

Species differences and geographic variation in the communal roosting behavior of *Prionostemma* harvestmen in Central American rainforests

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Abstract. Many species roost communally but the proximate causes and ultimate functions of this widespread behavior remain poorly understood. We studied the communal roosts of two undescribed species of harvestmen in the genus *Prionostemma* Pocock 1903 at a Caribbean rainforest site in southeastern Nicaragua. The species are quite similar in gross morphology but differ in body coloration, male genitalia, and roosting behavior. One species roosts primarily on spiny palms while the other species, which is darker in coloration, roosts inside buttress root cavities. In a mark-recapture study, the cavity-roosting species had higher levels of individual site fidelity than found previously in the spiny palm-roosting species, perhaps because suitable cavities are scarcer than spiny palms. The tree cavity aggregations were strongly male-biased, which our review of the literature suggests is unusual for harvestman roosts. The overall sex ratio of the spiny palm aggregations was 1:1, but some roost sites were strongly male biased while others were strongly female biased. Removing all harvestmen from 10 spiny palm roost sites shifted the overall sex ratio toward males on subsequent days, but the sites with skewed sex ratios remained skewed in the same directions despite complete turnover in roost membership. These results are discussed in relation to mechanisms of roost formation and possible sex differences in vagility, microhabitat preferences and sensitivity to disturbance. Both species also occur at La Selva Biological Station in Costa Rica but neither forms roosting aggregations in spiny palms or tree cavities there. A possible explanation for the geographic variation is that roosting patterns change over time through cultural drift.

Keywords: Aggregation, conspecific attraction, mark-recapture, Opiliones, sex ratio

Animals in diverse taxonomic groups congregate for the inactive period of the diurnal cycle, a behavior referred to as communal roosting (Eiserer 1984; Mallet 1986; Devries et al. 1987; Vulinec 1990; Alcock 1998; Bijleveld et al. 2010). Communal roosts may offer protection from predators through dilution or group defenses (Holmberg et al. 1984; Alcock 1998; Eisner 2004; Willemart & Gnaspini 2004). In some taxa, communal roosts may also provide thermoregulatory benefits (Beauchamp 1999), mating opportunities (Blanco & Tella 1999), opportunities for food sharing (Wilkinson 1984), or information about the location of food patches (Beauchamp 1999; Kerth & Reckardt 2003; Bijleveld et al. 2010). Harvestmen (Opiliones) are generally active at night and roost during the day (reviewed in Machado & Macias-Ordóñez 2007). Some species roost solitarily while others form aggregations ranging in size from a few individuals to hundreds (Holmberg et al. 1984; Cockerill 1988; Coddington et al. 1990; Machado et al. 2000; Willemart & Gnaspini 2004; Machado & Macias-Ordóñez 2007; Wijnhoven et al. 2007; Wade et al. 2011). The communal roosts of harvestmen can be dense aggregations, in which most individuals are clinging to other individuals, or loose aggregations in which most individuals are in contact with the substrate (reviewed in Machado & Macias-Ordóñez 2007). Some species roost in caves or other dark places (Holmberg et al. 1984; Willemart & Gnaspini 2004; Chelini et al. 2011), while other species roost on the exterior surfaces of rocks or vegetation exposed to sunlight (Coddington et al. 1990; Grether et al. 2014). The most frequently proposed functions of Neotropical harvestman roosting aggregations are safety from predators, through dilution and/or chemical defenses, and protection from desiccation (Coddington et al. 1990; Machado et al. 2000;

Willemart & Gnaspini 2004; Machado & Macias-Ordóñez 2007; Grether & Donaldson 2007; Wade et al. 2011; Chelini et al. 2011).

Studies of intra- and interspecific variation can provide insights into the proximate causes and ultimate functions of communal roosts (Chelini et al. 2012). In this paper, we compare the roosting aggregations of two syntopic species of *Prionostemma* Pocock 1903 (Eupnoi: Sclerosomatidae: Gargrellinae) harvestmen at Refugio Bartola, a lowland tropical rainforest site in southeastern Nicaragua. One of the species usually aggregates on the fronds and trunks of spiny palms (Arecaceae: *Bactris* spp., *Astrocaryum* spp.) in the forest understory (Fig.1; Donaldson & Grether 2007; Grether & Donaldson 2007), while the other species aggregates in cavities at the base of trees (e.g., Fabaceae: *Dipteryx panamensis*) that have buttress roots (Fig. 2). Both species form loose aggregations (Holmberg et al. 1984; Machado & Macias-Ordóñez 2007) in which most individuals' legs are in contact with the substrate and the legs are flexed. The species are quite similar in body size and anatomical proportions, but the cavity-roosting species is notably darker in coloration (Fig. 3). Based on scanning electron micrographs of male genitalia (Fig. 4), the same two undescribed species occur at La Selva Biological Station in Costa Rica (69 km to the SE), although neither is known to aggregate in spiny palms or tree cavities at La Selva (see Discussion). Following Proud et al. (2012), we refer to the species that aggregates in tree cavities at Refugio Bartola as *Prionostemma* sp. 1 and to the species that aggregates in spiny palms as *Prionostemma* sp. 2.

The population of *Prionostemma* sp. 2 at Refugio Bartola has been the subject of several short studies focused on clarifying the mechanisms of roost formation. Mark-recapture studies

