

## QUANTITATIVE SHIFTS IN ORB-WEB INVESTMENT DURING DEVELOPMENT IN *NEPHILA CLAVIPES* (ARANEAE, NEPHILIDAE)

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**ABSTRACT.** When there are direct conflicts in resource allocation to foraging effort versus growth and development, the relative allocation to foraging may change in a predictable manner with development. Orb-webs provide a physical record of resource allocation to foraging, and their synthesis requires the investment of physiologically important resources. Spiders in strongly seasonal habitats must complete development prior to the end of the season, and may be expected to alter foraging effort to maximize the probability of successful reproduction. Comparison of populations of the orb-weaving spider *Nephila clavipes* (Araneae, Nephilidae) in very seasonal versus less seasonal habitats allows testing for changes in allocation of resources to foraging effort during development. Orb-web size increases with increasing spider size, with little variation in slope among populations. However, in univoltine populations inhabiting strongly seasonal habitats, the size of the orb web is not a simple function of spider size: the rate of increase in orb-web size decelerates abruptly at a relatively small juvenile stage. Spiders in a less seasonal habitat did not decelerate foraging investment, and the pattern cannot be explained by changes in other aspects of orb-web structure. I postulate that the decline in relative investment into foraging is related to increased investment into juvenile female growth and development in circumstances where delayed maturation carries heavy fitness penalties.

**Keywords:** foraging, resource allocation, juvenile development

A central premise of all foraging models is that foraging investment reflects decisions concerning the allocation of resources between obtaining food and other physiological needs (Pianka 1981; Stephens & Krebs 1986). For logistical reasons, most optimal foraging studies and models examine only one developmental stage of an organism, and they extrapolate long-term fitness consequences from short-term optimization strategies (Houston & McNamara 1982; Stephens & Krebs 1986; eg. Bilde et al. 2002). However, if the conflicts between foraging effort and other processes change during development, resource allocation decisions may vary over the life-time of an individual (reviewed in Helfman 1990).

*Nephila clavipes* (Linnaeus 1767) (Araneae, Nephilidae) synthesizes the viscid orb web from protein strands and other organic compounds (Townley & Tillinghast 1988; Vollrath et al. 1990), many of them physiologically important (Higgins & Rankin 1999). Individuals rebuild their orb daily or nearly daily, so resource allocation to foraging is a dynamic process (Higgins & Buskirk 1992). The orb-web is a physical representation of the investment

into foraging because no foraging takes place off of the orb, and, at least in juveniles, the orb is used only for foraging. Orb-web size is a function of both the spider size and current foraging conditions (Higgins & Buskirk 1992; Sherman 1994; Pasquet et al. 1994; Higgins et al. 2001; Venner et al. 2000). However, current foraging success may not be the sole factor influencing orb-web investment (Higgins 1990, 1995).

In arthropods expressing environmentally-induced variation in development, resource allocation decisions may significantly alter growth rates and development. Many studies with diverse organisms have shown that foraging success can influence growth of juveniles and reproduction of adults (e.g., minnows, Siems & Sikes 1998; scrub jays, Fleischer et al. 2003). Fewer studies have considered the influence of development upon allocation of resources to foraging effort (apart from size-dependent factors such as changes in prey type or predation risk; however, see Cohen & Voet 2002). Habitat seasonality and individual growth and development have major effects on the fitness of individual *N. cla-*

*vipes* females. Female fecundity increases significantly with increasing female size (Higgins 2000). In univoltine populations, early maturing females are larger and have the opportunity to lay multiple egg sacs prior to the end of the season. Slowly growing females appear to be “making the best of a bad job” (Dawkins 1980), maturing late in the season at a small size with reduced reproductive success.

Laboratory experiments with small juvenile *N. clavipes* suggest that the spiders are making trade-offs between foraging and weight gain (Higgins 1995; Higgins & Rankin 1999). If the within-instar patterns of resource allocation are extrapolated over the entire developmental period, then when either resources or time are limiting, I predict that individual spiders will shift resources from foraging investment to growth and development, decreasing the likelihood of reproductive failure. I expect this to be most obvious in univoltine organisms inhabiting strongly seasonal areas, where season length limits the time available to reach maturity (Higgins & Rankin 1996; Higgins 2000). To investigate this possibility, I measured the foraging investment and foraging success by *N. clavipes* from five univoltine populations inhabiting highly seasonal Mexican sites and from a bivoltine population inhabiting a less seasonal Panamanian site. This comparison revealed that relative foraging investment is sharply reduced in larger juveniles and adult females in populations from strongly seasonal habitats but not in the population inhabiting the relatively less seasonal habitat. I consider several possible proximate and ultimate causes for the reduction in foraging investment.

#### METHODS

**Study organism.**—*Nephila clavipes* is a large orb-web building spider distributed from the south-eastern United States to Misiones, Argentina. Juveniles of both sexes and mature females build large, fine-meshed orb-webs typically suspended in a less-orderly labyrinth of barrier silk (Levi 1980; Higgins 1992a). Orb webs are renewed nightly between 2300 h and 0500 h, the exact time varying among populations (Higgins & Buskirk 1992). Older juvenile and mature females do not always replace the entire orb. The proportion of the orb area that is replaced each night depends on immediate weather conditions and the devel-

opmental stage of the individual (Higgins & Buskirk 1992). The orb web is synthesized from proteins (the silk component) and water-soluble organic compounds that are precursors or derivatives of physiologically important compounds such as neurotransmitters and cell-membrane components (Vollrath et al. 1990; Townley et al. 1991; Higgins & Rankin 1999; Higgins et al. 2001). To investigate the effects of seasonality on investment into foraging, I compared data concerning prey capture success and orb web size (radius) from six populations of *N. clavipes*, one in a less-seasonal site in Panama and five in strongly seasonal sites in Mexico (Table 1). Voucher specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D C.

