

Original Article

Sociality and resource use: insights from a community of social spiders in Brazil

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We explored the role of group living and cooperation in resource use in a spider community where 4 congeneric species of similar body size, but with behaviors ranging from near-solitary to fully social, co-occur. We found that the range of insect sizes captured by each species reflected their nest and colony size so that species with larger colonies and prey capture webs captured larger insects than less social species. Yet, among those species whose webs did not differ significantly in size—the 2 with the largest and the 2 with the smallest webs—one captured significantly larger insects than the other. This pattern was apparently due to differences in the extent to which nest mates cooperated in the capture of prey, as in only one of the species in each pair did the size of the insects captured increase with colony size. The 4 species were thus packed along the spectrum of available insect sizes from least to most social, with limited overlap between contiguous species. The pattern of resource use was thus more overdispersed than expected by chance, as would be expected if the species had been assembled or differentiated to avoid extensive dietary overlap. We consider alternative hypotheses to explain these patterns and suggest that group size and level of cooperation may play an important role in the dietary segregation of sympatric organisms. *Key words:* *Anelosimus*, community assemblage, cooperation, group foraging, prey size, resource partitioning, species coexistence. [*Behav Ecol* 22:630–638 (2011)]

INTRODUCTION

Group living in animals has well-known consequences in many aspects of an animal's life including its reproduction, predator protection, and foraging (Caraco 1979; Pulliam and Millikan 1982; Krebs and Davies 1993; Krause and Ruxton 2002). Group characteristics, such as cooperativeness and group size, play crucial roles in the way social species engage in these activities and, in particular, in defining their foraging patterns and resource use. Bigger groups, for example, may detect prey faster (Baird and Dill 1996), use less energy, and spend less time during prey capture (Creel S and Creel NM 1995) and decrease variability in hunting success (Krause and Ruxton 2002). In addition, bigger groups may be more successful with specific prey types (Hector 1986; Creel S and Creel NM 1995) and sizes (Caraco and Wolf 1975; Nudds 1978; Nentwig 1985; Rypstra 1990; Yip et al. 2008). For example, cooperative hunting in social carnivores—that is, African wild dogs, lions, wolves, and spotted hyenas—allows the capture of prey otherwise unattainable by solitary foragers (Kruuk 1972; Caraco and Wolf 1975; Nudds 1978; Creel S and Creel NM 1995). Sociality may thus play important roles not only in expanding the range of resources a species is capable of exploiting but also in creating obvious differences in resource use between species that differ in level of sociality. However, although a wide range of literature has shown differences in prey size use as a function of sociality (i.e., hunting group size

and level of cooperation) (e.g., Lamprecht 1981; Hector 1986; Baird and Dill 1996; Holekamp et al. 1997; Guevara and Avilés 2007; Powers and Avilés 2007; Yip et al. 2008), such studies have focussed on populations of single species inhabiting separate environments. In such cases, species comparisons are problematic as dietary differences could arise for reasons other than sociality if, for instance, the species occupy areas with marked differences in the size and type of available prey (i.e., low vs. high elevations, Guevara and Avilés 2007). Comparative analyses of closely related species that differ in relevant social traits (i.e., group size or level of cooperation), but share the same habitat, can help disentangle the roles of sociality in creating differences in resource use among social organisms.

The social spider genus *Anelosimus* (Theridiidae) is ideal to examine the role of sociality in resource use as local communities often contain species that vary in their level of sociality (Avilés 1997; Agnarsson 2006; Avilés et al. 2007). In general, the more advanced social species (nonterritorial permanent social, sensu Avilés 1997) form colonies containing dozens to thousands of spiders and may be able to capture larger prey than less social ones (i.e., subsocial or nonterritorial periodic social) whose colonies contain single-family groups of at most a few dozen individuals (Avilés 1997; Lubin and Bilde 2007). This would be due both to the greater size of their prey capture webs and the presence of more individuals to participate in cooperative prey captures (Nentwig 1985; Rypstra 1990; Powers and Avilés 2007; Yip et al. 2008). Yip et al. (2008), for instance, have shown that the size of insects captured by the Neotropical social spider *A. eximius* increases monotonically with colony size.

To assess the association between sociality and prey size use amongst co-occurring social species, we studied a striking

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Anelosimus community containing at least 5 species with minimal body size differences (body lengths within 0.1 mm of one another) but with levels of sociality ranging from almost solitary to fully social. We tested the hypothesis that the ranges of insect sizes captured by these sympatric spider species reflect their nest and colony sizes, as would be expected if larger nests are capable of intercepting larger insects and the presence of a greater number of individuals makes their cooperative capture possible. If level of sociality plays a role in the prey size captured, we predict that species with larger colonies and more developed cooperation will capture larger insects than less social species with smaller colonies. We then assess whether the various species capture prey selectively from the distribution of insect sizes present in their environment. We finally test whether the pattern of resource use by this *Anelosimus* community is more overdispersed than expected by chance and consider alternative hypotheses that might explain such a pattern. This community of closely related *Anelosimus* spiders represents a unique opportunity to examine how sociality may shape resource use in sympatric species and thus potentially play a role in reducing niche overlap among co-occurring organisms, a possibility not previously explored.

