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SHORT COMMUNICATION

Anelosimus oritoyacu, a cloud forest social spider with only slightly female-biased primary sex ratios

Leticia Avilés and **Jessica Purcell**: Department of Zoology University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia V6T 1Z4, Canada. E-mail: laviles.ubczool@gmail.com

Abstract. We examine the social characteristics and sex ratio of the recently described *Anelosimus oritoyacu* Agnarsson 2006. We find that this spider, whose nests occur on tree crowns and bushes in open fields near Baeza, Ecuador, lives in colonies that may contain from one to several thousand adult females and their progeny. It differs from most other social congeners in that it occurs at relatively high elevations (1800–1900 m) and its primary sex ratio, 2.5 females per male, is the least biased of any known social species in the genus. The low sex ratio bias may reflect a low colony turnover rather than high gene flow among colonies, as the colonies occurred in complexes that were few and far between, but appeared to be long-lived. The relatively small body size of adult females and a web that appears to allow the capture of insects from all directions, combined with individual and group foraging, may allow the formation of large colonies at an elevation where insects, albeit abundant, are for the most part small.

Keywords: Ecuador, Theridiidae, cooperation, life cycle, quasisocial, subsocial

The genus *Anelosimus* Simon 1891 is of particular interest in the study of spider sociality because it contains the largest number of non-territorial permanent-social (or quasisocial) species of any spider genus (Avilés 1997; Agnarsson 2006; Lubin & Bilde 2007). Among these, *Anelosimus eximius* Keyserling 1884, *Anelosimus domingo* Levi 1963, *Anelosimus dubiosus* Keyserling 1881, *Anelosimus guacamayos* Agnarsson 2006, *Anelosimus lorenzo* Levi 1979, and *Anelosimus rupununi* Levi 1956 have been the subject of one to several studies (e.g., Fowler & Levi 1979; Rypstra & Tirey 1989; Rypstra 1993; Avilés & Tufiño 1998; Marques et al. 1998; Avilés & Salazar 1999; Avilés et al. 2007; Purcell & Avilés 2007; Yip et al. 2007). Here we report on a new non-territorial permanent social *Anelosimus*, recently described by Agnarsson (2006) as *Anelosimus oritoyacu*. We show that although this species exhibits social organization similar to that of other social *Anelosimus* spiders, it presents some interesting differences. Along with *A. guacamayos*, *A. oritoyacu* occurs at what appears to be the elevational range limit for permanent sociality in this genus (Avilés et al. 2007) and its sex ratio is the least biased among known social *Anelosimus* (Avilés & Maddison 1991; Avilés et al. 2007). Here we present a brief account of the size and structure of *A. oritoyacu*'s nests and colonies, informal observations on the cooperative nature of its societies, and, given the relevance of sex ratios as indicators of population structure (Williams 1966; Nagelkerke & Sabelis 1996; Hardy 2002), estimates of its primary and tertiary sex ratios.

Location of nest complexes seen.—Over a period of six years (January 2002–June 2008) we located eight areas, all within a 10 km radius of Baeza, Ecuador (0°27′S, 77°53′W; 1800–1900 m elev.), that contained from 1–12 *A. oritoyacu* nests (median 3.5) each, for a total of 55 nest records (Table 1). When more than one nest was present within these areas, nests were typically clustered within meters of one another in what we refer to as "nest complexes." Distances between identified nest complexes ranged from 25 m to 3.5 km. Most nests were located on the crowns of trees or on bushes growing on open hillsides or roadsides. The nest complexes appeared remarkably stable over time—at two of the sites initially discovered in 2002, nests were still present in 2007 and 2008 (Table 1). In contrast, nest complexes in species such as *Anelosimus eximius* rarely last more than 2–3 years (L. Avilés unpublished data), and those of species such as *Theridion nigroannulatum* Keyserling 1884 usually last less than a year (Avilés et al. 2006)

