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Social organization of the colonial spider *Leucauge* sp. in the Neotropics: vertical stratification within colonies

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Abstract. A first step toward understanding why sociality has evolved in a particular taxonomic group is to establish comparison points by studying the organization of different social systems. We examined the social organization and spatial distribution of individuals in colonies of the undescribed colonial spider *Leucauge* sp. (Araneae: Tetragnathidae). The social organization of this species was typical of a colonial species, with spiders maintaining individual territories (orb webs) within a scaffolding of shared support lines maintained by the group. Furthermore, we observed a size-dependent vertical stratification of spiders within colonies, with large spiders occupying the highest positions, followed by medium, extra-small and small individuals, a spacing pattern that was consistent across colonies of all sizes. Spiders captured and consumed prey individually and displayed territorial behaviors involving web defense. This study provides a new example of a colonial spider species that shows a distinctive within-group spatial distribution. We discuss possible reasons underlying this species' spatial arrangement in the context of social evolution.

Keywords: Aggregation, group living, orb web, sociality, spatial distribution

Knowledge about the social organization of particular species provides key insight into the mechanisms and conditions involved in the evolution of sociality. Spiders have proven to be good model systems for the study of social evolution because they encompass a large range of social phenotypes (see Avilés 1997; Uetz & Hieber 1997; Lubin & Bilde 2007 for classic and recent reviews). The few species that express social tendencies fall into two broad categories defined by individuals' level of cooperation and group structure: 'colonial' and 'cooperative' (Avilés 1997; Uetz & Hieber 1997). Colonial (or territorial permanent-social) species are generally orb-weaving spiders that spin individual webs and form permanent groups with low dispersal rates. A colonial lifestyle is characterized by the grouping of individual webs that serve as foraging or multi-purpose territories depending on the species, and which are usually maintained by single individuals. Group members engage in individual activities on their webs (e.g., foraging, brood rearing), and cooperation is usually limited to the maintenance of shared framework silk that joins the different webs (but see Fernández Campón 2007 for an example of cooperative foraging). Conversely, cooperative (or non-territorial permanent social) spiders form permanent groups on communal webs without any spatial separation between group members, and individuals cooperate in various activities such as prey capture, web maintenance and parental care. Although both social structures have evolved independently multiple times, these two organizational schemes represent distinct evolutionary pathways to sociality (Lubin & Bilde 2007).

The social organization of a group of individuals may be characterized by various attributes, such as spatial arrangement, temporal pattern, behavioral interactions and genetic relationships. The characteristics of these social attributes depend largely on the tradeoffs between the benefits and costs of communal living. In colonial spiders, benefits of group living include decreased per capita silk investment due to a shared silk framework (Uetz & Hieber 1997), increased accessibility to areas of high prey availability (e.g., open space over bodies of water) otherwise out of the reach of solitary spiders (Buskirk 1975a; Smith 1983), enhanced predator warning (Uetz et al. 2002) and increased prey capture success due to the proximity between individual webs that may cause prey to 'ricochet' from one web to the next (Uetz 1989; Whitehouse & Lubin 2005). However, coloniality also involves costs, such as increased vulnerability to predators or parasites and competition for local resources including food and web space (Buskirk 1975a, b; Uetz & Hieber 1997; Rayor & Uetz 2000).

In this study, we document the colonial structure of a recently discovered and undescribed neotropical spider, *Leucauge* sp. (referred to as *Plesiometa* sp. in Avilés et al. 2001). This orb-weaving species has previously been categorized as 'colonial' by Avilés et al. (2001), based on limited data about its social organization. To address this shortcoming, we examined the social organization of *Leucauge* sp. colonies, focusing on group composition, colony architecture and the social dynamics involved in territory maintenance and foraging. Spatial structuring within colonies may reflect a need for individuals to maximize resource acquisition and survival in a group-living situation where competition and predation pressure may impose constraints. Based on our preliminary observations suggesting a spatial arrangement of individuals within colonies, we tested the hypothesis that the distribution of *Leucauge* sp. individuals within a colony is non-random with respect to spider size, a proxy for age class.