MATERIALS AND METHODS

Locality

Spider colonies and their prey capture patterns were studied in the protected reserve of Serra do Japi near Jundiá in the state of São Paulo, Brazil (lat 23°12'–23°22'S, long 46°57'–47°05'W and 650–1300 m elevation). This is a markedly seasonal semi-deciduous forest with leaf fall occurring especially during the dry and relatively cool autumn and winter seasons (from April to September). We conducted our prey capture surveys during the wet–warm season (summer) in November–December 2005 (mean monthly rainfall >100 mm) at 3 different sites within the reserve (Paraiso, Bauru, Bica), all located between 1000–1200 m elevation and covering about 3 Km². At these sites, spider colonies occur sympatrically, mainly on shrubs and trees located both in the interior and forest edge. Although there are some differences among the species on the exact position they occupy on the plant substrate and relative to the forest edge (Purcell J, Vasconcellos-Neto J, Gonzaga MO, Fletcher J, Avilés L, unpublished data), nests of all species can be found in close proximity from one another in all areas, often as close as a few centimeters apart. In addition to studying the prey captured by the colonies, we used 3 sampling methods—no-kill malaise traps, knockdown sticky traps,

and visual sampling—to assess the range of insect sizes present in the environment in areas around the study colonies.

Species descriptions

The species we studied belong to the genus *Anelosimus*, which, with 7–8 described permanent-social species, is the spider genus with the largest number of known social species, in addition to numerous subsocial and a few nearly solitary ones (Agnarsson 2006; Agnarsson et al. 2006). Species in this genus build tridimensional webs with vertical prey capture threads for the interception of insects later subdued by the spiders (Nentwig 1985; Avilés 1997; Agnarsson 2006; Yip et al. 2008). The webs are occupied either by a single family, in nearly solitary or subsocial species, or by multiple females and their offspring, in social ones. Colony members cooperate in the construction and maintenance of the nest, prey capture, and, in the more social species, brood care (Avilés 1997; Lubin and Bilde 2007).

Our study community at Serra do Japi contained species representing the full spectrum of social behaviors present in the genus, including the nearly solitary, *A. nigrescens* Keyserling; 2 subsocial species, *A. baeza* Agnarsson and *A. studiosus* Hentz; 1 species intermediate between social and subsocial, *A. jabaquara* Levi; and 1 social species, *A. dubiosus* Keyserling. *Anelosimus dubiosus* and *A. jabaquara* are close phylogenetic relatives, whereas the remaining 3 species belong to different subclades within the genus (Agnarsson 2006; Agnarsson et al. 2007). Geographically, *A. dubiosus* and *A. jabaquara* are known to occur only in Brazil at elevations between 600–1100 m (Agnarsson 2006) where they are often found in sympatry (Gonzaga and Dos Santos 1999). The remaining species have a more widespread distribution in the Americas, occurring in a range of habitats except in lowland tropical rainforests (Agnarsson 2006; Avilés et al. 2007). Although relatively common throughout its range (Agnarsson 2006), *A. studiosus* occurred at very low densities at Serra do Japi. We thus only report on the characteristics of the nests and prey capture patterns of the 2 nests from which data were obtained (Table 1) but do not include this species in the analyses. Because of the strong seasonality of Serra do Japi (see above), the populations of any given species are synchronized in their phenology, with the reproductive season, which is slightly offset among species (Marques et al. 1998; Purcell J, Vasconcellos-Neto J, Gonzaga MO, Fletcher J, Avilés L, unpublished data), roughly coinciding with the warm–wet season.

Our ranking from least to most highly social of *Anelosimus* species in this community is based on the instar at which individuals disperse from the natal nest. In the nearly solitary,

Table 1
Summary of nests and prey captured by 5 sympatric social spider species in Serra do Japi, Brazil

		<i>Anelosimus dubiosus</i>	<i>A. jabaquara</i>	<i>A. baeza</i>	<i>A. studiosus</i>	<i>A. nigrescens</i>
Level of sociality		Social	Intermediate Social–subsocial	Subsocial	Subsocial	Almost solitary
Number of nests		23	27	25	2	46
Range of longest axis of nest (cm)		6–120	11–80	2–30	7–23	2–13
Range of nest cross section (cm ²)		12–5655	78–2727	2–426	22–106	3–79
Total number of prey (range) recorded per colony	D	1–19	1–20	1–10	1–5	1–4
	N	1–9	1–7	1–6	0	1–2
Total number of prey recorded per species	D	108	174	53	6	59
	N	30	53	12	0	4
Range of prey size (body length mm) recorded	D	2–30	2–28	1–12	2–13	1–4
per species	N	4–24	2–30	1–10	0	1–4

Daily observation periods (day or night) ranged from 2 to 8 h. D = day, N = night.

A. nigrescens spiderlings disperse early in their lifecycle so that nests contain mostly single females with an egg sac or with recently hatched spiderlings; beyond the second or third instar individuals live solitarily (this study; Avilés L, unpublished observations). In the subsocial *A. baeza* and *A. studiosus* colonies are also initiated by single females, but the offspring remain in their natal nest for several instars before dispersing (this study; see also Powers and Avilés 2007, for *A. baeza*; and Jones and Parker 2000 and Viera et al. 2007, for *A. studiosus*). At the time of this study, *A. baeza* colonies were in the midst of their social phase, as they contained mostly subadult individuals following the death of their mother but prior to dispersal. Although differences in the prey size utilized may exist at other phases of *A. baeza*'s phenology (e.g., post-dispersal colonies containing single individuals), the timing of our study allowed us to observe the effects of group "living and cooperation in this species prey capture patterns while simultaneously assessing the prey capture patterns of the entire community." In *A. jabaquara* dispersal happens at the subadult to adult stages, but a fraction of females may remain in the natal nest to reproduce (Gonzaga and Vasconcellos-Neto 2001). In *A. dubiosus* females, on the other hand, apparently mature and mate within the natal nest, with the establishment of new colonies involving budding, in addition to the dispersal of solitary, possibly already inseminated, adult females (Marques et al. 1998). In *A. jabaquara* and *A. dubiosus*, therefore, a nest may be reoccupied by successive generations, and colonies may contain up to a few dozen adult females. The life cycles of these 2 species are offset by a month, with *A. jabaquara* undergoing dispersal and producing egg sacs earlier than *A. dubiosus* (Marques et al. 1998). This study took place just prior to *A. jabaquara*'s dispersal period when its nests and colonies were close to their maximum size (Table 1).

