

ECOLOGICAL STUDIES

I. HABITAT, LIFE CYCLE, AND WEB ECOLOGY OF THE SPIDER

NEPHILA CLAVIPES KOCH (ARANEIDAE)

II. THE RELATIONSHIP BETWEEN SELECTED WEB PARAMETERS,

WEIGHT GAIN, AND FECUNDITY IN THE SPIDER

NEPHILA CLAVIPES KOCH (ARANEIDAE)

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A Thesis

Presented to

The Faculty of the Department of Biology

University of Houston

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In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

Clovis Weldon Moore, Jr.

August 1975

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An Abstract of a Thesis  
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## Abstract

Aspects of the natural history and the relationship between weight and variation in selected web parameters in the orb weaving spider Nephila clavipes were investigated. Habitat, life cycle, prey, movements, population density, and variation in selected web parameters were among the aspects of the natural history of the spider studied. It was found that population densities were constant over most of the season, that movements were significantly non-random, and that variations in the selected web parameters show seasonal trends. When the selected web parameters were regressed onto weight over short periods of time, it was shown that a significant relationship existed, implying that Nephila clavipes may adjust its web to changing environmental conditions. Further, it was shown that movements are significantly related to the average daily weight gain at a given site.

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## Introduction

Habitat selection in spiders has interested many ecologists. Orb weavers, in particular, have received much attention, since their webs are easily observed and measured. The characteristics and placement of the web largely determine these spiders' success in obtaining prey, a poorly constructed or placed web leading to few prey. While physical structure of the habitat and microclimate can be important in web placement (Enders, 1973; Turnbull, 1973), once the web is constructed, characteristics of both the web and prey become important in determining the kind and amount of prey captured. Turnbull (1973) concluded that the spider has little ability to modify the web characteristic of its species. However, Witt (1963) has shown that both the environment and the physiological state of the spider influence the construction of the web in Araneus diadematus, and Eberhard (1971) has shown that environment influences the construction of the web of the spider Uloborus diversus. There is a possibility that some spiders build "better" webs than others, since even a cursory examination of habitat reveals spiders in all stages of development.

While evidence on web ecology is available on many orb weaving spiders, information on Nephila is largely lacking. Wilder (1866, 1868) described its habitat, prey, and method of erecting the web in South Carolina, and Krakauer (1972) has now provided its responses to thermal stress in its

Florida habitat. The natural history and web ecology of this spider is largely undescribed and in this paper I describe the life cycle of the spider on the South Texas Coastal Plains, with special attention to the habitat of Nephila at this location, the variation in selected web parameters, and the distribution of residence times in a study area.

### Study Area

This study was conducted at the University of Houston Coastal Center at Hitchcock, Texas, about thirty miles southeast of Houston on the coastal plains. During World War II the site was occupied by a naval training base and was deactivated in 1948. For a short period after 1948, part of the site was farmed and used for livestock grazing. The University of Houston acquired the site around 1950, and since that time the area has been allowed to go through secondary succession. The entire site is crossed by paved streets about fifteen meters wide, dividing the Center into blocks.

The Center consists of approximately 404.7 hectares of mixed vegetational types ranging from coastal prairie grasslands containing Big Bluestem (Andropogon sp.) and Little Bluestem (Andropogon scoparius) as the main constituents to a forest of Chinese Tallow (Sebum sebiferum). The soil base is a heavy black clay common to the coastal plains. In dry, hot weather this soil easily forms a hardpan that is broken by numerous cracks. In wet weather, the area is prone to minor flooding, but is generally well drained by a system of ditches.

The vegetation consists of Bacheris shrubs and Chinese Tallow trees. There are a few native hardwoods scattered throughout the area including Hackberry (Celtis sp.) and Willow (Salix sp.).

The fauna is diverse and consists of small mammals, other vertebrates, including reptiles (Anolis sp., Lampropeltis sp.), amphibians (Bufo sp., Rana sp.), birds (Corvus sp., Colinus sp.) and numerous invertebrates, including insects and arachnids. Large herbivores are excluded from the site by fences.

For detailed studies of Nephila clavipes, a 30.48 meter by 30.48 meter area in the southeast corner of the reservation was chosen. This area consists of an open forest of Chinese Tallow with a well defined understory of Goldenrod (Solidago sp.), bordered on two sides by paved roads and drainage ditches. The remaining two sides are open areas containing Solidago sp.. The ditches are lined with Tallow trees, while most of the inner area is covered with Solidago sp. and Rubus sp. with small amounts of Longisera japonicum. The area is surrounded by groves of Tallow trees with understories that vary from open to dense tangles of Rubus sp..

In addition to Nephila clavipes, other spiders present in the study area include representatives of the families Uloboridae, Mimetidae, Theridae, and Aranidae.



### Methods of Study

Web sites were marked with a site number on a piece of surveyor's tape, instead of stakes, offering the least possibility of increasing the number of available web sites. These tags were placed on the largest support near the upper right hand portion of the web. This method of placement allowed the investigator to differentiate individual web sites even where there were several spiders sharing a site. Sites were designated as the largest tree or shrub having the most support threads attached to it.

Individual spiders to be weighed were removed from their webs by chasing them onto a support thread, and capturing them in a wide-mouthed glass jar, caring not to damage the web. Small spiders were anesthetized with ethyl acetate, weighed on an electronic balance, and marked. Larger spiders were not anesthetized, but were placed in a petri dish of pre-determined weight.

To obtain data on individuals, spiders were marked with acrylic paints (Liquitex). The spiders were returned to the field approximately two hours after capture, each being placed in its own web. Returned spiders were observed for a period of one hour for signs of disturbance. Preliminary experimentation was undertaken to ascertain whether the paints and/or anesthetization were injurious to the spiders. Forty-five spiders were collected in the field and divided into nine groups of five each. Seven of the groups were painted

on the cephalo-thorax with different color paint in the manner outlined above. There were two control groups, one group was treated exactly as above, except that they were painted with water, and the remaining group was left untreated. The spiders were placed in one quart glass jars with cotton and gauze plugs. The jars were placed in a constant temperature chamber at 30 degrees Celsius. Spiders were watered daily, and the experiment was concluded when all spiders had died. Analysis of the data by single classification ANOVA showed no differences between the groups in log mean longevity ( $F = 1.22$ , d.f. = 8, 36,  $p > 0.25$ ). Hence, it was concluded that the method of treatment had no immediate effect upon these spiders. Another experiment was conducted in the field with marked spiders, since it was possible that the colors chosen would alter the survival probabilities. Forty spiders that were marked revealed no differences in length of survival by Analysis of Variance.

In addition to web height and mesh size, magnetic orientation and web dip were measured with a Brunton Pocket Transit. Orientation to the nearest degree was taken as that direction normal to the plane of the web to which the dorsal side of the spider faced. Dip was measured to the nearest degree by placing the extended body of the transit gently on the surface of the web. Vertical span was calculated from web span by adjusting for the angle of dip. Mesh size was measured by averaging the number of lines that intersected one centimeter of a ruler in two successive trials.

### Habitat

The genus Nephila occurs widely throughout the tropical regions of the world. While Petrunkevitch (1911) lists six species as occurring in the Americas, only one is present in the continental United States, Nephila clavipes. According to Comstock (1940), it is confined to the southeastern portion of the United States and in Texas it is limited to the southeastern portion of the coastal region (Brady, 1959). The habitat of Nephila clavipes is marshy area in open forest, or palmetto thicket, where their webs are built between trees and shrubs, often at heights of five meters or more above ground (Wilder, 1866; Brady, 1959; Krakauer, 1972).

