OIKOS 99: 377–385, 2002

Female gigantism in a New Guinea population of the spider *Nephila maculata*

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Higgins, L. 2002. Female gigantism in a New Guinea population of the spider *Nephila maculata*. – Oikos 99: 377–385.

In many arthropods, female clutch size is positively correlated with female size but the benefits of increased size are presumed to be counterbalanced by the mortality risks incurred through delayed maturation. The orb-weaving spiders of the genus *Nephila* are characterized in part by large female size, and among species female size declines with increasing latitude, suggesting that one important mortality risk associated with delayed female maturation is the end of the growing season. The best-studied species inhabit strongly seasonal habitats. To explore the hypothesis that female size is limited by season length, I collected data concerning size-dependent growth and development rates, prey capture success, predation risk, and female fecundity from a population of *N. maculata* inhabiting a nearly aseasonal habitat. Comparison of these data with observations from another *N. maculata* population and from congeners inhabiting more seasonal sites supports the hypothesis that female size in this genus may be limited primarily by season length. Combined with recent phylogenetic evidence that male size is an ancestral characteristic, these results indicate that sexual size dimorphism in this group has evolved due to fitness advantages of delayed female maturation.

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Identification of the selective forces that result in the evolution of extreme differences in body size between males and females has long been a source of discussion among biologists (reviewed and summarized in Hedrick and Temeles 1989). Adult size reflects life-history trade-offs between selection for large size and costs of delayed maturation (Roff 2001). In general, sexual size dimorphism (SSD) will evolve when males and females have different optimal body size at maturation, so long as the genetic correlation for size at maturity between the sexes is less than 1.0 (Lande 1980, Slatkin 1984). Because SSD is an emergent property of the relative sizes of males and females, and the evolutionary forces leading to changes in male or female size will vary among groups, the sources of differences in selection between the sexes are likely as diverse as the organisms expressing sexual size dimorphism.

Spiders have long attracted attention in the study of the evolution of SSD because females may be nearly ten times larger than the males, particularly in some orb-web spinning groups (Darwin 1871, Robinson and Robinson 1980, Elgar 1991, Vollrath and Parker 1992, Head 1995, Coddington et al. 1997, Prenter et al. 1997, Hormiga et al. 2000, Moya-Laraño et al. 2002). Even within the orb-spinning spiders, the models explaining the evolution of small males and large females are nearly as numerous as the authors who have addressed the problem. They fall into two broad categories, those proposing mechanisms for the evolution of male dwarfism and those proposing mechanisms for the evolution of female gigantism. These models are often presented as opposing hypotheses (Coddington et al. 1997, Vollrath and Parker 1997), although Lande's and Slatkin's models imply that they may co-exist (Lande 1980, Slatkin 1984).

Accepted 2 May 2002

ISSN 0030-1299

In orb-web spinning spiders, small male size is likely an ancestral trait, where male optimal size has apparently not varied while female optimal size has, producing some lineages with exceedingly large female size (Hormiga et al. 2000). Maintenance of male dwarfism likely reflects diverse mechanisms that are not mutually exclusive. Sound evidence exists for small male advantage due to female preference (Schneider et al. 2000), mortality selection (Vollrath and Parker 1992), and scramble competition (Moya-Laraño et al. 2002). It is also likely that small male size is favored because males are often kleptoparasites of the females, living on their webs and "stealing" insects; the competition for food would favor maintenance of different sizes of the males and females (Slatkin 1984, Hedrick and Temeles 1989).

Female gigantism has received much less attention than male dwarfism, perhaps because it appears obvious that fecundity selection will favor increased female size at maturity (Darwin 1871, Head 1995). However, selection for increased fecundity will only result in the evolution of large female size if there are no counteracting mortality factors favoring early maturation and hence smaller size (Stearns 1992, reviewed in Roff 2001: 198–210). Costs of delayed maturation include, but are not limited to, increased generation time and increased risk of pre-reproductive mortality caused by predation and the end of the growing season (Roff 1980, 1983, Stearns 1992, Higgins and Rankin 1996, Higgins 2000). However, some large arthropods apparently enter a size-refuge, outgrowing many if not most predators (Chase 1999). If a slight increase in development time yields large increases in size and size itself is a refuge from predation, then the selective advantages of increased fecundity might outweigh the disadvantages of delayed maturation. Under these circumstances, season length may be the major limiting factor to increased female size. When increased size is not of great benefit to male fitness (Vollrath and Parker 1992, Schneider et al. 2000, Moya-Laraño et al. 2002), or when males express less phenotypic variation in size at maturity (Fairbairn 1990), this fecundity advantage could lead to the evolution of female-biased SSD common in insects and spiders (Scriber and Slanski 1981, Head 1995).