**Censuses and study sites.**—I determined spider size and orb web investment during monthly or bimonthly censuses at each site. During the first census each year at each site, I located an area with at least 50 juveniles and returned to this area for subsequent censuses. At the end of each season when spiders were rare, I increased the total area searched. For each individual found, I made the following observations: spider size (leg I tibia-patella length, TPL, Higgins 1992b), proportion new silk in the orb ( $\leq 1/3$ ,  $\leq 1/2$ ,  $\leq 2/3$ ,  $\leq 3/4$ ,  $\leq 1$ ), maximum vertical orb radius (nearest 0.5 cm). In addition, I measured spiral strand density at Chamela, Nanciyaga, and Fortín de las Flores, counting the number of strands over two centimeters radius, ending 1 cm above the lower edge of the orb (Higgins & Buskirk 1992). I did not attempt to measure total capture area (as described in Herberstein & Tso 2000) for two reasons. First, the calculations are inappropriate for nephilid webs. The orb web of *Nephila* has branching radii, an exceedingly dense viscid spiral (Uetz et al. 1978) that varies in mesh size from hub to outer edge, and a shape that is strongly elliptical with little or no viscid spiral above the hub. Second, the measure of total capture strand is still an approximation that may not necessarily address the actual material investment into the orb. Spiders can and do vary the number of silk strands spun for a particular element of the web, resulting in webs that have the same physical dimensions but different material content as determined by dry weight of the web (pers. obs.). Observations

Table 1.—Climate data and seasonality of study sites. Climate data are from Garcia (1973), Bullock (1986) and Higgins (2000). Season length is determined as follows: seasonally cold sites—number of months with temperatures above 22 °C (coast), 20 °C (Fortín); seasonally dry sites—number of months with rainfall above 50 mm; Panama is distinct because, although dry and rainy seasons, the spiders are active throughout the year. The observed generation time is the number of months between peak number of unsexed juveniles and peak number of mature females in each year of the study, using midpoints if peaks were broad (from fig. 1, Higgins 2000). The population in Gigante Peninsula, Panama, is bivoltine with spiders present throughout the year.

Site	Coordinates	Altitude	Seasonality	Average season length (mo)	Observed generation time (mo)
Panama:					
Gigante Peninsula	9°N, 80°W	15 m	dry	12	dry: 6; wet: 6
Mexico:					
Playa Escondida	18°30'N, 95°W	5 m	cold	9	1989: 4.5
Nanciyaga	18°30'N, 95°W	100 m	cold	9	1989: 5; 1990: 4
Fortín de las Flores	19°N, 97°W	1000 m	cold	7	1989: 6; 1990: 5.5
Tehuacán	18°20'N, 97°30'W	1500 m	cold, dry	5	1990: 3.5
Chamela	19°30'N, 105°W	50 m	dry	6	1989: 5; 1990: 3.5

on predation load are not included in the current paper because there were no significant differences in predation rates on juveniles among the populations used in the current study (pers. obs.). Predator attack rates on juvenile *N. clavipes* decline significantly when TPL > 0.7 cm (Higgins 1992a).

In 1983–1984, I conducted censuses on Gigante Peninsula, part of the research station operated by the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama. This site is seasonally dry, but drought is mild and the population of *N. clavipes* is bivoltine with some spiders present throughout the year (Lubin 1978; Higgins 2000). In this study, each generation is labeled by the season in which it reaches maturity (i.e., the “rainy season” generation hatches in the dry season and matures in the early rainy season).

In 1989 and 1990, I conducted censuses in five sites along a transect spanning Mexico at approximately 19°N. The Mexican sites all have the same photoperiodicity, but differ in type of seasonality and in season length. Populations in all of the Mexican sites are typically univoltine, with the spiders emerging from the egg sacs as second instar juveniles at the initiation of the growing season (Hill & Christensen 1981; Higgins 2000). The various populations in Mexico experience qualitative-

ly different limits to the growing season. In seasonally cold sites (Playa Escondida, Nanciyaga, Fortín de las Flores), the growing season is limited by the arrival of strong cold fronts (nortes), which kill all individuals not protected within egg sacs. The first norte may arrive any time between early October and January and in some years, no nortes arrive at the coastal sites. The coastal populations at Playa Escondida and Nanciyaga are facultatively bivoltine (Higgins 1997). In Chamela, a seasonally dry site on the Pacific coast, the growing season is limited by the end of the rainy season, usually around October. The cessation of rains does not kill the spiders, and spiders may be found as late as three months after the last significant rainfall (Higgins 2000). Tehuacan, a mid-altitude desert in Puebla, has dry cold winters. Spiders in this site appear limited primarily by the arrival of the first norte (pers. obs.) and season length is estimated by temperature rather than rainfall.

**Foraging success.**—To determine the size range and diversity of insects captured, I recorded all cases of prey capture by spiders found during censuses and during prey capture surveys (see below). Prey observed to be in the orb web but ignored or actively rejected by the spiders were not included.

To determine diurnal prey-capture success at each site, I utilized dawn-to-dusk trap-line

surveys of spiders marked and measured the previous day (Turnbull 1962; Castillo & Eberhard 1983; Higgins 1987; Higgins & Buskirk 1992). I used a new group of spiders at new web sites in every survey. Each survey included at least 5 actively hunting animals within a circuit, such that I could visit all spiders within 15 minutes. The spiders observed during the survey were large juveniles (TPL  $\geq 0.5$  cm) and mature females. Spiders smaller than 0.5 cm TPL primarily capture very small insects requiring less than 15 minutes to consume, making the trap-line survey an inefficient method of recording foraging success. I estimated diurnal prey capture rates at least once each year at all sites except for Playa Escondida and Fortín de las Flores, where the surveys were run only in 1989. To test for variation in prey capture during the growing season, I made repeated surveys in Nanciyaga and Chamela in 1990 (3 and 2 surveys, respectively). These data are compared to published data on prey capture from Barro Colorado Island (Higgins & Buskirk 1992), as prey capture censuses were not conducted on Gigante Peninsula (separated from Barro Colorado Island by approximately 1 km).