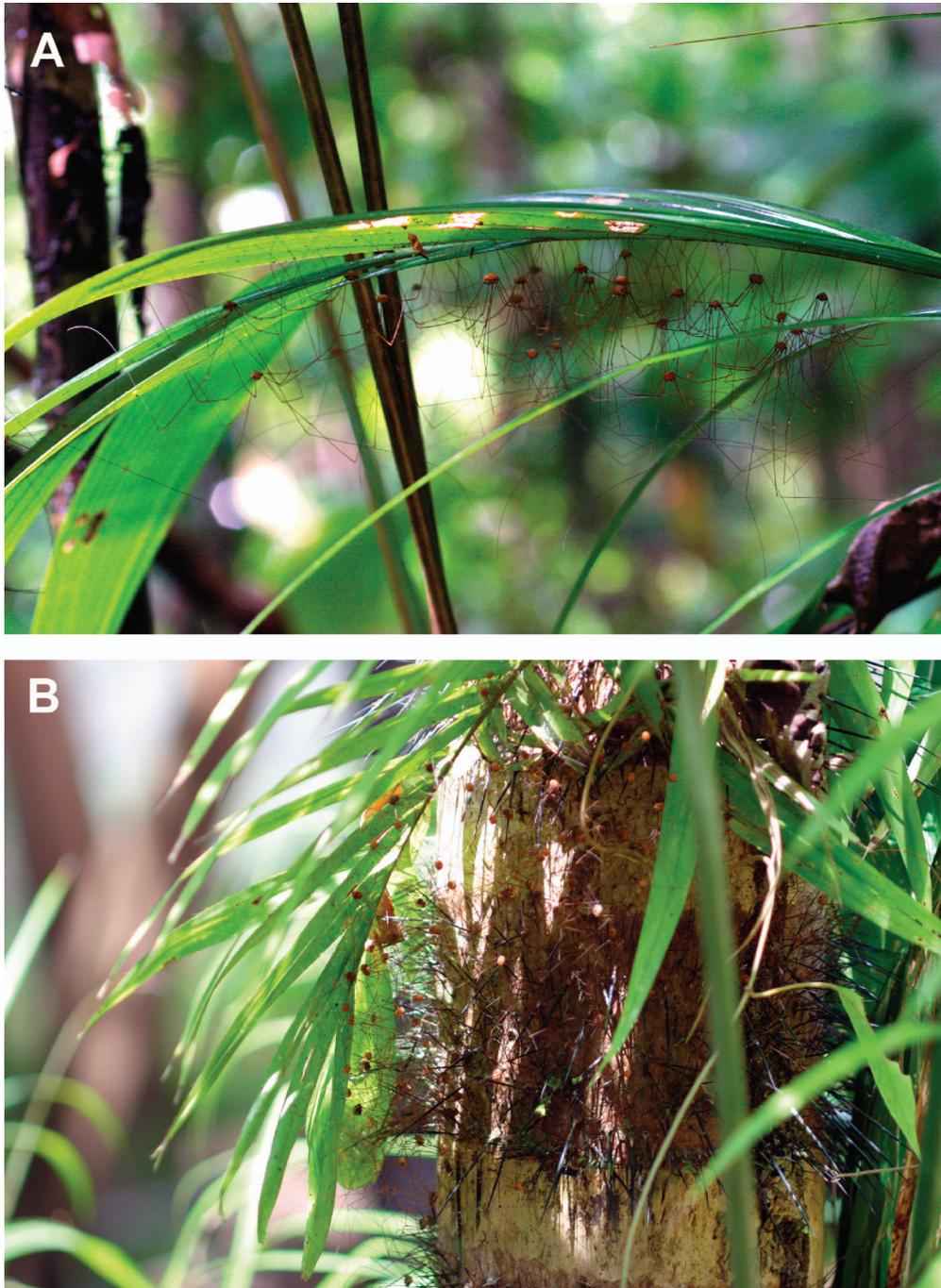


Figure 1.—*Prionostemma* roosting aggregations underneath a frond (A) and along the trunk (B) of spiny palms.

established that individual harvestmen are not roost-site faithful (Grether & Donaldson 2007; Teng et al. 2012), and yet aggregations have formed in the same locations for over 10 years (Teng et al. 2012; Grether et al. 2014). The long-term use of specific sites does not appear to be a product of habitat limitation. Most spiny palms do not attract harvestman aggregations, and those that do are not distinctive in the characteristics of the palms themselves or microclimate (Grether & Donaldson 2007; Teng et al. 2012). Based on roost site manipulations and experimental translocations, it has been deduced that these harvestmen preferentially settle in sites marked with conspecific

scent (Donaldson & Grether 2007; Teng et al. 2012). Thus, the location of the communal roosts appears to be traditional in that some sites are used in preference to others only because conspecifics roosted there in the past (Donaldson & Grether 2007). While the mechanism of roost site selection in *Prionostemma* sp. 2 may result in the repeated use of particular roosting sites for multiple years, the same mechanism could also cause populations to drift in roosting microhabitat over longer time scales. Our finding that the same species is present but does not roost in spiny palms at La Selva Biological Station provides tentative support for this cultural drift hypothesis (see Discussion).



Figure 2.—Distant (A) and close-up (B) photographs of a tree cavity with a *Prionostemma* roosting aggregation.

The aggregations of *Prionostemma* sp. 1 in buttress root cavities were first discovered at Refugio Bartola in February 2013 and have not been described previously. To begin to characterize the roosting behavior of this species, and to compare it to that of *Prionostemma* sp. 2, we made structured behavioral observations and conducted a mark-recapture study. Comparable data have already been published for *Prionostemma* sp. 2 (Donaldson & Grether 2007; Grether & Donaldson 2007; Teng et al. 2012), so we did not duplicate this work. Instead, we carried out a removal experiment at spiny palm aggregation sites (see Grether et al. 2014). In the context of the species comparison, the primary relevance of the removal experiment is that it yielded data on *Prionostemma* sp. 2 roost sex ratios, which have not been reported previously. To help place our findings into a broader context, we also analyze data on harvestman roost sex ratios reported in the literature.

METHODS

Study area.—This study was carried out in primary lowland rainforest at Refugio Bartola in southeastern Nicaragua (10.973°N, 84.339°W) from 2–20 February 2013. This private reserve is contiguous with Indio Maíz Biological Reserve, the largest remaining tract of primary rainforest in Central America (ca. 4500 km²). The climate is wet tropical, with about 4 m of rainfall per year, peak precipitation in June–August, and a dry season from February–April during which about 15% of the annual precipitation is recorded (Cody 2000). Approximately 69 mm of rain fell at Refugio Bartola during the study period.

Operational definitions.—We use the term roosting aggregation to refer to groups of two or more individuals resting in the same “site”. In the case of spiny palm roosts, we consider all of the spiny palms within 1 m of each other to belong to the same site (spiny palms tend to grow in clusters with broadly overlapping fronds). In the case of tree cavity roosts, we consider a single cavity to be a site. While roosting individuals of both study species are often close enough together to have overlapping legs (Figs. 2, 3), we did not use leg overlap as a criterion for determining aggregation membership (cf. Willemart & Gnaspini 2004).