Large female size has evolved at least once in the subfamily Nephilinae (Tetragnathidae) (Coddington et al. 1997, Hormiga et al. 2000). Increasing female size is highly correlated with increased fecundity across species and within species of spiders (Eberhard 1979, Craig 1987, Marshall and Gittleman 1994, Higgins 2000). Higgins has shown that female *Nephila clavipes* are large enough to be in a size refuge from most predators (1992a) and that fecundity per reproductive bout increases with increasing female size (1992b, 2000). Female size in this genus may be limited primarily by habitat seasonality: the females are balancing the risk of mortality due to the end of the season against the benefits of increased size (Miyashita 1990, Higgins 2000). Comparative analysis of published data from eight species of *Nephila* supports this hypothesis. Female size declines significantly as latitude increases from the equator, while male size does not vary (Fig. 1). If mortality due to the end of the season is a major factor influencing optimal female size and age at maturity, then one expects females in aseasonal sites to be released from even this limit to development. To explore the hypothesis that female size in *Nephila* may be limited by season length, I studied a population of *N. maculata* (Fabricious) in the relatively aseasonal habitat in lowland north Papua New Guinea, testing for a size-refuge from predation and for a fecundity advantage of increased size. I compare these results to an earlier study of the same species at the mid-altitude site Wau (point 1 on Fig. 1).

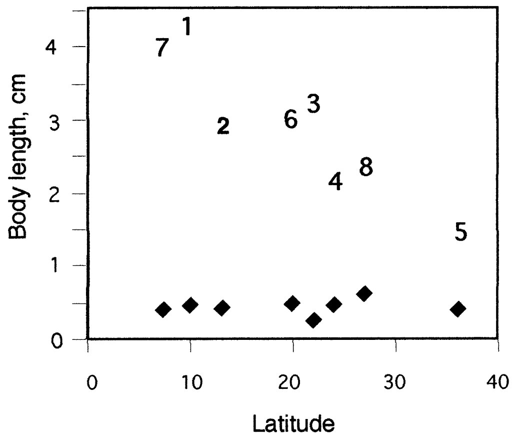

Fig. 1. Male and female body length for reported species of *Nephila* as a function of degrees latitude from the equator. Female body length (cm) = 46.18 − 0.816 (latitude) $R^2 = 0.850$, $F_{(1,6)} = 33.908$, $p = 0.001$; male body length (cm) does not vary with latitude ($p > 0.7$). Data correspond to the mean (M, if multiple measures are given), midpoint of the range (MPR, if a range is provided) or reported body length (if only one measurement is reported) for males and females of each species. Female data are indicated by numbers, males of each species are indicated by diamonds at the same latitude. Where a region rather than a point was given as the locality, the midpoint of the latitudinal range was used in the analysis. 1: *maculata* (M for females, MPR for males Wau, Papua New Guinea, Robinson and Robinson 1973); 2: *sexpunctata* (Matto Grosso Brazil; Levi and von Eickstedt 1989); 3: *senegalensis* (MPR Banjul, Gambia (laboratory reared); Clausen 1987); 4: *edulis* (MPR Patonga, New South Wales, Australia; Austin and Anderson 1978); 5: *clavata* (M females, MPR males Tokyo, Japan; Miyashita 1990, T. Miyashita, pers. com.); 6: *madagascarensis* (M Madagascar (laboratory reared) Bonnet 1929); 7: *pilipes* (Ibadan, Nigeria; Robinson and Robinson 1980); 8: *clavipes* (Florida, USA; Levi 1980).