METHODS

Study area.—We conducted this study in late August 2005 in the Jatun Sacha Biological Reserve (01°04′S, 77°36′W, elev. 400–440 m), in the Napo Province of eastern Ecuador in the

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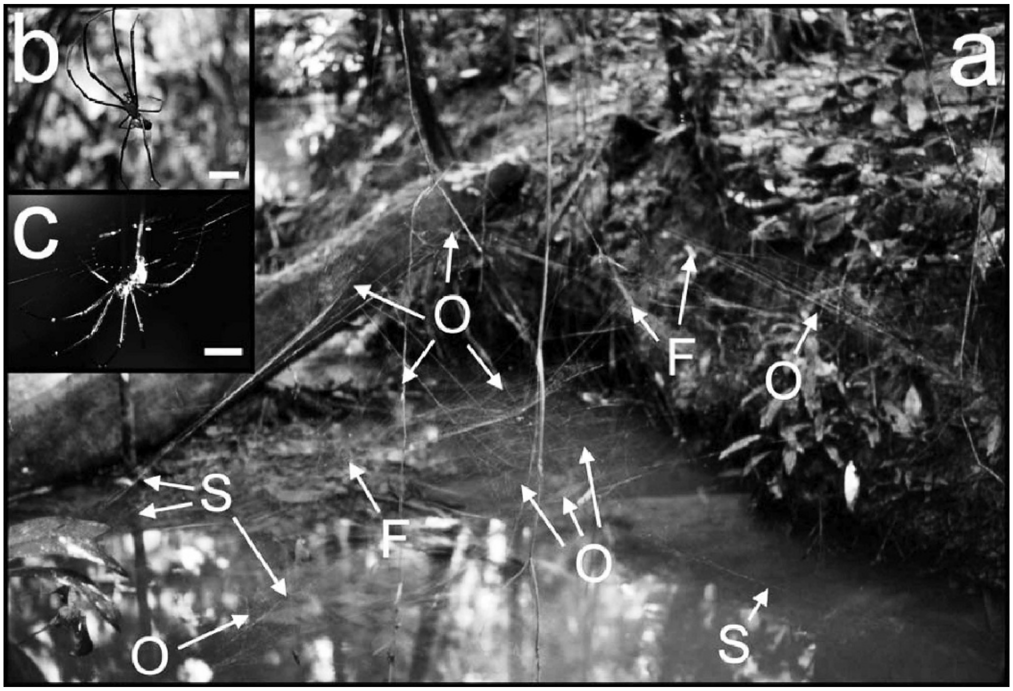

Figure 1.—a) *Leucauge* sp. above a stream in the lowland rainforest of Ecuador: several visible orb webs (O) are joined together by framework silk (F) and anchored to the vegetation with long support lines (S). b) Adult male and c) adult female *Leucauge* sp. spider on an orb web (scale bars = 10 mm). Photo credits: a) and c) L. Avilés; b) A. Larocque.

Amazon basin. The reserve comprises 2200 ha of 70% primary and 30% secondary tropical rainforest in a transitional region between the lower Andean slopes and the Amazonian lowlands (Jatun Sacha Foundation 2009).

Study species.—The orb-weaving spider *Leucauge* sp. (Araneae: Tetragnathidae) is a territorial permanent-social species found in neotropical rainforests. This species was first characterized in Ecuador by Avilés et al. (2001) and bears significant morphological resemblance to *Leucauge argyra* (Walckenaer 1841) (= *Plesiometa argyra*: Platnick 2009). *Leucauge* sp. spiders are black with a prominent white patch on the abdomen outlined with silver bands and red coloring on their prosoma (Fig. 1b, c). They spin individual orb webs that may reach close to 1 m in diameter and are usually found in riparian habitats of the rainforest above creeks or other bodies of water inside the forest (personal observation; Avilés et al. 2001). Colonies consist of clusters of individual orb webs joined together through a framework of shared silk scaffolding that is anchored to the vegetation on the banks of a body of water with thick silk threads (Fig. 1a). Their phenology and dispersal patterns are unknown, although we have observed spiders of all age classes in August.

Data collection and analysis.—This study consisted of two parts: a population survey of *Leucauge* sp. colonies ($n = 22$) at the study site and behavioral observations of a single colony.

