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Authors

Grether, Gregory F
Donaldson, Zoe R

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Communal Roost Site Selection in a Neotropical Harvestman: Habitat Limitation vs. Tradition

Gregory F. Grether & Zoe R. Donaldson

Department of Ecology & Evolutionary Biology, University of California, Los Angeles, CA, USA

Correspondence

Greg Grether, Department of Ecology & Evolutionary Biology, University of California, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, USA.
E-mail: ggrether@ucla.edu

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Abstract

Many species have been reported to form roosting (resting, sleeping) aggregations at 'traditional' sites, but the alternative hypothesis that specific sites are used repeatedly because of habitat limitation is rarely tested. We studied the roosting behavior of a species of harvestman (Opiliones, *Prionostemma* sp.) at a lowland rainforest site in Nicaragua. Both sexes roosted by day in spiny palm trees, dispersed at dusk to forage, and rejoined aggregations just before dawn. The distribution of harvestmen among spiny palms was significantly clumped, and harvestman density did not correlate with spiny palm density. Aggregations formed repeatedly in a small subset of the available spiny palms and the same sites were used in two different years (2001, 2003). Nevertheless, the membership of aggregations was fluid; individual harvestmen were found at multiple roosts and moved up to 0.2 km per night. Translocated animals often returned to the roost where they had been released or nearby roosts but were never found at previously unused sites. The high consistency of site use but low site fidelity of individuals suggests that roost sites differed conspicuously (to the harvestmen) from sites that were not used. We found no univariate or multivariate differences between used and unused sites, however, in the characteristics of the trees or microclimate. These results conflict with the habitat limitation hypothesis but are consistent with the traditional site use hypothesis. The tradition may be mediated by a site-labeling chemical, a mechanism that does not require individual site fidelity. We discuss these results in relation to the proposed functions of roosting aggregations.

Introduction

Communal roosting has been studied most extensively in birds and bats, but the behavior is taxonomically widespread (e.g., Reynierse et al. 1969; Cook et al. 1976; Pearson & Anderson 1985; Mallet 1986; Cockerill 1988; Miller 1989; Alcock 1998; Pimenta & Martins 1999; Gomes-Filho 2000; Grether & Switzer 2000). The location of communal roosts often appears to be traditional in that the same sites are used repeatedly while other seemingly suitable sites remain unused (e.g., Rau & Rau 1916; Vaughan & O'Shea 1976; Eiserer 1984;

Marzluff et al. 1996; Blanco & Tella 1999; Brooke et al. 2000; Switzer & Grether 2000; Harms & Eberhard 2003). Although the functions of communal roosts have been studied and discussed extensively (e.g., Waltz 1982; Mallet 1986; Rabenold 1987; Miller 1989; Vulinec 1990; Marzluff et al. 1996; Switzer & Grether 2000; Barta & Giraldeau 2001; Dall 2002; Wright et al. 2003), the proximate mechanisms of roost site selection, and the reasons for repeated use of specific sites, have received comparatively little attention.

Site fidelity, in general, is favored when the costs (e.g., energy, time, predation) of moving to a new

site are greater than the costs of returning to a potentially suboptimal site (Switzer 1993; Lewis 1995). When the benefits of returning to a site depend positively on the presence of conspecifics (Stamps 1988; Muller et al. 1997), the conditions favoring site fidelity are likely to be quite broad. Simple dilution (safety in numbers) could be sufficient to favor the continued use of suboptimal aggregation sites, if moving puts individuals at risk of facing predators alone (Treisman 1975). Thus, traditional site use may be adaptive even when it causes animals to return to suboptimal sites (Warner 1988, 1990; Grether & Switzer 2000).

In a rapidly changing environment, however, traditional site use has potentially disastrous consequences. Protection of suitable roosting habitat is recognized as a conservation priority for many species (e.g., birds, Donazar et al. 2002; Harms & Eberhard 2003; bats, Brooke et al. 2000; Barclay & Brigham 2001; Aguirre et al. 2003; Smith & Racey 2005; butterflies, Alonso-Mejia et al. 1997; Dennis 2004; dragonflies, McGeoch & Samways 1991). When traditional roost sites are destroyed, however, the existence of suitable alternative sites is only relevant if the animals recognize them as such. Thus, species that rely on traditional aggregation sites for survival or reproduction may be especially sensitive to habitat destruction. Traditional site use may also complicate efforts to translocate or reintroduce endangered species (e.g., condors; Donazar & Feijoo 2002).

According to Galef (2004), for a behavior to be called traditional, it must be demonstrated that the behavior is transmitted by social learning. We maintain, however, that traditional site use does not require learning (Donaldson & Grether in press). All that is required is that animals be attracted to a site as consequence of conspecifics using the site in the past. Thus, the tradition of returning to specific sites could be based solely on cues left behind by conspecifics. The alternative to traditional site use is that specific sites are used because they differ from unused sites in ways other than past usage. For brevity, we refer to this alternative hypothesis as the habitat limitation hypothesis, where 'habitat' refers to any relevant environmental factor other than conspecifics.