Prey capture by spider colonies

We surveyed spider nests every 1–1.5 h during the daytime (08:00 and 18:30) from 17 November to 02 December 2005. Additionally, we surveyed a subset of the colonies during the night between 19:30 and 24:30 (Table 1). We performed night surveys under red light by placing a red filter over the flashlights to avoid disturbance and behavioral interference to the spiders and to prevent attracting insects to the nests. Sampling periods ranged from 2 to 8 h starting at different times each day and night. During each survey, we examined each nest for new insect prey naturally caught in the web and/or being consumed by the spiders. Insects were classified to order and whenever possible to family. Insect length was measured to the nearest millimeter from the most anterior side of the head to the tip of the abdomen. Visually sampled specimens were assessed by eye to the nearest 5 mm. For consistency, all surveys were done by the same 2 observers.

Insects sampled from the environment

Concurrently with surveys of prey captured by the colonies, we sampled flying and vegetation-dwelling insects that could potentially form part of the spider diets (1 mm in length or longer). We used 3 collecting techniques: no-kill malaise traps, knockdown sticky traps, and visual searching. Six no-kill malaise traps (1.2 m height, 1.2 m base) made of fine-mesh gray tulle, and a superior collection bottle were set up at approximately 5–10 m away from existing spider colonies and at a minimum distance of 10 m from one another. A similar number of knockdown sticky traps (a double-sided sticky surface of 210 × 297 mm per side placed over 2 inferior slopping ramps that converged into a jar with alcohol) were set up equidistantly along each of the transects. Specimens caught in the malaise and sticky traps were removed at the

end of each observation period after 2–8 continuous hours of sampling (day 2–8 h, night 3–5 h) starting at different times each time. Each site was sampled at least 3 times in the day and once at night. All insects captured were taken to the laboratory for their identification and measurement. Visual searching was carried out at least 3 times during the day and once or twice during night hours. It involved actively searching for 5 consecutive minutes insects, and other arthropods flying or sitting on or under the surrounding vegetation at randomly selected points near the spider colonies. For all 3 collecting techniques, sampling bouts of identical effort and procedure were used at all sites by the same observer. Insects were classified and measured as done above with the prey caught by the colonies.

Nest and colony size

Because nest size is correlated with the number of individuals present in a colony in all *Anelosimus* species studied (appendices in Avilés et al. 2007; Powers and Avilés 2007; Purcell and Avilés 2007), we used nest size (cross section of the nest at the widest part of the basket, as in Purcell and Avilés 2007) as a surrogate for colony size. The length of the longest axis of *Anelosimus* nests ranged from 2 to 120 cm (surface area: 2–5655 cm²; Table 1).

Data analysis

We conducted a preliminary test of the effect of site (Paraiso, Bauru, Bica), time period (day or night), and sampling technique (colony, malaise, sticky, and visual) on insect length (natural log transformed millimeter) using a mixed model analysis of variance where colony/trap ID was treated as a random factor nested within site and technique. We found no effect of site ($F_{2,176} = 1.20$, $P = 0.3$) or site–technique interaction ($F_{2,3237} = 1.28$, $P = 0.3$) on insect length, but significant effects of time period ($F_{1,3237} = 1.28$, $P < 0.0001$) and technique–time period interaction ($F_{3,3237} = 5.7$, $P = 0.0007$). We further found that differences in the size of the insects sampled during the day and night held for the sampling techniques (primarily for visual sampling) but not for the spider colonies (independent contrasts: colony day vs. night $F_{1,3237} = 2.0$, $P = 0.2$). For comparisons of insect length captured by the different spider species, we thus combined day and night samples from all localities. Whenever sampling technique data were included in the analyses (i.e., selectivity and niche overlap analyses), we ran separate tests for day and night periods while combining samples from all localities. Although we found a significant effect of sampling technique ($F_{3,176} = 7.5$, $P < 0.0001$), we combined data from all techniques in analyses requiring an estimate of the entire range of insect sizes available to the spiders.

We used a 1-way analysis of variance, followed by Tukey–Kramer Honestly Significant Difference tests (overall $\alpha = 0.05$), to compare the size of the nests (natural log-transformed cross section of the nest, in square centimeter) and the sizes of the insects (natural log-transformed mean insect length in millimeter) captured by the spider colonies. For the insect tests, we used as our response variable the average size of insects captured per colony for the combined day and night samples, weighted by the number of insects entering in each estimate (Table 1). To assess the effect of colony size on the average size of the insects captured by the colonies, we first performed a linear regression for all species combined and then an analysis of covariance (ANCOVA) with species, colony size, and their interaction in the model. As a significant interaction between species and colony size was found, we finally performed separate regression analyses for each species.

To compare resource utilization in relation with resource availability for each of the species, we calculated Jacobs' selectivity index (Jacobs 1974), which standardizes the relationship between the proportion that each insect size class (insect size categories in millimeter, as shown in Figure 5) makes up of a species diet and the relative abundance of that insect size class in the combined environmental samples. The index ranges from -1 to $+1$. A positive value indicates that a given prey size is taken selectively, whereas a negative value indicates that a prey size is avoided.