Using Schoener's (1980) regressions of insect wet weight on body length for insects from tropical wet and tropical dry sites in Costa Rica, I estimated the total wet weight of prey captured by each spider during prey-capture surveys. Where prey were identified to order, I used the equation for that particular order. Hemiptera and Homoptera were not distinguished in my surveys and I used the equation from Hemiptera to estimate wet weight of these insects. I used the equations from the wet forest to estimate wet weight for insects captured in Playa Escondida, Nanciyaga and Fortin de las Flores and the equations from the dry forest to estimate wet weight of insects captured in Tehuacán and Chamela.

**Statistical Analysis of Orb Size.**—Orb radius as a function of spider size (TPL) is strongly heteroscedastic: variation in orb radius increases with increasing spider size (Higgins & Buskirk 1992). Square-root transformation of the orb radius effectively removed heteroscedasticity (Weisberg 1980), as was found in a prior analysis (Higgins & Buskirk 1992). Therefore, all subsequent analyses of orb web radius against spider size use square-root transformed data.

In all of the observations from the strongly-seasonal Mexican sites, orb radius was not a simple function of spider size but exhibited significantly reduced slope above TPL approximately equal to 0.5 (see below). Comparison of the investment into the orb among these populations involved three steps. First, I used ANCOVA to test whether the slopes above and below TPL = 0.5 cm were significantly different (all  $P < 0.001$ ). Second, to test whether the function of orb size on spider size differed significantly between years, I assumed that the bend point was 0.5 TPL, split the data at this point, and used ANCOVA to test for differences between years for those populations observed in both years (Playa Escondida, Nanciyaga, Fortín and Chamela). Where there were significant differences between years, I determined the best-fit bend point separately for each year. When there was no difference between years, the data were pooled for comparisons among sites.

In order to quantitatively assess the location of the best-fit bend point,  $\tau$ , I used Chappell's (1989) bend point analysis: using a series of values of the independent variable (spider size, TPL) as the bend point, separate regression analyses for data above and below each bend point were run and then the error sums of squares for the paired regressions were summed. The TPL value where the minimum summed ESS occurs is the best estimate of the bend point. In this analysis, intervals of 0.1 cm TPL were used.

Finally, to determine the similarity or dissimilarity among the populations, I used separate ANCOVAs to compare the regressions above and below the best-fit bend point of each population. Prior to running these final ANCOVAs, I verified that the preliminary tests for differences between years (which had used  $\tau = 0.5$ ) were valid for the best-fit bend points.

## RESULTS

**Foraging success.**—As has been observed earlier (Higgins & Buskirk 1992), larger spiders captured larger prey in all populations, but spiders of all sizes continued to capture prey in the smallest size category ( $\leq 2$  mm). To compare prey size among populations, the observations were divided into three groups according to spider size: TPL  $< 0.5$ ,  $0.5 \leq$  TPL  $< 1.0$ ,  $1.0 \leq$  TPL. Prey were grouped

Table 2.—Diurnal prey-capture rates. Median prey size was determined from all observations of prey captured during censuses and surveys. Mean number of prey caught and mean weight of prey caught refer to prey capture per 12 h diurnal foraging and are calculated only from the prey capture surveys. Panama prey capture data from Higgins & Buskirk (1992). Fortín mean weight of prey captured estimated from juvenile spider numbers of prey captured (Table 2a) and large spiders' median prey size; see text for details. <sup>1</sup>a posteriori *F* tests; within groups  $P > 0.3$ , among groups  $P < 0.03$ ; Panama and Fortín data were not included in statistical analyses.

Site, year	Surveys ( <i>n</i> )	Spiders ( <i>n</i> )	Median prey size, mm ( <i>n</i> )	Mean number (SE)	Mean weight, mg (SE)
<i>a. Juvenile spiders (0.5 &lt; TPL ≤ 1.0 cm)</i>					
Nanciyaga 1990	1	14	4 (55)	2.5 (0.43)	1.41 (0.38)
Fortín 1989	1	14	2 (29)	3.8 (2.6)	1.16 (0.23)
Chamela 1990	1	14	4 (23)	1.6 (0.44)	0.99 (0.37)
<i>b. Large juvenile and adult female spiders (TPL ≥ 1.0 cm)</i>					
Playa Escondida 1989	1	14	4 (13)	1.2 (0.30)	4.48 (3.30) a
Nanciyaga 1989	1	12	6 (59)	3.1 (0.62)	5.11 (2.32) a
1990	2	37	5 (124)	3.4 (0.31)	9.14 (2.09) a
Fortín (estimated)	0	0	6 (24)	4 (—)	6.84 (—)
Tehuacán 1990	1	9	10 (23)	3.0 (0.75)	17.44 (5.12) b
Chamela 1989	1	12	4 (58)	2.5 (0.60)	1.41 (0.41) a
1990	1	10	5 (26)	1.9 (0.28)	4.82 (2.94) a
BCI, Panama 1983 rainy	2	26	8	1.8 (9.8)	6.4 (6.7)
BCI, Panama 1983 dry	2	10	6	1.4 (1.1)	1.9 (3.2)

into 2 mm size classes (pooling larger size classes to reduce the number of empty cells). For the largest spiders, there were no differences between years in Chamela or Nanciyaga (maximum likelihood  $\chi^2 < 5.5$ ,  $P > 0.37$ ). Pooling across years for each site, comparisons revealed among-site differences in the size of prey captured by the largest spiders, but no differences in the size of prey captured by the smallest and intermediate-sized spiders (maximum likelihood  $\chi^2$  test:  $TPL < 0.5$ ,  $\chi^2 = 9.19$ ,  $df = 8$ ,  $P = 0.33$ ;  $0.5 \leq TPL < 1.0$ ,  $\chi^2 = 10.97$ ,  $df = 9$ ,  $P = 0.28$ ;  $TPL \geq 1.0$ ,  $\chi^2 = 39.97$ ,  $df = 16$ ,  $P = 0.001$ ).