Nest and web structure.—*A. oritoyacu*'s nests differed from those of most other social species in the genus in lacking a well differentiated basal basket and extensive superior prey capture webbing, as depicted, for instance, for *A. eximius* by Yip et al. (2008, fig. 1; see also photo in Avilés et al. 2001, fig. 9). Instead, *A. oritoyacu*'s webs consisted of a core area surrounding a piece of vegetation and prey capture strands running away from the core, including inferiorly from it (Fig. 1), much like the nests of *A. rupununi* (Avilés & Salazar 1999), a canopy species. Also as in *A. rupununi*, *A. oritoyacu*'s silk was of a lighter texture and whiter coloration than in most other congeneric species. This web structure may reflect the position of the webs on tree crowns, and the need to capture insects flying from the side and below the nests. *A. oritoyacu*'s nests, as well as those of *A. rupununi*, thus have characteristics that appear a response to the canopy location preferred by these species. The nests we observed ranged broadly in size. At least two nests, but possibly as many as seven, of the 55 recorded contained either a single adult female or what appeared to be the clutch of a single female. The majority of nests, however, were considerably larger. Several nests in the first nest complex seen in January 2002, for instance, measured on the order of 3–4 m in diameter and probably contained several thousand individuals. Among 20 nests measured (two in 2002, three in 2004, eight in 2007, and seven in 2008, from one, two, three, and five different colony complexes, respectively), the smallest measured 13 × 13 × 23 cm and the largest, 205 × 156 × 100 cm.

Colony age structure.—Of the five nests that we dissected (three in January 2002 from the initial nest complex found, one in December 2002 from a complex 300 m away from the former, and one in 2008 from a seven-nest complex found 500 m away from the original found), four contained a mix of juvenile and/or egg sacs, subadult, and adult spiders, suggesting that reproduction is not strongly synchronized within nests (Table 2); the remaining nest contained only subadult males and females (Table 2). We surveyed the age structure of seven additional nests, both in June–July (2004, 2008) and in December (2002, 2007) and found that adults and juveniles/egg sacs were present at both times. Taken together, these findings suggest that *A. oritoyacyu* either has a short generation time and/or that its life cycle is largely independent of the mildly seasonal rain patterns of the region (rainiest: May–July; least rainy: December–February; Neill 1999). Adult males were seen overlapping with adult females in at least eight colonies, suggesting that the opportunity for intracolony mating is present.

Table 1.—Location of nest complexes seen and the number of seen nests they contained at the date of inspection. Location code: BZ-TN = Baeza-Tena Road; BZ-LA = Baeza-Lago Agrio Road; BZ, TN and LA = towns of Baeza, Tena, and Lago Agrio, respectively. Km from Baeza shown after each location code.

Location code	Latitude	Longitude	Elevation (m)	Dates seen	# Nests in complex
BZ-TN 8.1	0.497083	77.873861	1822	Jan-02	4
				Dec-02	few
				Dec-07	several
				Jun-08	several
BZ-TN 8.1 +333 m	0.4955	77.876306	1881	Dec-02	2
BZ-TN 1.0	0.46322	77.87662	1866	Dec-02	12
				Dec-07	4
				Jun-08	3
BZ town				Jun-04	1
BZ-TN 4.5	0.4729	77.86819	1848	Dec-07	1
				Jun-08	2
BZ-LA 2.4	0.45157	77.88392	1818	Jul-04	2
BZ-LA 2.6	0.451395	77.88954	1823	Jun-08	1
BZ-LA 3.0	0.45152	77.88399	1842	Dec-07	8
				Jun-08	7
BZ-LA 3.0 + 25 m	0.45152	77.88399	1842	Dec-07	4
				Jun-08	4

