

# Tradition without social learning: scent-mark-based communal roost formation in a Neotropical harvestman (*Prionostemma* sp.)

Zoe R. Donaldson · Gregory F. Grether

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**Abstract** Most models of habitat selection assume that individual animals choose and either reuse or abandon sites based on a constant reassessment of site quality. When survival is a function of the presence of conspecifics, however, the benefits of returning to traditional sites may override resource assessment. Many animals form roosting aggregations at what appear to be traditional sites. At our study site in Nicaragua, the harvestman *Prionostemma* sp. forms diurnal roosting aggregations on a small subset of the available spiny palm trees. With respect to physical characteristics and microclimate, the spiny palms used by the harvestmen resembled a random sample of those available, yet the same subset of trees was used in two different years (2001, 2003). This suggests that the location of aggregation sites is traditional, not a product of habitat limitation. Individual harvestmen were not faithful to particular roost sites, however, which raises the question of how the tradition could be maintained over time. In this paper, we present evidence, derived from a series of small-scale field experiments, that the harvestmen mark roosting sites chemically and enter marked sites preferentially when searching for places to roost. We also show that the harvestmen are sensitive to changes in site quality (the presence of spines)

but will continue to use degraded traditional sites when no intact spiny palms are nearby. This system provides an example of how animal traditions could be maintained over multiple generations without learning. Site-labeling can be viewed as an external form of social memory.

**Keywords** Conspecific attraction · Habitat selection · Aggregation · Tradition · Pheromone · Chemotaxis · Daddy-long-legs · Opiliones

## Introduction

Classic models of habitat selection assume that individual animals choose and either reuse or abandon sites based on a constant reassessment of resource quality (Brown 1969; Fretwell and Lucas Jr. 1970). Animals employing this strategy should be found at locations that can be predicted from measurements of critical habitat features. Alternatively, if tradition plays a strong role in the repeatability of site usage, habitat measurements may not reliably predict patterns of spatial dispersion (Warner 1990). Switzer (1993) modeled the costs and benefits of site choice tactics under various conditions and showed that animals should be site faithful when the costs of moving and becoming familiar with a new area (e.g., energy, time, and predation) are greater than the costs of returning to a potentially suboptimal site. The conditions favoring site fidelity are likely to be even broader for species in which the benefits of returning to a site depend positively on the presence of conspecifics (Stamps 1988; Muller et al. 1997). Simple dilution (safety in numbers) could be sufficient to favor the maintenance of suboptimal aggregation sites, if relocating puts individuals at risk of facing predators alone (Hamilton 1971; Vine 1971).

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Z. R. Donaldson (✉)  
Neuroscience Program, Emory University,  
954 Gatewood Road, Room 5243,  
Atlanta, GA 30329, USA  
e-mail: zdonald@emory.edu

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

Galef (2004) argued that for a behavior to be called traditional, it must be demonstrated that the behavior is transmitted by social learning. This criterion makes sense when applied, for example, to tool use. If it was found that a particular form of tool use, such as chimpanzee termite fishing, developed without learning or was purely a product of individual trial-and-error learning, then there would be no reason to call the behavior traditional. We propose that a different criterion be used, however, to determine whether aggregation sites are traditional. Our criterion is that animals must be shown to be attracted to specific sites as a consequence of those sites being used by conspecifics in the past. By this definition, traditional site use does not require learning. The tradition of aggregating at specific sites could be maintained by cues left behind by conspecifics, such as odors. For example, odor cues have been implicated in the maintenance of sleeping aggregation sites in the bee *Idiomelissodes duplocincta* (Alcock 1998) and foraging routes in ants (Hölldobler and Wilson 1990) and Norway rats (Galef and Buckley 1996).