Methods

Study organism and study site

The orb-weaving spider *Nephila maculata* (Araneae: Tetragnathidae) is a very widely distributed species, found from southern China to northern Australia (Levi 1980) in low to mid-altitude tropical and temperate forests, both rainforest and seasonally dry. The Robinsons studied *N. maculata* at the mid-altitude site of Wau, Papua New Guinea (Robinson and Robinson 1973). At Wau, the spiders were found throughout the year, with peak abundance of immature individuals in the latter part of the rainy season (January–May). Mature females showed little variation in adult size (Table 1 in Robinson and Robinson 1973). Males were somewhat more seasonal, with peak abundance in the rainy season, and were considerably smaller than females (Fig. 18 in Robinson and Robinson 1973). *N. maculata* also occurs in the north coastal rainforests near Madang, Papua New Guinea. The climate at Madang is even less seasonal than Wau. The driest months in Madang are between the monsoons, May and August–September, but rainfall in each of these months exceeds 100 mm (DaSilva et al. 1994). Similarly, mean monthly temperatures vary annually only about 2°C (http://ferret.wrc.noaa.gov/las/main.pl/coads_climatology.nc). At Wau, Robinson and Robinson report about 30 mm of rain during the driest month of August. The temperatures were cooler at Wau than Madang, with similar range from maximum to minimum temperature.

Between 20 February and 3 April, 1993, I observed *N. maculata* in the forest owned by the village of Biatabag, southwest of the city of Madang. The village owns both areas of primary forest and garden areas where plots are cleared approximately every 15 years for planting. The spiders were most abundant in the older secondary forest of the garden areas. I used census techniques to monitor the age structure of the population, and repeated observations of marked individuals to determine prey capture rate, predation load, rate of weight gain (growth rate), and instar duration and growth per molt (development rate). I measured size-dependent fecundity by collecting gravid females, temporarily housing them in an insectory, and releasing them at the capture site after oviposition.

Population age structure

The age structure of the population was determined through five censuses during the study period. During each census, all individuals in the study area were measured (leg I tibia + patella length, TPL) and their sex and maturation status were determined (Higgins 1992b). Spiders smaller than 0.5 cm TPL with no male secondary sexual characteristics (swollen pedipalps) were classified as unsexed immatures. Juvenile males in the penultimate instar could be distinguished by their swollen but immature pedipalps and mature males by their mature, sclerotized pedipalps. Juveniles equal to or larger than 0.5 cm TPL were classified as immature females, as all the penultimate instar males I observed were smaller than this size. Sexually mature females were identified by the loss of the bottle-brush hairs on the legs and the heavily sclerotized epiginal plate on the abdomen (Robinson and Robinson 1973). Sexually mature individuals were relatively rarely observed in this study: males cohabit with females, and after reaching maturity the females tended to build their webs in the canopy of the forest (Higgins, pers. obs.), coming down to lay eggs in the soil (Robinson and Robinson 1973, Higgins, pers. obs.). Therefore, the frequency of sexually mature individuals is underestimated by the census technique.

Prey capture and predation

Prey capture success (mean and standard deviation of number of prey captured per 12 diurnal hours) was determined by diurnal trap-line surveys of marked individuals of TPL ≥ 0.5 cm on 4 March 1993 and 16 March 1993 (Turnbull 1962, Castillo and Eberhard 1983, Higgins and Buskirk 1992). I used new spiders at new web sites for each survey. The day prior to each survey, I located 10 spiders along a trapline, spaced such that I could observe all animals within 15 minutes. Starting at dawn the next day, I observed each actively hunting individual every 0.5 h until sunset. For each incidence of prey capture, I recorded prey size (2 mm increments) and spider response (capture, reject, ignore). Because these spiders masticate their prey, most prey could not be identified so prey type is not reported. The total range of prey sizes captured by spiders in this population was determined by combining all observations of prey captured by spiders during the trap-line surveys, censuses, and the daily observations of marked individuals. Insects that were ignored, rejected, or where captures failed are not included in the calculation of mean prey capture rate or median prey size.