Clutch size and sex ratio.—In 2004, we collected egg sacs from a single large colony and used the method described by Avilés & Maddison (1991) to sex the embryos they contained. Egg sacs were off-white in color, averaged 3.9 ± 1.2 mm in diameter ($n = 5$), and contained between 16 and 46 eggs ($n = 11$, median = 37, mean = 34, SE = 3.13). In cytological spreads of individual embryos we counted the number of chromosomes contained in at least three dividing cells to determine whether the individual was male or female ($n = 130$, four egg sacs, Table 2). As in other species in the genus, males had 22 and females, 24 chromosomes (20 autosomes plus two sex chromosomes for males, and four sex chromosomes for females). Samples with fewer than three scorable dividing cells were not included in this analysis. We found the primary sex ratio to be about 2.5 females to a male (Table 3). This sex ratio differs significantly from the expected 1:1 sex ratio of subsocial species (Avilés & Maddison 1991; but see Gunnarsson & Andersson 1992 for a solitary species with biased sex ratios) and from the 10:1 sex ratio found in other social *Anelosimus* species (e.g., *A. eximius* and *A. domingo,* Avilés & Maddison 1991; *A. guacamayos,* Avilés et al. 2007). The tertiary sex ratio of adult and subadult spiders from nests collected in 2002 and 2008 similarly showed a bias of between two and five females to one male (Table 1).

Spider size and instars.—We measured the length of the tibia + patella on leg pair 1 (TP1) and leg pair 2 (TP2), as well as the sternum length (SL) and weight for a haphazard sample of subadult and adult spiders collected from one nest belonging to the original complex seen in 2002. Lengths were measured to the nearest 0.1 mm using an SZH Olympus dissecting stereomicroscope. We measured weights to the nearest 0.0001g using a Mettler Toledo standard level balance. The average ± SE of each measurement is presented for each instar (Table 4). We found that *A. oritoyacu* males were adult at a size

Figure 1.—*Anelosimus oritoyacu*'s nests photographed near Baeza, Ecuador, and photographs of adult male (above) and female (bottom) spiders. Note the different scales of the male and female photographs.

Table 2.—Colony age structure breakdown and the tertiary sex ratio (total number of adult plus subadult females / total number of adult plus subadult males) for five dissected *A. oritoyacu* colonies.

Colony	Collection date	Nest size (cm)	% Collected	Contents (number)							Tertiary sex ratio
				Ad m	Sub m	Ad f	Sub2 f	Sub1 f	Juvs	Sacs	
BZ-TN 8.1-1	6 Jan 2002	45 × 25 × 14	100	27	14	12	47	29	36	0	2.15:1
BZ-TN 8.1-2	6 Jan 2002	40 × 18 × 17	100	9	21	16	28	17	51	3	2.03:1
BZ-TN 8.1-4	6 Jan 2002	–	100	32	6	42	28	67	0	4	3.61:1
BZ-TN 8.1 + 333-1	17 Dec 2002	–	100	0	13	0	27		0	0	2.08:1
BZ-LA 3.0-7	20 Jun 2008	–	30	15	11	16	44	76	45	4	5.23:1

Table 3.—Primary sex ratio of *Anelosimus oritoyacu*, reported as the proportion of males among developing embryos in four egg sacs. The proportions are compared with 1:1 and 10:1 sex ratio expectations (right two columns) using either the binomial exact test for each egg sac (rows 1–4) and the total sample (row 5) or the weighted Z-transform method (last row), which combines the probabilities of the four egg sacs, with each sac weighted by the number of embryos scored to give more weight to more precise estimates, as recommended by Whitlock (2005).

Egg sac	Total embryos	Total scored	# of Males	Proportion of males	$P_{1:1}$	$P_{10:1}$
1	24	21	7	0.33	0.09	0.003
2	41	34	8	0.24	0.001	0.02
3	37	31	8	0.26	0.005	0.01
4	46	44	14	0.32	0.007	< 0.001
Total:	–	130	37	0.28	$<< 0.001$	$<< 0.001$
Mean:	–	32.5	9.25	—	Z_s	Z_s
St. Dev.:	–	9.47	3.2	—	0.04	0.01

Table 4.—Instar measurements for subadult and adult males and females. The mean is shown with the standard error in parentheses. Measurements include tibia + patella for leg pair 1 (TP1) and leg pair 2 (TP2), sternum length (SL) and weight.