The alternative to traditional site use is that specific sites are used because of habitat limitation (i.e., scarcity of accessible and suitable sites). We acknowledge that it would be difficult, and perhaps pointless, to try to distinguish between these alternatives in species that enhance the suitability of their habitat (e.g., by building structures or caching food). For most species, however, the distinction between traditional site use and habitat limitation should be of substantial interest to ecologists. Warner (1990) showed that tradition interferes with resource assessment in the spawning site choices of bluehead wrasse (*Thalassoma bifasciatum*). In such systems, population mean fitness may actually increase after long-established traditions are disrupted. On the other hand, the loss of traditional sites can have disastrous consequences for species that rely on such traditions for survival or reproduction (e.g., dams preventing Pacific salmon from reaching traditional spawning sites; Nehlsen et al. 1991).

Communal roosting has been studied most extensively in birds and bats, but the behavior is widespread taxonomically (e.g., Reynierse et al. 1969; Cook et al. 1976; Pearson and Anderson 1985; Mallet 1986; Cockerill 1988; Miller 1989; Alcock 1998; Pimenta and Martins 1999; Gomes-Filho 2000; Grether and Switzer 2000). Whereas the functions of communal roosts have been investigated and discussed extensively (e.g., Waltz 1982; Mallet 1986; Rabenold 1987; Miller 1989; Vulinec 1990; Marzluff et al. 1996; Switzer and Grether 2000; Barta and 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.

The mechanisms through which animals locate aggregations may influence the degree of site fidelity of the

aggregations and their association with specific habitat features. A variety of visual, chemotactic, and phototactic stimuli have been proposed as cues for aggregation formation in arthropods (Delany 1959; Reynierse 1966, 1967; Reynierse and Ellis 1967; Reynierse et al. 1969; Grether and Switzer 2000). The spatial and temporal range, stability, and locatability of aggregation cues may influence the specificity and repeatability of the aggregation sites. For instance, if aggregation cues are located on immobile structures or substrates, such as a tree or cave entrance, aggregations should form at a given site with high predictability and rarely move unless the cue is destroyed (Gnaspini 1996). Alternatively, if the cues are mobile, such as the animals themselves or environmental conditions such as temperature or humidity that change frequently, the aggregation sites may also change frequently (Lewis 1995).

We studied the communal roosting behaviour of a *Prionostemma* sp. harvestman (Opiliones: Eupnoi: Sclerosomatidae: Gagrellinae [formerly Palpatores: Phalangioidea]; identified by Ana Tourinho, personal communication) in an intact lowland rainforest site in southeastern Nicaragua. As reported in Grether and Donaldson (2006), this species aggregates during the day, almost exclusively on the trunks and fronds of spiny palm trees (*Cryosophila warscewiczii* and multiple *Bactris* spp.) in the forest understory. After dark, the harvestmen disperse and forage solitarily; at dawn, the aggregations reform with a high degree of site fidelity. Unlike some other aggregating Neotropical harvestmen (Gnaspini 1995, 1996), this species leaves the diurnal roosting site every night, forms relatively small aggregations (<100 individuals), and does not appear to undertake brood care at the aggregation sites. During our study, aggregations formed repeatedly in a small subset of the available spiny palms, and the same sites were used in two different years (2001, 2003). In addition, the harvestmen preferentially clustered at specific but seemingly arbitrary positions within the spiny palms. Nevertheless, the membership of aggregations was fluid; individually marked harvestmen were observed moving between clusters within sites and were found at multiple roost sites, moving up to 0.2 km per night (Grether and Donaldson 2006). The high consistency of site use but low site fidelity of individuals suggested that spiny palms used as aggregation sites differed conspicuously (to the harvestmen) from those that were not used. However, we found no differences between used and unused sites in the characteristics of the trees themselves (height, spine density, etc.) or microclimate (wind, temperature, and humidity). These results argue against the habitat limitation hypothesis but also raise questions about how a tradition of roosting at particular sites could be maintained in this system.

