabilimentum or an eggsac chain (Fig. 5) show some tendency (ratio = 1.886) to remain motionless (no response) when disturbed and do not jump from the web (ratio = -2.711). Spiders that have either silk stabilimenta or eggsacs but are not aligned with these web structures jump from the web when disturbed (ratio = 2.711) and show some tendency not to remain motionless (ratio = -1.886). There is little difference between spiders that move to the edge of the web or shake the web in terms of their alignment with web structures (ratios < /1.96/).

Spiders that have an eggsac chain in the web are found aligned with that web structure (ratio = 2.117) more often than spiders with a linear stabilimentum (ratio = -2.117) (Fig. 6).

Spiders that had neither silk stabilimenta nor eggsacs in their webs had no web structures with which to align. This led to structural zeros in the data table matrix (Bishop et al. 1975) for the variables STABSAC and

ALIGNMENT. Because of this, the data for these spiders were analyzed separately. A two-way contingency table analysis was conducted comparing the interaction between the time of day and the response variables for these spiders. This analysis indicated independence between the two variables ($X^2 = 7.28$, d.f. = 6, $p = 0.2956$). Therefore, to detect any patterns among the four levels of the response variable for these spiders having neither stabilimenta nor eggsac chains, a second log-linear analysis fitted these data to a model that treated the TIME and the RESPONSE variables separately (i.e. no two-way or higher order interaction terms in the model).

The ratio of the log-linear parameter estimate to its standard error (Table 1) shows that spiders with no web structures jump from their webs when disturbed (ratio = 10.979). These spiders do not remain motionless when disturbed (ratio = -3.379), and they do not shake the web (ratio = -3.852).

Juvenile Survey:

As in the adult survey, four variables were recorded during the spiderling survey: time of day (T); presence of a silk stabilimentum (S); alignment with the stabilimentum (A); and response of the spiderling to disturbance (R). Each of these four variables (as in the adult survey) had several levels: TIME: 1 = morning, 2 =

afternoon, 3 = evening; STABILIMENTA: 1 = linear stabilimentum, 2 = no stabilimentum, 3 = circular stabilimentum; ALIGNMENT: 1 = aligned, 2 = not aligned, 3 = no stabilimentum to align with; RESPONSE: 1 = jumped from the web, 2 = moved to the edge of the web, 3 = remained in position or showed no response, 4 = shook the web.

Juvenile U. glomosus occasionally had a circular stabilimentum at the hub of their webs. A spiderling was considered aligned with this circular stabilimentum if it was resting entirely beneath this thickened silk "platform."

Figure 7a is a plot of carapace length and first femur length measurements collected by Opell (1987) to assess the stadia of field U. glomosus. Figure 7b is the plot of these same measurements for every 10th juvenile spider observed, and subsequently collected, during the juvenile survey. These plots show that all the juveniles were in either the third or fourth stadia.

To detect associations between the TIME, STABILIMENTA, ALIGNMENT, and RESPONSE variables, the juvenile survey data were fit to a log-linear model (Bishop et al. 1975, Fienberg 1987). This model was one that indicated two-way interactions between 4 pairs of variables: TIME and RESPONSE (TR); TIME and ALIGNMENT (TA); TIME and STABILIMENTA (TS); and STABILIMENTA and

ALIGNMENT (SA). This model had a G^2 value of 31.44 with 29 degrees of freedom and a p-value of 0.3449 (indicating a good fitting model). Adding the two-way interactions between RESPONSE and STABILIMENTA or between RESPONSE and ALIGNMENT did not contribute to the fit of the model. No higher order (i.e. three-way) interactions were found to significantly contribute to the fitness of the model.

Figures 8 - 11 illustrate these 4 interactions. The interpretation of these figures is the same as for Figures 2 - 6 of the adult survey analysis.

Figure 8 indicates that in the morning juvenile spiders do not shake their webs when disturbed (ratio = -4.418), and that they do not preferentially exhibit any one of the other three possible responses (ratios $< /1.96/$). In the afternoon, juveniles do not remain in position when disturbed (ratio = -2.455) and they do shake the web (ratio = 2.576). In the evening, juveniles do not jump from the web when disturbed (ratio = -2.146); they do not move to the edge of the web (ratio = -2.895); and they do shake the web (ratio = 2.290).

Figure 9 indicates that in the morning spiderlings are aligned with either the linear or the circular stabilimenta (ratio = 2.491 for spiderlings aligned; ratio = -2.491 for spiderlings not aligned). However in the afternoon they are not so aligned (ratio = -3.670 for spiderlings aligned; ratio = 3.670 for spiderlings not

aligned). There is no tendency for either alignment or for non-alignment in the evening (ratios $< /1.96/$).

Figure 10 shows that in the morning and afternoon there is no pattern to the kind of stabilimentum (linear or circular) found in juveniles' webs (ratios $< /1.96/$). In the evening, however, spiderlings tend to have linear (ratio = 2.993) rather than circular (ratio = -2.993) stabilimenta .

Figure 11 indicates that spiderlings with circular stabilimenta are more likely to be aligned (ratio = 3.645) than spiderlings with linear stabilimenta (ratio = -3.645). (In fact, only 3 of the 129 spiderlings with circular stabilimenta were not aligned with this web structure.)

Because spiderlings with neither linear nor circular stabilimenta in their webs had nothing to align with, the data table contained structural zeros for the variables STABILIMENTA and ALIGNMENT. Therefore, the data for these spiderlings' webs were analyzed separately. A two-way contingency table analysis compared the interaction between the TIME of day and the RESPONSE variables for these spiderlings. This analysis indicated responses of the spiderlings with no stabilimenta in their webs is correlated with the time of day ($X^2 = 23.805$, d.f. = 6, $p = 0.0006$, rejection of the null hypothesis of independence).

To detect the patterns of these interactions I calculated the parameter estimates and the corresponding ratio terms by fitting the saturated log-linear model with the two-way interaction term between time and response (Fig. 12). The G^2 value for a saturated model is always 0 (as are the degrees of freedom and the corresponding p-value).

Figure 12 shows that during the morning spiderlings without stabilimenta do not shake their webs in response to disturbance (ratio = -3.752) and show no preference for any one of the other three possible responses (ratios $< /1.96/$). In the afternoon these spiderlings shake their webs (ratio = 2.850), but show no preference for any of the other three possible responses (ratios $< /1.96/$). In the evening, spiderlings with no stabilimenta show some tendency not to move to the edge of the web (ratio = -1.850) but they show no other behavioral preference (ratios $< /1.96/$).

Filming:

Table 2 summarizes the behaviors recorded on film. All of the behaviors listed in the table occurred between 11:45 and 19:00. Jumping (as defined earlier) was shown by two different adult female spiders (#2 and #3). Neither female had eggsacs in her web. One female jumped from the web when contacted ventrally through the web by

a wasp, probably of the families Sphecidae or Pompilidae, but it is impossible to positively identify it from the film. The spider remained off the web for approximately 20 seconds before she began ascending. The predator-prey interaction occurred about 14:50 on September 4, 1987. The spider was resting in a cryptic posture at the hub of the web before she jumped. This entire behavioral sequence is illustrated in Figure 13.

A different female (#3) jumped from her web at approximately 18:00 on September 22. She also had no eggsacs and was resting in a cryptic posture at the edge of the web next to a wooden frame stick. A long antennae grasshopper (suborder Ensifera) (approximately 15 mm long) walked along the frame stick toward the spider. When one of the insect's antennae contacted the spider, she jumped from the web. She remained off the web approximately 3 minutes before beginning her ascent.

At about 18:00 and again at 19:00 on September 11, this same female (#3) shook her web (a behavior also described earlier). The cause was unknown (possibly an insect too small to be seen on film). Before shaking her web, this female was resting in a cryptic posture at the edge of the web next to a wooden frame. At 16:50 on September 28, this female was again resting in a cryptic posture at the edge of the web next to the wooden frame stick when a Reduviidae (approximately 20 mm long) walked

along the frame stick. The insect contacted the spider with an antenna, and the female responded to this contact by shaking her web. The Reduviidae stopped briefly then continued along the frame stick.

This female (#3) displayed an unusual behavior I have termed "centripetal saltation." When disturbed, she released her hold on the web with her first two pairs of legs and, using a dragline, propelled herself to another part of the web where she regained her hold. She showed this behavior five times on September 20 between 12:00 and 16:48 and two times on September 21 between 18:00 and 19:00. On all of these occasions, the spider was resting in a cryptic posture at the edge of the web next to the frame stick. Five of these centripetal saltations were triggered by contact with an approximately 3 mm long insect (probably an ant) crawling on the frame stick next to the spider. Two times the stimulus was indiscernible. This female also showed the behavior at about 16:00 on September 25 after being contacted by a similar small insect. On September 28, the female showed the centripetal saltation behavior after being contacted by the antenna of an approximately 12 mm long grasshopper walking along the frame stick.

Another female (#1) displayed an eggsac defense behavior (described in Chapter 3) on August 28 at about 18:30. The female was in a cryptic posture at the hub of

her web aligned with a long chain of eggsacs. A caterpillar (approximately 25 mm long) was seen crawling along the eggsac chain. The spider jerked the web several times (eggsac defense behavior) in response to the caterpillar, causing the caterpillar to fall from the eggsac chain.

On September 27 at about 14:30, this female (#1) shook her web in response to a small insect caught in the web. The spider, while shaking the web, approached the prey item and began wrapping it. Although similar, this prey capture shaking is distinguishable from the shaking disturbance behavior. Super 8 mm films showed that, when shaking the web prior to prey wrapping, spiders extend their first two pairs of legs and use them to manipulate the prey item. The shaking results principally from alternate flexion and extension of the third pair of legs and from alternate lowering and raising of the abdomen in the web plane. The fourth pair of legs serve primarily to hold onto the web. In contrast, the shaking response described earlier involves, primarily, alternate flexion and extension of the long front legs and, to a lesser extent, the second pair of legs. The third and fourth pairs of legs show no obvious involvement in generating these rhythmic oscillations.

As the wooden frames on which the filmed spiders were maintained were hung from a porch ceiling just below

an active Trypoxylon nest, wasps often flew very close to the spiders as they entered and left their nests. A flying wasp seen on film was scored as an encounter if it flew within 3 cm of the spider. Seventeen such "close encounters" were recorded. Three of these occurred around 09:00 on September 1; the remainder occurred between 12:00 - 17:00 on August 31, September 1, and September 17. In 16 of the 17 encounters, the spiders showed no response to the presence of the wasp, even when the wasp was flying very close to the spider. Only once did the spider respond to the presence of the wasp. On this occasion the Trypoxylon, while crawling along the ceiling from its nest, contacted the spider's web and the spider moved from the hub to the edge of the web.

DISCUSSION: SURVEYS AND FILMING

The results support the hypotheses that: 1) the jumping behavior is an effective predator avoidance strategy; 2) time of day does influence the disturbance behaviors shown by adult and juvenile U. glomosus; 3) for adult U. glomosus, alignment with the web structures does influence the disturbance behaviors shown by the spiders; and 4) both adult and juvenile spiders with no web structures do exhibit different frequencies of the disturbance behaviors than spiders with these web structures.

The survey analyses reveal the associations existing among the variables TIME, RESPONSE, STABSAC (or STABILIMENTA), and ALIGNMENT. However, when reviewing the results of these analyses, it should be kept in mind that only 4.0% of the adults showed the shaking response (regardless of the other variables) while most of the adults (50.2%) jumped from the web. Also, only 3.6% of the juveniles remained motionless (or showed no response) while the majority of the spiderlings (45.4%) moved to the edge of the web (regardless of the other variables).

The survey showed that adult U. glomosus which either had web structures but were not aligned with them or had no web structures, showed a strong tendency to jump from the web when disturbed. Those spiders that did have web structures and jumped tended to have linear stabilimenta rather than eggsac chains. This suggests that the web structures are enhancing the spider's crypsis and when the spider either does not have the structures or has them but does not utilize them to hide itself, it escapes from the plane of the web when disturbed. This also suggests that alignment with web structures and the jumping behavior are responses against visually hunting predators. The filming provided direct qualitative evidence that the jumping behavior is an effective avoidance strategy against visually hunting predators.

The surveys demonstrated that time of day does influence the disturbance behaviors shown by the spiders. During the morning, adult females with either linear stabilimenta or eggsacs shook the web but did not move to the edge of their webs. However, during the evening, they did move to the edge of their webs when touched. Regardless of the presence of a stabilimentum, third and fourth instars did not shake the web in the morning, shook the web in the afternoon, and did not move to the edge in the evening. If their web lacked a stabilimentum, they did not remain motionless in the afternoon, did not jump in the evening, and shook the web in the evening. The time of day did not influence the responses of adults without web structures. If they had web structures, adults were more likely to shake their webs in the morning; whereas juveniles both with and without web structures preferentially show this behavior in the afternoon and the evening. These results suggest that adults and juveniles may be under pressure from different groups of predators. Alternately, juveniles may change their responses during development due to physiological changes, or these responses may be learned.

Neither adults nor juveniles with web structures seem to prefer the jumping response during any part of the day. This supports the hypothesis that stabilimenta and eggsacs protect the spiders, and that those with

these structures are less likely to show a costly avoidance strategy (jumping). However, the evidence for this is stronger for adults than for juveniles. Although adults aligned with web structures tend to remain motionless when disturbed, those that are not aligned jump from the web.

The survey analyses suggest that eggsacs are better camouflage devices than stabilimenta. More spiders with eggsacs are found aligned with these web structures than are spiders with stabilimenta, and spiders with eggsacs show a much stronger tendency to remain motionless when disturbed than spiders with stabilimenta. An alternate explanation is that the spider is actually providing some kind of protection for the eggsac. This hypothesis is considered in a later chapter.

The interaction between response and stabilimenta and between response and alignment with the stabilimenta is not significant for juvenile U. glomosus. However, juveniles with circular stabilimenta are more often found aligned with the silk platform (i.e. situated directly beneath it) than spiderlings with linear stabilimenta. This supports the Robinsons' hypothesis (1970, see general introduction) that circular stabilimenta may make the spiderlings more cryptic to visually hunting predators. The filming provides indirect evidence to support the hypothesis that web structures are protecting

the spiders: although the jumping response was only seen twice in the 280 hours of filming, neither spider which showed this response had any web structures. The spiders which shook the web in response to disturbance also had no web structures.

INTRODUCTION: CONSISTENCY STUDY

In the population studies (the adult and juvenile surveys) I found that time of day influenced the disturbance behaviors expressed by the spiders. Because individual spiders observed during the surveys were not marked, there remains the unlikely possibility that these results were an artifact of sampling technique (i.e. sampling more consistent movers in the morning and more consistent shakers in the evening) rather than the result of individual spiders switching their behavioral responses. The purpose of this study was to determine how consistently the four responses to disturbance (jumping from the web, shaking the web, moving to the edge of the web, and remaining motionless) were expressed by individual Uloborus glomosis, both throughout a day and over a period of several days.

