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Notes on the biology of *Anelosimus pacificus* Levi, 1963 (Theridiidae, Araneae)—evidence for an evolutionary reversal to a less social state

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Abstract

All hitherto studied *Anelosimus* species are social, either temporarily (subsocial) or permanently (quasisocial); the genus represents the largest known clade of social spiders. We provide behavioural data on *Anelosimus pacificus* Levi, 1956 (Theridiidae, Araneae) a species that hitherto was known from only a few specimens collected half a century ago. *Anelosimus pacificus*, unlike its better known congeners, is solitary for the majority of its lifespan with the juveniles passively receiving maternal care before dispersal at an early instar. Given the phylogenetic position of *A. pacificus*, this is an example of a behavioural reversal to a less social (solitary) state, and the first such reversal documented in spiders. Interestingly, linked with this is a reversal in other traits. *Anelosimus pacificus* web architecture, use of sticky silk, the ability of juveniles to emerge from the egg sac, and build and maintain webs without help from the mother, all more resemble traits in typical solitary theridiids than those in its social congeners. These observations may help elucidate what factors contribute to the evolution of sociality in spiders.

Keywords: *Anelosimus pacificus*, Araneae, behaviour, evolution of sociality, Theridiidae

Introduction

The cobweb spider genus *Anelosimus* Simon, 1891 represents a model system for the study of sociality and its evolution (reviewed by Avilés 1997, see also Agnarsson 2006). The genus contains almost exclusively social species, ranging from temporary social, or subsocial, to permanently social, or quasisocial. Sociality is generally thought to evolve via the “maternal care route”, in other words, maternal care precedes subsociality, which in turn precedes quasisociality in the evolutionary history of social lineages (e.g. Burgess 1978; Schneider 2002; Agnarsson 2002, 2004; Buskirk 1981). The social species all start

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their lives emerging from an egg sac in the mother's nest. The mother protects and provides for the spiderlings and she may either feed them actively by regurgitation, or passively by leaving them dead prey. Subsocial spiderlings remain in the natal nest until dispersal near adulthood while quasisocial spiders reach adulthood and mate within the natal nest (Avilés 1997). Hence, the switch to quasisociality is accompanied with a switch to inbreeding (Bilde et al. 2005). Presumably due to the long term negative consequences of inbreeding, quasisociality appears to represent an evolutionary dead-end (Agnarsson et al. in press). Consistent with this hypothesis, although there have been many independent origins of social behaviour (e.g. Bilde et al. 2005; Agnarsson et al. in press; Avilés et al. 2006) there is no direct evidence for the secondary loss of quasisociality, i.e. a reversal to less social, or solitary behaviour, in any spider lineage. To date, there is furthermore no evidence for a reversal from subsocial to compulsory solitary living in spiders. Here we report on some behavioural notes providing evidence for solitary behaviour, with maternal care lasting only a couple of juvenile instars, in *Anelosimus pacificus* Levi, 1956, a species that has not been collected since its original description and was hitherto known only from seven Mexican and Jamaican specimens. Given its phylogenetic position (Agnarsson 2006; Agnarsson et al. 2007) this represents the first observation of a reversal to mostly solitary behaviour in an *Anelosimus* species.

Methods

Definition of solitary versus social behaviour

Some degree of maternal care, beyond care of egg sac, is widespread and common in theridiid spiders. In most cases, however, juveniles appear to be passive receivers of care and disperse from the natal nest at an early instar (I–III after emerging from the egg sac) without contributing to the colony. In most *Anelosimus* species (subsocial and quasisocial), in contrast, juveniles stay in the natal nest until near or after adulthood and actively cooperate and contribute to common colony tasks. We here follow Agnarsson et al. (in press) in distinguishing between these systems on the basis of cooperation, referring to the former as solitary behaviour with extensive maternal care. It should be noted, however, that our conclusion of an evolutionary reversal in social behaviour does in no way depend on these definitions (whether termed “less social” or “solitary:”); these definitions are offered merely for clarity.