Given that individual harvestmen are not strongly site faithful and, in any case, are relatively short-lived, how

could the pattern of roost site usage remain stable for years? Two hypotheses seem plausible: (1) suitable roosting sites are in limited supply, site suitability changes little over time, and we have failed to identify the key variables that determine whether a spiny palm is suitable, or (2) the harvestmen mark roosting sites chemically and enter marked sites preferentially when searching for places to roost. To investigate the mechanisms used by the harvestmen to locate aggregation sites and to determine whether these mechanisms lead to the continued use of degraded sites (a hallmark of traditional site use), we carried out a series of roost site manipulations.

## Materials and methods

### Study site

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

### Leaf litter replacement

How do these small, terrestrial, solitary foragers find aggregation sites 1–5 m above the forest floor? One possibility is that they deposit a scent trail when leaving the roost at night and then follow the same or a different trail back to an aggregation site before dawn. If so, removing the leaf litter around the base of a roosting tree, after the animals have dispersed at night, should obscure the scent trail and disrupt the formation of the aggregation in the morning.

In 2001, we removed all leaf litter within a 1.5-m radius of the base of two established aggregation sites (RD3 on 30 April and B10 on 1 May) and also from two control sites. In 2003, we removed all leaf litter within a 3-m radius of the base of two established aggregation sites (O12 on 29 April and Y2 on 30 April) and also from two control sites. A control site consisted of a spiny palm that was not occupied by harvestmen previously during this study and which was similar in height to and 10–15 m from the aggregation site with which it was paired. Leaf litter from the aggregation site was moved to the paired control site, and leaf litter from the control site was discarded (>10 m from either site). We replaced the leaf litter at the aggregation site with leaf litter from an area without spiny palms to avoid the possible interfering effects of residual

scent that might be present at the base of palms used as aggregation sites in the past. Any scent gradient in the leaf litter would have been disrupted when the leaves were moved from aggregation site to control site because the orientation of the leaves was changed. The results were interpreted with this limitation in mind.

### Tree replacement

The goal of this experiment was to determine whether the harvestmen are likely to use spatial cues or scent marks to locate aggregation sites. If the harvestmen mark aggregation sites with volatile chemicals deposited solely at the site, then moving a tree a few meters from its original location should not greatly affect aggregation formation. Conversely, if the harvestmen mainly rely on spatial memory or a scent trail in the leaf litter surrounding aggregation sites, then moving a tree a few meters could greatly disrupt aggregation formation.

On 1 May 2001, after determining that the harvestmen had dispersed for the night, we cut down two established aggregation palms (O5 and RD1) as close to the base of the tree as possible. The base of the trunk was then whittled to a point, and the trees were driven into the ground about 3 m away from their original locations and secured with ropes to three nearby trees. The compass orientations of the relocated palms were kept as similar as possible to the original orientations. Both trees lost about 25 cm of height, and one frond on O5 was damaged, but the spines were undamaged. All trees within a 10-m radius of the original site were censused for the remainder of the study (8 days).

This experiment was repeated in 2003 with important modifications. After the harvestmen had dispersed for the night on 27 April 2003, the palm at O5n was cut down as close to the base as possible and moved away 3–4 m. Then, the tree was immediately returned to its original position and compass orientation where it was secured with ropes and left in place for 48 h. This served to control for the disruption caused by cutting and transporting the tree (which itself could interfere with aggregation formation). After the harvestmen had dispersed for the night on 29 April 2003, the palm was moved 3.75 m away from its original location and again secured in its original compass orientation. Another spiny palm of the same species and similar size, but which was not used as a roosting site by harvestmen, was then cut down, placed upright on the stump of the original aggregation tree, and secured with ropes. This second tree served as a position control. If the harvestmen primarily use spatial cues to relocate aggregation sites, they would be expected to settle in the control tree. Conversely, if aggregation formation is mediated by a site-labeling scent, they would be expected to return to the original tree. The cut trees and all spiny palms within a 10-m radius were surveyed for the remainder of the study.