If these behaviors are primarily responses to wasp predation pressure, I expected that individual spiders would switch their behavioral strategy from morning to afternoon to evening as wasps are most active during the morning and afternoon. I also expected the pattern of switching for each behavior to be similar to that detected in the adult survey. If the behaviors either occur randomly or in response to generalized predators such as birds or other spiders (which are active all day

long), I expected no behavioral switching among the individuals.

Hoffmaster's (1982 a) study suggested that the shaking response is particularly effective against nonflying visually hunting predators such as other spiders. My survey and filming studies suggested that the jumping response is particularly effective against wasp predation. If this is the case, I expected to detect behavioral switching among spiders that more consistently displayed the jumping response but not among those that more consistently showed the shaking response.

METHODS AND MATERIALS: CONSISTENCY STUDY

Forty-nine adult female U. glomosus without eggsacs were collected from shrubbery on the Virginia Tech campus. (Although many of these females subsequently produced eggsacs, this factor was not considered in the analysis.) Twenty-five of these spiders were collected in mid-July, 1987 and assigned to group I. The others were collected in late July and formed group II. All were maintained in a wooded area in Blacksburg, Virginia under natural light, temperature, and humidity conditions.

Spiders in group I were individually identified by applying small dots of green and red enamel paint to their dorsal abdominal surfaces. These dots were observed by holding a long-handled dental mirror beneath

the spider. Group I spiders were established on six arachnothrombi, each of which provided a vertical series of 25 wooden dowel rods spaced 12 cm apart (Fig. 14). Each rod was 8 mm in diameter and 50 cm long. These spiders chose their own web attachment sites on this apparatus. The arachnothrombi were kept in a 3 x 3 x 3 m screened enclosure to prevent dispersal away from the test area.

Group II spiders were kept in 31 x 16.5 x 9 cm plastic shoeboxes covered with mosquito netting and placed under a taut plastic tarpaulin roof just outside the screened enclosure housing group I spiders. I began testing group I on July 13, and group II 7 days later. Group I spiders were removed and the experiment terminated after 19 days of testing. Group II spiders were tested for 39 days.

For both groups, I disturbed all spiders in the morning (08:00 -10:00) of day 1 of the tests and recorded their behaviors. On day 2 I disturbed all the spiders in the afternoon (12:00 - 14:00) and on day 3 I disturbed them in the evening (16:00 - 18:00). Spiders were not disturbed on day 4 to ensure 24 hours between tests. This 24 hour testing sequence was chosen to prevent the degeneration of the behaviors from too frequent disturbances. On day 5, the 3-day cycle, hereafter referred to as a block, was resumed (Table 3). Group I

spiders were run for 5 blocks (15 days of actual testing) and group II spiders for 10 blocks (30 days of actual testing).

To supplement their diet, I fed all spiders with several fruit flies (Drosophila species) blown into their webs, either after testing in the evening of the three day cycle or on the fourth (non-test) day. Temperature was recorded every day observations were made. The mean temperature during the morning tests was 19.8 °C (s.d. = 5.86); the mean during the afternoon tests was 27.9 °C (s.d. = 5.48); and the mean during the evening tests was 27.0 °C (s.d. = 6.43).

As a stimulus I dropped water on the venter of each spider from a Pasteur pipette (with an average tip diameter of 1.20 mm) held 1 cm above the spider. This method was suggested by W. G. Eberhard (personal communication) as a more standardized contact stimulus than the rubber bulb used in the previous survey study. Preliminary tests showed no difference between either stimulus in triggering the behaviors. After stimulating the spider, I recorded its response to this disturbance as either: jumping out of the web, moving to the edge of the web, showing no response, or shaking the web.

If a spider died or disappeared before half of the observations were completed, then all the previous observations for that individual were eliminated from the

data set. Therefore, a spider from group I had to survive through block 3 for its behaviors to be included in the analyses and one from group II had to survive through block 5. Observations for 22 group I and for 21 group II spiders were used in the final analyses.

Because there were too few observations per individual to statistically determine the consistency of that spider's responses, the data were pooled. To evaluate the consistency of the behaviors between blocks (i.e., over the entire testing period) I conducted two log-linear analyses (Fienberg 1987, Bishop et al. 1975). One analysis compared the four behavioral categories during blocks 1 through 5, pooling the data for the 43 spiders for a total of 631 observations. Since group I spiders were discontinued after block 5, the second analysis compared blocks 6 through 9 for the 21 group II spiders for a total of 231 observations.

To determine the consistency of the behaviors between the time periods (morning, afternoon, and evening) I pooled the observations for each of the four behavioral categories made during each of the three time periods across all 43 spiders for a total of 862 observations. I conducted a log-linear analysis of these data to detect any patterns of behavioral switching that might have occurred.

RESULTS: CONSISTENCY STUDY

Over the entire testing period, spiders jumped in response to contact 53.0% of the time, they moved to the edge of the web 5.8% of the time, they remained motionless (no response) 17.0% of the time; and they shook the web 24.1% of the time. Data tables of these results are presented in Appendix 3.

Consistency Over Time:

To evaluate the consistency of the behaviors over the first five blocks for groups I and II combined, I used a two-way contingency table analysis comparing the interaction between the BLOCK and the RESPONSE variables. This analysis indicated that the pattern of these spiders' responses changed over the 15 day course of these observations ($X^2 = 23.860$, d.f. = 12, $p = 0.0213$, rejection of the null hypothesis of independence).

To detect the patterns of these interactions I calculated the parameter estimates and the corresponding ratio terms by fitting the saturated log-linear model with the two-way interaction term between BLOCK and RESPONSE (Fig. 15). (For the interpretation of Figures 15 - 17, see Chapter 1 results.) The G^2 value for a saturated model is always 0 (as are the degrees of freedom and the corresponding p-value).

Figure 15 shows that the jumping response increases

with time, occurring less frequently in Block 1 (ratio = -3.473) than in Block 4 (ratio = 2.511). It also indicates that more spiders show a tendency to remain motionless, or show no response, by Block 5 (ratio = 1.911). According to this analysis, the moving and shaking responses do not change over the course of these observations (ratios $< /1.96/$) and the only change in the frequency of no response occurs in Block 5.

To evaluate the consistency of the behaviors for the 21 group II spiders over the last four blocks (6 - 9), I used a two-way contingency table analysis comparing the interaction between the BLOCK and RESPONSE variables. This produced a Pearson's chi-square value of 24.697 with 9 degrees of freedom ($p = 0.0033$) leading me to reject the null hypothesis of independence between the two variables.

To detect the pattern of these interactions I calculated the parameter estimates and the corresponding ratio terms by fitting the saturated log-linear model with the two-way interaction term between BLOCK and RESPONSE. Figure 16 shows that the jumping response occurs more frequently in Block 6 (ratio = 2.941) and that there is no change in this behavior from Block 7 - Block 9 (ratios $< /1.96/$). It also demonstrates an increasing tendency for spiders to remain motionless or show no response over the course of the study: Block 6

ratio = -2.865 and Blocks 8 and 9 have ratios of 2.156 and 2.104 respectively. Moving and shaking responses do not change over the course of these observations.

Consistency Between Time Periods:

To evaluate the consistency of the behaviors from morning to afternoon to evening for groups I and II combined, I used a two-way contingency table analysis comparing the interaction between the TIME and RESPONSE variables. This analysis indicated that spider response is influenced by the time of day ($X^2 = 33.432$, d.f. = 6, $p < 0.00001$).

To detect the patterns of these interactions I conducted a third log-linear analysis for the saturated model with the two-way interaction term between TIME and RESPONSE. Figure 17 indicates that spiders which jump from the web do not show this response in the morning (ratio = -5.541) but do exhibit this behavior in the afternoon (ratio = 2.919) and the evening (ratio = 2.333). Spiders which move to the edge of the web when disturbed do so in the morning (ratio = 2.233). There is no important change in the frequency of this behavior in the afternoon or the evening (ratios $< /1.96/$). Spiders which show no response or remain motionless when disturbed do so in the morning (ratio = 2.107). There is no change in the frequency of this behavior in the

afternoon or the evening (ratios $< /1.96/$). Likewise, there is no change in the frequency of the shaking response from morning to afternoon to evening (ratios $< /1.96/$).

DISCUSSION: CONSISTENCY STUDY

Consistency Over Time:

If the 43 spiders consistently showed the same behaviors over the course of the entire testing period, there should have been no change in the frequencies of the four responses from Blocks 1 through 9. This was the case only for spiders that moved to the edge of their webs and for spiders which shook their webs when disturbed. There was, however, an increase in the frequency of jumping over time: there were fewer jumpers in Block 1 and more by Blocks 4 and 6. There was no clear trend in the frequency of spiders remaining motionless or showing no response when disturbed, although this response, also, was clearly not consistent over time: there were more spiders remaining motionless by Block 5, fewer during Block 6, then an increase by Blocks 8 and 9.

These results suggest that as some spiders age, they change their responses to disturbance. The underlying causes of these changes may be physiological or environmental. For example, spiders that switch from

jumping or shaking or moving to remaining motionless when disturbed may be exhibiting an habituation to the stimulus. Despite the 24 hour testing regime, these spiders may have learned that the contact stimulus was not threatening. Alternately, as a spider ages, it may switch from energetically costly behaviors to energetically conservative behaviors (remaining motionless) to partition its energy resources most adaptively. Nutritional state may also influence the expression of these behaviors. Although the spiders used in these studies were maintained under a standard feeding regime, their weights were not monitored over the course of the study.

Spiders which exhibited a greater frequency of jumping from the web over time may have become sensitized to the stimulus or may be inherently more sensitive to direct disturbance. Alternately, these spiders may have been more effective than others in catching prey or may be younger adults that can afford to expend energy in potentially expensive escape behaviors.

Consistency Between Time Periods:

If the 43 spiders consistently showed the same responses to disturbance from one time period to another, there would have been no changes in the frequencies of the four responses from morning to afternoon to evening.

This was the case only for spiders that shook the web when disturbed. Spiders that jumped from the web did not show this response when tested in the morning, but did jump in the afternoon and the evening. In the morning, spiders moved to the edge of the web or remained motionless.

These results do not support my hypothesis that the jumping behavior is primarily a response to wasp predation but do support my hypothesis that the shaking behavior is a response to predation by nonflying, generalist predators. The jumping behavior (as discussed in the General Introduction) appears to be an expensive behavior, both energetically and strategically. Therefore, it would be to a jumper's benefit to relinquish this behavior during the evening when the stimulus is least likely to be a wasp (Coville 1987) in favor of moving to the edge of the web or shaking the web, tactics that appear more effective (and less expensive) against nonflying predators active in the evening. However, the analysis suggests that spiders that jump from the web in the afternoon and evening move to the edge of the web or remain motionless in the morning.

It is likely that the spider does not depend on an internal clock to decide whether or not to jump from its web when disturbed, but, rather, relies on the exposure of its website to sunlight since sunlight has a direct

influence on the activity patterns of spider hunting wasps. According to Coville (1987), "activity is influenced by temperature, weather, and exposure of the nest to sunlight." Their foraging activity is also influenced by these factors; for example, wasps do not normally forage during overcast conditions (Coville 1987, pers. obs.). There is indirect evidence to support this idea of a sunlight influenced behavior pattern. First, this study was conducted in a wooded area that received only indirect mottled sunlight until about 11:00 every day. In addition, part of the filming (Chapter 1) was conducted inside the same enclosure that previously housed the Consistency spiders. During the filming, I introduced 5 mud-dauber wasps (family Sphecidae) into the enclosure with their mud nests in order to film their interaction with uloborids also in the enclosure. During the entire 3 weeks they were in this shaded enclosure, the wasps were never active before 11:00.

This does not, however, explain why the Consistency spiders showed a preference for the jumping behavior in the evening when wasps would again be inactive (during the filming the wasps in the enclosure stopped activity about 17:00 - 17:30 every day). It may be that, in the evening, spiders slowly decrease their sensitivity to stimuli triggering the jumping behavior just as wasps slowly decrease their foraging activities. As it only

took 1/2 to 1 hour to record observations for all the spiders, I may have tested them during the peak in their evening sensitivity before it began declining.

Nonflying, visually hunting predators such as spiders, ants, and reduviids are active all day long. If the shaking behavior is a response to these predators, then spiders should show this response throughout the day. The results indicate that spiders which shake the web do not switch their behavioral strategy: the behavior is seen at the same frequency throughout the day.

This study provides empirical support for the hypothesis that jumping from the web, shaking the web, and moving to the edge of the web evolved in response to predation pressure. More specifically, the groups of predators each behavior is most effective against can be postulated. The results support the idea that spiders switch their behavioral tactics throughout the day according to what group of predators is most active.

INTRODUCTION: EGGSAC DEFENSE STUDY

In the adult survey (Chapter 1) I found that female Uloborus glomorus with eggsac chains in their webs remained aligned with those eggsacs throughout the day and remained motionless next to the eggsacs when disturbed. Hoffmaster (1982a) described similar behavioral patterns among female Philoponella (=Uloborus) republicana with eggsacs: these spiders did not drop (jump) out of the web in response to jumping spider (Salticidae) attacks. Instead, they moved to the edge of the web, taking the eggsac with them. This was possible because their single, lenticular eggsacs are suspended from, but not anchored into, the web as are those of U. glomorus. Females with eggsacs did not respond to hummingbird (Trochilidae) attacks. Hoffmaster suggests that these behavioral differences between females with and those without eggsacs ". . . is adaptive; by modifying the behavioral response to predation, the spider can protect its investment in the eggmasses."

A chain of lenticular eggsacs greatly enhances a U. glomorus female's crypsis (at least to a human observer). The survey results suggest that alignment with an eggsac chain may protect a female from visually hunting predators. However, this tending behavior also places the female in a position to protect her reproductive

investment by warding off egg predators and parasitoids.

Such eggsac tending behavior is common among wandering spiders in the families Lycosidae, Pisauridae, Salticidae, Thomisidae, Gnaphosidae, Clubionidae, and Oxyopidae (Eberhard 1974, Matlack and Jennings 1977, Gertsch 1979, Fink 1987, Austin in press). Although eggsac tending is most common among wandering spiders, it has also been observed among the web builders Agelenidae (Kaston 1948) and Uloboridae (Patel and Bradoo 1981, Hoffmaster 1982a).

Like the silken eggsacs themselves, this guarding behavior may function to protect the juvenile instars from predation and parasitism (Austin and Anderson 1978, Austin in press). For example, Austin (in press) found that the brooding behavior of female Clubiona robusta L. Koch (Clubionidae) functioned to increase "the survival of eggs or juveniles in nests and to protect them from predation by ants and other potential predators." In this example, females guarding eggsacs killed all intruders greater than 2 mm long that entered the nest. Similar aggressive behavior was described by Eberhard (1974) for brooding females of the salticid Lyssomanes jemineus Peck and Wheel. Patel and Bradoo (1981) say that "the cribellar silk around the cocoon of Uloborus ferokus [Bradoo] effectively prevents and interferes with the ovipositional activity of its eggparasite Idris sp."