Population survey: We collected the following population data over two days: (1) number of spiders per colony and, for each spider therein, (2) spider body size, (3) height of the spider from the ground and (4) location within the colony. Spider body size, measured with a ruler as total body length (distance from the front of the prosoma to the tip of the abdomen), reflects both developmental stage and feeding history in spiders (Jakob et al. 1996). We grouped spiders into four size classes based on the overall distribution of observed body lengths: large ('L', average length: 11–12 mm), medium ('M', 7–9 mm), small ('S', 5–6 mm) and extra-small ('XS', 3–4 mm). L spiders were adult females and males, M spiders were sub-adults and both S and XS spiders were juveniles of various instars. We measured a spider's height from the ground as the distance from the surface of a body of water directly below a colony to the center of the spider's body. Spider location within the colony was categorized as on (1) an orb, (2) a support strand within the silk framework, (3) a dragline produced by the spider and attached to the web complex or (4) plant substrate at the periphery of a colony (usually the underside of a leaf). We collected these data on days without rain.

For analysis, we first checked the data for normality and heteroscedasticity and applied transformations where appropriate. We excluded three colonies with fewer than five spiders from the analyses (see Fig. 2). To examine differences in the distribution of spider sizes among colonies we used a log-likelihood ratio test with William's correction for small sample sizes (Sokal & Rohlf 1995). We used a logistic regression model to test the effect of colony size on spider size distributions within colonies. We assessed the relationship between a spider's size and its location within a colony using a log-likelihood ratio test with William's correction. Finally, we used a general linear model (GLM) to examine the effects of colony size and spider size on a spider's height above the ground (log-transformed), using averages for each spider size class within each colony to avoid pseudoreplication. We also assessed the relationship between colony size and the average height from the ground (log-transformed) of all spiders within a colony using a GLM and Spearman's rank correlation.

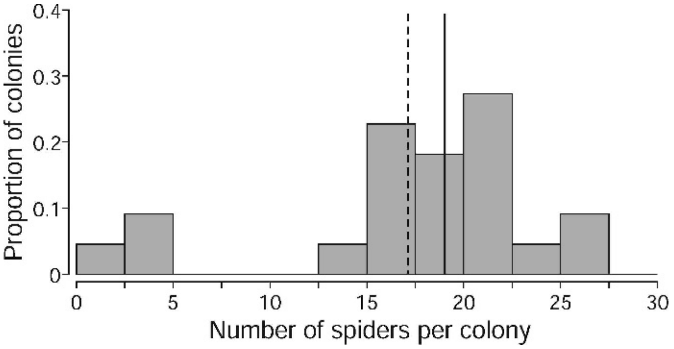

Figure 2.—Distribution of *Leucauge* sp. colony sizes (n = 22 colonies). The plain vertical line indicates the median colony size and the dashed vertical line the mean colony size.

Behavioral observations: The behavioral component of the study consisted of the observation of a single colony for 10 h per day (0700–1700 hours) on two consecutive days. Our purpose was to record foraging activities and territorial interactions among colony members. The focal colony was chosen for ease of access, median colony size and the presence of all age classes (21 adults, subadults and juveniles). It was located on a sunny tree fall over a small creek. We observed the colony continuously over 10 h, and for each individual web in the colony we recorded (1) all successful prey capture events and the identity of the spider(s) involved in a capture and (2) the number of territorial interactions and the identity of both the intruding and resident spider. We continuously observed interactions between spiders until they led to a clear outcome (e.g., stay versus retreat). To increase our sample size, we also monitored prey capture at another colony of similar size. We estimated prey size (total body length) visually and recorded the prey's taxonomic order. Prey biomass (dry weight) was calculated from total body length using insect-order specific regression models developed by Sage (1982). For analysis, we combined prey size and biomass data from both colonies.