## Frond replacement

The harvestmen formed aggregations repeatedly not only on specific trees but routinely clustered at specific locations within a tree. At a few sites, aggregations formed on particular fronds. This permitted us to carry out a within-tree version of the tree replacement experiment by moving individual palm fronds. The experiment involved moving a frond with a history as an aggregation site (frond 1) to a different position within the same tree and then replacing it with a frond of similar size and in similar condition from a tree of the same species that was not being used as a roost (frond 2). A third frond, meeting the same criteria, was placed at a randomly chosen position within the roosting tree (frond 3; Fig. 1a). These manipulations were done at night while the harvestmen were away from the roost. All fronds were secured in place using wire, and live fronds were kept from wilting by placing the severed end in a small water-filled plastic vial covered with parafilm (American National Can, Menasha, WI). If the harvestmen primarily use scent marks to locate aggregation sites, then

they would be expected to return to frond 1. If instead they rely primarily on spatial cues, they would be expected to return to frond 2. Frond 3 served as a control for both scent marks and position effects. Five frond replacements were carried out; once at site BD2 on 1 May, twice at R4 on 30 April and 1 May, and twice at BD24 on 5 May 2003. These sites were surveyed daily for the remainder of the study.

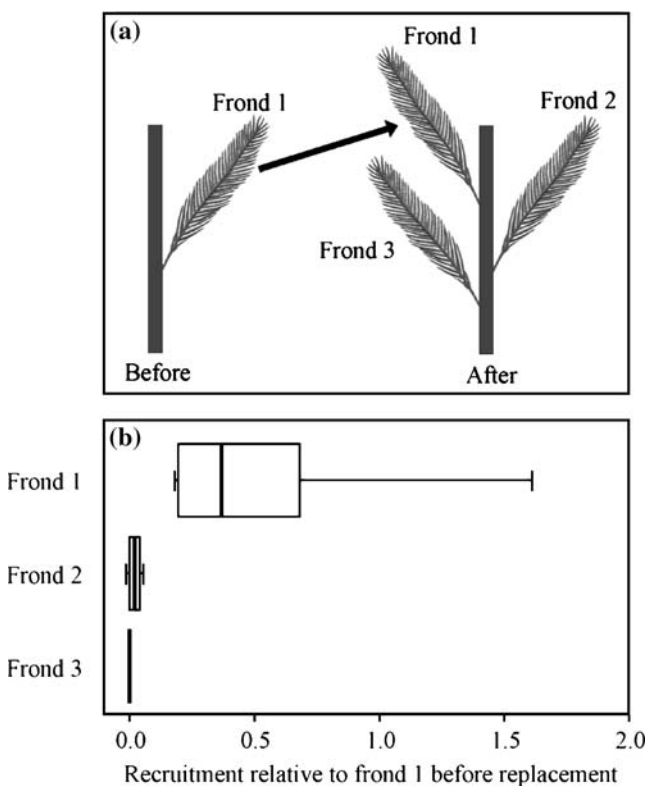
## Spine removal

Spines are the most obvious feature that distinguish roosting sites from non-spiny palms (which were not used by harvestmen). Moreover, spines appear to provide protection against predatory vertebrates, such as anoline lizards (personal observation; see “Discussion”). Therefore, spine removal should substantially decrease site quality, allowing us to test the harvestmen’s response to degraded sites.

To create a situation where the harvestmen would have to travel a considerable distance to locate an intact spiny palm, we removed spines from all palms at R16 and O5b on 7 May 2001. O5b consisted of a single tree, and R16 consisted of three spiny palms. At the start of the experiment, R16 had been continuously used as an aggregation site with little change in aggregation size for at least 10 days, and O5b had been in use for at least 5 days. At least 90% of the spines were removed with a machete, from the base of the tree to the top of the trunk, after all harvestmen had dispersed for the night. The spines were left where they fell at the base of the tree. Both sites were censused for the next 2 days.

To reduce the cost to the harvestmen of moving to an intact tree, we shaved one or two selected trees within roosting sites that consisted of multiple trees. In this scenario, the harvestmen needed to travel less than a meter from a shaved tree to encounter an intact tree. Spines were removed from one of eight trees at O12, two of ten trees at Y15, two of seven trees at Y19, and one of three trees at R6. Spines were removed using scissors and left where they fell at the base of the tree. These sites were monitored for 3 to 7 days after spine removal.

