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Post-embryonic development of the sub-social spider *Anelosimus* cf. *studiosus* (Araneae, Theridiidae)

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Summary

Post-embryonic development has been studied exclusively in solitary spiders. Sociality could minimise development inside the egg-sac, because premature spiderlings would be cared for cooperatively. Here, we describe the post-embryonic development of a Uruguayan sub-social spider, *Anelosimus* cf. *studiosus*. Fifteen egg-sacs were removed from their mothers, opened and the eggs raised in humid chambers. Nine females with their egg-sacs were kept as controls. Three consecutive instars were observed: prelarva, larva and nymph. Prelarvae were detected on average 16.58 days after oviposition, and moulted to larvae 1.38 days later. The larval period lasted 2.85 days before moulting to the first nymphal instar, giving a total of 20.73 days on average after oviposition. Spiderling emergence from the egg-sac in the control group took 20.77 days. The results suggest that the mother opens the egg-sac immediately when she perceives nymphal movements. No reduction in the number or duration of instars was observed compared with solitary theridiid spiders, but it is suggested that this might occur in other more social theridiid spiders.

Introduction

Post-embryonic developmental instars inside the egg-sac are very variable in arachnids (Hammen, 1978; André & Jocqué, 1986; Canard & Stockman, 1993), including spiders (Foelix, 1996). Diverse non-motile, low motile and motile instars have been named using different terms, generating many attempts to standardise their terminology (Vachon, 1957; Galiano, 1967; Valerio, 1974; González, 1979; Emerit, 1984; Downes, 1987). However, the old terms used by Vachon (1957) have been followed by many authors, being considered clear and unequivocal, and are also used here. This author followed the terms used for insects, as larva or nymph, but referring to very different forms. The motionless form which can be seen through the chorion was called the prelarva, showing incomplete leg segmentation (Fig. 1), barely differentiated spinnerets and undeveloped reproductive organs. The prelarva tears the chorion using its palpal "egg teeth" and immediately moults, changing into the larval instar. The larva has little mobility but complete leg segmentation (Fig. 2), the cheliceral fangs are differentiated but lack the poison channel, the spinnerets are differentiated but lack spigots, and the reproductive organs are undeveloped. Finally, the larva moults into the nymph which is a complete juvenile form (Fig. 3), with cheliceral fangs with poison channel, functional spinnerets, and developed but non-functional reproductive organs. Nymphs emerge from the egg-sac and live independently, moult several times, reaching adulthood when they develop functional reproductive organs. However, other intermediate forms have been described in some spider species, such as prelarva II, larva I, larva II, prenymph, etc. The emerged nymphs are usually described as juveniles, young or spiderlings, as proposed by Bonnet (1981).

Social spiders live in communal nests and their members cooperate in nest construction and maintenance, and prey capture (Avilés *et al*., 2001). Newly emerged spiderlings inhabit a large and "safe" maternal web, often being protected and fed by regurgitation from their mother, during their early instars. This predictable and protected environment, as well as the prolonged maternal care, could produce the early emergence from the egg-sac of immature spiderlings which would be unable to survive by themselves in other conditions. This would involve a shorter development time inside the egg-sac (few and/or brief instars) compared with solitary spider species.

The genus *Anelosimus* is one of a few genera of spiders that contain solitary, subsocial and social species. Sub-social spiders provide good models for investigating potential selection pressures that could have been involved in the evolution of sociality. *Anelosimus* cf. *studiosus* is a sub-social spider from Uruguay which is part of the "*studiosus* group". This species is very close to *A. studiosus* (Hentz) and its taxonomic status is now under revision (I. Agnarsson, in litt.).

In this paper we describe the post-embryonic development of *Anelosimus* cf. *studiosus*. As far as we know, there are no previous analyses of post-embryonic

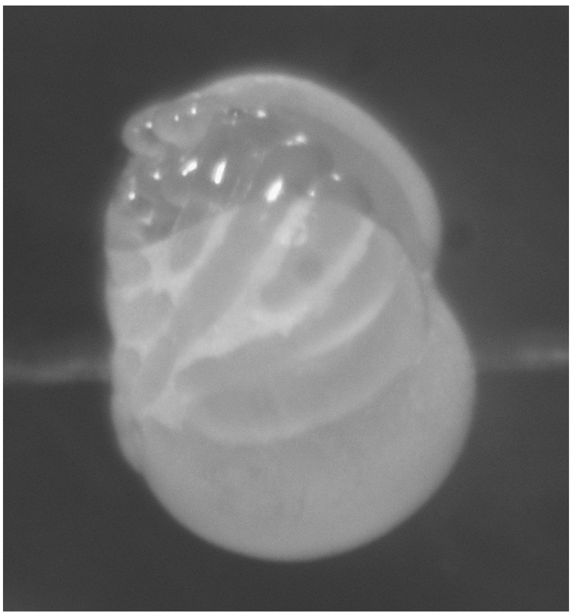

Fig. 1: Hatching prelarva of *Anelosimus* cf. *studiosus*, tearing the chorion.

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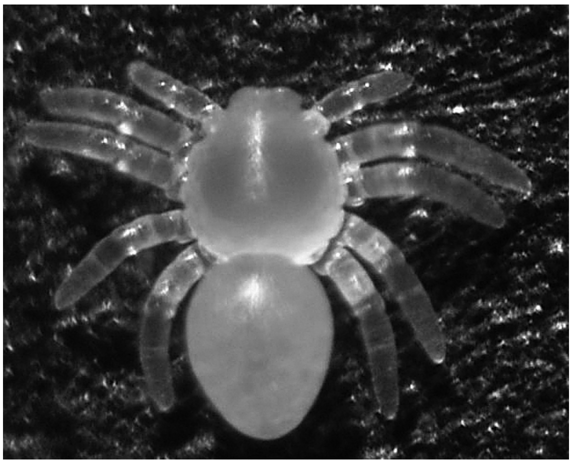

Fig. 2: Larva of *Anelosimus* cf. *studiosus*.

development in a social theridiid spider, but several in solitary species (Downes, 1987) that allow the comparison of differences and similarities between them.