We studied the communal roosting behavior of *Prionostemma* sp. harvestmen in an intact lowland rainforest site in southeastern Nicaragua. This species aggregates during the day on the trunks and fronds of spiny palm trees (*Cryosophila warscewiczii* and multiple *Bactris* spp.) in the forest understory. Prelimin-

ary observations showed that the harvestmen dispersed from the roost sites at night and predictably reformed aggregations at the same sites by dawn. As we show in this paper, the pattern of site use was highly non-random. The same small subset of spiny palm trees was used by the harvestmen in two different years.

Our main goal in this paper is to distinguish between two alternative proximate explanations for the repeated use of particular sites: habitat limitation vs. tradition. If the distribution of aggregation sites were a product of habitat limitation, then spiny palms used as aggregation sites ought to differ in measurable ways (e.g., physical characteristics, microclimate) from spiny palms that were not used. To positively establish a role for tradition, it would be necessary to show how the tradition is perpetuated. A tradition of roosting at specific sites could be maintained by (1) direct conspecific attraction coupled with individual site preferences, or (2) indirect conspecific attraction via site-labeling. These are not mutually exclusive hypotheses but instead different mechanisms that could lead to the same pattern. To examine the roost site fidelity of individual harvestmen, we tracked the movement of marked individuals and experimentally translocated animals between sites. Roost site manipulations were used to test for site-labeling. Results from the latter experiments are reported in Donaldson & Grether (in press) and discussed below.

Methods

Study Site

This study was carried out in primary lowland Caribbean rainforest at Refugio Bartola in southeastern Nicaragua (10.97 N, 84.16 W, elevation 30 m) from Apr. 26 to May 9, 2001 and Apr. 22 to May 6, 2003, near the end of the dry season. This area typically receives about 4 m of rainfall per year; ca. 3 mm of rain fell during the study period in 2001 and 38 mm fell during the study period in 2003 (M.L. Cody, pers. comm.). For more information about the study site, see Cody (2000).

Taxonomy

Opiliones is a poorly known group, especially in Central America. We sent specimens to several experts but were unable to obtain a species identification. Ana Tourinho kindly identified the specimens to genus (Opiliones, Eupnoi, Sclerosomatidae,

Gagrellinae [formerly Palpatores: Phalangoidea], *Prionostemma*) and remarked that this is either an undescribed species or one that had previously been misclassified as belonging to a different genus (*Tamboicus*) (A. Tourinho, pers. comm., 4 Jan. 2006). Voucher specimens are available.

Site Selection and Monitoring

In both years of the study, we began by searching for harvestmen aggregations along the existing trail system at Refugio Bartola. All such aggregations were found in spiny palm trees >1 m in height. Each roosting site was paired with a matched control site, which consisted of the nearest spiny palm, or cluster of spiny palms, that was not occupied by harvestmen at the time it was discovered. The paired design ensured that our comparisons of site characteristics and microclimate were not confounded by spatial heterogeneity. The mean distance between roost and control sites was 12.7 m (range: 2.5–50 m). All roost sites and control sites were censused on a daily or near daily basis from the date of discovery until the end of the study period. During a census, we counted the number harvestmen, recorded any identifying marks (see below), and noted the position of the aggregation within the site. Behaviors other than resting, including interactions between conspecifics and responses to other species, were recorded on an ad libitum basis. The accuracy of visual counting was verified by capturing all animals at a site by hand; animals that could not initially be reached by hand could usually be chased within reach with a stick. Thereafter, visual counting was employed, when possible, to minimize disturbance. Ten roost–control site pairs were monitored in 2001 and 20 were monitored in 2003 (Fig. 1). In addition to the daily censuses, which were conducted during daylight hours, we also visited roosting sites at dusk, night and dawn to record the daily activity cycle.

Habitat Availability

To evaluate the degree to which harvestmen were clumped among the available spiny palms, we counted harvestmen on all spiny palms within 17 forest transects. To ensure that the transects were located within suitable habitat, we centered them on known roosting sites. Each transect consisted of four 20 m by 5 m spokes projecting north, south, east, and west of a known roosting site. To test for clumping of harvestmen among the spiny palms encountered during the transects (excluding the known roosting