Instar	*n*	TP1 (mm)	TP2 (mm)	SL (mm)	Weight (mg)
Male					
Subadult	6	1.25 (0.0224)	1.02 (0.0307)	0.7 (0.000)	3.53 (0.243)
Adult	7	1.86 (0.023)	1.39 (0.0254)	0.779 (0.0149)	3.87 (0.167)
Female					
First Subadult	4	1.43 (0.025)	1.16 (0.0239)	0.738 (0.0125)	3.43 (0.330)
Second Subadult	4	1.69 (0.375)	1.36 (0.0239)	0.9 (0.000)	4.43 (0.325)
Adult	14	2.129 (0.0266)	1.66 (0.0195)	1.04 (0.0116)	5.52 (0.229)

corresponding to the second subadult female instar (Table 3, Fig. 1), suggesting that males mature one instar earlier than females, as is the case with other tropical *Anelosimus* (e.g., Avilés 1986; Avilés et al. 2007).

Interestingly, *A. oritoyacu* appears to exhibit significantly less sexual size dimorphism than other Ecuadorian social *Anelosimus* (Fig. 2) (mean male: female body length ratio = 0.79 for *A. oritoyacu*; 0.68 for *A. guacamayos*; 0.66 for *A. domingo*; 0.65 for *A. eximius*; total body lengths of 15 to 31 specimens per species measured to the nearest 0.1 mm). This is due to adult *A. oritoyacu* females being relatively small compared to females in these other species (mean ± SE, *oritoyacu*: 3.65 ± 0.11 mm, *n* = 7; *eximius*: 4.84 ± 0.06 mm, *n* = 21; *guacamayos*: 4.04 ± 0.07 mm, *n* = 21; *domingo*: 3.49 ± 0.08 mm, *n* = 15), while *A. oritoyacu* males are relatively large (*oritoyacu*: 2.90 ± 0.19 mm, *n* = 8; *eximius*: 3.14 ± 0.08 mm, *n* = 10; *guacamayos*: 2.76 ± 0.12 mm, *n* = 4; *domingo*: 2.29 ± 0.08 mm, *n* = 12). The significance of this pattern is unclear.

Conclusions and discussion.—In conclusion, the size, duration, and demographic composition of *A. oritoyacu* colonies, including their female biased sex ratios, are consistent with this being a non-territorial permanent social species with colonies that last for multiple generations. The estimated 2.5 females per male primary sex ratio further suggests that some degree of intracolony mating must be taking place in this species, as is typical of species with this level of sociality (Avilés 1986, 1993, 1997). It is interesting, however, that *A. oritoyacu*'s sex ratio is the least biased among known permanent social *Anelosimus*, as other species typically exhibit sex ratios of 10:1 (*A. eximius*, *A. domingo*: primary sex ratio), 5:1 (*A. guacamayos*: primary sex ratio), and 3:1 (*A. dubiosus*: sex ratio among subadults to adults). Avilés (1993) showed through computer simulations that the most highly biased sex ratios arise when the degree of isolation of the colony lineages and their rate of turnover (i.e., rate of colony extinction and replacement) are the greatest. Sex ratios that are only slightly biased would thus arise if there were some degree of gene flow among the colonies' lineages and/or their rate of turnover were relatively low. Without genetic data to assess population structure on *A. oritoyacu*, at the moment we cannot ascertain which of these two (or combination of these two) factors plays the most important role in determining the low sex ratio bias of this species. However, the fact that *A. oritoyacu*'s nest complexes were few and far between does suggest that the likelihood that dispersing males would find nests of unrelated females (i.e., belonging to a different complex) are low to non-existent. On the other hand, the fact that *A. oritoyacu*'s nests and colonies appear relatively long-lived compared to those of other social *Anelosimus* suggests that a low rate of colony turnover may be the parameter most likely responsible for the low sex ratio bias observed, a prediction that requires further testing.

