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New communal roosting tradition established through experimental translocation in a Neotropical harvestman

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'Tradition' has been invoked to explain instances in which animals aggregate repeatedly in the same locations for no apparent reason, but alternative explanations, such as cryptic habitat selection, are difficult to rule out. Distinguishing among these hypotheses requires field experiments. We studied a species of harvestman (*Prionostemma* sp.) that forages solitarily at night and forms roosting aggregations in spiny palms by dawn. Aggregations have formed repeatedly in the same sites for over a decade, and yet the aggregation sites do not appear to differ from unused sites in tree characteristics or microclimate. Previous research suggested that the harvestmen find aggregation sites by detecting chemicals left behind by conspecifics. If so, it should be possible to establish new aggregation sites simply by moving harvestmen to new locations. We carried out such an experiment and, as predicted, release sites attracted harvestmen at much higher rates than did matched control sites. Most individuals that came to release sites were new recruits, and one site continued to attract several harvestmen for at least 7 days, suggesting that a new roosting tradition was established. We also revisited the question of whether any other factors, besides past usage, predict site use. Among sites used by the harvestmen, the size of the aggregations was strongly predicted by microclimate and spiny palm characteristics. Together these findings support the hypothesis that attraction to conspecific cues is the primary mechanism responsible for the long-term stability of aggregation sites, while also suggesting that site characteristics play a previously unrecognized role. Understanding how site traditions develop may have direct applications in conservation.

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Communal roosting has been studied most extensively in birds (Bijleveld et al. 2010), but it occurs in many other animals as well (Pearson & Anderson 1985; Mallet 1986; Devries et al. 1987; Miller 1989; Alcock 1998; Pimenta & Martins 1999; Brooke et al. 2000; Gomes-Filho 2000; Grether & Switzer 2000; Willemart & Gnaspini 2004; Machado & Macías-Ordóñez 2007). While much has been written about the potential costs and benefits of roosting communally (e.g. Vulinec 1990; Alcock 1998; Beauchamp 1999; Switzer & Grether 1999; Grether & Donaldson 2007; Machado & Macías-Ordóñez 2007; Bijleveld et al. 2010), relatively little is known about the proximate mechanisms underlying the formation and maintenance of communal roosts.

The locations of communal roosts often appear to be 'traditional' because the same sites are used repeatedly while other seemingly suitable sites remain unused (Vaughan & O'Shea 1976; Eiserer

1984; Miller 1989; Alcock 1998; Blanco & Tella 1999; Switzer & Grether 1999; Brooke et al. 2000). The alternative to traditional site use is that aggregations form where they do only because suitable roosting habitat is limiting. Habitat limitation is impossible to rule out without manipulative field experiments (Warner 1990), because the animals might be responding to unmeasured environmental cues or complex combinations of cues. To establish that site use is indeed traditional, it must be shown that the use of specific sites is in some way transmitted from one individual to another, which also requires experiments. While it might seem obvious that birds and mammals learn about the locations of communal roosts from conspecifics, it is not obvious that social learning is the basis of communal roosting in invertebrates.

Research on communally roosting insects is generally consistent with the social learning hypothesis. The repeated use of particular aggregation sites is usually hypothesized to arise from some combination of habitat selection, learned site preferences, and direct visual or olfactory conspecific attraction (butterflies: Jones 1930; Mallet 1986; dragonflies: Miller 1989; bees: Alcock 1998; owlflies: Gomes-Filho 2000; damselflies: Grether & Switzer 2000).

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Other mechanisms are possible, however, and largely untested. For example, a tradition of aggregating at specific sites could arise from attraction to cues left behind by conspecifics, with no need for individual site preferences, direct conspecific attraction, or learning.

Here we report the results of an experiment that was designed to test a specific hypothesis about how roosting aggregations form in a Neotropical harvestman. Aggregations of unrelated individuals are rare in arachnids in general but common in the harvestman order Opiliones (Coddington et al. 1990; Machado & Macías-Ordóñez 2007). At our study site in southeastern Nicaragua, the abundant local species of *Prionostemma* (Eupnoi: Sclerosomatidae: Gagrellinae; not described below the genus level) aggregates in the crowns and along the trunks of spiny palm trees (*Bactris* sp., *Astrocaryum* sp.) in the forest understory (cf. Coddington et al. 1990). These harvestmen form loose, mixed-sex aggregations in which the legs of most individuals are in contact with the substrate, dissimilar to the dense multilayered aggregations seen in some other species of Gagrellinae (reviewed in Machado & Macías-Ordóñez 2007). Aggregations break up around dusk, as the animals leave to forage solitarily, and form again just before dawn (Grether & Donaldson 2007). The membership of the aggregations is quite fluid. Individual harvestmen move distances of up to 0.2 km per night and show low roost site fidelity (Grether & Donaldson 2007; also see Coddington et al. 1990). Nevertheless, only a small fraction of the available spiny palms (about 1 in 11) is used for roosting on a given day, and the same trees are used day after day (Grether & Donaldson 2007). The spiny palms used for roosting do not appear to differ from those that are not used, either in the characteristics of the trees or in microclimate (Grether & Donaldson 2007). Past site use appears to be the only reliable predictor of future site use. While this suggests that the roosting sites are traditional, the low site fidelity of individual harvestmen indicates that social learning is unlikely to be the mechanism.