Roost measurements and behavioral observations.—Using flashlights, we searched for harvestman roosts at the base of 114 buttressed trees. At the first seven tree cavities in which *Prionostemma* roosting aggregations were found, we measured air temperature, surface temperature, and percent humidity both within the cavity and outside the cavity using a hygrothermometer and infrared thermometer (Extech Instruments Waltham, MA USA). In addition, we measured the height, width, depth and compass orientation of the cavity, and the tree’s circumference at breast height. To characterize the behavior of the harvestmen in the cavity roosts, we used scan sampling (Altmann 1974). Under red light, we observed six of the cavity roosts used in the mark-recapture study for 15 minutes, recording at 1-minute intervals the number of harvestmen that were stationary or engaged in the following behaviors: walking within the cavity; bobbing (moving body up and down, a likely anti-predator behavior; Holmberg et al. 1984; Grether and Donaldson 2007); ventral rubbing (pressing

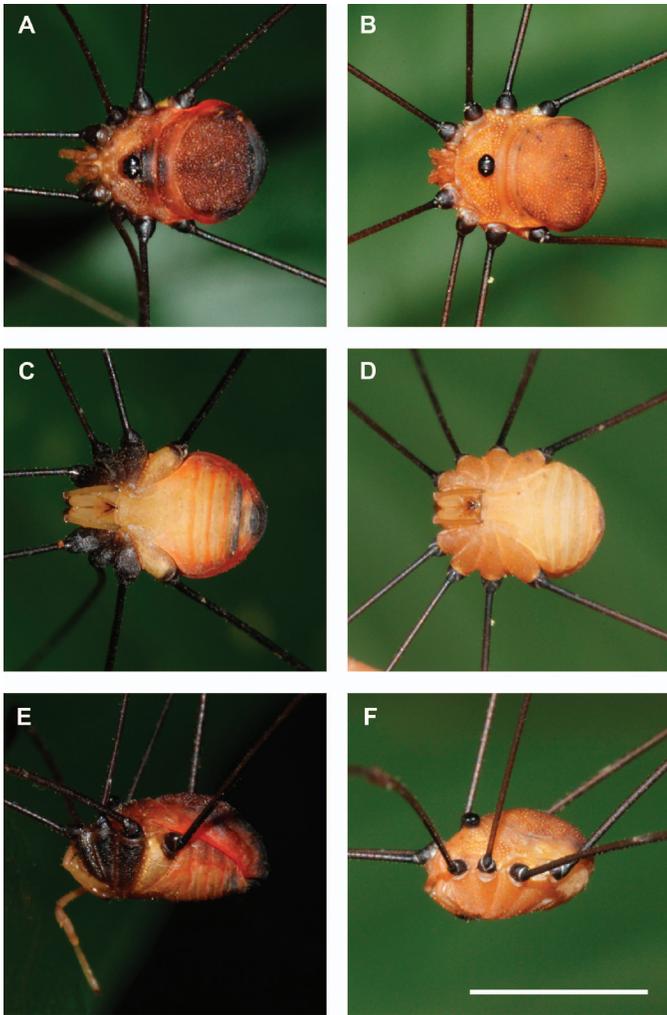


Figure 3.—Photographs of two *Prionostemma* species at Refugio Bartola, Nicaragua. Two female specimens are each shown in dorsal (A, B), ventral (C, D), and lateral (E, F) views. The female on the left was found in a tree cavity roost (*Prionostemma* sp. 1) and the female on the right was found in a spiny palm roost (*Prionostemma* sp. 2). *Prionostemma* sp. 2 is more uniform and lighter in coloration than *Prionostemma* sp. 1. The black coxae (I–III) and red and black patches on the abdomen of the *Prionostemma* sp. 1 specimen are typical of this species. Scale bar = 5 mm.

against substrate and moving body forward, a possible scent-marking behavior; Donaldson and Grether 2007; Willemart and Hebets 2011); and leg threading (moving leg through mouth parts, a self-grooming behavior; Edgar 1971; Pereira et al. 2004; Teng et al. 2012).

Mark-recapture study.—To measure daily turnover in the tree cavity aggregations, and to check for movement between nearby tree cavity and spiny palm roosts, we marked and recaptured harvestmen at seven tree cavity roosts (two other tree cavity roosts were found too late in the study period to be included in the mark-recapture study). All harvestmen in a cavity were captured by hand between 0900 and 1630 h and placed in a mesh cage (Bioquip Products). Individuals that initially were too deep inside the cavity to be captured were flushed out with a stick. The harvestmen were sexed, inspected for ectoparasitic larval mites, marked on the dorsal surface of

the abdomen with small dots of paint (Marvy Decocolor, Uchida of America, Torrance, CA) in color combinations corresponding to the capture date and location, and then released in their original cavities. This procedure was carried out on three consecutive days at each aggregation site and a final recapture was done on the fourth day. On all four days at each site, we also searched for marked harvestmen on all buttress roots and spiny palms within a 10 m radius. Recaptured individuals were given additional paint dots corresponding to the location and date of recapture. During this study, we marked 257 harvestmen.

Removal experiment.—Concurrent with the mark-recapture study, we captured and removed all of the harvestmen from 10 spiny palm roosts on at least four consecutive days and for up to six consecutive days if the site continued to attract new harvestmen. The animals were captured by hand and held temporarily in a mesh cage. Individuals that initially were too high to be captured were chased down with a wooden pole. The harvestmen were sexed, marked on the dorsal surface of the abdomen with small dots of paint identifying the capture location, and released at least 50 m away from the aggregation site on the trunk of another spiny palm. During the experiment, we removed 989 harvestmen (37–224 per site).

At each removal site, we took a standard set of measurements, including canopy cover, crown height, spine density, and trunk diameter (the first three factors have been found to correlate with the size of *Prionostemma* sp. 2 aggregations; Teng et al. 2012). Canopy cover was measured with a concave spherical densiometer (Forestry Suppliers Inc, Jackson, MS, USA). Crown height was measured with a graduated pole, and trunk diameter was measured with a ruler, on all of the spiny palms at a site. Spine density was measured by placing a 4 cm² wire quadrat on the trunk of the palms and counting all spines originating within the quadrat. The quadrat was placed at three different heights above the ground (0.8, 1.15, and 1.55 m) in the four cardinal directions around the trunk. If a site had more than five spiny palms within 1 m of each other, spine density was measured on half of the trees chosen at random. One observer made all measurements of a particular type. Site averages for spine density, crown height and trunk diameter were used in the analysis.