Austin (1985) suggests that ". . . assuming that parasitoids and predators of spider eggs have had a long association with their prey, one may expect that such relationships have coevolved, i.e. parasitoids and predators having evolved morphological and behavioural adaptations to breach the eggsac barrier and spiders counteracting this with structurally more complex egg sacs and behavioural adaptations." Uloboridae eggsacs are known to host three different genera of hymenopteran parasitoids and predators: Idris (Scelionidae), Eurytoma (Eurytomidae), and Arachnopteromalus (Pteromalidae) (Austin 1985). Arachnopteromalus dasys Gordh was originally collected from the eggsacs of the uloborid Octonoba sinensis (Simon) (= Uloborus octonarius Muma) (Gordh 1976). I have since collected this species from the eggsacs of U. glomosus in Montgomery County, Virginia. The potential clearly exists for the development of such behavioral adaptations against eggsac parasitism described by Austin. I propose that the strong tendency of female U. glomosus to remain aligned with their eggsacs throughout the day, even when disturbed, is just such a behavioral adaptation, functioning to protect the eggsacs against parasitoids and predators.

METHODS AND MATERIALS: EGGSAC DEFENSE STUDY

Twenty-two adult female U. glomosus with eggsac

chains containing at least two unhatched eggsacs were collected from shrubbery on the Virginia Tech campus in mid-July, 1987. (One spider died before testing began.) Each spider was allowed to build webs on a horizontal 10 x 10 cm wooden frame set inside 10 x 10 x 9 cm plastic freezer containers covered with saran wrap. These containers were kept in an environmental chamber on a 14:10 light:dark cycle. Females were fed and watered regularly and monitored every day to detect the emergence of the small (2.5 mm long) parasitoid wasps, Arachnopteromalus dasys. When the wasps emerged they were individually placed in 5 cm diameter, 7 mm deep plastic petri dishes. Each was provided with a small piece of cotton moistened with dilute honey water.

To determine if the female spiders exhibited protective behavior against these eggsac parasitoids, I placed a wasp on the eggsac furthest from each female, being careful not to touch the eggsacs, and noted how long it took the female to respond to the presence of the wasp. The first response of the female (if any) was recorded along with the eggsac the wasp was on when the female detected it. I also recorded any subsequent (second) behaviors that occurred up to 5 minutes later. The data were analyzed using chi-square tests of independence. Super 8 mm movies were taken of four females responding to the presence of A. dasys on their

eggsacs and the movies used to describe the behaviors.

This experiment was repeated using second and third instar spiderlings instead of wasps. I chose spiderlings closest in size to the parasitic wasps. Eleven of the original 21 females were tested; the remainder had since died.

RESULTS: EGGSAC DEFENSE STUDY

Adult A. dasys began emerging from the eggsacs of two females (#11 and #8) on July 5 at about 10:00. By July 30, 5 wasps had emerged from the eggsacs of female #4, 7 wasps from the eggsacs of female #8, and 16 wasps from the eggsacs of female #11. None of the remaining females had parasitized eggsacs. However, parasitic wasps may have previously emerged from some of the eggsacs that had hatched before I collected them. Therefore, these observations do not yield unequivocal estimates of the rates of parasitism.

Table 4 summarizes the results of placing wasps on the females' eggsacs (females had up to 9 eggsacs in their chains). The most common initial response shown by the spiders was a jerking behavior somewhat similar to the disturbance shaking behavior (see the general introduction for a description of this latter response). The jerking response, when compared to the other first responses pooled, occurs more frequently than expected if

the behavior is a random response among the spiders ($X^2 = 5.76$, d.f. = 1, $p < 0.02$).

Of the three spiders from whose eggsacs the wasps emerged (females #4, #8, and #11): #4 died before testing began; #11 was very sensitive to the presence of the wasp on her eggsacs, jerking the web almost immediately and subsequently turning and walking along the eggsac chain; and #8 took 1 minute to respond at which time she jerked the web twice and subsequently moved away from the eggsac chain.

Super 8 mm films showed that this jerking response, unlike the shaking response to disturbance, is not stimulated by direct contact. A female was typically aligned with her eggsac chain in the posture shown in Figure 1a. The 4th pair of legs or the abdomen touched the most recently constructed eggsac and probably detected the wasp's movement on the eggsacs. There was no association between the eggsac that the wasp was on and the response of the female: 9 out of the 16 times the females initially jerked the web when the wasp was on the last or second to last eggsacs (i.e., the oldest eggsacs, 5 of which were hatched); the remaining 7 times, the wasp was on one of the 3 eggsacs closest to the female, 1 of which was hatched.

The jerking response had two distinct elements: the female flexed all four pairs of legs at the

tibia-metatarsus joints, thus raising her body toward the web; she then extended the legs at these joints. This rapid stilting behavior lowered the spider's body away from the web surface and caused the whole web to oscillate sharply. Unlike the shaking response to disturbance which the spider repeated in rapid succession during the course of several seconds, this jerking behavior was a single event with longer pauses between occurrences.

Three of the spiders showed no response during the five minute trial. Two of the spiders first turned and walked along the eggsac chain. This behavior was the most common second response (13 out of 21 spiders showed it), although a X^2 test of independence comparing this second response with the other four second responses combined resulted in a X^2 value of 1.19 with 1 degree of freedom ($p > 0.1$) leading me to fail to reject the null hypothesis of independence and indicating that this turning response is not shown by a significant number of the spiders. As 15 spiders showed this behavior during the 5 minute trial, it is worth describing. After jerking the web, the spider turned, faced the first eggsac, and began walking along the chain. Sometimes, while walking, a spider paused and jerked the web. As they walked, the spiders stretched their long front legs around the sides of the eggsac chain, touching and sweeping the eggsacs

with the tarsi. Neither during the jerking behavior nor during the leg sweeping did I see a wasp become dislodged from the eggsacs, although while the spider jerked the web, the wasps crouched down and lowered their antennae.

When the 11 surviving females were tested using spiderlings rather than wasps, I found that 5 of the adults initially jerked their webs; 5 showed no response throughout the 5 minute trial; and one turned and faced its eggsacs. Three females who had first jerked their webs also showed this behavior as a second response; 2 showed no second response; and one turned towards the eggsacs.

DISCUSSION: EGGSAC DEFENSE STUDY

Most female U. glomus actively defend their eggsacs against parasitoids. The jerking behavior and the leg sweeping response have not been described previously. Since none of the wasps observed in this study were dislodged when the spider jerked the web, it would seem, at first, that this behavior is not a very effective response against eggsac parasitism. However, it may prevent the wasps from inserting their ovipositors in the eggsacs. Since all the wasps used in this study were separated as soon as they emerged, they were all virgins and, probably, for this reason, did not attempt oviposition. As two of the females from whose eggsacs

the wasps emerged showed the jerking response, it is unclear just how effective the jerking response is, although it takes only one fertile wasp to do a great deal of damage to an eggsac chain.

In the VHS filming study (Chapter 1) I observed both the jerking response and the leg sweeping by a female with a chain of eggsacs. This spider was responding to a caterpillar crawling over the eggsac chain. The jerking behavior proved quite effective at dislodging this insect. In the present study, five females jerked the web in response to spiderlings crawling over the eggsacs. From these observations, it seems that, although the jerking behavior may have evolved primarily as a response against eggsac parasitoids and predators, females cannot distinguish between parasitoids, harmless insects, and progeny crawling along their eggsacs. In other words, they are not responding to a very defined set of stimuli produced only by hymenopteran parasitoids (i.e., A. dasys). Instead they are responding to detectable stimuli produced by anything moving along the eggsac chain.

INTRODUCTION: STIMULUS STUDY

The survey and filming study (Chapter 1) showed that, in Uloborus glomus, the jumping response is an effective avoidance strategy against hymenopteran predators such as wasps of the families Sphecidae or Pompilidae. However, it is unclear what stimuli trigger this response and the other disturbance responses (shaking the web, and moving to the edge of the web). Most orb-weaving spiders, including U. glomus, have poor eyesight but some can perceive changes in light intensity (Foelix 1982). Foelix even mentions that some orb-weavers drop out of their webs when someone approaches them. I have occasionally observed this in U. glomus. Therefore, vision, or perception of the predator's shadow, is one possible stimulus for jumping.

Alternately, air-borne or web-borne vibrations may elicit these behaviors. Air-borne vibrations are primarily detected through long sensory setae called trichobothria, located on the walking legs and pedipalps, whereas slit sense organs, located in the cuticle of the legs, are responsible for detecting web-borne vibrations and, to a lesser extent, air-borne vibrations (Barth 1982). These two types of sensory organs detect vibrations of less than 1 kHz. Trichobothria respond to frequencies of 45 Hz and greater (Harris and Mill 1977)

whereas slit sense organs are sensitive to frequencies as low as 1 Hz (Bohnenberger 1981).

Frings and Frings (1966) exposed three orb-weaving araneid species (of the genera Araneus and Argiope) to a wide range of frequencies of both air-borne and web-borne vibrations and described the elicited behaviors. They found that spiders attacked the stimulus, shook the web, or dropped (jumped) from the web when exposed to web-borne vibrations; they jerked their webs, extended their legs, or shook the web in response to air-borne vibrations. Klarner and Barth (1982) describe individuals of the araneid Nephila raising their first two pairs of legs in response to a buzzing fly held above the spiders. They considered this behavior a defensive response (presumably against flying predators).

Hoffmaster (1982b) studied the effects of low frequencies (0.017 - 14 Hz) on the occurrence of attack, pumping (shaking), and dropping (jumping) behaviors in a species of the araneid Argiope. She found that the majority of spiders which jumped or shook the web did so in response to a vibrational stimulus (a vibrating glass rod) contacting the abdomen. Few of the Argiope jumped from the web, but, of those that did, most were also responding to vibrational stimuli contacting the abdomen. This example suggests that direct contact stimuli may elicit escape or defensive responses in orb-weaving

spiders.

The purpose of the present study was to determine what stimuli (visual, air-borne, web-borne, or tactile) are primarily responsible for eliciting the jumping, moving, and shaking responses shown by U. glomosus. Previous studies (Chapters 1 and 2) indicated that contact stimuli were sufficient to elicit these responses, however these results do not preclude the possibility that other stimuli may also be involved.

METHODS AND MATERIALS: STIMULUS STUDY

This study was conducted in an experimental room under natural light at an average temperature of 70.6 °F (s.d. = 4.53) between 18 September and 7 October 1987. Fourteen 2nd and 3rd instar lab-reared spiderlings and 9 adult females (survivors from the Consistency Study - Chapter 2) were used. The 14 spiderlings were all siblings, having emerged from the eggsacs of one of the adults used in the study. All 9 adults had eggsac chains.

Since predatory wasps emit both visual and vibrational stimuli, I decided to use a tethered wasp as an preliminary stimulus. This decision was based on the assumption that if spiders did not respond to an organism emitting all the stimuli I was interested in, they would not respond to the separate stimulus components.

Therefore, a spider hunting wasp, family Pompilidae, was collected and a long piece of thread glued to its thorax in such a way that wing movement was not impaired. To prevent the wasp from flying in wide circles (i.e. to concentrate its movements), I lowered a clear plastic drinking straw over the thread and used this as a "handle."

To test the responses of the spiderlings to a contact stimulus I dropped water on the venter of each juvenile from a modified Pasteur pipette (with an average tip diameter of 0.51 mm) held 1 cm above the spiderling. Since all the adults had been used for the Consistency Study (Chapter 2), I had an accurate record of each individual's responses to a contact stimulus and did not re-test these spiders' responses. I tested the spiderlings' responses to the contact stimulus on two different days (trials 1 and 2). Several days later I tested the juveniles and the adults with the tethered pompilid wasp. The buzzing wasp was slowly lowered until its legs (hanging down from its body) were within 1 - 3 cm of the adult or the spiderling. The wasp was never allowed to actually contact the spider. This test was repeated on two separate days for a total of three trials.

The day after the final trial with the wasp, I again tested all 23 spiders for their responses to the

contact stimulus (water droplet). I used a Pasteur pipette with an average tip diameter of 1.20 mm for the adult spiders. The data were analyzed using a two-way contingency table analysis.

Earlier in the year (June and July 1987), I measured the wingbeat frequency of tethered Sphecidae wasps of the genera Sceliphron, Trypoxylon, and Chalybion and, later, of the Pompilidae wasp used in this study. I recorded the wasps directly into a Sona-Graph 7029-A sound spectograph.

RESULTS: STIMULUS STUDY

The data are summarized in Table 5. Data listed under Trial 1 for the adults are from the last observations recorded for these 9 individuals during the Consistency Study (Chapter 2). One of the spiderlings used in Contact Stimulus Trial 1 had no web and could not be tested. This individual had made a web by Trial 2 so all 14 spiderlings were tested.

Most of the juveniles and 7 of the adults showed some kind of active behavior (jumping or moving or shaking) in response to the droplet of water during the initial contact stimulus trial. During the three trials with the tethered wasp, only 2 spiderlings ever showed an active behavior in response to these visual and vibratory stimuli. None of the adults showed an active response to

the wasp during any of the three trials. In the final trial all of the spiderlings and 7 of the adults actively responded to the contact stimulus of a water droplet.

To determine the statistical significance of these results, I pooled: the Contact Stimulus Trial 2 observations for the spiderlings with the Contact Stimulus Trial 1 observations for the adults; the Tethered Wasp Trial 1 observations for the spiderlings with the observations for the adults; and the Contact Stimulus Trial 3 observations for spiderlings with the observations for the adults. Within each trial, I pooled all the observations for the three active behaviors giving me the two RESPONSE categories: active response and no response. I chose these trials because they were the least biased towards rejection of the null hypothesis of independence between the RESPONSE variable and the TRIAL variable (initial trial with the contact stimulus, trial with the tethered wasp, and final trial with the contact stimulus). The two-way contingency table analysis comparing RESPONSE with TRIAL resulted in a X^2 value of 35.80 with 2 degrees of freedom ($p < 0.005$) leading me to reject the null hypothesis of independence. This indicates that the response of the spiders is influenced by whether the stimulus is a contact stimulus or the set of stimuli produced by wasps.

Recordings of wingbeat frequencies showed that Sceliphron (Sphecidae) has frequency bands ranging from 75 - 275 Hz; Trypoxylon (Sphecidae) produced bands of 200 - 300 Hz; Chalybion (Sphecidae) has a band around 70 Hz; and the pompilid wasp produced frequency bands of 136 - 480 Hz.