Material and methods

Spiders were collected as sub-adults in Montevideo, Uruguay, from a perennial native tree (*Rapanea laetevirens*, Myrsinaceae: "canelón"). They were raised under laboratory conditions until reaching adulthood, being fed mainly with fruit flies (*Drosophila* spp.). Twenty-four mated females laid egg-sacs. Fifteen egg-sacs were removed from their mothers and opened. The eggs from each egg-sac were placed in small petri dishes with wet cotton-wool until they reached the first nymphal instar (experimental group). The presence of the prelarval instar was detected by transparency through the chorion. The timing of hatching from the chorion, moulting to larva and to first nymphal instar, were recorded. Simultaneously, as a control group, nine mothers were kept with their own egg-sacs, and the timing of both egg-laying and nymphal emergence (assisted by their mother's chewing on the egg-sac) were recorded.

Mean room temperature during the experimental period was 24°C (range 22–26°C). Voucher specimens were deposited in the Arachnological Collection of the Faculty of Sciences, Montevideo, Uruguay.

Normal distribution (Shapiro–Wilks test) and homogeneity of variance (Levene test) were tested with the PAST statistical package, version 1.24 (Hammer *et al.*, 2004) and analysed with parametric tests. Normally distributed data are presented as mean ± SD.

Results

The prelarval instar (Fig. 1) was first detected by transparency at a mean of 16.58 ± 1.66 days after egg-laying ($n=13$), and it shed the chorion and immediately moulted to the larval stage (Fig. 2) at 18.00 ± 1.96 days after laying ($n=13$). The larval instar had a mean duration of 2.85 ± 0.90 days. Moulting to the nymphal instar (Fig. 3) occurred 20.73 ± 2.02 days after egg-laying ($n=15$). Juveniles from the control group emerged 20.77 ± 3.63 days after egg-laying ($n=9$). No significant differences were found between the experimental and control groups using the t-test for two independent samples ($t=0.039$, df=22, $p=0.97$).

Discussion

The results indicate that *Anelosimus* cf. *studiosus* has the minimal number of instars known for spiders inside the egg-sac: only one prelarval, larval and nymphal instars (category II of Downes, 1987). This pattern of post-embryonic development is similar to that found in some solitary theridiids such as *Theridion (Nesticodes) rufipes* Lucas, *Achaearanea decorata* (L. Koch) and *Latrodectus hasselti* Thorell by Downes (1987), and in *Achaearanea tepidariorum* (C. L. Koch) by Valerio (1974). Neotropical species of *Latrodectus*, *Tidarren* and *Steatoda* show two prelarval instars inside the egg-sac (González, 1979, 1981, 1982, 1987; González *et al.*, 1998), but this difference in the number of prelarval instars could be artificial, according to whether or not the authors recognise the shedding of the embryonic cuticle as a true moult (Valerio, 1974; Galiano, 1991). Valerio (1974) stressed the brevity of the larval instar (quiescent, first instar) in theridiid spiders and stated a possible trend toward the elimination of this instar. Therefore, we considered the larva to be a good candidate for reduction of duration or elimination in our subsocial spider. However, in spite of the high level of investment by the mothers in caring for the egg-sac and feeding the juveniles (Viera *et al.*, 2006), the subsocial condition of *Anelosimus* cf. *studiosus* did not seem to affect the number of instars. Early juveniles (first nymphal instar) of *A.* cf. *studiosus* are able to adopt a free lifestyle, and are capable of capturing small prey in favourable conditions, indicating an important degree of development and some possibility of survival without their mother (Ghione *et al.*, 2004), similar to the solitary spiders of the family. On the other hand, other social and also some subsocial *Anelosimus* species are unable to capture prey before the third nymphal instar (Brach, 1977), suggesting that they emerge from the egg-sac in

Fig. 3: First nymph of *Anelosimus* cf. *studiosus*, or first complete juvenile form.

earlier stages of development. Thus, a smaller number of instars could be expected in these species. However, *Anelosimus* cf. *studiosus* could have shortened the duration of its embryonic and/or post-embryonic development. Available data on the duration of embryonic development (oviposition to eclosion) are scarce in theridiids: we found only the work of Umaña (1987), which indicated 12 days for *Theridion (Nesticodes) rufipes*. The larval period seems to be uniformly brief in the family, being 2 days in *A. tepidariorum* following Valerio (1974), 3 days in *T. rufipes* according to Umaña (1987) and 3 days in *Tidarren sisyphoides* (Walckenaer) according to González (1982); however, *Steatoda retorta* González spent 4.5 days (González, 1987) and *Latrodectus* spp. 7 days (González, 1979, 1981) in the larval instar. *Anelosimus* cf. *studiosus* did not seem to shorten the larval period. Further research on both embryonic and post-embryonic development in solitary and especially social theridiid spiders is needed to elucidate these hypotheses.

Spiderlings of the experimental group reached the nymphal stage after a similar time period to that at which the control females opened their egg-sacs, suggesting that the presence of nymphs inside the egg-sac is very brief. In this species, females continuously carried the egg-sac, grasping it with chelicerae and pedipalps (Viera *et al.*, 2006) and they could easily perceive nymphal movements after moulting and immediately tear the egg-sac, as was indicated by Fujii (1978, 1980) and Vannini *et al.* (1986) for lycosids.

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