I estimate predation risk from the frequency of intact, abandoned orb webs. As in *N. clavipes* (Higgins 1992a), *N. maculata* consume and recycle the materials of the orb web prior to voluntary web site abandonment. Spiders were classified as having suffered a predation attempt if, 24 h after the spider had been observed on an intact orb web, I found an empty intact or slightly damaged orb web. Note that these estimates of predation risk do not distinguish between successful and unsuccessful attacks. The classification of such an event as an attack was occasionally supported by additional evidence such as marked, autotomized legs in the web.

Predation risk is a function of spider size (Higgins 1992a), so prior to statistical analysis I grouped observed spiders into three size/age classes ($TPL < 0.5$ cm: unsexed immatures; $0.5 \text{ cm} \leq TPL < 1.0$ cm: juvenile males and small juvenile females; $TPL \geq 1.0$ cm: large juvenile females and mature females). Mature males do not build orb webs and were not included in the estimation of predation risk. The risk of predator attack was calculated in two manners. First, I calculated risk as the cumulative frequency of abandoned, intact orb webs for all animals observed in each size class throughout the study period. Second, to estimate the risk of attack per unit time for spiders in different size classes, I selected 14 2-day periods approximately 7 d apart. Each set of spiders was unique; if a spider was observed more than once I used only the first observation. The predation per unit time was estimated by the number of intact, abandoned orbs on day 2 compared to the total number of spiders observed in each size class on day 1 of each period.

Growth and development

Two aspects of life history were observed in this population: juvenile growth and development rates, and the size at sexual maturity of males and females. Because females take an estimated 6 months to reach sexual maturity, age at sexual maturity was not measured during this study. During censuses, all unmarked individuals greater than 0.3 cm TPL were marked with Testors® nonmetalic enamel and their web sites were flagged. Marked individuals were observed nearly daily until no longer found. Juveniles smaller than 0.3 cm TPL could not be safely marked, but their web sites were flagged and they were also observed nearly daily until no longer found. The open nature of the study area allowed me to relocate many marked individuals through successive web sites and over several days. A total of 176 individuals were marked during the study. For animals found more than once, the average duration of observation was 10 days (s.d. 2.8, range 6–24).

Juvenile development rate in arthropods is a function of three inter-related factors (Higgins and Rankin 1996): the rate of weight gain, growth per molt, and the intermolt interval (the time between successive ecdyses). It is possible to monitor all three variables without removing individuals from their webs. These spiders gain weight by storing reserves in their abdomens and mass is highly correlated with spider size (TPL) and the volume of the abdomen. Abdomen volume (av, cm^3) was calculated as a cylinder from the length and maximum width of the abdomen and mass was estimated using published equations for *N. clavipes* ($\text{mass (g)} = 0.012 + 0.081 \ TPL^3 + 0.784 \ av$; Higgins 1992b). Growth per molt was measured as the slope of the regression of postmolt TPL on premolt TPL. The intermolt interval was determined for 11 marked individuals that were observed nearly daily from one ecdysis to a second.

Female fecundity

Female fecundity is a function of TPL and of prelaying weight (which is also a function of TPL). To simplify these relationships and avoid non-independent analyses, I estimated the function of fecundity upon weight, and weight upon size (TPL). As mentioned above, mature female *N. maculata* spin in the forest canopy and were difficult to observe in secondary forest. To determine female fecundity, I collected six females from the canopies of fruit trees on the edge of Baitabag village. The spiders were returned to these fruit trees after laying. *Nephila maculata* lay their eggs buried in the soil (Robinson and Robinson 1973). To collect egg sacs, I placed each of the gravid females in a 66 cm long screened cube with a small potted plant. All the spiders buried their egg sacs in the pots. These spiders lay very large egg sacs (all $> 3\,000$ eggs), so I estimated egg number from total clutch weight (after removal from the silken egg sac) by weighing and counting approximately 20% of eggs in each clutch.