Finally, to eliminate any cost associated with relocating, we performed a within-tree version of the experiment. After determining the area on the trunk normally occupied by an aggregation at Y0a, we removed the spines from half of that area and monitored the site for the next 4 days.



**Fig. 1** Frond replacement experimental design and results. (a) Schematic illustration of the experimental design. Frond 1 had a history as an aggregation site. Frond 2 served as a replacement control of similar size and condition. Frond 3 is a second control meeting the same criteria as frond 2, but placed randomly within the site to control for habitat limitation. (b) Effects of frond replacement on harvestman recruitment relative to frond 1 before replacement. Box plots showing median (vertical line), interquartile range (box), and range of values (error bars) for each frond treatment group

## Results

### Leaf litter replacement

The number of harvestmen returning to the established aggregation sites was lower on the day after leaf litter

replacement, compared to the immediately preceding day, in all four trials (Fig. 2). The reduction in recruitment was greater in 2003 than in 2001, perhaps because a larger clearing radius was used in 2003. In two of four replicates of this experiment, harvestmen were found at the control sites (i.e., the sites to which leaf litter from the aggregation sites was moved) the day immediately after leaf litter replacement (four individuals at B10 control and two at Y2 control). These results are consistent with the hypothesis that the harvestmen use scent trails, although it is possible that the reduction in recruitment was merely a disturbance effect (e.g., some harvestmen might have been present in the leaf litter at the time that it was moved). What we can infer from these results is that the harvestmen do not rely entirely on scent trails to locate roosting sites. Aggregations still formed at the original roost sites after the leaf litter (which completely covered the ground around roosting sites) was replaced. Thus, other cues, such as airborne scent gradients or spatial landmarks, must also play a role in aggregation formation.

#### Tree replacement

On the day before palms RD1 and O5 were moved, they contained 30 and 16 harvestmen, respectively. On the next morning, both trees were completely empty. No harvestmen were found on palm RD1 or any other spiny palms within a 10-m radius of the original site for the remainder of the study. Palm O5 also remained empty for 6 days, but on days 7 and 8, a small cluster of five harvestmen re-appeared in this tree. On the morning after the manipulation, however, an aggregation of 15 harvestmen was found 0.6 m away from the original location of palm O5 in a smaller palm that had not been used as a roosting site for at

least 3 days before. This new roosting site (O5b) continued to be used for the remainder of the study.

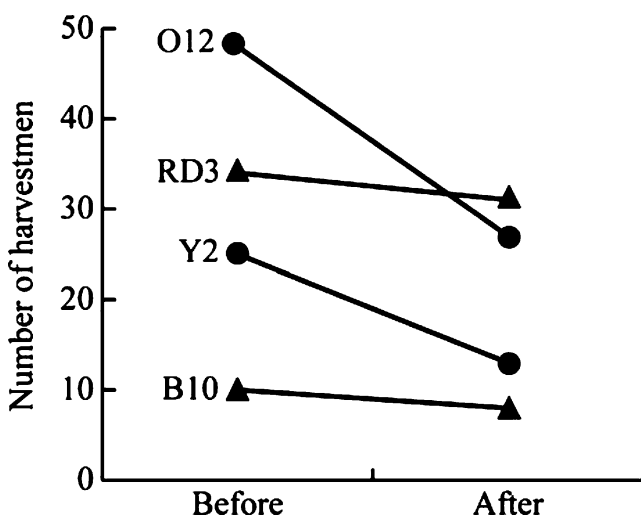
In 2003, we modified the experiment to separate the effects of cutting the tree from moving it and also to separate position effects from tree-specific effects (see “Materials and methods”). On the day before palm O5n was cut (27 April 2003), it contained 27 harvestmen. After this tree was cut and before it was moved to a new location, 15 harvestmen roosted there on 28 April, and 18 roosted there on 29 April. On 1 May, after the tree was moved and a control tree was put in its place, the number of harvestmen roosting on the original tree dropped to three and remained low (0–3) for the rest of the study (7 days). No harvestmen were found on the control tree over the same time period.

