On the biology and behaviour of *Nephila* senegalensis senegalensis (Walckenaer, 1837)

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Summary

An adult female and 4 egg-sacs of *Nephila senegalensis* senegalensis (Walckenaer) were received from Gambia, West Africa. Notes were made on the biology and behaviour of this female, and of the individuals which emerged from the eggs.

The species appears to have a generation length of one year. A female is capable of producing at least 4 egg-sacs per season, corresponding to about 4500 eggs. The spiderlings apparently moult once before emerging from the egg-sac, and begin to disperse and construct their first orb-web in the third instar.

Connected to the orb-web is a ventral barrier web. The adult male will accept food, but constructs no orb-web. Courting and mating behaviour was observed. Net-strumming does not occur, and opportunistic mating is not the rule. As the male is smaller than the smallest prey accepted by the female, these observations fit the hypothesis that net-strumming simulates the vibrations of prey. The male has a copulatory posture not known in any other *Nephila* species. Egg-laying and production of the egg-sac is described. The male is figured.

Introduction

In December 1975 Henrik M. Skou brought me an adult female *Nephila senegalensis senegalensis* (Walckenaer, 1841) (designated female-1) collected a few days earlier near Banjul, Gambia, West Africa, and in April 1976 he brought four egg-sacs from the same area. From these about 760 spiderlings emerged, of which a female (female-2) and a male reached maturity and mated. Female-2 laid eggs, of which a number hatched, and four individuals reached maturity.

Drawings were made of the male, and notes were made on age and generation, fecundity, spiderlings, web, mating and egg-laying.

Materials and methods

Female-1 was kept in a glass jar with an inner side length of 19.5 cm. The spiderlings from the egg-sacs of April 1976 were kept in a similar jar, and 21 were separated individually in glass jam-jars of varying sizes, closed with gauze. Female-2 and the male of the first brood were, when mature, transferred to a cage ($50 \times 25 \times 45$ cm) with glass on the front and nylon netting on the other sides, and a 19.5 cm glass jar respectively. The second brood was kept in the cage just mentioned, in which it was laid, and in insect boxes ($24.5 \times 24.5 \times 4.5$ cm), with part of the sides replaced by gauze.

All of the spiders were kept at my home in Copenhagen, and for the first 2-3 months they were sprayed with tepid water every morning and evening. The temperature was generally around 20°C, and in winter the relative humidity was usually about 40%, while in summer it fluctuated around 60%. During

June, July and August in both 1976 and 1977 the spiders were not studied.

The spiders were fed with *Drosophila melanogaster* Meigen, various insects collected in the field, *Calliphora vicina* Robineau-Desvoidy, and the desert locust *Schistocerca gregaria* Forskål.

Results

Descriptions

The female of N. s. senegalensis has been described by Walckenaer (1841), and by several later authors. The male of N. s. senegalensis has been described by Simon (1885), Berland (1936) and Villiers (1946).

I give here the lengths and weights of the two sexes for the sake of a better understanding of the interactions between them; and as there are few previous illustrations of the male, drawings of the palp and abdomen are included.

Female

Total lengths: 32, 26 and 16 mm. Wet-weights (alcohol): 1619, 1140 and 220 mg. The female of 16 mm was very poorly nourished, and certainly atypical. The mean length of the two larger females is 29 mm, while the mean weight is 1380 mg.

Male (Fig. 1)

Total lengths: 4.5, 4.5 and 4.7 mm (mean 4.6 mm). Wet-weights: 5.5, 6.6 and 6.4 mg (mean 6.2 mg). Legs I and II are relatively much longer in the male than in the female.



Fig. 1: Male N. s. senegalensis. A Left palp, prolateral view; B Left palp, retrolateral view; C Abdomen, dorsal view. Scale lines = 1 mm.



Fig. 2: Web of newly emerged, isolated juvenile. Scale line = 1 cm.

When fresh, the palpal organs (Fig. 1a, b) were so darkly pigmented that details could not be seen. The drawings were made after two years in 70% alcohol.