Donaldson & Grether (2007) hypothesized that the harvestmen find aggregation sites by detecting chemical cues left by conspecifics on previous days. Attraction to conspecific scent marks is the sort of positive feedback mechanism that could cause animals to continue aggregating at particular sites indefinitely, with or without individual site fidelity (Alcock 1998). Harvestmen have chemosensory structures on their legs and pedipalps (Willemart et al. 2009), and some species, including our study species, have been observed rubbing body parts against the substrate, a potential scent-marking behaviour (Donaldson & Grether 2007; Willemart & Hebets 2011). However, a role for chemical cues in aggregation formation has not been directly demonstrated in harvestmen (Machado & Macías-Ordóñez 2007; Willemart et al. 2009). If Donaldson & Grether's (2007) hypothesis is correct, it should be possible to establish new aggregation sites simply by moving harvestmen to previously unused spiny palm trees. The prediction is that sites where harvestmen were released will attract more harvestmen on subsequent days than matched control sites where no harvestmen were released. In addition to testing this prediction with a field translocation experiment, we examine the stability of roost site use over a 10-year period and revisit the question of whether any factors, besides past usage, are predictive of the location or size of the roosting aggregations.

METHODS

Study Area and Timing

This study was carried out at Refugio Bartola, a Caribbean rain forest site in southeastern Nicaragua located at the confluence of the Rio San Juan and the Rio Bartola (10.97°N, 84.16°W; elevation

30 m). The translocation experiment (described below) was carried out from 21 January to 11 February 2011, near the beginning of the dry season. The comparison of roost site use over time and the analysis of predictors of aggregation size (described below) were based on data collected from 22 April to 6 May 2003, near the end of the dry season. This area typically receives about 4 m of rainfall per year; ca. 38 mm fell during the study period in 2003 and ca. 74 mm of rain fell during the study period in 2011.

Comparison of Roost Site Use between Years

First, to avoid confusion, we explain exactly what we mean by a 'site'. The spiny palms within which the harvestmen roost usually grow in clusters, and harvestmen are often found in multiple trees within a cluster. We considered spiny palms with trunks within 1 m of each other to belong to the same site. During the 2011 study period, we attempted to find all 18 of the roost sites that were monitored in the 2003 study period. We successfully relocated 15 roost sites and recorded visual estimates of the number of harvestmen present at each site on 1 or 2 days (means were used in the analysis). At one site, the spiny palm trees were gone. Two sites could not be relocated with confidence because trail markers were missing.

Habitat Characteristics and Microclimate

In deciding which habitat characteristics to measure, we considered that preferred roosting sites might offer protection from predation, overheating or desiccation. We measured the density, length and orientation of the spines and the height of the trees because these factors seem most likely to affect the vulnerability of the harvestmen to vertebrate predators, such as lizards (Donaldson & Grether 2007). The hypothesis that harvestmen select sites that offer protection from overheating or desiccation led us to measure forest canopy cover, air temperature, wind speed and relative humidity. In 2003, spine density was estimated by painting circles (diameter 3.5 cm) at three points along the trunk and counting all spines originating within the circles. Circles were placed 1.6, 1.8 and 2.0 m above the ground unless the trunk height was less than 2.0 m, in which case they were placed as close to the crown as possible and 20 and 40 cm below. In 2011, spine density was estimated by placing a 4 cm² wire square at three different heights (0.8, 1.15 and 1.55 m) along the trunk in the four cardinal directions and counting all spines originating within the square. To characterize the orientation of the spines, each spine was classified as being within 20 degrees of the horizon (flat), >20 degrees above the horizon (up), or >20 degrees below the horizon (down). The proportions of upward and downward pointing spines were used in analyses. To characterize the number of trees at a site, all spiny palms with trunks within 1 m of each other were counted. Canopy cover was measured from the middle of each site with a concave spherical densiometer (Forestry Suppliers, Inc., Jackson, MS, U.S.A.). Air temperature, wind speed and relative humidity were measured once per day per site during the 2003 study period using a Kestrel 3000 meter (Nielsen-Kellerman, Inc., Chester, PA, U.S.A.). Measurements were taken within 10 cm of the trunk and as close to a roosting aggregation as possible without disturbing the animals. Site averages were used in the analysis.

Translocation Experiment Overview and Site Selection

The purpose of the translocation experiment was to determine whether releasing harvestmen at formerly unused sites would attract harvestmen to these sites on subsequent days. In overview, the experiment involved moving harvestmen from existing

aggregation sites into a randomly chosen half of 16 unoccupied but apparently suitable sites; the remaining eight sites served as controls. We then monitored harvestman recruitment at the release and control sites on subsequent days.

Source sites for the translocation were clusters of spiny palms with aggregations of 20–300 harvestmen (mean \pm SD = 94.4 ± 89.5 , $N = 11$). Release sites were in areas of the forest with spiny palms (*Bactris* sp.) of species used by the harvestmen but where no harvestmen were found on the previous 2 days. Individual trees of the same *Bactris* species, and similar in height and diameter, were selected to serve as paired release and control sites. After the matched pairs were selected, treatments were assigned by random coin toss.