Within sites, there was very little variation between years or among repeated surveys in number of prey captured per spider per day (Table 2). In Chamela and Nanciyaga, diurnal prey capture did not vary significantly among surveys in 1990 (ANOVA of log-transformed number of insects captured/spider/survey; Chamela:  $F_{(1,22)} = 1.23$ ,  $P = 0.28$ ; Nanciyaga:  $F_{(2,48)} = 0.92$ ,  $P = 0.41$ ), or between 1989 and 1990 (Chamela:  $F_{(1,34)} = 0.89$ ,  $P = 0.35$ ; Nanciyaga:  $F_{(1,61)} = 0.07$ ,  $P = 0.80$ ). Therefore, observations within each site were combined for comparisons among sites. Diurnal prey capture rates varied among sites ( $F_{(4,131)} = 4.83$ ,  $P = 0.001$ ), being significantly lower at

Playa Escondida (a posteriori contrast:  $F_{(1,131)} = 10.37$ ,  $P = 0.002$ ), and somewhat lower at Chamela than the other three sites.

The wet-weight of prey captured per spider per day varied among sites for the larger females, but did not vary among sites for the smaller spiders (Table 2). Because larger spiders capture larger prey, I compared total wet weight of prey captured among sites separately for surveys with intermediate sized spiders ( $0.5 \text{ cm} \leq \text{mean TPL} < 1.0 \text{ cm}$ ) and surveys with large spiders (mean  $TPL \geq 1.0 \text{ cm}$ ). Three prey-capture surveys were conducted for intermediate-sized spiders: Fortín de las Flores (August), Nanciyaga (May), and Chamela (August). These spiders captured on average 1 mg prey/diurnal survey at all three sites (ANOVA:  $F_{(2,39)} = 0.39$ ,  $P = 0.68$ ). The large spiders captured significantly different amounts of prey at the different sites (Table 2; comparing Playa Escondida, Nanciyaga, Tehuacán, Chamela. ANOVA:  $F_{(3,89)} = 3.79$ ,  $P = 0.013$ ). This appears due largely to the very high prey capture rate and large median prey size at Tehuacán (a posteriori contrast of wet weight captured: Chamela vs. Tehuacán,  $F_{(1,89)} = 10.22$ ,  $P = 0.001$ ; [Playa Escondida and Nanciyaga] vs. Tehuacán  $F_{(1,89)} = 5.86$ ,  $P = 0.002$ ). Due to problems obtaining the con-

tinuous access required for prey-capture surveys, no prey capture surveys were conducted at Fortín de las Flores during the period when larger females were present in the population. For subsequent comparisons among populations, I estimated wet weight of prey captured by large females in Fortín in the following manner: median prey size caught by spiders  $TPL \geq 1.0$  was 6 mm in Fortín ( $n = 13$ ), and the mean weight of 6 mm prey in Fortín was 1.71 (SE = 0.11). Assuming that the mean number of prey captured per diurnal survey by juveniles, 4 insects, is constant over the season (as observed in Chamela and Nanciyaga), the wet weight of prey captured per day in Fortín by the larger females can be estimated as 6.84 mg.

**Foraging Investment.**—Foraging investment is altered by three aspects of orb-web structure: proportion of new silk in the orb, spiral strand density, and orb web size. The variation in proportion of new silk spun each day is not considered in the current paper, as it did not differ from what has been described elsewhere (Higgins & Buskirk 1992). Larger spiders are more likely to partially renew the orb web, and the radius of partially renewed orbs is larger than the radius of wholly renewed orbs by spiders of the same size. Therefore, I included only completely renewed orbs (more than 75% new) in the comparison of orb size and spiral strand density among the sites.

Examination of the relationship between orb radius and spider size (taking the square root of orb radius to reduce heteroscedasticity) revealed a different pattern in Panama compared to all Mexican sites (Figs. 1, 2). In Gigante, Panama, orb size increased with increasing spider size, and the relationship between orb size and spider size did not differ between the two generations (Table 3a). Pooling across generations and comparing orb-web investment between large and small spiders showed no difference in slope (Table 3b): orb radius (square-root transformed) was a simple straight-line function of spider size (Fig. 1). In contrast, in all Mexican populations, larger spiders built smaller orbs that would be expected from extrapolating from the observed investment by small juveniles (Fig. 2).