Analysis of harvestman communal roost sex ratios from the literature.—We searched the primary literature for reports of the sex ratio of harvestman communal roosts. For inclusion in our statistical analysis, a report needed to contain one of the following kinds of data on the sex ratio at communal roosts: the number of individuals of each sex, the total number of individuals and the sex ratio, or the sex ratio and its standard deviation. We did not impose our operational definitions of terms such as aggregation and roosting site (see above) on other studies but instead accepted the definitions used in the original studies. For example, some researchers define aggregations as groups of three or more individuals with overlapping legs (e.g., Willemart & Gnaspini 2004). However, we do not believe this compromised the validity of our literature review. In cases of multispecies aggregations (e.g., Machado & Vasconcelos 1998; Chelini et al. 2012), we analyzed the data for each species separately. Because a sample size of five is the minimum required to establish whether a sex ratio deviates significantly from 1:1 with a

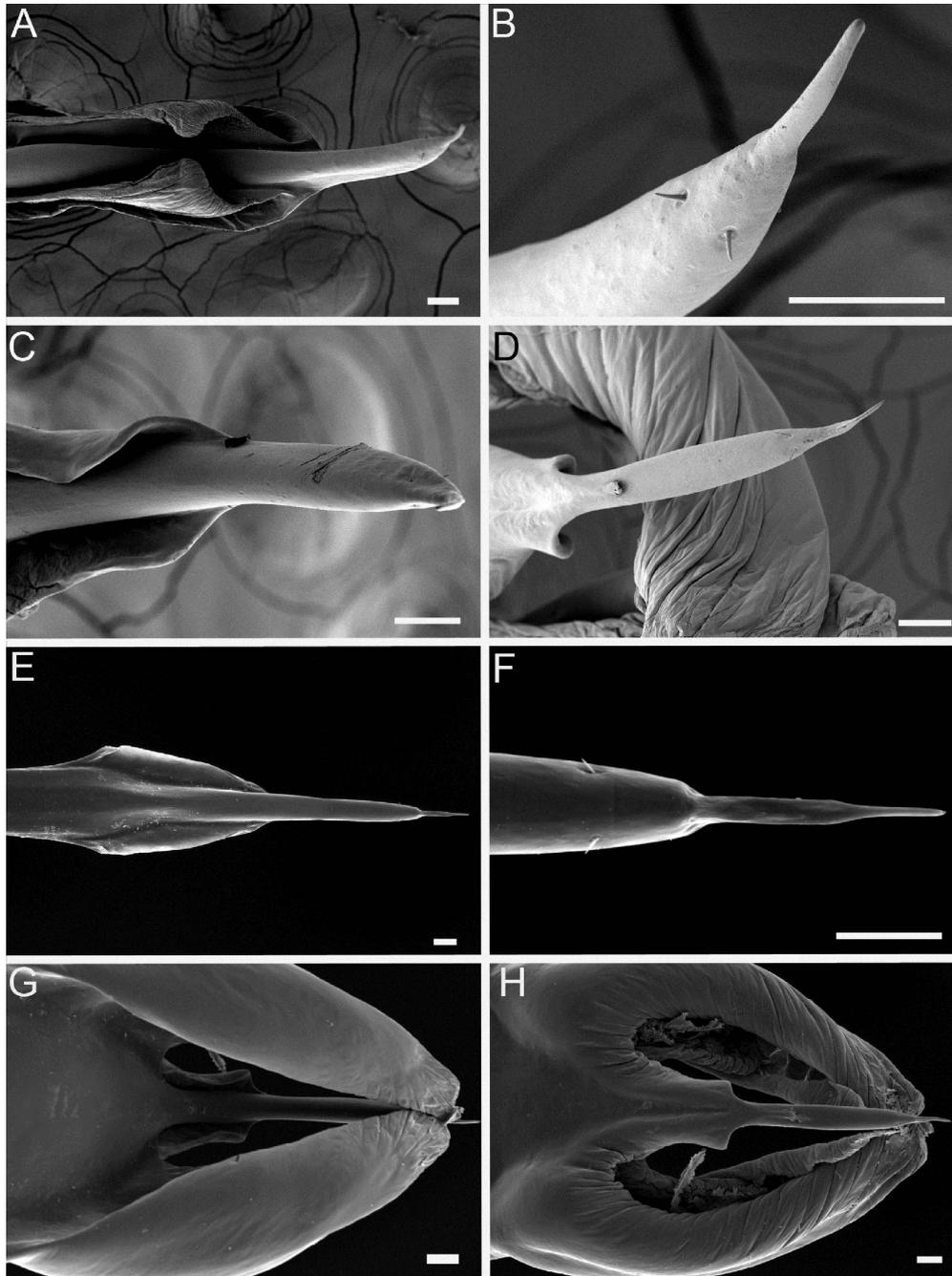


Figure 4.—Scanning electron micrographs of male genitalia. The genitalia of the species of *Prionostemma* that typically roosts in spiny palms at Refugio Bartola, Nicaragua (A, B) is very similar to that of *Prionostemma* sp. 2 (Proud et al. 2010) at La Selva, Costa Rica (E, F) in both shape and proportion. There is a small difference in the shape of the stylus – in panel F the stylus attenuates but in panel B it does not. Nevertheless, these are probably the same species. The curling of the alates (winglets) just before the glans on the Nicaraguan specimen (A) is an artifact. The species that roosts in tree cavities at Refugio Bartola (C, D) is undoubtedly the same species as *Prionostemma* sp. 1 at La Selva (G, H). The large structure at the base of the penis (best seen in panel H), the lateral expansions (alates), and the stylus are identical in size and shape, as viewed from both dorsal (C, G) and ventral perspectives (D, H), to *Prionostemma* sp. 1 at La Selva. Scale bar = 50 μm .

binomial test, we excluded sex ratios based on sample sizes smaller than five. We also excluded sex ratios based on samples that likely included solitary roosting or non-roosting harvestmen (e.g., Tsurusaki 2003). Because harvestmen can live for years as adults (Gnaspini 2007), we did not pool data from repeated visits to the same sites and instead analyzed

data from different months and seasons separately. In the case of the study of Mestre and Pinto-da-Rocha (2004), we chose one month per season that best represented the average sex ratio of all the months in that season. In the case of the study of Willemart and Gnaspini (2004), we pooled data from different aggregation sites but analyzed each collection date

Table 1.—Summary of mark-recapture study results. From left to right: the day of the study, the total number of harvestmen captured, the number that were unmarked until that day (i.e., not captured previously), the number that were marked from any previous capture, the percentage that were marked from any previous capture, the number returning on the next day, and the percentage returning on the next day.

Day	Total	Unmarked	Marked	% Marked	Returning	% Returning
1	172	172	—	—	96	55.8%
2	141	45	96	68.1%	69	48.9%
3	108	25	83	76.9%	30	27.8%
4	57	15	42	73.7%	—	—

separately because the sex ratio varied significantly within seasons.

Statistics.—Wilcoxon signed-rank tests were used to compare the microclimate inside and outside of cavities, because these data are paired by site. Skillings-Mack tests (nonparametric equivalents of repeated measures ANOVAs) were used to compare the change in harvestman numbers over time, because there were more than two time points. Binomial tests were used to compare the observed sex ratios to 0.5. Fisher exact tests were used to test for associations between nominal variables (e.g., sex and mite presence). Spearman rank correlations were used to test for correlations between continuous variables (e.g., roost sex ratio and canopy cover). For comparisons involving small sample sizes (e.g., number of roosts), we computed the *P*-values by permutation. All reported *P*-values are two-tailed. Ranges, means and standard deviations are provided to facilitate comparisons to other studies. Stata 12.1 (StataCorp, College Station, TX, USA) was used for the computations.

