Natural History Miscellany

Altitudinal Patterns of Spider Sociality and the Biology of a New Midelevation Social *Anelosimus* Species in Ecuador

Leticia Avilés,[1,*] Ingi Agnarsson,[1,2,†] Patricio A. Salazar,[1,‡] Jessica Purcell,[1,§] Gabriel Iturralde,[3,‖] Eric C. Yip,[4,#] Kimberly S. Powers,[5,**] and Todd C. Bukowski[5,††]

1. Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada;
2. Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada;
3. Escuela de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador;
4. Department of Entomology, Cornell University, Ithaca, New York 14853;
5. Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721

abstract: To the extent that geography correlates with particular environmental parameters, the geographical distribution of phylogenetically related social and nonsocial organisms should shed light on the conditions that lead to sociality versus nonsociality. Social spiders are notorious for being concentrated in tropical regions of the world, occupying a set of habitats more restricted than those available to the phylogenetic lineages in which they occur. Here we document a parallel pattern involving elevation in the spider genus *Anelosimus* in America and describe the biology of a newly discovered social species found at what appears to be the altitudinal edge of sociality in the genus. We show that this is a cooperative permanent-social species with highly female-biased sex ratios but colonies that are one to two orders of magnitude smaller than those of a low-elevation congener of similar body size. We suggest that the absence of subsocial *Anelosimus* species in the lowland rain forest may be due to an increased probability of maternal death in this habitat due to greater predation and/or precipitation, while absence of a sufficient supply of large insects at high elevations or latitudes may restrict social species to low- to midelevation tropical moist forests. We refer to these as the "maternal survival" and "prey size" hypotheses, respectively, and suggest that both in combination may explain the geographical distribution of sociality in the genus.

Keywords: biogeography of sociality, elevation, latitude, social evolution, social spiders, sex ratio, group foraging, Theridiidae.

* Corresponding author; e-mail: laviles@zoology.ubc.ca.

† E-mail: iagnarsson@gmail.com.

‡ E-mail: salazar@zoology.ubc.ca.

§ E-mail: purcell@zoology.ubc.ca

‖ E-mail: jluna@hoy.net.

E-mail: ecy7@cornell.edu.

** E-mail: ksp@deainc.com.

†† E-mail: toddbukowski@yahoo.com.

Spider sociality is a rare phenomenon (about 0.06% of spider species) but one that has nonetheless evolved repeatedly (Avilés 1997; Agnarsson et al. 2006; Johannesen et al. 2007). Nonterritorial permanent-social spiders, also known as quasi-social or simply "social" (e.g., Avilés 1997; Lubin and Bilde, forthcoming), are scattered in several distantly related families and hence differ in many morphological, behavioral, and physiological traits. They are found in diverse habitats and on most continents and hence experience a variety of environments. Many species occur in tropical moist forests (e.g., Levi et al. 1982; Riechert et al. 1986; Avilés et al. 2001), while others inhabit dry thornbush or semideserts (e.g., Kraus and Kraus 1988; Crouch and Lubin 2000). Despite these differences and multiple independent origins, social spider species exhibit striking similarities in their behavior and population structure (reviewed in Avilés 1997). Colony members cooperate in nest building and maintenance, prey capture and feeding, and brood care. Unlike most social insect societies, where individuals disperse out of the natal nest to mate (Wilson 1971), social spider colonies grow through the internal recruitment of new offspring generations produced by male and female spiders who remain within their natal nest to mate. New colonies arise through the budding or fission of existing colonies. Colonies are thus isolated population lineages that grow, proliferate, and become ex-

tinct without mixing with one another. As shown by Avilés (1993), such population structure and dynamics, combined with the greater proliferation success of more female-biased (i.e., faster-growing) colonies, may have allowed the evolution of the highly female-biased sex ratios that characterize the permanent-social spiders (reviewed in Avilés 1997). In contrast, related subsocial (or periodic-social) species form colonies that contain the offspring of a single female, disperse before mating, and have 1 : 1 sex ratios (Kraus and Kraus 1988; Avilés and Maddison 1991; Avilés and Gelsey 1998; Evans 2000; Bilde et al. 2005; Agnarsson 2006; Avilés and Bukowski 2006; Viera et al. 2006).

Interestingly, all social spider species appear to occupy a set of habitats more restricted than those available to the phylogenetic lineages in which they occur. Most notably, they are all concentrated in tropical regions of the world (reviewed in Avilés 1997), while related subsocial species extend into the temperate zones (e.g., Kraus and Kraus 1988; Avilés and Gelsey 1998; Agnarsson 2006; Viera et al. 2006; Jones et al. 2007). Here we demonstrate a parallel pattern involving elevation. We show that social species in the genus *Anelosimus* (Agnarsson 2006) in Ecuador occur exclusively in the lowland rain forest up to midelevation cloud forests, while subsocial species are absent from the lowland rain forest but are common at higher elevations. We also report on a newly discovered social species, *Anelosimus guacamayos* Agnarsson 2006 (for its taxonomic description, see Agnarsson 2006), found at higher elevations than previously studied species in the genus. We first show that this is a cooperative permanent-social species by demonstrating that it forms colonies that contain multiple adult females and their offspring, exhibits cooperative prey capture and feeding, and has female-biased sex ratios. We then test the hypothesis that this species is somehow "less social" than a lower-elevation social congener of similar body size, *Anelosimus eximius* Keyserling 1884 (Agnarsson 2006), by comparing the colony size distribution and spacing of spiders within nests in these two species. Uetz and Hodge (1990), in comparing two species of orb-weaving colonial (noncooperative) spiders from Mexico in the genus *Metepeira* (Araneidae), found that spiders in a prey-poor environment, where they were predicted to be less social, lived solitarily or in small groups, with greater spacing among group members, when compared with spiders in a prey-rich environment, where groups were bigger and spacing smaller (Uetz and Hodge 1990). We thus consider that the presence of a greater proportion of nests with solitary females, smaller colony sizes, or greater spacing of spiders within the nests, a possible indicator of mutual tolerance (Uetz and Hodge 1990), may be indicative of a "lower" level of sociality in the higher-elevation species.