DISCUSSION: STIMULUS STUDY

This study demonstrates that most adult and juvenile U. glomosus actively respond to a contact stimulus and remain motionless in their webs in response to the visual and vibratory stimuli of a tethered wasp. This supports Hoffmaster's (1982b) findings that contact stimuli are more effective in triggering the shaking and jumping responses in Argiope. It also suggests that spiders conserve their energy resources when faced with ambivalent or harmless stimuli (such as a large insect flying or hovering over them) but readily react to potentially life-threatening stimuli (such as a large object directly contacting them).

The frequency of the wingbeats of the various sphecid and pompilid wasps were all within the range detectable by trichobothria (Barth 1982). Therefore, the spiders were clearly able to perceive the wasps hovering above them.

It may be that spiders, when they detect the

vibratory stimulus of a hunting wasp, freeze (if they are active) or tense in preparation to respond if contacted. Since all the spiders observed in this study were already motionless in their webs, resting in cryptic postures, when exposed to the tethered wasp, I detected no such preparatory freezing. Spiders first exposed to tethered wasps and then contacted might be more immediately responsive to the contact than spiders contacted first. This could easily be tested.

SUMMARY

This study had five objectives: 1) to determine the frequency of three putative predator avoidance behaviors in adult and juvenile Uloborus glomosus and to determine what factors influence the expression of these behaviors, 2) to determine how consistently individuals express these disturbance behaviors throughout a day and over a period of days, 3) to obtain direct evidence that these hypothesized predator avoidance mechanisms actually enable a spider to avoid visually hunting predators, 4) to determine what stimuli are necessary or sufficient to trigger the active escape (jumping from the web) and the startle (shaking) responses, and 5) to investigate the influence of eggsacs upon an attending female's behavior. Each objective is discussed more fully below.

1) I found that time of day, presence of a web structure (stabilimentum or eggsac chain), and alignment with the web structure each influence the disturbance behaviors shown by U. glomosus adults and juveniles. However, adults and juveniles (3rd and 4th stadia) are not influenced by these factors to the same extent. For example, time of day does not influence the behaviors shown by adults that lack web structures (these spiders jump from the web when disturbed), whereas time of day

does influence the behaviors shown by juveniles without web structures. These results suggest that adults and juveniles may respond to different groups of predators or that ontogenetic changes influence the development of these behaviors.

In the survey study I hypothesized that the jumping behavior occurs more frequently during the morning and afternoon when wasps are most active and that the shaking response occurs at the same frequency through the day, as nonflying predators are active throughout the day.

Although the results did not contradict my hypotheses, they did not clearly support them: neither adults nor juveniles showed a preference for the jumping behavior during any part of the day. Adults (with web structures) shook the web in the morning; juveniles shook the web in the afternoon and the evening but not in the morning.

However, the consistency study did support the hypothesis that shaking occurs at the same frequency throughout the day. Additionally, I found that individual U. glomosus jumped from their webs in the afternoon and the evening but changed their responses in the morning. Although these results seem to contradict my hypothesis that jumping should occur more frequently in the morning and afternoon, spiders may be responding not to the clock-time during which wasps are most active, but to wasp activity as it is influenced by the exposure

of the habitat to sunlight.

Similar reasoning might explain why the survey results and the consistency study results do not agree. Several banks of shrubbery, where the surveys were conducted, were bounded on two sides by campus buildings that shaded the sunlight for most of the day, while other banks had buildings adjacent to but not in front of them and were shaded during only part of the day. If the shading at the consistency site affected those spiders' responses, it is reasonable that the variability in the exposure of the survey spiders to sunlight also affected their responses.

The results of the surveys suggest that the presence of web structures and the alignment of spiders (at least adults) do protect the spiders from visually hunting predators. My results do not support two predictions of the Robinsons' hypothesis (1970, 1973, 1978) that stabilimenta function, primarily, to strengthen webs. If this were the case, spiders with and without these web structures would show similar responses to disturbance, which they do not. Also, if the Robinsons' hypothesis was correct, alignment with web structures would not influence the spiders' responses to disturbance, which it does. For example, when a web structure, with the potential for making a spider more cryptic, is present and the spider is aligned with that

structure, it is less likely to exhibit the jumping response.

The juvenile survey results do support the Robinsons' hypothesis (1970) that the circular stabilimentum platform produced by some spiderlings functions to conceal the spiderling from visually hunting predators. All but three of the 129 spiderlings with a circular stabilimentum in their webs rested directly beneath this web structure. However, since a circular stabilimentum is invariably built at the hub of the web, this tendency to remain in position beneath the stabilimentum may reflect the advantage of staying at the center of the web in terms of prey detection.

2) I found that individual spiders did not show the same responses at all times of the day nor over a period of days. During the consistency study the frequency of jumping and of spiders showing no response changed. This may be due either to habituation to the stimulus or to nutritional differences between the spiders. Spiders that jumped in the afternoon and the evening switched to moving to the edge or showing no response in the morning. These latter results are discussed more fully under 1) above.

3) I filmed a predator-prey interaction between a

spider hunting wasp (either a sphecid or a pompilid) and a uloborid. In this sequence the wasp hovered over and then attacked the spider; the spider did not respond until it was contacted by the wasp but then jumped from its web. Although the wasp continued to follow the spider out of the field of view, approximately three minutes later, the spider ascended its dragline to the web, successfully eluding the predator.

4) Contact stimuli rather than vibratory or visual stimuli cause U. glomosus to jump from, shake, or move to the edge of the web.

5) Uloborus glomosus females with eggsacs actively protect those eggsacs against parasitoids. They show a distinct jerking behavior and some show a leg sweeping response. These behaviors may prevent oviposition by hymenopteran parasitoids and possibly function to dislodge the wasp. Although the behaviors may have evolved in response to specialized hymenopteran parasitoids, the stimuli that trigger them are not specific to these hymenopterans; progeny and harmless insects walking over the eggsacs can also trigger these behaviors.

The results of this study support the hypotheses

that the disturbance behaviors shown by U. glomosus as well as the presence of certain web structures and the alignment of the spiders with these structures are all predator avoidance strategies. They also support the hypothesis that visually hunting predators are exerting the selection pressure necessary to maintain these strategies in the population. This study also suggests that researchers should be cautious in applying a predator avoidance function to behaviors based on indirect evidence. For example, the tendency of females to remain aligned with their eggsacs could be interpreted primarily as a predator avoidance mechanism since females are so cryptic next to these eggsac chains. However, I found that the females are also actively protecting their eggsacs from parasitoids.

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FIGURES

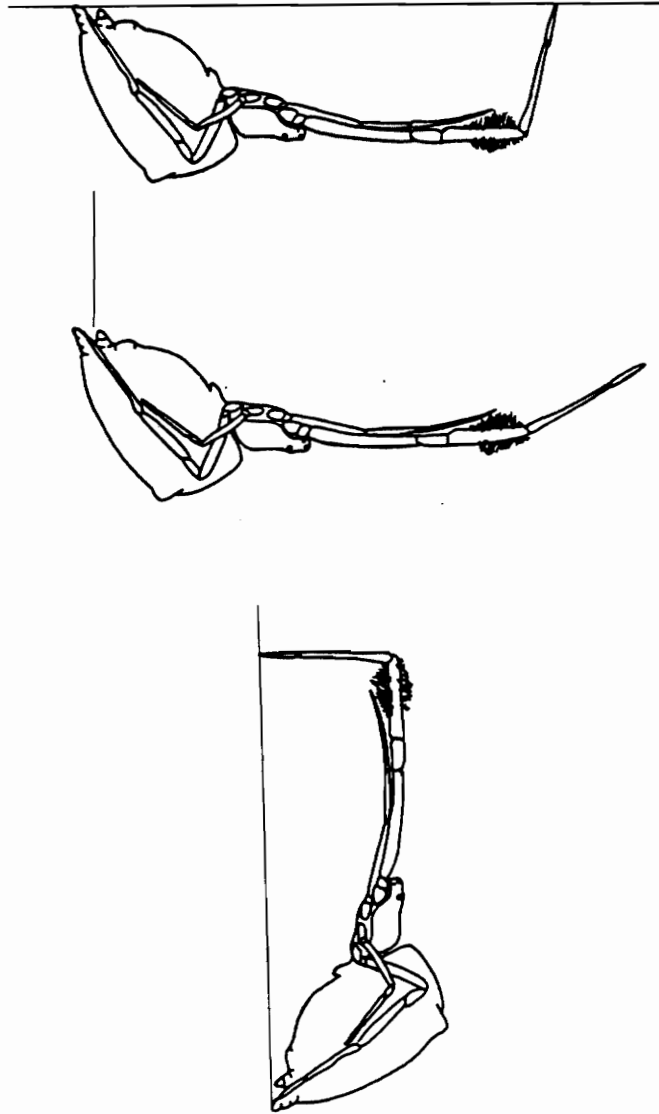
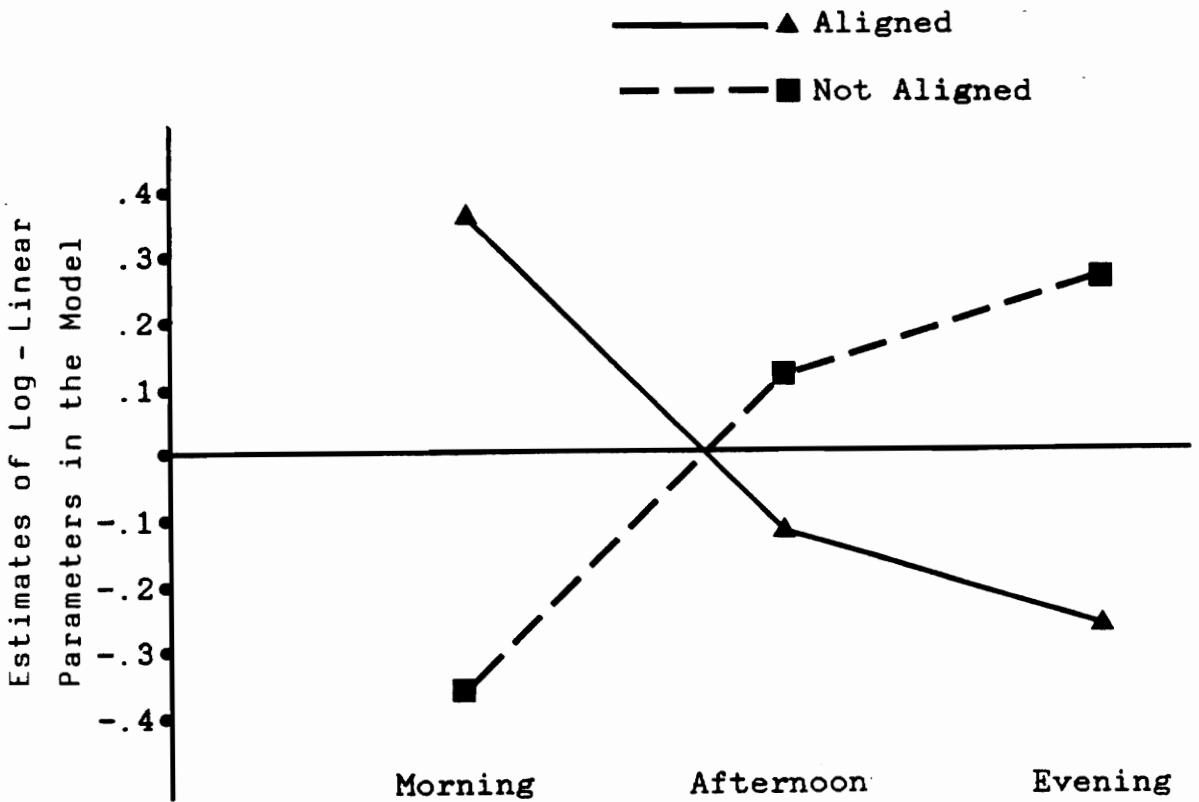


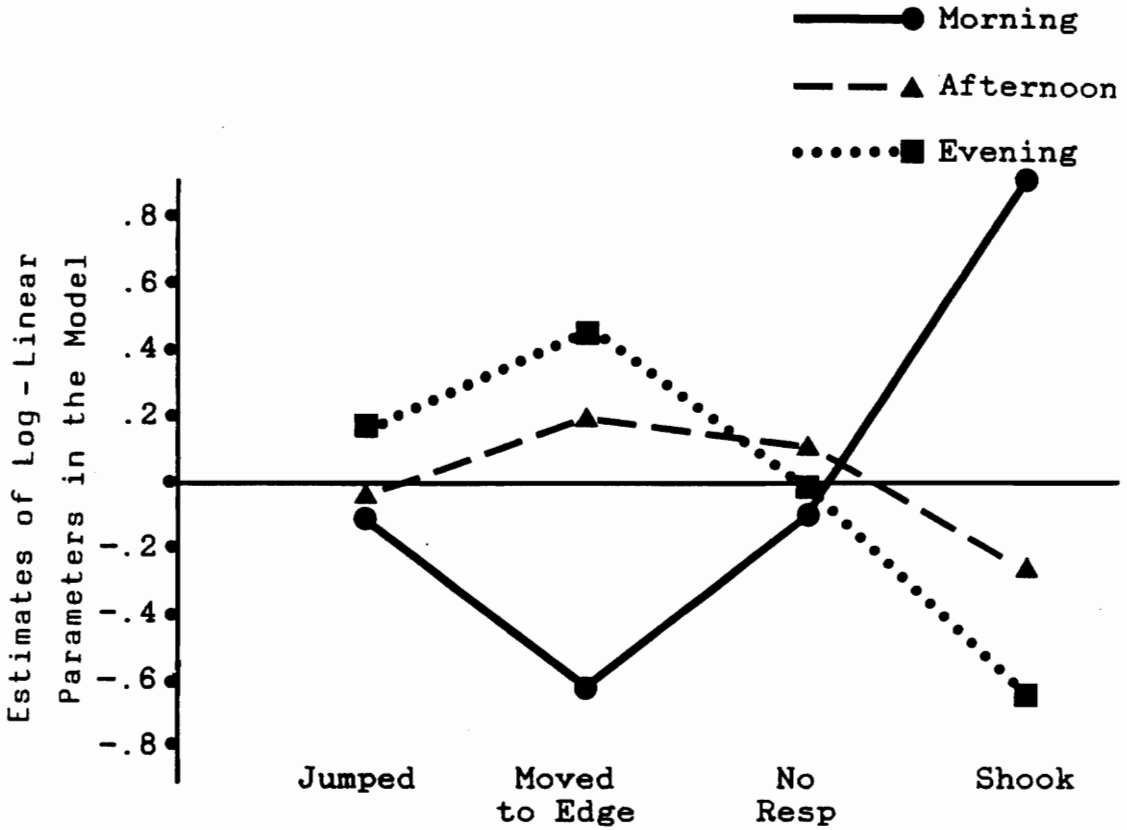
Figure 1. Postures involved in the jumping behavior.
(a) Cryptic posture at the hub of the web (legs bent 80°);
(b) cryptic posture at the end of the dragline, after jumping
(legs bent 25°); (c) ascending the dragline (legs bent 90°).