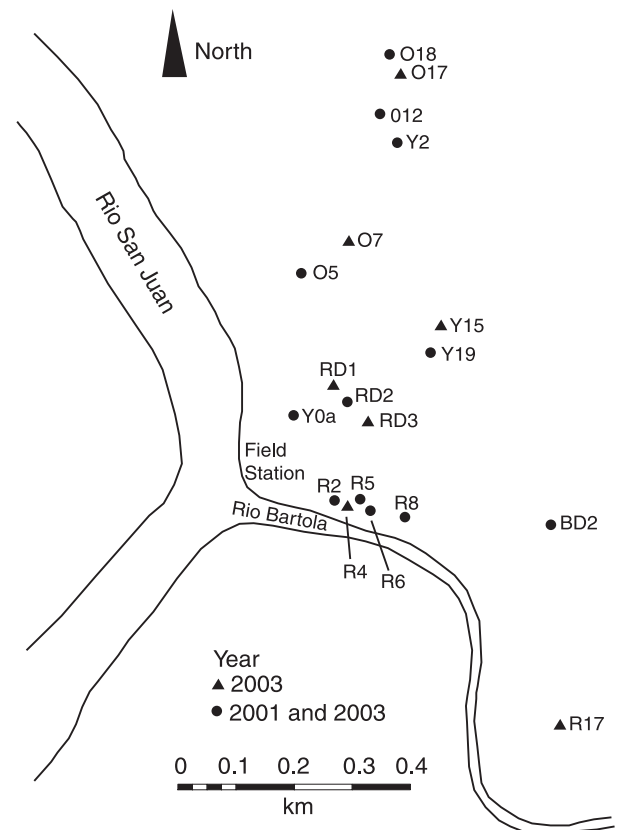


Fig. 1: Map of study area. Locations of roosting sites were obtained with a GPS receiver and overlaid on a map of the study area provided by M.L. Cody

sites), we compared the observed distribution to a Poisson distribution separately for each transect and also for all transects pooled. In a Poisson distribution, the ratio of the variance to the mean (the coefficient of dispersion, or CD) equals 1. An observed CD > 1 indicates clumping, while an observed CD < 1 indicates dispersion. To test the significance of the pooled CD, we used a Monte Carlo simulation in which the observed number of harvestmen was randomly assigned to the observed number of possible roosting sites. This was iterated 10 000 times to generate a distribution of CDs expected under random settlement.

Consistency of Site Usage Across Years

Seven of the ten roost–control site pairs established in 2001 were also monitored in 2003; the remaining three pairs were not monitored in 2003 because the roost sites were physically damaged by our experimental manipulations in 2001 (Donaldson & Grether in press). We based year-to-year comparisons on

visual census data up to the date that the harvestmen at the roost site were first captured in a given year, to avoid the possibly confounding influence of handling effects (see below). To test the null hypothesis that site usage in 2001 was independent of site usage in 2003, we classified each of the 14 sites as 'used' or 'not used' by harvestmen aggregations and applied Fisher's exact test. To examine the consistency of site occupancy across years, we calculated the Spearman rank correlation between mean aggregation size at roost sites in 2001 and 2003. One roost site (R17) had to be excluded from this analysis because data on the size of the aggregation were lost.

Site Characteristics and Microclimate

To determine whether the spiny palms in which harvestmen roosted differed in their physical characteristics from spiny palms that were not used as roosts, we compared the monitored roosting sites to the paired control sites with respect to canopy openness, the number of spiny palm trees at the site, tree height, trunk height, trunk diameter, mean spine length, and mean spine density. Canopy openness, which is influenced by the spiny palms themselves as well as by overstory trees, was measured from the middle of each site with a concave spherical densiometer (Forestry Suppliers Inc., Jackson, MS, USA). Tree height (the highest point of the tree) and trunk height (from the ground to where the trunk separated into individual fronds) were measured with a graduated pole or clinometer. Trunk diameter 1.5 m from the ground was measured with a ruler (± 1 cm). To estimate mean spine length and density, we painted circles (diameter 3.5 cm) at three points along the trunk and counted and measured the length of all spines within the circles. Circles were placed 2.0, 1.8 and 1.6 m above the ground unless the trunk height was less than 2 m, in which case spines were measured as close to the crown as possible and 20 and 40 cm below. In clusters of five or more palms, half the trees were measured, with preference given to trees that contained the largest number of harvestmen. At control sites, we chose trees within clusters at random, excluding trees shorter than 2 m. A complete set of measurements was obtained for 16 roost-control pairs and most measurements were obtained for 18 pairs. Because trunk height and tree height were strongly correlated ($r = 0.91$, $n = 35$), only tree height was included in the analysis.

To test for microclimate differences between roosting and control sites, air temperature, relative humidity,

and wind speed were measured once per day at each monitored site during the 2003 study period using a Kestrel 3000 meter (Nielsen-Kellerman Inc., Chester, PA, USA). Wind speed was measured for 1 min and the peak and average wind speeds were recorded. At roosting sites, measurements were taken within 10 cm of the trunk and as close to a roosting aggregation as possible without disturbing the animals. Control site measurements were matched to the paired roosting site in time of day, distance from the trunk, distance from the ground, and compass orientation. The minimum, maximum, and mean of each variable at each site was calculated and treated as a separate variable in the analysis.