Age and generation

The mean age of the females at death was 317 days after emergence from the egg-sac (range: 300-351 days), and the mean age of the males was 217 days (range: 200-250 days). Female-2 became adult at day 190, and one male at day 180. The first egg-sac was laid 38 days after female-2's final moult, and the first juvenile emerged 19 days later. 144 days after the final moult of female-2 a much larger number of juveniles emerged from egg-sac number 2, and after 254 days a second-instar juvenile was seen.

Number of egg-sacs

Female-1 laid one egg-sac. The four egg-sacs brought to me were in a lump, and probably were produced by the same individual. Female-2 produced four egg-sacs with a mean interval of 20 days (range: 19-22 days).

Number of eggs per egg-sac, and emerged spiderlings

The numbers of eggs in the egg-sacs laid by female-2 were 1553, 1499, 773 and 671 (mean 1124). The four egg-sacs brought to me produced a total of 760 spiderlings (the mean of three estimates: 650, 690 and 940).

Early instars

Numerous empty sloughs were observed inside the egg-sacs. The first instar outside the egg-sac (i.e. 2nd instar) has the abdomen filled with yolk, and does not feed or produce an orb-web. They do make a web though, consisting of diffuse threads spun communally across the cage. Isolated juveniles spin a similar, but smaller web (Fig. 2). In the daytime they are rather active, generally occupied by extending the web, and at dusk they gather into large aggregations, which seem to correspond to each egg-sac. Second instar spiderlings would readily drink from droplets of water on the threads.

On several occasions a peculiar behaviour was observed. The spiderlings would suddenly shake the web in concert, so that the whole structure vibrated violently. It looked like the reaction seen in many webbuilding spiders when they are disturbed, but in this case a disturbing factor was not perceived.

The first moult outside the egg-sac was seen 11 days after the emergence of the spiderlings, and most spiderlings moulted 17 days after emergence.

Third instar spiderlings no longer aggregate in the evening, but spread throughout the cage and are more active. At this stage they produce their first orb-web. Isolated specimens made their first orb-webs 1-4 days after the moult, while the first orb-web seen in the cage with the bulk of the spiderlings was seen 18 days after the first exuviae were observed.

One of the 3rd instar spiderlings was seen eating its coiled-up web. This behaviour was also observed in female-1, where the whole process was seen from the coiling-up of the web, until it had disappeared into the mouth of the spider, and prolonged observation did not reveal any spitting out of remains.

The 3rd instar spiderlings were rather cannibalistic, their victims usually being their 2nd instar siblings.

Orb web

The web of the adult female in its natural environment had a diameter of 1-1.5 m (H. M. Skou, pers. comm.). The web is an asymmetric orb-web with few adhesive threads above the hub, and placed at an angle to the vertical of about 40° . The adhesive threads are yellowish. Above and on the side of the web facing upwards there was a barrier web.

None of the adult males was seen to produce an orbweb, but they ate *Drosophila* that came within reach. One male was seen touching remains of prey in the web of the female.

Mating

The moment the male entered the cage of female-2 he started moving legs I and the pedipalps up and down, nearly vibrating them, while climbing up the female's web. Within a few minutes he reached the female whose abdomen he touched posteriorly, and then withdrew. He then moved around in the web above her, jerking, and about ten minutes after his introduction into the cage, he mounted up the ventral side of her abdomen to the epigynal area, vibrating his front legs, and started tapping her epigyne with the pedipalps. A few seconds later he inserted one of his palps. This is the usual way of introducing mating, and was observed on several later occasions. Only one palp is inserted at each mating, while the other is raised. I



Fig. 3: Copulatory posture of the male. Scale line = 5 mm.



Fig. 4: Egg-sac production. A The silken basket wherein the eggs are laid; **B** The female on the egg-sac. Scale lines = 1 cm(A), 2 cm(B).

have, however, on one occasion seen the male introducing palps alternately in rather rapid succession, while the female was busy biting a prey. During mating the male palp can be seen to swell and collapse every c. 3 seconds, and his two pairs of front legs touch legs I and II of the female, and sometimes also her chelicerae. At intervals he also taps them. While copulating the abdomen of the male is turned to the side corresponding to the palp in use (Fig. 3).