Observations

Anelosimus pacificus, although hitherto never collected in Costa Rica, is apparently common along its Pacific coast. Webs were encountered, typically at the tips of branches of *Ficus* spp. at the beachfront. Data were collected at two localities: Parrita (N 9.5167 W 84.3167, February 2005, G. Barrantes and W. Eberhard, and 10–11 September 2005, I. Agnarsson and L. J. May-Collado) in the Puntarenas province, and Playa Hermosa (N 10.57941° W 084.67635°, 15–16 September 2005, I. Agnarsson and L. J. May-Collado) in the Guanacaste province, both on the Pacific coast of Costa Rica. Webs were photographed in the field, and the contents of webs examined, and the age of juveniles, or instar number, estimated roughly based on their size. Three adult spiders, two with their egg sacs, were taken to the laboratory where they were maintained for about two months and observations made on the adults and the behaviour of their spiderlings.

Results and discussion

Web

The webs of most subsocial and quasisocial species are similar, a dome-shaped sheet reinforced with dead, or sometimes living, leaves and above the sheet aerial threads that intercept insects in flight (Agnarsson 2006). The aerial threads usually lack visible sticky silk (but see Marques et al. 1998). *Anelosimus pacificus* (Figure 1A, B), however, builds webs unlike those of any social *Anelosimus* (Figure 1C). Rather, they resemble webs of many solitary theridiids, a three-dimensional mesh surrounding vegetation, with sticky droplets (visible with a 10X hand lens) distributed throughout the mesh. The retreat is somewhat unusual, two leaves sandwiched together with silk, as in the related *A. kohi* Yoshida, 1993 from SE Asia (Agnarsson & Zhang 2006). In captivity, the adult female constructed her web on the tip of an herb twig. The first web was a small mesh built at first among the petioles, with threads then extended to some other leaves. The spider used the base of the petioles as her retreat. Some days later she used the base of some leaves as her retreat, and the size of the mesh increased conspicuously.

