

## Ecological and seasonal variations in a free-moving population of the golden-web spider, *Nephila clavipes*

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### Summary

Spiders live in various ecotypes and may change location as a function of the season or stage of their life cycle. This study examined seasonal and maturational population differences occurring in a temperate population of *Nephila clavipes* in three contiguous ecotypes: hardwood forest, forest fringe, and open cleared spaces. Transects were examined weekly for two years during the period when *Nephila* were active. Spiders and their webs were described and counted. During the spring most spiderlings were located in the forest fringe; however, by the mating season spiders were more evenly dispersed across the three ecotypes with larger adult females found mainly in the clearing. Webs in cleared areas contained mainly adult females and were more likely to be aggregated than forest or forest fringe webs. Forest and forest fringe aggregations usually consisted of juvenile spiders. The implications of the present findings for the interaction of habitat, web structure and feeding are discussed and compared to similar studies conducted on tropical *Nephila*.

### Introduction

Some spider species occupy different habitats during different seasons of the year. For example, funnel-web spiders from the southeastern United States move away from lava flows and into grassland once the summer sun makes the lava flows too hot. When cooler temperatures occur in the fall, the funnel-web spiders return to the lava flows (Riechert, 1974). Spiders also occupy different habitats during particular phases of their life cycle. Female wolf spiders in Europe move from the forest to cleared areas after egg laying, leaving the young and sub-adult animals in the leaf debris of the woods (Edgar, 1971). Tropical *Nephila maculata* spiderlings live in

grassy cleared areas throughout the year (Robinson, Lubin & Robinson, 1974), whereas adults are found primarily along trails and open spaces within the forest (Robinson & Mirick, 1971).

Unlike tropical *Nephila clavipes*, which may have at least two generations per year (Vollrath, 1980), temperate *N. clavipes* have an annual cycle of a single generation where the adults die each fall. Adults dwell in the forest (Moore, 1977), in cleared areas around power lines (Krakauer, 1972), and at the forest edge (Moore, 1977). Like their tropical counterparts, adult temperate *Nephila* build their webs above the herbaceous layer. Although studies have partially examined the life cycle and habitat of temperate *N. clavipes* (Krakauer, 1972; Moore, 1977), previous research has focused solely on adult populations. The present study was designed to examine growth, movement patterns and aggregation patterns in a free-moving population of *N. clavipes* from dispersal until adult death in early winter.

Temperate *N. clavipes* spiderlings usually overwinter in egg sacs from September-March. After emergence spiderlings remain together for about five weeks in a series of communal webs (Hill & Christenson, 1981). After dispersal, spiderlings build their own individual webs where they capture prey for the first time (Hill & Christenson, 1981). *N. clavipes* shows extreme sexual dimorphism in size; males mature at about 8 mm in cephalothorax-abdomen length and females at about 22 mm in length. Adult males abandon their own webs and search for female webs where they vie for the hub position, an area about 5 cm above the female (Christenson & Goist, 1979; Vollrath, 1980). Peripheral males remain on support strands further from the female. The female is sexually receptive for about 48 hrs following her final moult and later in adulthood primarily when feeding on large prey. About one month after her final moult, the female leaves her web and lays her first egg clutch which she abandons after construction. Females usually lay their eggs in the boxelder trees found at the edge of the forest and probably lay two egg clutches in a season. A month later the eggs hatch; spiderlings moult for the first time about a week later. By the end of December, all adult *Nephila* are dead. The second instars overwinter in the egg sacs and then emerge in the spring.