Results

Age structure of the population

The age structure of the population changed very little over the 30 d between the first census and the last census (Fig. 2). All age classes were present at each census during the study, including relatively large numbers of recently dispersed second and third instar juveniles (TPL ca 0.1 cm). Although these data represent only a short portion of the year, the stable age structure is in marked contrast to shifting age structures of populations and species in more seasonal habitats, where dispersing small juveniles rarely co-occur with mature individuals (*N. clavipes* Higgins 2000, *N. edulis* Austin and Anderson 1978, and *N. clavata* Miyashita 1986). At Wau, although Robinson and Robinson report that all stages of *N. maculata* were present throughout the year, they observed seasonal shifts in numbers of both juveniles and sexually mature individuals, with juveniles rare from May to November, and adults rare from December to April (Fig. 8 in Robinson and Robinson 1973).

Table 1. The number of predator attacks on marked individuals, as a function of the size of the individual and the size distribution of the population. Frequency (over all observed attacks), and rates of predator attack for 24 h and 12 d intervals are also presented for each size class. The frequency of attack is highly dependent upon size (likelihood ratio $\chi^2 = 11.80$, df = 2, $p = 0.003$).

	Size class		
	TPL < 0.5 cm	0.5 = TPL < 1.0	TPL = 1.0 cm
Number observed (% of population)	93 (53%)	33 (19%)	50 (28%)
Predator attacks observed (% of attacks)	22 (73%)	7 (27%)	1 (3%)
Number of spider-days	317	146	235
Predator attack rate/24 h	0.057	0.034	0.009
Predator attack rate/12 d	0.68	0.41	0.10

Prey capture and predation

The prey capture rates and median prey sizes of *N. maculata* in Madang fell within the ranges observed for *N. clavipes* in wet tropical habitats, and the mean was higher than that observed in Wau (*N. clavipes*: mean capture rate ranged from 1.2 to 4 items/12 h, median size ranged from 4–8 mm; Higgins, pers. obs., Higgins and Buskirk 1992; Wau *N. maculata* mean = 1.86 prey/day, Table 2 in Robinson and Robinson 1973). Two diurnal surveys of prey capture were run during the study; for descriptive purposes, I present pooled data from the two surveys. Juveniles preparing to molt do not hunt and observations from these spiders were excluded from the analysis of prey capture. A total of 13 actively-hunting individuals were observed for a total of 149 spider-hours. Mean prey capture rate per 12 h was 3.22 items (s.d. = 2.18). Mean prey size, estimated from all observed prey captures during the entire study, was 5.48 mm (N = 105; s.d. = 4.03; median = 4 mm).

Predator attack rates declined as the spiders increased in size (Table 1). Among all 176 individuals marked during the study, 73% of the 30 cases of probable predator attack occurred in juveniles with TPL < 0.5 cm (disappeared leaving intact or slightly damaged orb the day after being observed). Likewise, the risk of predator attack per 24 h was roughly 6 times higher for the smallest individuals compared to large and mature females. By multiplying these attack rates by 12 d, the average intermolt duration at this site (see below), I can estimate the risk of attack per instar for individuals in each size class (Table 1).

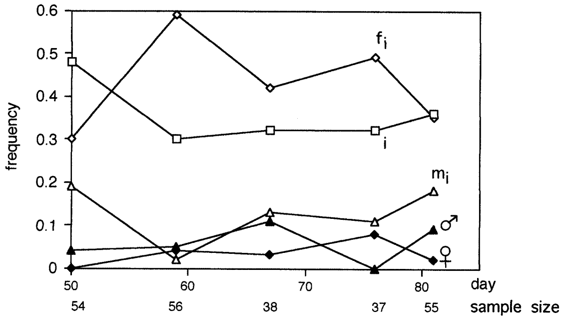

Fig. 2. The frequency of each developmental group in the population, plotted by Julian date; the total number of individuals observed at each census is recorded as sample size. i: unsexed juveniles; f_i: juvenile females; m_i: juvenile males (penultimate instar); males and females.

Growth and development

Growth rate was measured by three interdependent variables: rate of weight gain, intermolt duration, and change in size at the molt. The rate of weight gain, mg/day, was calculated by determining the change in weight between two successive observations (minimum 6 d, range 6–14 d) and dividing by the number of days in the interval. There was no relationship between the rate of weight gain and the time interval between observations ($F_{(1,25)} = 0.96$, $p = 0.34$) and this term was dropped from the final analysis. Regression analysis showed that larger spiders gained weight more rapidly (Fig. 3).