We calculated prey size overlap between species pairs using the Pianka (Pianka 1973) and the Czechanowski (Feinsinger et al. 1981) indices with values ranging from 0 (no overlap) to 1 (complete overlap). For this purpose, we divided the insect length data into 15 size classes to generate a data matrix of the number of prey items in each size class (in the columns) captured by each species (in the rows) as well as by the combination of sampling techniques. To assess whether the observed overlap values reflected a resource utilization pattern more overdispersed than expected by chance, we compared the observed data matrix with "pseudo-communities" generated by Monte Carlo simulations. We used primarily the RA2 randomization algorithm (Lawlor 1980), which relaxes the niche breadth for each species, but retains the zero structure of the matrix under the assumption that even in the absence of species interactions certain prey size classes may be unavailable for some species in the system. For the day data only, we also used RA4 (Lawlor 1980), a highly conservative algorithm that retains both niche breadth and zero structure. Although RA4 is not recommended for general use because of its proneness to type II error (failing to reject a null hypothesis that is false), patterns that are significant with this algorithm are expected to be "quite strong" (Winemiller and Pianka 1990; Gotelli and Entsminger 2009). In producing the null pseudo-communities, both algorithms were run under the assumption that different insect size categories were available to the spiders proportional to their frequency of occurrence in the environment, as assessed with the combination of sampling techniques. We performed 10 000 Monte Carlo simulations of niche overlap for each species pair. Observed overlap values were then compared with these simulated null values.

All statistical tests were performed using the statistical software JMP IN (Windows NT Version 5.1). Monte Carlo simulations and overlap tests were conducted using the software EcoSim 7.72 (Gotelli and Entsminger 2009).

RESULTS

There were significant differences in the size of the nests of the 4 *Anelosimus* species (mean area of the cross section of the nest \pm 95% confidence interval [CI] in square centimeter, back-transformed values: *A. dubiosus* 812.4 ± 1.5 , *A. jabaquara* 735.1 ± 1.3 , *A. baeza* 54.6 ± 1.6 , and *A. nigrescens* 24.5 ± 1.6 ; $F_{3,148} = 65.2$, $P < 0.0001$), with the 2 most social species having significantly larger nests than the 2 least social ones (Figure 1). Nest sizes of the social *A. dubiosus* and the intermediate social-subsocial *A. jabaquara*, or those of the subsocial *A. baeza* and the almost solitary *A. nigrescens*, however, were not significantly different from one another (Tukey–Kramer tests; Figure 1).

Nonetheless, the 4 spider species differed in the insect size they captured (mean insect length \pm 95% CI in millimeter, back-transformed values: *A. dubiosus* 10.0 ± 1.1 , *A. jabaquara* 8.2 ± 1.1 , *A. baeza* 4.1 ± 1.1 , and *A. nigrescens* 2.1 ± 1.2 ; $F_{3,148} = 117.9$, $P < 0.0001$; Figure 1). The average size of the insects caught increased with level of sociality, with all pairwise comparisons being significantly different from one another (Tukey–Kramer tests; Figure 1). The size range of the prey captured by colonies of the 4 species is given in Table 1.

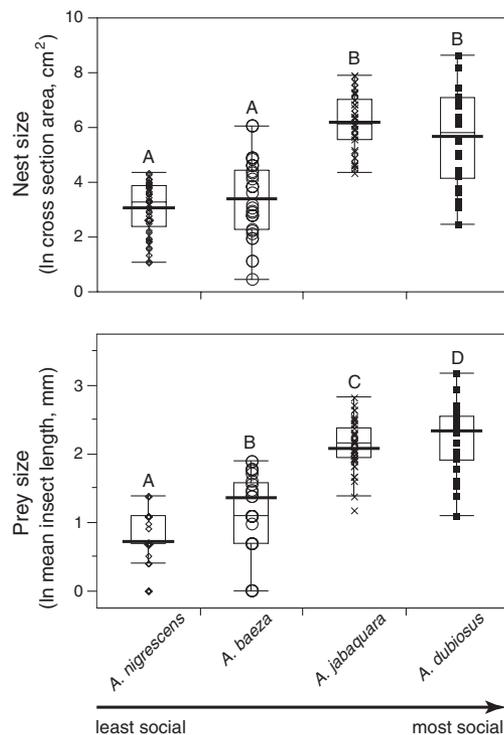


Figure 1

Quantile boxplots showing the distribution of nest sizes, and the size of insects captured by 4 sympatric *Anelosimus* spider species in Serra do Japi, Brazil (from least to most social: *A. nigrescens*, *A. baeza*, *A. jabaquara*, and *A. dubiosus*). Thick overhanging lines represent the means of the distributions. Nonsignificant differences are indicated by similar letters, as obtained by Tukey–Kramer Honestly Significant Difference tests (overall alpha = 0.05).

There was a positive correlation between prey and nest size across all 4 species ($F_{1,28} = 79$, $P < 0.0001$; Figure 2), with no effect of time period or nest size–time period interaction on this pattern ($F_{1,28} = 0.05$, $P = 0.8$ and $F_{1,28} = 0.07$, $P = 0.8$, respectively). An ANCOVA revealed significant main effects of species groups ($F_{1,144} = 16.8$, $P < 0.0001$) and nest size ($F_{1,144} = 8.0$, $P = 0.005$). A significant interaction between species and nest size ($F_{3,144} = 2.8$, $P = 0.04$) indicated that the slopes of the relationship between prey size and colony size differed among the species. Further regression analyses of individual species showed that the size of the insect captured increased with nest size for *A. dubiosus* ($r^2 = 0.27$, $t = 3.2$, $P = 0.003$; Figure 3) and *A. baeza* ($r^2 = 0.25$, $t = 3.0$, $P = 0.005$; Figure 3) but not for *A. jabaquara* ($r^2 = 0.004$, $t = 0.4$, $P = 0.7$; Figure 3) or *A. nigrescens* ($r^2 = 0.0007$, $t = -0.2$, $P = 0.9$; Figure 3).

