

Development and survivorship of male *Nephilengys cruentata* (Araneae: Tetragnathidae) in the laboratory

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Summary

The development and survivorship of male *Nephilengys cruentata* was studied in the laboratory. There are three colour phases in the transition from juvenile to adult: penultimate instar, immature adult, which lasts a few days, and mature adult coloration. Juvenile males build orb webs which are used to capture prey, while adults do not build webs, but feed relatively frequently on prey in females' webs. The average time from egg to adult moult was 84.3 days (SE=2.1, $n=48$, range=58–126 days). Mean body length of males was 4.4 mm (SE=0.2, $n=28$, range=3.5–6 mm). Adult male *N. cruentata* lived on average 122.1 days (SE=21.8, $n=13$, range=26–238 days).

Introduction

Nephilengys cruentata (Fabricius, 1775) is one of the largest orb-weavers in the world, and it is one of the three nephiline species that occur in the Neotropics, the other two being *Nephila clavipes* (L.) and *Nephila sexpunctata* Giebel (Levi & Eickstedt, 1989). Despite its high level of synanthropism (Neiman, 1991; see also Robinson & Robinson, 1980) little is known of its biology, and most of the available data refer to females (Bauab-Vianna, 1970; Robinson & Robinson, 1980; Edmunds & Edmunds, 1983; Ades, 1984; Ades *et al.*, 1986, 1990; Japyassú *et al.*, 1988; Japyassú & Ades, 1990, 1992; Ades & Lederman, 1994; Santos-Filho, 1994; Valva & Santos-Filho, 1996; Cunha & Santos-Filho, 1996), but see Bauab-Vianna (1970), Robinson & Robinson (1978, 1980) and Levi & Eickstedt (1989) on males.

Bauab-Vianna (1970) studied the development of both sexes from hatching to adulthood, and reported that males undergo 5–6 moults while females undergo 8–9; thus males are protandric and take 110 days from egg to adult while females take 210 days.

Robinson & Robinson (1980) studied the mating behaviour of two species of the genus *Nephilengys*, *N. malabarensis* (Walckenaer) and *N. cruentata*. They described the approach of the *N. malabarensis* male to the female, but stated that they never saw the details of copulation either in *N. malabarensis* or in *N. cruentata*. They observed male–male interactions (fights and chases) in *N. cruentata* and stated that the male approaches the female in her retreat and moves about juddering.

Robinson & Robinson (1978) devised a functional classification of the mating behaviour of araneid spiders, including *N. cruentata* in their group A, which comprises

spiders in which courtship occurs entirely at the hub of the web. Furthermore, they stated that *Nephilengys* males lose (or remove) the major part of their pedipalps during or after copulation, and that they live in a sterile state on the web of the female, where they fight with other (fertile) males and may drive these off, and that eunuchs could be protecting their parental investment. Levi & Eickstedt (1989) also found eunuchs in collections from Brazil.

Sexual dimorphism in spiders has received much attention recently, and the scarcity of data on male spiders for comparative purposes has been pointed out (Elgar, 1991; Vollrath & Parker, 1992; Andersson, 1994; Head, 1995; Coddington *et al.*, 1997). In this paper I examine the development and survivorship of *Nephilengys cruentata* males in captivity as part of an ongoing project on the life history of this species (Santos-Filho, 1994; Valva & Santos-Filho, 1996; Cunha & Santos-Filho, 1996).

Material and methods

The development of *N. cruentata* was studied as the time taken from egg hatching until the final moult. No attempt was made to count the number of moults. Two clutches of eggs (groups 1 and 2), collected from a population established in 1992 (Santos-Filho, 1994), and laid on 4 and 27 September 1995 respectively, were held by scotch tape to the ceiling of two small glass aquaria, with volumes of 6 l and 16.7 l respectively, which were turned upside down, with their open end on a table. A ball of moist cotton wool was kept inside the aquaria, which were aerated by periodically lifting them from the table and allowing the air to be renewed. As hatching extends over a few days, the date of hatching was established as the first day that hatchlings could be observed within the nest, an envelope of loose silk which surrounds the clutch. The onset of hatching was recognised as when the eggs became detached from each other, the fine talcum-like powder that cements the eggs together fell down, and the appearance of the clutch was of a loose aggregate of eggs, hatchlings and empty white egg-shells. The spiderlings of each clutch were raised together in each of the aquaria (mass-rearing), and drosophilids were added as food, almost daily. Once they moulted into adults the date of moult was recorded. Body length (prosoma+opisthosoma) was measured to the nearest 0.5 mm and the number of legs recorded, for a sub-sample of 28 males, pooled from both clutches. Measurements were made with males inside thin glass vials stoppered with cotton wool and held against a ruler under 20 × magnification.