At the Coastal Center, Nephila clavipes occurs in the greatest concentrations in the open forest, sometimes extending a short distance into surrounding high shrub layer. However, Nephila have never been found by the investigator at any great distance from the trees, either in the shrubs (Bacheris sp.) or in the grasslands. Nephila is also found, generally at considerable heights (5-7 meters), with its webs bridging large open spaces over the roads and drainage ditches. Judging from concentrations of spiders, the preferred location seems to be within the drip line of the canopy, where the relative humidity is no lower than about 80%. Wilder (1868) noted that the spider has a positive phototactic response and the investigator's own observations confirms that Nephila prefers an exposure varying from light shade to moderate

sunlight. However, some individuals can be found exposed for long periods of the day.

Krakauer (1972) reported that large females (0.45-1.62 g) under full exposure to a heat source resulting in a mean body temperature of  $36.78 \pm 0.30^{\circ} \text{C}$ , were observed to extrude a drop of fluid from the mouth and manipulate it with the chelicerae. In addition, they oriented their posture to minimize the heat load. Krakauer (1972) also found that the critical thermal maximum showed a significant negative correlation with weight.

My observation of unfed spiders confined in glass cases at a constant temperature ( $25-27^{\circ} \text{C}$ ) and low humidity survived only 2-3 days, but lived to 35 days in high humidity (90%) environments. Adult Nephila become inactive below a temperature of  $10^{\circ} \text{C}$ , and die if the temperature is  $0^{\circ} \text{C}$  or less.

In summary, the preferred habitat of Nephila clavipes is moderately open to exposed location offering supports for their large webs. The preferred microclimate is highly humid, and such that the spider's body temperature remains generally below  $36.78^{\circ} \text{C}$ . The significant negative relationship found in direct sunlight more often than will the very large specimens, since the lethal temperature seems to depend upon weight.

### Life Cycle

While it is unknown whether Nephila lives longer in more tropical environments, Nephila clavipes has a maximum life span of one year in this area, as does Argiope sp., Araneus sp., and the majority of web-building spiders. In contrast, species of Lycosa typically have a two-year life span (Edgar, 1970). The Nephila females deposit their egg masses from October through November, although Wilder (1868) reported some females laying as early as September. The egg masses vary from ovoid to a truncated cone in shape and are covered with a white powdery substance. When freshly laid, eggs are cemented together rather firmly, but become more easily separated as hatching nears. Individual eggs are approximately 1 mm in diameter, yellow in color, spherical in shape, and have a mean fresh weight of  $1.0704 \pm 0.2345$  mg (4408 eggs in 9 cases). Each egg mass is wrapped in a single layer of yellow silk, forming a cocoon. The cocoon is wrapped in a leaf which is bound securely to a branch with silk. Within a few weeks, the yellow color of the silk weathers to a dull brown, making it difficult to detect among the dead leaves. The eggs are most often found on a living branch about the size of a pencil, usually only 4-5 meters from the web site. However, I have found egg cases up to 10-20 meters from the nearest current web site. Other egg sites are bushes and vines near the web site and, occasionally, the web itself (one case out of 18 egg cases found). This behavior contrasts with that of

Argiope sp. which consistently lay their egg cases in or very near the web (Comstock, 1940). Egg cases are found at all heights from about 38 cm above ground level to the tops of 9 meter trees. I could find no marked preference for any one height.

Of 4408 eggs examined (9 cases) 3.9% were obviously inviable, being dark and shriveled. On three occasions I have found egg cases parasitized by a mantispid, an egg parasite of ground dwelling spiders (Borrer et al., 1970). Significantly, these egg masses were located less than 46 cm above ground level. There may be other sources of mortality at this stage, but none are known to me. Thus mortality appears to be due mainly to a single predator (16.7% in 18 cases), with some mortality due to inviability of the eggs (3.9% in 9 cases).

Mortality in the 4th stadium is largely due to an unknown spider of the family Mimetidae, the therid Romphacea sp., and to other Nephila. Examination of 35 mud dauber nests revealed no Nephila but many Argiope sp. and other spiders. On many occasions I have found adult Nephila females dead in their webs, but I could find no wounds, and no parasites emerged or were evident from 20 such spiders I kept on glass containers for several weeks at ambient temperatures.

The eggs hatch in about one month after deposition and the spiderlings remain in the egg case until the following May or June. During that time they undergo a molt, and the color changes from yellow to green (Table 1). The number of layers of the egg case increases during this time, presumably

Table 1

Life Cycle of Nephila clavipes

Table 1  
Life Cycle

Stage	Duration	Size	Shape	Color
Egg	1 month	1 mm in diameter	Spherical	Yellow, with white powder on exterior
1st stadium	1-2 weeks	1 mm in diameter	Short legs, covered with black bristles Typical spider abdomen	Base is yellow, with faint black streaks on abdomen
2nd stadium	5 months	1-2 mm	Legs longer than 1st stadium, covered with black bristles; globose abdomen	Yellow to bright green as time passes
3rd stadium	variable	3 mm	Typical spider shape with globose abdomen	Green with black on abdomen
4th stadium	variable	6-7 mm	Elongate abdomen like adults, with relatively simple pattern of streaks. Thorax bare or covered with fine hairs	Abdomen is black and yellow; thorax is yellow
5th stadium	variable	variable (weighs more than 50 mg)	Typical <u>Nephila</u> shape; Males and females distinguishable. "Bottle brushes" on legs of female, males have swollen pedipalps	Abdomen is black and white. Pattern is more complex. Suggestion of white bar on ant. of abdomen, thorax is yellow
6th stadium	variable	variable	Typical <u>Nephila</u>	Females: black on ant. end, white bar is next, ground color is yellow to gold. Six white spots. Thorax covered with silver hairs. Males: Dark brown, no "bottle brushes"



a response to cold. The young hatch in June and make a temporary tangle web near the egg case site. They remain at this site for about one week, and undergo a second molt, before dispersing.

Dispersal of spiders occurs in two ways. Aerial dispersal or "ballooning" is the more spectacular and is common among spiders (Bristowe, 1939), but many spiders simply walk away (Edgar, 1970). Nephila apparently utilizes an intermediate method. Silk threads are floated in the wind, until they contact some structure, then the line is made fast and the spider walks across it. The distance covered will, of course, depend on the openness of the area and the direction of the wind.

Following dispersal, the spiderlings spin orb webs from 2.5 to 5 cm in diameter using dead standing material for supports. In the study area, this material was usually Solidago stalks from the previous season, although some webs were made in the forks of small, dead branches of the Chinese Tallow trees. A further molt occurs, changing the shape of the abdomen from globose to elongate. The males begin to develop functional sex organs in June to July and are subsequently found in the webs of females. Apparently, the sexually mature males do not commonly spin webs, even though they are fully capable of producing silk. However, I have observed, on a few occasions a mature male inhabiting a small web which was apparently its own. The males are very small

(~1 cm in length) and live as commensals in the webs of the females. Wilder (1866) thought that the males took no food, but I have observed them feeding on the females' prey and capturing small prey that the female ignores (mainly small dipterans).

Before the males mature, all spiders tend to build their webs with one or more edges in common, constituting a "hotel". Apparently, this is a mechanism to enable the males and females to find one another, because as the males mature, they move into a female's web. The "hotels" begin to break up in July and the female spiders maintain webs that do not share any support threads. "Hotels" begin to reform during the latter part of August to September and are common thereafter until the first frost. During the latter period, the surplus males present in the webs of females may distribute themselves to the webs of females that mature during this time.