#### Fronde replacement

Overall, there was a significant effect of frond treatment on recruitment (Fig. 1b; Friedman’s test,  $\chi^2$  corrected for ties = 9.33,  $P=0.01$ ,  $N=5$ ). Harvestmen always returned to frond 1 (the original aggregation site) and sometimes in large numbers (range, 4–60 individuals). In four cases, the number of harvestmen roosting on frond 1 decreased after the frond was moved and, in one case, the number increased (Wilcoxon matched pairs test,  $W=3$ , two-tailed  $P=0.31$ ,  $N=5$ , for the comparison of the mean recruitment to frond 1 for 3 days before the manipulation to that for 3 days afterwards). On four occasions, over a 3-day period, one or two harvestmen were found on frond 2, but no harvestmen were found on frond 3. The much greater recruitment to frond 1 in comparison to either of the other two fronds ( $W=0$ , one-tailed  $P=0.03$ ,  $N=5$ ) strongly suggests that the harvestmen mark local aggregation sites chemically. The difference in recruitment to fronds 2 and 3 was not significant ( $W=0$ , two-tailed  $P=0.25$ ,  $N=3$  after dropping ties) but is suggestive of a position effect (Fig. 1b).

#### Spine removal

If removing the spines immediately reduced recruitment to zero, this would imply that site suitability overrides scent-mark-based chemotaxis. Conversely, if removing the spines had little effect on roost settlement, this would suggest either that the harvestmen use other cues besides spines to identify suitable sites or that chemotaxis overrides site suitability. Removing spines may also remove scent, so a moderate reduction in recruitment after spine removal would not differentiate whether the harvestmen were responding to the removal of spines or to the removal of scent. To circumvent this problem, we varied the distance that the harvestmen would have to travel to reach an intact



**Fig. 2** Effects of leaf litter replacement on harvestman recruitment. Triangles represent sites altered in 2001 (1.5-m clearance radius). Circles represent sites altered in 2003 (3-m clearance radius)

site (with spines) from a degraded site (without spines). If the harvestmen use olfaction to locate aggregation sites but are also responsive to changes in site suitability, then travel distance should influence how quickly degraded sites are abandoned.

Spine removal was always followed by a reduction in aggregation size (Fig. 3; Wilcoxon matched pairs test comparing harvestmen numbers on the day before spine removal versus the day after spine removal,  $W=0$ , two-tailed  $P=0.016$ ,  $N=7$ ). Over the same time interval, harvestmen numbers always increased on the unshaved control trees, or in the case of Y0a, the unshaved portion of the trunk ( $W=0$ , two-tailed  $P=0.06$ ,  $N=5$ ). At four of the seven sites, the number of animals roosting on the shaved trees (or shaved portion of the trunk) quickly dropped to

zero or nearly zero. At the remaining three trees, harvestmen continued to use the shaved trees, albeit in reduced numbers. Two of the trees in the second category had no intact spiny palms nearby. Thus, spine removal appeared to have a weaker effect on roost settlement when the distance to the nearest intact spiny palm was greater.