The survivorship of another group of 13 adult males with known date of adult moult was followed after their emergence as adults until their deaths. Males were kept singly in small plastic boxes (0.7 l; $n=10$) and in glass aquaria (6 l, 16.7 l; $n=3$), with ($n=3$) or without ($n=10$) females present. These males comprised 10 virgins, and 3 males which had copulated and lost their palpal organs. Six males were not marked, and 7 males were marked with water-based ink pens, while 4 males had 7 legs and

9 males had 8 legs. Within each enclosure a moist cotton wool ball was kept and frequently moistened; enclosures were frequently aerated, and non-eaten food removed. Males were offered live and freshly killed drosophilids almost daily, and occasionally, newly hatched *N. cruentata* spiderlings, as food.

Male coloration was described from direct observations of live individuals, and complemented by macrophotography of juvenile and adult males. Observations of free-living males in the population provided additional data on feeding by males and male size range; the search for, and description of, sperm webs was made with a hand-held 20 × magnifier. Statistical analyses followed Sokal & Rohlf (1981). Non-parametric Mann-Whitney and Kruskal-Wallis tests were employed; *t*-tests were also used, when only summary statistics in the literature were available. Multiple factor ANOVA could not be used to test for the effects of variables on survivorship because sample sizes were small.

Results

Transition juvenile-adult

Immature males can already be distinguished by their 4th moult (Bauab-Vianna, 1970), and at the last instar before the adult moult they are light grey in general appearance. These immature males have the cephalothorax and abdomen mottled in white, brown and black; the legs, which are translucent, have light brown and black transverse bands; their pedipalps are also translucent, but the tips of the palpal organs are already dark brown, though morphologically different from the adult's. Their eyes are black and there are two black stripes which run from near the eyes, obliquely, to the posterior region of the prosoma. During the juvenile phase males build regular orb webs, but as they approach the last moult some may build refuges and thus develop a semi-orbicular web. A few days before the final moult males stop mending and rebuilding their webs. Immediately after their final moult males have a light beige cephalothorax and light brown abdomen, and their pedipalps are dark brown. A few days (2–3) after moulting the cephalothorax acquires a honey brown colour and the abdomen turns a darker reddish brown, while the pedipalps turn to a very dark brown, and the legs become black distally, from the patella onwards, except for legs IV, in which the black extends to the femur. On the anterior portion of the dorsum of the opisthosoma males show patterns of melanic dots and blotches, which vary individually and can be used for individual recognition. Adult males did not build regular orb webs, but instead they built a tangle of threads within the boxes, on which both dead and live drosophilids became entangled relatively easily. Males fed as adults relatively frequently and were able to subdue live prey, such as drosophilids, spiderlings, and even juvenile and adult *N. cruentata* males. Adult males maintain the ability to produce silk in relatively large quantities, as judged by the dense tangle of threads they produce inside boxes. When living on female webs a

