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NOTES ON THE SOCIAL STRUCTURE, LIFE CYCLE, AND BEHAVIOR OF *ANELOSIMUS RUPUNUNI*

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ABSTRACT: Observations on the colony structure, life cycle, and behavior of *Anelosimus rupununi* in eastern Ecuador point to a level of social organization similar to that of *Anelosimus eximus* and *Anelosimus domingo*, confirming its status as a non-territorial, permanently-social species. *Anelosimus rupununi* colony members were seen to cooperate in prey capture and transport, to feed communally, and to take turns in tending the egg sacs. Sex ratios were also highly female-biased. There were, however, some interesting differences with these other species. *Anelosimus rupununi* egg sacs were grouped as part of maternal care efforts, with grouped sacs being more likely to be tended than ungrouped sacs. Males and females apparently matured at the same instar, males appeared shorter-lived than females, and individuals within the nests were clearly synchronized with each other in the stage of their life cycle. Also, as would be expected from its notably smaller body size, *A. rupununi*'s life cycle appeared shorter than that of *A. eximius*.

Understanding the evolution of animal social systems often requires exploring within a comparative framework both the environmental conditions that may have selected for social living and the suite of traits that in particular phylogenetic lineages may have facilitated or hindered the transition from one level of social organization to another (Crespi & Choe 1997). Spiders appear ideal for this exploration because they have given rise to several independent derivations of complex social behavior involving cooperation in nest building, prey capture, feeding, and brood care (for a recent review, see Avilés 1997). Additionally, the genera that contain these cooperative species—also known as ‘‘non-territorial permanent social’’ or ‘‘quasisocial’’—contain species with other levels of social organization. The genus *Anelosimus* Simon 1891 (Araneae, Theridiidae) in America, in particular, includes at least four non-territorial permanent-social species, which are mostly tropical, and several periodic-social or solitary species that inhabit both tropical and temperate areas of the New World (Levi 1956, 1963, 1972; but see Furey 1998). Among these, only the permanent-social *Anelosimus eximius* Keyserling 1884 has been relatively well studied (see references cited in Avilés 1997). Other species have received comparatively little attention (see Brach 1977; Fowler & Levi 1979; Nentwig & Christenson 1986; Smith 1987; Rypstra & Tirey 1989; Avilés & Maddison 1991; Furey 1998; Avilés & Gelsey 1998).

Here we present observations on the colony structure, life cycle and behavior of *Anelosimus rupununi* Levi 1956 in eastern Ecuador. This species had been previously reported from Trinidad, British Guiana, northwestern Peru, Brazil and Paraguay (Levi 1963), although the Paraguayan specimens apparently correspond to misidentified *A. lorenzo* Levi 1979 (Fowler & Levi 1979). No previous records existed from Ecuador where this study was conducted. The only published information on *A. rupununi* was a photograph of a nest (Levi 1972) and the suggestion that the species is ‘‘probably quasisocial’’ because it forms extensive colonies (Fowler & Levi 1979). Fowler & Levi (1979) noted that the apparently closely related *A. lorenzo* forms perennial colonies that may contain hundreds of individuals that cooperate in prey capture, feeding and brood care. Here we confirm that *A. rupununi* has a level of social organization comparable to that of the permanent-social *A. eximius* and *A. domingo* Levi 1963. We note, however, some interesting differences between *A. rupununi* and these two species. In particular, in *A. rupununi* individuals within the nests are relatively well synchronized in the stage of their life cycle and group their egg sacs as part of maternal care efforts.

We discovered colonies of *A. rupununi* at two sites in eastern Ecuador, the Yasuni National Park (YNP) and the Jatun Sacha Biological Station (JSBS). The YNP (including the adjacent Waorani Reserve) comprises 1,662,000 hectares of primary rainforest. We visited the area near the confluence between the Tiputini and Tivacuno rivers (0°41′S, 76°24′W, 210–250 m elevation) where the Estación Científica Yasuní (ECY, Pontificia Universidad Católica del Ecuador) is located. The JSBS is located on the southern banks of the Upper Napo River (1°4′S, 77°36′W, 450 m) and comprises 2000 hectares of mostly primary forest surrounded by farms. At both sites we searched for colonies of *Anelosimus* spp. both within the forest and along the forest edge. At the YNP (19–23 July 1997) we inspected 4 km inside the forest, 10 km along the Tiputini river, and 7 km along the ECY-Tibacuno road. At the JSBS (9–17 July and 3–9 August 1997 and April 1998), we inspected 6 km inside the forest, 55 km along the Arajuno, Napo, and Huambuno rivers, and 20 km along the Tena-Ahuano road. Additionally, the colonies located at the JSBS in mid-July 1997 were monitored bi-weekly until mid-February 1998 or until their extinction.