Methods

Altitudinal Patterns of Anelosimus Sociality

Through surveys along several hundred kilometers of roads and visits to natural reserves and other point localities in Ecuador, we recorded the presence of *Anelosimus* species at elevations ranging from 4 to 3,000 m (table A1 in the online edition of the *American Naturalist*). Areas surveyed included several main and secondary roads on the eastern slopes of the Andes, three roads on the western slopes, six natural reserves or other point localities in eastern Ecuador, 10 in the highlands, and three in the west. Areas visited below 700 m elevation correspond to lowland tropical rain forest and those between 700 and 2,500 m, east and west of the Andes, to lower montane rain forest or cloud forest (see Neill 1999). Highland areas surveyed ranged from 2,200 to 3,000 m, with vegetation types ranging from upper montane rain forest to semidesert. Voucher specimens have been deposited in the collections of the Museum of Comparative Zoology, the Museo Ecuatoriano de Ciencias Naturales, the Museo de Invertebrados de la Pontificia Universidad Católica del Ecuador, the Smithsonian Natural History Museum, and the University of British Columbia (see table A2 in the online edition of the *American Naturalist*).

Anelosimus guacamayos Biology

We obtained data on the age composition and tertiary sex ratio (juveniles to young adults) of *Anelosimus guacamayos* colonies through the collection of entire ($N = 15$ in 1999; $N = 7$ in 2002) or partial (15%–50% of $N = 4$ nests in 2002) nests from the area in eastern Ecuador where we first discovered the species in August 1999, that is, Cocodrilos, in the Napo Province, 0.63°–0.65°S, 77.8°W, 1,740–1,940 m elevation. We also obtained a preliminary estimate of *A. guacamayos*'s primary sex ratio from cytological preparations of 45 embryos randomly chosen from five egg sacs collected from the Cocodrilos area in 1999 (four sacs from a colony with 39 adult females and one from a colony with three adult females). Clutch size data were obtained from four of these sacs (three from the large colony and one from the small colony), plus three sacs collected in 2003.

We collected nests after measuring and drawing their aerial and lateral cross sections (as in Purcell and Avilés 2007, their fig. 1) and classified the spiders they contained by instar and sex on the basis of size and secondary sexual characters. Males were distinguishable from females because of their enlarged palpi starting in their fourth instar outside the sac. Females matured in their seventh instar, one instar later than males. In order to minimize biases due either to differential maturation of juvenile males and

females or to earlier mortality of adult males, we used in our tertiary sex ratio estimates only colonies ($N = 8$) where most or all juveniles had already differentiated and where adults were not old enough for males to have started to die. For the primary sex ratio, we obtained embryo chromosome preparations using the methodology of Avilés and Maddison (1991). In *Anelosimus*, males have 22 (20 + XX) and females 24 (20 + XXXX) chromosomes (Avilés and Maddison 1991). All preparations used in our estimate received identical counts by two independent scorers.

Also at the Cocodrilos site, we observed 14 prey capture attempts and eight captures during 3.5 h of observations of one large-sized and one medium-sized nest (large colony: 2226–2326 and 1146–1305 hours; medium colony: 0958–1114 hours), both in January 2002. We also obtained records of 179 prey feeding events over a period of 18 days in June 2003 (from $N = 15$ colonies) and 6 days in July 2004 ($N = 8$ colonies).

Comparison with *Anelosimus eximius*

In order to compare the *A. guacamayos* and *A. eximius* colony size distributions, we used methods that allowed unbiased sampling of nests of different sizes. In the case of *A. guacamayos*, this involved complete censuses of all nests present within four 200 × 5-m quadrats selected to be centered in areas of high nest density at the Cocodrilos site. We used two census dates in our analyses, one randomly chosen among 19 available (September 2003; $N = 21$ nests), to parallel data collection methods used for *A. eximius*, and the other corresponding to the mean date of the start of egg laying for colonies in a quadrat (January–June 2003, depending on quadrat; $N = 47$ nests), to account for the greater synchrony in the life cycle stages of individuals within *A. guacamayos* nests (length of egg laying period within nests, least squares mean and standard error, back-transformed from natural logs: in *A. guacamayos*: 4.8, 4.5–5.2 weeks, $N = 46$ nests at Cocodrilos; in *A. eximius*: 8.2, 7.1–9.4 weeks, $N = 17$ nests at J. M. Durini lumber plantation; colony size included as a covariate in the model). In the case of *A. eximius*, we used two randomly laid transects plus one transect laid in an area of high nest density (for details, see Purcell and Avilés 2007) at each of four sites representing two elevations and two habitat types: lowland forest edge at the Cuyabeno Nature Reserve (220–340 m elevation, Sucumbíos Province, 0.03°S, 76.2°–76.3°W; $N = 23$ nests), lowland forest interior at the Cuyabeno Nature Reserve (as before) and at Jatun Sacha (400 m elevation, Napo Province, 1.07°S, 77.61°W), and upper-elevation forest edge along the Vía a Loreto (980–1,160 m elevation, Napo Province, 0.7°S, 77.76°–77.58°W; $N =$

61 nests), an area in the vicinity of Cocodrilos where *A. eximius* occurs only at the forest edge (Purcell and Avilés 2007). In our analyses, we combine the two lowland forest interior sites (Cuyabeno interior and Jatun Sacha; $N = 41$ nests) because there were no significant differences between them in the proportion of solitary females (binomial exact test: $P = .23$) or colony size (Wilcoxon test: $\chi^2 = 2.31$, $P = .13$).