Mating occurs after the last of 6-7 molts of the female. I have observed several matings. The males approach the females boldly while she is motionless at the hub of the web. I have seen males attempting to copulate the unreceptive females and she merely plucked at the web. The male is never pursued or eaten. Mating is complete in thirty to forty-five minutes.

I found the sex ratio to be near 1:1, but the males are distributed as a Poisson ( $G = 1.4884$ ,  $p > 0.1$ ) over the webs of the females. The number of males per web varies from none to

to six. However, in the latter case a single male stays near the female, and apparently is her mate, and seems to keep the other males on the periphery of the web. I have observed that these surplus males are subject to greater predation by a therid, Romphacea sp., than the center male.

The Nephila life cycle ends with the first series of days of mean low temperatures below 10° C.

## Prey

In agreement with numerous previous studies of spider prey (Bilsing, 1920; Turnbull, 1973), the list of prey items taken by Nephila clavipes includes representatives of nearly all orders of Insecta. The most conspicuous exceptions are grasshoppers, crickets, and coleopterans. Dipterans and hymenopterans make up the bulk of the diet, supplemented by lepidopterans, mainly Noctuid moths. Spider activity is mainly diurnal beginning shortly before dawn and extending until shortly after dark.

The list of prey (Table 2) taken shows a progressive change with time and development of the spider. In late May through July, when the majority of spiders weigh 30 to 300 mg, the diet is mainly large dipterans (Sarcophagidae, Muscidae, Bibionidae, Asilidae). Through August, the bulk of the diet was made up of lepidopterans (Noctuid moths). From September on, the bulk of the diet was Apis mellifera with Odonata, and Vespidae also being trapped and consumed.

Nephila clavipes, like Argiope sp., normally occupies the underside of the web in a head down position. When a prey strikes the web, the spider locates the prey by plucking at the web. Thus far, the sequence agrees with that of Argiope argentata studied in detail by Robinson (1969). The web plucking step is often difficult to see as a separate act since it is usually followed immediately by a rush toward the prey.

At this point, the spider bites the prey with a long bite (lasting a few seconds) that quickly stills the captured insect. These orb-weavers prefer a frontal attack, but will bite anywhere unless the prey is unduly large. If the prey is small, it is plucked from the entrapping web and carried directly to the hub, where it is consumed. If the prey is large, it will be wrapped in a few strands of silk, suspended from the rear legs (pair IV) of the spider, and transported to the hub. There, the spider executes a 180° turn, attaches the prey bundle to the web, and begins to feed on it. If more prey strike the web, the spider may drop its current prey and attack a second. Generally, the second and subsequent prey will be wrapped and left at the site of capture. I have seen as many as four prey packages in the web at one time. After feeding, the spider will cut the prey bundles loose from the web and let them fall to the ground. If other prey are present, the spider will retrieve one of them and continue feeding until all prey are consumed. After feeding, the spider will clean her legs, pulling them through her chelicerae several times, and then assume a quiet state of waiting for further prey.

While this is an adequate description of a usual sequence, I have observed several occasions when the spider did not attack another prey until she finished with the current package, and on one occasion I observed a spider, apparently not feeding, repeatedly ignore prey striking the web.

Table 2  
Relative Abundances of Prey Captured

	June	July	August	September	October	November
Diptera	27	67	3	22		
Orthoptera		17				
Odonata			2		1	2
Coleoptera			2			
Lepidoptera			84	13		
Nephila		16	1			
Homoptera	13		1	3		
Hemiptera			1		1	2
Hymenoptera	55		5	62	98	93
Neuroptera						2

### Web Height

Eberhard (1971) demonstrated a significant relationship between the size of a spider and web height in Uloborus diversus. He explained this phenomenon as a result of the damaging effect of wind upon the more fragile webs of small sized spiders. Enders (1974) showed increased height above ground with age in Argiope trifasicata and A. aurantia, and attributed it to the growth of the vegetation in which the web was sited. Nephila webs sited in Solidago showed an increase in web height with vegetation, for May and early June. During this period, the webs were always 1-3 inches above the surrounding vegetation. However, Nephila webs on the twigs of Tallow trees, which are generally above the surrounding vegetation showed no tendency to increased web height during this period. Therefore, growth in surrounding vegetation could be responsible for increasing web height in Nephila.

Table 3 shows a systematic increase in bottom heights from May through September, followed by a decrease in mean height during October and November. This increase, after early June, cannot be related to vegetative growth since I could detect no relationship between web height and vegetative height ( $r = 0.12$ ,  $p > 0.05$ ). There are several possible explanations for this increase: prey items and/or their flight patterns could be changing during the season, or there could be a simple relationship between the size of the spider and web height, or the increase is possibly correlated with mean

monthly temperature. The second explanation is probably invalid because there is no general correlation between web height and spider weight while the web height of the spiders increases during the year. The monthly summary of relative prey abundances (Table 2) shows three changes in principal prey that could correspond with the monthly changes in web height, so prey could be a cause of this increase. However, I feel that a more plausible mechanism is that Nephila uses hot air currents to float silk vertically. Thermal currents over the streets and bare ground in the study area would certainly be sufficient to carry the silk highways used by Nephila up during the summer months and cause them to drop during the cooler periods of the fall months. Thus, I conclude that changes in prey flight heights, and/or thermal differentials may account for the change in web heights in Nephila during the season.



Table 3  
Monthly Averages for Web Parameters

Month	n	Bottom Height 1	Rest Height 1	Orientation 2	Dip 3	Weblines 4
May	124	30.21 $\pm$ 0.85	34.45 $\pm$ 0.88	-	-	-
June	100	37.55 $\pm$ 1.31	42.84 $\pm$ 1.29	168.80 $\pm$ 16.33	73.03 $\pm$ 1.45	18.42 $\pm$ 0.41
July	204	45.96 $\pm$ 1.06	56.24 $\pm$ 1.08	162.48 $\pm$ 5.61	73.12 $\pm$ 0.49	14.42 $\pm$ 0.27
Aug.	207	46.83 $\pm$ 1.36	57.93 $\pm$ 1.38	175.23 $\pm$ 6.02	70.40 $\pm$ 0.48	13.80 $\pm$ 0.35
Sept.	340	52.50 $\pm$ 1.16	63.05 $\pm$ 1.20	150.55 $\pm$ 4.21	70.49 $\pm$ 0.38	-
Oct.	42	51.02 $\pm$ 1.71	60.25 $\pm$ 1.65	182.33 $\pm$ 13.32	65.75 $\pm$ 1.72	-
Nov.	46	46.33 $\pm$ 2.12	53.01 $\pm$ 2.01	128.65 $\pm$ 12.02	68.54 $\pm$ 1.26	-

- 1 inches  
2 north = 0°  
3 from horizontal  
4 per cm

### Magnetic Orientation

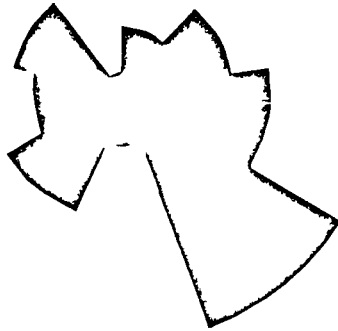
Eberhard (1971) found preferred web orientations in Uloborus diversus, as a result of the prevailing wind at his experimental sites. In my studies on Nephila, wind is probably not a strong factor influencing magnetic orientation of the webs, since the study area was surrounded on all sides by belts of trees. Krakauer (1972) reported that spiders in exposed locations orient their webs normal to the incidence of maximum sunlight. However, spiders occupying more shaded sites were oriented in all compass directions. I found no consistent trend in mean magnetic orientation during the year (Figure 1). This lack of a trend also makes it unlikely that the position of the sun has a direct effect upon web orientation in the study area, since the study occurred between the vernal and autumnal equinoxes when the solar position moves southward.

