Sex-linked differences in the growth of *Nephila clavipes*

Fritz Vollrath

Department of Zoology, Universitetsparken B135,
DK 8000 Århus C, Denmark
and
Department of Zoology, South Parks Road,
Oxford OX1 3PS, UK

Summary

Raising *Nephila clavipes* under controlled conditions revealed that males grew significantly more slowly than females. This difference was independent of diet. A comparison with other studies showed that the pattern of growth in *Nephila* spiderlings is comparable to *Tetragnatha* and *Metellina,* although some *Nephila* species may have fewer male instars and more female instars than these genera.

Introduction

Males of the golden silk spider, *Nephila clavipes*, range in body dimensions and weight from 10 to 50% of those of the females (Vollrath, 1983). With very few exceptions, all spiders show some degree of sexual dimorphism, but extreme sexual size dimorphism is confined to a few genera (e.g. *Nephila*, *Argiope*, *Mastophora*, *Tidarren*, *Misumena*, *Abanitis*—see Vollrath, 1998). These genera are distributed over a wide range of families (e.g. Tetragnathidae, Araneidae, Theridiidae, Thomisidae, Atypidae) and we may assume that the trait "extreme sexual dimorphism" is independently derived many times (Coddington *et al*., 1997). Traditionally, this form of dimorphism has been termed male dwarfism (Darwin, 1894; Vollrath, 1998). However, in two recent papers, Coddington, Hormiga and Scharff presented a new cladistic analysis which suggests that, specifically in *Nephila*, the males are not dwarfs but the females giants (Hormiga *et al*., 1995; Coddington *et al*., 1997). These authors seem to imply that there was strong selection for large body size in females and little selection on male size (Coddington *et al*., 1997). Coddington, Hormiga and Scharff are right in assuming strong selection for large female size because this is the rule in spiders (as in most other

invertebrates) where female size typically correlates with fecundity (Vollrath, 1987; Head, 1995). However, several studies have shown that in *Nephila clavipes* there is also the potential for strong selection on male size (Robinson & Robinson, 1973; Christenson & Goist, 1979; Vollrath, 1980; Christenson, *et al*., 1985; Vollrath, 1987; Christenson & Cohn, 1988; Cohn *et al*., 1988; Higgins, 1989; Christenson, 1989, 1990; Cohn, 1990; Vollrath & Parker, 1992; Elgar & Fahey, 1996; Uhl & Vollrath, submitted). Confusingly, many of these studies suggested that, on balance, most selection pressures would favour large size also in males; specified selection pressures where the larger males did on the whole better against their smaller peers were, for example, travel and web tenancy (Vollrath, 1980), male fighting (Robinson & Robinson, 1973; Christenson & Goist, 1979; Vollrath, 1980) and access to females and their reproductive output (Christenson, 1990). However, other selection pressures seem to favour small size in males, for example, mortality during copulation (Elgar & Fahey, 1996; but see Uhl & Vollrath, submitted) and, very strongly, mortality during development (Vollrath, 1985; Vollrath & Parker, 1992).