To compare spacing of spiders within nests, we used both density and average nearest neighbor distances (NNDs). We estimated density by dividing the volume of the nest (approximated with the formula for an ellipsoid) by the total number of adult female spiders it contained. NNDs were estimated on a random sample of adult females in a nest by using a thin ruler from the outside of the web to avoid disturbing the spiders. All NND estimates for both species were done during the day to ensure comparability because spacing patterns could differ between day and night. Both measures were standardized by spider body size by dividing the Euclidean distance by the typical length of adult *A. eximius* (4.6 mm) or *A. guacamayos* (4.05 mm) females (spider sizes as given in Agnarsson 2006). The *A. guacamayos* data were collected at the Cocodrilos site ($N = 19$ nests for the density measures; $N = 7$ for NND). For *A. eximius*, we used data for Cuyabeno edge ($N = 24$ for density; $N = 6$ for NND) and interior populations ($N = 40$ for density; $N = 7$ for NND), Jatun Sacha interior populations ($N = 14$ for density; $N = 7$ for NND), and Vía a Loreto edge populations ($N = 13$ for density only). Cuyabeno and Jatun Sacha forest interior populations were combined in the analyses because they exhibited no significant differences in spider spacing between them (for the contrast in spider density within nests between the two sites: $F = 0.85$, df $= 1,95$, $P = .36$).

Statistical Analyses

We used a one-sided Kolmogorov-Smirnov test (R, ver. 2.2.1) to compare the colony size distributions and a binomial exact test (http://faculty.vassar.edu/lowry/binomialX.html) to compare the proportion of solitary females between *A. guacamayos* (random or egg laying dates) and each of the three *A. eximius* elevation/habitat type combinations. After excluding colonies with solitary females, we also used a Wilcoxon test to compare median colony sizes between the two species. The *P* values were corrected for each set of three comparisons using the Bonferroni correction.

We used ANOVA, with colony size as a covariate (ln number of adult females), to test for differences in both spider density and NND within nests (both variables natural-log transformed) across the two species and the two

habitat types (edge and interior for *A. eximius* at the low-land sites; edge for *A. guacamayos* and *A. eximius* at its higher-elevation sites [density only for the latter]). We used a Tukey-Kramer a posteriori multiple-comparisons test to determine which of the different species/habitat type combinations were significantly different from one another.

Results

### Altitudinal Distribution of Anelosimus *Sociality*

Anelosimus guacamayos nests were found on the eastern slopes of the Andes at elevations ranging from 991 to 1,940 m (from north to south: 1,290–1,329 m in the El Chaco area, 1,750–1,940 m in the Cocodrilos area, 991–1,248 m in the Puyo area, and 1,415–1,900 m in the Limón area; table A2), all in open habitat along the road or on landslide sites but not in forests. All of these areas correspond to lower montane cloud forest (Neill 1999). In contrast, the social *Anelosimus eximius*, *Anelosimus domingo*, and *Anelosimus rupununi* were found in lowland rain forest, at elevations no greater than 1,300 m (maximum documented elevation for *A. eximius*: 1,300 m; for *A. domingo*: 910; and for *A. rupununi*: 800 m; fig. 1; table A2). Only the recently described *Anelosimus oritoyacu* Agnarsson 2006 (L. Avilés and J. Purcell, unpublished data) occurred at an elevation similar to the one for *A. guacamayos* (1,800–1,950 m). Subsocial species, on the other hand, were common at altitudes above 1,000 m but, apart from *Anelosimus baeza*, were absent from areas below 900 m (higher for

some species). At elevations between 1,000 and 2,000 m, both social and subsocial species occurred in sympatry (fig. 1; table A2), with nests of the two types often found alongside each other, although subtle microhabitat differences cannot be ruled out (J. Purcell and L. Avilés, unpublished observations).

A. guacamayos *Social System*

As in other species in the genus, *A. guacamayos* nests were basket shaped, with a dense basal sheet, a scaffolding of irregular webbing in the interior, and superior vertical and oblique prey capture lines connecting the nest to the surrounding vegetation. Fifty-three percent of the nests surveyed at a random date and 52% of those surveyed at the peak of the egg laying period contained multiple adult females and their offspring (range = 2–600 females plus offspring). The remaining nests contained a single adult female with or without offspring. No nests contained single subadult or juvenile individuals, indicating that individuals do not disperse to establish new nests in preadult stages. If all age classes are included, the largest nest recorded contained 233 adult females plus 2,680 subadults and juveniles and measured 2.6 m × 0.4 m × 0.5 m. The size of a nest (area of the ellipse corresponding to the cross section at the widest part of the basket) was correlated with the number of spiders it contained (fig. A1 in the online edition of the *American Naturalist*).

Both the primary and the tertiary sex ratios were highly
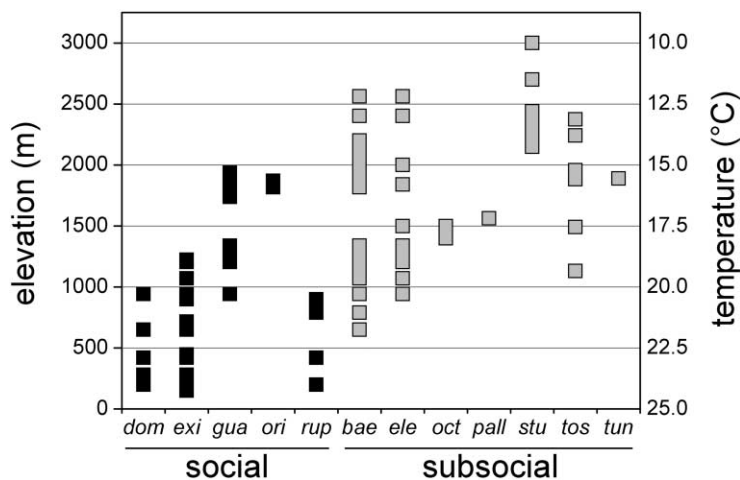
Figure 1: Altitudinal pattern of sociality in the spider genus *Anelosimus* in Ecuador, with associated mean annual temperatures. Social and subsocial *Anelosimus* species listed in alphabetical order within each category; abbreviations are as follows: *dom* = *domingo*, *exi* = *eximius*, *gua* = *guacamayos*, *ori* = *oritoyacu*, *rup* = *rupununi*, *bae* = *baeza*, *ele* = *elegans*, *oct* = *octavius*, *pall* = *pallatanga*, *stu* = *studiosus*, *tos* = *tosum*, *tun* = *tunguragua*. See Agnarsson (2005, 2006) for taxonomic descriptions and Avilés et al. (2001) for a review of the biology of the Amazonian species (for further details and more recent studies, see Rypstra and Tirey 1989; Avilés and Tufiño 1998; Avilés and Salazar 1999; Powers and Avilés 2007; Purcell and Avilés 2007). Mean annual temperatures based on Neill and Jørgensen (1999).