Prior to the translocations, we estimated the number of harvestmen present at source sites and took the following measurements on the two palms with the largest aggregations at each site: crown height, maximum height, spine density, spine orientation and distance from the nearest human trail. At release and control sites, we took the same measurements and also measured trunk diameter, canopy cover and distance to the closest natural aggregation. Because crown height and maximum tree height were strongly correlated ($r = 0.98$), only crown height was included in analyses.

There were no significant differences between release and control sites in any of the habitat characteristics measured (Wilcoxon signed-ranks tests: canopy cover: $T = 11$, $N = 8$, $P = 0.38$; crown height: $T = 16$, $N = 8$, $P = 0.84$; trunk diameter: $T = 14$, $N = 8$, $P = 0.64$; distance to trail: $T = 15$, $N = 8$, $P = 0.74$; distance to nearest aggregation: $T = 13$, $N = 8$, $P = 0.55$; tree count: $T = 10$, $N = 8$, $P = 0.31$; mean spine density: $T = 15$, $N = 8$, $P = 0.74$; proportion of upward spines: $T = 12$, $N = 8$, $P = 0.46$; proportion of downward spines: $T = 6$, $N = 8$, $P = 0.11$). The trunk-to-trunk distance between trees within matched pairs ranged from 1.5 to 7.5 m (mean \pm SD = 4.1 ± 2.1 m, $N = 8$ pairs). Release–control site pairs were separated from each other by more than 10 m and by more than 20 m from their respective source sites. The average crown height of trees at source sites ranged from 1.1 to 4.4 m (mean \pm SD = 2.9 ± 0.9 m, $N = 11$). The average crown height of trees at release–control sites ranged from 1.5 to 5.8 m (mean \pm SD = 3.1 ± 1.3 m, $N = 8$ pairs). The average diameter of trees at source sites ranged from 0.14 to 0.20 m (mean \pm SD = 0.16 ± 0.02 m, $N = 6$). The average diameter of trees at release–control sites ranged from 0.14 to 0.16 m (mean \pm SD = 0.15 ± 0.02 m, $N = 8$ pairs).

Translocation Procedure

At source sites, harvestmen were captured by hand and placed in 38-litre clear plastic bags. At release sites, individuals were marked on the dorsal surface of the opisthosoma with colours specific to the site and date of release using Decocolor paint markers (Uchida of America Corp., Torrance, CA, U.S.A.) and released one by one on the tree trunk. Each individual was observed for 30 s before the next animal was released; after the last animal was released, the group was observed for 5 min (see Behaviour Sampling Protocol below). At sites 1–3, we conducted one initial translocation followed by a supplementary translocation on the following day. Early results suggested that additional supplementation might be needed to establish a new roosting tradition, and thus at sites 4–8, we conducted one initial translocation followed by two supplementations (i.e. harvestmen were released on 3 consecutive days). All of the animals released together were from the same source site; some source sites were used to seed multiple release sites. All translocations were carried out between 0930 and 1300 hours. The number of harvestmen released at a given site on a given day ranged from 20 to 28

(mean \pm SD = 21.7 ± 2.1). One harvestman was killed immediately after release by a *Paraponera clavata* ant, one was caught in a spider web, two died for unknown reasons, and 455 were released successfully. Marking the translocated animals enabled us to distinguish returning individuals from new recruits. We continued monitoring experimental and control sites, recording the number of harvestmen present and their marks, if any, for 2–7 days after the last supplementation (mean \pm SD = 4.4 ± 1.8 days). In 11 instances we were unable to determine whether a harvestman was marked or not. In the data analysis, we included these cases in the count totals but excluded them from the counts of unmarked harvestmen.

Behaviour Sampling Protocol

To characterize the immediate response of the harvestmen to being released at a new site, we attempted to observe each harvestman for 30 s and record whether it (1) dropped to the ground, (2) moved up or down within the tree, or performed any of the following behaviours: (3) ventral rubbing (pressing ventrum against the substrate and moving body forward, a possible scent-marking behaviour; Donaldson & Grether 2007; cf. Willemart & Hebets 2011), (4) leg threading (moving the leg through the mouth parts; a self-grooming behaviour; cf. Edgar 1971; Pereira et al. 2004), or (5) bobbing (moving the body up and down rapidly; a possible antipredator behaviour that these harvestmen show when disturbed by vertebrates, including humans; Grether & Donaldson 2007). Of 455 harvestmen released, 51 moved out of view before 30 s elapsed but their observed behaviours were included in the count totals. In the data analysis, we calculated the proportion of harvestmen performing each behaviour in each release session (i.e. at a given site on a given day), and then averaged across the 21 release sessions. To characterize the behaviour of the group after all individuals were released, we took five instantaneous scan samples (Altmann 1974) 1 min apart. During a group scan, we recorded the behaviour of each visible harvestman using the behavioural categories described above, except that we did not record the direction of movement. We started taking group scans in the seventh of the 21 release sessions. Counts from the five scans taken during a given release session were pooled to calculate the proportion of times that each behaviour was observed and then the data were averaged across the 15 sessions.