We used paired t-tests to compare roost sites to paired control sites one variable at a time. This approach increases the probability of making a type I error (falsely rejecting the null hypothesis of no difference) but maximizes the probability of detecting a true univariate difference if one exists. Discriminate function analysis (DFA) was used to determine whether roost sites could be distinguished from control sites using a linear combination of site characteristics or microclimate variables. Variables were log-transformed, as needed, to meet parametric assumptions. Non-parametric Wilcoxon matched pairs signed ranks tests (not presented) yielded identical results, with respect to significance at the 0.05 level, as the paired t-tests.

Translocation Experiment

To test the member-specificity of roosts and the site-specificity of individuals, we moved marked harvestmen between pairs of roosting sites. On Apr. 27, 2001, entire roosting aggregations were captured at R5 ($n = 59$) and O7 ($n = 31$) and animals were assigned at random to one of two treatment groups: 'residents' were released at their original site while 'translocated individuals' were released at the other site. Thus, after the manipulation, R5 and O7 each contained roughly half of their original occupants and half of the other site's original occupants. On May 1, the experiment was repeated at sites Y13 ($n = 43$) and R5. Only unmarked individuals from R5 ($n = 35$) were used so that the marked individuals from the first experiment could still be monitored independently (for exact sample sizes, see Fig. 3).

To mark entire aggregations, we first captured and held the animals in plastic terraria to prevent some from escaping while others were being marked. Marks consisted of minute dots of acrylic paint placed on the

legs and/or posterior dorsal surface of the body. Each treatment group was given a unique mark, as coded by the color and/or position of the dots; individuals within a treatment group were not given unique marks in this experiment. We transported the animals between sites in inflated 4 l plastic bags. To control for handling effects, residents and translocated individuals were detained for the same length of time. After release, each translocated individual was observed for 2 min and any interactions with other harvestmen were recorded. Roost censuses were made on the night and morning following the manipulation, as well as on successive days for the remainder of the study period.

Movement Patterns

To obtain data on individual roost site fidelity and inter-roost movement, we marked 240 harvestmen with numbered, color-coded tags across four roost sites (R5, RD3, O17, and O7; see Fig. 1) between Apr. 24 and Apr. 26, 2003. The color of a tag identified the site and the number identified the individual. Marked individuals were recorded during daily roost censuses for the remainder of the study. Tags were made from paper laminated with plastic and affixed caudal to the dorsal ocelli using non-toxic water-based glue (Elmer's Products Inc., Columbus, OH, USA) (Fig. 2). To evaluate whether marking, per se, influenced the return rate, we compared the number of harvestmen roosting at a site on the day on which the animals were marked to the number present on the days immediately before and after marking.

Discrete aggregations frequently formed at two or more locations within a single roost site. To determine whether individuals are site-faithful to particular aggregations, we used aggregation-specific marks at two sites. At site RD3, where aggregations formed on two specific trees within a cluster, we used numbered tags of two different colors to code aggregation membership ($n = 84$, blue; $n = 14$, orange). At site Y0a, where the harvestmen formed two discrete aggregations at different places on the same tree trunk, we marked the upper ($n = 72$) and lower ($n = 21$) aggregations with green and orange fluorescent dust, respectively.

Results

Activity Pattern

The majority of harvestmen dispersed from the day-roosts between 17:30 and 17:50 h in the evening and regrouped before dawn between 05:30 and 06:00 h. Inside the forest, the aggregations appeared to be stable over the course of the day. However, at the two forest edge sites (Y0a, Y0b), the size of the aggregation shrank noticeably on some afternoons, perhaps because these sites were exposed to much higher maximum air temperatures ($>35^{\circ}\text{C}$) and lower humidities ($<49\%$) than the interior forest sites.

Habitat Availability

Harvestmen were clumped among the available roosting sites, and spiny palm density was not predictive of harvestmen density. A total of 202