Insects caught by the colonies ranged in size from 1 to 30 mm (prey capture events $n = 400$ day, $n = 99$ night; Table 1). This range covered most of the spectrum of insect sizes sampled from the environment, as only 4 of 2931 insects obtained with the 3 sampling methods (day and night samples) were larger than 30 mm. The largest insect, seen by visual sampling, measured 43 mm. The range of insect lengths obtained by the sampling techniques were 1–25, 1–26, and 1–43 mm for malaise traps ($n = 1695 + 126$), sticky traps ($n = 635$), and visual search ($n = 476$), respectively. Jacobs' indexes were positive for only small prey items for the 2 least social species (day samples only; Figure 4), indicating an apparent bias toward the capture of smaller prey relative to the insect sizes available in the environment. The 2 most social species had positive selectivity index values for larger prey sizes but not for smaller insect sizes (day samples only; Figure 4) thus

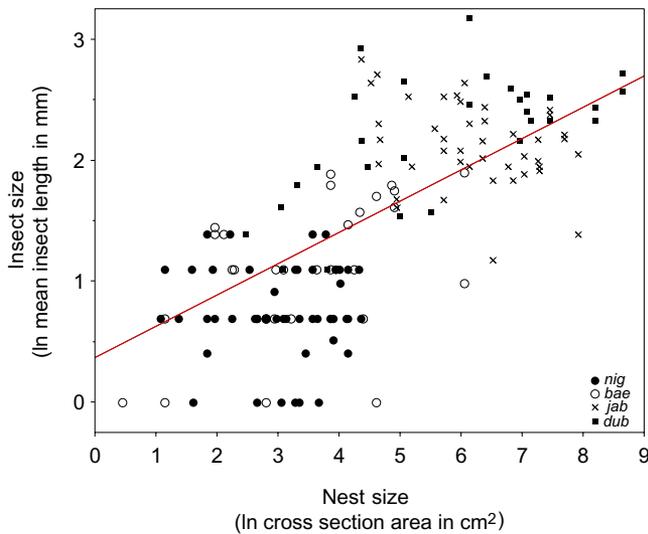


Figure 2

Regression of mean size of the insects caught by a given colony (shown as the ln-transformed mean insect length, in millimeter) on nest size (ln-transformed cross section area in square centimeter) for the combined nests of 4 sympatric social and subsocial *Anelosimus* species (*dub* = *A. dubiosus*, *jab* = *A. jabaquara*, *bae* = *A. baeza*, and *nig* = *A. nigrescens*) in Serra do Japi, Brazil (regression $r^2 = 0.54$, $t = 13.2$, $P < 0.0001$).

indicating segregated use of prey resources in relation to prey availability.

Analysis of niche overlap with both the Pianka and Czechanowski indices, and the RA2 algorithm showed overlap values significantly smaller than expected by chance in the range of prey sizes utilized by most species pairs, even for species contiguous in the sociality scale (Table 2; Figure 5). This general pattern held during the day and night, despite the smaller sample sizes of the latter. The only consistent exception was the *A. nigrescens*–*A. baeza* pair for which overlap indices were non significantly different during both time periods. Comparable results were obtained with the conservative RA4 algorithm applied to day samples, with only 2 additional (and mixed) exceptions: *A. jabaquara* and *A. baeza* were not significantly different with the Pianka index and *A. dubiosus* and *A. jabaquara* with the Czechanowski index. The distribution of prey sizes captured by the species was thus more overdispersed than expected by chance (overall RA2 for Pianka: day, observed = 0.13, expected = 0.46, $P_{\text{obs}} \leq P_{\text{sim}} < 0.0001$; night, observed = 0.18, expected = 0.45, $P_{\text{obs}} \leq P_{\text{sim}} < 0.0001$; for Czechanowski: day, observed = 0.14, expected = 0.33, $P_{\text{obs}} \leq P_{\text{sim}} < 0.0001$; night, observed = 0.18, expected = 0.34, $P_{\text{obs}} \leq P_{\text{sim}} < 0.0001$), consistent with a hypothesis of nonrandom patterns of resource use in this community.

DISCUSSION AND CONCLUSION

This study shows that interspecific differences in nest and colony size, for the most part, reflected differences in level of sociality in 4 sympatric spider species of the genus *Anelosimus*, with the 2 least social species having significantly smaller nests than the 2 most social ones (Figure 1). These differences, in turn, translated to differences in the size of the prey captured by the spiders. Interestingly, however, although the nests of the 2 least social and of the 2 most social species did not differ significantly from one another in size, the size of the insects they captured did (Figure 1). Thus, the social *A. dubiosus* captured on average significantly larger insects than the intermediate social–subsocal *A. jabaquara* and the subsocial

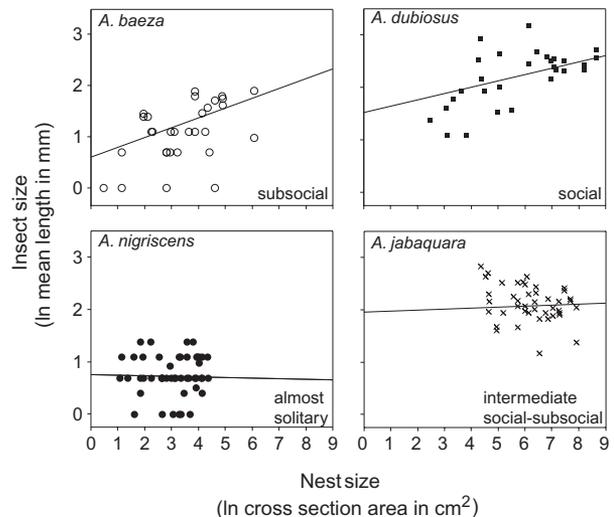


Figure 3

Regression of mean insect prey size (given as the ln-transformed mean insect length, in millimeter) on nest size (ln-transformed cross section area in square centimeter) for nests of 4 sympatric species of *Anelosimus* in Serra do Japi, Brazil (regressions: *A. dubiosus* $r^2 = 0.27$, $t = 3.2$, $P = 0.003$; *A. jabaquara* $r^2 = 0.004$, $t = 0.4$, $P = 0.7$; *A. baeza* $r^2 = 0.25$, $t = 3.0$, $P = 0.005$; and *A. nigrescens* $r^2 = 0.0007$, $t = -0.19$, $P = 0.9$).