Statistical Analysis

Wilcoxon signed-ranks tests were used to compare (1) the average number of recruits per day at paired release and control sites and (2) the habitat characteristics of paired release and control sites. The goal of the latter analysis was to examine whether the experimental treatment was confounded with some other factor that might influence harvestman recruitment, even though the treatments were assigned at random. The conservative approach in this case was not to use a correction for multiple tests.

To test for multivariate differences between source and release sites, we used nonparametric k th-nearest-neighbour discriminate analysis (Rencher 2002). All six variables that were available for source sites (crown height, spine density, proportion of upward spines, proportion of downward spines, tree count and distance from trail) were first standardized to a mean of zero and variance of 1.0, k was set to 3, and leave-one-out estimation was used.

A count-based regression model was used to examine whether the number of harvestmen present at roost sites could be predicted based on site characteristics. Because the data were overdispersed relative to a Poisson distribution, and because only sites with harvestmen present were included in the analysis (i.e. no zeros), we

used zero-truncated negative binomial regression. Separate regression analyses were carried out on the 2003 and 2011 data sets. In both data sets, most roost sites were clusters of *Bactris* palms. Restricting the analysis to *Bactris* proved necessary to obtain stable results because the non-*Bactris* sites (three in 2003 and one in 2011) were outliers with respect to tree size and spine density. In addition to analysing data from the 2 years separately, we pooled data between years and included a year term in the model. Spine density differed significantly between years, perhaps because of differences in the way spine density was measured (no other site characteristics differed significantly between years). Spine density was therefore standardized within years, by subtracting the mean and dividing by the standard deviation, for the combined-years analysis. Models with all available site characteristics were fitted initially and then variables were removed sequentially until only those with significant coefficients (i.e. $P < 0.05$) remained. Computation of Akaike Information Criterion (AIC) scores confirmed that this procedure resulted in the best-fit models (not shown). Statistical analyses were carried out using Stata 10.1 (StatCorp, College Station, TX, U.S.A.).

RESULTS

Comparison of Roost Site Use within and between Years

In our resurvey of roost sites used in 2003, all 15 of the relocated roost sites were still being used by the study species in 2011. Most potential roost sites (i.e. isolated spiny palms or clusters of spiny palms) were vacant in both years. In a survey of 17 radial transects centred on existing roost sites in 2003, harvestmen were found in only 19 (9.4%) of 202 potential roost sites (Grether & Donaldson 2007). With a probability of 0.094 of any given site being used, the probability of all 15 roost sites being occupied again in 2011, merely by chance, is very low (binomial test: $P < 0.0001$). We did not carry out a systematic survey of possible roost sites in 2011, but even if 50% of potential roost sites were occupied in 2011, it would still be highly improbable for all 15 of the 2003 roost sites to be occupied again merely by chance (binomial test: $P < 0.0001$). The average number of harvestmen at the 15 relocated roost sites did not differ significantly between years (Wilcoxon signed-ranks test: $T = 35$, $N = 15$, $P = 0.16$), and the trend was towards larger numbers of harvestmen in 2003 (mean \pm SD = 48.2 ± 10.2 , range of means 3.5–127.5, $N = 15$) than in 2011 (27.8 ± 11.0 , range of means 2–173, $N = 15$).

Despite the consistency between years in which sites were used by the harvestmen, the average number of harvestmen present at the 15 roost sites in 2003 was not predictive of the number present in 2011 (Spearman rank correlation: $r_s = -0.11$, $N = 15$, $P = 0.69$). On a shorter timescale, however, the number of harvestmen present on one day was strongly predictive of the number present on subsequent days (2003: $r_s = 0.92$, $N = 18$, $P < 0.0001$, with an interval of 1–12 days between counts; 2011: $r_s = 1.0$, $N = 5$, $P < 0.0001$, with an interval of 12–16 days between counts; Fig. 1).

Habitat Correlates of Roost Site Use

The question of whether spiny palms that are used by the harvestmen differ from those that are not used, either in the characteristics of the trees themselves or in microclimate, was a major focus of Grether & Donaldson's (2007) study. No correlates of roost site use were found in their study, except that the average number of spiny palms was greater at occupied sites than at vacant sites. We did not attempt to replicate that study in 2011 fully, but we tested for differences between source sites and release sites in canopy cover and several tree characteristics (including spine