female biased: 38 females and seven males, or 15.5% males, for the primary sex ratio (7.5%–27.2% males, 95% confidence interval [CI]) and 759 females and 89 males, or 10.5% males, for the tertiary sex ratio (8.8%–12.4% males, 95% CI). On the basis of their CIs, both figures are significantly different from a 1 : 1 sex ratio but not significantly different from one another or from a third sex ratio estimate obtained among subadults to young adults in colonies at the Cocodrilos site censused between January and October 2003 (9.2% males, 5.5%–14.1%, 95% CI; Iturralde 2004). The average number of eggs per sac was 33.1 ± 2.3 SE (range = 26–45, $N = 7$ egg sacs).

With the exception of one case where a single adult female captured a 3-mm fly, other prey capture events involved the joint participation of three to 22 spiders of various ages ($N = 13$ events with more than one spider, median = 7). There was a significant correlation between the size of an insect (range = 3–30 mm) and the number of spiders involved in its capture ($r = 0.66$, df = 1, $P = .01$), as well as with the number of spiders feeding on it (one to 28 spiders in 186 feeding events seen in 25 colonies; $F = 40.9$, df = 1,160, $P < .0001$, $R^2 = 0.42$, with colony included in the model as a random effect). In five of seven complete capture and feeding sequences observed, a greater number of individuals (a 30%–275% increase) fed on than participated in the capture of a particular prey item.

Comparison with A. eximius

Anelosimus guacamayos had a significantly greater proportion of nests with solitary females when compared with *A. eximius* populations in the lowlands, in both edge (Cuyabeno River) and interior (Cuyabeno forest and Jatun Sacha) habitats (binomial exact test: $P < .0001$ for both comparisons), but not when compared with populations in the upper-elevation Vía a Loreto area ($P = .2$; fig. 2*A*). Nonetheless, the *A. guacamayos* colony size distribution consisted of colonies that were one to two orders of magnitude smaller than those of *A. eximius* at any of the areas surveyed (fig. 2*B*), whether all or only colonies with more than one female were included in the analyses (Kolmogorov-Smirnov test of entire distribution at a random date vs. *A. eximius* lowland edge: $D = 0.81$, $P < .0001$; lowland forest: $D = 0.71$, $P < .0001$; upper elevation: $D = 0.48$, $P = .0001$; corresponding Wilcoxon tests for nests with more than one female only: $\chi^2 = 18.4$, $P < .0001$; $\chi^2 = 13.8$, $P = .0002$; $\chi^2 = 6.3$, $P = .012$; similar P values for tests with colonies during the egg laying period; significance level corrected to 0.0167 to account for three multiple comparisons in each test).

There were significant differences in the spacing of adult female spiders within nests in a comparison across the *A.*

guacamayos and the three *A. eximius* populations surveyed (for the species/habitat type effect on spider density within nests: $F = 9.67$, df = 3, 97, $P < .0001$; fig. 3; for the nearest neighbor test: $F = 7.13$, df = 2, 22, $P = .004$; data not shown). These differences, however, were due to differences between forest interior and forest edge populations, regardless of species type, rather than to a difference between species (Tukey-Kramer test not significant; fig. 3). Thus, *A. eximius* forest interior colonies in the lowland sites had the spiders more closely packed together (NND least squares mean ± standard error = 4.4 ± 0.5 adult female spider body lengths) than either *A. eximius* forest edge colonies in the lowlands (7.8 ± 1.1 spider body lengths) or at higher elevations or *A. guacamayos* colonies (7.4 ± 1.1 spider body lengths; data not shown). Spider spacing within nests did not differ between the *A. guacamayos* population studied and those of *A. eximius* high- or low-elevation edge populations (fig. 3).