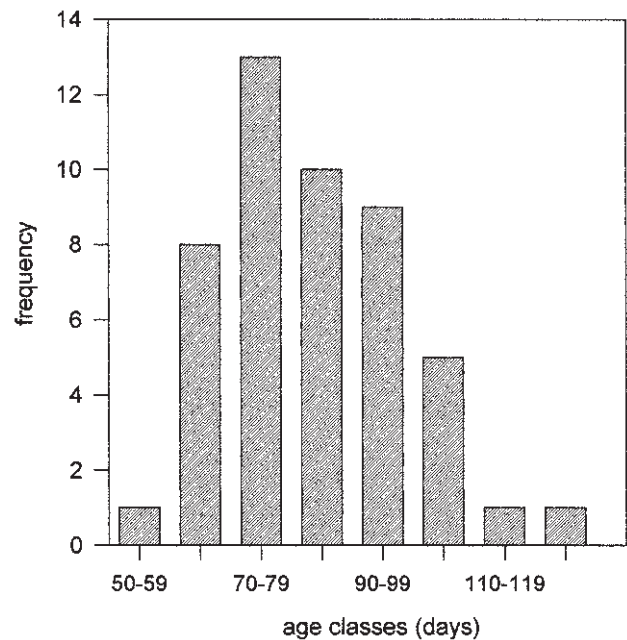


Fig. 1: Frequency distribution of the age at adult moult in male *Nephilengys cruentata*.

common behaviour pattern observed in males is their frequent silk deposition, in which they lower the tip of the abdomen, touch the spinnerets on the substrate and thus lay silk while they walk over and inside the female's refuge.

Sperm induction was not observed, but sperm webs were found in webs of males that had recently moulted into adults, but only after acquiring adult coloration. The sperm webs were built near the hub of the male's juvenile orbicular web, which remains occupied for a few days after moulting; they were made between two adjacent radii, and the direction of the silk threads laid between them was parallel to the adhesive threads; the number of sperm webs found per web was up to 8 or 9. Some of the sperm webs were regular in shape, roughly rectangular, while others were more irregular. No webs similar to these were found in the webs of immature males. Sperm webs were not found in female webs, but as the latter are large and complex, with silk barriers and the silk refuge, they could easily have been missed.

Development

In group 1, in the smaller cage, a total of 19 males moulted into adults, the fastest taking 66 days and the slowest 110. On average the development from hatching to adult took 84.9 days (SE=2.7). A total of 29 males moulted to adults in group 2, range 58–126 days, mean 83.9 days (SE=3.1). There was no significant difference in time to adult moult between the two groups ($z = -0.49$, $p = 0.63$, $n = 48$), which were therefore pooled in the following analyses. The age at adult moult (Fig. 1) was normally distributed (Shapiro-Wilks statistic=0.96, $df = 48$, $p = 0.31$). The pooled mean age at adult moult was 84.3 days (SE=2.1, $n = 48$). The number of males that moulted per day ranged from 1 to 3 (mean=1.7, SE=0.1, $n = 48$).

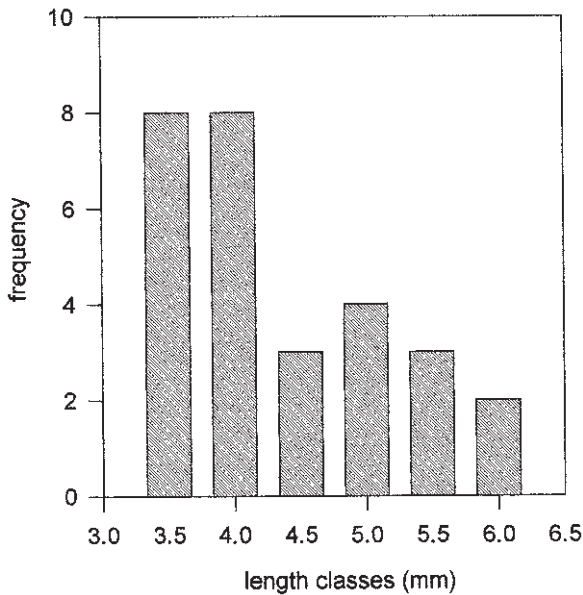


Fig. 2: Frequency distribution of body length in adult male *Nephilengys cruentata*.

Body length in the two groups was: group 1: mean=4.3 mm, SE=0.3, range=3.5–5.0 mm, $n=7$; group 2: mean=4.4 mm, SE=0.2, range=3.5–6.0 mm, $n=21$. There was no significant difference in body length between the two groups ($z = -0.16$, $p=0.87$, $n=28$); the pooled mean body length was 4.4 mm (SE=0.2, $n=28$), and the distribution of body lengths deviated significantly from normality (Shapiro–Wilks=0.87, $p<0.01$). The distribution showed a positive skewness (0.66), indicating that small males were relatively more common (Fig. 2). No correlation between body length and age at moult was found ($r = -0.014$, $p=0.94$, $n=28$).