Fortunately, *Nephila clavipes* has a wide spread of male sizes; this allows us to measure size-dependent fitness by experimentally
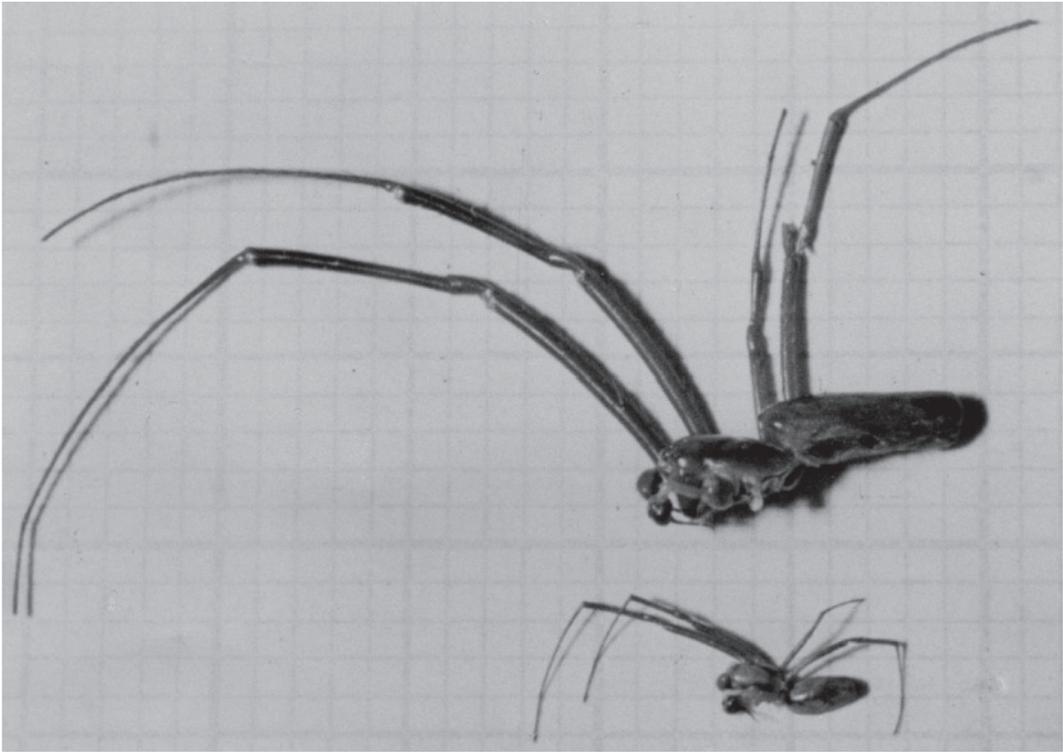
Fig. 1: *Nephila clavipes* brothers from the same egg sac fed either well or poorly during their development.

studying the conflicting selection pressures on males of different sizes both in the field and the laboratory. Note that this is much more difficult in the females, where it is nearly impossible to measure fitness in the field. We can even experimentally address the notion that size has evolved mostly in the females. My examination of the growth pattern in *Nephila* and related genera might help to shed some light on this particular question.

In the life history of an animal with distinct growth by moulting, it is not only the absolute size at maturity and the number of moults that matters, but also the time spent in each instar (the interval between moults or rate of growth) and the growth achieved during each moult (the ratio of growth). Clearly, growth rate and ratio are somewhat interrelated and, together with the animal's decision on the amount of fat reserves either to go into growth or be retained as reserves, determine the pattern of growth. In this study, I examine this pattern for males and females with an eye for any information relevant for the question of sex-dependent selection pressures on enhanced or delayed growth. Thus, coupled with a brief foray into the literature for data on (other) tetragnathids, my ontogenetic study aims to contribute to the question of developmental constraints and, possibly, the evolution of size in spiders.

In *Nephila clavipes*, the males go through fewer moults than females to reach maturity (4 or 5 moults for males, 7 or 8 moults for females). Yet in the field, most males of a cohort mature only a few weeks before most females of the same cohort (Vollrath, 1980). Note that males do not mate with females of a later generation but with females of their own cohort. The slight protandry strongly suggests that the males have a different pattern of growth to the females. To test the hypothesis of sex-based differences of life history strategies, I hatched, from the same cocoon, juveniles of both sexes and raised them, in isolation, on three diets: rich, poor and

mixed. Hormiga *et al*. (1995) have placed the nephilines into the tetragnathids; therefore, I decided to compare *N. clavipes* with some typical metid–tetragnathids. The comparative data were taken from the detailed studies by Juberthie (1955) and Schaefer (1976), who examined growth in a wide range of spiders and over a range of abiotic conditions, some resembling the conditions under which I raised *Nephila* .

Material and methods

Mated females of *Nephila clavipes* were collected in the field in Panama and transferred to the laboratory to obtain eggs which were raised under controlled conditions (27 °C, 70% rH, LD 12:12). The diet varied according to treatment: (1) rich (fruit flies *ad libitum* for the young instars and small crickets for the older instars), (2) poor (1–2 prey every 4 days), or (3) mixed (several days *ad libitum* feeding followed by several days starvation). The young raised on the rich and poor diets were siblings taken from one egg sac, the young raised on the mixed diet were sibs taken from another egg sac. Spiders were kept individually in small PVC cups (20 cl for the young instars) and wooden frames (30 × 30 × 10 cm or 50 × 50 × 25 cm for the larger instars). All were measured after each moult (weighed, and anaesthetised with CO_2 to measure the length of patella–tibia on leg 1 under the microscope). Moults were counted as post-eclosion instars.