There is, however, a bimodal distribution of orientations (Figure 1), one centering upon the north-northeast sector, and the stronger, centering upon the southeast-southwest sector. Conspicuously, the north-northwest sector is avoided by a majority of the population. The fact that some webs are oriented toward the non-preferred sector indicates that suitable supports exist for such orientation. We might consider that changing preferred flight direction of the prey influences web orientation, but the lack of consistent directionality in the wind at the study site, and the apparent changes in orientation from September through November, when the preferred

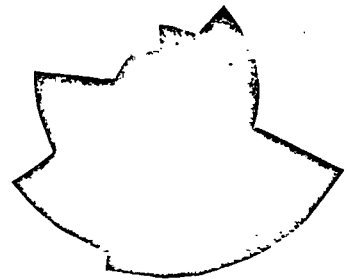
Figure 1  
Monthly Orientation Frequencies

# MONTHLY ORIENTATION FREQUENCIES

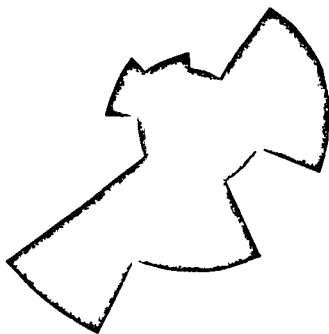
JUNE



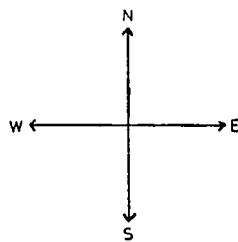
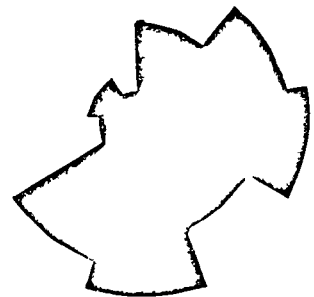
JULY



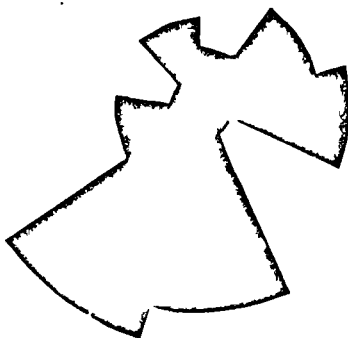
AUGUST



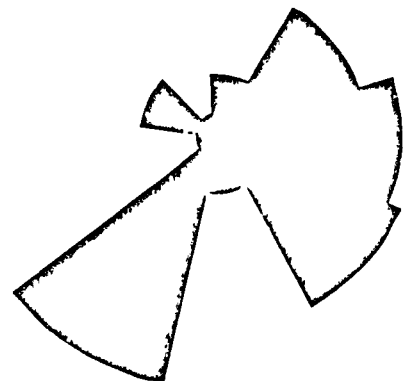
SEPTEMBER



OCTOBER



NOVEMBER



prey is Apis mellifera, makes such a conclusion unlikely, although it cannot be excluded entirely. The study area is bordered to the east by an open Tallow forest, to the south and the south-southwest by an open field with a shallow belt of Tallow trees between and to the west-north by dense Tallow forests. It is therefore possible that prey come preferentially from the more open areas to the east-south-west sectors.

## Dip

The dip (vertical alignment) of an orb web determines the area intercepted (Krakauer, 1972), the more nearby vertical webs giving greater sweep. However, a vertical web is more exposed to possible wind damage (Langer, 1969; Eberhard, 1971), and spiders building such a web must compromise between maximum catch effectiveness, while minimizing web damage by wind.

Eberhard (1971) examined the dip of webs of Uloborus diversus and found that webs exposed to the desert winds were more nearly horizontal than webs in protected sites, but could find no relationship between size of spider and dip of web. Table 3 shows an apparent trend of decreasing dip throughout a season. The changes are small but consistent from June to October, and are consistent with a relationship between spider weight and dip, since there is an increase in mean weight of the spiders through this period. However, I found no correlation between log-weight and dip, and I conclude that there is no relationship between dip and weight.

Krakauer (1972) suggested a relationship between heat load in Nephila and the dip of the web. Table 3 indicates that there may be an interaction between thermal factors and dip, since the dip decreases throughout the summer months with increasing heat loads. Further field work is necessary to resolve such a relationship.

### Movements

The factors that influence the movement of web-building spiders are largely unresolved (Eberhard, 1971). Turnbull (1964) indicated that, at least indoors, spiders never abandon a web site if sufficient food is available. Eberhard (1971) studied web longevity in the desert and found that webs were either replaced within two days or the site was abandoned. He also found that webs were replaced more frequently following feeding than following fasting, and that smaller spiders replaced their webs more frequently than larger spiders. Enders (1973) released marked Argiope aurantia and observed that animals that built webs remained at or near the site for several weeks.

I measured movement as duration of stay in the study area, and frequency distributions of such durations-of-stay calculated on a monthly basis (Table 4). Each frequency distribution was tested for goodness-of-fit, by G statistic, to a Poisson distribution of random durations-of-stay. The distributions were significantly different from Poisson ( $P < .001$  in all cases), and the coefficient of dispersion reveals that the distributions are markedly clumped, implying a difference in web sites within the study area.

Table 4  
Summary Table for Residence Times/spider-site

Month	n	mean	C. D.	G-Statistic
July	84	1.357	2.763	24.184***
August	42	4.524	8.639	35.939***
September	61	6.917	5.431	81.089***
October	51	7.137	6.866	47.298***
November	43	9.186	6.917	18.730***