RESULTS

Social organization and colony architecture.—Colonies ranged in size from 2–27 spiders, with a median group size of 19 (Fig. 2). Most colonies contained multiple adult females, adult males, sub-adults and juveniles. A colony typically consisted of a collection of individual orb webs arranged in a three-dimensional pattern and connected by a framework of silk forming a web complex (Fig. 1a). Orb webs were organized into multiple non-horizontal planes oriented either at the same angle or at different angles from each other (differences in orientation < 90°). Neighboring webs were closely arrayed and often faced similar directions (some were as close as 10 cm apart). The horizontal dimensions of a colonial web complex were usually proportional to the width and topology of the body of water above which they were placed and ranged from 0.5–3 m. Web complexes had a dense three-dimensional core with flattened edges connecting to the vegetation at the water's edge (Fig. 1a), and colony height was proportional to the number of spiders (see 'Spatial arrangement within colonies').

Web size (i.e. orb diameter) scaled positively with spider size: larger spiders occupied larger webs (personal observation). Individuals maintained individual territories (orb webs), although they were commonly seen moving between webs while travelling to other parts of the web complex, and some spiders did not own a web. When disturbed, spiders would typically flee along shared support silk threads to common retreats in the vegetation at the end of the anchor points to the substrate. Web owners regularly maintained their orb webs (i.e., as the need arose), and both spiders that owned webs and web-less spiders maintained the support silk framework. Web building was most common in the early morning and evening.

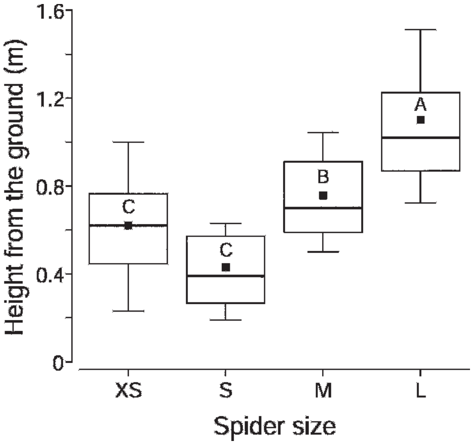

Figure 3.—Distribution of *Leucauge* sp. spiders' heights from the ground (i.e., the water surface) as a function of body size (XS = extra-small; S = small; M = medium; L = large). Boxplots show medians (thick lines), means (filled squares), 25th and 75th percentiles (bottom and top of boxes) and 10th and 90th percentiles (cap of lower and upper whiskers). Letters inside the boxes denote differences between body-size classes based on Bonferroni-adjusted pairwise contrasts (see Results).

Spatial arrangement within colonies.—There was significant heterogeneity across colonies in the proportion of spiders of different size classes (large, medium, small and extra-small; $G_{adj} = 78.39$, $P = 0.02$, $df = 54$). However, the distribution of spider sizes across colonies was independent of colony size ($\chi^2 = 6.43$, $df = 3$, $P = 0.09$) except that extra-small spiders tended to be more common than small ones in large colonies ($\chi^2 = 5.67$, $P = 0.02$). Large- and medium-sized spiders were more likely to occupy an orb, and small and extra-small spiders were more likely to be found on the framework, a dragline or the underside of peripheral leaves ($G_{adj} = 120.58$, $df = 9$, $P < 0.0001$).

A spider's vertical position within a colony was positively correlated with its size class ($F_{3,68} = 22.54$, $P < 0.0001$; Fig. 3). Large spiders assumed the highest positions in a colony (mean height ± SD: 1.10 ± 0.35 m, $n_L = 108$), followed by medium-sized spiders (0.76 ± 0.26 m, $n_M = 70$). Small spiders occurred closest to the bottom of the web complex (0.43 ± 0.22 m, $n_S = 73$) whereas extra-small spiders clustered in between medium and small spiders (0.63 ± 0.28 m, $n_{XS} = 114$), apparently lacking individual orb webs. Therefore, from highest to lowest, the spiders from each size class were distributed as L > M > XS > S within a colony, with adults closer to the top and juveniles closer to bottom of the web complex. Bonferroni-adjusted contrasts revealed significant pairwise differences between each size class ($P < 0.05$) except between XS and S ($P = 0.38$; see Fig. 3). The correlation between height from the ground and spider body size held for colonies of all sizes as there was no significant interaction between spider size and colony size ($F_{3,68} = 0.94$, $P = 0.43$). Furthermore, the average height at which spiders of each size class occurred across colonies did not vary with colony size ($F_{1,68} = 2.82$, $P = 0.10$). However, the overall height from the ground of spiders in each colony increased with colony size ($F_{1,17} = 5.25$, $P = 0.03$), suggesting that colonies grow vertically. This relationship was stronger when the three smallest colonies with fewer than five spiders were included in the analysis ($r_s = 0.71$, $n = 22$, $P = 0.0002$).