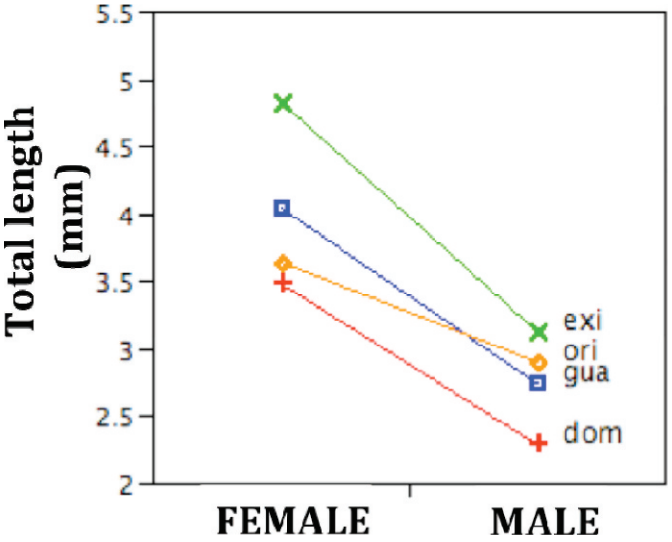

Figure 2.—Least square means for the total length of male and female spiders of four social *Anelosimus* species found in Ecuador (ex = *A. eximius*; ori = *A. oritoyacu*; gua = *A. guacamayos*; dom = *A. domingo*). Note that the size difference between *A. oritoyacu* males and females is significantly smaller than that found in the other three species, as confirmed by a significant interaction between species and sex ($F_{3,72} = 13.3$; $P = < 0.0001$) in a mixed model ANOVA including, in addition to the two factors and their interaction, colony identity as a random effect.

Another interesting aspect of the biology of this species is that, along with *A. guacamayos* (which occurs at up to 1,940 m elev.), it occurs at the elevational range limit for sociality in the genus (Avilés et al. 2007). Our earlier studies (Guevara & Avilés 2007; Powers and Avilés 2007) suggest that absence of an abundant supply of large insects at high elevations and latitudes may restrict social *Anelosimus* species to low-to mid-elevation tropical moist forests. The reason is that large insects, which are caught cooperatively by larger colonies, are needed to compensate for a decline in the surface area per unit volume of the prey capture snares—and thus of the number of insect prey per capita—as colony size increases (Yip et al. 2007). So, how can *A. oritoyacu* manage colonies containing thousands of individuals at an elevation where there are proportionally few large insects compared to lower elevation areas where social *Anelosimus* thrive? We suggest at least three non-mutually exclusive hypotheses to be tested in future studies. 1) Because *A. oritoyacu* females are small compared to most other *Anelosimus* species (see above and Fig. 2), the supply of insects larger than the spiders may still be significant at the elevations at which it lives. 2) There may be proportionally less loss of surface area per unit volume of *A. oritoyacu*'s webs as colonies grow because its webs appear to capture insects from all directions, rather than just from above, as in the more typical *Anelosimus* species with a basal basket-shaped nest (e.g., *A. eximius*, see drawing in Yip et al. 2007). 3) Although insects are on average smaller at higher elevation cloud forest areas, such as the one we studied (e.g., Guevara and Avilés 2007), our earlier studies show that insect density (number of insects per unit area) in these areas is greater than in the lowland tropical rainforest (Powers & Avilés 2007), so that the overall biomass of potential prey is either the same (E. Yip & L. Avilés unpublished data) or somewhat greater (Powers & Avilés 2007) than at lower elevations. Given an abundance of small insects, through individual and cooperative prey capture, both of which we have witnessed (L. Avilés unpublished data), the spiders may be able to sustain large social colonies if other aspects of their fitness are substantially enhanced by group living. During the course of this study we obtained preliminary evidence that females may care indiscriminately for each other's egg sacs, as we witnessed multiple instances of egg sac switching over a 24-h period in artificially established groups (four) of five color-coded females and their sacs (L. Avilés unpublished data). Above and beyond any benefits that may arise from cooperative prey capture, offspring fitness could thus be enhanced by the availability of surrogate caregivers in the event of the mother's death (e.g., Jones et al. 2007). These are all ideas that will need to be formally explored in future studies.

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