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### Study area

The study was conducted at the F. Edward Hebert Center of Tulane University, located 20 km south of New Orleans, Louisiana. Transects traversed three ecological habitats where *N. clavipes* built their webs. The woods area was hardwood, bottomland forest consisting primarily of red maple (*Acer rubrum*), hackberry (*Celtis laevigata*), American elm (*Ulmus americana*) and green ash (*Fraxinus pennsylvanica*). The forest fringe, between the woods and clearing, consisted primarily of softwood including boxelder (*Acer negundo*), low shrubs and dead saplings. The cleared area consisted of annual flowering plants, giant ragweed (*Ambrosia trifida*), brazilian vervain (*Verbena brasiliensis*), black willow (*Salix nigra*), common ragweed (*Ambrosia artemisiifolia*) and ironweed (*Sida rhombifolia*). The three areas were adjacent to one another; thus each transect line contained a portion of each area. We inspected transects weekly from 8 April to 9 December 1978 and from 9 April to 4 November 1979. The study area was continuous with other areas containing *Nephila*; the same movement patterns were observed in the *Nephila* in these surrounding areas.

### Methods

During 1978 we initially strung six transect lines, but added lines as the density of spiders decreased, so that by September there was a total of fifteen lines. These lines were used for the remainder of the 1978 season and for all of the 1979 season. In 1979 lines were randomly selected for inspection from the fifteen transects provided that at least 100 spiders on their own webs were described or all fifteen transects were used. Once data collection began on a line, we finished the line regardless of when the 100 spider limit was reached.

Each of the fifteen transect lines measured 1 m in width and 55 m in length. The lines averaged 36 m in the woods, 6 m in the forest fringe, and 13 m in the clearing. At the beginning of the season when the spiders were numerous, four persons censused each line. One pair started at the woods end of a line and the other pair at the clearing. Members of a pair looked inwards on the 1 m wide line, each member examining the half a metre closest to him. As the number of spiders decreased and their size increased, two persons censused a line starting at opposite ends.

In 1978 we collected the following information

	1978						1979					
	Early		Mid		Late		Early		Mid		Late	
	$\bar{X}$	s.d.	$\bar{X}$	s.d.	$\bar{X}$	s.d.	$\bar{X}$	s.d.	$\bar{X}$	s.d.	$\bar{X}$	s.d.
<b>Woods</b>												
Undiffer.	6.1	(3.1)	0.3	(0.5)	0	(0)	19.8	(11.1)	7.6	(1.2)	0	(0)
Juv. ♀	0.4	(0.7)	0.9	(0.6)	0	(0)	0.3	(0.6)	0.7	(0.7)	0.1	(0)
Ad. ♀	0	(0)	0.2	(0.1)	0	(0)	0	(0)	0.1	(0)	0.07	(0)
Sol. ♂	0.2	(0.6)	0.7	(0.8)	0	(0)	0.2	(0)	1.1	(0.2)	0	(0)
♂ on ♀ web	0	(0)	0.5	(0.3)	0	(0)	0	(0)	0.4	(0.5)	0	(0)
<b>Forest Fringe</b>												
Undiffer.	9.1	(5.0)	0.8	(1.6)	0	(0)	62.9	(50.4)	10.1	(1.7)	0	(0)
Juv. ♀	1.0	(0.2)	1.3	(0.2)	0	(0)	0.6	(0.1)	0.9	(0.1)	0	(0)
Ad. ♀	0	(0)	0.4	(0.3)	0.2	(0.2)	0	(0)	0.2	(0.2)	0.2	(0.1)
Sol. ♂	0.5	(1.4)	1.0	(1.4)	0	(0)	0.4	(0.1)	0.9	(0.1)	0	(0)
♂ on ♀ web	0	(0)	1.2	(0.9)	0	(0.1)	0	(0)	0.6	(0.6)	0	(0)
<b>Clearing</b>												
Undiffer.	1.7	(1.0)	0	(0.1)	0	(0)	17.3	(17.0)	0.1	(0.2)	0	(0)
Juv. ♀	0	(0)	0.4	(0.3)	0	(0)	0	(0)	0.6	(0.1)	0	(0)
Ad. ♀	0	(0)	1.0	(0.8)	0.7	(0.7)	0	(0)	0.5	(0.3)	0.3	(0.3)
Sol. ♂	0	(0)	0	(0)	0	(0)	0	(0)	0.3	(0.1)	0	(0)
♂ on ♀ web	0	(0)	1.8	(1.0)	0.1	(0)	0	(0)	0.6	(0.4)	0.1	(0.2)