RESULTS

Roost characteristics and behavioral observations.—We found *Prionostemma* sp. 1 aggregations in nine (7.9%) of 114 buttressed trees examined. Solitary harvestmen of Cosmetidae species (e.g., *Cynorta* spp. Koch 1839, *Eucynorta* spp. Roewer 1912) were often found on the surface of the roots and in the gaps between them, but the *Prionostemma* aggregations were found only in cavities (i.e., holes) just above ground level. The cavities with *Prionostemma* aggregations seemed relatively narrow (mean \pm sd, 0.34 \pm 0.15 m, $n = 7$) and deep (0.58 \pm 0.12 m, $n = 7$), compared to unused cavities. Trees with cavity roosts ranged in circumference from 1.25–8.14 m (mean \pm sd, 3.72 \pm 2.38 m, $n = 7$). Canopy cover readings taken at the base of the trees ranged from 92.7–96.7% (mean \pm sd, 94.4 \pm 1.4%, $n = 7$). The daytime surface temperature was consistently 1–2 °C lower inside the roosting cavities (mean \pm sd, 25.0 \pm 0.8 °C) than immediately outside (mean \pm sd, 26.3 \pm 1.4 °C; Wilcoxon signed-rank test, $T = 0$, $n = 7$, $P = 0.018$). There were no significant differences in daytime air temperature or humidity inside the roosting cavities (air temperature, 27.0 \pm 0.8 °C; humidity, 86.1 \pm 6.0%) compared to immediately outside (air temperature, 27.0 \pm 0.8 °C, Wilcoxon signed-rank test $T = 2$, $n = 7$, $P = 0.29$; humidity, 88.7 \pm 10.3%, $T = 1$, $n = 7$, $P = 0.08$). During behavioral observations made at the aggregation sites during the day,

Table 2.—Numbers of females (N_f) and males (N_m) and the sex ratio, calculated as the proportion female (P_f), at tree cavity roosts on the first day of the mark-recapture study, sorted from the most male-biased to the least male-biased. Binomial tests (BT) compare the observed sex ratio to 0.5. Two-tailed *P*-values are shown for samples with $n \geq 5$. With a sequential Bonferroni correction for multiple tests (Holm 1979), across the six *P*-values in the table, the criterion for statistical significance at $\alpha = 0.05$ is $P < 0.05$.

Tree cavity	N_f	N_m	P_f	<i>P</i>
1	2	18	0.1	0.0004
2	1	8	0.11	0.04
3	3	16	0.16	0.004
4	10	44	0.19	< 0.0001
5	8	28	0.22	0.001
6	8	23	0.26	0.01
7	1	2	0.33	—

most individuals were either stationary (mean of the site scan sampling means, 77.5%) or bobbing (19.2%). Some individuals were walking within the cavity (2.0%), but no leg-threading, ventral rubbing, foraging, or reproductive behaviors (e.g., mating, egg laying) were observed.

Mark-recapture study.—The maximum daily return of *Prionostemma* sp. 1 to the cavity roost where they were marked (i.e., from one day to the next) ranged from 44.4–77.4% per site ($n = 7$; mean \pm sd, 59.4 \pm 12.1%). Marked harvestmen were recaptured on 221 occasions and always in the same cavity where they were originally marked.

Despite the relatively high return rates, capturing and marking *Prionostemma* sp. 1 evidently reduced their likelihood of returning. The total number of *Prionostemma* found in the cavity roosts decreased from 172 on the first day to 141 on the second day, 108 on the third day, and 57 on the fourth day (Table 1). The change over time in harvestmen numbers was highly significant (Skillings-Mack test, SM = 15.3, simulation $P < 0.0001$). As the total number of harvestmen declined, the proportion of harvestmen that carried marks from any previous day's capture remained relatively stable but the proportion of harvestmen returning on the next day declined over time (Table 1).

Because recaptured individuals were given new marks on each day, we were able to infer that some individuals returned repeatedly to the same cavity. Of the 57 harvestmen found in the final recapture, 42 (73.7%) were present on a prior day, 32 (56.1%) were present on at least two prior days, and 17 (29.8%) were present on all three prior days.

Within the 10-m radii of the seven cavity roosts in the mark-recapture study, there were 35 other buttressed trees and 40 spiny palms. *Prionostemma* aggregations were found in one (2.8%) of these buttressed trees and two (5%) of the spiny palms. Only two harvestmen in the mark-recapture study were found away from the buttressed tree where they were marked. One was found on the trunk of another buttressed tree and the other was found in a spiny palm aggregation. In both cases, the marked individuals were within the 10-m radius of the cavity where they were marked (as opposed the 10-m radius of a different roost cavity).

The sex ratio at cavity roosts was strongly male-biased both overall (50 females, 207 males, proportion female = 0.24; binomial test $P < 0.0001$) and at all seven of the mark-recapture sites (Table 2; proportion female among all animals

Table 3.—Numbers of females (N_f) and males (N_m) and the proportion female (P_f) at spiny palm roosts prior to the first removal and after the first removal. Roost sites are sorted by P_f prior to the first removal, from the most male-biased to the most female-biased. Binomial tests (BT) compare the observed sex ratio to 0.5. Fisher's exact tests compare the pre-removal sex ratio to the post-removal sex ratio. Two-tailed P -values are shown. With a sequential Bonferroni correction for multiple tests (Holm 1979), across all 30 P -values in the table, the criterion for statistical significance at $\alpha = 0.05$ is $P < 0.003$.

Spiny palm	Prior to first removal				After first removal				Fisher's exact P
	N_f	N_m	P_f	P	N_f	N_m	P_f	P	
1	1	24	0.04	< 0.0001	3	9	0.25	0.14	0.09
2	5	37	0.12	< 0.0001	1	18	0.05	0.0008	0.65
3	15	91	0.14	< 0.0001	11	107	0.09	< 0.0001	0.30
4	8	34	0.19	< 0.0001	6	30	0.17	0.0007	1.0
5	17	14	0.55	0.72	28	50	0.36	0.02	0.09
6	58	36	0.62	0.03	13	46	0.22	< 0.0001	< 0.0001
7	43	25	0.63	0.04	11	30	0.27	0.004	< 0.0001
8	31	7	0.82	0.0001	17	2	0.89	0.007	0.70
9	56	7	0.89	< 0.0001	41	17	0.71	0.002	0.02
10	16	2	0.89	0.001	15	7	0.68	0.13	0.15

marked, range 0.10–0.28). There was no significant variation among roost sites in the sex ratio of harvestmen marked during the first capture (Fisher's exact test, $P = 0.77$) or across all of the harvestmen marked during the study ($P = 0.27$), nor did the overall sex ratio change significantly over time from the first capture to the last recapture (Fisher's exact test, $P = 0.53$). Of the 221 recaptures, 50 (22.6%) were female, which did not differ significantly from the overall sex ratio (binomial test $P = 0.69$). Thus, males and females exhibited similar levels of individual site fidelity.