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

ALIGNMENT	TIME		
	Morning	Afternoon	Evening
Yes	2.733	-0.946	-2.168
No	-2.733	0.946	2.168

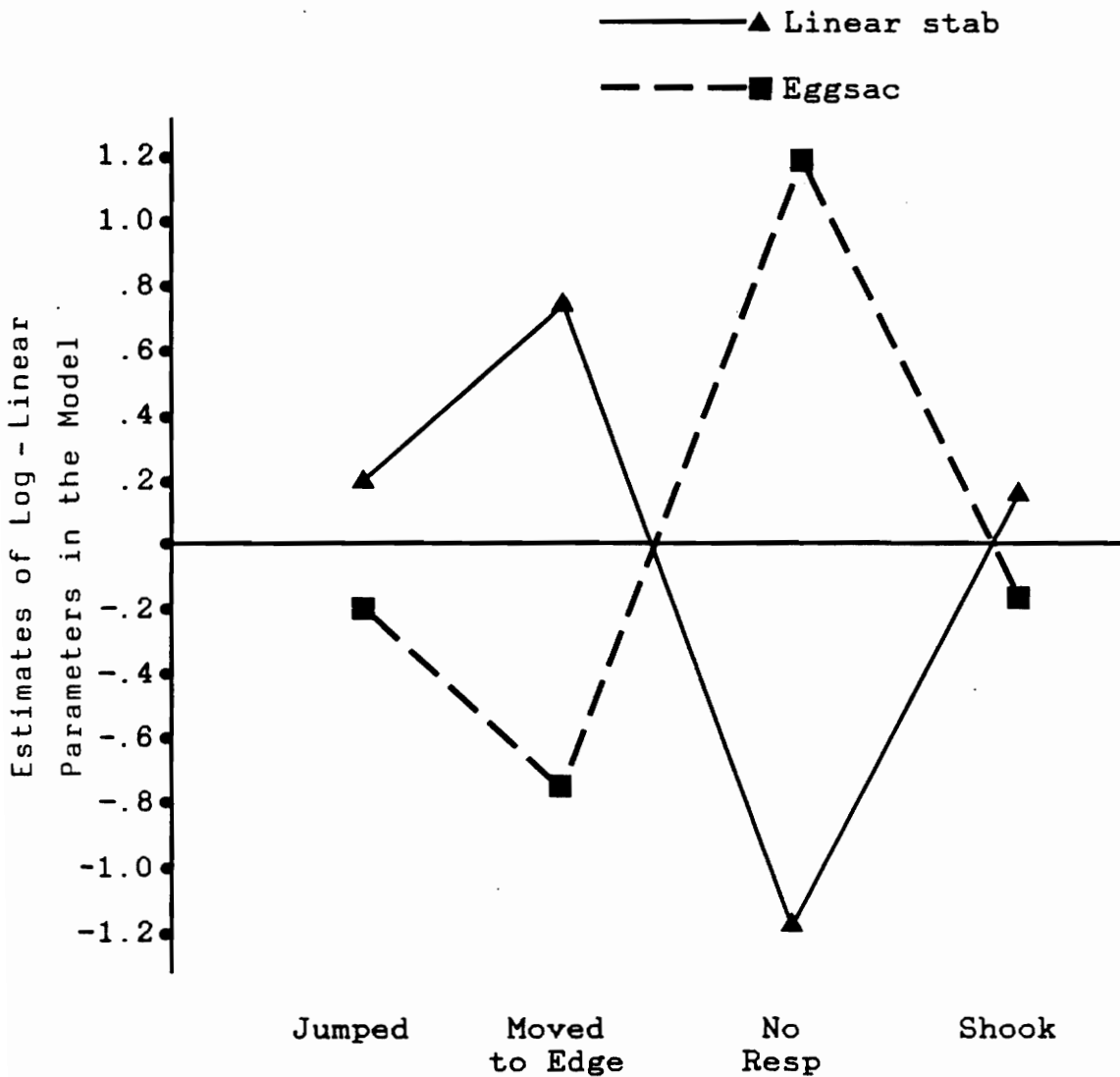
Figure 2. Association between the TIME and ALIGNMENT variables for adult *Uloborus glomus* from the log-linear model for these data. The upper figure presents the parameter estimates for each of the two behaviors (aligned and not aligned) at each time of day. The lower table indicates which levels of the two variables contribute most to the significant association between the variables.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

RESPONSE	TIME		
	Morning	Afternoon	Evening
Jumped	-0.785	-0.321	0.864
Moved Edge	-2.879	0.817	1.819
No Resp	-0.733	0.703	-0.056
Shook	2.432	-0.564	-1.149

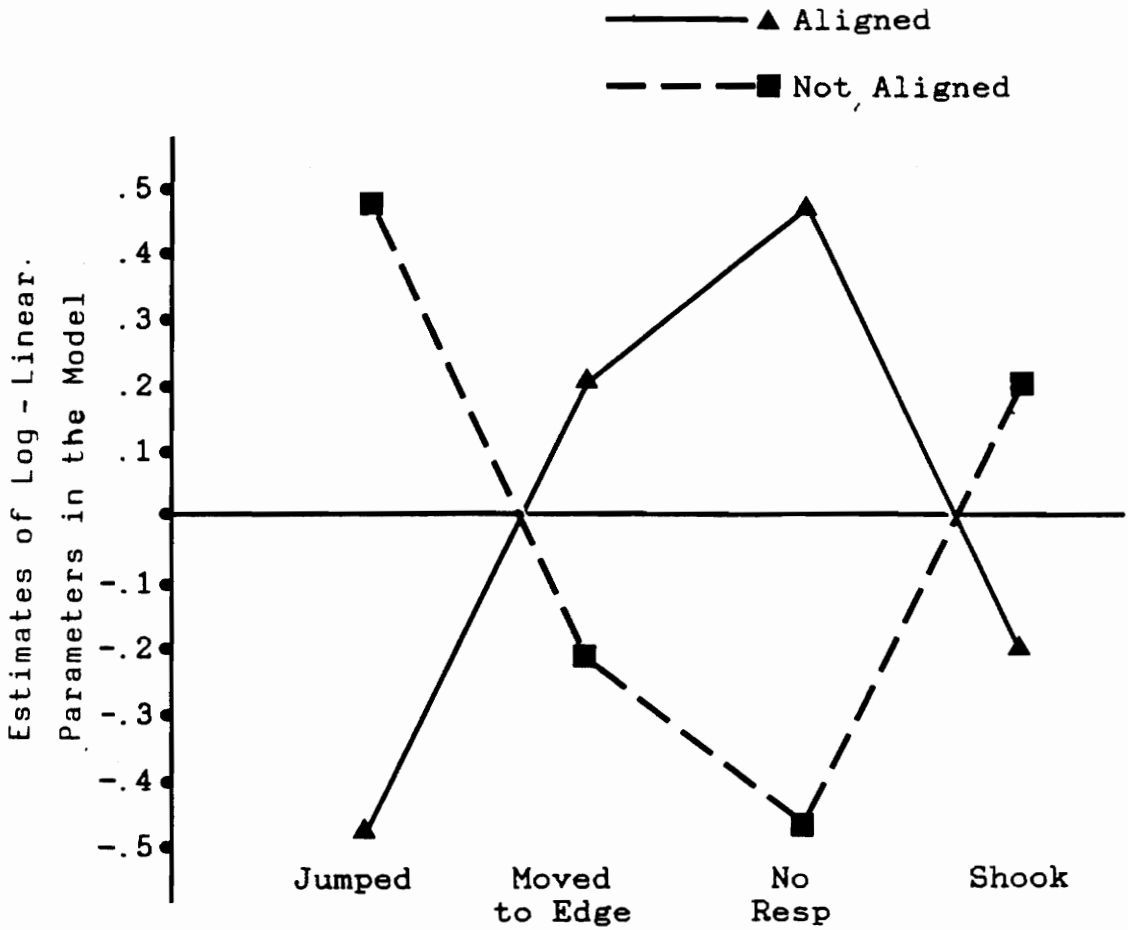
Figure 3. Association between the TIME and RESPONSE variables for adult *Uloborus glomus* from the log-linear model for these data.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

STAB/SAC	RESPONSE			
	Jumped	Moved	No Resp	Shook
Linear stab	1.839	4.674	-7.856	0.967
Eggsac	-1.839	-4.674	7.856	-0.967

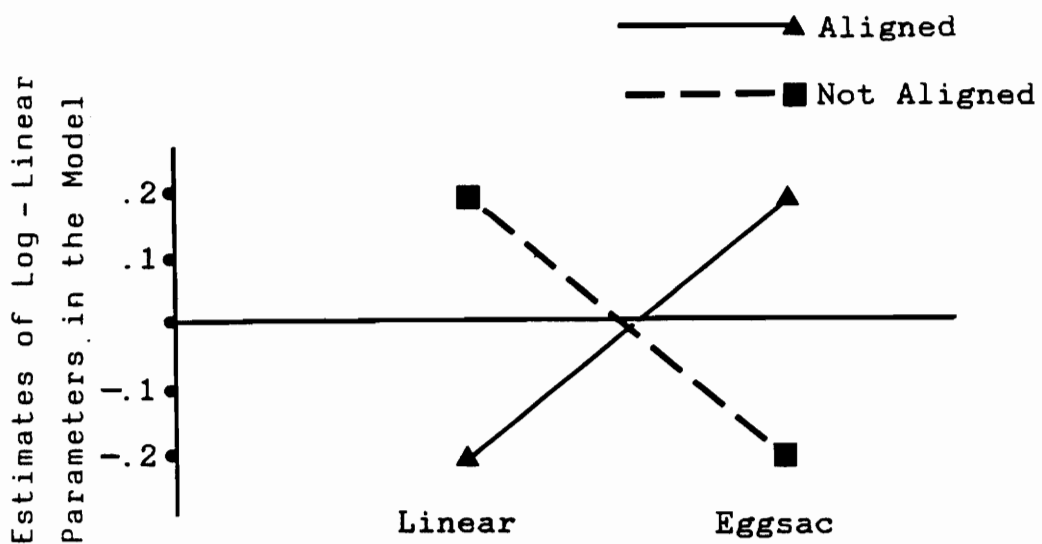
Figure 4. Association between the RESPONSE and STAB/SAC variables for adult Uloborus glomosis from the log-linear model for these data.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

ALIGNMENT	RESPONSE			
	Jumped	Moved	No Resp	Shook
Yes	-2.711	0.726	1.886	-0.482
No	2.711	-0.726	-1.886	0.482

Figure 5. Association between the RESPONSE and ALIGNMENT variables for adult *Uloborus glomosis* from the log-linear model for these data.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

ALIGNMENT	STAB/SAC	
	Linear stab	Eggsac
Yes	-2.117	2.117
No	2.117	-2.117

Figure 6. Association between the STAB/SAC and ALIGNMENT variables for adult Uloborus glomus from the log-linear model for these data.

