Oecologia (2000) 122:51–59

Linden Higgins

The interaction of season length and development time alters size at maturity

Received: 30 December 1998 / Accepted: 1 September 1999

Abstract An end-of-season penalty, with late-maturing individuals being smaller than early-maturing individuals, has been observed in a variety of univoltine terrestrial arthropods. The current study extends these observations, utilizing multiple populations of a single sexually dimorphic species to examine the ecological correlates and fitness consequences of late maturation at a small size. The orb-weaving spider, *Nephila clavipes*, inhabits a broad range of habitats that vary from mild to strong seasonality. Because males mature several instars earlier than females, they can reach maturity much earlier in the growing season. Within a cohort, I found that female size at maturity was negatively correlated with timing of maturation in strongly seasonal sites. At a less seasonal site, there was no correlation between female size and timing of maturation within a cohort. In most populations studied, male size was not correlated with the timing of maturation within a cohort. Within populations in strongly seasonal sites, late-maturing females had reduced fecundity. The probability of copulation, survivorship from maturity to first clutch, clutch size relative to female size, and the number of possible clutches were all reduced with delayed maturation. The probability of prereproductive death for late-maturing females was strongly affected by stochasticity in the timing of the end of the growing season.

Key words Life-history · Phenology · Sexual dimorphism · Fitness · *Nephila clavipes*

L. Higgins[1] (✉)
Centro de Ecología, Universidad Nacional Autonoma de México,
Apartado Postal 70-275, Ciudad Universitaria, C.P. 04510,
Mexico
e-mail: linden@ent.umass.edu
Fax: +1-413-5452115

Present address:
[1] Department of Entomology, Fernald Hall,
University of Massachusetts at Amherst,
Amherst, MA 01003, USA

Introduction

Classic life-history theory predicts a positive correlation between age and size at sexual maturity (reviewed in Roff 1992; Stearns 1992). In this paper, I offer an explanation of why the opposite pattern can be found – a negative correlation between age and size at sexual maturity. The classic life-history models make the critical assumption that juvenile development is a genetically determined trait that is fixed within an individual (i.e., Istock 1967; Wilbur 1980). Consequently, these models predict that large size will be achieved by delaying maturation at the cost of increased generation time. In contrast, in most arthropods studied, individuals respond plastically to food availability and other environmental variables (reviewed in Higgins and Rankin 1996), giving rise to large differences in size and age at sexual maturity among individuals.

In univoltine arthropods, several authors have found that within a cohort, late-maturing individuals are smaller, implying a negative correlation between size and age at sexual maturity (the butterflies *Lasiommata* spp., Nylin et al. 1996 and *Euphydryus editha*, M. Singer, personal communication; mole crickets, Forrest 1987; the spiders *Nephila edulis*, Miyashita 1986, 1991 and *Stegodyphus lineatus*, Schneider 1997; the beetle *Stator limbatus*, C. Fox, personal communication). The present study extends these observations, examining ecological correlates and fitness consequences of late maturation in the spider *Nephila clavipes*.

This spider is particularly well suited to studying the interaction between age and size at sexual maturity. It is distributed in habitats differing greatly in seasonality, allowing comparative studies across habitats. Much of the variation among populations appears due to environmentally induced variation in growth and development (Higgins 1992, 1993, 1995). Additionally, there is great sexual dimorphism in size at sexual maturity (Christenson and Goist 1979; Robinson and Robinson 1980; Vollrath and Parker 1997). Sexual size dimorphism in this species is correlated with differences in number of juvenile stages

Table 1 Location of each site, altitude (meters above sea level), climatological conditions and number of generations

Site	Study period	Coordinates	Altitude (m)	Annual rainfall (m)	Summer temp. (°C)	Season-ality	Length[a], months	Diurnal prey capture[b]	Number of generations per year
Panama									
Gigante Peninsula	Feb. 1985– Feb. 1986	9°N, 80°W	100	3.5[c]	Wet: 26.9[c] Dry: 27.2[c]	Dry	Wet: 7 Dry: 5	Wet: 1.8 Dry: 1.4	2
Eastern Mexico									
Los Tuxtlas	Aug. to Dec. 1986	18°30’N, 95°W	50	4.4[d]	25.4[d]	Cold	9	2.4	1–2
Playa Escondida	1989	18°30’N, 95°W	5	4.4[d]	25.4[d]	Cold	9	1.2	1–2
Nanciyaga	1989, 1990	18°30’N, 95°W	100	4.4[d]	25.4[d]	Cold	9	3.1	1–2
Fortín de las Flores	1989, 1990	19°N, 97°W	1000	2.2[d]	21.5[d]	Cold	7	3.8	1
Tehuacán	1990	18°20’N, 97°30’W	1500	0.5[d]	20.0[d]	Cold, dry	5	3.0	1
Western Mexico									
Arroyo Frio	1989	19°15’N, 101°30’W	1200	–	–	Cold, dry	5	–	1
Chamela	1989, 1990	19°30’N, 105°W	50	0.7[e]	25.6[e]	Dry	6	1989:2.5, 1990:1.8	1

[a] Seasonally cold sites: average number of months with temperature above 22°C (coast), 20°C (Fortín); seasonally dry sites: average number of months with rainfall above 50 mm

[b] Mean prey capture rates observed per 12 h; LE Higgins, unpublished work, Higgins and Buskirk (1992)

[c] Dietrich et al. (1982)

[d] Garcia (1973); data from the nearest weather station, not from the actual study site

[e] Bullock (1986), S.H. Bullock, personal communication

between males (maturing at an early instar) and females (maturing at a late instar). This permits a comparison within species of individuals with very different development times. I found that in strongly seasonal habitats, female size declined over time in each cohort but male size did not. Neither male nor female size declined over time within a cohort in less seasonal habitats. I also found that the fitness consequences to females of late maturation are severe in strongly seasonal habitats.