The mean mating period was 8 ± 1.6 min. (S.E., n = 7). Often mating was terminated by the female getting restless, and the male would slide down his dragline or, less often, rush up on the dorsal side of her abdomen, and from there quietly climb onto the web above her. At times they mated at intervals of about one hour. During the intervals he usually occupied a position in the web just above her, often between her two hind legs, where he sat grooming himself. Prior to mounting is often a period of moving around with characteristic jerks, or rhythmical swaying, and vibrating the anterior legs and the pedipalps. Now and then he reaches out a leg to touch the apex of the female's abdomen, after which he passes the leg through his chelicerae. Often he also moves around the barrier web.

During the two days the male spent with the female, they were seen mating 11 times.

Nothing has been seen that could be interpreted as sperm induction.

Egg-laying

The whole process of egg-laying and egg-sac construction was observed on one occasion (female-2). First the spider produced a slightly inclined silken sheet in a top corner of the cage. On the underside of this she built a basket of white silk, wherein the eggs were laid (Fig. 4A). The basket was then closed, and this inner part was then covered with a thick layer of white silk forming a somewhat elongated egg-sac (Fig. 4B). The basket was made by fastening threads while turning in a circle. She would pull out threads with legs IV, alternately, so far out that the threads when fastened formed loops, which gave the egg-sac a fluffy appearance. She constantly touched the edge of the basket with the palps, so the diameter of the basket corresponded to the distance from the palps to the spinnerets when her body was bent, i.e. c. 15 mm. The production of the basket started at 01.00, and was finished at 05.30. At 06.55 egg-laying began, and terminated at 07.10. For a while afterwards there was a white droplet in the genital aperture. She immediately started to cover the mass of eggs with the same kind of looped silk as previously. At 09.20 she started fastening threads at the base of the egg-sac, and now she also rested at intervals. At 10.00 the construction was so large, that she could sit upon it, and at this point she was also fastening threads some distance from the egg-sac. At 10.40 the spider finished her work, and returned to the orb-web to remove foreign bodies from it.

Discussion and Conclusions

Generation

Most spiderlings emerged about one year after the emergence of their mother (190 + 144 = 334 days). Taking into consideration that the offspring, either as eggs or unemerged spiderlings, are capable of surviving for a prolonged period (at least 153 days) it seems reasonable to assume that the species in Gambia has a life cycle of one year, the spiderlings emerging at the beginning of the rainy season, during which they grow to the adult stage. The eggs, or 1st instar spiderlings, then survive the harsher period of the dry season. This conclusion is in accordance with the observations of Villiers (1946) on *N. s. senegalensis*, and de Jager (1960) on *N. s. annulata* Thorell (misidentified as *N. clavipes*).

Eggs

It can be concluded that a female is capable of producing at least 4 egg-sacs in its life-time, corresponding to about 4500 eggs or about 1100 eggs per egg-sac.

Early instars

The relatively low number of spiderlings which emerged is probably the result of too low relative humidity. Austin & Anderson (1978) observed an optimal r.h. for the hatching of N. edulis eggs of 75%.

When compared with the observations on morphology and behaviour of the first stages in *Nephila edulis*, *N. maculata* and *N. senegalensis annulata* (Austin & Anderson, 1978; de Jager, 1960; Robinson & Robinson, 1973, 1976) it seems clear that the emerging stage corresponds to the second instar after hatching.

It seems that preventing 3rd instar spiderlings from dispersing inhibits their orb-web building behaviour. Dispersal and orb-web building behaviour thus seem to be positively and negatively correlated with density, respectively, leading to reduced intraspecific competition.

Web

It appears that the barrier web corresponds to the structure which Robinson & Robinson (1973) call "the

ventral barrier web".

Probably the male lives on small insects caught in the female's web, and possibly on some of the female's prey. This is in accordance with observations on *N. maculata* (Robinson & Robinson, 1976), and may be usual for *Nephila* spp.

Mating

The male changed behaviour immediately when he came into contact with the female's web. Probably the new behaviour was triggered by pheromones on the threads of the web. This phenomenon has also been reported for *N. maculata* (Robinson & Robinson, 1973, 1976). Also, the observation of the male touching the female and then drawing his tarsi through his chelicerae strengthens the hypothesis of the male receiving chemotactic stimuli.