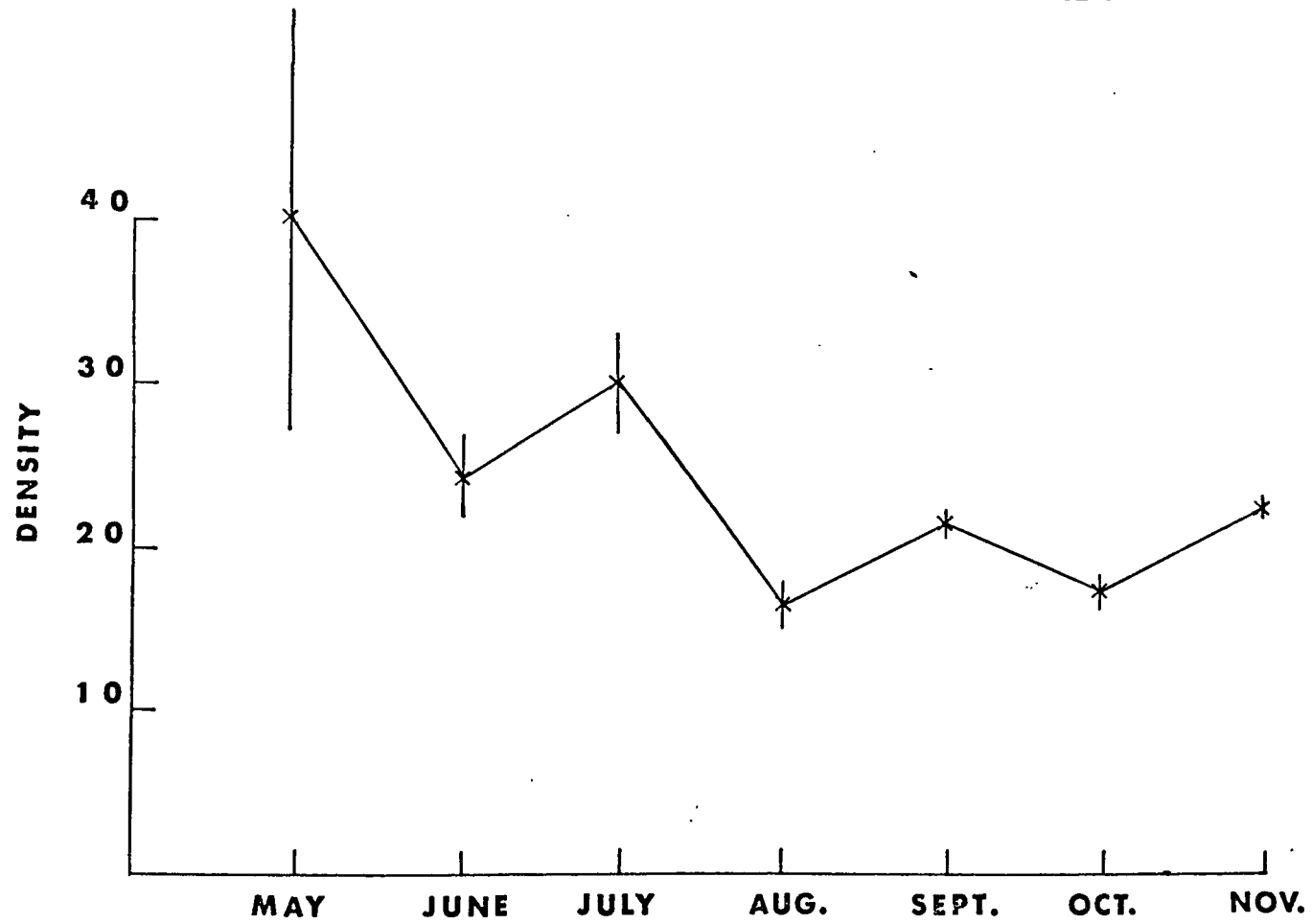
### Population Density

Figure 2 shows the mean numbers of Nephila in the study area by month. The relatively high numbers in May reflects new hatches and its large standard error is, undoubtedly, the result of successive hatches and concomitant dispersal of young spiders. The lowered mean numbers for June and July are the result of the high mortality rates of young spiders, plus the changing web site requirements during this period of active growth and maturation. Further, the males are beginning to mature, and will not be reflected in the counts. From August through November the average numbers show very small changes in magnitude, and no consistent trend in direction. This relative constancy of numbers implies a limited number of "adequate" web sites in the study area, and the possible lack of significant sources of mortality for adult Nephila females. The very small standard errors for this period reflects the increased residence time during the season at this site (Table 4).

Figure 2

Average Density per 0.929 hectares

**Figure 2**  
**AVERAGE DENSITY IN THE STUDY AREA**



### Density of Weblines

Mayer (1953) was able to increase the weight of a spider by fastening a small weight to the dorsum of the abdomen, and found that such "heavier" spiders built webs with wider meshes than before. Witt and Baum (1960) established a similar relationship between weight and mesh size and between size of web and leg length in Araneus diadematus and Neoscona vertebrata.

Regression analysis of 1973 data confirmed such a relationship in Nephila (Table 5). The regression equation,  $\ln D = -0.215393 \ln Wt. + 3.74526$ , shows that heavier spiders tend to build webs with a lower webline density, hence increasing mesh size, than lighter spiders. The reasons for such a relationship are unclear. Perhaps, as Witt and Baum (1960) suggested, the silk production capacity of the spider increases more slowly than does the body weight and leg length, forcing the spider to build a larger web with larger mesh size. Another possible explanation is that spiders seek to maximize the energy profit by building a web that retains prey greater than a certain threshold size regulated by the mesh size of the web. Of course, factors other than body weight certainly determine mesh size in Nephila, since the regression explains about 56% of the variance of the webline density.

Table 5  
Density of Weblines vs Body Weight

Source	df	SS	MS	F <sub>s</sub>
Explained	1	5.54043	5.54043	172.10004***
Unexplained	133	4.28167	.03219	
Total	134	9.82210		

### Summary

The preferred habitat of Nephila clavipes resembles that of Argiope aurantia (Enders, 1973) in that both prefer an ecotonal habitat. However, Nephila prefers vegetation which is sparse-to-moderate in density and height, in or near open stands of trees, while Argiope aurantia and A. argentata prefer a habitat with low dense vegetation and moderate-to-little shade (Enders, 1973; Robinson, 1969). The preferred microclimate is highly humid, and such that the spider's body temperature generally remains below 36.78° C. Smaller Nephila will be more often found at sites exposed to full sunlight, than will the larger specimens, since the lethal temperature is negatively related to body weight (Krakauer, 1972).

In the only published field account of web parameters, in Uloborus diversus, Eberhard (1971) demonstrated that the dip and height of the web was influenced by two factors, wind speed and the size of the spider. On the other hand, dip of Nephila webs is independent of weight (size) and does not seem to be influenced by wind. In A. aurantia, web height is shown to be influenced by height of vegetation at the site during the growing season and, further, by sexual maturity (Enders, 1974). My observations show that web height in Nephila is also influenced by vegetation growth when located in Solidago sp., but that there is no correlation between web height and weight.

Eberhard (1971) showed that orientation of web placements

in Uloborus diversus were dependent upon wind direction, while Krakauer (1972) cited evidence that the magnetic orientation of Nephila webs depended upon the angle of maximum exposure to the sun. In the study area, there is no evidence of a consistent orientation of webs, related either to wind or sunlight exposure. Likewise, I could not find a consistent relationship between weight and web orientation.

Data on movements of spiders between web sites is very scarce (Eberhard, 1971). Turnbull (1964) showed that Achaearenea tepidariorum never abandoned a web site if sufficient food were available, Enders (1973) presented evidence that in A. aurantia residence times were also high. In Nephila residence times are clumped. In the early part of the season Nephila moves often but average residence time increases during the summer.

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Ecological Studies:

II. THE RELATIONSHIP BETWEEN SELECTED WEB PARAMETERS,  
WEIGHT GAIN, AND FECUNDITY IN THE SPIDER  
NEPHILA CLAVIPES KOCH (ARANEIDAE)

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## Introduction

Spiders, like most invertebrates, exhibit a positive correlation between female size and fecundity (Peterson, 1950; Turnbull, 1962; Kessler, 1971). In semelparous forms this provides a direct correlation between size and fitness, and moreover, because of relatively constant growth efficiencies among stadia, spider size (and therefore fitness) can be in turn related to effectiveness in prey capture.

In orb weaving spiders, the web is the only means of detecting and capturing prey and therefore fitness depends in large part upon the appropriate construction of webs and their placement in the environment. Individuals which construct inappropriate webs or place them in poor sites would be selected against by virtue of their smaller sizes and hence one should be able to detect crucial elements of web ecology in these spiders by analyses of corresponding weight gains in field situations.

In determining the role of web ecology in growth of spiders, several factors need to be considered. First, a spider might consistently choose web sites where there is an abundance of prey. Turnbull (1964) found that the cob web spider Achaeranea tepidariorum, constructed webs in various suitable places only to abandon them when a certain minimum number of prey were not captured. Thus, prey were not a factor in selecting a web site, only in deciding whether to move or stay. From a review of extensive literature on

web placement, Turnbull (1973) concludes that there are two major requirements in web siting: (1) suitable structures for support of the web, and (2) microclimate at the site. Thus, initial site selection is not likely to be influenced by prey abundance, but duration of stay may be correlated with such abundances.