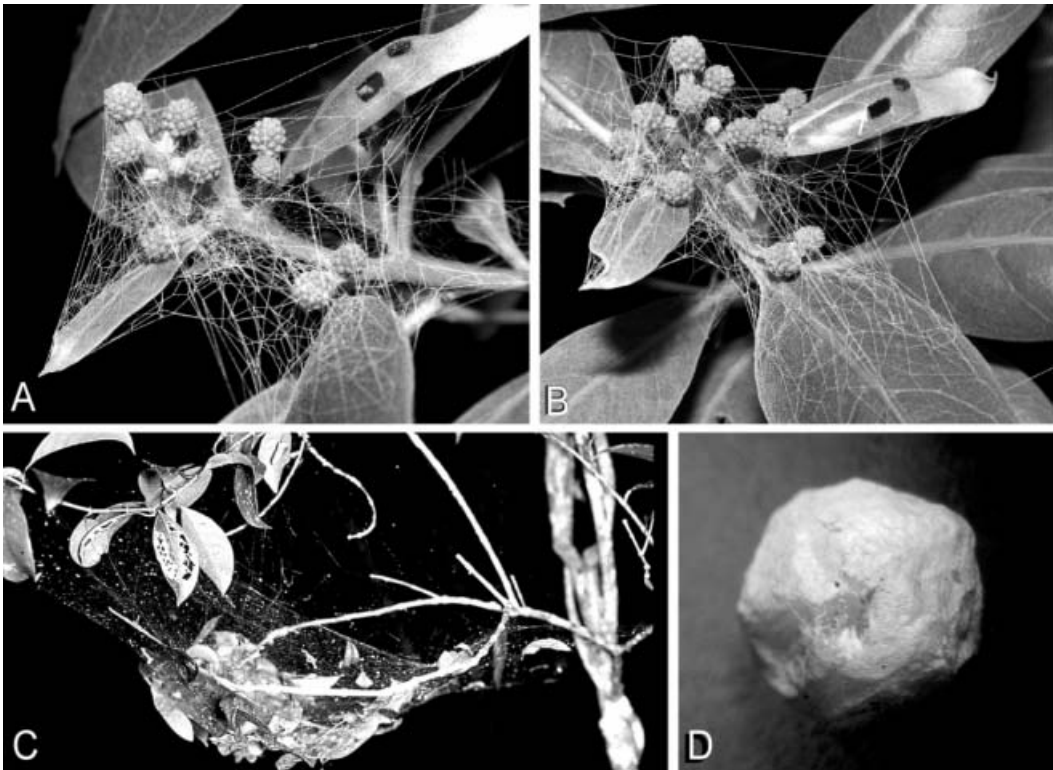


Figure 1. A, B, solitary *A. pacificus* web, a flimsy tangle of silk lines with conspicuous globules of glue throughout; C, web of the subsocial *A. may* Agnarsson, 2005, a typical *Anelosimus* 'basket' web with dense silk sheet containing living and dead leaves, and aerial threads above, without visible glue; D, the bright white *A. pacificus* egg sac. All webs have been dusted with corn starch to enhance the visibility of the silk lines.

Egg sac

In captivity the spider laid eggs enveloped in a globular white egg sac (Figure 1D); the egg sac was hidden in the sandwiched-leaf retreat. Three egg sacs found in Parrita were also found hidden within the retreats. From one of the egg sacs emerged ca. 26 spiderlings. Note that most *Anelosimus* species have dull grey or greenish egg sacs (Agnarsson 2005, 2006; Agnarsson & Kuntner 2005); however, white eggs have been documented in the phylogenetically proximate *A. kohi* and *A. linda* Agnarsson, 2006 from Malaysia (Agnarsson & Zhang 2006) and *A. vittatus* (C. L. Koch, 1836) from Europe (pers. obs.).

Attack behaviour

The attack behaviour of the adult spider on several flies was observed. Two *Drosophila* flies were dropped on the web at about the same time. The spider rapidly attacked the first fly, flinging some sticky threads on the fly and then bit it. As soon as the prey was subdued, the spider moved toward the second fly, biting and taking it to the retreat where she began to feed upon it. The wrapped fly was taken to the retreat after the spider had discarded the carcass of the other fly. A blow fly (Calliphoridae) placed on the web was immediately attacked (<5 s). The fly was bitten at the tip of its abdomen and stopped moving at once, indicating an effective venom. The prey was then taken to the spider's retreat.

The attack behaviour of *A. pacificus* differs notably from the behaviour of the subsocial *A. studiosus* (G. Barrantes pers. obs.). *Anelosimus studiosus* (Hentz, 1850) approached each prey cautiously ($n=6$). Prey attacked by *A. studiosus* took much longer to stop moving (up to 4 min), despite being bitten at least three times. Additionally, *A. pacificus* wrapped prey using more viscid threads than *A. studiosus*; the latter uses very little silk to wrap prey. The attack behaviour of *A. pacificus* more resembles that of solitary species in other related genera, e.g. *Achaearanea tepidariorum* (C. L. Koch, 1841), *A. tessellata* (Keyserling, 1884), or *Nesticodes rufipes* (Lucas, 1846) (G. Barrantes pers. obs.).

Emergence of nymphs

Two freshly collected egg sacs were maintained in a plastic bag until nymphs emerged. The nymphs of *A. pacificus* do not need their mother to break apart the external wall of the egg sac, contrary to the nymphs of the subsocial *A. studiosus* where the mother helps nymphs to emerge from the egg sac.

Maternal care, cooperative behaviour and dispersal

Two days after nymphs emerged a blow fly was dropped on the web. The fly was rapidly attacked by the mother, and taken to the retreat where the nymphs began to feed on it soon after. The adult spider moved away while the nymphs fed. The fly was bitten several times before being left for the nymphs to feed upon, as is common in other theridiids (e.g., *A. tessellata*, *Theridion evexum*, Keyserling, 1884, *N. rufipes*). Another blow fly was placed on the web five days later. The fly was rapidly attacked by the adult spider but this time several second instar nymphs arrived at the prey soon after their mother began the attack. They began to "feed" on the prey but then it was carried to the retreat where most of the nymphs had remained.

In captivity, the adult spider abandoned the web and nymphs and moved to another nearby plant. The nymphs (possibly second or third instar) dispersed during the next day.