Discussion

That elevation parallels latitude for a variety of biogeographical patterns is a well-recognized fact in biogeography (e.g., Stevens 1992; Jimenez-Castillo et al. 2007; Swenson and Enquist 2007). Here we show that the global pattern of spider sociality being concentrated in tropical areas of the world (reviewed in Avilés 1997) is paralleled by a similar pattern involving elevation. We show that social species in the spider genus *Anelosimus* in Ecuador predominate in lowland rain forests up to midelevation cloud forests, while subsocial species are common at higher elevations but are absent from the lowland rain forest (fig. 1). The pattern extends beyond the genus, as all other social spider species known for Ecuador (e.g., *Tapinillus* sp. [Avilés 1994], *Aebutina binotata* [Avilés 2000], and *Theridion nigroannulatum* [Avilés et al. 2006]) occur below 1,300 m (reviewed in Avilés et al. 2001). A pattern of decreasing sociality with increasing elevation also applies within species, as populations of *Anelosimus eximius* toward the upper end of its elevational range (1,000–1,300 m) have both a greater proportion of solitary females and smaller average nest sizes than do populations in the lowlands (Purcell and Avilés 2007; fig. 2). An absence of social species outside the latitudinal range of 10.2°N and 23.5°S is also clear in the genus (e.g., Agnarsson 2006). The northernmost representatives are the putatively social *Anelosimus puravida* in Costa Rica (Agnarsson 2006) and *A. eximius* in Panama (Vollrath 1986); the southernmost representatives are *Anelosimus lorenzo* in Paraguay (Fowler and Levi 1979) and *Anelosimus dubiosus* in Brazil (Marques et al. 1998). Subsocial species, in contrast, extend as far north as 31.5° in Arizona (Avilés and Gelsey 1998) and 38.6° in the eastern United States (Furey 1998; Jones et al. 2007) and as far
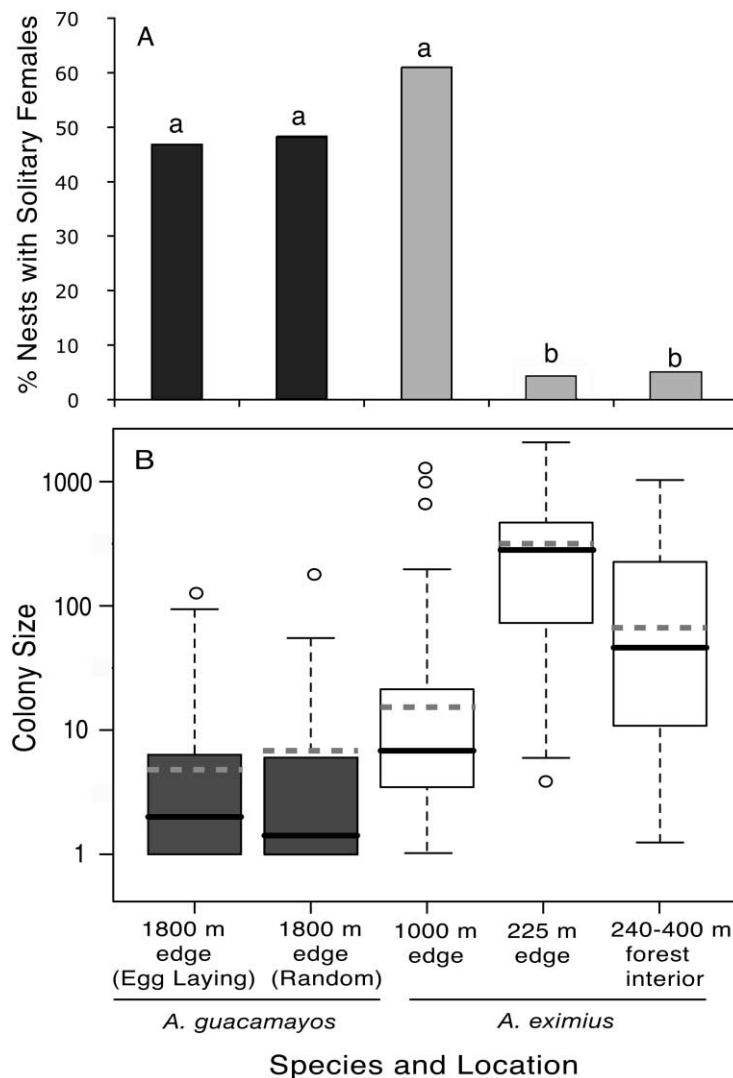
Figure 2: *A,* Proportion of nests with solitary females in the *Anelosimus guacamayos* population along the road at Cocodrilos (1,800 m), compared with *Anelosimus eximius* populations in midelevation edge (Vía a Loreto, 1,000 m), lowland edge (Cuyabeno River, 225 m), and lowland forest (Cuyabeno forest, 240 m, and Jatun Sacha, 400 m). Lowercase letters show significant binomial exact test differences between either of the *A. guacamayos* samples and each of the *A. eximius* populations. *B,* Median and quantile boxes showing the distribution of colony sizes (shown as the $\log_{10}$ total number of adult and subadult females) in the *A. guacamayos* population and the *A. eximius* populations in the three habitats. Shown also (*gray dashed lines*) are the medians of the distributions once nests with solitary females have been removed from the analysis. In both tests, the *A. guacamayos* population is represented either by a randomly chosen date among those surveyed ("random") or by a date corresponding to the peak of the egg laying period for each quadrat ("egg laying").

south as 34.5° in Uruguay and 31.4° in Argentina and southern Brazil (Viera et al. 2006). Interestingly, the subsocial *Anelosimus studiosus* occurs at low elevations at high latitudes (North America, southern South America) but mostly between 1,000 and 3,000 m in tropical America (I. Agnarsson, personal observation; see also Agnarsson 2006).

The concentration of social *Anelosimus* species in the low- to midelevation moist forests is particularly intriguing

as the genus is common at high latitudes and is most speciose at elevations above 1,000 m in the tropics (Agnarsson 2005, 2006; Agnarsson and Kuntner 2005; Agnarsson and Zhang 2006). Why would social *Anelosimus* or, for that matter, most social spider species be concentrated in the lowland tropics? We suggest that two separate patterns need to be addressed and that these patterns— absence of subsocial species in the lowland tropical rain forest and absence of social species at high elevations and
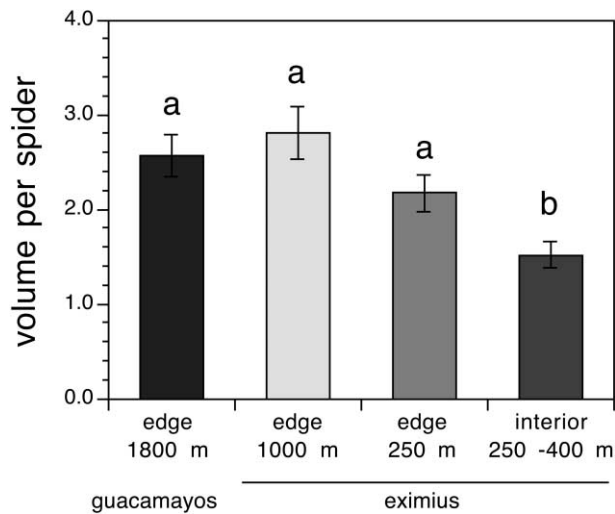
Figure 3: Nest volume per adult female spider (ln volume in adult female length units) for *Anelosimus guacamayos* populations in Cocodrilos, Ecuador, compared with *Anelosimus eximius* populations in the Vía a Loreto (edge habitat, 1,000 m elevation), Cuyabeno River (edge habitat, 250 m elevation), and combined Cuyabeno forest and Jatun Sacha forest (forest interior habitat, 250 and 400 m elevation, respectively) habitats. Bars shown with different letters are significantly different under a Tukey-Kramer test.

latitudes—respond to different factors for which elevation and/or latitude may be coarse predictors. We refer to the hypotheses potentially explaining these patterns as the "maternal survival" (Jones et al. 2007) and "prey size" (Powers and Avilés 2007) hypotheses, respectively.