Materials and methods

Study organism

Nephila clavipes is a widely distributed spider, found from the southeastern United States to Missiones, Argentina, occurring in a variety of habitats (Levi 1980). In strongly seasonal habitats, spiderlings hatch from eggs laid at the end of the growing season and spend most of the first instar inside the silken egg sac, emerging at the beginning of the next growing season (Christenson and Wenzl 1980; Barnes et al. 1992). Juveniles larger than leg 1 tibia+patella length (TPL) equalling 0.5 cm are females, as males are in either the penultimate or mature stage at or prior to this size (Higgins 1993). I refer to smaller juveniles as “unsexed”. Post-embryonic development is plastic, with environmentally induced variation in both the duration and the number of instars prior to maturation (Higgins 1992, 1993, 1995). This plasticity allows both age and size at sexual maturity to vary in response to environmental conditions (Higgins and Rankin 1996). The study populations differed in growth rate (rate of weight gain), development rate (instar duration), and in size at sexual maturity (personal observation, Higgins 1993). Common garden experiments with animals from four Mexican populations (Nanciyaga, Fortín, Tehuacán, Chamela) revealed that growth and development rates did not differ when the spiders were held under similar conditions and fed the same amount (Higgins 1993). Under experimental conditions, individuals gaining weight more slowly spend more time in each instar, so reduced weight gain slows development (Higgins 1995). There are no molts following sexual maturation.

This spider is extremely sexually dimorphic. Females mature after eight to ten juvenile instars, in 3–5 months, and males mature after three to five juvenile instars. Consequently, males mature at a significantly smaller size (Christenson and Goist 1979; Robinson and Robinson 1980; Vollrath 1980; Vollrath and Parker 1997). Females usually mate within 48 h of maturation (Christenson and Goist 1979; Robinson and Robinson 1980; Christenson et al. 1985). Twenty to 25 days are required for a female to produce each egg sac and as many as five egg sacs can be laid without repeated insemination (Christenson et al. 1985; Higgins 1992). Clutch size is positively correlated with female size and somatic weight (Higgins 1992). Mean egg weight for a clutch is variable but not correlated with female size, prelaying weight or hatchling size (personal observation). Except in areas with very mild seasonality, such as Panama, the adults perish at the end of each growing season (defined by the period of rains in seasonally dry areas, by warmth in seasonally cold areas), leaving eggs and juveniles protected from the elements within egg sacs.

Study sites

I studied populations of *N. clavipes* from one site in Panama and seven disjunct sites in Mexico (Table 1): Gigante Peninsula in Barro Colorado National Monument, Panama, and seven sites along an east-west transect in Mexico, from the Veracruz coast (east) to the Jalisco coast (west). In Mexico, the three coastal Veracruz sites are disjunct, separated by cattle pastures. Playa Escondida and Los Tuxtlas are separated by approximately 1 km,