Survivorship

On average adult males lived 122.1 days (SE=21.8, $n=13$), but lifespan ranged from 26 to 238 days. The survivorship curve was approximately linear, suggesting that males suffered an approximately constant mortality rate, except at the end of the curve where there was an abrupt change beyond 220 days (Fig. 3). The type of enclosure the males spent their lives in had no effect on lifespan ($\chi^2=1.36$, $p=0.71$, $df=3$), and no effect of marking was found ($z = -1.00$, $p=0.32$, $n=13$). The presence of a female also did not affect survivorship ($z = -0.62$, $p=0.54$, $n=13$). The loss of the palpal organ(s) due to autotomy did not significantly affect adult lifespan ($z = -1.57$, $p=0.12$, $n=13$), though males without palpal organs tended to live longer. Finally, the number of legs also did not affect survival ($z = -0.51$, $p=0.61$, $n=13$).

Discussion

Juvenile *N. cruentata* males are efficient sit-and-wait predators in their orbicular webs, as is the case with *Nephila clavipes* males (Myers & Christenson, 1988), and their predatory behaviour does not differ substantially from that of juvenile females (pers. obs.). The absence of

web renewal near moults has also been noted for *N. clavipes* males (Myers & Christenson, 1988). The ontogenic change in coloration is useful in obtaining newly moulted adults for field studies.

The semi-orbicular webs built by juvenile males in small plastic boxes could be the result of the limited space available, but more likely represent normal ontogenic variation, as females also usually change from building orbicular webs to semi-orbicular webs as they develop (Japyassú, 1993). Even though the tangles of threads made by adult males can function as relatively good traps for flying insects in small plastic boxes, nearly all prey captured by free-living males were seized in the capture region of the female's web, though one adult male captured a juvenile conspecific male away from any web (pers. obs.). Thus, although the statement that adult orb-weaver spider males do not feed is common (e.g. Bristowe, 1958; Savory, 1977), many in fact do so (Eberhard *et al.*, 1978; Cohn & Christenson, 1988; Suter, 1985; this study).

The average time to adult moult in male *N. cruentata* was much shorter than that reported by Bauab-Vianna (1970). Unfortunately she did not mention the measure of central tendency used, nor the sample size, so more direct comparisons are precluded. As development in spiders is generally very sensitive to the amount of food (Vollrath, 1980), the shorter developmental time found here could be due to the abundant food offered. Nonetheless, the observed developmental time in *N. cruentata* may be regarded as long when compared with *Nephila clavipes* under a rich diet (33.3 ± 7.2 days, $n=11$), but similar to this species when offered a poor diet (82.0 ± 17.2 days, $n=12$; Vollrath & Parker, 1992), though differences in mean temperature between the localities cannot be ruled out. The fastest males in the present study developed in half the time required by the slowest, and the relatively large variance in

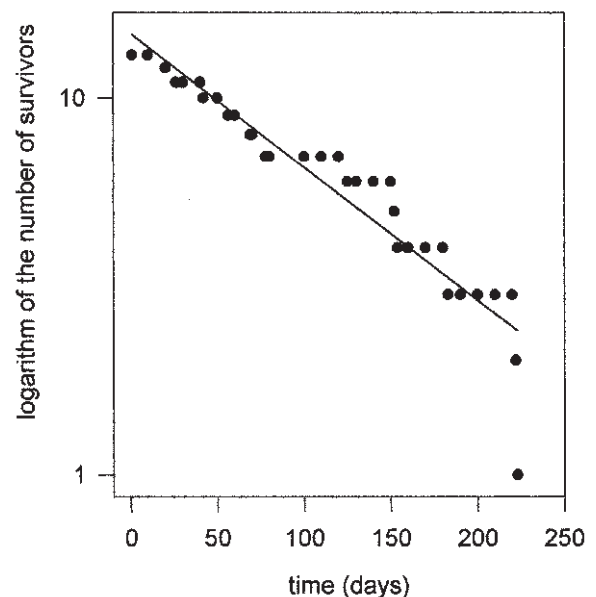


Fig. 3: Survivorship curve of male *Nephilengys cruentata* in captivity. The equation fitted to the data is: $\log \text{survivors} = 1.17135$ (SE=0.02995) $- 0.00355$ (0.00023) days; $n=33$, $p<0.00005$, $r^2=0.89$.