Prior to determining the best-fit bend point,  $\tau$ , for the Mexican populations, I tested for differences between years at each site assum-

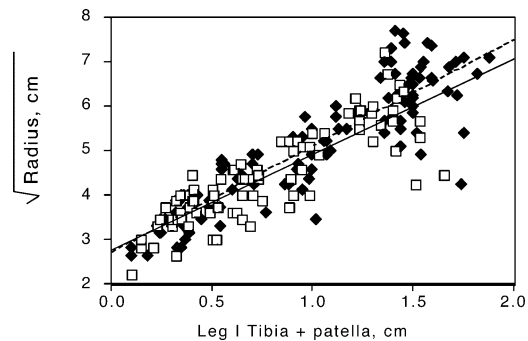


Figure 1.—Orb radius (square root transformed) as a function of *Nephila* size (TPL) in Gigante Peninsula. Black diamonds (dash line): wet season; the generation maturing in the early rainy season; white squares (solid line): dry season; the generation maturing in the early dry season. There is no difference in orb size between the generations.

ing a bend point of  $TPL = 0.5$ . These preliminary analyses revealed significant differences in slope between years for smaller spiders at Fortín de las Flores and for larger spiders at Playa Escondida (ANCOVA. Fortín: small spiders  $F_{(1,256)} = 5.32$ ,  $P = 0.022$  and large spiders  $F_{(1,74)} = 0.119$ ,  $P = 0.73$ ; Playa Escondida: small spiders  $F_{(1,162)} = 0.239$ ,  $P = 0.625$  and large spiders  $F_{(1,49)} = 5.92$ ,  $P = 0.02$ ). Although there was a significant difference between years among large spiders at Chamela, this was most likely due to absence of observations between  $TPL = 0.4$  and  $TPL = 0.7$  for 1989 (Fig. 2), and I dropped the Chamela 1989 observations from the subsequent analyses of orb size. Preliminary analyses revealed no differences between years at Nanciyaga (small spiders  $F_{(1,72)} = 1.699$ ,  $P = 0.20$  and large spiders  $F_{(1,124)} = 0.116$ ,  $P = 0.73$ ). In all cases, where there was no difference between slopes there was also no difference in intercept (all year effects  $P \geq 0.06$ ).

Because there were significant differences in the slopes between years observed at Fortín de las Flores and Playa Escondida, I considered the 1989 and 1990 data separately when determining the best-fit bend point,  $\tau$ , for these data sets (Table 4). I first compared the best-fit bend points to the *a priori* estimate of  $\tau = 0.5$  cm using *t*-tests. At all sites except Fortín in 1990, the value of  $\tau$  was not statistically different from  $TPL = 0.5$  cm (*t*-test: all  $P \geq 0.5$ ; Table 4). In Fortín in 1990, the bend point occurred at a significantly smaller spider

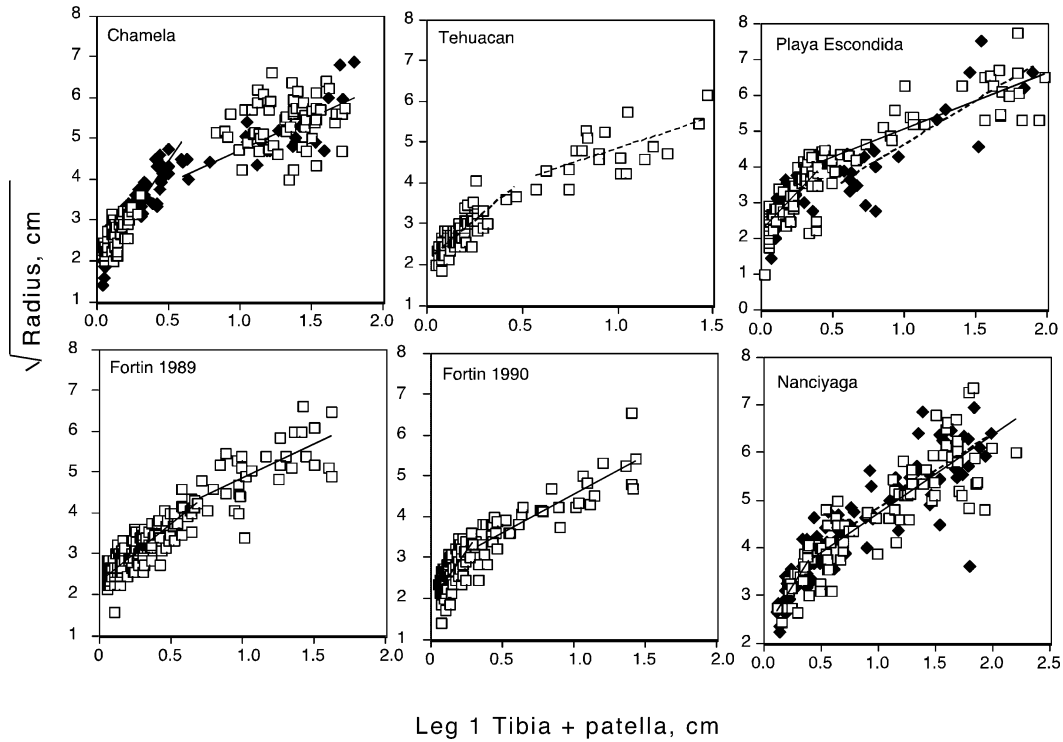


Figure 2.—Orb radius (square root transformed) as a function of *Nephila* size (TPL) in Mexican populations. Where two years of data are plotted in the same graph (Chamela, Nanciyaga, Playa Escondida), squares (solid line):1989; diamonds (dashed line):1990. No regression is plotted for the Chamela 1989 data as there is a gap in the data between TPL of 0.4 and 0.7, but the data are presented for comparison.