Table 1: Number of spiders per 10 m in each ecotype. Spiders are classified as undifferentiated, juvenile females (Juv. ♀), adult females (Ad. ♀), males occupying their own webs (Sol. ♂), or males on female webs (♂ on ♀ web).

from each web located on the transect line: the spider's size and sex, number of males on a female's web, number and position of missing legs, numbers and kinds of captured prey, the spider's activity, orb damage, presence of barrier strands and their positions dorsal and/or ventral to the resident, whether the barrier strands contained debris, and occurrence of webs connected by common support strands. We classified each spider as follows: unknown sex (less than 10.5 mm in cephalothorax-abdomen length), female (greater than 10.5 mm in length), and male (presence of enlarged pedipalps). Orb damage was recorded on a scale from 0 to 6: 0 = no holes in the viscid spiral, 1 = a few small holes, 2 = ¼ of the spiral missing, 3 = ¼ to ½ of the spiral missing, 4 = ½ to ¾ of the spiral missing, 5 = ¾ to all of the spiral missing, and 6 = only a few barrier strands remaining. In 1979 we recorded two additional measures: whether the orb's hub was less than or greater than 1 m from the ground, and a measure of hub to hub distance between connected webs.

### Analysis of results

When 1978 results were replicated in 1979, then

1978				1979			
Date	♂	♀	♂/♀	Date	♂	♀	♂/♀
17/6	1.0	9.5	0.1	17/6	3.0	6.5	0.5
24/6	10.0	8.0	1.2	24/6	7.7	7.7	1.0
1/7	9.2	11.2	0.8	1/7	19.3	11.3	1.7*
8/7	15.0	8.0	1.9*	8/7	21.7	11.0	2.0*
				11/7	Hurricane Bob		
15/7	7.0	6.5	1.1	15/7	9.2	3.8	2.5*
22/7	11.0	7.4	1.5	22/7	7.6	3.6	2.1*
29/7	9.4	8.1	1.2	29/7	5.1	3.6	1.4
5/8	6.8	6.3	1.1	5/8	2.8	2.8	1.0
12/8	6.2	5.1	1.2	12/8	2.1	3.0	0.7
20/8	3.9	3.4	1.1	19/8	1.4	2.5	0.6
26/8	2.9	4.3	0.7	26/8	1.2	1.8	0.7
2/9	0.9	2.8	0.3	1/9	0.9	1.7	0.6
9/9	0.6	3.1	0.2	9/9	0.3	1.1	0.2
16/9	0.1	3.0	0.0	16/9	0.1	0.7	0.1
23/9	0.0	2.3	—	23/9	0.1	0.5	0.2

Table 2: Sex ratios. Male and female columns reflect the average number of spiders per line on a particular day, ♂/♀ column is the sex ratio, and asterisks indicate ratios significantly ( $p < 0.01$ ) different from a 1:1 ratio and favouring males.

just the latter are reported. If there was a discrepancy between the years, then results are given for both years. The study was divided into three time segments: (1) early season, during which animals matured (April-June), (2) mid season, when mating occurred (July-August), and (3) late season, when females laid eggs (September-December). Season x ecotype ANOVAs were conducted on all dependent variables. Chi-squares were conducted on frequency data including analyses for the pattern of missing legs, types of spiders found in web aggregations, and number of spiders in an aggregation. Sex ratios were analysed using Chi-squares corrected for continuity.

### Results

#### Population density

In the early season more spiderlings were located in the forest fringe per 10 m<sup>2</sup> than in the woods or clearing ( $F(2,74) = 3.80$ ;  $p = 0.027$ ). By the mating season the number of spiders decreased, and spiders were more evenly dispersed across the three areas. Late in the season spider numbers dropped even more, with most of the remaining females residing in the clearing (see Table 1).