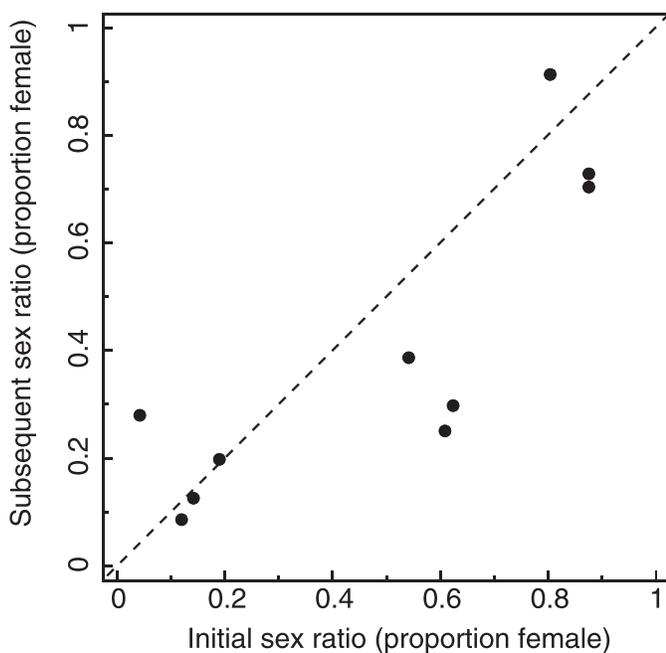


Figure 5.—Variation in, and effects of the removal treatment on, the sex ratio at spiny palm roosting sites. Each point represents the sex ratio (proportion female) before and after the removal treatment commenced at 10 established aggregation sites. The dashed line has a slope of 1 and thus points below the line indicate that the sex ratio decreased after the removal treatment began. See text for statistical results.

Red ectoparasitic larval mites were found on 21 (8.2%) of the 257 individuals marked in cavity roosts. The maximum number of mites per individual was three and most mites (24 of 26) were attached to legs. There was no significant sex difference in mite prevalence (16 of 207 males and 5 of 50 females; Fisher's exact test, $P = 0.57$). Mite prevalence varied significantly among sites (Fisher's exact test, $P < 0.0001$). No mites were found infesting harvestmen at four of the seven sites. At the site with the highest mite prevalence, 14 of 45 individuals (31.1%) had at least one mite. By comparison, mites were rare at the *Prionostemma* sp. 2 spiny palm aggregations during this study (fewer than 1 in 50 individuals; G.F.G et al., pers. obs.).

Removal experiment.—The removal treatment had an unexpected effect on the sex ratio at *Prionostemma* sp. 2 roosts. While the overall sex ratio was approximately 1:1 at the first removal (Table 3; 250 females, 277 males, proportion female = 0.49; binomial test $P = 0.26$), it was significantly male-biased in subsequent removals (total count: 146 females, 316 males, proportion female = 0.37; binomial test $P < 0.0001$). A sex ratio shift of this magnitude is very unlikely to have occurred by chance (Fisher's exact test, $P < 0.0001$). Seven of the 10 sites had strongly skewed sex ratios (female biased, $n = 3$; male biased $n = 4$), and despite complete turnover in roost membership, the initial and subsequent (i.e., post-removal) sex ratios were strongly correlated across sites (Fig. 5, Spearman rank correlation $r_s = 0.79$, $n = 10$ sites, $P = 0.008$). As shown in Fig. 5, three sites that initially had weakly female-biased sex ratios all shifted to having male-biased sex ratios, three sites that initially had strongly female-biased sex ratios remained strongly female-biased, and four sites that initially had strongly male-biased sex ratios remained strongly male-biased. None of the measured site characteristics correlated significantly with the initial roost sex ratio (canopy cover $r_s = 0.22$, $n = 10$, $P = 0.53$; spine density $r_s = -0.02$, $P = 0.95$; crown height $r_s = 0.44$, $P = 0.20$; trunk diameter $r_s = -0.52$, $P = 0.14$).

All 989 of the harvestmen removed during this experiment were marked and released on other spiny palms. For the duration of the study, none of the marked harvestmen returned to the site where they were initially captured.

However, six marked individuals, from three different release sites, were found inside the same tree cavity in the mark-recapture study. The distance between the release sites and this tree cavity ranged from 28–45 m and the harvestmen were found there 1–2 days after they were released.

Harvestman communal roost sex ratios from the literature.— We found data on the sex ratios at communal roosts of 12 harvestman species in the published literature. Most of the reported communal roost sex ratios did not deviate significantly from 1:1 (Table 4). Significantly female-biased communal roost sex ratios were found in *Goniosoma albiscriptum* Mello-Leitão 1932 at one of seven sampling dates in 2000 (Willemart & Gnaspini 2004) and in a multi-year study of *Goniosoma longipes* Roewer 1931 (Machado et al. 2000), both at caves in southeastern Brazil. Tsurusaki (2003) reported significantly male-biased sex ratios in general collections of two harvestman species in Japan, but whether these species form roosting aggregations was not stated. *Prionostemma* sp. 1 appears to be the only known example of a harvestman with strongly male-biased communal roost sex ratios.

DISCUSSION

Roosting behavior (Mestre & Pinto-da-Rocha 2004; Willemart & Gnaspini 2004), sex ratios (Chelini et al. 2012), and mite infestation levels (Townsend et al. 2006) are all known to vary seasonally in harvestmen, so it cannot be assumed that the species differences that we observed hold year round. With that caveat, the preferred roosting microhabitats of the two *Prionostemma* species at Refugio Bartola during the dry season could scarcely be more distinct. All of the *Prionostemma* sp. 1 aggregations that we found were inside cavities at the base of buttressed trees, while *Prionostemma* sp. 2 aggregations are usually found several meters above the ground in spiny palms (Grether & Donaldson 2007). Some marked individuals were found moving between tree cavity and spiny palm aggregations, however, and a review of photos taken of roosting aggregation in previous years yielded three additional cases of individuals with the coloration of *Prionostemma* sp. 1 in spiny palm aggregations (G.F.G., pers. obs.). The extent to which these species intermingle at roost sites remains to be quantified. Solitary individuals of Cosmetidae harvestmen (e.g., *Cynorta*, *Eucynorta*) are often found in *Prionostemma* aggregations as well (unpublished data).