Territorial behavior.—We observed 20 attempts by eight different web-less spiders to displace web-holding individuals (“attacks”) on six different webs within the focal colony. Most of these attacks (16/20, 80%) took place on webs located in the center of the web complex and involved adult spiders. Responses to attacks followed an escalating pattern of agonistic behavior typically seen in colonial species (Buskirk 1975b; Hodge & Uetz 1995). Upon approach by an intruder, resident spiders positioned at the hub of the orb web would typically orient towards the intruder. The resident spider would then either contract all eight legs simultaneously, resulting in a rhythmic pulsing lasting 5–10 s that forced the intruder to halt and brace itself, or pluck the web by repeatedly jerking web radii with the front legs that also forced the intruder to brace itself (on two occasions jerks caused intruding spiders to fall out of the orb web). If intruders persisted and approached closer, the resident spider would rush out to face the intruder at the periphery of the web in a one-on-one encounter lasting from < 1 s to 3–4 s, with legs and pedipalps entangled in a blur of activity. After such an encounter, the loser would retreat a short distance and the victor would scramble to the hub of the orb. Resident spiders most often won these encounters, repelling 85% (17/20) of attackers and maintaining their ownership of a web. Spiders not occupying orbs were generally tolerant of each other as close approach and even touching was observed on framework lines of the web complex without any agonistic interactions.

Foraging behavior.—In the focal colony, we observed 23 prey capture events by 11 different spiders on 10 different orb webs. In the second colony we observed an additional 23 prey capture events. Most prey entered the web complex from the side; a few entered from the bottom. Spiders captured and consumed prey individually without cooperating. In both colonies, prey were mostly dipterans with a few hymenopterans and lepidopterans, and ranged from 1–15 mm in length (dry mass = 0.17–25.87 mg) with a majority of prey being small (median length = 2 mm; median dry mass = 0.32 mg; Fig. 4). Few prey were ≥10 mm in length (focal colony: 2/23, 8.7%; second colony: 3/23. 13.0%), but these accounted for 46.7% (focal colony) and 72.5% (second colony) of the total prey biomass. Because these data represent a small prey sampling effort, the exact shape of the distributions should be considered with caution, whereas the overall pattern is robust.

Prey capture occurred throughout the day: 13/23 (56.5%) captures took place between 0800–1200 hours and the remainder (43.5%) took place between 1300–1700 hours; no prey were captured between 1200–1300. In the focal colony, five different spiders captured one prey each and six spiders captured two to four prey each. Spiders occupying webs located in the center of a colony secured 11 out of 23 (47.8%) prey captures, and those at the periphery had 12 out of 23 (52.2%) prey captures. We once observed a spider successfully stealing a prey item captured by another spider; no other conflict over prey between spiders was observed.