A. baeza captured on average significantly larger insects than the almost solitary *A. nigrescens* (Figure 1). Given that the 2 most social species are very similar in terms of nest structure and body size (Marques et al. 1998) and occupy the same microhabitat (Purcell J, Vasconcellos-Neto J, Gonzaga MO, Fletcher J, Avilés L, unpublished data), we propose that differences in the size of insects captured may result from differences in the extent of cooperative prey capture in these 2 species, with *A. dubiosus* being more cooperative than *A. jabaquara*. This is suggested by the fact that the social *A. dubiosus* captured increasingly large insects as colony size increased, whereas the intermediate social–subsocal *A. jabaquara* did not (Figure 3). Such a pattern would arise if an increasing number of individuals participated in prey capture in larger *A. dubiosus* but not in *A. jabaquara* colonies due to either differences in the density of individuals within nests and/or their degree of cooperativeness, hypotheses that we are currently investigating (Harwood G, Avilés L, in preparation). Earlier studies, in fact, suggest that *A. dubiosus* may be, in general, more cooperative than *A. jabaquara*. Marques et al. (1998), for instance, have shown that in *A. dubiosus*, young from different broods mix at a young age and appear to be fed by regurgitation by multiple females, whereas in *A. jabaquara*, the brood of different females tend to remain in separate retreats until a relatively late instar. Along the same lines, compared with *A. jabaquara*, *A. dubiosus* is suggested to exhibit greater tolerance of conspecifics (Marques et al. 1998), a factor that is expected to be key in enabling higher levels of cooperation and more complex social behaviors in spiders, in general (Shear 1970; Kullmann 1972). Differences in the extent of cooperation may also underlie the different slopes for *A. baeza* and *A. nigrescens* (Figure 3), as nests of the latter species contained mostly single adult females, with or without a very young brood.

Our findings also show that the 4 co-occurring species used resources differentially by capturing prey items toward the small or large end of the available range of insect sizes as a function of their level of sociality (Figure 4). The small size of their nests and colonies may intuitively explain why large insects are not captured by the less social species. However, for

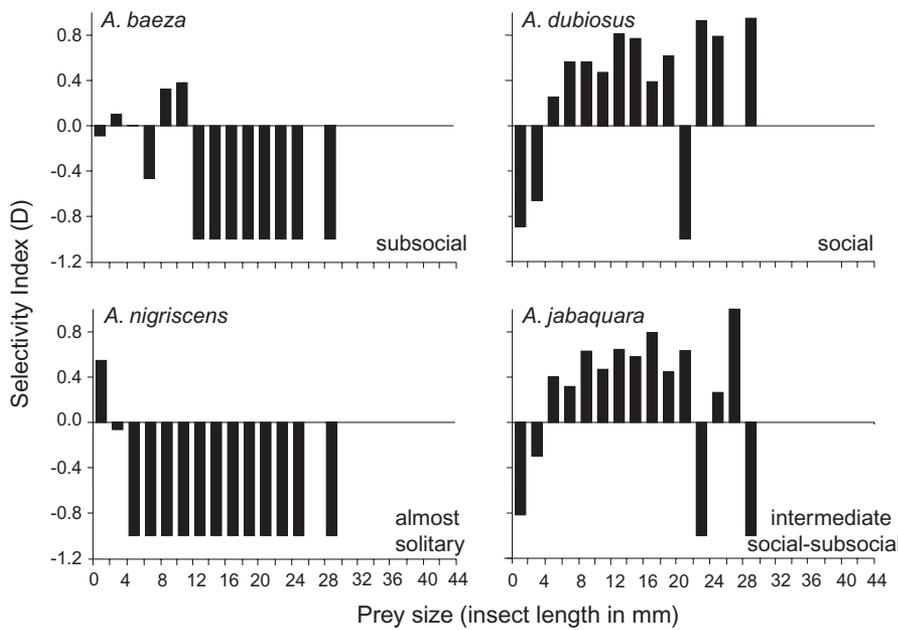


Figure 4
Comparison between the prey size utilized by 4 sympatric *Anelosimus* spider species and the distribution of insect sizes sampled at Serra do Japi, Brazil using 3 sampling techniques (day samples only). Prey selectivity (D) is represented by Jacobs' index. Positive values indicate selectivity for the given prey size, and negative values indicate avoidance of a given prey size by the species.

more social species, given that their large colonies can capture both large and small prey, the apparent bias toward large prey deserves more attention. One possibility is that these large colonies ignore or reject potentially unprofitable small prey, concentrating instead on prey that can better fulfill the nutritional requirements of the colony. Increased sociality may thus confine the species to the large prey niche, leaving less social species with small colonies alone in exploiting small prey. Small insects may also be harder to detect in large nests (i.e., larger prey is more visible than small prey in large webs), thus having a greater opportunity to escape. Finally, as observed in other *Anelosimus* communities (Salomon M, unpublished data), particular species may have greater density of silk in their webs, thus being better able to retain small prey. We note that these various possibilities are not necessarily mutually exclusive. On the other hand, we did not detect any differences in the size of the insects available in the different microhabitats occupied by the colonies, ruling out environmental differences as an explanation for the observed patterns.