Mean intermolt duration was 12.7 d (s.d. = 3.12, range 7d–17 d) for 11 individuals observed for one complete intermolt period (ecdysis through ecdysis;

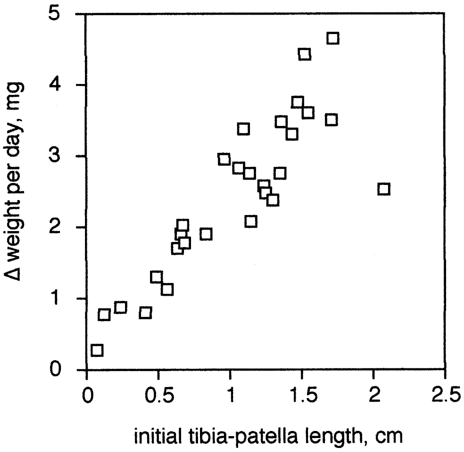

Fig. 3. The rate of weight gain per day is a function of spider size ($\Delta wt/d = 0.513 + 1.88$ TPL, $F_{(1,26)} = 78.26$, $p < 0.001$ $R^2 = 0.751$).

sizes range 0.66–1.5 cm TPL, mean TPL = 0.97 cm, s.d. = 0.3). Only individuals observed on both days of ecdysis are included. The timing of ecdysis is determined by observation of premolt status the prior day (failure to build a new orb, large swollen abdomen), the presence of a marked molted exoskeleton in the web, and the absence of a mark on the individual. The duration of the intermolt tended to increase with spider size (TPL) but the relationship was nonsignificant. Similarly sized individuals varied greatly in instar duration (e.g. one individual of TPL = 1.1 molted in 7 d, another individual of TPL = 0.77 molted in 17 d). This variation is likely due to differences in prey capture success (Higgins 1995, Higgins and Rankin 2001).

The rate of growth per molt, calculated as the slope of the regression of postmolt size on premolt size, was 1.267 (N = 60). It varied little with size or developmental stage (Fig. 4). This value falls within the range of observations from various populations of *N. clavipes* (1.19–1.31; Higgins 1992b, 1993).

Males matured at a mean size of 0.49 cm (N = 12, s.d. = 0.06, range 0.42–0.6), after approximately 4 juvenile instars (not including the non-spinning "larval" stage occurring in the egg sac). Females in the forest matured at a mean TPL of 2.062 cm (N = 11, s.d. = 0.26, range 1.66–2.45); the larger females passing through about 10 juvenile instars. Mature females with TPL as large as 2.8 cm, approximately 1 instar larger than the largest observed forest females, were found in Baitabag village during the study of female fecundity (Fig. 5).

The females in Madang are larger than the females observed at the higher altitude site in Papua New Guinea. At Wau, the Robinsons measured total leg length and weight, making direct comparison with these data somewhat difficult. The Wau spiders had a mean weight of 3.38 g (range 2.7–4.25), compared to a mean weight of 4.06 g in Madang (range 2.5–6.9; note that all Madang females were heavily gravid). Comparing variation in leg length or TPL (which are not altered by degree of gravidity as body length and weight are) reveals a much larger range in size in Madang compared to Wau (Wau median leg 1 total length = 8.25, range = 0.7 cm (8%), N = 11, Robinson and Robinson 1973; Madang female median TPL = 2.23, range = 1.14 cm (50%), N = 17).

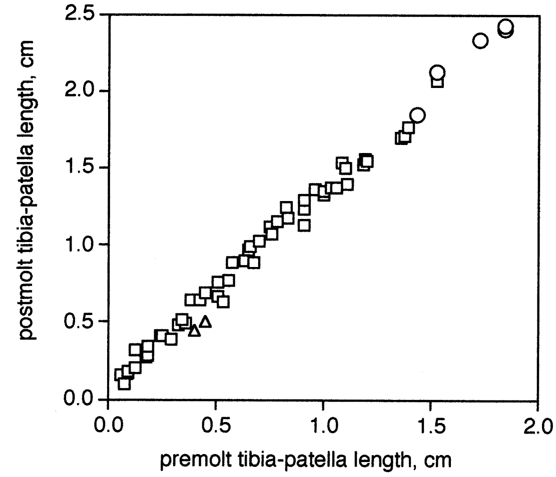

Fig. 4. Postmolting size is a function of premolt size ($TPL_2 = 0.078 + 1.267\ TPL_1$. $F_{(1,58)} = 5232.7$, $p < 0.001$, $R^2 = 0.989$). Squares: molts to juvenile stage; triangles: male molt to sexual maturity; circles: female molt to maturity.