Results

Diet had a strong effect, not only on the males (Fig. 1), which ranged from 3 to 8 mm in size (length patella–tibia), but also on the females, which ranged from 9.5 to 17 mm in length. On all diets the males always grew more slowly than females (or, if you wish, the females faster than the males). This basic sex difference in the rates of growth was obvious when studying a range of males and females qualitatively during their full ontogeny (Fig. 2) as well as when examining quantitatively one particular juvenile instar (Table 1).
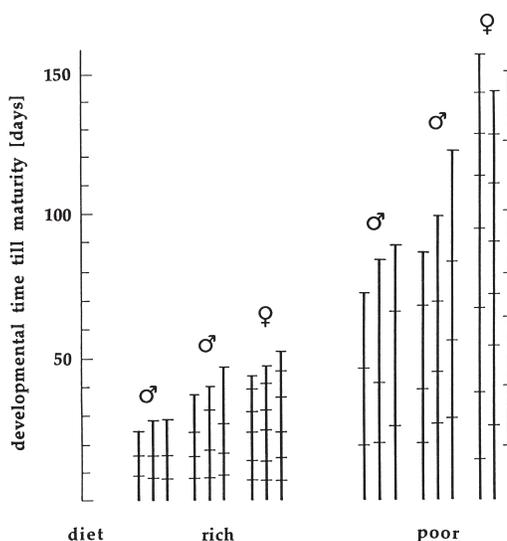

Fig. 2: Growth of *Nephila clavipes* siblings raised under two opposing diets (rich and poor). Shown are the fastest and slowest males and females. Note that males mature in either the fifth or sixth post-eclosion instar whereas the females typically mature in 8 moults except when they are starved in which case they may add an additional instar (Vollrath, 1987). The average developmental time until maturity of the three fastest and three slowest individuals from the second post-eclosion instar (when the animals were taken into the experiment) was for males and females 42.7 ± 5.7 and 51.5 ± 2.1, respectively, on the rich diet; 96.5 ± 26.3 and 143.0 ± 6.0, respectively, on the poor diet.

diet	sex	(*n*)	time	difference
rich	males	(11)	8.0 ± 0.6	15%
	females	(18)	6.8 ± 0.5	
poor	males	(17)	26.7 ± 6.7	22%
	females	(12)	20.9 ± 4.7	
mixed	males	(48)	17.6 ± 5.0	15%
	females	(48)	15.0 ± 3.3	

Table 1: Growth in subadult male and female *Nephila clavipes*. Males took significantly longer than females to complete the (for them) pre-penultimate instar 3 (rich: $P < 0.001$; poor: $P < 0.05$; mixed: $P < 0.05$) yet were of comparable size (length of patella/tibia, mm) and weight (mg) to females (all paired t-tests not significant).
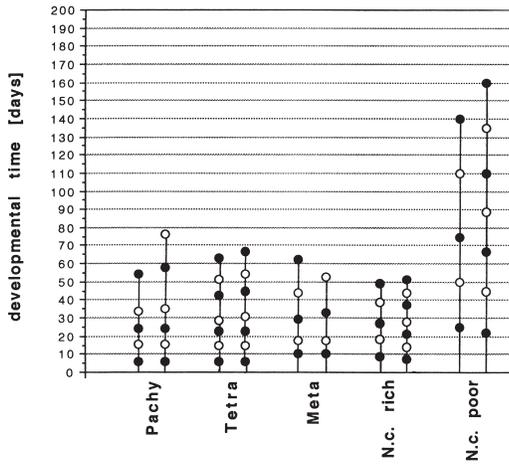
Fig. 3: Pattern of growth in a range of metid--tetragnathid spiders. Shown is the developmental time from the second post-eclosion instar until maturity under controlled conditions. Moults are indicated by circles with alternating moults shown black and white. Note that the first post-eclosion moult is not shown. For each species the left column shows the growth in the males, the right column the growth in the females. My own data on *Nephila clavipes* (N.c.) is given for animals on either a rich or a poor diet. The data on *Pachygnatha clercki* (Pachy), *Tetragnatha montana* (Tetra) and *Metellina segmentata* (Meta) are taken from Schaefer (1976) who raised the animals at 27 °C, 16/8 LD and with ample food.