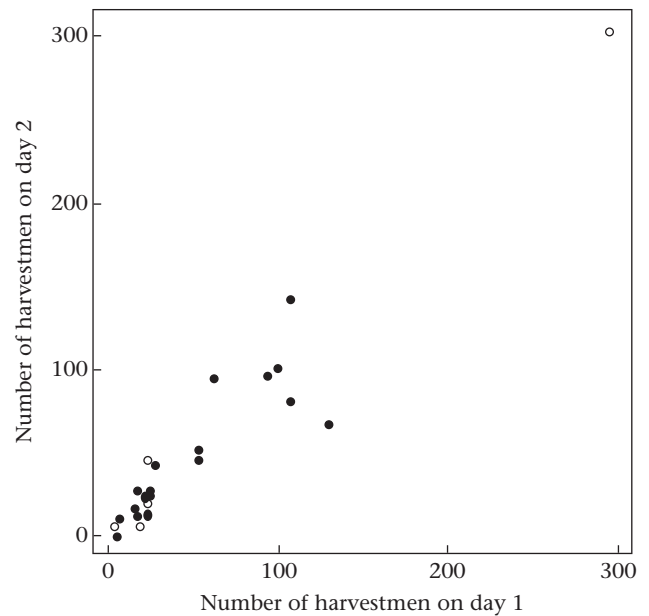


Figure 1. Consistency of roost site occupancy by harvestmen on short timescales. Estimated number of harvestmen at roost sites on 2 different days, 1–16 days apart, in 2003 (solid circles) and 2011 (open circles). See text for statistical analysis.

orientation and distance from the nearest human trail, which were not measured in the previous study). Univariate tests revealed one potentially significant difference: spine density was higher at source sites than at release sites (Mann–Whitney U test: $U = 69.5$, $N_1 = 11$, $N_2 = 8$, $P = 0.03$). No significant difference was found for crown height ($U = 44$, $P = 0.52$), tree count ($U = 63$, $P = 0.13$), spine orientation ($U = 57.5$, $P = 0.27$) or distance to the nearest trail ($U = 58$, $P = 0.27$), and spine density was not significant following Bonferroni correction for multiple tests ($k = 5$; adjusted $\alpha = 0.01$). Nonparametric discriminant analysis correctly classified only 36.4% of source sites and 12.5% of release sites, for an overall error rate of 73.7%. Thus, with the possible exception of a difference in spine density between occupied and vacant sites, the measured habitat characteristics did not explain why some sites were used by the harvestmen and others were not.

Restricting the analysis to sites that were used by the harvestmen, spine density was a significant predictor of harvestman numbers in both years (Table 1). Crown height, canopy openness and mean air temperature also emerged as significant predictors in the 2003 data set (Table 1). Larger trees with greater spine densities, at sites with relatively closed forest canopies and lower mean temperatures, had more harvestmen. Trunk diameter, wind speed and relative humidity were not significant predictors of harvestman numbers (zero-truncated negative binomial regression: $P > 0.05$; stepwise results not shown). With data from the 2 years combined (and restricted to site characteristics measured in both years), spine density and crown height were significant predictors of harvestman numbers (Table 1, Fig. 2). The year term was significant in the combined model, but there were no significant differences between years in the slope of harvestman counts on spine density or crown height (i.e. no significant interactions; not shown).

Translocation Experiment Results

The behaviour of the harvestmen immediately after release was quite variable (means \pm SD, all $N = 21$): $6.2 \pm 6.0\%$ dropped to the

Table 1

Variables predicting the number of harvestmen present at natural roost sites (restricted to *Bactris* trees) in zero-truncated negative binomial regressions (likelihood ratio tests for overdispersion: all $P < 0.001$)

Variable	Estimate	SE	z	P
2003 (14 sites)				
Crown height	0.759	0.103	7.35	<0.001
Spine density	1.625	0.594	2.74	0.006
Canopy openness	-0.042	0.011	-3.86	<0.001
Air temperature	-0.404	0.092	-4.40	<0.001
Intercept	13.190	2.698	4.89	<0.001
Model	Likelihood ratio: $\chi^2_4=27.05$, $P<0.0001$			
2011 (10 sites)				
Spine density	3.731	1.054	3.54	<0.001
Intercept	3.059	0.383	7.98	<0.001
Model	Likelihood ratio: $\chi^2_1=8.08$, $P=0.004$			
Both years (24 sites)*				
Crown height	0.506	0.140	3.61	<0.001
Spine density	0.288	0.128	2.26	0.024
Year	0.692	0.255	2.71	0.007
Intercept	2.141	0.461	4.65	<0.001
Model	Likelihood ratio: $\chi^2_3=19.90$, $P=0.0002$			

* Spine density was standardized within years for the combined-years analysis (see Fig. 2 for graphical depiction of the results).

ground, $47.3 \pm 22.6\%$ moved up in the tree, $24.7 \pm 15.8\%$ moved down but stayed in the tree, $30.6 \pm 28.4\%$ performed ventral rubbing and $48.0 \pm 23.5\%$ bobbed (these percentages sum to greater than 100% because some individuals performed multiple behaviours). The bobbing category can be split into what might be two distinct behaviours: bobbing while walking ($27.6 \pm 19.9\%$) and bobbing in place ($23.7 \pm 18.8\%$). The only behaviour in our ethogram that was not observed 30 s post-release was leg threading. After all the harvestmen were released, during the group scans (means \pm SD, all $N = 15$): $4.9 \pm 4.7\%$ of the harvestmen were moving, $1.8 \pm 2.5\%$ performed ventral rubbing, $11.4 \pm 11.0\%$ performed leg threading, $1.7 \pm 1.7\%$ bobbed in place and $80.1 \pm 11.3\%$ were stationary. No harvestmen was observed to drop to the ground or bob while walking during the group scans. While data from the 30 s focal samples and the 5 min group scan samples are not directly comparable, it is apparent that there was a shift in activity shortly after release; most individuals stopped performing antipredator behaviour (bobbing) and some began self-grooming (leg threading).