Table 3.—Orb web size as a function of spider size in Gigante, Panama, where y is the square root of orb radius and x is leg I tibia + patella length.

a. Comparison of generations				
Dry season	$y = 2.78 + 2.11 x$		$F_{(1,105)} = 190.35$	$P < 0.001$
Rainy season	$y = 2.88 + 2.21 x$		$F_{(1,54)} = 102.58$	$P < 0.001$
ANCOVA				
Source	SS	df	F	P
TPL	96.29	1	294.73	< 0.001
Generation	0.044	1	0.14	0.71
TPL x gen	0.05	1	0.15	0.70
Error	51.95	159		
b. Comparison of spiders smaller and larger than TPL = 0.5 cm				
TPL < 0.5 cm	$y = 2.49 + 2.98 x$		$F_{(1,54)} = 35.68$	$P < 0.001$
TPL ≥ 0.5 cm	$y = 2.76 + 2.25 x$		$F_{(1,205)} = 184.37$	$P < 0.001$
ANCOVA				
Source	SS	df	F	P
TPL	14.37	1	43.56	< 0.001
Size class	0.251	1	0.76	0.39
TPL x class	0.282	1	0.85	0.36
Error	52.45	159		

Table 4.—Values of best-fit bend points,  $\tau$ , and 95% confidence intervals (CI) for each population. \* In Fortín in 1990,  $\tau$  is significantly different from 0.5 ( $t = 2.509$ ,  $P < 0.05$ ).

Site	$\tau$	95% CI
Playa Escondida 1989	0.4	0.079
Playa Escondida 1990	0.5	0.184
Nancyaga	0.4	0.078
Fortín 1989	0.7	0.125
Fortín 1990	0.3*	0.046
Tehuacán 1990	0.5	0.106
Chamela 1990	0.6	0.069

size. Prior to running ANCOVA comparisons among populations, I also tested whether the differences between years found at Fortín de las Flores and Playa Escondida using *a priori* assumption of  $\tau = 0.5$  persisted with the best-fit bend point, by repeating the ANCOVA analysis comparing the slopes of the regression of orb-web radius on TPL between years for each site. In both cases, the results were the same: there were significant differences in slope between years for large spiders at Playa Escondida and small spiders at Fortín. For all subsequent tests, I kept the data of these sites separated by year.

In all of the Mexican sites, the rate of increase of orb radius with spider size decelerated significantly in spiders larger than  $TPL = 0.5$ . Further comparisons among Mexican populations therefore considered spiders of  $TPL < \tau$  separately from spiders of  $TPL \geq \tau$ . The analyses of covariance for orb radius by spiders of  $TPL < \tau$  and spiders of  $TPL \geq \tau$  revealed significant interactions between spider size and site, indicating that the slopes of the regressions were significantly different among sites (Tables 5, 6). However, a posteriori comparisons show that the significance of the population  $\times$  TPL factor is due to grouping of the populations rather than unique foraging investments in each population. Among spiders  $TPL < \tau$ , those in Fortin de las Flores in 1989 increased orb-web size more slowly (lower slope) than any other population (Table 6a). Among spiders  $TPL \geq \tau$ , the populations split into two groups (Table 6b). Even where significant, the differences among these populations are much less than the differences between large and small spiders. Comparing Fortin de las Flores (1989) to Chamela (1990;

Table 5.—Analysis of foraging investment: Analysis of covariance of orb-web size among populations, with spider size as covariate. a include data from Playa Escondida, Nancyaga, Fortín 1989, Fortín 1990, Tehuacán, Chamela; b include data from Playa Escondida 1989, Playa Escondida 1990, Nancyaga, Fortín, Tehuacán, Chamela.

Source	<i>df</i>	Mean square	<i>F</i>	<i>P</i>
a. Spiders with $TPL < \tau$				
TPL	1	75.201	760.26	<0.001
Site	5	0.874	8.84	<0.001
TPL $\times$ site	5	1.881	19.02	<0.001
Error	607	0.099		
b. Spiders with $TPL \geq \tau$				
TPL	1	75.01	256.17	<0.001
Site	5	1.45	4.95	<0.001
TPL $\times$ site	5	0.86	2.93	0.013
Error	327	0.29		

the highest slope), the slope in Fortin is 43% of the slope found for Chamela. Similarly, comparison of the lowest and highest slopes for spiders  $TPL \geq \tau$  (Tehuacan vs. Playa Escondida) revealed 37% difference. All within-population decelerations were greater (Table 6b).

There remains the possibility that the spiders in a given population always invest more in the orb, even if the relative investment declines with increasing spider size. This would be reflected as concordance between the small and large spiders ( $< \geq \tau$ ) in each population across all populations. To test for concordance, I used Kendall's coefficient of concordance (Siegel & Castellan 1988), comparing the rank orders of populations according to the slopes from the regression analyses of orb size on spider size.

The slopes of the regressions on either side of the bend point vary with the actual point at which each data set is split into two groups, therefore I first ran a sensitivity analysis testing for changes in rank-order of populations when altering the value of  $\tau$ . I divided each data set at the maximum and minimum of the 95% confidence interval around each best-fit bend point and calculated the slopes for small and large spiders (keeping the years separate for Playa Escondida and Fortín). I then compared the rank orders of the populations for large or small spiders among three sets of



Table 6.—Analysis of foraging investment: regression equations of orb-web size on spider size for all Mexican sites. Letters (a, b) in the regression column refer to groups with *slopes* that are not significantly different. Small spiders: within group a, interaction effect  $F_{(4,455)} = 0.86$  adjusted  $P = 0.97$ ; between groups interaction effect  $F_{(1,622)} = 62.43$  adjusted  $P < 0.002$ . Large spiders: within groups, interaction effect (a)  $F_{(2,204)} = 0.022$ , adjusted  $P = 0.99$ ; (b)  $F_{(2,116)} = 1.58$ , adjusted  $P = 0.21$ . Between groups interaction effect  $F_{(1,328)} = 9.92$ , adjusted  $P = 0.004$ . The percent change is calculated as the change from high slope to low slope as a percent of the larger slope.