The hypothesis of Jones et al. (2007), that cooperative breeding should be favored in environments where a single female has a high probability of dying before her offspring are able to care for themselves, may explain the absence of subsocial species in the lowland rain forest but for reasons other than those relevant to the species for which this hypothesis was proposed. Jones et al. (2007) argue that the greater incidence of multiple-female nests at higher latitudes in the subsocial *A. studiosus* (a reverse latitudinal cline) may reflect the more protracted development of the offspring at latitudes where temperatures are lower. Although temperature trends in relation to spider sociality run in the opposite direction along the altitudinal cline we describe here (fig. 1), the probability of maternal death during offspring development may be greater in the lowland tropical rain forest than at higher elevations or latitudes, by virtue of potentially greater rates of predation in this habitat. Heavy and frequent precipitation in the lowland rain forest may also contribute to the failure of single-female nests and may thus be an additional factor selecting for cooperative breeding in this

habitat, in particular in genera, such as *Anelosimus* or *Agelena* (Riechert et al. 1986), in which nests and prey capture snares require heavy investment in silk. Consistent with the hypothesis that the lowland rain forest may be an unsuitable environment for a subsocial or solitary lifestyle in the genus, Avilés and Tufiño (1998) showed that females of the social *A. eximius* living solitarily cannot replace themselves in this environment. In contrast, group living females in the same habitat (Avilés and Tufiño 1998) or solitary females of *Anelosimus arizona* in a dry temperate habitat (Avilés and Gelsey 1998) produce significantly more than one surviving adult female offspring per capita.

In addition to predation and precipitation, a third unrelated factor that may in turn be responsible for the absence of social species at higher elevations and latitudes is prey size (Powers and Avilés 2007). Powers and Avilés (2007; see also Guevara and Avilés 2007) have recently shown that insects in the lowland rain forest are considerably larger than insects at either higher elevations or higher latitudes (e.g., average insect weight [mean and standard error] in malaise trap samples, back-transformed from natural-log least squares means: 4.7, 4.2–6.5 mg at 1.07°S, 77.61°W, 400 m vs. 1.9, 1.7–2.2 mg at 0.60°S, 77.86°W, 2,073 m and 1.6, 1.2–2.0 mg at 31.49°N, 110.32°W, 1,524 m) and that areas lacking social species are not necessarily prey poor (for details, see Powers and Avilés 2007; for insect size distributions obtained with multiple sampling techniques at the same two elevations in Ecuador, see Guevara and Avilés 2007). Interestingly, an upper-elevation cloud forest site where only a subsocial species lives was found to have at least as much, if not more, total biomass available per unit area and time than the lowland rain forest. Here, however, insects were mostly small (Guevara and Avilés 2007; Powers and Avilés 2007). Because small insects do not require multiple individuals for their capture (e.g., Rypstra 1990), such environments may thus not provide a sufficient incentive for the development of large cooperative spider societies. It is thus not absence of sufficiently high overall biomass but rather absence of a sufficient supply of large insects at higher elevations and higher latitudes that may restrict social species to their lowland tropical habitat (Powers and Avilés 2007).

Because it cannot be elevation or altitude per se that explains the distribution of social and nonsocial species, it is not surprising that the altitudinal and latitudinal patterns are imperfect. Thus, a number of subsocial *Anelosimus* species live at low elevations in the dry coastal areas of Ecuador, where, interestingly, social species are absent (Agnarsson 2006). Presumably, independent of altitude, some environmental variables are shared between the high-elevation habitats and the dry coastal habitats that facilitate the occurrence of subsocial species but disfavor sociality. On the basis of the factors we have hypothesized

to be potentially relevant, we can then predict that the insect size distribution in these areas does not contain a sufficient supply of large insects and that single females are able to at least replace themselves in this environment, as predation rates and/or precipitation rates may be sufficiently low.

The discovery of *Anelosimus guacamayos*, the biology of which we report here for the first time, is interesting in this context because it occurs at what could be the altitudinal edge of sociality in the genus. Here we show that this is a typical nonterritorial permanent-social spider (sensu Avilés 1997), with nests that contain multiple adult females and their offspring, cooperative prey capture, and sufficient population subdivision to have led to its strongly female-biased sex ratio (Avilés 1993; Iturralde 2004). Consistent with the hypothesis that higher elevations are less conducive to sociality in the genus, however, we found that *A. guacamayos* colonies were one or two orders of magnitude smaller than those of its lower-elevation congener of similar body size, *A. eximius* (fig. 2*B*), indicating dispersal at smaller colony sizes (P. Salazar, G. Iturralde, and L. Avilés, unpublished data) and possibly lower levels of tolerance among nestmates. Spacing among female spiders within nests, however, appeared to be related not to tolerance or food availability (e.g., Uetz and Hodge 1990) but rather to factors that differ between forest edge and interior habitats, regardless of elevation. We found that *A. guacamayos*, an edge species, had individuals that were spaced similarly to those of forest edge populations of *A. eximius* at low and high elevations, while *A. eximius* had more closely packed spiders in the forest interior than in the forest edge (fig. 3). Because we have found no difference in prey abundance or size between edge and interior habitats in the lowland rain forest (for density: $F = 0.07$, df $= 1, 11$, $P = .79$; for insect size: $F = 0.56$, df $= 1, 11$, $P = .47$; six malaise traps placed over five [nonconsecutive, randomly selected] days at either river edge or forest interior sites at the Cuyabeno Nature Reserve; trap ID included as a random effect in the model; E. Yip and L. Avilés, unpublished data; methodology as in Powers and Avilés 2007), we suspect that these patterns reflect instead differences in the architecture of the vegetation substrates between edge and interior habitats (Purcell and Avilés 2007). The discovery of *A. guacamayos* also adds to the growing pool of known social spider species (Avilés 1997; Avilés et al. 2001, 2006; Lubin and Bilde, forthcoming) and to the number of independent origins of sociality within the genus and among spiders as a whole (Avilés 1997; Agnarsson 2004, 2006; Agnarsson et al. 2006; Johannesen et al. 2007).