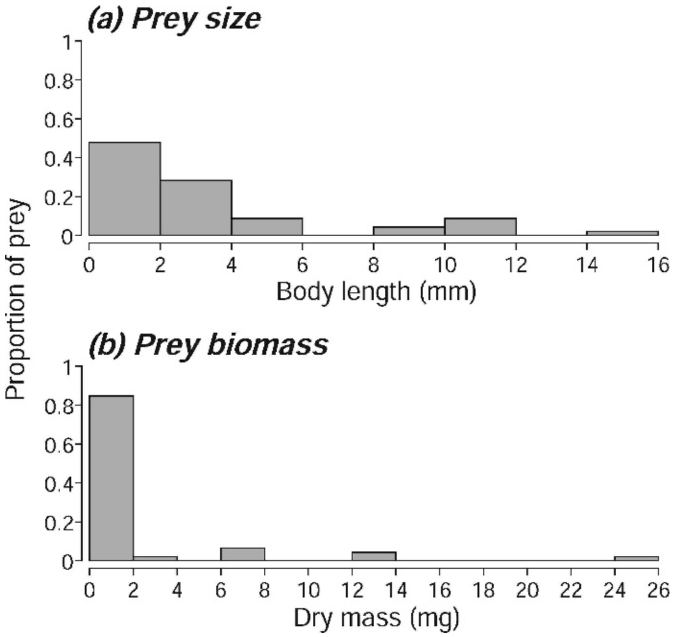

Figure 4.—Distribution of prey captured by *Leucauge* sp. spiders in terms of a) size and b) biomass.

DISCUSSION

This study presents the first empirical evidence of a colonial social organization in the recently discovered neotropical spider *Leucauge* sp. (Avilés et al. 2001). In colonies from the lowland rainforest of Ecuador, spiders maintained individual orb web territories within a framework of shared silk and engaged in individual prey capture. Our population survey showed that the spatial distribution of individuals within colonies is vertically stratified, supporting our hypothesis of a non-random spatial distribution. Colonies were vertically stratified according to spider size so that large spiders positioned themselves closest to the top, medium-sized spiders were found below large ones, and small spiders occupied webs that were closest to the bottom of the colony. Extra-small spiders occurred within the vertical range of small and medium spiders, as they usually did not own a web but instead lived as floaters in the colony’s framework (i.e., an orb-less silk matrix within the colony’s web complex). This non-random spatial distribution of individuals within colonies suggests that the social organization of *Leucauge* sp. follows a hierarchical arrangement, which may be explained in at least three non-mutually exclusive ways.

First, this size-dependent spatial distribution may result from environmental opportunity within a habitat. In *Leucauge* sp. colonies, larger spiders spin larger orb webs, as with other colonial (e.g. *Metabus gravidus* Pickard-Cambridge 1899 (Buskirk 1975a); *Metepeira incrassata* Pickard-Cambridge 1903 (Rayor & Uetz 2000) and usually solitary orb-weaving species (e.g., *Cyclosa* spp. Menge 1866 (Miyashita 1997); *Leucauge mariana* (Taczanowski 1881) (Eberhard 1988); *Nephila clavipes* (Linnaeus 1767) (Higgins & Buskirk 1992)). The highest positions in a colony may better accommodate large orb webs, causing size-related variation in space occupation. Likewise, habitat parameters such as topography and the availability and orientation of web attachment points may affect spacing patterns within spider colonies. For example, in *Metabus gravidus* colonies, the average height of individual orb webs depends on the water current of the stream beneath a colony and the distance between the stream banks (Buskirk 1975a). Further research is needed to determine how the physical characteristics of habitats occupied by *Leucauge* sp. colonies affect their spatial organization.

Alternatively, the spatial stratification of individuals within *Leucauge* sp. colonies may be the result of interactions among colony members. The spatial arrangement of co-occurring spiders within a habitat is commonly thought to reflect competition between individuals for the occupancy of profitable locations (Wise 1993). Along these lines, Herberstein (1998) showed through a manipulative experiment that competition for habitat space between two co-occurring species of web-building linyphiid spiders leads to vertical stratification of species within the habitat. Likewise, competition among conspecifics may produce spatial structure within a colony. Leborgne & Pasquet (1987) showed that the spatial organization of *Zygiella x-notata* (Clerck 1757) spiders living in aggregations is density-dependent. At high densities, cohabitation between spiders of different sizes involved modulations in web size because the presence of large spiders with large webs caused smaller individuals to spin smaller webs.

Similar competitive interactions correlated with individual differences in age and size may affect spatial structuring in group-living species. In the colonial species *Metepeira incrassata*, spiders distribute themselves in a size-dependent pattern (Rayor & Uetz 1990). Large females compete for prime positions close to the core of the colony that afford the best protection from predators, whereas smaller immature spiders live closer to the edge of the web complex where both prey and predators are more common. This spatial arrangement reflects a tradeoff between the foraging and protective requirements of different age classes and results in a hierarchical distribution across different parts of the web complex based on competition for specific environmental conditions. In *Leucauge* sp. colonies, individuals may compete for the highest locations, and larger spiders may dominate due to their size advantage, just as in *M. incrassata* colonies (Rayor & Uetz 2000). To determine if the spatial arrangement of spiders within *Leucauge* sp. web complexes is based on competitive interactions, we would need to conduct field manipulations of spider size composition within colonies and environmental conditions (e.g., predation pressure) at different heights above the ground.