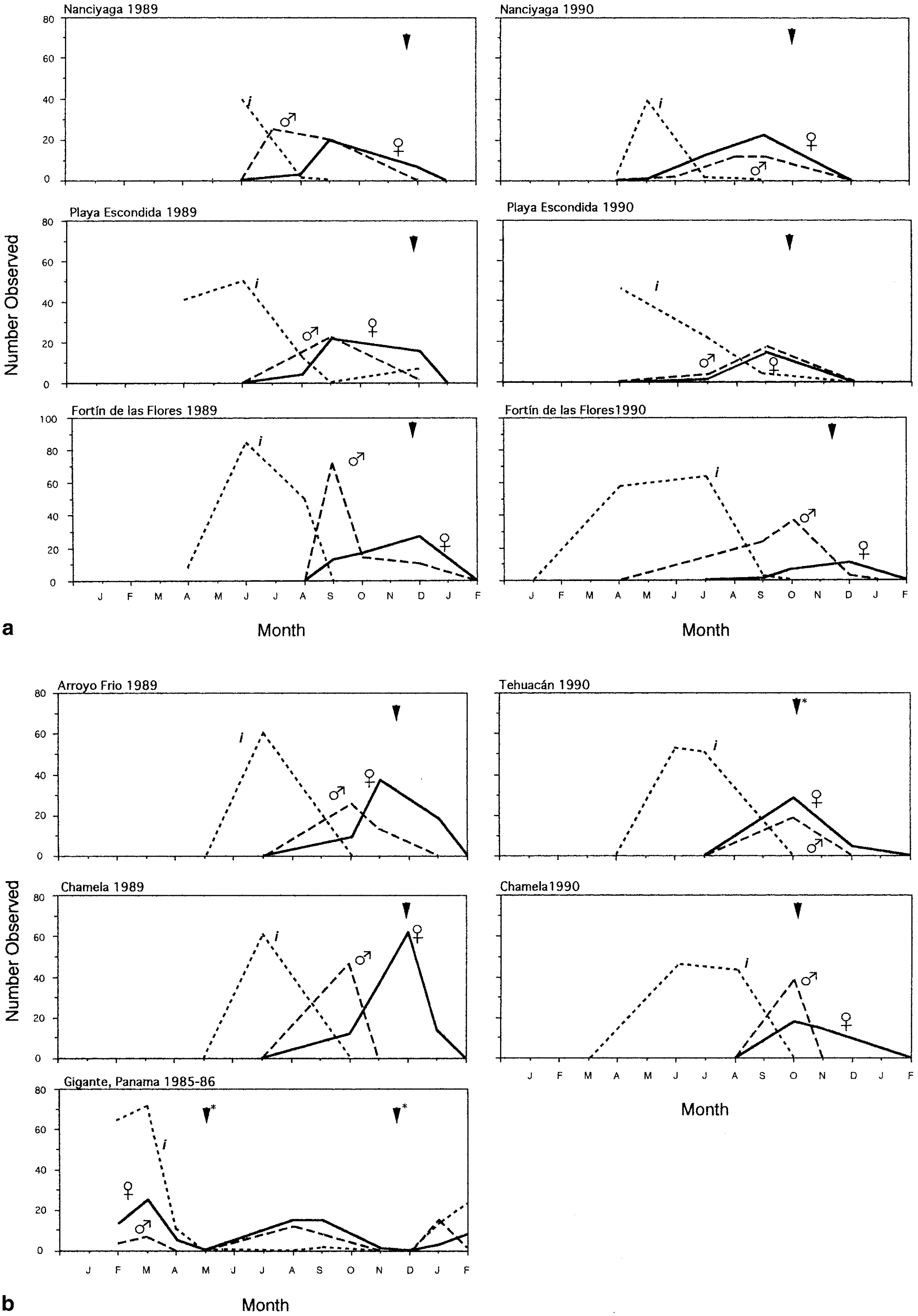

Fig. 1 Observed phenologies of small juveniles (*i*), mature males and mature females in Gigante Peninsula, Panama and along the 19° latitude in Mexico. The *arrows* indicate timing of seasonal shifts. For Panama, two *arrows* mark the onset, in May, and the end, in December, of the rainy season. In Playa Escondida, Nanciyaga and Fortín, the *arrow* indicates the arrival of the first cold storm, and in Tehuacán, Arroyo Frio and Chamela, the *arrow* indicates the last rains. *Arrows* marked by an *asterisk* are taken from the climatological data (Garcia 1973; Dietrich et al. 1982). The timing of the last rain in Arroyo Frio is taken from observations in Chamela

and Nanciyaga is 13 km south. The four remaining sites are separated by more than 40 km each. Mean diurnal prey-capture rates ranged from one to almost four prey items per day (Table 1; Higgins and Buskirk 1992; L.E. Higgins, unpublished work). Vegetation type at these sites included orchards (Fortín de las Flores and Arroyo Frio), second growth lowland tropical rainforest (Playa Escondida, Nanciyaga and Gigante Peninsula, Panama), old growth lowland tropical rainforest (Los Tuxtlas), old growth lowland seasonally dry tropical forest (Chamela), and columnar cactus desert (Tehuacán).

Within Mexico, there is great variation in type and severity of the seasons (Garcia 1973), but all sites have approximately the same photoperiodicity. In the four eastern Mexican sites, the seasonality experienced is in temperature: nocturnal winter temperatures can drop to 15°C on the coast and 0°C at 1000 m. The growing season begins between March and April on the coast, April and May at 1000 m, and ends with the arrival of the first northern storm, between September and December, which kills most adults. In the two western Mexican sites, the rainfall is seasonal with a severe dry season (normally no rain at all from February to May; S.H. Bollock, personal communication). The growing season begins with the first rains, usually in June, and ends with the last rainfall, usually in October or November. The spiders can survive several weeks of drought. The central plateau of Tehuacán is both dry and cold from October to May (Garcia 1973; Peters Recagno 1993).

The voltinism of *N. clavipes* differs between the Panamanian and the Mexican populations. All of the Mexican populations are normally univoltine with one summer generation (approximately May to November; although the coastal Veracruz populations can be bivoltine in years with mild winters; Higgins 1997). In Panama, the seasonality is mild compared to the Mexican sites and there is relatively little annual variation in photoperiod. This population is bivoltine with two distinct generations (Lubin 1978; Fig. 1, present paper). One generation hatches in the late dry season and matures in August/September, during the rains. The other generation hatches in the rainy season and matures in January/February after the rains have ended. I refer to the former as the rainy-season generation, and the latter as the dry-season generation.

Phenology, size at maturity, and female fecundity

To determine the phenology and to estimate the age and size at maturation in each population, I conducted monthly or bimestrial censuses throughout at least one generation. In Panama, Nanciyaga, Playa Escondida, Fortín, and Chamela, I collected data from two generations and in Los Tuxtlas, Tecuacán, and Arroyo Frio, from one generation. Data from Los Tuxtlas from 1989 and 1990 are not included in these analyses because the spiders disappeared due to unknown causes following the peak of unsexed juveniles in April 1989 (only four immature and mature females were found in August 1989). Field assistants searching only for mature females made the January 1990 and 1991 (end of season) visits to Nanciyaga and Playa Escondida.

At the initiation of each generation at each site, I located a study area with a high density of unsexed juveniles (approximately 50/30 m^2). At each site, I returned to the same study areas for censuses throughout the remainder of the season. As the emphasis of the study was on the age structure of the population rather than density, I increased the total area searched when spiders were rare. During each visit, I measured and classified into an age category all spiders found in the census area. Spider size was measured as leg I tibia+patella length (TPL) to the nearest 0.01 cm±2% (measured with Helios needle-nosed calipers; Higgins 1992), without removing spiders from the webs. The spiders were classified as unsexed immatures when the TPL was less than 0.5 cm, penultimate instar males (distinguished by swollen but not mature pedipalps), juvenile females, and mature males and females. The presence of a dark, heavily sclerotized epigynal plate in females indicates sexual maturity. Using flat enamel paints, I marked mature females with individual codes and males with a color code indicating the census date. Repeated observations of the same individuals were excluded from the analyses of size at maturity.

The primary goal of this study was to determine whether size at sexual maturity changed over time within a cohort. The best statistical treatment is one that allows simultaneous evaluation of change in size at maturity over time in all sites and years of observation. However, between years and among sites, differences in the size of mature animals on a given calendar date could have two causes: they could be due to differences in the beginning of the growing season, differences in growth and development rates, or both. To simultaneously investigate the consequences of differences in growth and development rates within populations at all sites, I needed to set time zero as the beginning of the growing season. The actual cues that trigger juvenile emergence are unknown, so rather than use weather data, I used the peak of unsexed juveniles (or the midpoint if the peak was broad) as an indicator of the beginning of the growing season for almost all sets of observations. There was no distinct peak of juveniles in Panama and the 1986 study in Los Tuxtlas did not include the early portion of the generation, so I analyzed the data from these two sites separately using census month as the covariate. Similarly, male size at sexual maturity was analyzed with time since peak juvenile abundance as the covariate except for Panama and Los Tuxtlas where census month was used as the covariate.