Two species in the Southern Hemisphere that occur at the latitudinal edge of sociality in the genus—*Anelosimus dubiosus* and its close relative *Anelosimus jabaquara*—also appear less social than congeners closer to the equator. *Anelosimus jabaquara* has an intermediate level of sociality, with mostly subsocial elements. The majority of its colonies consist of a single mother and her offspring, offspring dispersal occurs for the most part before mating, adult females show aggression toward one another, and sex ratios are only slightly female biased (Marques et al. 1998). The rupture of the social phase, however, appears not to be obligatory because smaller females may remain in the natal nest and form colonies that may last for several generations (Gonzaga and Vasconcellos-Neto 2001). *Anelosimus dubiosus* is permanently social, showing tolerance and cooperation between adults and more biased sex ratios (Marques et al. 1998). But, like *A. guacamayos*, dispersal also appears to occur at colony sizes that are one or two orders of magnitude smaller than those of *A. eximius*, and a greater portion of females live solitarily (Marques et al. 1998).

Although the trend is by no means universal (e.g., Kaspari and Vargo 1995), a correlation between greater levels of sociality and lower altitude or latitude has been noted both within and among species for a variety of other social organisms, including cooperative breeding birds (Brown 1987), wasps (Reeve 1991), bees (Packer 1990; Eickwort et al. 1996; Richards 2000; Cronin and Schwarz 2001), thrips (Kranz et al. 2002), and others. Exploring the ecological factors responsible for such patterns in a system as eminently tractable as the genus *Anelosimus* (e.g., Avilés and Tufiño 1998; Avilés and Bukowski 2006; Jones et al. 2007; Powers and Avilés 2007) should thus shed light on how out of the interaction between organisms and their environments the biogeographical patterns of sociality, and sociality itself, emerge.

Literature Cited

Agnarsson, I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). Zoological Journal of the Linnean Society 141:447–626.

———. 2005. A revision and phylogenetic analysis the American *ethicus* and *rupununi* groups of *Anelosimus* (Araneae, Theridiidae). Zoologica Scripta 34:389–413.

———. 2006. A revision of the New World *eximius* lineage of *Anelosimus* (Araneae, Theridiidae) and a phylogenetic analysis using worldwide exemplars. Zoological Journal of the Linnean Society 146:453–593.

Agnarsson, I., and M. Kuntner. 2005. Madagascar: an unexpected hotspot of social *Anelosimus* spider diversity (Araneae: Theridiidae). Systematic Entomology 30:575–592.

Agnarsson, I., and J. X. Zhang. 2006. New species of *Anelosimus* (Theridiidae, Araneae) from Africa and Southeast Asia, with notes on sociality and color polymorphism. Zootaxa 1147:1–34.

Agnarsson, I., L. Avilés, J. A. Coddington, and W. P. Maddison. 2006. Social theridiid spiders: repeated origins of an evolutionary dead-end. Evolution 60:2342–2351.

Avilés, L. 1993. Interdemic selection and the sex ratio: a social spider perspective. American Naturalist 142:320–345.

———. 1994. Social behavior in a web-building lynx spider, *Tapinillus* sp. (Araneae, Oxyopidae). Biological Journal of the Linnean Society 52:163–176.

———. 1997. Causes and consequences of cooperation and permanent sociality in spiders. Pages 476–498 *in* J. C. Choe and B. J. Crespi, eds. The evolution of social insects and arachnids. Cambridge University Press, Cambridge.

———. 2000. Nomadic behaviour and colony fission in a cooperative spider: life history evolution at the level of the colony? Biological Journal of the Linnean Society 70:325–339.

Avilés, L., and T. C. Bukowski. 2006. Group living and inbreeding depression in a subsocial spider. Proceedings of the Royal Society B: Biological Sciences 273:157–163.

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

Avilés, L., and 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). Journal of Arachnology 19:126–135.

Avilés, L., and P. Salazar. 1999. Notes on the social structure, life cycle, and behavior of *Anelosimus rupununi*. Journal of Arachnology 27:497–502.

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

Avilés, L., W. P. Maddison, P. A. Salazar, G. Estévez, P. Tufiño, and G. Cañas. 2001. Arañas sociales de la Amazonía ecuatoriana, con notas sobre seis especies sociales no descritas previamente. Revista Chilena de Historia Natural 74:619–638.

Avilés, L., W. P. Maddison, and I. Agnarsson. 2006. A new independently derived social spider with explosive colony proliferation and a female size dimorphism. Biotropica 38:743–753.

Bilde, T., Y. Lubin, D. Smith, J. M. Schneider, and A. A. Maklakov. 2005. The transition to social inbred mating systems in spiders: role of inbreeding tolerance in a subsocial predecessor. Evolution 59:160–174.

Brown, J. L. 1987. Helping and communal breeding in birds. Princeton University Press, Princeton, NJ.

Cronin, A. L., and M. P. Schwarz. 2001. Latitudinal variation in the sociality of allodapine bees (Hymenoptera; Apidae): sex ratios, relatedness and reproductive differentiation. Australian Journal of Zoology 49:1–16.

Crouch, T. E., and Y. Lubin. 2000. Effects of climate and prey availability on foraging in a social spider, *Stegodyphus mimosarum* (Araneae, Eresidae). Journal of Arachnology 28:158–168.

Eickwort, G. C., J. M. Eickwort, J. Gordon, and M. A. Eickwort. 1996. Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). Behavioral Ecology and Sociobiology 38:227–233.

Evans, T. A. 2000. Male work and sex ratio in social crab spiders. Insectes Sociaux 47:285–288.