a. Spiders with $TPL < \tau$				
Site	Regression	R <sup>2</sup>	Rank order of slopes	
Playa Escondida 1989	$y = 2.21 + 4.22 x$ <b>a</b>	0.59	5	
Playa Escondida 1990	$y = 2.17 + 4.47 x$ <b>a</b>	0.66	6	
Nanciyaga	$y = 2.22 + 3.95 x$ <b>a</b>	0.55	4	
Fortín de las Flores 1989	$y = 2.31 + 2.96 x$ <b>b</b>	0.77	1	
Fortín de las Flores 1990	$y = 1.93 + 3.69 x$ <b>a</b>	0.54	2	
Tehuacán	$y = 2.11 + 3.93 x$ <b>a</b>	0.63	3	
Chamela 1990	$y = 1.88 + 5.22 x$ <b>a</b>	0.89	7	

b. Spiders with $TPL \geq \tau$				
Site	Regression	R <sup>2</sup>	Rank order of slopes	% change
Playa Escondida 1989	$y = 3.48 + 1.57 x$ <b>a</b>	0.74	2	-62%
Playa Escondida 1990	$y = 2.19 + 2.43 x$ <b>b</b>	0.70	7	-46%
Nanciyaga	$y = 3.20 + 1.59 x$ <b>a</b>	0.68	3	-60%
Fortín de las Flores 1989	$y = 3.21 + 1.65 x$ <b>b</b>	0.38	4	-44%
Fortín de las Flores 1990	$y = 2.66 + 1.89 x$ <b>b</b>	0.76	5	-49%
Tehuacán	$y = 3.31 + 1.53 x$ <b>a</b>	0.39	1	-61%
Chamela	$y = 2.64 + 1.92 x$ <b>b</b>	0.31	6	-63%

slopes (breaking the data at the best  $\tau$ , lowest  $\tau$  and highest  $\tau$ ). Kendall's coefficient of concordance showed significant concordance among the rank orders for both the small and the large spiders (small spiders: Kendall's coefficient = 0.73,  $df = 6$ ,  $P = 0.041$ ; large spiders: Kendall's coefficient = 0.92,  $df = 6$ ,  $P = 0.011$ ). This indicates that the rank order of populations according to relative orb size (slope) is insensitive to the exact position of the bend point in each data set. I then tested for rank-order concordance between small spiders and large spiders in each population using the slopes calculated with the best-fit  $\tau$ . Among the Mexican sites, there is no correlation among populations between large and small spiders (Table 6; Kendall's coefficient = 0.696,  $df = 6$ ,  $P = 0.21$ ).

It is possible that the change in rate of increasing orb size with growth is correlated with a shift in orb-mesh size, resulting in a constant material investment. If this is the case, then I expect a similar "bent line" pattern in orb-mesh density with increasing spider size. To test this, I compared mesh density

for spiders of different sizes in three sites with strong "bends" in orb-web radius: Chamela, Fortín de las Flores and Nanciyaga. There was significant variation among sites (Fig. 3). In all populations, spiral strand density declines with increasing spider size. Among these sites, the decline was steepest at Fortín and shallowest at Chamela (Fig. 3). There is no indication that the relationship is not a simple straight line.

## DISCUSSION

When environmental factors other than foraging success, such as short season length, limit the probability of successful survival or reproduction, these factors may alter the decisions of resource allocation into foraging, especially when variation in foraging success is included in the analysis (Caraco 1980; Houston & McNamara 1982; Stephens & Charnov 1982; Johansson & Rowe 1999). Such factors have been taken into account in some models, such as risk-sensitivity models (reviewed in Stephens & Krebs 1986) and state-sensitive models (Mangel & Clark

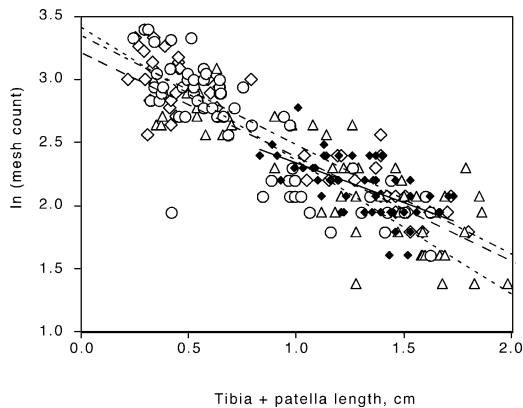


Figure 3.—Spiral strand density vs. *Nephila* size (Leg 1, TPL), new orbs only, for three Mexican populations. Triangles (dashed line): Nanciyaga 1989; circles (dotted line): Fortín 1989; black diamonds (solid line): Chamela 1989; and open diamonds (dot-dash line): Chamela 1990. Although there are significant differences among sites in slope and intercept (slope:  $F_{(2,164)} = 4.16$ ,  $P = 0.017$ ; intercept:  $F_{(2,164)} = 3.70$ ,  $P = 0.027$ ), the relationship of strand density to spider size is a simple straight line.

1988). One important result from these models is that short-term optimization strategies may not maximize fitness. Rather, animals are predicted to alter their foraging strategy based upon the probability of gaining sufficient energy to survive and reproduce. Most of these models, however, still only consider the foraging behavior of a single developmental stage. Resource allocation decisions occur throughout development. Consideration of the fitness consequences of developmental changes in resource allocation will improve our understanding of the long-term affects of variation in resource use (Perrin & Sibley 1993). Investigation of orb size over the entire developmental period of juvenile *N. clavipes* revealed that the relative investment into foraging is not necessarily constant: in populations inhabiting strongly seasonal areas, relative orb-web investment declined as spiders grow. This deceleration in foraging investment was not correlated with shifts in orb renewal or with changes in mesh size. Comparison with the bivoltine population in Gigante (current paper) and the 1985 observations from the facultatively bivoltine population in Los Tuxtlas (Higgins & Buskirk 1992) indicate that the shift in allocation to

foraging effort may reflect changes in priorities that are influenced both by seasonality and by foraging success.