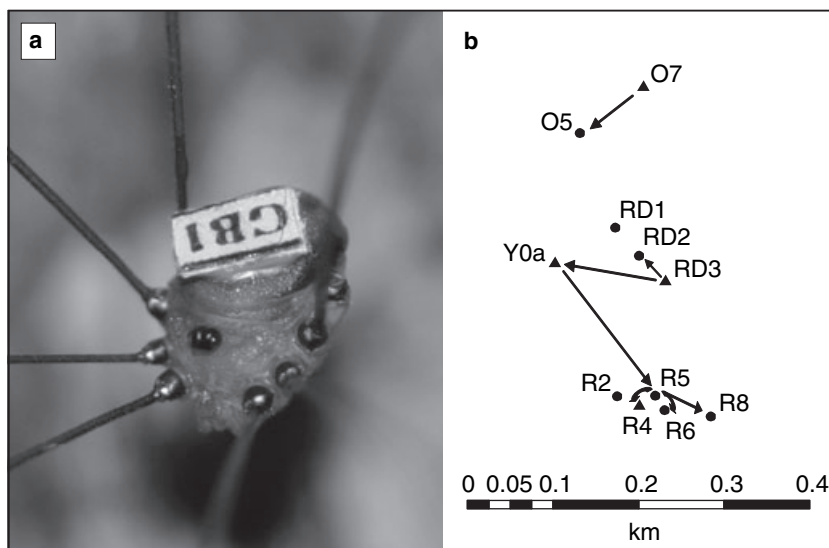


Fig. 2: (a) An individually marked harvestman. (b) Movement of marked harvestmen among sites over an 11-d period. Arrows denote direction of movement. Triangles represent sites where harvestmen were individually marked. Circles denote unmarked sites. In this figure, sites O5 and O7 appear closer to the other sites than they actually are. See Fig. 1 for the location of these sites within the study area

potential roosting sites (spiny palms or clusters of spiny palms) were found in the forest transects; 19 of these sites (9.4%) were occupied by harvestmen (range, 1–10 harvestmen; $\bar{x} \pm \text{SE}$, 3.3 ± 0.5). The CD values for individual transects ranged from 2.0 to 8.2 and the pooled CD was 4.6. The Monte Carlo simulation generated a range of pooled CD values from 0.7 to 1.5 ($\bar{x} = 1.0$; $n = 10\,000$ iterations). Thus, the observed CD was significantly larger than that expected under random settlement ($p < 0.0001$). Across transects, spiny palm density (number per transect) was not correlated with the density of harvestmen (Spearman $r_s = 0.36$, $p = 0.15$, $n = 17$). These results are consistent with a local aggregation model of roost settlement, as opposed to a long-distance aggregation model in which areas with the highest densities of spiny palms attract the most harvestmen.

Consistency of Site Usage Across Years

Site usage was remarkably consistent across years. All seven of the roost sites monitored in 2001 and 2003 contained harvestmen aggregations in both years and no aggregations were found at control sites in either year. The probability of the same sites being used in both years by chance alone is quite low (Fisher's exact test, $p = 0.0006$). Roost sites with large aggregations in 2001 also tended to have large aggregations in 2003 but the correlation between mean aggregation size in the two years was marginally non-significant ($r_s = 0.77$, $n = 6$, $p = 0.08$), perhaps because of the small sample size.

Site Characteristics and Microclimate

Aggregations were found in multiple species of spiny palms spanning a wide range of tree heights, trunk diameters, spine lengths, spine densities, and canopy openness. We found no evidence that roost sites differed from control sites in their physical characteristics or microclimate, except for a possible difference in the average number of trees per site. Of the six tree characteristics examined, four were significantly correlated between roost and control sites (tree count $r = 0.37$, $p = 0.12$; canopy openness $r = 0.66$, $p = 0.002$; mean tree height $r = 0.69$, $p = 0.001$; mean tree diameter $r = 0.66$, $p = 0.002$; mean spine length $r = 0.39$, $p = 0.15$; mean spine density $r = 0.78$, $p < 0.001$), which indicates that the paired design successfully controlled for some spatial heterogeneity in these characteristics. Only tree count differed significantly between roost and control sites (Table 1; paired t-tests on log-transformed variables; tree count $t = 2.21$, $p = 0.04$, $df = 18$; all other $p > 0.4$); none of the differences would be significant if corrected for multiple tests. On average, roost sites contained 1.9 more trees than control sites; however, the range of tree counts was identical for roost and control sites. DFA on the full set of variables correctly identified roost and control sites as such only 54% of the time (MANOVA $F_{6,26} = 0.46$, $p = 0.81$). No significant univariate or multivariate differences in microclimate were detected between roost and control sites (Table 1; uncorrected paired t-test; p-value range: 0.08–0.86). Based on the full set of eight microclimate variables, DFA correctly

Table 1: Tree characteristics and microclimate at the monitored roost sites and paired control sites

Variable	Roost site				Control site				n
	Mean	SD	Minimum	Maximum	Mean	SD	Minimum	Maximum	
Canopy openness (%)	29.6	26.2	8.3	94.6	25.0	21.2	8.3	96.7	18
Tree count	4.9	3.4	1	11	3.1	2.8	1	11	18
Mean tree height (m)	6.0	3.7	2.6	19.1	5.4	1.3	3.8	8.0	18
Mean tree diameter (cm)	55.8	51.3	22.0	220.0	52.4	28.8	30.5	126.7	18
Mean spine length (mm)	25.8	11.3	10.0	60.1	29.9	22.5	9.2	92.8	17
Mean spine density (cm ²)	0.7	0.3	0.3	1.4	1.0	1.3	0.2	4.5	17
Average wind speed (m/s)	0.4	0.2	0.0	0.7	0.4	0.3	0.0	1.1	19
Maximum wind speed (m/s)	0.5	0.3	0.0	0.9	0.5	0.4	0.0	1.2	19
Mean relative humidity (%)	73.5	9.1	50.3	95.0	72.5	8.8	51.7	91.0	22
Minimum relative humidity (%)	64.4	12.7	45.0	95.0	63.9	12.7	44.0	91.0	22
Maximum relative humidity (%)	83.7	12.2	51.0	99.0	82.3	11.3	54.3	97.0	22
Mean temperature (°C)	30.3	1.3	27.4	32.8	30.4	1.2	27.9	32.6	22
Minimum temperature (°C)	27.6	2.4	23.6	32.8	27.8	2.3	24.2	32.8	22
Maximum temperature (°C)	32.1	1.8	27.4	36.2	32.2	1.7	28.2	32.8	22