In mark-recapture studies, *Prionostemma* sp. 1 showed much higher daily return rates (up to 77%) than *Prionostemma* sp. 2 (up to 26%; Grether & Donaldson 2007). A likely explanation is that suitable tree cavities are scarce compared to spiny palms. Another possible explanation is that cavity roosts are easier for the harvestmen to relocate.

We found ectoparasitic larval mites on 8% of the *Prionostemma* sp. 1 and on less than 1% of the *Prionostemma* sp. 2. Whether this is causally related to the species difference in roosting habitat is unknown but seems possible. Species differences in larval mite infestation rates have previously been linked to species differences in foraging habitats (Townsend et al. 2008).

We have found evidence for handling effects in both species (see Grether & Donaldson 2007 for the *Prionostemma* sp. 2 evidence), but the rapid decrease over time in the number of *Prionostemma* sp. 1 at the mark-recapture sites leaves little

doubt that capturing these animals makes them less likely to return to the same site. Harvestmen have been shown to have spatial associative learning ability (dos Santos et al. 2013) and may avoid sites where they have previously been disturbed. Another possible explanation is that captured harvestmen release defensive chemicals (Machado 2002; Machado et al. 2002; Eisner 2004; Rocha et al. 2013) that persist at the site of disturbance and make it less attractive for roosting. In any case, the decreasing return rate over time (Table 1) suggests that these harvestmen would rapidly abandon a site where they were disturbed repeatedly.

Perhaps the most interesting species difference found in our study at Refugio Bartola is the difference in roost sex ratios. The *Prionostemma* sp. 1 aggregations were strongly male biased (76% male), which may be rare in harvestmen. The communal roosts of some insects are male biased (Alcock 1998; Switzer & Grether 1999), but our review of the literature turned up no other harvestman examples (Table 4). Most harvestmen aggregation sex ratios reported in the literature do not differ significantly from 1:1, but female biases have been reported in several Laniatores species (Table 4). In some cases, the sex ratio at communal roosts may merely reflect the population sex ratio (Chelini et al. 2012), and female-biased population sex ratios may be indicative of facultative parthenogenesis (Tsurusaki 1986, 2003). Willemart and Gnaspini (2004) found that the communal roosts of *Goniosoma albiscriptum* (Laniatores: Gonyleptidae) were more female-biased than the population sex ratio and hypothesized this is because males are more aggressive and less gregarious than females. *Goniosoma albiscriptum* roosting aggregations break up during the peak reproductive season, perhaps because females become intolerant of conspecifics while guarding their eggs and males become intolerant of all other males (Willemart & Gnaspini 2004). A similar mechanism could potentially account for male-biased roost sex ratios, if males continued to roost communally while females roosted away from aggregation sites to guard their eggs. We did not encounter egg-guarding females during our study, however. Thus, the male-bias of *Prionostemma* sp. 1 communal roosts is a mystery that merits further study.

Although the overall sex ratio of *Prionostemma* sp. 2 roosts did not differ from 1:1, most of the aggregation sites were strongly sex biased. In the removal experiment, sites that initially had weakly female-biased sex ratios became male-biased while sites with strongly skewed sex ratios remained skewed in the same directions despite complete turnover in roost membership (Table 3, Fig. 5). A possible explanation for the shift in the overall sex ratio is that males are more vagile than females, as has been reported for other species of harvestmen and for arachnids generally (reviewed in Willemart and Gnaspini 2004). If removing the harvestmen from an aggregation site temporarily depletes the local pool of potential recruits, males may move into the area first, resulting in a temporary male bias in the roost sex ratio. But why would some sites attract mainly females? Sex differences in roost-site preferences could potentially explain the pattern, but none of the roost characteristics that we measured were predictive of the sex ratio. Another possible explanation is that the sexes differ in their scent-marking chemicals and are most strongly attracted to same-sex scent. The latter hypothesis could be

Table 4.—Sex ratios of harvestman roosting aggregations reported in the literature. Abbreviations in column titles: Mo., month; N_{ag} , number of aggregations sampled; N_f , number of females; N_m , number of males; P_f , proportion female; Sig., significance level of statistical test versus $P_f = 0.5$; Ref., source of data. Country codes: BR, Brazil; NL, Netherlands; NI, Nicaragua; US, United States. Season codes: Sp, spring; Su, summer, W, winter; F, fall. P -values for 2-tailed tests: NS $P > 0.1$; § $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Reference codes: 1, Machado and Vasconcelos 1998; 2, Mestre and Pinto-da-Rocha 2004; 3, Willemart and Gnaspi 2004; 4, Machado et al. 2000; 5, Machado 2002; 6, Chelini et al. 2012; 7, Cockerill 1988; 8, Wijnhoven et al. 2007; 9, this paper. Dashes indicate that the information was not provided. Binomial tests were used if harvestmen counts were provided; in lieu of counts, if means and standard deviations were provided, we tested whether the 95% confidence interval of the roost sex ratio included zero. The horizontal dashed line separates the suborders; species above the line are in the suborder Laniatores; species below the lines are in the suborder Eupnoi.