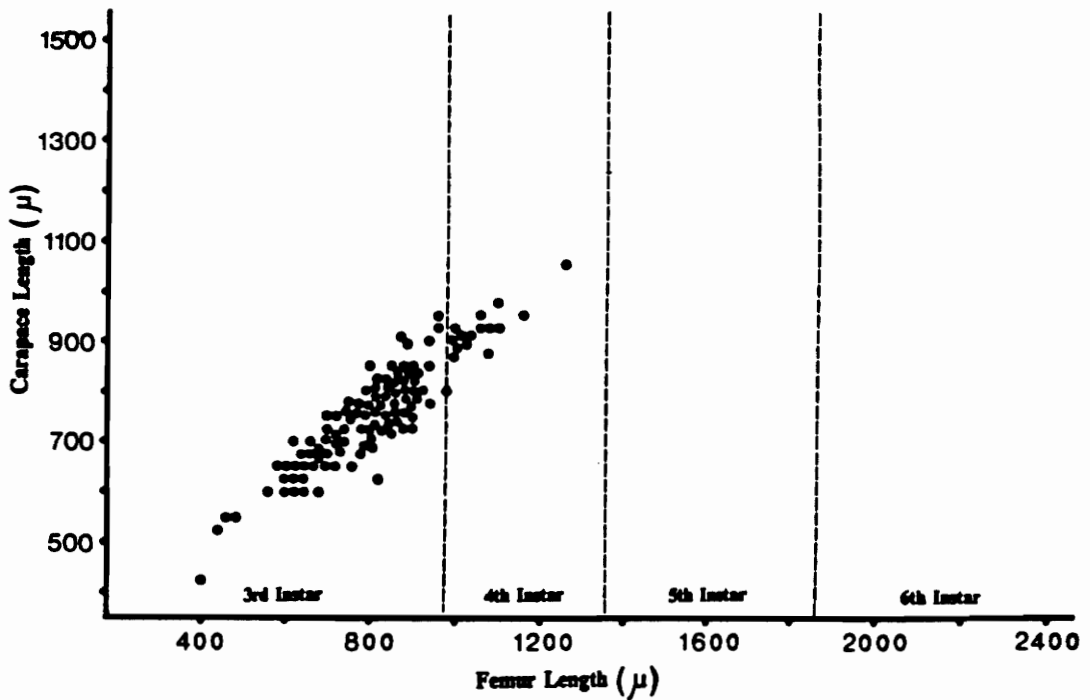
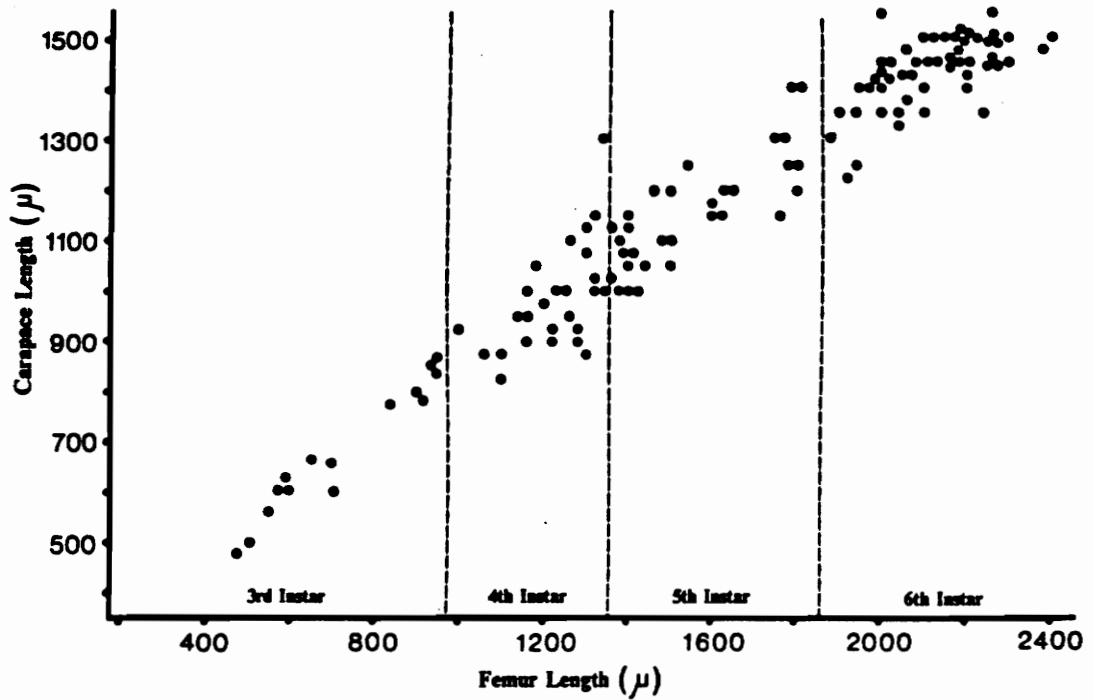
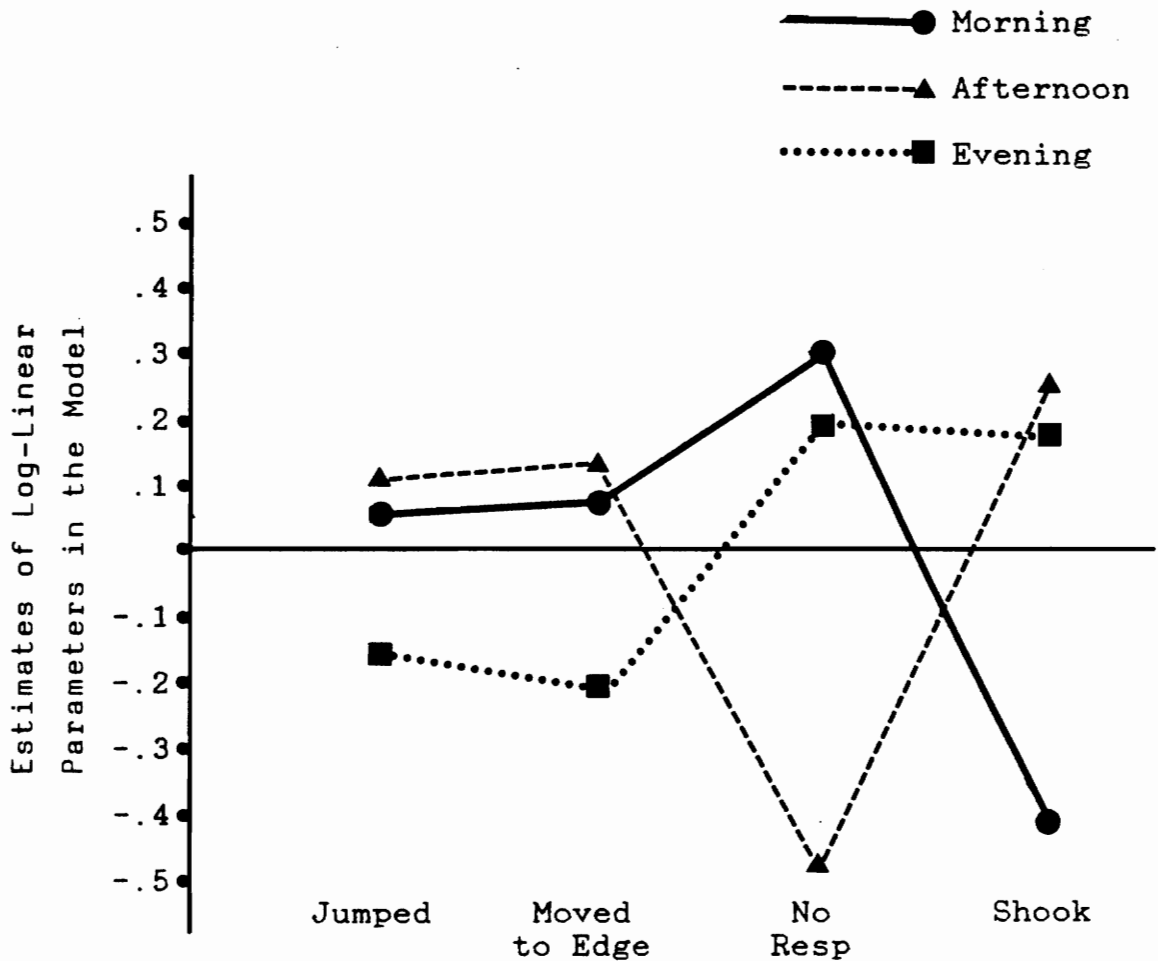


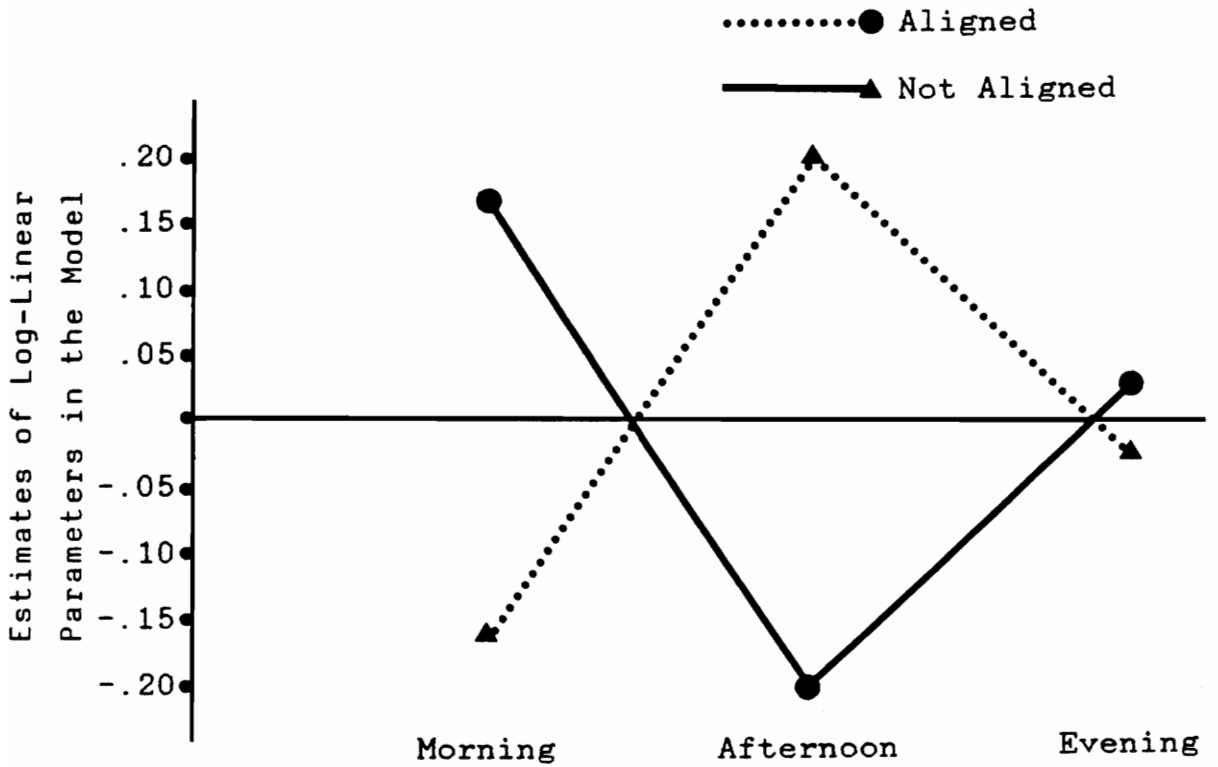
Figure 7. (a) Plot of growth of field U. glomus collected by Opell (1987). (b) Plot of juvenile U. glomus collected during juvenile survey.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

RESPONSE	TIME		
	Morning	Afternoon	Evening
Jumped	0.646	1.262	-2.146
Moved Edge	0.951	1.609	-2.895
No Resp	1.758	-2.455	1.260
Shook	-4.418	2.576	2.290

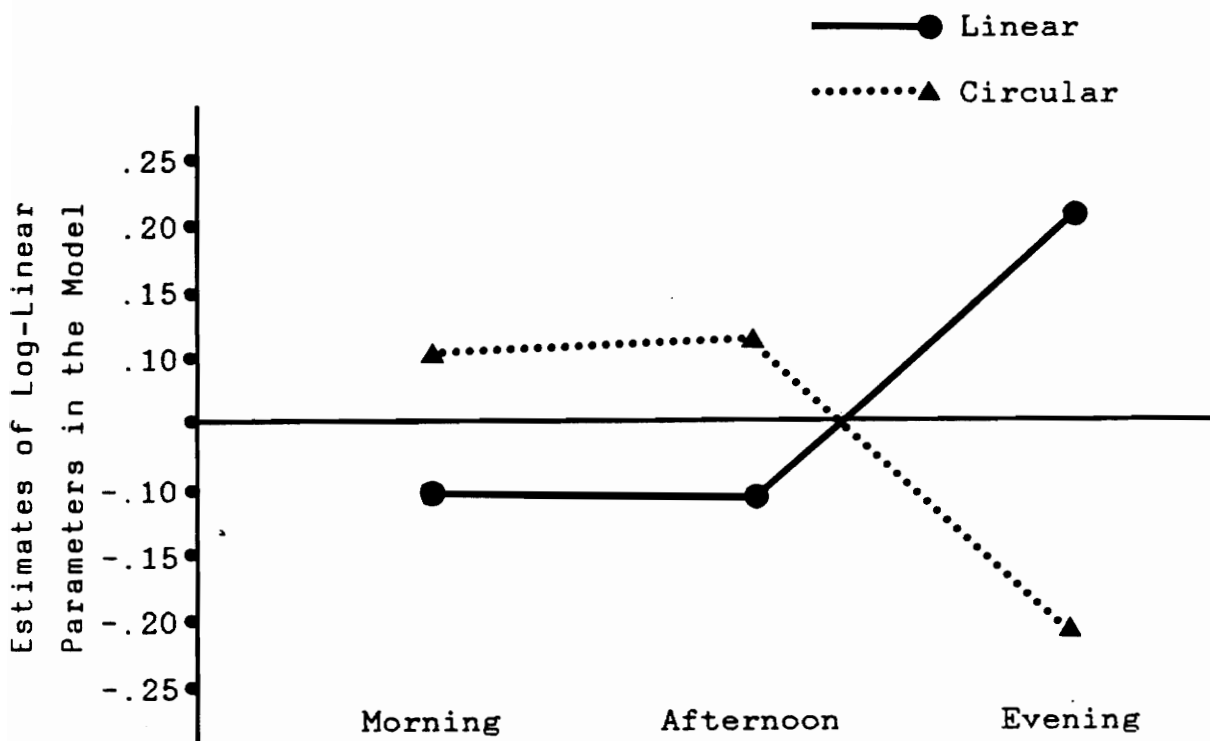
Figure 8. Association between the TIME and RESPONSE variables for juvenile Uloborus glomosis from the log-linear model for these data.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

ALIGNMENT	TIME		
	Morning	Afternoon	Evening
Yes	2.491	-3.670	0.654
No	-2.491	3.670	-0.654

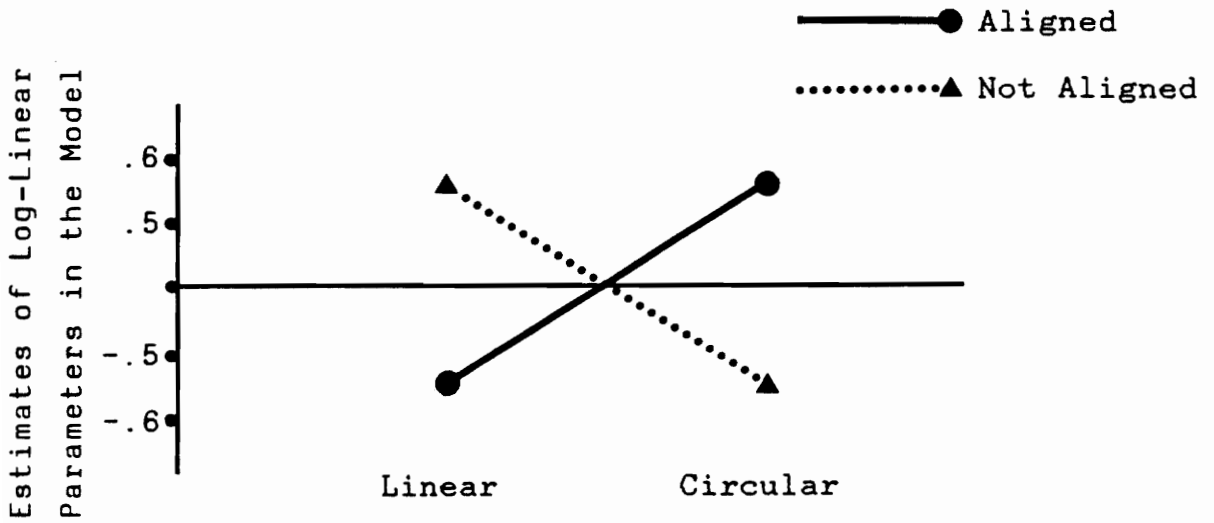
Figure 9. Association between the TIME and ALIGNMENT variables for juvenile *Uloborus glomus* from the log-linear model for these data.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

STABILIMENTA	TIME		
	Morning	Afternoon	Evening
Linear	-1.530	-1.607	2.993
Circular	1.530	1.607	-2.993