	3	4	5	6	7	8	9	10	ref
N c			M	M		F	F		V
T m				F	M F	M F			J,S
T n				M F	M F				J
P c			M	M F	F				S
M s		M F	M F	M					S

Fig. 4: Number of moults in tetragnathid spiders. M = males, F = females, N c = *Nephila clavipes*, T m = *Tetragnatha montana*, T n = *Tetragnatha nigrita*, P c = *Pachygnatha clercki*, M s = *Metellina segmentata*. References: Juberthie (1955), Schaefer (1976), Vollrath (1983). The data have been normalized to show the instar that leaves the egg sac; i.e. all have one extra larval instar inside the egg sac.

Discussion

The observed sex difference in growth suggests either that the males had a different foraging behaviour and ate less per day than the females, or that they ingested similar amounts but had a higher metabolism. At present we have no data to support a choice between these possibilities. However, I see no good reason to assume a higher metabolism in immature males; instead, I note that risk-adverse foraging behaviour (which would reduce growth rate) would reduce mortality since foraging activity and predation risks are likely to be correlated. Thus, spiders typically would grow and mature as rapidly as possible in order to reduce predation risks in the immature stage (e.g. Hutchinson *et al.*, 1997). Our *N. clavipes* males, however, provide an example where the rate of growth is clearly not maximized, because immature females manage to grow significantly faster. We may assume that the males hold back on their rate of growth and I can conjure a plausible adaptationist argument to explain why males and females might have different foraging/feeding strategies: the males might grow more slowly in order to match mature at the same time as the females do. There is an additional benefit associated with this strategy: not only is foraging dangerous and each additional day potentially costly, but moulting itself can also be highly dangerous and reducing the number of moults would result in reduced mortality (Hutchinson *et al.*, 1997).

Under controlled conditions, males grew inherently more slowly than females; this explains the observation that, in the field in Panama, mature *N. clavipes* belonging to the same generation overlap, even though the males have fewer instars. In my field site the peak of male maturation preceded female maturation by about 2 weeks (Vollrath, 1980); this slight protandry can be explained by the combination of (1) slower growth per instar in the males which have 5/6 moults after eclosion, and (2) faster growth per instar in the females which have 8/9 moults.

This brings us to the next question: whether, in *N. clavipes* over phylogenetic time, male growth has slowed and instar number decreased or whether female growth has accelerated and instar number increased. Following Hormiga *et al.* (1995) and Coddington *et al.* (1997) I will

assume that *Nephila* belongs to the taxon Tetragnathidae. If we compare data on growth within this family (Fig. 3) we see that *Nephila* females neither grow faster nor males more slowly than other members of this family if fed well. It is surprising that the large *Nephila* females take no longer to mature then the considerably smaller *Metellina* or *Tetragnatha* females. This similarity in growth rates might be taken as support for Coddington, Hormiga and Scharff's argument that *Nephila* females have increased body size during the evolution of this genus.

However, the pattern of growth in *Nephila clavipes* and other metid–tetragnathids does not support such a conclusion unambiguously (Fig. 4). Whereas other metid–tetragnathids have overlapping male and female instar numbers, *N. clavipes* does not; clearly, selection has led to a bimodal pattern of maturation instars in this as in other nephilids but not, as far as we can see, in other metid–tetragnathids (Vollrath & Parker, 1997). Moreover, although *N. clavipes* females can have one instar more than *Tetragnatha montana,* two more than *T. nigrita* and *Pachygnatha clercki* and up to four more than *Metellina segmentata,* the males of this species have 1–2 instars fewer than *T. montana,* up to one fewer than *T. nigrita* and *P. clercki,* and about as many as *M. segmentata.* Obviously, to judge whether males have decreased, or females increased, the number of growth stages, one would have to establish whether the ancestor's pattern of growth was more like that of *T. montana* or that of *M. segmentata.* To me, it seems likely that in *Nephila* both sexes have evolved. The increase in female size and instar numbers is easily explained by the fitness advantage (more eggs) of larger females. It is more difficult to explain the smaller size and instar number in males because of the selection parameters studied, some favour large and some favour small males. In the end it might be most diffiult to explain the wide range of male sizes which in *Nephila clavipes* display a most disconcerting degree of opportunism in their phenotypic expression.

References

CHRISTENSON, T. E. 1989: Sperm depletion in the orb-weaving spider *Nephila clavipes*. *J. Arachnol.* **17**: 115–118.

CHRISTENSON, T. E. 1990: Natural selection and reproduction: a study of the golden orb-weaving spider. *In* D. A. Dewsbury (ed.). *Contemporary issues in comparative psychology.* Sunderland, MA: Sinauer: 149–174.