Fowler, H. G., and H. W. Levi. 1979. A new quasisocial *Anelosimus* spider from Paraguay. Psyche 86:11–18.

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

Gonzaga, M. O., and J. Vasconcellos-Neto. 2001. Female body size, fecundity parameters and foundation of new colonies in *Anelosimus jabaquara* (Araneae: Theridiidae). Insectes Sociaux 48:1–7.

Guevara, J., and L. Avilés. 2007. Multiple sampling techniques confirm differences in insect size between low and high elevations that may influence levels of spider sociality. Ecology 88:2015–2033.

Iturralde, G. 2004. Aspectos evolutivos de la proporción de sexos en arañas sociales de la Amazonía ecuatoriana (Evolutionary aspects of sex ratio in social spiders from Amazonian Ecuador). Licenciate thesis, Ponticia Universidad Católica del Ecuador, Quito.

Jimenez-Castillo, M., S. K. Wiser, and C. H. Lusk. 2007. Elevational parallels of latitudinal variation in the proportion of lianas in woody floras. Journal of Biogeography 34:163–168.

Johannesen, J., Y. Lubin, D. R. Smith, T. Bilde, and J. M. Schneider. 2007. The age and evolution of sociality in *Stegodyphus* spiders: a molecular phylogenetic perspective. Proceedings of the Royal Society B: Biological Sciences 274:231–237.

Jones, T. C., S. E. Riechert, S. E. Dalrymple, and P. G. Parker. 2007. Fostering model explains variation in levels of sociality in a spider system. Animal Behaviour 73:195–204.

Kaspari, M., and E. L. Vargo. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. American Naturalist 145:610–632.

Kranz, B. D., M. P. Schwarz, D. C. Morris, and B. J. Crespi. 2002. Life history of *Kladothrips ellobus* and *Oncothrips rodwayi*: insight into the origin and loss of soldiers in gall-inducing thrips. Ecological Entomology 27:49–57.

Kraus, O., and M. Kraus. 1988. The genus *Stegodyphus* (Arachnida, Araneae): sibling species, species groups, and parallel origin of social living. Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 30:151–254.

Levi, H. W., Y. D. Lubin, and M. H. Robinson. 1982. Two new *Achaearanea* species from Papua New-Guinea with notes on other theridiid spiders (Araneae Theridiidae). Pacific Insects 24:105–113.

Lubin, Y. D., and T. Bilde. Forthcoming. The evolution of sociality in spiders. Advances in Animal Behavior.

Marques, E. S. A., J. Vasconcellos-Neto, and M. B. De Mello. 1998. Life history and social behavior of *Anelosimus jabaquara* and *Ane-*

losimus dubiosus (Araneae, Theridiidae). Journal of Arachnology 26:227–237.

Neill, D. A. 1999. Vegetation. Pages 13–25 *in* P. M. Jørgensen and S. León-Yánez, eds. Catalogue of the vascular plants of Ecuador. Missouri Botanical Garden, St. Louis.

Neill, D. A., and P. M. Jørgensen. 1999. Climate. Pages 8–13 *in* P. M. Jørgensen and S. León-Yánez, eds. Catalogue of the vascular plants of Ecuador. Missouri Botanical Garden, St. Louis.

Packer, L. 1990. Solitary and eusocial nests in a population of *Augochlorella striata* (Provancher) (Hymenoptera; Halictidae) at the northern edge of its range. Behavioral Ecology and Sociobiology 27:339–344.

Powers, K. S., and L. Avilés. 2007. The role of prey size and abundance in the geographical distribution of spider sociality. Journal of Animal Ecology 76:995–1003.

Purcell, J., and L. Avilés. 2007. Smaller colonies and more solitary living mark higher elevation populations of a social spider. Journal of Animal Ecology 76:590–597.

Reeve, K. 1991 *Polistes*. Pages 99–148 *in* K. G. Ross and R. W. Mathews, eds. The social biology of wasps. Comstock, Ithaca, NY.

Richards, M. H. 2000. Evidence for geographic variation in colony social organization in an obligately social sweat bee, *Lasioglossum malachurum* Kirby (Hymenoptera; Halictidae). Canadian Journal of Zoology 78:1259–1266.

Riechert, S. E., R. Roeloffs, and A. C. Echternacht. 1986. The ecology of the cooperative spider *Agelena consociata* in equatorial Africa (Araneae, Agelenidae). Journal of Arachnology 14:175–191.

Rypstra, A. L. 1990. Prey capture and feeding efficiency of social and solitary spiders: a comparison. Acta Zoologica Fennica 190:339–343.

Rypstra, A. L., and R. S. Tirey. 1989. Observations on the social spider, *Anelosimus domingo* (Araneae, Theridiidae), in southwestern Perú. Journal of Arachnology 17:368–371.

Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. American Naturalist 140:893–911.

Swenson, N. G., and B. J. Enquist. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. American Journal of Botany 94:451–459.

Uetz, G. W., and M. A. Hodge. 1990. Influence of habitat and prey availability on spatial organization and behavior of colonial web-building spiders. National Geographic Research 6:22–40.

Viera, C., S. Ghione, and F. G. Costa. 2006. Regurgitation among penultimate juveniles in the subsocial spider *Anelosimus* cf. *studiosus* (Theridiidae): are males favored? Journal of Arachnology 34:258–260.

Vollrath, F. 1986. Environment, reproduction and the sex ratio of the social spider *Anelosimus eximius* (Araneae, Theridiidae). Journal of Arachnology 14:266–281.

Wilson, E. O. 1971. The insect societies. Belknap, Cambridge, MA.

Natural History Editor: Henry M. Wilbur

From the Cocodrilos area in Napo, Ecuador. *Left*, nest of the newly discovered social spider *Anelosimus guacamayos* being surveyed by one of the coauthors (photograph by G. Iturralde). *Top right*, *Anelosimus guacamayos* adult female; *bottom right*, *A. guacamayos* adult male (*scale bars* = 2 mm; photographs by W. P. Maddison).