Proximally, changes in orb-web structure might cause changes in orb-web size. Orb radius in *N. clavipes* is negatively correlated with the amount of new silk and spiral strand density, and larger spiders tend to build widely-meshed, incompletely renewed orbs (Higgins & Buskirk 1992). However, these factors cannot explain the observed sudden deceleration in foraging investment. Although the bend point occurs at about the size at which the spiders become more likely to partially renew the orb (Higgins & Buskirk 1992), only data from completely renewed orbs were included in the present analyses. Nor is this a reflection of a shift in mesh size, as strand density is a simple linear function of spider size.

Among the Mexican sites visited in 1989–1990, the striking pattern is how little variation there is among populations. Among smaller spiders, spiders of a given size built significantly smaller webs at Fortín in 1989 compared to other sites, but no environmental factors are correlated with this: prey capture is higher in number, but lower in median weight resulting in no significant difference in mean weight of prey captured. Comparing the larger spiders among populations and between years in Mexico, the populations fell into two distinct groups but again there are no correlated differences either in prey capture (only Tehuacan differed in prey capture) or season length. By comparing data across a larger time and geographic scale, the possible roles of both factors in determining resource allocation can be tentatively described.

Marginal increases in resource allocation to weight gain and development will be favored if they result in marginal increases in fitness (Perrin 1992). There are two arguments for why shifting resources from foraging to growth could increase female fitness. First, decreases in orb investment may not decrease prey capture (Higgins & Buskirk 1992), so holding web size relatively constant after a certain size is achieved may not greatly alter the probability of foraging success. Second, there are great fitness advantages of early maturation and of large female size. It is notable that the developmental stage at which the spiders in Mexico decreased relative investment

into the orb web, approximately the fifth juvenile instar, is long before female maturation. At this developmental stage, most males have reached sexual maturity but females will pass through three or more additional instars prior to maturing. Under high rates of weight gain, fifth instar females need at least 36 days to mature, and then 21 days to lay the first egg sac (Higgins 2000, 2002). Spiders in strongly seasonal environments must reproduce prior to the end of the season.

Comparison among these univoltine Mexican populations, the bivoltine population in Panama, and the 1985 observations from Los Tuxtlas (a mild year in coastal Veracruz with very high prey capture; Higgins & Buskirk 1992) better illustrate the potential importance of both season length and prey capture success in determining allocation of resources to web building. The comparison of orb-web size between the population in Gigante, Panama, and populations in Mexico supports the hypothesis that the animals in strongly seasonal environments may be shifting resources away from foraging to improve the chances of reproduction. The prey-capture success recorded in Panama falls within the range of observations from the Mexican sites (Table 2), but the climate is much less seasonal. Although this region of Panama is seasonally dry, one generation of spiders hatches, emerges, and passes through several instars during the dry season and the end of the rains does not kill larger juveniles and mature females of the next generation. Thus, the seasonality does not strongly affect the life cycle, nor was there any reduction in female fecundity associated with delayed maturation (Higgins 2000). With no penalty for delayed maturation, there was also no pattern of reduced investment to orb-web building as spiders in this site grew.

Prey capture success is also apparently important in determining developmental patterns of resource allocation to orb building. Los Tuxtlas field station (UNAM) is within 20 km of Nanciyaga and Playa Escondida and has similar climate and forest structure (it was not used in the current study due to local, temporary reduction in spider abundance; pers. obs.). During a 1985 study, the spiders in Los Tuxtlas captured nearly twice as much prey compared to prey capture for spiders in the same region in the current study (ca 12 mg/day in 1985 vs. ca 5 mg/day in 1989 and 9

mg/day in 1990) and there is no indication in the 1985 data of any change in the relative investment into the orb during the course of development (Higgins & Buskirk 1992). It is potentially important that the end of the season at these sites, governed by the arrival of the northern storms (nortes) is apparently unpredictable.

One can gain a sense of the relative importance of prey capture rates and seasonality by comparing the 1985 data from coastal Veracruz with the 1990 data from Tehuacán. Although the growing seasons at both Tehuacán and coastal Veracruz end with cold temperatures, the nortes do not always reach central Veracruz and these populations are facultatively bivoltine (Higgins 1997). In contrast, the Tehuacan growing season is predictably short and always terminated by cold winter temperatures (Higgins 2000). In 1990, spiders in Tehuacan had even higher prey capture success than Los Tuxtlas in 1985, but the Tehuacan spiders still exhibited a very strong decline in orb-web size.

These results are very different from similar, experimental, results of foraging investment under time constraints in the damselfly larvae (Johansson & Rowe 1999). In these actively hunting predators, time constraints resulted in increased investment into foraging. The difference may reflect the more direct competition for resources between web and body in the spider, or differences in variation in success with similar foraging investment. First, there are direct trade-offs in materials between orb-web synthesis and growth and development in *N. clavipes* juveniles (Higgins & Rankin 1999). Web components such as protein and choline are required for web construction as well as for physiological functions. Second, building a larger orb web does not necessarily increase chance of foraging success. Increased foraging effort (time and energy spent searching) by active foragers may have a less direct impact upon growth and a more certain pay-off. Only further research in a wider array of foragers will determine if this dichotomy is widely applicable.

Life-time strategies of allocation of resources among different, conflicting requirements during growth, development and reproduction are indicated by these observations to be more complex than what can be modeled as extensions of short-term optimization strategies.

Optimization theory (reviewed in Perrin & Sibly 1993) can provide a conceptual framework for experimental examination of resource allocation, as applied to plants by Iwasa & Roughgarden (1983). Such models are more difficult to apply to animals, as the measurement of allocation into different organ systems is usually destructive. Web-building spiders, with a physical record of the decisions regarding foraging investment, may prove more amenable to the study of the interface between life-history strategies and behavioral strategies.

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