CHRISTENSON, T. E., BROWN, S. G., WENZL, P. A., HILL, E.M. & GOIST, K. C. 1985: Mating behaviour of the golden orb-weaving spider, *Nephila clavipes* : 1. Female receptivity and male courtship. *J. comp. Psychol.* **99**: 160–166.

CHRISTENSON, T. E. & COHN, J. 1988: Male advantage for egg fertilisation in the golden orb-weaving spider (*Nephila clavipes*). *J. comp. Psychol.* **102**: 312–318.

CHRISTENSON, T. E. & GOIST, K. C. 1979: Costs and benefits of male-male competition in the orb-weaving spider *Nephila clavipes*. *Behav. Ecol. Sociobiol.* **5**: 87–92.

CODDINGTON, J. A., HORMIGA, G. & SCHARFF, N. 1997: Giant female or dwarf male spiders? *Nature, Lond.* **385**: 687–688.

COHN, J. 1990: Is it the size that counts? Palp morphology, sperm storage, and egg hatching frequency in *Nephila clavipes* (Araneae, Araneidea). *J. Arachnol.* **18**: 59–71.

COHN, J., BALDING, F. V. & CHRISTENSON, T. E. 1988: In defence of *Nephila clavipes* postmate guarding by the male golden orb-weaving spider. *J. comp. Psychol.* **102**: 319–325.

DARWIN, C. 1894: *The descent of man and selection in relation to sex.* 2nd ed. London: J. Murray.

ELGAR, M. A. & FAHEY, D. F. 1996: Sexual cannibalism, competition, and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). *Behav. Ecol.* **7**: 195–198.

HEAD, G. 1995: Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (Class Araneae). *Evolution, Lancaster, Pa.* **49**: 776–781.

HIGGINS, L. E. 1989: Effect of insemination on the morphology of the internal female genitalia of the spider *Nephila clavipes* (Araneae: Araneidae). *Ann. ent. Soc. Am.* **82**: 748–753.

HORMIGA, G., EBERHARD, W. G. & CODDINGTON, J. A. 1995: Web-construction behaviour in Australian *Phonognatha* and the phylogeny of nephiline and tetragnathid spiders (Araneae: Tetragnathidae). *Aust*. *J*. *Zool*. **43**: 313–364.

HUTCHINSON, J. M., MCNAMARA, J. M., HOUSTON, A. I. & VOLLRATH, F. 1997: Dyar's rule and the investment principle: the consequences of a size-dependent feeding rate when growth is discontinous. *Phil*. *Trans*. *R*. *Soc*. *Ser. B* **352**: 113–138.

JUBERTHIE, C. 1955: Sur la croissance post-embry-onaire des araneides, croissance lineaire du corps et dysharmonies de croissance des appendices. *Bull*. *Soc*. *hist*. *Nat*. *Toulouse* **90**: 83–102.

ROBINSON, M. H. & ROBINSON, B. 1973: Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithson*. *Contrib*. *Zool*. **149**: 1–76.

SCHAEFER, M. 1976: Experimentelle Untersuchungen zum Jahreszyklus und zur Über-winterung von Spinnen (Araneida). *Zool*. *Jb*. (*Syst*.) **103**: 127–289.

UHL, G. & VOLLRATH, F. Submitted: Sexual cannibalism and extreme male size variability in *Nephila* (Araneae). *Zool*. *Anz*.

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

VOLLRATH, F. 1983: Relative and absolute growth in *Nephila clavipes*. *Verh*. *naturw*. *Ver*. *Hamburg*. *N.F.* **26**: 277–289.

VOLLRATH, F. 1985: Web spider's dilemma: a risky move or site dependent growth. *Oecologia* **68**: 69–94.

VOLLRATH, F. 1987: Growth, foraging and reproductive success. *In* W. Nentwig (ed.). *Ecophysiology of spiders*. Berlin: Springer: 57–370.

VOLLRATH, F. 1998: Dwarf males. *Trends Ecol*. *Evol*. In press.

VOLLRATH, F. & PARKER, G. 1992: Sexual dimorphism and distorted sex ratios in spiders. *Nature, Lond*. **360**: 156–159.

VOLLRATH, F. & PARKER, G. 1997: Giant female or dwarf male spiders? A reply. *Nature, Lond*. **385**: 688.