#### Sexual differentiation and sex ratio

In both years we could distinguish females in the woods by the first of June, in the forest fringe by mid June, and in the clearing by late June. Males were identifiable about a week later than females; they also appeared first in the woods, then in the forest fringe and finally in the clearing. Interestingly, solitary males were never found in the clearing during 1978 and only a few ( $n = 15$ ) mid season during 1979 (Table 1). In each of the habitats males appeared on female webs during the first week of July. During the mating season female webs in each area averaged about one male each; only 19% of female webs contained more than one male. Females on webs with males were larger ( $\bar{X} = 19.9$  mm) than females on webs without males ( $\bar{X} = 18.0$ ;  $F(1,78) = 6.24$ ;  $p = 0.001$ ). All males had abandoned their own webs by the end of August, and most males had died by the end of September (Table 2). Females had died by the end of December.

We examined the proportion of males to females for both years. During the peak of the mating season,

i.e. the first two weeks of July, the ratio was in favour of males, but by mid-August the ratio began to favour females (Table 2). On 11 July 1979 the study site was affected by 50 mph winds from a passing hurricane. Female webs collapsed, and the next day females were found on flowering plants. Male numbers dropped from 21.7 before the storm to 10.3 animals per line two days later. Female numbers dropped from 11 to 4.3 animals per line. Female numbers were more severely affected by the storm than male numbers as reflected in the increased sex ratios (see Table 2). The drop in the number of males per line from July 8th to 15th in both 1978 and 1979 was by about one-half. In contrast, the drop in the number of females for the same period was slight in 1978 but severe in 1979.

### Morphology

Undifferentiated spiderlings grew about 1.5 mm per month during the spring (Fig. 1). Females grew at a much faster rate than males. Males reached their maximal size in June whereas females continued growing until August. Females located in the clearing were longer in cephalothorax-abdomen length ( $\bar{X}$  =

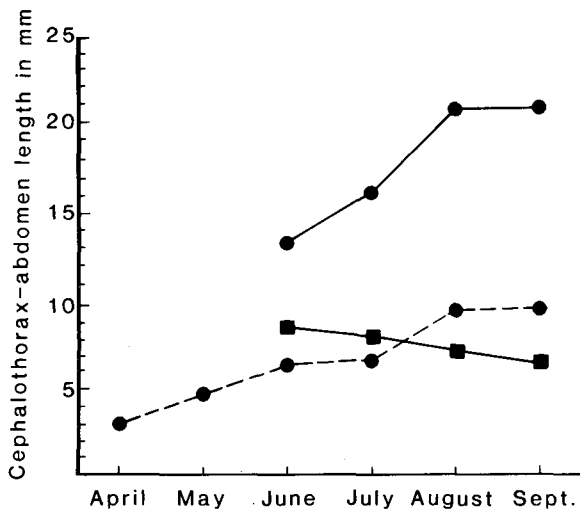


Fig. 1: Growth curves during 1979: undifferentiated spiderlings (stippled lines with circles), males (solid lines with squares), and females (solid lines with circles). Cephalothorax-abdomen length was measured in mm for each spider. Males and females were not differentiated until June.

21.4 mm) than females in the forest fringe ( $\bar{X}$  = 17.8 mm) or woods ( $\bar{X}$  = 17.5 mm;  $F(2,78) = 11.23$ ;  $p = 0.001$ ).

Over the two-year period out of a total of 4717 spiders examined, 518 spiders were missing one leg, 129 two legs, and 30 three legs. The first pair of legs were most likely to be missing ( $\chi^2(3) = 199.39$ ;  $p < 0.001$ ). The proportion of spiders with missing limbs did not differ among the habitats. Hub and peripheral males on female webs were more often missing limbs than solitary males ( $F(2,74) = 3.78$ ;  $p = 0.023$ ).