developmental time could have implications for mating opportunities. Females of *N. cruentata* in São Paulo populations lay clutches almost all year round, and as females may survive up to two years after the adult moult, generations overlap (pers. obs.); thus populations are age-structured, and there is an almost continuous, though low, input of newly moulted adult females into the populations, which thus comprise adult females of various ages and reproductive histories. It may therefore be advantageous for males to spread out their time of entry into the population (Parker, 1985). Alternatively, the observed variance in development could simply be the result of unidentified factors, each with a small influence, as suggested by the normal distribution of times to adult moult.

Elgar (1991) reported that the mean male length for seven species of the subfamily Nephilinae in the genera *Herennia*, *Nephila* and *Nephilengys* ranged from 3.0 to 6.0 mm. The mean length of *N. cruentata* males was slightly less than that reported for *N. malabarensis* (4.8 mm), and the mean size of *N. cruentata* did not differ ($z = -1.1$, $p = 0.27$, $n = 8$) from the mean size of all seven species (4.7 mm, $SD = 0.90$, $n = 7$). Therefore *N. cruentata* males (4.4 mm) are not inordinately large or small, though intraspecific variation is high, as the range of *N. cruentata* male sizes found in nature, from 3 to 6 mm, spanned the reported interspecific variation in mean length; the deviation from normality of the distribution of male sizes is possibly a result of the frequencies of males with 5 and 6 moults, but this deserves further investigation.

The absence of any relationship between body size and age at adult moult was unexpected, as it is common in several arthropods, and generally the earlier adults are either particularly small or large, but in the sheet-weaver spider *Pityohyphantes phrygianus* (C. L. Koch) males are larger than females, in spite of emerging earlier in the season (Gunnarsson & Johnsson, 1990). No seasonal variation in mean male size, as reported by Vollrath (1980) for *Nephila clavipes*, could be shown, because of the short interval during which the clutches were laid from which the males originated.

The lifespan of adult males was extremely variable, the oldest male living almost ten times as long as the shortest lived one. As a senescent type of survivorship curve would have been expected in the absence of predators, parasites, adverse biotic factors and abundant food, the approximately constant mortality rate found indicated that captive conditions were not optimal; the most probable factor that could have caused such a result is low relative humidity, as males are extremely sensitive to desiccation, and although the cotton wool balls were kept damp, they may have been less damp than necessary. Alternatively, as Cohn & Christenson (1988) found that feeding increased male longevity in *Nephila clavipes*, it could be that the diet of *N. cruentata* males was not entirely appropriate. The abrupt change of the survivorship curve shape at its end strongly suggests that there is a maximum lifespan, around seven months, which was reached by a few males. Cohn & Christenson (1988) studied the survivor-

ship of male *N. clavipes* after adult emergence in large screened boxes, under different feeding regimes, and found extremes of an average of 21.6 days ($SD = 7.2$, $n = 6$) for non-fed males to an average of 68.8 days ($SD = 12.7$, $n = 4$) for males kept with females. The mean longevities of *N. clavipes* males kept with females and *N. cruentata* males did not differ ($t = 1.32$, $p > 0.2$, $df = 15$). However, Christenson *et al.* (1987) mention eight control males, also maintained in large screened boxes in one irradiation experiment, that lived on average 52.6 days ($SD = 13.6$), and this mean longevity differed significantly from that of male *N. cruentata* ($t = 2.45$, $p < 0.05$, $df = 19$). As it is not possible to combine their data for the different food regimes a more thorough comparison of mean longevities could not be made but, again, temperature and humidity differences between localities could have affected mean longevities; also, no maximum longevities were mentioned by them. Cohn & Christenson (1988) also reported that cohabitation with females increased the longevity of males, possibly due to their feeding on prey captured by females. Unfortunately, the small sample size of males followed throughout their lives made the absence of any effects of the presence or absence of females, marking, loss of palpal organs, and the number of legs on survivorship only suggestive.

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