Web architecture.—We located eight nests of *A. rupununi*, all of them in forest edge or open and disturbed areas. A nest at the YNP occurred on the crown of a tree that hung over the Tiputini River. The seven nests located at the JSBS occurred on trees or bushes in farms adjacent to the preserve. We could not locate any nests in the forest interior where, in contrast, we located numerous *A. domingo* and *A. eximius* nests. The nests of *A. rupununi* differed from those of *A. eximius* in several respects: they were made of silk of a whiter and lighter appearance, contained almost no dry leaves and did not have a definite top-bottom polarity. In fact, rather than being basket-shaped, with a basal sheet and extensive silk lines extending upwards, the nests of *A. rupununi* enveloped pieces of vegetation on all sides and had only short if any lines extending upwards. This architecture may result from the location of the nests in areas with no other vegetation above. This architecture, combined with the spatial distribution of the nests, suggests that *A. rupununi* is a forest edge or canopy species.

Individual instars.—Spiders of all instars were of a generally dark brown or black coloration that obscured the dorsal abdominal pattern characteristic of *Anelosimus*. Based on the state of the genitalia, general size, and body proportions, we classified the later-instar spiders into ‘‘juveniles,’’ ‘‘subadults’’ and ‘‘adults.’’ Measurements of the tibia plus the patella of leg I yield a multimodal distribution that supports this *a priori* classification of instars (Fig. 1). Based on these data, it appears that after the last undifferentiated juvenile instar, both males and females have only one subadult instar before acquiring sexual maturity. This situation differs from that found in *A. eximius* and *A. domingo* where females are significantly larger than males as a result of having one additional subadult instar before maturing (Avilés 1986; unpubl. data). Egg sacs were subspherical in shape (2.00 × 2.00 × 2.75 mm, $n = 1$), of an off-white coloration, and tended to be bundled in groups of up to eight sacs (see below). Possibly as a camouflage mechanism, the sac bundles contained debris attached to their surface that gave them a flower like appearance. Egg sacs contained from 8–13 eggs (mean ± SE: 10.6 ± 0.6 eggs; $n = 13$). No parasitoids were present inside the sacs examined.

Colony age structure and life cycle.—The four nests whose contents we inspected contained from a single adult female to close to 3000 spiders. The age distribution within the two largest nests (Table 1) suggested a definite synchronization in life cycle stage among individuals within a colony. When seen in July 1997, the YNP colony contained mostly adult females and egg sacs, while the JS 1 colony contained primarily subadult females and no egg sacs.

The synchronization in life cycle stages within the JS 1 colony continued throughout the period it was observed (Fig. 2). Six weeks after it was first recorded, the spiders in this colony had matured and laid their eggs. By week 10, the first spiderlings had emerged from the sacs, and by week 16 some of these spiderlings had reached the adult instar. In the mean time, the maternal females had decreased in number and were apparently all gone before their offspring reached the sub-