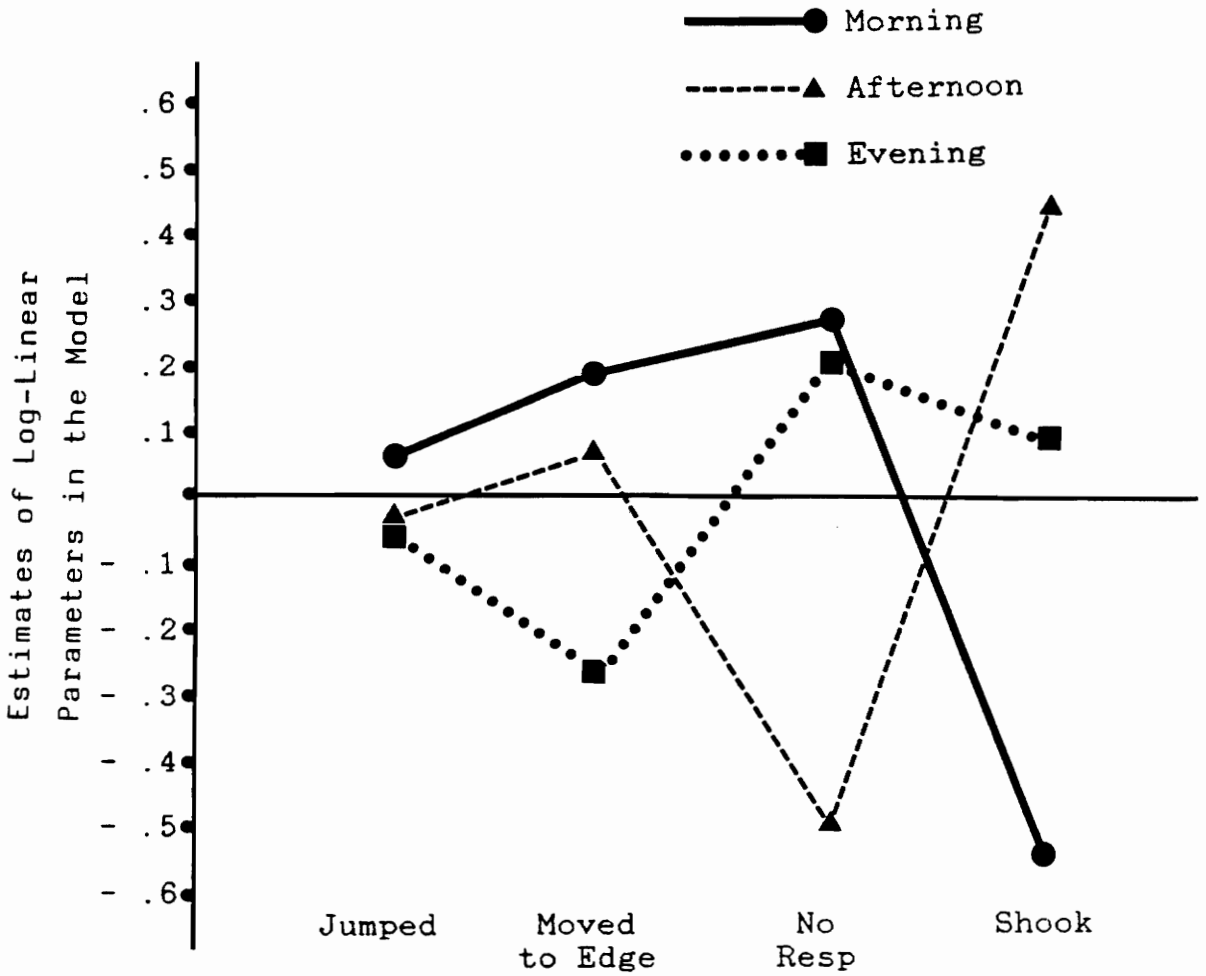
Figure 10. Association between the TIME and STABILIMENTA variables for juvenile Uloborus glomosis from the log-linear model for these data.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

ALIGNMENT	STABILIMENTA	
	Linear	Circular
Yes	-3.645	3.645
No	3.645	-3.645

Figure 11. Association between the STABILIMENTA and ALIGNMENT variables for juvenile *Uloborus glomosis* from the log-linear model for these data.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

RESPONSE	TIME		
	Morning	Afternoon	Evening
Jumped	0.463	-0.130	-0.246
Moved Edge	1.696	0.540	-1.850
No Resp	1.103	-1.491	0.703
Shook	-3.752	2.850	0.575

Figure 12. Association between the TIME and RESPONSE variables for juvenile *Uloborus glomosis* with no stabilimenta in their webs from the log-linear model for these data.

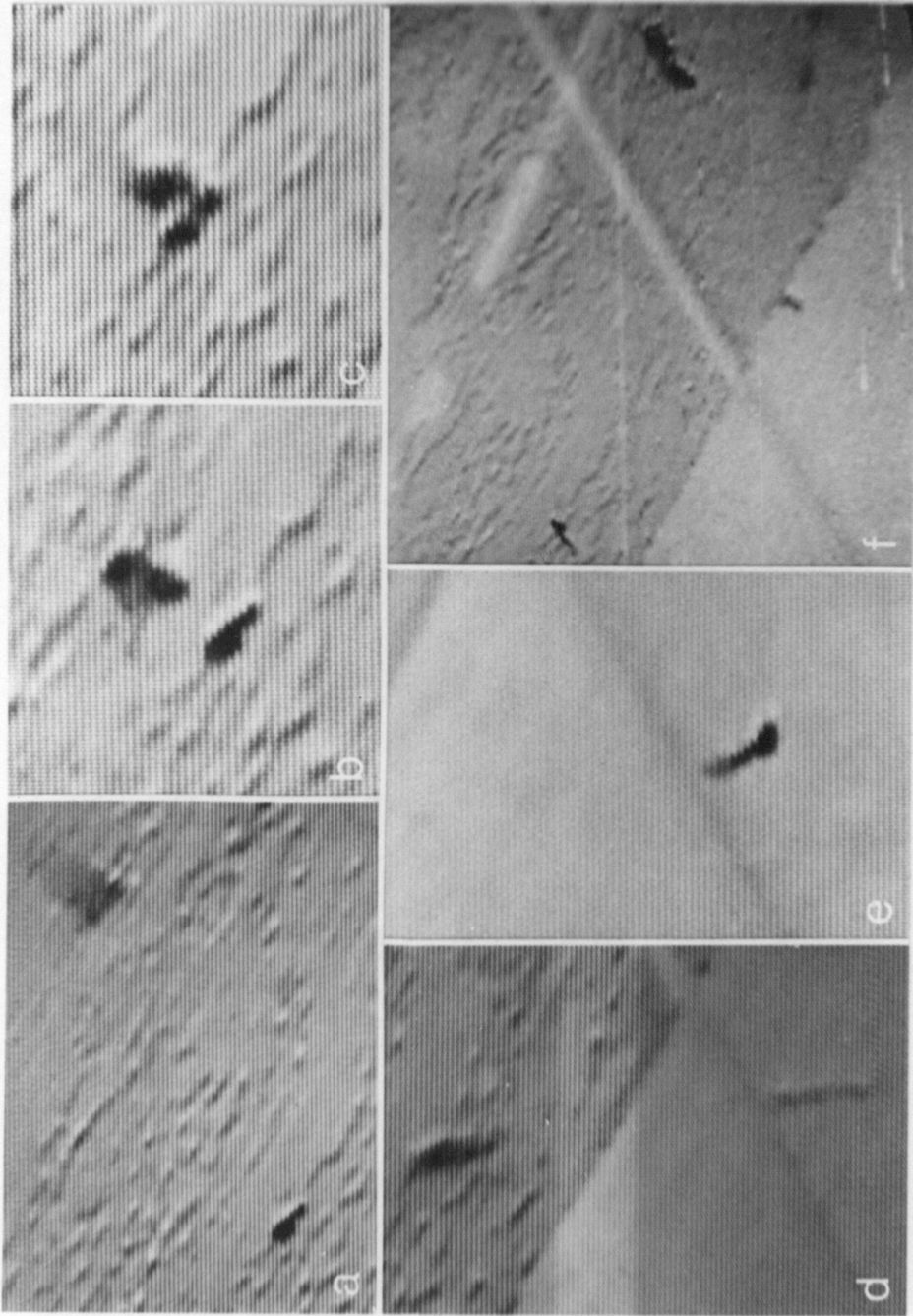


Figure 13. Photographs of the filmed predator-prey interaction between an adult spider and a spider-hunting wasp. (a) Wasp approaching the spider; (b) wasp hovering over spider; (c) wasp attacking spider; (d) spider jumping, wasp following; (e) spider ascending her dragline; (f) spider back at the hub, wasp flying away (bottom right corner).

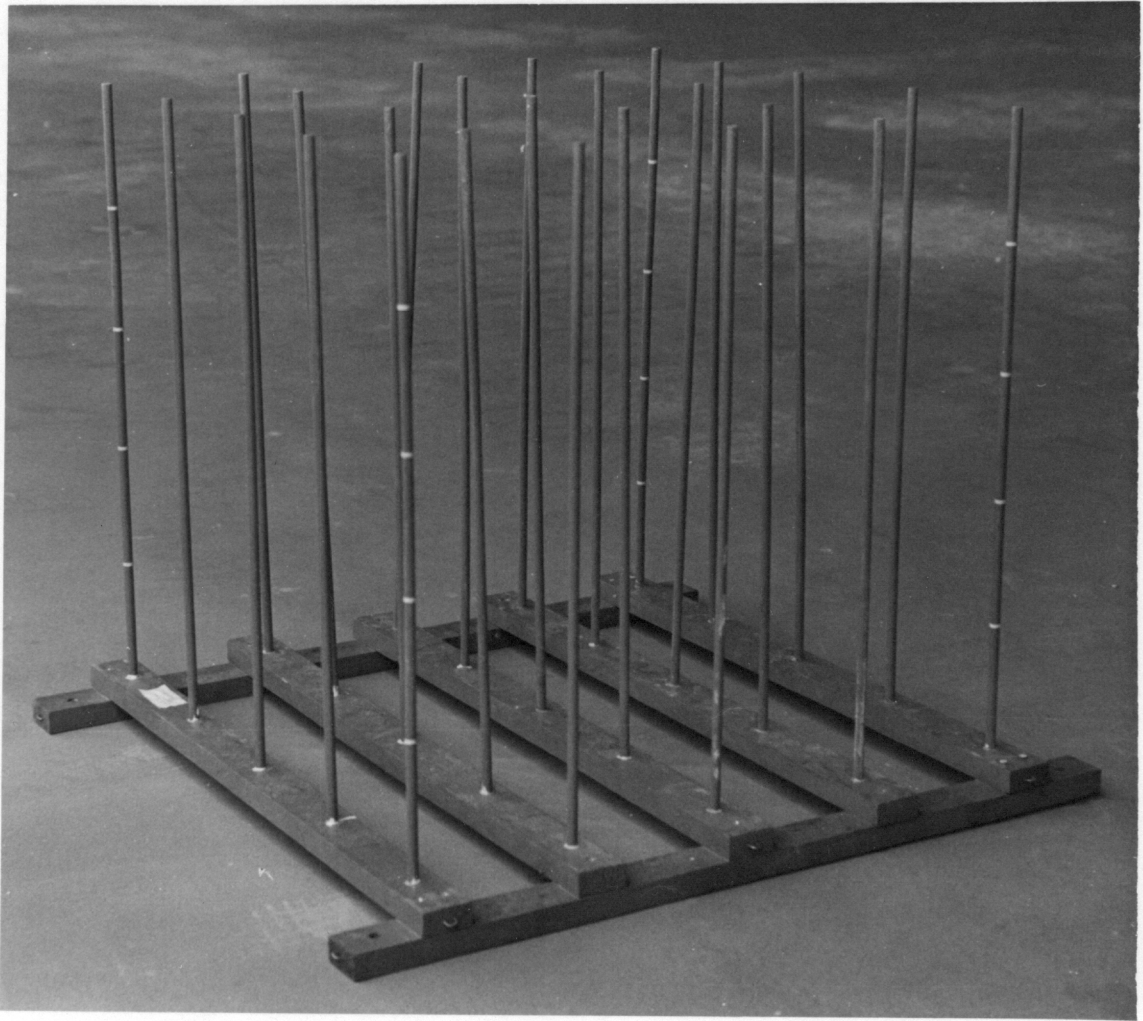
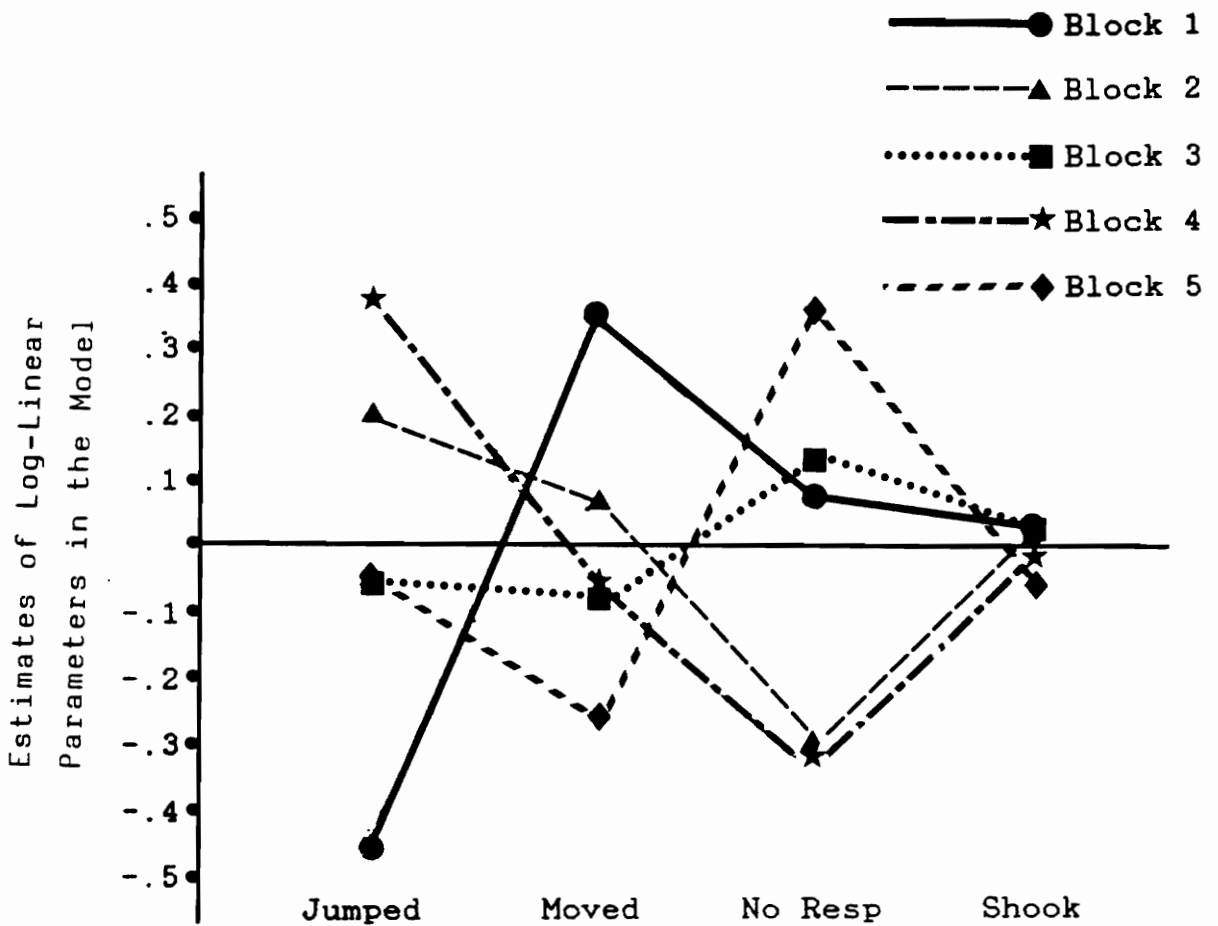