The analysis of these data rests on the assumption that unmarked mature females and mature males found in each census have matured in situ since the prior census and are not immigrants. This assumption is supported by three aspects of the natural history of these spiders. First, mature female *N. clavipes* are highly web-site tenacious (Vollrath 1985) and rarely move more than 20 m between web sites (personal observation). Second, the females are very large (reaching 3 g when gravid) and their webs span 1–3 m, making exhaustive searches of these study areas feasible. It was not uncommon to relocate previously marked females during censuses. Third, mature males live on the webs of females; males moving from web to web have very high mortality (Vollrath 1980; Christenson 1990). Lastly, immigration of unmarked, older mature females into a study site would tend to obscure any patterns of changing size with time, except in the unlikely case that all immigrants were consistently larger or smaller than non-immigrants.

In 1989, I tested for an influence of the timing of maturation on female clutch size among the Mexican populations. During the censuses, I collected unmarked, heavily gravid females (distinguished by weight and web characteristics; Higgins 1990), moved them to a laboratory at the Center of Ecology, UNAM, Mexico City, and fed them ad libidum until eggs were laid. No spiders that waited longer than 10 days in the laboratory before laying were included in the analysis to reduce any laboratory effect. Assuming that these females had matured since the prior census, the clutch collected represents each individual's first reproductive bout, and can be used to examine the effect of time-of-maturation on reproductive output.

Results

Phenology

In most Mexican sites, the first mature individuals were found 3 months after the peak of unsexed juveniles. Mature male abundance peaked earlier than female abundance at most of the Mexican sites, but not in Panama (Fig. 1). In the seasonally dry sites of Mexico (Tehuacán, Arroyo Frio, Chamela), late females reached maturity at or after the end of the rainy season and males disappeared before late females matured. In the seasonally cool sites (Playa Escondida, Nanciyaga, Fortín de las Flores), the end of the season is marked by the arrival of

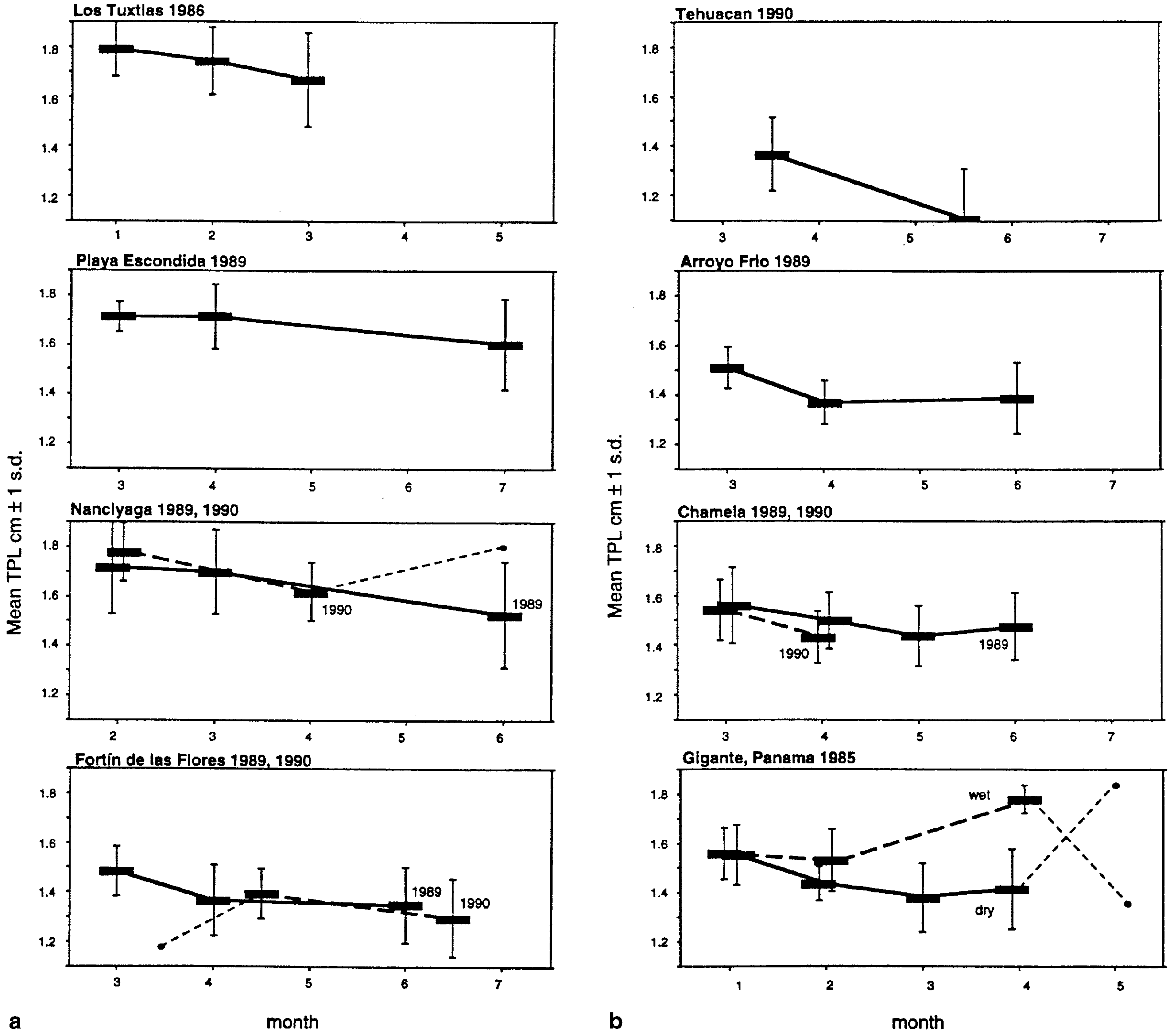

Fig. 2 Mature female size (mean TPL±SD) versus months since peak of unsexed juveniles in each population. Single *points connected with dotted lines* indicate censuses with solitary females. For Panama and Los Tuxtlas, the month of census is used as either there was no strong peak of unsexed juveniles or the peak was not observed (month 1=July in Los Tuxtlas, January in the Panama dry generation, and June in Panama wet)

a northern storm, which usually kills all individuals outside of an egg sac. In these seasonally cool sites, some males were usually present in the population throughout the time females were present.