On the days following the translocations, harvestmen entered release sites, on their own accord, significantly more often than they entered the matched control sites (Wilcoxon signed-ranks test: $T = 1$, $N = 8$ release–control site pairs, $P = 0.0078$; Fig. 3). All eight release sites attracted some harvestmen (range 0–12 per day; mean \pm SE of daily site means = 1.90 ± 0.70) while only three of eight control sites did (range 0–2 per day; mean \pm SE = 0.14 ± 0.10). Unmarked harvestmen were found in at least seven of the eight release sites (range 0–11 per day; mean \pm SE = 1.17 ± 0.52) but in only one of the control sites (range 0–1 per day; mean \pm SE = 0.016 ± 0.016 ; Wilcoxon signed-ranks test: $T = 0$, $N = 8$ pairs, $P = 0.0039$; Fig. 3). Most harvestmen that entered release sites were unmarked (at least 60 of 94 records; $\geq 63.8\%$) while only one of eight harvestmen found at control sites was unmarked (12.5%). Two marked harvestmen were found at one control site on one day, but the remaining six cases of recruitment to control sites involved solitary individuals. Marked harvestmen were found at the site where they had been released on a previous day (34 records) or at the nearest control site (seven records), but never at other release or control sites. The maximum number of harvestmen returning to their release site on the day immediately following release was 20% of the number released, and the mean \pm SE return rate was $2.75 \pm 1.09\%$ ($N = 21$ release dates).

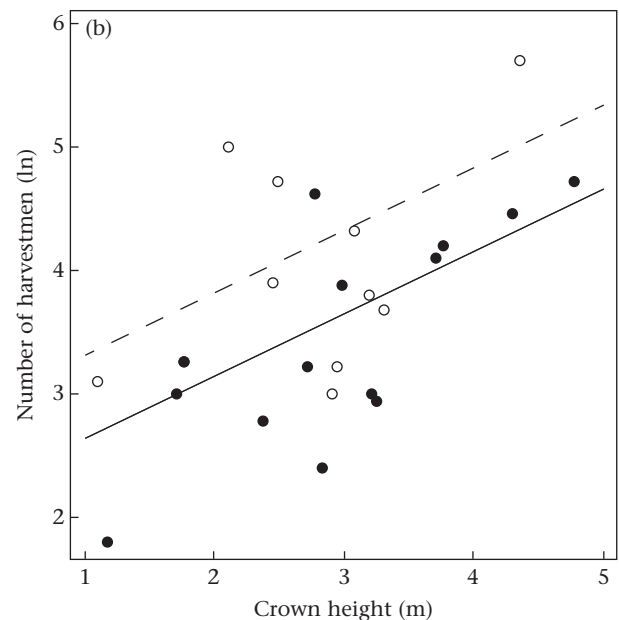
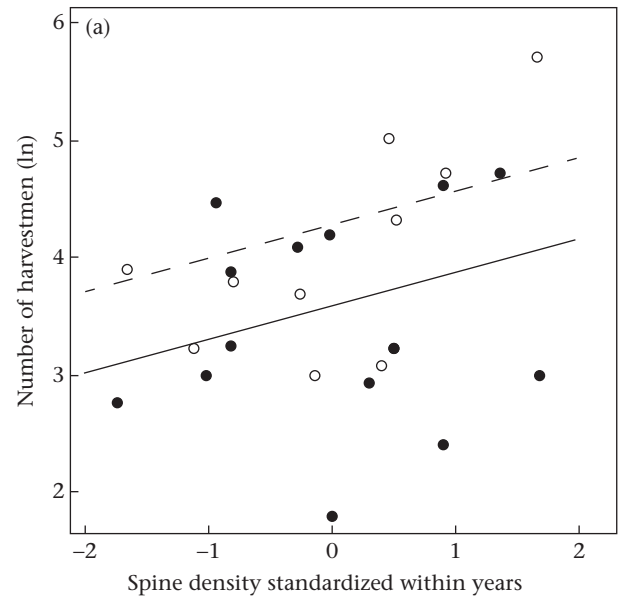


Figure 2. Relationship between the number of harvestmen present at roost sites (ln-transformed) and the (a) average spine density and (b) crown height of palms at those sites in 2003 (solid circles, solid lines) and 2011 (open circles, dashed lines). Best-fit lines are from zero-truncated negative binomial regressions for the combined-years analysis (see Table 1).

Site 1 continued to attract several harvestmen ($5\text{--}12$ per day; mean \pm SD = 6.8 ± 2.9) for at least 7 days after the supplementary translocation, up to the last census, suggesting that a new roosting tradition had become established. Most harvestmen found at this site were new recruits. From the fourth day forward, 90–100% of the harvestmen recruited to the site were unmarked. On days 4 and 6, all five harvestmen at the site were unmarked. On days 5 and 7, respectively, 11 of 12 (92%) and 9 of 10 (90%) harvestmen roosting at the site were unmarked. Although this new aggregation remained relatively small during our study, even sites with smaller aggregations in 2003 were still in use in 2011. Three other release sites attracted smaller numbers of harvestmen (1–4 per day; mostly unmarked) up to the last census, while the remaining four release sites were vacant at the last census.