Second, Kajak (1967) concluded that Araneus quadratus and A. cornutus live the majority of the time in a superabundance of prey, and that the amount of food caught depended, in large measure, on the web itself, raising the question of which parameters of the web are most likely to be involved with differing effectiveness in prey capture. Witt and Reed (1965) showed that in Araneus diadematus the number of radii, width/length ratio of the catching zone and the length of the radii were independent of spider weight, but that area of the catching zone, mesh width and thread length were all functions of spider weight. Enders (1974) observed an apparent increase in web heights in Argiope aurantia and A. trifasciata with age, but concluded that growth of the surrounding vegetation had forced these spiders to move their webs upward during the season, and that web height was not a direct function of age or weight. Langer (1969) considered the theoretical aspects of spider web construction based upon physical considerations and concluded that wind and precipitation should have an influence on the width/length ratio of the catching zone, and upon the angle of inclination (dip).

Thus while the importance of the web and its placement to spider fitness are generally accepted, we are less certain as to what characteristics of the web itself may be important and what elements of environment cue spiders to optimal sites. The purpose of this study was to examine these elements of the web ecology of the orb weaving spider Nephila clavipes. In particular I wished to test whether the parameters of web height, web size (span), magnetic orientation, or angle of inclination could be related to weight of spiders in their natural environment and whether weight gain at any given site, reflecting prey capture success, was related to residence times at these sites.

### Methods of Study

Web sites were marked with a site number on a piece of surveyor's tape, instead of stakes, offering the least possibility of increasing the number of available web sites. These tags were placed on the largest support near the upper right hand portion of the web. This method of placement allowed the investigator to differentiate individual web sites even where there were several spiders sharing a site. Sites were designated as the largest tree or shrub having the most support threads attached to it.

Individual spiders to be weighed were removed from their webs by chasing them on to a support thread, and capturing them in a wide-mouthed glass jar, caring not to damage the web. Small spiders were anesthetized with ethyl acetate, weighed on an electronic balance, and marked. Larger spiders were not anesthetized, but were placed in a petri dish of pre-determined weight.

To obtain data on individuals, spiders were marked with acrylic paints (Liquitex). The spiders were returned to the field approximately two hours after capture, each being placed in its own web. Returned spiders were observed for a period of one hour for signs of disturbance. Preliminary experimentation was undertaken to ascertain whether the paints and/or anesthetization were injurious to the spiders. Forty-five spiders were collected in the field and divided into nine groups of five each. Seven of the groups were painted

in the manner outlined above. There were two control groups, one group was treated exactly as above, except that they were painted with water, and the remaining group was left untreated. The spiders were placed in one quart glass jars with cotton and gauze plugs. The jars were placed in a constant temperature chamber at 30 degrees Celsius. Spiders were watered daily, and the experiment was concluded when all spiders had died. Analysis of the data by single classification ANOVA showed no differences between the groups in log mean longevity ( $F = 1.22$ , d. f. = 8, 36,  $p > 0.25$ ). Hence, it was concluded that the method of treatment had no immediate effect upon these spiders. Another experiment was conducted in the field with marked spiders, since it was possible that the colors chosen would alter the survival probabilities. Forty spiders that were marked revealed no differences in length of survival by Analysis of Variance.

In addition to web height and mesh size, magnetic orientation and web dip were measured with a Brunton Pocket Transit. Orientation to the nearest degree was taken as that direction normal to the plane of the web to which the dorsal side of the spider faced. Dip was measured to the nearest degree by placing the extended body of the transit gently on the surface of the web. Vertical span was calculated from web span by adjusting for the angle of dip. Mesh size was measured by averaging the number of lines that intersected one centimeter of a ruler in two successive trials.



## Results

To determine which web parameters contribute most to weight gain, web parameters were correlated with themselves and with spider weight through the season, followed by step-wise multiple regression of spider weight onto these parameters. Data were appropriately transformed and tested for normality before statistical analyses, including the use of the natural log of spider weight.

Table 1 gives the intercorrelations among variables averaged over the season, and Table 2 gives the results of step-wise regression for separate 5-day intervals throughout the season. The proportion of the total variance explained by the regression generally increases from June through late August, indicating that the variables become more important as the size of spiders increased.

In late June, span and orientation explain 40% of the variance in the weights of Nephila. At this time, the spiders are still residing in "hotels" and the occasional male exhibits mature external sex organs. Span is more important variable at this time explaining about 31% of the variance. By the middle of July, the "hotels" have largely broken up, and most of the males have matured. The females have become more solitary and most have males residing in their webs. The proportion of the total variance explained by the regression drops to about 32%, with still the most important variable, but explaining only about 19% of the variance. However, orientation has increased in importance

Table 1

Mean Correlation Coefficients between Span (S), Bottom height (B),  
Rest Height (R), Magnetic Orientation (O), Dip (D), and Weight (Wt)  
Averaged over the Season

	Span	B	R	O	D	Ln Wt
Span	-	$0.013 \pm 0.066$	$0.215 \pm 0.064$	$-0.140 \pm 0.065$	$-0.039 \pm 0.066$	$0.629 \pm 0.051$
B		-	$0.975 \pm 0.015$	$0.127 \pm 0.066$	$0.021 \pm 0.066$	$0.138 \pm 0.065$
R			-	$0.045 \pm 0.066$	$0.051 \pm 0.066$	$0.268 \pm 0.064$
O				-	$0.002 \pm 0.066$	$-0.151 \pm 0.065$
D					-	$-0.110 \pm 0.066$
Ln Wt						-

n = 231  
df = 201

Table 2

Step-wise Multiple Regression Analysis of ln Spider weight onto  
Span (S), Orientation (O), Dip (D), Rest Height (R), and Bottom Height (B)

Date	N	F	Computed F-statistic	Variable	Regression Equation	% total variation explained	% variance explained by span
26 June 1973	31	4.18	14.45 5.37	S O	1.18 S - 2.160 O + 3.55	40.00	30.95
17 July 1973	21	4.38	5.74 4.47	S O	0.73 S - 2.56 O + 5.67	31.67	19.17
24 July 1973	44	4.10	23.88 6.67	S R	0.83 S + 0.17 R + 1.56	42.49	34.73
31 July 1973	32	4.17	33.23	S	1.10 S + 1.98	50.97	50.97
15 Aug 1973	17	4.54	19.35	S	1.27 S + 1.17	53.42	53.42
22 Aug 1973	11	5.12	103.34	S	1.40 S + 0.52	91.10	91.10
29 Aug 1973	12	4.96	17.13	S	1.19 S + 1.83	59.45	59.45
25 Aug 1972	21	4.38			no significant regression		
8 Sept 1972	26	4.26	20.92 6.12 5.38	S O D	1.16 S - 0.32 O + 1.17 D + 0.85	61.46	44.34
18 Sept 1972	16	4.60	18.26	B	0.020 B + 4.53	53.51	0.00

in the regression equation now explaining about 12% of the variance. Figure 1 shows that the preferred orientation is more diffuse than in June, indicating that this correlation is real and not the spurious result of some other operant mechanism in the population. Further, the majority of these spiders were occupying sites in the interior of the study area. The relative importance of orientation at this time may be a reflection of preferred flight direction of potential prey.

By the end of July, the spiders have occupied sites both on the exterior and the interior of the study area. The character of the prey has begun to change from Dipterans to Lepidopterans (Table 3). The Lepidopterans probably use the trees and shrubs in the study area for refuges or perhaps even feeding, but apparently fly at a different height than the Dipterans. The regression equation (Table 2) shows that height above ground explains part of the weight variance. But again the more important variable in the regression is the span, explaining about 35% of the weight variance.