Net strumming as reported for N. edulis and N. madagascariensis (Austin & Anderson, 1978; Robinson & Robinson, 1973), was not observed. This strengthens the hypothesis that net strumming simulates the vibration of prey, as the female was never seen to make any attempt to catch the male. Also, the female would not accept prey smaller than Calliphora vicina whose live-weight was well above the wet-weight (alcohol) of the males (C. vicina: $34 \pm 1.1 \text{ mg}$ (S.E., n = 20; N. s. senegalensis males: 6.2 mg (range 5.5-6.4 mg, n = 3). [The difference between live-weight and alcohol-weight in spiders is too small to influence the above conclusion (Clausen, 1983).] In N. edulis and N. madagascariensis, where the female is often aggressive towards the male, the males are relatively larger, and net strumming, opportunistic mating, slow advance to female, and moving to the other side of the female's web are the rule, while the opposite seems to be true for N. senegalensis and N. maculata in which the female usually is not aggressive toward the male.

The copulatory posture of N. s. senegalensis (Fig. 3) lies between that of N. pilipes and the other Nephila species (Robinson & Robinson, 1980). Maybe the turning of the abdomen is related to the increase in pressure necessary for the function of the palp during copulation.

Egg-laying

The general pattern of egg-laying and production of the egg-sac observed here is in accordance with the observations of Villiers (1946) on N. s. senegalensis, and corresponds quite well to what is seen in N. madagascariensis (Bonnet, 1930). There are, though, certain differences between N. s. senegalensis and N. madagascariensis. In the latter the egg-sac usually is produced on a vertical silk carpet, which 2

results in a much more elongated shape, because the egg-mass is drawn downwards by gravity, and the female cannot support it so well with her abdomen. This might explain why *N. madagascariensis* does not make the base sheet in the shape of a basket. Bonnet (1930), however, saw a few *N. madagascariensis* egg-sacs produced on horizontal carpets, and one might speculate that the latter position is the most original, as it has been observed in other Araneidae (Bonnet, 1930; Nielsen, 1932). Another difference appears to be the way in which the threads are drawn from the spinnerets and fastened. *N. s. senegalensis* fastened the threads each time they were drawn out by legs IV, while *N. madagascariensis* apparently drew threads from the spinnerets 4-5 times before fastening (Bonnet, 1930).

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References

- AUSTIN, A. D. & ANDERSON, D. T. 1978: Reproduction and development of the spider *Nephila edulis* (Koch) (Araneidae: Araneae). *Aust.J. Zool.* **26**: 501-518.
- BERLAND, L. 1936: Mission de M. A. Chevalier aux îles du Cap Vert. 1. Araignées. *Revue fr. Ent.* **3**(1): 67-88.
- BONNET, P. 1930: Les araignées exotique en Europe. II. Bull.Soc. zool.Fr. 55: 53-77.
- CLAUSEN, I. H. S. 1983: Weight-length relations of eight species of spiders (Araneae) from Denmark. *Ent. Meddr.* 50: 139-144.
- JAGER, S. de 1960: Nephila, a highly intelligent spider. Afr.wild Life 14: 205-208.
- NIELSEN, E. 1932: The biology of spiders. Copenhagen, Levin & Munksgaard.
- 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.
- ROBINSON, M. H. & ROBINSON, B. 1976: Ecology and behavior of Nephila maculata: A supplement. Smithson. Contrib. Zool. 218: 1-22.
- ROBINSON, M. H. & ROBINSON, B. 1980: Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pac.Insects Monogr.* 36: 1-218.
- SIMON, E. 1885: Etudes arachnologiques. 18e mém. XXVI. Matériaux pour servir à la faune des arachnides du Sénégal. Annls Soc.ent.Fr. 5: 345-396.
- VILLIERS, A. 1946: Observations preliminaires sur Nephila senegalensis. Notes afr. 30: 1-3.
- WALCKENAER, C. A. 1841: Histoire naturelle des insectes. Aptères 2: 1-548. Paris.