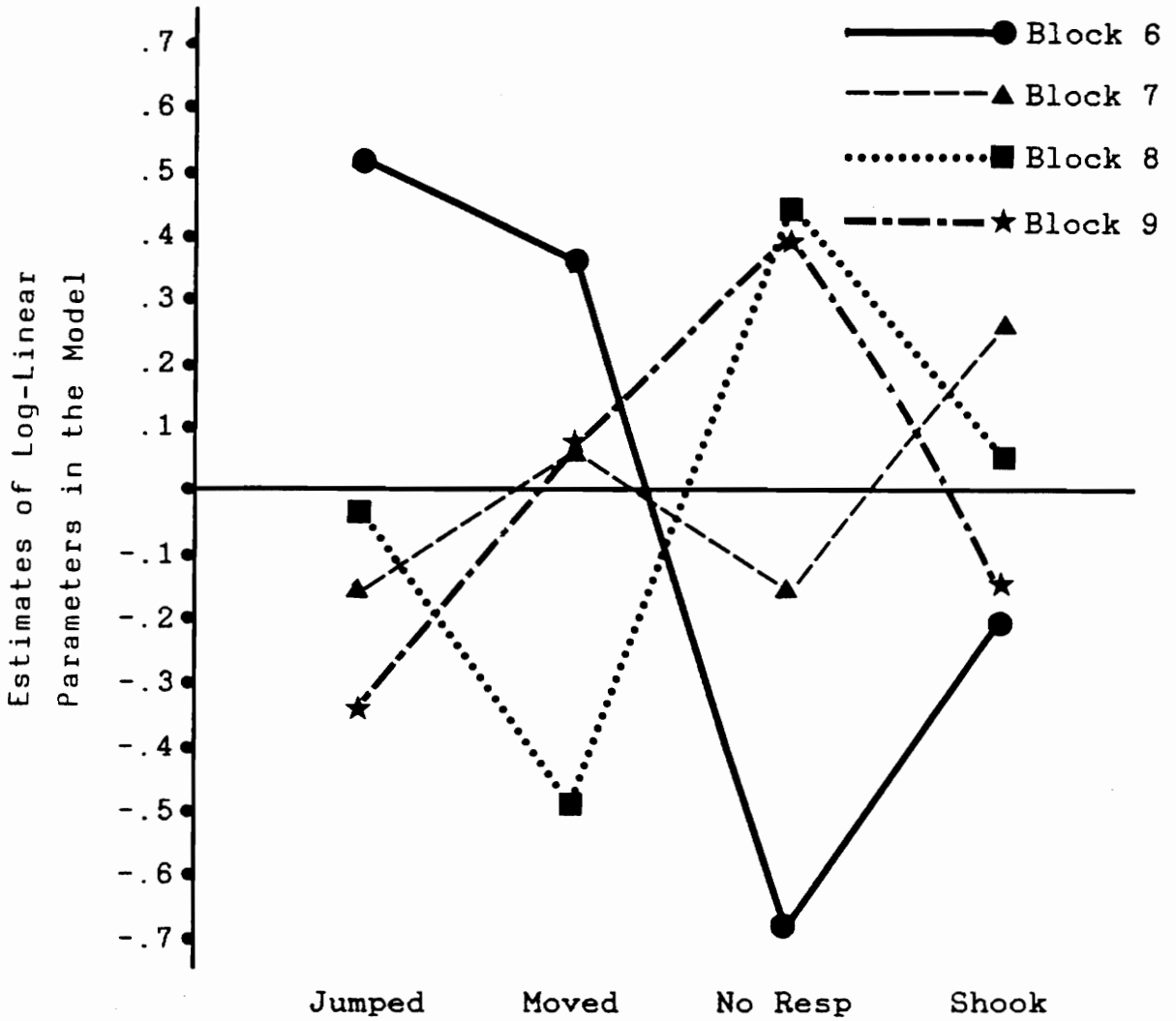
Figure 14. Arachnothrombus.



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

RESPONSE	BLOCK				
	Block 1	Block 2	Block 3	Block 4	Block 5
Jumped	-3.473	1.351	-0.454	2.511	-0.372
Moved Edge	1.385	0.238	-0.289	-0.187	-0.823
No Resp	0.514	-1.245	0.676	-1.264	1.911
Shook	0.143	0.084	0.125	-0.092	-0.230

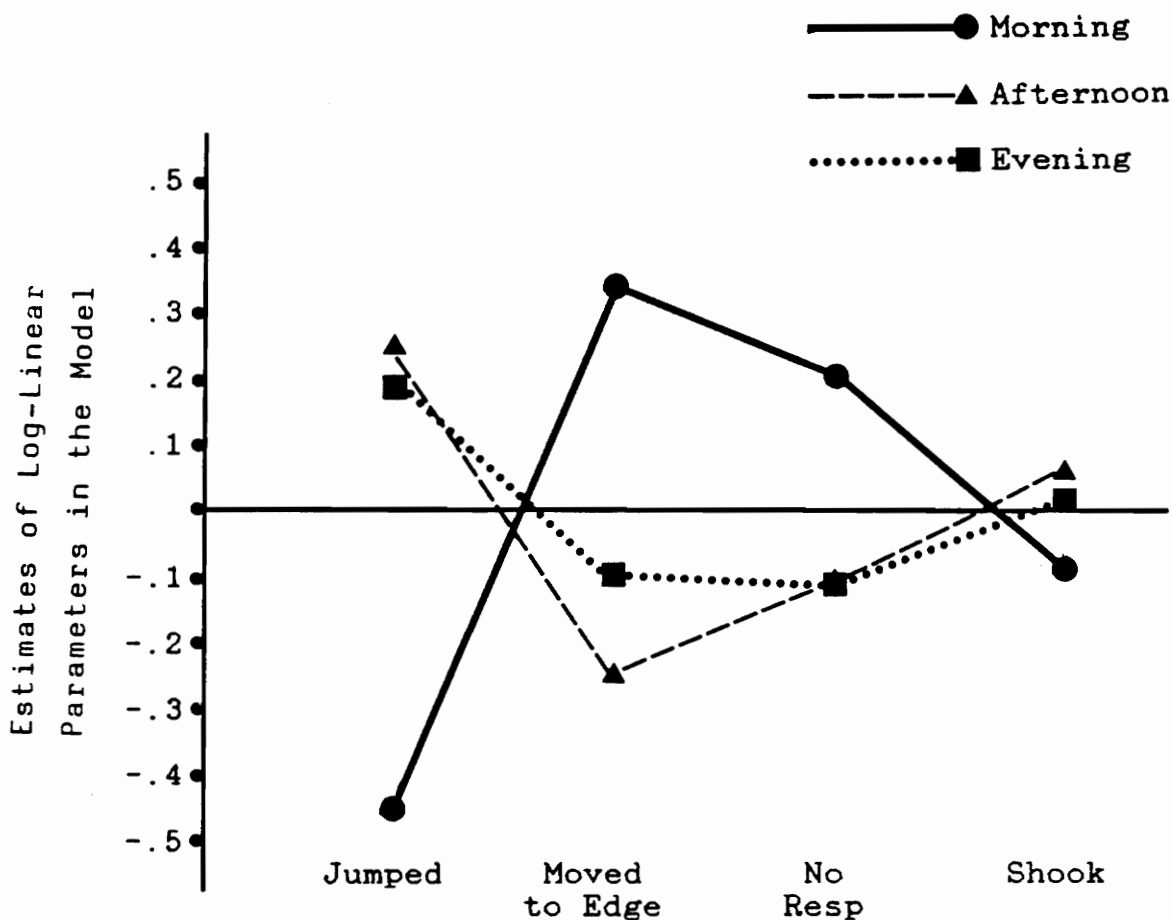
Figure 15. Association between the TIME and BLOCK variables for Consistency Study *Uloborus glomus* from the log-linear model for these data. (For blocks 1 - 5.)



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

RESPONSE	BLOCK			
	Block 6	Block 7	Block 8	Block 9
Jumped	2.941	-0.853	-0.086	-1.659
Moved Edge	1.360	0.177	-1.365	0.251
No Resp	-2.865	-0.756	2.156	2.104
Shook	-0.951	1.402	0.304	-0.634

Figure 16. Association between the TIME and BLOCK variables for Consistency Study *Uloborus glomosis* from the log-linear model for these data. (For blocks 6 - 9.)



**RATIO OF THE LOG-LINEAR PARAMETER ESTIMATE
TO ITS STANDARD ERROR**

RESPONSE	TIME		
	Morning	Afternoon	Evening
Jumped	-5.541	2.919	2.333
Moved Edge	2.233	-1.290	-0.581
No Resp	2.107	-0.867	-0.972
Shook	-1.023	0.800	0.139

Figure 17. Association between the TIME and RESPONSE variables for Consistency Study *Uloborus glomosis* from the log-linear model for these data.

TABLES

Table 1. Response variables for adults with neither stabilimenta nor eggsac chains.

	RESPONSE			
	Jumped	Moved	No Resp	Shook
Parameter Estimates	1.394	0.235	-0.737	-0.891
Ratio Terms	10.979	1.471	-3.379	-3.852

Table 2. Summary of filming.

BEHAVIOR	STIMULUS		
	Contact by Hymenopteran	Contact by Other Insect	Unknown
Jumping	1	1	0
Centripetal Saltation	0	7	2
Shaking Web	0	1	2
Eggsac Defense Behavior	0	1	0
Shaking Web During Prey Capture	0	1	0

TOTAL # FILMING HOURS ~ 280

Times wasp seen flying within 3 cm of spider with no resp from spider = 16

Times spider responded from stimulus of flying wasp = 1 (moved to edge of web)

Table 3. Consistency study sampling procedure.

	Morning	Afternoon	Evening
Day 1	X		
Day 2		X	
Day 3			X
Day 4			
Day 5	X		
Day 6		X	
Day 7			X
:			
:			
:			

TABLE 4. Summary of eggsac defense behaviors by 21 females.

1st Resp	Jerked Web	Turned and Walked Along Eggsac Chain	No Resp
Range of Time of 1st Resp (from 0)	2" - 4'10"	2" - 1'20"	0" - 5'
% Females Showing Resp	76.2	9.5	14.3
2nd Resp	Turned and Walked Along Eggsac Chain	Jerked Web	Moved Away From Eggsacs
Range of Time of 2nd Resp (from 0)	10" - 5'55"	17" - 1'30"	1'15"
% Females Showing Resp	61.9	14.3	4.8
			Assumed Cryptic Post
			No Resp
			1'30"
			0" - 5'
			4.8
			14.3

Table 5. Summary of responses to a contact stimulus and a tethered wasp.

Resp.	Contact Stimulus			Tethered Wasp			Contact Stimulus
	Trial 1	Trial 2	Trial 3	Trial 1	Trial 2	Trial 3	
ACTIVE	92.3	71.4	14.3	0	0	0	100
% SPIDERLINGS	0	14.3	0	0	0	0	14.3
Moved	0	14.3	0	0	0	0	0
(N = 14*)	92.3	42.9	14.3	0	0	0	85.7
NO RESP	7.7	28.6	85.7	100	100	100	0
ACTIVE	77.8		0	0	0	0	77.8
% ADULTS	33.3		0	0	0	0	44.4
Moved	0		0	0	0	0	11.1
(N = 9)	44.4		0	0	0	0	22.2
NO RESP	22.2		100	100	100	100	22.2

*Except for Contact Stimulus, Trial 1, where N = 13.

APPENDICES

APPENDIX 1

Observed frequency table for the adult survey. Total number of observations is 595.

ALIGN	STABSAC	RESP	TIME			
			MORNING	AFTERNOON	EVENING	
Yes	Linear	Jumped	30	19	21	
		Moved	7	12	7	
		No Resp	3	5	1	
		Shook	5	1	0	
	Eggsac	Jumped	37	23	16	
		Moved	1	3	6	
		No Resp	74	57	38	
		Shook	4	1	0	
	No	Linear	Jumped	4	8	11
			Moved	2	0	1
			No Resp	0	1	0
			Shook	0	0	0
Eggsac		Jumped	1	6	5	
		Moved	0	0	0	
		No Resp	2	1	0	
		Shook	0	0	1	
*		Neither	Jumped	32	58	28
			Moved	11	17	9
			No Resp	7	7	0
			Shook	2	8	2

* Spiders with no web structures with which to align.

APPENDIX 2

Observed frequency table for the juvenile survey. Total number of observations is 1800.

ALIGN	STAB	RESP	TIME		
			MORNING	AFTERNOON	EVENING
Yes	Linear	Jumped	90	85	114
		Moved	121	124	156
		No Resp	13	7	17
		Shook	40	82	119
	Circular	Jumped	9	13	8
		Moved	23	23	13
		No Resp	3	0	2
		Shook	6	14	12
No	Linear	Jumped	8	25	14
		Moved	20	42	27
		No Resp	0	1	4
		Shook	7	19	27
	Circular	Jumped	0	0	0
		Moved	0	0	0
		No Resp	0	0	0
		Shook	2	0	1
*	Neither	Jumped	63	34	22
		Moved	152	79	37
		No Resp	11	3	4
		Shook	32	49	23

* Spiders with no stabilimenta with which to align.

APPENDIX 3

Observed frequency table for the consistency over time. Total number of observations is 862.

BLOCK	RESPONSE			
	JUMPED	MOVED	NO RESP	SHOOK
1	57	9	20	37
2	82	5	10	27
3	74	5	18	32
4	91	4	9	24
5	72	4	22	29
6	33	8	8	12
7	17	6	14	20
8	17	3	22	14
9	14	6	24	13

Observed frequency table for the consistency between time periods. Total number of observations is 862.

RESP	TIME		
	MORNING	AFTERNOON	EVENING
Jumped	116	172	169
Moved	26	11	13
No Resp	70	38	39
Shook	76	67	65

VITA

Paula E. Cushing was born February 17, 1964 in Alexandria, Virginia to Col. Joseph and Paula M. Cushing. She lived in Alexandria for 18 years and received all her early schooling there. She received her Bachelor of Science degree from Virginia Polytechnic Institute and State University in June, 1985.

When she was eight she declared she would become a naturalist. She later clarified her goals and stated she would be a biologist. She has narrowed her field still further and now claims to be an invertebrate ethologist. She began her invertebrate zoology career at a young age when she collected her first dead insects, placing them in a box with a clear lid. The summer after high school she interned at the Smithsonian Institution's Insect Zoo. She also worked as a volunteer naturalist with the Fairfax County Park Authority. The park, discovering that she worked at the Insect Zoo, asked her to give a presentation on spiders. (She was careful not to mention to the D.C. bus driver that she was transporting a tarantula from the Insect Zoo to the park.) This began her career in arachnology.

The winter of her first year in college she began working for Dr. Brent D. Opell who further stimulated her

interest in the field of arachnology. She spent her three years as an undergraduate working for Dr. Opell on such subjects as spider vision and respiration and became known as the Spider Lady.

Paula plans to continue studying the behavior of spiders and other invertebrates. She is interested in the adaptive significance of invertebrate behaviors and hopes to study ant-mimicing spiders for her doctoral degree. However, before pursuing her Ph.D. she plans a two month romp in Europe with her brother and a three month stay in Panama working as a Research Assistant (studying spiders, of course).

Paula Elizabeth Cushing