Family	Species	Location	Mo. (season)	N_{ag}	N_f	N_m	P_f	Sig.	Ref.
Gonyleptidae	<i>Despirus montanus</i>	Serra do Cipó, Minas Gerais, BR	Nov (Sp)	5	26	16	0.62	NS	1
Gonyleptidae	<i>Discocyrtus sp. 1</i>	Curitiba, Parana, BR	Aug (W)	—	8	4	0.67	NS	2
Gonyleptidae	<i>Discocyrtus sp. 1</i>	Curitiba, Parana, BR	Nov (Sp)	—	9	6	0.60	NS	2
Gonyleptidae	<i>Discocyrtus sp. 1</i>	Curitiba, Parana, BR	Dec (Su)	—	5	4	0.56	NS	2
Gonyleptidae	<i>Discocyrtus sp. 1</i>	Curitiba, Parana, BR	May (F)	—	7	6	0.54	NS	2
Gonyleptidae	<i>Eugynides sp.</i>	Serra do Cipó, Minas Gerais, BR	Nov (Sp)	5	15	23	0.39	NS	1
Gonyleptidae	<i>Geracormobius sp.</i>	Curitiba, Parana, BR	Jan (Su)	—	5	4	0.56	NS	2
Gonyleptidae	<i>Goniosoma albiscriptum</i>	Ribeirão Pires, São Paulo, BR	Apr (F dry)	1	24	3	0.89	***	3
Gonyleptidae	<i>Goniosoma albiscriptum</i>	Ribeirão Pires, São Paulo, BR	May (F dry)	1	9	9	0.50	NS	3
Gonyleptidae	<i>Goniosoma albiscriptum</i>	Ribeirão Pires, São Paulo, BR	Jun (W dry)	1	24	12	0.67	§	3
Gonyleptidae	<i>Goniosoma albiscriptum</i>	Ribeirão Pires, São Paulo, BR	Jun (W dry)	1	17	7	0.71	§	3
Gonyleptidae	<i>Goniosoma albiscriptum</i>	Ribeirão Pires, São Paulo, BR	Jul (W dry)	1	18	8	0.69	§	3
Gonyleptidae	<i>Goniosoma albiscriptum</i>	Ribeirão Pires, São Paulo, BR	Jul (W dry)	1	9	3	0.75	NS	3
Gonyleptidae	<i>Goniosoma albiscriptum</i>	Ribeirão Pires, São Paulo, BR	Aug (W dry)	1	4	3	0.57	NS	3
Gonyleptidae	<i>Goniosoma longipes</i>	Florestal Itapetinga, São Paulo, BR	Mar–Jun	28	—	—	0.64	*	4
Gonyleptidae	<i>Goniosoma aff. proximum</i>	Ilha do Cardoso, São Paulo, BR	—	82	—	—	0.52	NS	5
Gonyleptidae	<i>Ilhaia cuspidata</i>	Curitiba, Parana, BR	Aug (Sp)	—	131	131	0.50	NS	2
Gonyleptidae	<i>Ilhaia cuspidata</i>	Curitiba, Parana, BR	Sep (Sp)	—	159	127	0.56	§	2
Gonyleptidae	<i>Ilhaia cuspidata</i>	Curitiba, Parana, BR	Dec (Su)	—	136	149	0.48	NS	2
Gonyleptidae	<i>Ilhaia cuspidata</i>	Curitiba, Parana, BR	May (F)	—	445	390	0.53	§	2
Gonyleptidae	<i>Serracutisoma spelaeum</i>	Intervales, São Paulo, BR	Jan, Feb, Apr–Oct	28	—	—	0.55	—	6
Gonyleptidae	<i>Serracutisoma proximum</i>	Intervales, São Paulo, BR	May–Sep (W dry)	7	—	—	0.61	—	6
Leiobunidae	<i>Leiobunum townsendi</i>	Austin, Texas, US	Sep (Su)	1	157	167	0.48	NS	7
Leiobunidae	<i>Leiobunum sp.</i>	NL	—	—	349	304	0.53	§	8
Sclerosomatidae	<i>Prionostemma sp. 2</i>	Refugio Bartola, Rio San Juan, NI	Feb (W dry)	10	250	277	0.47	NS	9
Sclerosomatidae	<i>Prionostemma sp. 1</i>	Refugio Bartola, Rio San Juan, NI	Feb (W dry)	7	33	139	0.19	***	9

tested with single-sex group translocations. If females are more strongly attracted to female scent than are males, sites where only females are released should attract more female than male recruits on subsequent days.

In contrast to the sharp habitat distinction that we found at Refugio Bartola, at La Selva Biological Station both *Prionostemma* species are typically found on the vertical surfaces of medium to large tree trunks or buttresses and nearby shrubs (Proud et al. 2012). Harvestman roosting behavior can change seasonally (Holmberg et al. 1984; Chelini et al. 2011), so it is important to consider whether the reported differences between sites could be an artifact of the timing of the research conducted at the two sites. At Refugio Bartola, *Prionostemma* sp. 2 has been studied between the months of January and May, which includes the dry season (February–April) and parts of the wet season. Spiny palms are used as roosting sites throughout this period, and the observation that the locations of the communal roosts are stable from one year to the next (Teng et al. 2012; Grether et al. 2014), combined with what is known about the mechanism of roost formation (Donaldson & Grether 2007), indicates that spiny palms are used as aggregation sites year-round at this site. That is, if the communal roosts were abandoned for part of the year, they would presumably form in different spiny palms in different years, because individuals are not roost-site faithful and suitable spiny palms are not limiting (Donaldson & Grether 2007; Grether & Donaldson 2007; Teng et al. 2012). At La Selva Biological Station, harvestmen have been studied in both the dry and wet seasons, and one of us has searched for Sclerosomatidae aggregations in spiny palms and the buttresses of large trees during both seasons and encountered none (V.R.T., pers. obs.). Thus, we are confident that *Prionostemma* roosting behavior differs between the sites.

How might population differences in roosting patterns arise? We first consider a sort of null model of the roost formation process. If individual harvestmen had no microhabitat preferences and roost formation was based solely on conspecific attraction (including scent-mark detection), then the locations of roosting sites would be expected to drift randomly over time through chance colonization events. Under this null model, we would expect communal roosts to form repeatedly at the same locations but not exclusively in a specific microhabitat. Aggregations would be expected to persist longer at sites where the harvestmen survived at higher rates, however, and this could lead to a pattern in which, at any given time, most aggregations formed in microhabitats that offered protection from predators, desiccation, etc. Thus, geographic variation in roosting patterns could arise simply through chance events and variation in the factors that influence survival rates in different microhabitats (predator species, climate, etc.). A more realistic model would have individuals searching for roosting aggregations in the microhabitats where they are most likely to form, either because of associative learning or because microhabitat preferences evolve to track roosting patterns, or some combination of these mechanisms. Nevertheless, the sort of cultural drift envisioned in the null model seems likely to play some role in population differentiation.

One way to investigate the relative importance of habitat preferences versus conspecific attraction would be to seed new

Prionostemma aggregations in different kinds of vegetation, using the group translocation method (Teng et al. 2012), and follow their fate. At Refugio Bartola, *Prionostemma* sp. 2 aggregations occasionally form on non-spiny understory plants (e.g., Rubiaceae: *Psychotria*) but not in the same places in different years (G.F.G., pers. obs.). The aggregations in spiny palms may persist longer than those in other types of vegetation simply because palm spines offer protection from predators, such as anoline lizards (Grether & Donaldson 2007). There is also evidence, however, that these harvestmen prefer spiny palms per se. When spines were experimentally removed from established roosting sites, the aggregations shifted rapidly over to previously unused spiny palms, if any were nearby (Donaldson & Grether 2007). Thus, it would be interesting to examine whether a tradition of roosting in spiny palms, once introduced, would spread through the *Prionostemma* sp. 2 population at La Selva Biological Station.

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