Female size at maturity

Females in Mexico, but not in Panama, showed declining size at sexual maturity as the season progressed (Fig. 2). At Playa Escondida in 1990, all but one of the mature females were found in the September census, and I excluded these data from the analysis of changing size within a cohort. Testing whether females reached maturity at different sizes within each cohort involved analysis of covariance of spider size (TPL) with time (months since juvenile peak or census date) as the covariate. Preliminary analysis of covariance with time since the peak of unsexed juveniles as covariate showed no difference between 1989 and 1990 in female size at maturity at Nanciyaga, Fortín, and Chamela (all $P > 0.1$). Therefore, the final analyses of adult female size through time among all sites observed in 1989 and 1990 did not distinguish between years.

The final analyses of covariance show a statistically significant decline in female size with time in all of the Mexican sites but not in Panama (Table 2). In Panama, females maturing in the dry season were smaller than females maturing in the wet season, but size did not change over time (census date) within a cohort (Table 2).

Table 2 ANCOVA of mature female size covarying with time since beginning of season

Source	*SS*	*df*	*F*	*P*
Gigante, Panama				
Time	0.001	1	0.028	0.87
Generation	0.26	1	14.09	<0.001
Error	1.6	87		
Los Tuxtlas, Mexico				
Time	0.13	1	6.73	0.012
Error	1.21	62		
Playa Escondida, Nanciyaga, Fortin de las Flores, Tehuacan, Arroyo Frio and Chamela, Mexico				
Site	0.69	5	6.90	0.001
Time	0.64	1	37.14	0.001
Site×time	0.17	5	1.84	0.1
Error	7.16	387		

Table 3 ANCOVA of female size in hilltops and arroyos in Chamela over time since peak of juveniles

Source	*SS*	*df*	*F*	*P*
Time	0.256	1	18.34	<0.001
Habitat	0.128	1	9.153	0.003
Year	0.037	1	2.684	0.103
Year×time	0.065	1	4.633	0.033
Year×habitat	0.001	1	0.006	0.939
Error	2.132	153		

Table 4 ANCOVA of male size at maturity

Source	*SS*	*df*	*F*	*P*
Gigante, Panama				
Time	0.002	1	0.142	0.707
Generation	0.127	1	10.74	0.001
Error	2.412	201		
Los Tuxtlas, Mexico				
Time	0.75	1	45.93	0.001
Error	0.85	52		
Playa Escondida, Nanciyaga, Fortín and Arroyo Frio				
Time	0.00	1	0.00	0.996
Site	0.606	3	12.154	<0.001
Error	4.522	266		

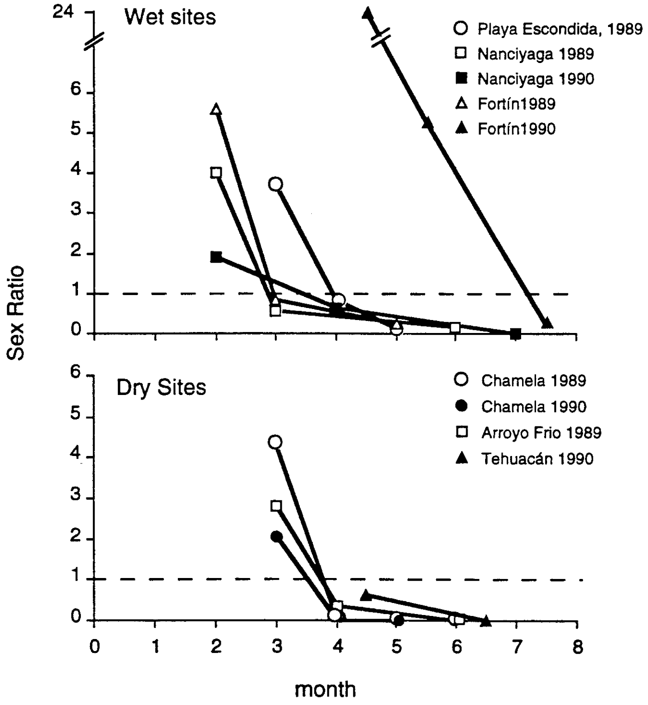

Fig. 3 The sex ratio (number of mature males/number of mature females) observed in each month following the peak of unsexed juveniles. The sex ratios are not reported when no mature females were found. Mature female abundance peaks in most sites between months 4 and 5. In Fortín in September, 1990 (month 4), only one mature female was found

Tested independently, spider size at Los Tuxtlas declined significantly over time (census date; Table 2). Among the remaining sites in Mexico, there was significant variation in female size at maturity among populations and a significant decline in female size over the course of the season (time since juvenile peak), but no difference in the rate of decrease in size among sites (no interaction effect; Table 2).

A posteriori contrasts of female size among the Mexican sites observed in 1989/1990 revealed that females were largest in the coastal Veracruz sites (Playa Escondida, Nanciyaga), significantly smaller in Chamela, and smallest in the higher altitude areas (Fortín, Tehuacán, Arroyo Frio; ANOVA within groups all $P>0.40$, among groups all $P\leq 0.002$).