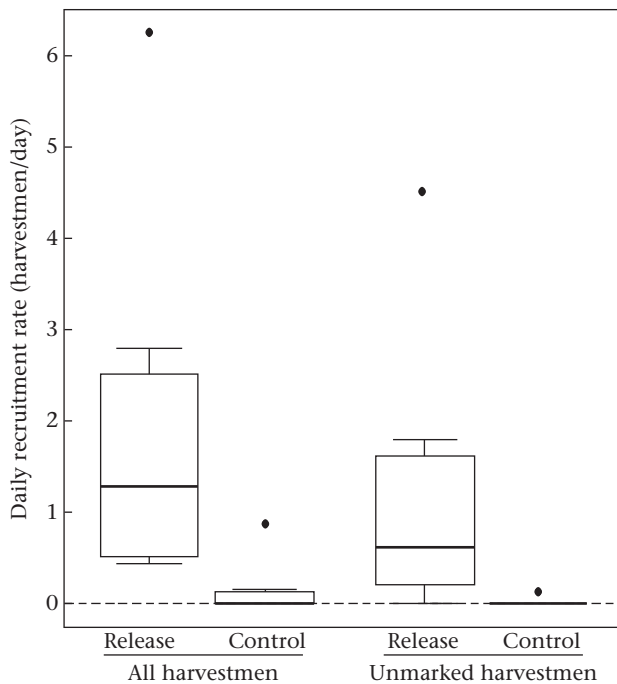


Figure 3. Translocation experiment results. Daily recruitment rate of harvestmen to release sites and matched control sites. See text for statistical comparison. Box plots depict the median (thick horizontal line), interquartile range (box), upper and lower adjacent values (error bars) and outside values (points). $N = 8$ sites per category.

After the translocation experiment, half of the release sites were occupied by harvestmen at the last census and half were vacant. The occupied sites did not differ significantly from vacant sites in spine density (Mann–Whitney U test: $U = 12.5$, $N_1 = 4$, $N_2 = 4$, $P = 0.20$) or crown height ($U = 10$, $P = 0.68$), but there was a difference in canopy cover ($U = 16$, $P = 0.028$). All four occupied release sites had greater canopy cover (mean \pm SE = $93.9 \pm 0.7\%$) than the unoccupied release sites ($90.2 \pm 1.2\%$), for a mean difference of $3.7 \pm 1.4\%$. This difference was not significant, however, after Bonferroni correction ($k = 3$; adjusted $\alpha = 0.017$).

We did not systematically check source sites, but two harvestmen were found at their source site 4 days after the translocation.

DISCUSSION

The work we present here supports the hypothesis that chemical-based conspecific attraction can lead to traditional site use that persists across multiple generations. The initial evidence for long-term roost site usage in *Prionostemma* sp. was that the status of 12 spiny palm sites, half used and half unused by the harvestmen, did not change between 2001 and 2003 (Grether & Donaldson 2007). In our resurvey of 18 roost sites used in 2003, 15 were still being used by harvestmen in 2011 (including five used in 2001). Remarkably, over the entire 10-year period, some roost sites were destroyed or otherwise lost from the study, but none of the remaining sites was abandoned by the harvestmen. Donaldson & Grether's (2007) inference that the harvestmen find aggregation sites by detecting chemical cues left by conspecifics was based on the results of a series of roost site manipulations. The most convincing experiment involved moving fronds within spiny palms (at night, when the harvestmen were away). Fronds that had been used for roosting continued to be used even after they were moved to a different position in the tree, while previously unused fronds that were placed in the original position of the used fronds

continued to be unused. Another experiment in which entire trees were moved yielded similar results. While these experiments established a probable role for site-labelling chemicals, they stopped short of showing that prior usage, alone, is sufficient to attract new harvestmen to a site. Conceivably the harvestmen could have selected the roosting sites based on other, unmeasured environmental cues. In the current study, by translocating harvestmen to new sites, we directly tested the prediction that prior usage alone is sufficient to induce aggregation formation. Release sites consistently attracted new (unmarked) recruits at much higher rates than matched control sites (Fig. 3). In fact, most of the harvestmen found at the release sites were unmarked, and on some days, only unmarked harvestmen were present. This suggests that cues left by the translocated individuals were sufficient to induce aggregation formation. Furthermore, it appears that a new communal roosting tradition became established at least at one release site.