An analysis of the overall pattern of prey usage by *Anelosimus* species in this spider community shows that it is more overdispersed than expected by chance. Nonrandom prey size segregation was detected overall and between most species pairs when observed patterns were tested against a null model that randomizes niche breadth but conserves prey size classes

(the RA2 algorithm, Lawlor 1980), and for daytime samples, a more conservative model that retains both niche breadth and prey size classes utilized (the RA4 algorithm; Lawlor 1980) (Table 2). Such nonrandom patterns of prey utilization as a function of level of sociality raise interesting questions regarding the mechanisms responsible for them. Although the relatively high density of nests of the 4 most common *Anelosimus* species at Serra de Japi—an average of 0.1 nests per meter square in some areas (Purcell J, unpublished data), makes species interactions a plausible mechanism influencing at least some aspects of the space, time, or dietary resource use by this community, it is unclear whether the observed patterns might reflect processes directly aimed at reducing dietary overlap or may be an indirect product of community assemblage in response to factors other than diet.

Whether insects could plausibly be a limiting factor for *Anelosimus* spider species in Sierra do Japi has yet to be determined. There is evidence, however, that prey availability and the size distribution of insects in the environment influence the range of colony sizes that can be sustained in particular habitats (Guevara and Avilés 2007; Powers and Avilés 2007). Thus *Anelosimus* species with large colonies are only sustainable in areas such as the lowland rainforest where large insects are abundant (Guevara and Avilés 2007; Powers and Avilés 2007; Yip et al. 2008). A paucity of large insects at Serra do Japi, where only 0.54% of the insects were larger than

Table 2
Values of PK and CN indices of overlap for the prey size used by 4 species of social spiders in Serra do Japi, Brazil

Species		<i>Anelosimus dubiosus</i>	<i>A. jabaquara</i>	<i>A. baeza</i>	<i>A. nigrescens</i>
<i>A. dubiosus</i>	PK		0.0842, $P < 0.0001$	0.0550, $P < 0.0001$	0.0027, $P = 0.0002$
	CN		0.2666, $P = 0.0001$	0.0779, $P = 0.0001$	0.0026, $P < 0.0001$
<i>A. jabaquara</i>	PK	0.3616, $P = 0.04$		0.2443, $P = 0.02$	0.0219, $P = 0.003$
	CN	0.4760, $P = 0.3$		0.2162, $P = 0.02$	0.0154, $P = 0.005$
<i>A. baeza</i>	PK	0.1131, $P = 0.007$	0.3645, $P = 0.08$		0.3933, $P = 0.4$
	CN	0.1128, $P = 0.005$	0.3131, $P = 0.07$		0.2737, $P = 0.4$
<i>A. nigrescens</i>	PK	0.0021, $P = 0.02$	0.0287, $P = 0.005$	0.2253, $P = 0.1$	
	CN	0.0045, $P = 0.02$	0.0394, $P = 0.01$	0.1596, $P = 0.07$	

P represents the probability of observing, just by chance, the given niche overlap value or smaller using the randomization algorithm RA2. Above the diagonal values represent day patterns and below the diagonal, night patterns. Pianka, PK; Czechanowski, CN.