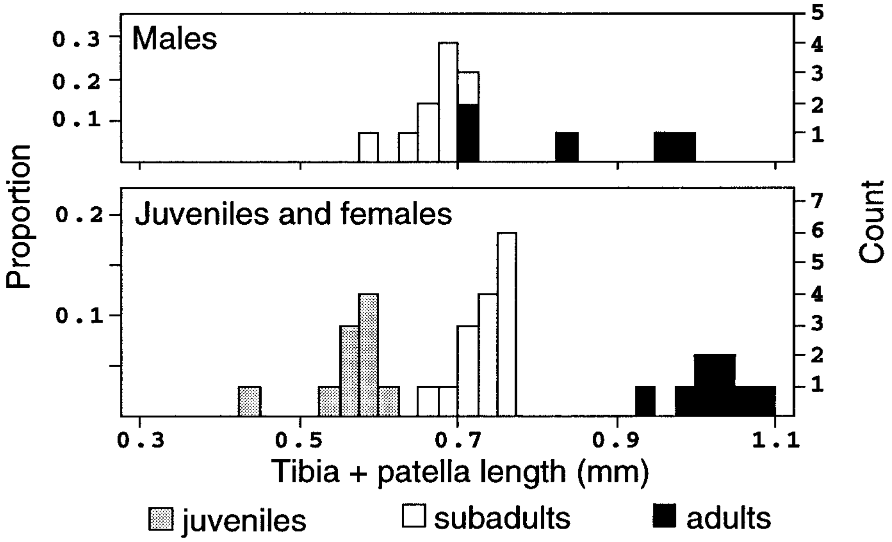

Figure 1.—Tibia + patella (leg pair I) measurements of late-instar *Anelosimus rupununi* spiders separated *a priori* into ''juveniles,'' ''subadults,'' and ''adults'' based on the state of their genitalia, size, and body proportions. Mean total body length (± SE) for the different instars and sexes are as follows: late-instar juveniles = 1.39 ± 0.03 mm; subadult females = 1.76 ± 0.02 mm; subadult males = 1.59 ± 0.05 mm; adult females = 1.81 ± 0.01 mm; adult males = 1.75 ± 0.05 mm.

adult instar. No new sacs appeared in the colony between weeks 14–18. Males appeared much shorter-lived than females, as no adult males were noted in this colony during the periods of egg sac and offspring development. Consistent with this observation, almost no males were present in the YNP colony when it contained primarily adult females and egg sacs (Table 1).

A shorter male lifespan in *A. rupununi* contrasts with the situation in *A. eximius* where males and females have adult lives of comparable length (Avilés 1986). The synchronization of life cycle stages within *A. rupununi* colonies also contrasts with the situation in *A. eximius* and *A. domingo*, where, although separate, the generations within the colonies are less clearly distinct (Avilés pers. obs.). Strong internal synchronization of life cycle stages has also been described for other permanent-social species such as *Achaearanea wau* Levi, Lubin & Robinson 1982 (Lubin & Robinson 1982), *Stegodyphus dumicola* 1898 (Seibt and Wickler 1988), and *Aebutina binotata* Simon 1892 (Avilés in press).

During the six months following its discovery, the spiders at the JS 1 colony completed one and a half generation cycles (Fig. 2). Mature spiders of the offspring generation remained at the original site and in early December—four months after the onset of the prior egg-laying cycle—started to lay their own eggs. *Anelosimus rupununi*, therefore,

Table 1.—Size and inhabitants of *Anelosimus rupununi* nests when first seen in July 1997 at the Yasuni National Park (YNP) and the Jatun Sacha Biological Station (JS).

Colony	Nest size (cm)	% scored	Sacs	Juv.	Females		Males	
					Subad.	Adult	Subad.	Adult
YNP	88 × 45 × 12	100	244	14	5	229	0	4
JS 1	130 × 95 × 80	10	0	25	224	27	10	12
JS 2.1		100	10	present	0	7	0	0
JS 3		100	0	0	0	1	0	0