Why would the highest positions in a web complex be the most coveted ones? One likely explanation is based on the fact that groups of colonial spiders are commonly viewed as ‘foraging societies’ that form to increase individuals’ foraging potentials (Whitehouse & Lubin 2005). In a foraging society, individuals may compete for locations within a colony where prey availability is higher or prey are more profitable. This may be especially true in tropical forests, where insect abundance, diversity and size vary with the height above ground, even at small spatial scales (Stork & Blackburn 1993; Basset et al. 2001). For example, Buskirk (1975a) found important spatial differences in insect species composition and abundance associated with the distance above and around streams occupied by *Metabus gravidus* spider colonies in tropical riparian habitats. Therefore, *Leucauge* sp. spiders positioned at different vertical locations within colonies may have access to different insect prey communities. In populations of *Leucauge venusta* (Walckenaer 1841) spiders from southern Mexico, the vertical distribution of webs on coffee plants is correlated with prey size and availability; large spiders build webs at an average height of 150 cm where prey are larger than at ground level, whereas small spiders build webs close to the ground where prey are smaller but more abundant (Hénaut et al. 2006). If rainforest habitats occupied by *Leucauge* sp. colonies have a similar spatial distribution of prey, large prey would be more common at the top of colonies compared to the bottom, which large adult spiders living close to the top may capture more easily than smaller subadult or juvenile spiders. Likewise, juveniles living closer to the bottom may have access to small but abundant prey.

Another possible explanation for the greater intrinsic value of high positions within a colony invokes the architectural properties of a colonial web complex. Spiders living higher up in a web complex may enjoy more architectural stability because they are less susceptible to sources of physical disturbance such as seasonal changes in water levels that may destroy webs.

Differences in the timing of web building between spiders of different sizes may also create heterogeneity in the spatial positioning of individuals. Rayor & Uetz (2000) found evidence for a sequential web-building pattern correlated with spider age and size in the colonial spider *M. incrassata*, with larger individuals securing prime web sites sooner at the expense of smaller ones. Similarly, the different positions occupied by *Leucauge* sp. spiders may depend on their age and web-building abilities. We found that individuals actively defend their webs against intruders, suggesting that they may also compete temporally to secure favorable positions. Individuals may then shift positions as they grow to progressively occupy more competitive locations. Further research is needed to examine this hypothesis in more detail.

Spatial positioning ultimately depends on compromises between the foraging, protective and structural costs and benefits procured by different locations within of a colonial web complex. For example, locations with a higher incidence of large insects may also be more exposed to predatory insects, from which larger spiders may be better protected and thus afford to live in. Conversely, small spiders may settle where the prey and predator fauna may be more suitable.

It is not known whether coloniality provides any individual fitness benefits to *Leucauge* sp. spiders, such as reduced web-building costs. In a congeneric species found in secondary forests of central Costa Rica, *Leucauge mariana*, spiders form local aggregations of adults during the dry season and tend to live solitarily the rest of the year (W. G. Eberhard, pers.

comm.; Valerio & Herrero 1977). In these aggregations, individual orbs lack the surrounding tangle lines that support the web and are solidly anchored to the substrate through shared support silk strands. Therefore, the main benefit invoked for group living in these colonies is an economy of silk (Valerio & Herrero 1977).

In summary, this study documents the colonial social organization of *Leucauge* sp. spiders. We showed that colonies follow a size-dependent spatial arrangement with a positive vertical stratification correlated with spider body size. The characterization of a spatial pattern within colonial spider groups provides further evidence that social groups are organized in specific ways to meet environmental challenges, and provides insight into the forces that shape the evolution of social systems. Future research should determine the underlying causes and mechanisms responsible for this observed spatial structure by conducting manipulative experiments and ecological studies.

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