For paired t-test results, see text.

identified roost and control sites as such only 58% of the time (MANOVA $F_{8,29} = 0.27$, $p = 0.86$).

Experimental Translocations

The results of the translocation experiment suggested that the harvestmen are able to enter new roost sites without aggression from residents; once an individual has roosted at a new site, it is about as likely as residents to return to the site. No chasing, biting, or other forms of aggression were observed when the translocated harvestmen were released into an existing aggregation. On the day immediately following the translocations, some individuals from both the resident and translocated groups returned to the tree on which they had been released, with the exception of the O7 residents (Fig. 3). None of the differences in return rates between residents and translocated individuals approached statistical significance, but a smaller proportion of the residents returned in three out of four trials. On subsequent days, the number of returning marked animals fluctuated between 0% and 20% of the original number marked, while the overall size of the aggregations remained fairly constant (not shown). No translocated individuals were found back at their original roost site. Two individuals marked for the first translocation (Apr. 27, 2001) were found at other established roosting sites. One individual from R5 appeared at site RD1 on Apr. 28 (ca. 222 m from R5) and one

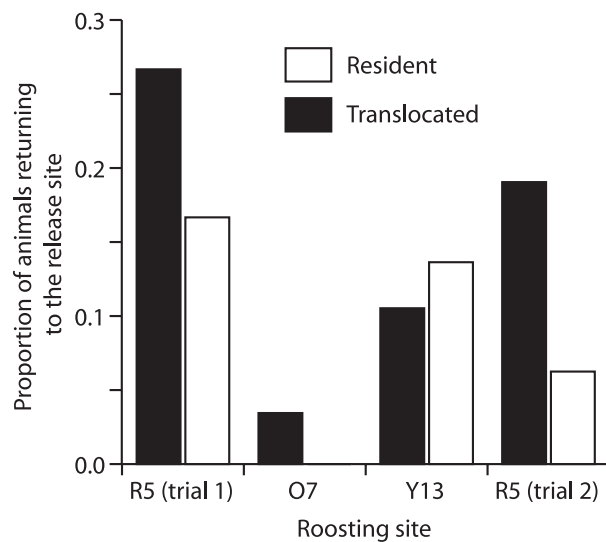


Fig. 3: Results of the translocation experiment. Bars show the proportion of marked harvestmen returning to the release site on the day after the manipulation. Sample sizes (number of marked harvestmen) from left to right in the figure: 15, 30, 29, 16, 19, 22, 21, 16

individual from O7 was found at site O5 on May 9 (ca. 88 m from O7).

Movement Patterns

Our mark-resighting study in 2003 confirmed that movement between sites occurred naturally and that daily turnover of roost membership was quite high. Of the original 240 harvestmen marked with numbered tags, 57 (23.8%) were positively identified during future censuses and 15 of these (26.3%) were found in other monitored roosting sites 13–130 m from the site where they were marked (Fig. 2). The maximum daily return of individuals to the site where they were marked ranged from 15.0% to 26.3% per site. Of the 92 harvestmen marked with fluorescent dust at site Y0a, 42 (45.6%) returned to Y0a and four (4.3%) were found at site Y0b (20 m from Y0a) on the day after they were marked, and one was found 6 d later at site R4 (190 m from Y0a).

The low return rates of individually marked animals can partially be attributed to handling effects. At all four sites where the harvestmen were marked with numbered tags, the total number of animals roosting at the site decreased on the day after marking by 34.4–67.7% ($\bar{x} \pm \text{SE}$, $47.4 \pm 7.8\%$). This does not simply reflect the continuation of a population trend because three of these sites showed increased occupancy on the day of marking compared with the previous day (5.3% decrease at one site; 5.7–80.0% increase at the other sites; $\bar{x} \pm \text{SE}$, $30.5 \pm 19.3\%$). Moreover, the maximum rate of return of marked animals occurred not on the day immediately after marking but 1–3 d later, which suggests that the harvestmen initially avoided sites where they had been marked.