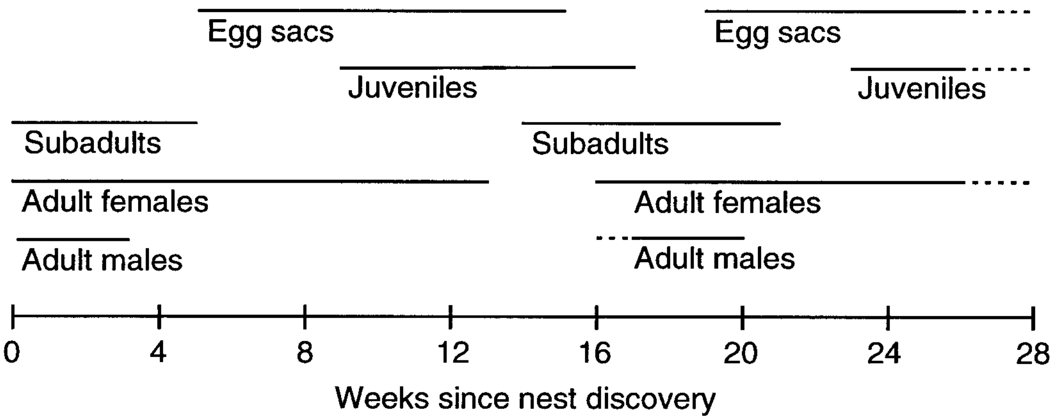

Figure 2.—Idealized life cycle of an *Anelosimus rupununi* colony based on bi-weekly inspections of a nest discovered at the Jatun Sacha Biological Station in mid-July 1997. Lines mark the presence of individuals of particular life cycle stages within the colony.

may complete three generations a year, in contrast with *A. eximius* that completes only between 2.4–2.6 generations a year at this same latitude (Avilés 1986).

Sex ratio.—We estimated the tertiary sex ratio in a colony that contained primarily subadult spiders and, thus, would not have been affected by the shorter life span of adult males (Colony JS 1, Table 1). We are assuming that the collected $\frac{1}{10}$ fraction of this colony is representative of the whole, as spiders of all instars appeared homogeneously distributed throughout the nest. The sex ratio among the 273 subadult and adult spiders in this sample was 8% males (4.7–12.5%, 95% c.i.) (Table 1). This value is strikingly similar to the 9% and 8% males reported as the sex ratio among developing embryos in *A. eximius* and *A. domingo*, respectively (Avilés & Maddison 1991).

Sacs per female.—Given the synchronization in life cycle stages within *A. rupununi* nests, the ratio of sacs to females during the peak of the egg laying period may be a reasonable representation of the number of sacs produced per female. The two colonies censused at this stage contained 1.04 and 1.40 sacs per female, respectively (Table 1). In contrast, estimates of the egg sac production in *A. eximius* that take into account its more protracted egg-laying period indicate that females in this species typically produce fewer than one sac per female (Avilés & Tufiño 1998; see also Vollrath 1986). The fecundity of *A. rupununi*, therefore, may be higher than what its small adult female body size and small number of eggs laid per sac would lead us to suspect.

Behavior.—We conducted casual observations on prey capture and feeding in the YNP colony after it was collected whole and brought intact to the field station (the colony enveloped a stiff piece of vegetation and, thus, maintained its original shape and structure). Following the artificial introduction of prey items in the nest, we recorded two cooperative prey capture events. In one event seven spiders participated in biting and subduing a cricket that was 4–5 times larger than the individual spiders. In another event three females cooperated in moving a captured membracid towards the nest's interior. In both cases, communal feeding followed. Groups of communally feeding spiders were also observed in other colonies in the field.

A behavior not previously observed in species in the genus *Anelosimus* consisted in the bundling of the egg sacs in groups. Also in the YNP colony (see above), we observed a female in the process of completing an egg sac and attaching it to a nearby pair of bundled sacs. The egg sac was initially suspended from the web as the spider crawled around it adding to its surface silk she pulled from her spinnerets. After the sac was completed, the spider detached it and brought it towards a pre-existing pair of sacs. After attaching the sac to the pair, the spider mounted guard by the new-formed trio.

Out of the 244 sacs present in this colony

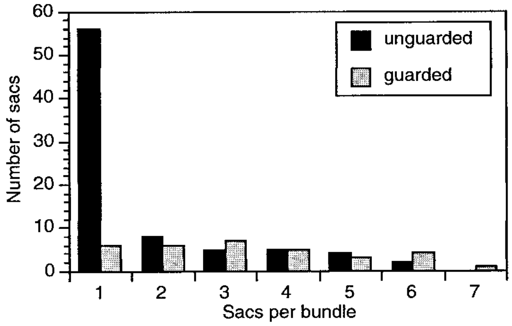

Figure 3.—Frequency distribution of guarded and unguarded egg sac bundles present in the YNP nest five days after it was collected whole.

when collected, 182 — or 75% —occurred in groups of 2–7 sacs (Fig. 3). The remaining sacs were single. When we started dissecting the colony in the laboratory five days after its collection, we noted that 31 out of the 234 females in the nest were involved in sac guarding. However, 105 of the 244 sacs were being guarded as grouped sacs were significantly more likely to be tended than ungrouped sacs (median number of sacs per bundle among guarded sacs = 3, among unguarded sacs = 1; Mann-Whitney U = 1975, $P < 0.0001$) (Fig. 3). Usually a single female mounted guard by each sac bundle, apparently relayed by other individuals. During a one hour observation period we noted that females repeatedly moved away from the sacs they were tending as a second female with whom they exchanged leg touches approached the area. Sac bundling was also observed in the Jatun Sacha colonies. The 10 sacs present in the JS 2.1 colony (Table 1), for instance, occurred in a group of eight and a group of two.