### Web parameters

A higher proportion of webs had both dorsal and ventral barrier strands in early and mid season than in late season ( $F(2,74) = 157.87$ ;  $p < 0.001$ ; Table 3). The barrier strands of the web were also more likely to contain debris items ( $F(2,74) = 102.71$ ;  $p < 0.001$ ), and those items were more likely to be arranged in a vertical linear manner early in the season ( $F(2,74) = 8.63$ ;  $p < 0.001$ ; Table 3). More woods and forest fringe webs were less than 1 m from the ground than clearing webs ( $F(2,74) = 45.4$ ;  $p < 0.001$ ); however, by mid season spiders built webs higher, regardless of where they were found ( $F(2,74) = 23.71$ ;  $p < 0.001$ ; Table 3). There were no significant seasonal differences in orb damage.

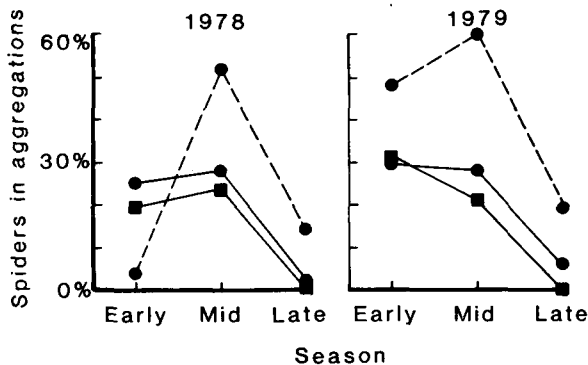


Fig. 2: Proportion of spiders that shared common support strands among the three ecotypes during early, mid and late seasons. Clearing spiders are represented by stippled lines with circles, fringe spiders by solid lines with squares, and woods spiders by solid lines with circles.

### Prey items

Prey types observed in female webs during July and August in both years were analysed. We divided prey into large items including large flies, beetles, bees, butterflies, dragonflies and cicadas, and small types including gnats, small flies, mosquitoes and small moths. Clearing spiders caught more large prey types than woods or forest fringe spiders (Woods = 37% large prey, Forest fringe = 7% large prey, and Clearing = 89% large prey,  $\chi^2(2) = 11.76$ ;  $p = 0.003$ ;  $n = 50$ ).

### Spider sociality

Clearing spiders built webs connected by common support strands more often than woods or forest fringe spiders (Fig. 2). The percentage of connected webs peaked at mid season and declined considerably by the end of the season. The average distance between the hubs of spiders in an aggregation was 31 cm; the distance did not vary significantly between the areas.

The number of webs connected together did not differ significantly between the areas. Usually only two webs were connected ( $n = 368$ ); however, there were situations where three webs ( $n = 100$ ) and four or more ( $n = 94$ ) were joined. The types of spiders found in aggregations varied between the areas. In the woods and forest fringe 94% and 93% of web aggregations, respectively, included solitary males and small spiderlings, while in the clearing 59% of the web aggregations consisted only of adult females ( $\chi^2(4) = 189.06$ ;  $p < 0.001$ ).

### Discussion

The number of spiders in a particular ecotype

varied depending on which phase of the life cycle the spiders were in. Egg sacs are usually laid in the forest fringe, and spiderlings thus disperse from there (Christenson & Wenzl, 1980). Immediately after dispersal, most spiderlings were still located in the forest fringe. This suggests that these *Nephila* spiderlings dispersed by playing out silk strands and travelling short distances along them rather than by ballooning, since ballooning usually results in spiderlings travelling a considerable distance from their departure point (Tolbert, 1977). Perhaps the reason is that the forest fringe has a lower canopy and more shrubs that would provide potential web supports for the spiderlings' small webs than the forest or clearing.

As the season progressed and spiders reached maturity, they became more evenly dispersed across the three areas. By mid season, the woods and forest fringe female populations consisted primarily of juveniles while the clearing population consisted primarily of adult females. Spiders captured more large prey in the clearing than in the woods or forest fringe.