Coddington et al. (1990) studied a *Prionostemma* sp. that roosts in spiny palms at a high-elevation (1440 m) cloud forest site in Costa Rica (Monte Verde). Whether this is the same species that roosts in spiny palms at our lowland (30 m) rainforest site in Nicaragua remains to be determined, but the behaviour of the two populations appears to be similar. Coddington et al. (1990) carried out an experiment in which harvestmen from a single aggregation were captured, marked and released within 10 m of the aggregation site. The next morning, a few marked harvestmen were found back at the original site but more were found in other aggregations 50–85 m from the original site. From these results, Coddington et al. (1990, page 217) inferred that the harvestmen can locate aggregations from great distances but probably do not have a homing ability. They further suggested that aggregations are probably not limited by the availability of sites and that individuals select particular aggregation sites. Coddington et al. (1990) did not speculate further about the mechanism of roost site selection. Our research on the same or a closely related species provides a possible explanation for why aggregations form repeatedly at particular sites: the harvestmen prefer to roost at sites where they encounter conspecifics or chemicals left by conspecifics.

While attraction to conspecific chemical cues appears to be the primary reason that *Prionostemma* sp. aggregations form repeatedly at particular sites, we found that habitat variables helped predict which sites attracted the largest aggregations. Within the forest understory, whether a spiny palm was used as an aggregation site was not predictable, but among sites that were used by the harvestmen, the size of the aggregation depended on the height and spine density of the tree (Fig. 2), canopy cover and air temperature (Table 1). The positive effect of spine density is consistent with Donaldson & Grether's (2007) finding that the harvestmen eventually abandoned trees from which the spines had been removed. Trees with greater spine densities probably provide better protection from vertebrate predators, such as the lizard *Norops lemurinus* (Donaldson & Grether 2007).

The positive effect of canopy cover and the negative effect of air temperature may reflect the fact that harvestmen are very susceptible to desiccation (Santos 2007). Although desiccation may not be as much of a problem in tropical rainforest as in more arid environs, our study in 2003 was carried out near the end of Nicaragua's long dry season. Grether & Donaldson (2007) noticed that aggregations shrank between the morning and afternoon hours at sites on the forest edge but not at interior forest sites where the temperature was more stable. Presumably harvestmen at the forest edge sites were retreating into the forest in the heat of the afternoon, but this did not cause the forest edge sites to be abandoned. Harvestmen were still roosting at both of these sites in 2007 (G. F. Grether, personal observation). By 2011, one of the forest edge sites had been destroyed, but the other site was still in use. For

another possible example of harvestmen avoiding desiccation during the dry season, in this case by roosting closer to a water source, see Machado et al. (2000).

Continued use of degraded sites is one of the hallmarks of traditional site use (Warner 1990). Once started, a tradition of roosting at a particular site might persist long after the site becomes unsuitable as a result, for example, of reductions in forest canopy cover caused by natural tree falls or logging. When the harvestmen settle into roosts at dawn, it may be impossible for them to assess whether climatic conditions will be tolerable later in the day. Even if individuals avoid low-quality sites that they have visited in the past, the chemical cues they leave behind might continue draw in naïve conspecifics. If so, this is a particularly dangerous form of traditional site use because the animals might be attracted to sites where conspecifics perished. By comparison, the tradition in bluehead wrasse, *Thalassoma bifasciatum*, of spawning at particular sites ended when the animals using those sites were experimentally removed and replaced with fish from another reef (Warner 1988). This would also be the predicted result for other species in which animals learn about the locations of traditional roosts by detecting conspecifics visually and/or acoustically (e.g. Mallet 1986; Miller 1989; Grether & Switzer 2000; Kerth & Reckardt 2003; Béchet et al. 2010). If a similar removal experiment was carried out on *Prionostemma* harvestmen, we predict that the roosting tradition would continue. This is a specific example of how the proximate mechanisms of habitat selection are relevant for predicting how animals will respond to habitat degradation (Mihoub et al. 2011; Van Dyck 2012).

Protection of roosting habitat is recognized as a conservation priority for many species (McGeoch & Samways 1991; Alonso-Mejia et al. 1997; Dellasala et al. 1998; Brooke et al. 2000; Barclay & Brigham 2001; Donazar et al. 2002; Aguirre et al. 2003; Harms et al. 2003; Dennis 2004; Smith & Racey 2005; Curtis & Machado 2007; Lambertucci 2008), but when traditional roosting sites are degraded or destroyed, the availability of alternative sites is only relevant if the animals will use them (Donazar & Feijoo 2002). Understanding how new site traditions develop, and how naïve animals find aggregation sites, may be of considerable value in applied conservation (and perhaps also in the management of certain pest species). Several species of harvestman are threatened with extinction because of habitat destruction (Curtis & Machado 2007). Destruction of traditional roosting sites might be contributing to the decline of some species. Species that form mass aggregations in caves, which are often impacted by human activities, seem particularly vulnerable. Attempting to reduce such impacts should be the first course of action, but in some cases it might be advisable to carry out translocations to establish new aggregation sites.

While this study brought us closer to understanding *Prionostemma* sp. communal roosts, many questions remain unanswered. Which chemicals are deposited at the roost sites? Do the harvestmen only detect substrate-bound chemicals, or can they also detect airborne chemicals, and if so, at what distance from an aggregation site? How much time do the harvestmen spend searching for aggregation sites? What is the predation rate on solitary individuals compared to individuals in aggregations? To what extent do the correlations between aggregation size and site characteristics result from habitat selection versus differential mortality? We raise these questions with the goal of stimulating further research on these highly tractable but understudied animals (Machado et al. 2007).

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