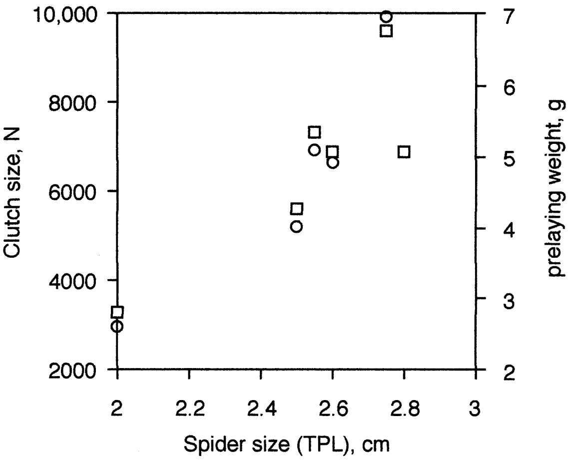

Fig. 5. Prelaying mass and clutch size are functions of adult females size (mass = $-7.98 + 5.11$ TPL; $R^2 = 0.833$ $F_{(1,3)} = 14.93$, $p = 0.01$) squares: clutch size; circles: prelaying weight.

Fecundity

Female fecundity increased with increasing female size (Fig. 5). Six females were collected in Baitabag village to determine size-dependent fecundity, five of these were weighed to the nearest mg prior to laying (one initiated oviposition behavior almost immediately after being collected). Female fecundity (number of eggs laid per clutch) is a function of prelaying mass (N eggs = 1459.2 (mass) − 344.22; $R^2 = 0.99$, $F_{(1,4)} = 423.9$, $p < 0.001$), and prelaying mass is a function of female size (Fig. 5). Clutch mass was approximately 85% of the somatic mass of the spiders, measured as the mass of the spider following oviposition. One of these spiders was relocated after release, and laid a second egg sac 21 d after the first.

Discussion

The classic life-history trade-off assumed for delaying maturation and increasing size at sexual maturity is the increased risk of pre-reproductive mortality (Stearns 1992, Roff 2001). However, *Nephila maculata* females in Madang may suffer few disadvantages by delaying maturation. There are no obvious weather factors that limit development, females outgrow most predators well before maturation, and fecundity increases rapidly with increasing female size. The size refuge from predation combined with the fecundity advantages of increased size are both likely driving forces in the evolution of female gigantism in this group.

Not all female *N. maculata* in Madang matured at the same large instar. All of the animals observed molting to maturity in the secondary forest study site were smaller than the largest gravid females found at Baitabag village, and the smaller forest animals matured at least two instars earlier than the large village females. The causes of early maturation by the spiders in the forest are unknown. One possibility is that prey capture rates are lower in the forest understory than in the village. In *N. clavipes*, microhabitat differences in prey capture and rainfall are correlated with differences in size at maturation within a population (Higgins 2000): females capturing less prey spend more time in each juvenile instar and mature at a smaller instar compared to females capturing more prey, which pass rapidly through juvenile development and mature at a larger instar. Females in Madang were much more variable in size at maturity than females in Wau, indicating that there is little variation in the number of juvenile instars among females at Wau females. Synchrony of maturation at Wau could be driven by the slightly greater seasonality at this mid-altitude site. The smaller size of females in Wau could reflect either phenotypic plasticity in development driven by environmental factors such as cooler temperatures or lower prey capture rates, or genetic differences among populations. Only further direct study will elucidate whether these differences are due to genetic differences, environmental differences, or an interaction of the two.