## Discussion

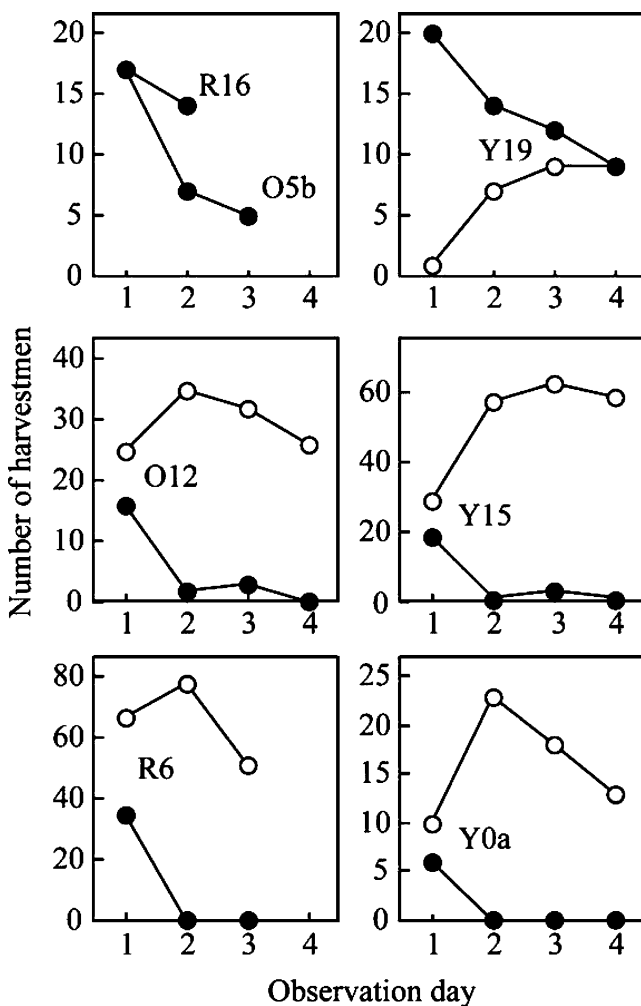
Taken together, our field experiments show that aggregation formation in this species of harvestmen is likely mediated by a chemical that the animals deposit directly on the roosting sites. Such a chemical can be viewed as an external form of social memory that fosters long-term (multi-generational) persistence of aggregation sites without the requirement of individual site fidelity (or any form of learning). Our results further suggest that this mechanism of aggregation formation leads to some degree of “cultural inertia” (Boyd and Richerson 1985), but does not completely override individual resource assessment.

### Evidence for a site-labeling chemical

When communal site use is traditional, the mode of social transmission will likely affect the duration of site use. For instance, traditional roosts in the rubyspot damselfly (*Hetaerina americana*) appear to be perpetuated by a combination of individual site preferences and visual conspecific attraction (Grether and Switzer 2000). This mode of transmission corresponds with the relatively short duration (weeks) of communal site maintenance in this species (Switzer and Grether 2000). The much longer persistence of communal sites in the harvestmen that we studied suggests a more stable mode of social transmission, such as site-labeling.

Our approach to testing for site-labeling chemicals was to move and/or replace materials that were potentially labeled and then measure the response of the harvestmen to these changes. This technique is similar to that used by Alcock (1998) to investigate the mechanisms of communal roost formation in the bee *Idiomelissodes duplocincta*. Because of the destructive nature of these experiments, the sample sizes are small, but taken together, the results support a role for a site-labeling chemical.

More specifically, our results are consistent with a model of roost formation in which individual harvestmen follow a chemical gradient that is weak within the leaf litter and strong within the particular regions of the palms where aggregations routinely form. Consistent with this model, we observed the strongest and most consistent behavioral response in the frond replacement experiment (Fig. 1). Conversely, replacement of leaf litter within a limited radius



**Fig. 3** Effects of spine removal on harvestmen recruitment. *Filled symbols* represent trees that were shaved between day 1 and day 2; *unfilled symbols* represent trees (or parts of trees) that were not shaved. Site names are given in the respective panels. Note that all trees were shaved at sites R16 and O5b (top left panel), and only a portion of one tree was shaved at site Y0a (bottom right). These two panels represent the extremes with respect to the distance that the harvestmen had to travel to reach a site with intact spines

surrounding the base of the tree would be expected to only partially disrupt aggregation formation, as we observed (Fig. 2).