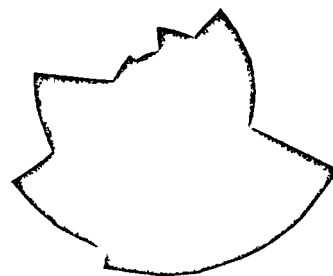
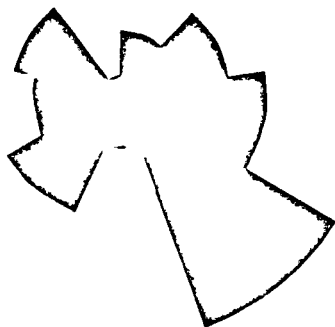
Through August, when Lepidopterans are the most important prey for Nephila, all adjustments in web height and orientation have been made and span becomes the only variable explaining a significant proportion (51% to 91%) of the weight variance. Now, the spider with the largest catching area, as measured by the span, is the most successful. The increasing regression coefficient for the August data underscores the

Figure 1  
Monthly Orientation Frequencies

# MONTHLY ORIENTATION FREQUENCIES

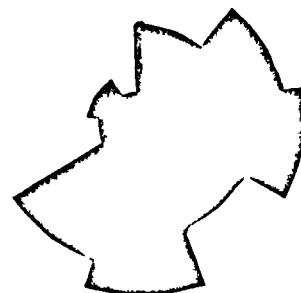
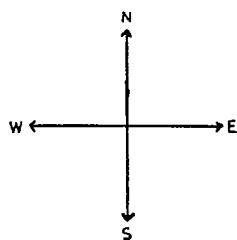
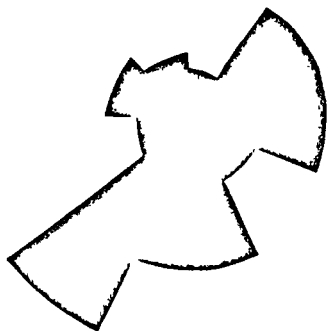
JUNE

JULY



AUGUST

SEPTEMBER



OCTOBER

NOVEMBER

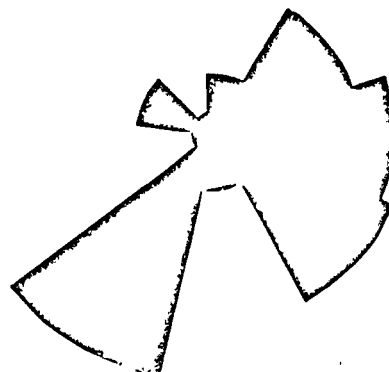
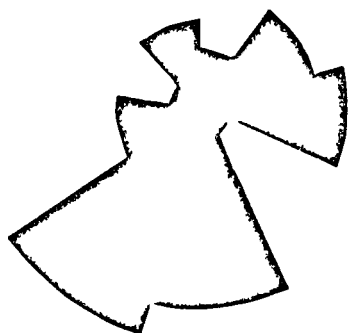


Table 3  
Relative Prey Abundances

	June	July	August	September	October	November
Diptera	27	67	3	22		
Orthoptera		17				
Odonata			2		1	2
Coleoptera			2			
Lepidoptera			84	13		
Nephila		16	1			
Homoptera	18		1	3		
Hemiptera			1		1	2
Hymenoptera	55		5	62	98	93
Neuoptera						2

increasing importance of span in explaining the weight variance. Apparently, a larger web increases the chances for prey capture.

At the end of August, when a new prey resource is beginning to be exploited, Table 3, the proportion of the total variance explained by the regression equation drops to about 60%. The spiders are beginning to build "hotels" and web sites on the interior of the study area are being abandoned. The important web sites are now on the exterior of the study plot. A large web is still an advantage to Nephila but the requirements are beginning to change.

In early September, the regression equation explains about 61% of the weight variance in Nephila. Span is still the significant variable in the regression explaining about 44% of the variance. Now, however, orientation (10%) and dip (7%) have become significant. This is during the period when the character of the prey is changing, and adjustments must be made.

By mid September, the regression equation explains about 54% of the weight variance, and span is no longer a significant factor in the regression. The only significant variable is bottom height, or height above ground level of the web. Thus, there are weight-related changes in web height occurring during this period. Perhaps, these adjustments are related to changes in prey items that are occurring at this point.

In summary, it is most important that a spider have the



largest possible web through the period of most rapid growth and sexual development, that is from June through August. Early in the season, there is an advantage to having a large web properly oriented, perhaps due to directionality in the flight of the prey. During the remainder of the season, the advantage is to the spider with the largest web and neither orientation nor height above ground is a significant factor.

### Residence Times

The factors that influence the amount of time that a spider spends at a given site are uncertain (Eberhard, 1971). Turnbull (1964) indicates that, at least indoors, A. tepidarorum never abandons a web site if sufficient food is available. In field studies on Uloborus diversus Eberhard (1971) found that 83 percent of the web sites were occupied over a five day period, and his data indicate no significant differences between size classes of spiders. Enders (1973) released Argiope aurantia and observed that the animals that built webs remained at or near the site for several weeks.

To determine whether certain web sites are more suitable than others, I utilize a goodness-of-fit to a Poisson distribution, which would be generated under a regime of random movements of spiders among equally attractive web sites. Residence time distributions per spider per site were calculated on a monthly basis (Table 4), and tested for goodness-of-fit by G-statistic (Sokal and Rohlf, 1969). It is apparent that the distributions were significantly clumped for all cases ( $P < .001$ ), implying that some web sites are more suitable than others and movement is speeded up in less suitable sites and slowed in better ones.

The consistent trend toward increased mean residence time as the season progresses indicates a possible relationship between weight and residence time. Regression calculated between log (weight) and log (residence time) were not

Table 4  
Summary Table for Residence Times/spider-site

Month	n	mean	C. D.	G-statistic
July	84	1.357	2.763	24.184***
August	42	4.524	8.639	35.939***
September	61	6.917	5.431	81.089***
October	51	7.137	6.866	47.298***
November	43	9.186	6.917	18.730***

Table 5  
Analysis of Variance  
Residence Time vs Weight Gain

Source	df	SS	MS	F <sub>s</sub>
Explained	1	10.26627	10.26627	33.29***
Unexplained	48	14.80342	0.30840	
Total	49	25.06969		

Regression Equation

Residence time vs Weight gain

$$\ln (\text{Days}) = 0.35304 \ln (\text{Weight gain}) + 1.14092$$

standard error of b =  $\pm$  0.06119

significant ( $b = -0.0003 \pm 0.20613$ ,  $F = 0.05$ ) indicating that heavier spiders do not remain at a site longer than lighter ones.

Turnbull (1964) suggested that weight gain may be a factor in the residence time of web building spiders. Accordingly, regression analysis was employed to delineate a relationship between residence time and weight gain, calculated as the algebraic sum of all gains and losses, excluding the loss of weight due to egg laying. The regression (Table 5) shows that the weight gained at a site explains 41% of the variance in residence time. A regression analysis calculated on average daily weight gain versus residence time was significant ( $b = 0.276 \pm 0.129$ ,  $F = 4.54$ ,  $.01 < P < .05$ ), implying that the average daily rate of weight gain influences residence time.

## Discussion

Spiders cannot alter the basic web pattern (Turnbull, 1974), but experiments by Witt (1963) Witt and Reed (1965), and Witt and Baum (1960) all indicate that at least some parameters of the web are alterable. Mesh size is a function of the weight of the spider and thread supply, but under starvation conditions a spider strives to maintain as large an area as possible with diminishing thread supply and so increases the web mesh size (Witt, 1965). Added weight results in a full sized web with fewer radii and spiral turns (Christiansen et al, 1962). Colebourn (1974) observed that Araneus diadematus is capable of repositioning the support thread, thereby affecting the orientation of the web. Finally, of course, the spider can move to a new site and construct a new web. My own observations on Nephila indicate that these spiders are capable of changing the height, orientation and dip of a web, and also can move to a new site.