Chamela has dry rolling hills dissected by moist arroyos. Observations of spiders in the arroyos, where they were most abundant, provided the data for the above analyses. However, spiders also occur on the hill tops, and in each month I conducted additional censuses in the drier areas and I can use these data to explore the role of microhabitat type in determining size at sexual maturity. Juveniles emerged from the egg sacs at the same time in both habitat types each year. I found that in both habitat types, the decrease in size over time was statistically significant and there was no interaction between time and habitat ($P>0.5$), so the time by habitat interaction term was dropped from the final analysis. Analysis of covariance demonstrated that in each month, mature female spiders on the hill tops were significantly smaller in both years (Table 3). The significance of the time×year interaction term reflects the fact that in each habitat type, late-maturing females tended to be smaller in 1990, a drier year than 1989.

Male size at maturity

Except at Los Tuxtlas, male size at sexual maturity did not decrease over time within a cohort (Table 4). Males were present at only one census date at Tehuacán and

Chamela, and these sites were not included in these analyses. There was no difference between 1989 and 1990 in male size at maturity at Playa Escondida, Nanciyaga, or Fortín (ANCOVA, all $P>0.40$). Therefore, I combined the observations from the 2 years in the final test for variation over time among sites in Mexico (time since peak juvenile abundance as the covariate). As in the analysis of female size, I analyzed the data from Panama and Los Tuxtlas separately using census month as the covariate. Only at Los Tuxtlas did male size decline over time. This may reflect the influence of a few outliers: the few males that matured in September were unusually small (mean TPL=0.29 cm±0.01, compared to 0.65 cm±0.03 in July).

A posteriori comparisons, pooling across time, were used to test for differences in male size among cohorts. Male size at maturity varied among populations and, in Panama and Chamela, between generations. In Panama, males maturing in the dry season were smaller than those maturing in the wet season (mean TPL±SEM; dry season 0.46 cm±0.01, wet season 0.54 cm±0.025; Table 2). In Chamela, the males were significantly smaller in 1990, a drier year than 1989 (mean TPL±SEM; 1989, 0.73 cm±0.014, 1990, 0.61 cm±0.02). However, the correlation between microhabitat and spider size observed for females at Chamela was not observed for the males [ANOVA: year, $F_{(1,62)}=25.44$, $P<0.001$; microhabitat, $F_{(1,62)}=2.12$, n.s.].

The Mexican populations observed in 1989/1991 varied in mature male size [Chamela 1989 and 1990 considered separately; ANOVA: $F_{(6,337)}=18.17$, $P<0.001$]. A posteriori contrasts showed that the males were largest in the western sites in the wet year (Chamela and Arroyo Frio 1989; TPL≈0.7 cm), intermediate in Nanciyaga and in Chamela in 1990 (TPL≈0.6 cm), smaller in Playa Escondida and Fortín (TPL≈0.55 cm), and smallest at the mid-altitude desert site Tehuacán (TPL≈0.4 cm; within groups $P>0.40$; among groups $P<0.02$).

Fitness consequences of variation in female size and age at maturity

The life-time fecundity of an individual female *N. clavipes* depends upon the probability of copulation, the number of eggs laid per clutch, and the number of clutches. By all three measures, females maturing late in a seasonal habitat have reduced fitness. The probability of copulation was higher with early maturation because peak male abundance occurred before peak female abundance (Fig. 1) and non-virgin males may be infertile (Christenson 1989). In all of the Mexican sites, by the time mature female abundance peaked, the sex ratio was less than 1:1 (male:female; Fig. 3). Mature males disappeared before the end of the growing season and were not found again until the following year. Even in Panama, where males were present for longer periods of time, virgin females unattended by males were found at the end of each generation (Higgins 1989).

To test for effects of female size at sexual maturity on clutch size, I collected egg sacs from 51 females during the 1989 and 1990 seasons. Over all sites, clutch size increased with increasing female size, although female size explained a small proportion of the total variance (number of eggs=–34.6+503.7 (TPL) ; $R^2=0.17$, $F_{(1,48)}=9.66$, $P<0.001$).

Independent of female size, females collected later in the growing season laid smaller clutches than females collected early in the growing season. Twenty-six females collected during 1989 censuses in Chamela, Fortín and Playa Escondida met the criteria for testing for an effect of time of maturation on female fecundity (found unmarked during a census, laid eggs within 10 days of collection). Females were collected at three censuses at each site, but the data from females collected during the last two censuses at Fortín and Chamela had to be combined within each site due to small sample sizes. Kruskal-Wallis tests for heterogeneity showed that within each site there was no variation in female size at maturation among different census dates (TPL; all $P>0.40$). There was a significant decline in clutch size over time at Chamela and Playa Escondida, and a non-significant trend towards smaller clutch sizes in Fortín [Playa Escondida ($n=10$) Kruskall-Wallis=7.63, $P=0.022$; Fortín ($n=9$) Mann-Whitney $U=16$, $\chi^2=2.16$, $P=0.14$; Chamela ($n=7$) Mann-Whitney $U=9$, $\chi^2=3.86$, $P=0.05$]. This decline in clutch size was not accompanied by any change in mean egg weight (clutch weight/egg number) at any site (all $P\geq0.06$).

Female fecundity is also determined by the number of clutches laid. Females can live as long as 5 months after sexual maturity, laying one clutch of 600–800 eggs every 21–25 days (Higgins 1992). However, the end of the season limits female longevity and hence the number of clutches, and late-maturing females may not lay at all. For example, in Los Tuxtlas in 1986, 30 marked mature females were observed nearly daily until oviposition or for 21 days. In this year the first northern storm arrived very early, in September. All of the 22 females that were mature in August were observed to lay, and none of the 8 that matured in September were observed to lay. All free-living spiders disappeared during or shortly after the storm and were presumed dead.

Discussion

For animals in habitats where the growing season ends with a killing frost or drought, individuals must achieve a resistant life-stage prior to the end of the growing season. In many univoltine arthropods, this means that individuals must mature and reproduce before a critical point during the growing season. If, in a spatially as well as temporally heterogeneous habitat, an individual has had “bad luck” in site choice, reduced growth rates (weight gain) may slow development relative to the passage of time within the growing season. This could be particularly critical for relatively sessile organisms like ant lions and many spiders (Turnbull 1962; Beck and Conner 1992; Gotelli 1997; Schneider 1997). As development is plastic in many arthropods, in turn slow growth can stimulate maturation at a smaller size, resulting in a pattern of declining adult size with time during a generation (Miyashita 1986, 1991; Forrest 1987; Schneider 1997; C. Fox, personal communication; M. Singer, personal communication). These small, late-maturing individuals likely have lower fitness relative to more rapidly growing, early-maturing individuals.