The natural rate of turnover must also be quite high, however. At the site where the animals were marked with fluorescent dust, which requires relatively little handling, the number of animals increased (4.1%) on the day after marking, yet the return rate of marked individuals was still less than 50%. Furthermore, although we attempted to mark all harvestmen present at the sites included in the mark-resighting study, most animals found at these sites on the day after marking were unmarked (6–59 unmarked individuals, representing 61–91% of the number present; $\bar{x} \pm \text{SE}$, 29.6 ± 10.1 unmarked individuals or $70.2 \pm 5.9\%$). This was also true for the sites used in the translocation experiment (9–42 unmarked individuals, representing 77–90% of the number present; $\bar{x} \pm \text{SE}$, $23.3 \pm 7.1\%$ or $83.2 \pm 2.6\%$).

At the two sites where we marked different aggregations (within the site) with different colors, there was no significant tendency for individuals to return to the aggregation where they had been marked (Fisher's exact test, $p = 0.2$ at site Y0a and $p > 0.9$ at site RD3). Thus, individuals do not appear to be site faithful to particular aggregations within roosting sites.

Discussion

Tradition vs. Resource Assessment

Past usage appeared to be the only reliable predictor of whether a spiny palm was used as a day roost by the harvestmen. Roost aggregations formed repeatedly in a small subset of the available spiny palms, and the only monitored sites that changed status between 2001 and 2003 were ones that we had experimentally disrupted in 2001 (Donaldson & Grether in press). Random settlement simulations confirmed that the distribution of harvestmen among spiny palms was significantly clumped. Individuals experimentally translocated between roosts often returned to the roost where they had been released or nearby roosts but were never found at previously unused sites. These observations would be consistent with the hypothesis that only a small subset of the available spiny palms were suitable for roosting (i.e., the habitat limitation hypothesis), but we found no univariate or multivariate differences between used and unused spiny palms in physical characteristics or microclimate. Either we failed to identify the key variable(s) that determine whether a spiny palm is suitable, or the roosting behavior of this species has a strong traditional component.

The movement patterns that we observed offer clues as to how a tradition of roosting at specific sites could be maintained. Although the locations of the roosts were very stable over time, roost membership was highly unstable. In our mark-resighting study, turnover from one day to the next always exceeded 50% and individual harvestmen were found in roosting sites as far as 0.2 km apart. Nevertheless, aggregations were found repeatedly not only in specific spiny palms but also at specific locations within the trees (e.g., specific fronds). It would be difficult to reconcile these results with a mechanism involving individual site preferences (i.e., homing) and direct conspecific attraction (whether visual or olfactory). An absence of homing was also suggested by the translocation experiment results; translocated individuals were just as likely as residents to return

to the release site. By comparison, the traditional roosts of rubyspot damselflies (*Hetaerina americana*) appear to be perpetuated by individual site preferences and direct (visual) conspecific attraction (Grether & Switzer 2000). The locations of the damselfly roosts drift on a time scale of weeks (within suitable habitat), as would be expected from this mode of social transmission (Switzer & Grether 2000). The harvestmen movement data are consistent, however, with a mechanism involving indirect conspecific attraction via site-labeling.

Harvestmen have well-developed scent glands and aggregation formation is one of many proposed functions of the glandular secretions (Holmberg 1986; Kury & Pinto-da-Rocha 2002). We observed harvestmen rubbing the sides and posterior end of their carapace against palm fronds, which is suggestive of scent-marking behavior. To test for scent-marking, we moved and/or replaced materials that were potentially scent-marked and then measured the response of the harvestmen to these changes. Alcock (1998) used a similar approach to investigate the mechanisms of communal roost formation in the bee *Idiomelissodes duplocincta*. Our results (and Alcock's) support the site-labeling hypothesis. For example, by moving individual fronds within spiny palm trees, we found that a frond's history of usage as an aggregation site had a much larger effect on subsequent recruitment than the position of the frond within the tree (Donaldson & Grether in press). Scent-marking could result in a positive feedback loop: the more animals using a site, the more scent gets deposited and the greater the attraction radius. This could explain the marginally non-significant trend that we observed for sites to maintain their general level of use across years.

One of the hallmarks of traditional site use is that it can lead to the continued use of degraded sites, as was suggested in Warner's (1988, 1990) study of spawning site use in bluehead wrasse (*Thalassoma bifasciatum*). Spines are the most obvious feature of spiny palms that distinguish them from non-spiny palms (which were not used by the harvestmen). Moreover, the spines appear to provide protection against predatory vertebrates, such as anoline lizards (G. F. Grether and Z. R. Donaldson pers. obs.). When spines were removed from trees that had been used as aggregation sites but trees with intact spines remained nearby, recruitment quickly decreased to zero or near zero on the shaved trees and increased on the unshaved trees (Donaldson & Grether in press). In contrast, when all of the trees at a site were shaved, harvestmen continued returning to the

shaved trees, albeit in reduced numbers. Although wholesale spine removal is not a natural occurrence, these results suggest that degraded sites may continue to be used for some time unless suitable alternatives are nearby.