The regressions of body weight on web parameters demonstrate that body weight depends upon these web parameters to a significant degree. The fact that kinds of prey available to these spiders changes throughout the season argues that we are seeing real responses by the spiders to changing external conditions. Further, even in a series of regressions where there is a single significant parameter, changing proportions of the weight variance explained by the measured parameter lends credibility to the hypothesis that the spiders

are adjusting their webs with respect to the prey, and that the heaviest spiders are the ones that are the most successful in this endeavour. Movements, as measured by residence times, are another method for obtaining an increase in prey. The web is the only means possessed by a web-building spider of assessing the productivity of its immediate environment and, consequently, the movements of a spider are random with respect to its prey (Turnbull, 1964). Hence, if the length of time that a spider stays at a given site depends upon the availability of prey, then the distribution of residence times will be random if the probability of catching sufficient prey is the same at each site. Distributions of residence times are indeed non-random, and imply that some sites in the study area are better, in some sense, than others. The success of a spider in capturing prey will be reflected in increased weight (Kajak, 1967), therefore increased weight gain during the time spent at a given site will be related to residence time at that site. Regression of  $\ln$  (weight gained) on  $\ln$  (residence time) was significant (Table 5), indicating that, in Nephila, residence time is dependent on the availability of prey at a site. However, this result is also subject to the interpretation that heavier spiders remain at a site longer than lighter ones. Regression of  $\ln$  (weight) onto  $\ln$  (residence times) was calculated and indicated that there is no significant ( $b = -0.0003$ ,  $F = 0.05$ ) relationship. Therefore, I conclude that prey availability as measured by

the weight gained at a given site is the major factor influencing residence time in Nephila clavipes. Thus, Nephila effects changes in the web parameters that result in increased weight, presumably due to an increase in consumption of prey, and movements, as measured by residence times, are related to weight gain.

Size in Nephila would be related to fitness if fecundity increased with female size. The regression equation relating the number of eggs to female size was  $\ln(\text{number of eggs}) = 0.96 \ln(\text{female mass}) + 0.34$ , accounting for 81% of the variance in fecundity among spiders ( $P < .001$ ). Thus, the female that could alter its web so as to increase the amount of prey caught and consumed per unit time might increase its fitness relative to others in the population (Schoener, 1971). However, its relative fitness would only increase if the subsequent egg and juvenile mortality were independent of the numbers of eggs, either by reduction to some arbitrarily low number of survivors or by losing some percentage of the current crop. In either case, the heavier female would be disproportionately represented in the next generation. Even if in a large hatch of young spiders, a large number were eaten by their siblings, the survivors might thereby gain an advantage in being larger than the survivors from a small hatch. The life cycle of Nephila renders this a distinct possibility, since, after hatching from the cocoon, the young remain together for a period of time after they begin feeding.



Another possible advantage in large females is that they may have greater pick among available males, perhaps selecting more aggressive males, since I have observed multiple males in some webs but not in others. To test this hypothesis data from 25 females taken during 25 August 1972 to 30 August 1972 were used to calculate the frequency distribution of males. The results ( $G = 1.4884$ ,  $P > 0.1$ ) show that the data fit a Poisson distribution implying that the number of males in a females' web is the result of a random process. The correlation between spider size and the number of males calculated from the same data was not significant ( $r = 0.325$ ,  $df = 23$ ,  $P > .05$ ).

Thus, we conclude that Nephila is capable of altering the measured web parameters to yield an increased consumption of prey, as measured by body weight, that there is a range of abilities to effect these alterations, and that increased body weight is reflected in increased egg production thereby increasing the relative fitness of the female.

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## Appendix A

Intercorrelations between Ln Weight, Square Root  
Span, Bottom Height, Rest Height, Orientation,  
and Dip for Five Day Intervals

Correlations                      Table 1  
26 June 1973                      Five Day Interval

n = 31

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	-0.064	0.190	-0.268	0.083	0.577**
Bottom Height		-	0.966**	0.263	0.381*	-0.072
Rest Height			-	0.197	0.419*	0.080
Orientation				-	0.062	-0.156
Dip					-	-0.279
Log Weight						-

## Correlations

Table 2  
17 July 1973

Five Day Intervals

n = 21

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	-0.160	0.041	0.405	-0.017	0.482*
Bottom Height		-	0.979**	-0.049	-0.181	-0.044
Rest Height			-	0.024	-0.152	0.034
Orientation				-	-0.248	0.218
Dip					-	-0.399
Log Weight						-

## Correlations

Table 3  
24 July 1973

Five Day Interval

n = 44

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	-0.028	0.201	-0.171	0.170	0.602**
Bottom Height		-	0.973**	0.084	-0.296*	0.274
Rest Height			-	0.046	-0.223	0.413**
Orientation				-	0.008	-0.188
Dip					-	0.047
Log Weight						-

Correlations

Table 4  
31 July 1973

Five Day Intervals

n = 32

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	0.096	0.358*	-0.272	-0.096	0.725**
Bottom Height		-	0.963**	0.077	0.123	0.305
Rest Height			-	-0.002	0.123	0.482**
Orientation				-	0.111	-0.219
Dip					-	-0.037
Log Weight						-



Correlations

Table 5  
15 August 1973

Five Day Interval

n = 17

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	-0.088	0.168	-0.120	-0.354	0.751**
Bottom Height		-	0.966**	-0.076	0.136	0.015
Rest Height			-	-0.110	0.086	0.210
Orientation				-	-0.208	0.051
Dip					-	-0.203
Log Weight						-

## Correlations

Table 6  
22 August 1973

Five Day Interval

n = 11

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	0.347	0.564	0.049	-0.405	0.959**
Bottom Height		-	0.969**	0.459	-0.057	0.224
Rest Height			-	0.406	-0.118	0.448
Orientation				-	0.071	0.045
Dip					-	-0.345
Log Weight						-

Correlations

Table 7  
29 August 1973

Five Day Interval

n = 12

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	-0.108	0.102	0.281	-0.391	0.795**
Bottom Height		-	0.977**	-0.371	-0.144	0.162
Rest Height			-	-0.331	-0.203	0.331
Orientation				-	-0.645*	-0.093
Dip					-	-0.284
Log Weight						-

## Correlations

Table 8  
25 August 1972

Five Day Interval

n - 21

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	-0.194	-0.073	-0.506	0.010	0.279
Bottom Height		-	0.992	0.591	0.147	-0.304
Rest Height			-	-0.006	0.165	-0.278
Orientation				-	0.000	-0.160
Dip					-	-0.340
Log Weight						-

Correlations                      Table 9  
8 September 1972                      Five Day Interval

n = 26

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	-0.074	0.064	-0.110	-0.083	0.682**
Bottom Height		-	0.986**	0.219	0.330	0.056
Rest Height			-	0.227	0.402*	0.173
Orientation				-	0.324	-0.408*
Dip					-	0.110
Log Weight						-

Correlations

Table 10  
18 September 1972

Five Day Interval

n = 16

	Span	Bottom Height	Rest Height	Orientation	Dip	Log Weight
Span	-	0.676	0.733	-0.218	-0.070	0.600
Bottom Height		-	0.996**	-0.191	-0.388	0.731*
Rest Height			-	-0.201	-0.349	0.752*
Orientation				-	0.060	-0.329
Dip					-	-0.148
Log Weight						-