In Parrita, webs with small nymphs only were found in February 2005, while solitary females, females with egg sacs and females with tiny juveniles, estimated to represent instars I and/or II after eclosing from the egg sac, were seen in September 2005. In Playa Hermosa, only solitary webs were seen, containing either an adult female, an adult male, or a juvenile. The solitary juveniles were believed to represent III or IV instars. While sparse and anecdotal these observations clearly imply solitary behaviour with extensive maternal care spanning only the first couple of instars outside the egg sac. It should be noted here that in social *Anelosimus* species, such as *A. eximius*, juveniles start to contribute to the common tasks of the colony only after reaching instar III (Vollrath 1986), hence it seems likely that cooperative behaviour is mostly or entirely absent in *A. pacificus*.

Phylogeny and reversal to solitary behaviour

All *Anelosimus* species hitherto studied in any detail are either subsocial or quasisocial and these include representatives from both “basal” and “distal” *Anelosimus* lineages (Agnarsson 2006). Here we document for the first time solitary behaviour in an *Anelosimus* species. Solitary behaviour is also suspected in two South American species *A. ethicus* (Keyserling, 1884) and *A. nigrescens* (Keyserling, 1884) based on limited field observations (L. Avilés pers. comm.). The phylogeny of Agnarsson et al. (2007) places *A. pacificus* as sister to the “*ethicus* group” (see Agnarsson 2006) containing *A. ethicus* plus *A. nigrescens*, hence the three supposedly solitary species form a clade. This phylogenetic hypothesis rejects the idea that solitary behaviour in the three is primitive, as could be the case if the three were sisters to the remaining *Anelosimus* species; rather, the three are nested well within the genus, while social behaviour optimizes to the base of the *Anelosimus* phylogeny (i.e. is primitively present, see Agnarsson 2006; Agnarsson et al. 2007). Hence, their solitary (or less social) behaviour is derived. Interestingly, this reversal to solitary behaviour is accompanied with a reversal in other traits; both web configuration, emergence of nymphs from egg sacs, and the attack behaviour of *A. pacificus* more closely resemble that of solitary species of related genera than any of the social *Anelosimus* species. This includes a reversal to using sticky silk in the web, and abundant silk with large viscid globules to wrap prey. This suggests that the sparse use of sticky silk by social *Anelosimus* species is not due to an inability to lay sticky silk, but rather a “choice” not to do so. For instance, *A. studiosus* uses silk with large viscid globules to wrap dangerous prey (e.g., *Pseudomyrmex* ants), but viscid globules are not visible when wrapping non-threatening prey (G. Barrantes pers. obs. and W. G. Eberhard pers. comm.).

Our findings suggest that detailed studies of the two European *Anelosimus* species (*A. vittatus* and *A. pulchellus*) might be particularly valuable, as the pair form the sister clade to the one containing the three solitary *Anelosimus* species. Both European species are poorly known, with anecdotal evidence suggesting subsociality in *A. vittatus* (see Agnarsson & Zhang 2006) although it is not known how long juveniles remain in the natal nest. Given their phylogenetic position, it would not be surprising if future studies unravelled in these species a social level somewhat intermediate between “typical” subsocial and the system found in *A. pacificus* and relatives.

The unrelated spider genus *Stegodyphus* (Eresidae) also contains solitary, subsocial, and social species (Kraus & Kraus 1988; Bilde et al. 2005). It may be that this genus offers an independent opportunity to examine the consequences of reversal to solitary behaviour on other behavioural traits. However, to date no phylogenetic hypothesis for *Stegodyphus* exists, and while existing evidence suggests several independent origins of sociality (Kraus

& Kraus 1988; Johannesen et al. 2002; Bilde et al. 2005), it remains to be seen if sociality has ever been lost within the genus.

Concluding remarks

We have provided the first evidence for a reversal in behaviour from social to solitary in a spider lineage. Linked with this is a reversal in other traits, such as web type, use of sticky silk, and the ability of juveniles to emerge from the egg sac, and build and maintain webs without help from the mother. However, it remains to be seen if the solitary *A. pacificus* have secondarily regained the aggression towards conspecifics that is typical of other solitary theridiids. The suppression of conspecific aggression, or at the very least aggression towards kin, is an essential step in the evolution of social behaviour in spiders. If *A. pacificus* show aggression towards siblings early on, this would suggest that a reversal to solitary behaviour could be triggered by “tinkering” with the onset of aggression, while the set of traits necessary to survive as a solitary spider seem to be readily regained.

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