Evolutionary Scenarios

The low site fidelity of individual harvestmen was an unexpected result, given the long-term stability of roost sites, and it raises an interesting evolutionary question. How could individuals benefit from producing a chemical that seeds the formation of an aggregation that they might not join? Several evolutionary scenarios seem plausible. First, scent-marking might originally have evolved to enable individuals to return to previously used solitary roosting sites. This could have subsequently led to the evolution of communal roosting and relaxed selection on individual site fidelity (owing to the relative ease of locating heavily-scented aggregation sites). Second, the marking chemical might have evolved as an aggregation pheromone used by early-arriving harvestmen to attract conspecifics during the same roosting period. Such an aggregation pheromone would have to persist long enough to seed aggregation formation on the following day, to explain our results. Third, the marking chemical might be a pheromone that evolved in some other context (e.g., mate attraction) with the right properties to also serve as an aggregation cue. Finally, the marking chemical may merely be an unmodified waste product that happened to be persistent enough, and yet of sufficient volatility, to allow a chemotactic response to evolve. Sorting out these (and perhaps other) evolutionary scenarios would require a comparative (phylogenetic) approach and more data than is currently available on the roosting behavior and scent glands of harvestmen (Opiliones).

Possible Functions of Harvestmen Roosting Aggregations

Our study was not designed to distinguish among the possible functions of harvestmen roosting aggregations and, at present, few hypotheses can be removed from consideration. The following discussion is offered in the spirit of encouraging further research on this understudied taxon.

First, aggregations may form simply because animals use the presence of conspecifics as a cue for locating high-quality habitat, where 'habitat quality' refers to the entire suite of factors that influence fitness (e.g., prey availability, predation risk; Danchin

et al. 2004). According to this 'null' hypothesis, the aggregations themselves serve no purpose and are merely a byproduct of the conspecific attraction mechanism. Alternatively, or in addition, individuals may benefit from the presence of conspecifics in one or more ways.

The response of the harvestmen to disturbance strongly suggests that the day roost aggregations provide anti-predation benefits. When we approached or reached into an aggregation too quickly, the harvestmen bobbed up and down by rapidly contracting and extending their legs. Once a few individuals began bobbing, the behavior quickly spread through the aggregation. Bobbing was also observed during three encounters with natural predators. In one case a scorpion and in another case a paraponerine ant (*Paraponera* sp.) grabbed the leg of a harvestmen, triggering localized bobbing and movement away from the site of attack. In both cases, the attacked individual dropped from the tree and, in the case of the ant, jettisoned the captured leg. The third case involved an anoline lizard (*Norops lemurinus*) that attacked and consumed one harvestman. The lizard was perched on a spineless frond and captured a harvestman just outside the limit of the spines at the base of the frond. In this case, bobbing spread through the entire aggregation and harvestmen closest to the site of the attack moved away. Bobbing clearly makes capturing the harvestmen more difficult. It might also serve as an alarm signal, a predator deterrent signal, or a predator confusion display. Harvestmen in an aggregation may also benefit from dilution (Treisman 1975) and there is the potential in this system for selfish herding (i.e., jostling for protected positions within an aggregation; Hamilton 1971; Vine 1971).

Roosting aggregations may also serve as sexual rendezvous sites. In some cavernicolous species of harvestmen, mating occurs at the day roosts and eggs are deposited on the cave walls and guarded by the parents (Gnaspini 1995, 1996; Machado & Oliveira 1998; Machado 2002). We saw copulations at the *Priostonemma* day roosts but did not observe egg-laying. In this regard, it would be valuable to know whether production of the site-labeling chemical is sex-limited, whether reproduction is seasonal, etc.

In the bird literature, the most popular explanation for roosting aggregations is that they serve as places to gather information about local mating or foraging opportunities. Under the information center and recruitment center hypotheses, naïve members of a roost follow knowledgeable members to newly discovered food (Ward & Zahavi 1973; Marzluff et al.

1996; Richner & Heeb 1996). As hunter-scavengers, harvestmen meet the basic assumptions of these hypotheses, but we never saw them follow each other from the roost and all harvestmen that we encountered away from the roost at night were solitary. The habitat copying hypothesis holds that roost members use 'public information' about the performance of conspecifics to decide whether or not to return to a particular site (Danchin et al. 2004). For example, harvestmen might be able to detect odors associated with foraging or mating activity among roost mates. If so, this could be one of the benefits of visiting multiple aggregation sites.

Finally, the thermoregulation hypothesis, which has most frequently been applied to the aggregations of temperate insects (Copp 1983; Eiserer 1984; Vulinec 1990) seems unlikely to apply in the tropical lowlands, and in any case, *Prionostemma* roosting aggregations probably are not dense enough to trap heat.

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