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LITERATURE CITED

Avilés, L. 1986. Sex-ratio bias and possible group selection in the social spider *Anelosimus eximius*. American Nat., 128:1–12.

Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. Pp. 476–498, *In* The Evolution of Social Behavior in Insects and Arachnids. (J. Choe & B. Crespi, eds.). Cambridge Univ. Press, Cambridge.

Avilés, L. In press. Nomadic behavior and colony life cycle in a cooperative spider. Biol. J. Linn. Soc.

Avilés, L. & W.P. Maddison. 1991. When is the sex ratio biased in social spiders?: Chromosome studies of embryos and male meiosis in *Anelosimus* species (Araneae, Theridiidae). J. Arachnol., 19:126–135.

Avilés, L. & G. Gelsey. 1998. Natal dispersal and demography of a subsocial *Anelosimus* species and its implications for the evolution of sociality in spiders. Canadian J. Zool., 76:2137–2147.

Avilés, L., & P. Tufiño. 1998. Colony size and individual fitness in the social spider *Anelosimus eximius*. American Nat., 152:403–418.

Brach, V. 1977. *Anelosimus studiosus* (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. Evolution, 31:154–161.

Crespi, B.J. & J.C. Choe. 1997. Explanation and evolution of social systems. Pp. 499–524, *In* The Evolution of Social Behavior in Insects and Arachnids. (J. Choe & B. Crespi, eds.). Cambridge Univ. Press, Cambridge.

Fowler, H.G. & H.W. Levi. 1979. A new quasisocial *Anelosimus* spider (Araneae, Theridiidae) from Paraguay. Psyche, 86:11–17.

Furey, R.E. 1998. Two cooperatively social populations of the theridiid spider *Anelosimus studiosus* in a temperate region. Anim. Behav., 55:727–735.

Levi, H.W. 1956. The spider genera *Neottiura* and *Anelosimus* in America (Araneae: Theridiidae). Trans. American Micros. Soc., 75:407–422.

Levi, H.W. 1963. The American spiders of the genus *Anelosimus* (Araneae, Theridiidae). Trans. American Micros. Soc., 82:30–48.

Levi, H.W. 1972. Taxonomic-nomenclatural notes on misplaced theridiid spiders (Araneae: Theridiidae), with observations on *Anelosimus*. Trans. American Micros. Soc., 91:533–538.

Lubin, Y.D. & M.H. Robinson. 1982. Dispersal by swarming in a social spider. Science, 216:319–321.

Nentwig, W. & T.E. Christenson. 1986. Natural history of the non-solitary sheetweaving spider *Anelosimus jucundus* (Araneae: Theridiidae). Zool. J. Linn. Soc., 87:27–35.

Rypstra, A.L. & R.S. Tirey. 1989. Observations on the social spider *Anelosimus domingo* (Araneae, Theridiidae), in Southwestern Peru. J. Arachnol., 17:368–371.

Seibt, U. & W. Wickler. 1988. Bionomics and social structure of ‘‘Family Spiders’’ of the genus *Stegodyphus*, with special references to the African species *S. dumicola* and *S. mimosarum* (Araneida, Eresidae). Verh. naturwiss. Ver. Hamburg, 30:255–303.

Smith, D.R. 1987. Genetic variation in solitary and cooperative spiders of the genus *Anelosimus* (Araneae: Theridiidae). Pp. 347–348, *In* Chemistry and Biology of Social Insects. (J. Eder & H. Rembold, eds.). Verlag J. Peperny, Munich.

Vollrath, F. 1986. Eusociality and extraordinary sex ratios in the spider *Anelosimus eximius* (Araneae: Theridiidae). Behav. Ecol. Sociobiol., 18:283–287.

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