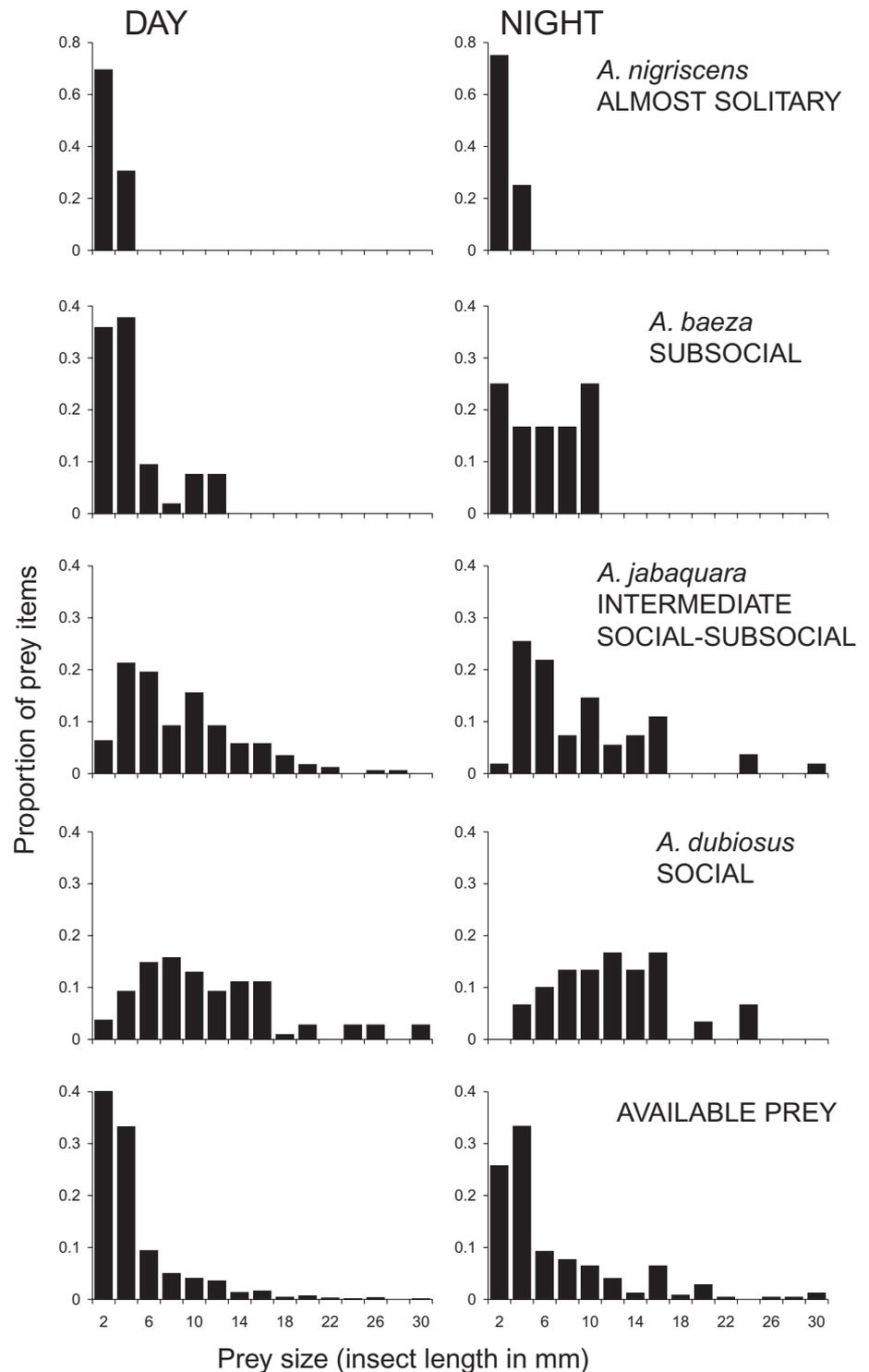


Figure 5

Resource utilization curves corresponding to day and night periods. Shown are the proportions of prey items of different size categories (in millimeter) consumed by 4 different sympatric species of *Anelosimus* spiders, and the prey size sampled from the environment.

25 mm (this study; compared with 8.5% of the insects in the lowland rainforest, data from Guevara and Avilés 2007), may limit not only the size but also the number of large colonies that can be sustained in this habitat. It is more difficult to envision how small insects, which are much more abundant, could be a limiting factor for small colonies. However, considering that small colonies occur at greater densities and tend to be clustered (following dispersal, all 5 species produce small daughter colonies in the vicinity of their source colony) (e.g.,

Vollrath 1982; Avilés and Gelsey 1998; Powers and Avilés 2003), the occurrence of interference competition for available insects among nearby nests is plausible. Evidence for food competition in spiders is mixed (Horton and Wise 1983; Riechert and Cady 1983; Wise 1984, 1993; Fasola 1999) but has been demonstrated experimentally in some cases (e.g., Brown 1981; Spiller 1984; Herberstein 1998).

Alternatively, the observed dietary segregation as a function of level of sociality may be an indirect product of community

assemblage in response to factors other than food resources. For example, patterns of microhabitat use by social and subsocial *Anelosimus* species at Serra do Japi (Purcell J, Vasconcellos-Neto J, Gonzaga MO, Fletcher J, Avilés L, unpublished data) suggest that substrate requirements, dictated by species differences in nest sizes, as well as competition for nesting sites within microhabitats, may influence the numbers and types of species present in this habitat, indirectly leading to the observed diet segregation patterns.

We should note that the diet-segregation and substrate-requirements/competition hypotheses need not be mutually exclusive. It is possible, for instance, that once the species with greater and lower levels of sociality came to primarily occupy the forest interior and the forest edge, respectively (Purcell J, Vasconcellos-Neto J, Gonzaga MO, Fletcher J, Avilés L, unpublished data), additional processes may have acted to further separate along spatial, temporal, or dietary axes the species within each of these microhabitats. Further studies, however, are needed to establish the likelihood that species interactions may be or could have been an organizing factor in this community and the extent to which such interactions may have involved competition for nesting sites versus available prey. A test of the hypothesis that prey is a limiting factor for *Anelosimus* species in this community, for instance, could involve artificially increasing the density of nests in some areas and decreasing it in others to determine whether prey intake, and thus growth and survival of individuals and colonies in manipulated versus control areas, is affected in the expected manner. A test of the competition-for-nesting-sites hypothesis, on the other hand, could involve selectively removing the nests of one of the species in some areas to determine if those substrate locations are subsequently colonized by colonies of the remaining species.

Evidence for the role of sociality in the prey size use of social organisms is robust (Nudds 1978; Lamprecht 1981; Nentwig 1985; Hector 1986; Gittleman 1989; Rypstra 1990; Creel S and Creel NM 1995; Baird and Dill 1996; Yip et al. 2008). In particular, the ability of larger hunting groups with increased cooperation to utilize larger food sizes than smaller groups or solitary individuals has been demonstrated in many social taxa. In spotted hyenas (*Crocuta crocuta*), for example, although a single individual can capture prey up to 3 times its body weight, group hunting is required to capture larger prey, such as zebra or buffalo (Cooper 1990; Holekamp et al. 1997; Trinkel 2010). Similarly, in pale chanting goshawk (*Melierax canorus*), social hunts allow capture of large prey (rodents), whereas only smaller prey (lizards and birds) can be subdued during solitary hunts (Malan 1998).

The potential role of sociality as an organizing factor in communities of co-occurring organisms, on the other hand, has received little attention. Nonetheless, there is evidence that in sympatry group size differences may lead to differential exploitation of resources in Mediterranean scavenger ant communities, where species that recruit large foraging groups are more successful at exploiting larger prey than species that recruit small groups (Cerdá et al. 1998). In addition, an effect of group-level attributes on species competition has been suggested in acacia ant communities where colony size increases a species position in the competitive hierarchy, with competitive interactions taking the form of wars of attrition with ~1:1 mortality (Palmer 2003, 2004). Although these studies did not analyze systematically the direct role of sociality in the context of prey size use and niche segregation, they point to the potential importance of sociality as an organizing factor in the assemblage of these communities.

In summary, we have shown that in a community of social spiders in Brazil species with more advanced levels of sociality and larger nest and colony sizes captured distinctly larger prey than less social species with smaller nests and colonies. For spe-

cies closer in the sociality scale, the average insect size captured differed even when the size of their nests and the ranges of insects sizes utilized overlapped (Figure 1). We suggest that this pattern may result from differences in levels of cooperativeness among colony members in species with similar nest sizes, a hypothesis that will require further testing. These results are consistent with the suggestion that differences in emerging properties of groups, such as colony size and degree of cooperation, can potentially create significant differences in resource use in co-occurring closely related species, thus potentially playing a role in community assemblage. This is an exciting and previously overlooked possibility deserving deeper empirical investigation in this and other animal communities.

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