In the present study, late females were smaller than early females in all seven univoltine populations inhabiting highly seasonal environments; late females were the same size as early females only in the bivoltine population found in the relatively less seasonal habitat in Panama. In all but one set of observations, early and late males were the same size. The differences observed between females in Panama and in Mexico, and between the sexes in Mexico, may reflect differences in the relative time spans of development and the growing season. For male *N. clavipes*, the growing season is long relative to the total development time and there may be no penalty associated with slowed development: slowly growing males can reach maturity at the same instar as more rapidly growing males. It may be only when the growing season is curtailed very early, as in Los Tuxtlas in 1986, that late males are smaller than earlier males. For female *N. clavipes*, the usual development time approaches the length of the growing season in all Mexican sites. Slowly growing females are faced with a trade-off between target size and the increased cost of delaying maturation. These data are consistent with the hypothesis that late females are reducing the probability of complete failure to reproduce by maturing at a smaller size. This tropical end-of-season penalty is similar to the phenomenon of severe time stress observed in some northern temperate butterflies (Nylin et al. 1996).

Habitat heterogeneity, such as variation in food availability, is likely a major cause of variation in size and age at sexual maturity within populations of terrestrial arthropods. It can cause differences in emergence times or differences in weight gain. Late emergence could reflect slower embryonic development or failure to receive the cues signaling the initiation of the growing season. Slow weight gain causes an individual to pass through each instar slowly or take more instars to reach a given size whereas rapid weight gain causes an individual to pass through several instars quickly and mature early (reviewed in Higgins and Rankin 1996). Regardless of whether the intermolt duration or the number of instars changes in response to variation in weight gain, within a cohort, well-fed and rapidly growing individuals reach a large size and mature early relative to the end of the season.

The role of microhabitat quality and variation among years in determining size at maturity is particularly apparent among female *N. clavipes* at Chamela. At this site, two distinct habitat types are found, the wet arroyos and dry hilltops, and the 2 years of study differed in total rainfall. Although the spiders in the two habitats had similar emergence dates, in each month females on the hilltops matured at a smaller size (presumably due to a lower abundance of insects). Late females and all males matured at a smaller size in the drier year.

In males, size at maturity may be more important than timing of maturity in determining reproductive success. Male reproductive success is correlated with dominance rank, which in turn is strongly influenced by male size (Christenson and Goist 1979; Vollrath 1980). As mean male size does not vary over time within a cohort, there is no penalty for late maturation related to size-determined competitive ability. However, changes in the sex ratio and in the frequency of virgin females during the growing season may interact in a complex fashion to alter male reproductive success when maturation is delayed.

Late-maturing female *N. clavipes* in strongly seasonal habitats have reduced fecundity for several reasons: they are smaller, produce smaller clutches for their size, and they have a shorter period of time in which to reproduce. The relatively small egg sacs laid by late females may reflect the energy limitations imposed by deteriorating habitat quality at the end of the season. This could be true even if the clutches collected in this study were not the first reproductive effort of each female, as clutch size has been observed to decline with successive clutches (T.E. Christenson, personal communication). In addition to these correlates of reduced fecundity, late-maturing females are less likely to encounter a male. Even if males are present when a late female matures, they may be old and perhaps infertile (Christenson 1989).

Slowly growing females are “making the best of a bad job” (Dawkins 1980; Eberhard 1982; Maynard Smith 1982; West-Eberhard 1989). In strongly seasonal environments, late females do not fully compensate for the poor conditions experienced as juveniles and are expected to have much lower reproductive success. Although not allowing full compensation for low growth rates, developmental plasticity that allows maturation with some chance of reproduction under deteriorating conditions must be viewed as adaptive (Reznick 1990). Such plasticity may play a key role in the ability of some arthropod species to survive under a wide range of environmental conditions.

Acknowledgements I am grateful for voluntary field assistance through the years from P. Batra, A. Benitaz, H. Macias C., L. Martínez, and J. Villarreal. C. Pease provided insight and support throughout the project and analysis. R. Buskirk, N. Cappacino, C. Cordero, H. Drummond, C. Fox, M. Franco, N. Fowler, F. Hensley, M. Morris, J. Soberón, and several anonymous reviewers commented upon earlier versions of the manuscript. In Mexico, several people generously allowed me to work on their property: L. Forbes and S. Ayala (Fortín), C. Rodriguez (Nanciyaga), F. Aguilar (Arroyo Frio), and the management of Hotel Playa Escondida. Permission to work at Los Tuxtlas and Chamela was granted by the Instituto de Biología, UNAM, and permission to work at Tehuacán cactus garden was granted by the Instituto Nacional de Ecología. This work was supported by the University of Texas Graduate Fellowship program, a National Science Foundation dissertation improvement grant (BSR-8413831), a Smithsonian Tropical Research Institute short-term fellowship, an Organization of American States PRA fellowship, and a fellowship from the Centro de Ecología, Universidad Nacional Autonoma de México. The data were prepared for publication while working in the laboratory of M.A. Rankin supported by a grant from the National Science Foundation (no. IBN 9220934).