In comparison to the females, male *N. maculata* are very small. There may be little advantage to large male size and perhaps some fitness advantage for small males (Schneider et al. 2000, Moya-Laraño et al. 2002). Although male–male competition in *N. clavipes* favors the larger male (Vollrath 1980, Christenson and Cohn 1988), there may be little opportunity for male–male competition because the sex ratio of adult *N. maculata* at Madang was close to unity and no females were found with more than one cohabiting male. Although no data were collected concerning male survival after maturation, males do not get large enough to escape predation and may be exposed to the same selective pressures that have been postulated to favor male dwarfism in *N. clavipes* (Vollrath and Parker 1992, 1997). Seasonality is not likely to be a major selective force determining male size because male development likely requires only a fraction of the growing season experienced by these spiders (Higgins 2000). Thus, it is not surprising that male size does not vary with latitude among *Nephila* species. Despite the wide range of female size among species in this genus, males are all about the same size, reflecting the fact that small male size is an ancestral characteristic of the subfamily Nephilinae (Hormiga et al. 2000), and that optimum male size may be very similar across all of these species.

Seasonality may be a major selective force limiting female size in *Nephila* because female development requires nearly the entire growing season in seasonal habitats (Higgins 2000). There is relatively little risk of mortality due to predation for large juvenile female *N. maculata* or *N. clavipes* (current paper, Higgins 1992a) and this may be typical for most *Nephila*. In the two best studied species, *N. clavipes* and *N. clavata*, differences in adult female size appear to reflect balancing selection between the advantages of delayed maturity (increased size and fecundity) and disadvantages of delayed maturity (risk of death due to seasonal shifts; Miyashita 1990, Higgins 2000). *N. maculata* in Madang, with little risk of death due to seasonal shifts, achieves a much larger size than species of *Nephila* in seasonal habitats.

Delaying maturation by one instar would have few disadvantages and potentially great advantages for *N. maculata* females in the coastal rainforests of northern New Guinea. Development in this population proceeds relatively rapidly, on average, about 12 days per instar, and the survival rate for each additional instar is at least 90%. The reproductive consequences of delaying maturation by even one instar are enormous. If one considers a female of 2.0 cm TPL, an additional instar of growth would increase her size to 2.6 cm TPL. This 30% increase in size could result in a 140% increase in prelaying (gravid) weight, which corresponds to 156% increase in the number of eggs laid. On average, each 0.5 cm increase in size will yield a potential increase in prelaying weight of 2.55 g and each additional gram gravid weight will yield a potential increase of nearly 1 500 eggs per clutch, if egg size is constant.

The only obvious penalty for delayed maturation is increased generation time. However, one additional instar of about 2 weeks duration is perhaps inconsequential in an organism with a total development time of nearly 6 months. These observations of *N. maculata* in lowland rainforests of northern Papua New Guinea support the fecundity selection hypothesis, that the fitness advantages of delayed maturation favor the evolution of female gigantism. Since male size is constant within the subfamily Nephilinae (Hormiga et al. 2000), evolution of female gigantism is likely the driving force leading to sexual size dimorphism in this group. The question remains concerning why females are not even larger than observed: what selective forces balance the advantages of further delay of maturation? A variety of factors could be involved: increasing generation time may select against increased delays beyond one or two instars, or there could be increased mortality risk associated with biomechanical and physiological limits to size particularly in ecdysis. There also could be mechanical limits to size, as these are long-limbed, slender spiders living on silken orb webs. Additionally, increased size would require proportional increases in food intake that might slow development through additional large instars. Lastly, it is possible that there may be mechanical and genetic limits to the absolute amount of size dimorphism that can evolve between the sexes.

Acknowledgements – The field research described herein was supported by a grant from the Christenson Research Institute. The people of Baitabag graciously allowed me to work on their lands, and my field assistant Batzeba was a valuable companion and excellent natural historian. Discussion with a variety of people has been important in the development of this paper, and I particularly wish to thank M. Baker, E. Jakob, N. Johnson, J. Moya-Laraño, and E. Temeles. Two annonymous reviewers provided helpful comments; one reviewer's recommendations resulted in the analysis presented in Fig. 1, greatly improving the manuscript. C. Pease provided patient support throughout.

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