Three types of sociality are found in spiders: sociality based on aggregation and tolerance, cooperative behaviour, and reproductive traits (Buskirk, 1981). *N. clavipes* appeared to tolerate one another within aggregations. Clustering may aid in defence against predators (Alcock, 1975) although currently there are no data to support this hypothesis in spiders (Buskirk, 1981), and aggregations of webs might even attract predators and parasites (Lubin, 1974). Moore (1977) hypothesized that *Nephila* "hotels" aid males in locating females. This study did not support Moore's hypothesis since woods and forest fringe solitary females had the same average number of males per web as clearing females. Buskirk (1981)

Web measure	Woods			Forest fringe			Clearing		
	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
Barrier Web	0.87	0.61	0.12	0.84	0.80	0	0.88	0.57	0.04
Debris	0.61	0.29	0.15	0.55	0.22	0	0.67	0.07	0
Linear Debris	0.08	0.09	0	0.06	0.03	0	0.18	0	0
< 1 m high	0.73	0.46	0.50	0.73	0.31	0.38	0.25	0.07	0
Orb damage	0.82	0.88	1.10	0.92	1.52	0.88	0.72	0.72	1.33

Table 3: Proportions of spiders in various ecotypes that occupied webs with barrier webs, debris within their barrier webs, linearly arranged debris in their barrier webs, and webs built less than 1 m from ground. Also included is an average measure of orb damage.

suggested that silk conservation and increased strength of web supports might be advantageous in web aggregations. This might have been true in the case of large aggregations of females in the clearing since the main sources of web support in the clearing were dead stalks of giant ragweed. These stalks are not as strong as the tree branches and trunks which are used as support in the woods and forest fringe. It is also possible that aggregations occur in the flight paths of insects. It could be that aggregations occurred because of limited support structures; however, there appeared to be an adequate number of support structures for individual webs in the clearing. Small spiderlings tended to aggregate in the woods and forest fringe; aggregating might occur in these ecotypes because of limited web sites.

Tropical *N. maculata* from New Guinea mate and lay eggs during the entire year (Robinson & Robinson, 1973). In contrast, tropical *N. clavipes* from Cerra Gelara hill in Panama have two distinct generations per year (Vollrath, 1980). Spiderlings in Panama disperse in April, their numbers peak in May, mating occurs in July with a sex ratio of 3:1 in favour of males, and most spiders are dead by October. Temperate *N. clavipes* are similar; however, while temperate spiderlings are overwintering in their egg cases, their tropical counterparts are repeating the above cycle from November to March. These three distinct life cycles may be related to differences in prey availability between the three regions. Prey numbers are greatest during the dry season in New Guinea while prey weight is greatest during the wet season, suggesting that as a whole prey availability is relatively stable throughout the year (Robinson & Robinson, 1973). In Panama there are two peaks in environmental quality, a measure Vollrath (1980) derived from rainfall and prey abundance data, which correspond to the two *Nephila* mating seasons. In a temperate climate insect prey are available in the spring and summer but are limited during the cooler fall and winter months.

It is difficult to make habitat comparisons between these studies since habitat types are not always well defined. Robinson, Lubin & Robinson (1974) report that immature *N. maculata* are found in tropical woodland, grassland, and montane environments, and Vollrath (1980) reports finding immature male *N. clavipes* in grassland. We, in

contrast, found few juveniles and scarcely any solitary males in the clearing. These differences could be due to climatic differences such as wind or rainfall between the regions or habitat differences between the areas which are not defined. Adult tropical *N. maculata* are only found in tropical woodland (Robinson, Lubin & Robinson, 1974) while temperate adult *N. clavipes* are found in woods and cleared areas. *N. maculata* are larger than *N. clavipes* and thus may require tree branches and trunks to provide support for their webs whereas *N. clavipes* can build webs using alternative sources of support. Also *N. maculata* are never found in aggregations which might be an additional source of web support while temperate *N. clavipes* are often found in aggregations in the clearing.

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