References

Barnes J, Higgins L, Sagrosky CW (1992) Predation of *Nephila clavipes* (Linnaeus) (Araneae: Tetragnathidae) eggs and review of genus *Pseudogaurax* (Diptera: Chloropidae), with a description of two new species. J Nat Hist 26:823–834

Beck MW, Conner EF (1992) Factors affecting the reproductive success of the crab spider *Misumenoides formosipes*: the covariance between juvenile and adult traits. Oecologia 92:287–295

Bullock S (1986) Climate of Chamela, Jalisco, and trends in the south coastal region of Mexico. Arch Meteorol Geophys Bioklimatol Ser B Theor Appl Climatol 36:297–316

Christenson TE (1989) Sperm depletion in the orb-weaving spider *Nephila clavipes*. J Arachnol 17:115–118

Christenson TE (1990) Natural selection and reproduction: a study of the golden orb-weaving spider. In: Dewsbury DA (ed) Contemporary issues in comparative psychology. Sinauer, New York, pp 149–174

Christenson TE, Goist KC (1979) Costs and benefits of male-male competition in the orb-weaving spider *Nephila clavipes*. Behav Ecol Sociobiol 5:87–92

Christenson TE, Wenzl PA (1980) Egg-laying of the golden silk spider, *Nephila clavipes*: a functional analysis of the egg sac. Anim Behav 28:1110–1118

Christenson TE, Brown SG, Wenzl PA, Hill EM, Goist KC (1985) Mating behavior of the golden orb-weaving spider *Nephila clavipes*. I. Female receptivity and male courtship. J Comp Psychol 99:160–166

Dawkins R (1980) Good strategy or evolutionary stable strategy? In: Barlow GW, Silverberg J (eds) Sociobiology – beyond nature/nurture. Westview Press, Boulder, pp 331–367

Dietrich WE, Winsor DM, Dunne T (1982) Geology, climate, and hydrology of Barro Colorado Island. In: Leigh EG Jr, Rand AS, Windsor DM (eds) The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, DC, pp 21–59

Eberhard WG (1982) Beetle horn dimorphism: making the best of a bad lot. Am Nat 119:420–426

Forrest TG (1987) Insect size tactics and developmental strategies. Oecologia 73:178–184

Garcia E (1973) Modificaciones al Systema de Classificación Climatica de Köppen. Universidad Nacional Autonoma de Mexico Press, Mexico City

Gotelli NJ (1997) Competition and coexistence of larval ant lions. Ecology 78:1761–1773

Higgins LE (1989) Factors influencing the shape of the internal female genitalia in the araneid spider *Nephila clavipes*. Ann Entomol Soc Am 82:748–753

Higgins LE (1990) Variation in foraging investment during the intermolt and before egg laying in the spider *Nephila clavipes*. J Insect Behav 3:773–783

Higgins LE (1992) Developmental plasticity and fecundity in the orb-weaving spider *Nephila clavipes*. J Arachnol 20:94–106

Higgins LE (1993) Constraints and plasticity in the development of juvenile *Nephila clavipes* in Mexico. J Arachnol 21:107–119

Higgins LE (1995) Direct evidence for trade-offs between foraging and growth in a juvenile spider. J Arachnol 23: 37–43

Higgins LE (1997) Fenología facultativa de *Nephila clavipes* en Los Tuxtlas. In: González E, Dirzo R, Vogt R (eds) Historia Natural de "Los Tuxtlas". Universidad Nacional Autonoma de Mexico Press, Mexico City

Higgins LE, Buskirk RE (1992) A trap-building predator exhibits different tactics for different aspects of foraging behavior. Anim Behav 44:485–499

Higgins LE, Rankin MA (1996) Different pathways in arthropod post-embryonic development. Evolution 50:573–582

Istock CA (1967) The evolution of complex life cycle phenomena: an ecological perspective. Evolution 21:592–605

Levi HW (1980) The orb-weaver genus *Mecynogea*, the subfamily Metinae and the genera *pachynatha*, *Glenognatha* and *Azilia* of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae). Bull Mus Comp Zool Harv Univ 149:1–75

Lubin YD (1978) Seasonal abundance and diversity of web-building spiders in relation to habitat structure on Barro Colorado Island. J Arachnol 6:31–35

Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge

Miyashita T (1986) Growth, egg production and population density of the spider *Nephila clavata* in relation to food conditions in the filed. Res Popul Ecol Kyoto 28:135–149

Miyashita T (1991) Direct evidence of food limitation for growth rate and body size in the spider *Nephila clavata*. Acta Arachnol 40:17–21

Nylin S, Gotthard K, Wiklund C (1996) Reaction norms for age and size at maturity in *Lasiommata* butterflies: predictions and tests. Evolution 50:1351–1358

Peters Recagno EM (1993) Variaciones microclimaticas de un desierto intertropical en el centro de México: Algunas implicaciones sobre la vegetación. Thesis, Universidad Nacional Autonoma de México

Reznick DN (1990) Plasticity in age and size at maturity in male guppies (*Poecilia reticulata*): an experimental evaluation of alternative models of development. J Evol Biol 3:185–203

Robinson M, Robinson B (1980) Comparative studies of the courtship and mating behavior of tropical araneid spiders. Pac Insects Monogr no. 36

Roff DA (1992) The evolution of life histories. Chapman & Hall, New York

Schneider JM (1997) Timing of maturation and the mating system of the spider, *Stegodyphys lineatus* (Eresidae): how important is body size? Biol J Linn Soc 60:517–525

Stearns SC (1992) The evolution of life histories. Oxford University Press, London

Turnbull AL (1962) Quantitative studies of the food of *Linyphia triangularis* Clerck (Araneae: Linyphiidae). Can Entomol 94: 1233–1249

Vollrath F (1980) Male body size and fitness in the web-building spider *Nephila clavipes*. Z Tierpsychol 53:61–78

Vollrath F (1985) Web spider's dilemma: a risky move or site dependent growth. Oecologia 68:69–72

Vollrath F, Parker GA (1997) *Reply to* Giant female or dwarf male spiders (Coddington JA, Hormiga G, Scharff N). Nature 385:688

West-Eberhard MJ (1989) Phenotypic plasticity and the origins of diversity. Annu Rev Ecol Syst 20:249–278

Wilbur HM (1980) Complex life cycles. Annu Rev Ecol Syst 11:67–93