Whereas our sample size of translocated trees was too low to draw firm conclusions, the results of this experiment complement the frond and leaf litter results. The lack of recruitment to the control tree in 2003 indicates that cues specific to individual trees, such as site-labeling chemicals, are important for roost site recruitment. This was also suggested by the eventual return of harvestmen to one of the translocated trees in 2001 and the continued, albeit highly reduced, use of the translocated tree in 2003. The 2003 version of this experiment also showed that cutting the tree, per se, did not cause the harvestmen to reject it. One further piece of supporting evidence is that we frequently observed harvestmen rubbing the sides and posterior end of their carapace against palm fronds at the aggregation sites, a possible scent-marking behavior.

#### Resource assessment versus tradition

Long-term use of traditional sites may lead to continued use of suboptimal sites, such as spawning sites maintained at degraded coral heads by bluehead wrasse (Warner 1990). The exclusive use of spiny palms suggests that the harvestmen benefit from some characteristic(s) common to these trees. Simple safety in numbers (dilution) could be achieved almost anywhere. Spines are the most obvious feature that could protect harvestmen from predators. Two of the three predatory attacks that we observed were by arthropods (scorpion and paraponerine ant) that could easily navigate through the spiny trunk. The only vertebrate predation we observed was by an anoline lizard (*Norops lemurinus*) that caught and ate a harvestman on a spineless frond.

Based on the assumption that spines are the key feature of spiny palms that make them suitable as roosting sites, we removed spines from selected roosting sites and recorded the responses of the harvestmen. We found that the harvestmen continued roosting in shaved palms (in reduced numbers) if there were no intact spiny palms nearby. However, recruitment usually dropped to zero or nearly zero when intact spiny palms were nearby (Fig. 3). Thus, damaged trees were more likely to be rejected if the costs of relocating to a nearby aggregation were minimal. The two palms shaved in 2001 were not used as roosting sites in 2003 (although the spines had regrown), which indicates that degraded sites are eventually abandoned even in the absence of nearby intact sites. These results are consistent with the hypothesis that roost site selection in this species involves a combination of conspecific cueing and resource assessment. If roosts were selected based on resource assessment alone, degraded sites should have been abandoned immediately, regardless of the proximity of intact

sites. Conversely, in the absence of resource assessment, degraded sites should continue to be used regardless of the distance to intact sites.

#### Evolutionary scenarios

The low site fidelity of individual harvestmen begs the question of how a communal roosting mechanism based on site-labeling could have evolved in this species. The basic challenge is to determine how individuals could benefit from producing a chemical that fosters the formation of an aggregation that they might not join. Several possible evolutionary scenarios are consistent with the available data. First, the marking scent may have evolved as an aggregation pheromone used by early-arriving harvestmen to attract other individuals during the same roosting period. To explain our results, such an aggregation pheromone would have to persist long enough to seed aggregation formation on the following day. Second, 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 the selection on individual site fidelity (owing to the relative ease of locating heavily-scented aggregation sites). Third, the marking scent 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. Finally, the marking scent may be a pheromone that evolved in some other context (e.g., mate attraction) with the right properties to also serve as an aggregation cue. We offer this not as an exhaustive list of possible evolutionary scenarios but instead to illustrate that there are a number of ways that scent-mark-based aggregation behavior could arise in a species with low individual site fidelity.

#### Some possible functions of harvestman roosting aggregations

Our informal observations are consistent with the idea that *Prionostemma* day roost aggregations provide anti-predation benefits. When we reached into an aggregation too quickly, the harvestmen bobbed up and down by rapidly contracting and extending their legs. During encounters with actual predators, bobbing quickly spread through the aggregation, and harvestmen closest to the site of the attack moved away. Bobbing clearly makes capturing the harvestmen more difficult and might also serve as an alarm signal, a predator deterrent signal, or a predator confusion display. Harvestmen in an aggregation also presumably benefit from dilution (Treisman 1975), and there is the potential in this system for selfish herding behavior (Hamilton 1971; Vine 1971).

Harvestmen aggregations might also serve as sexual rendezvous sites. In some cavernicolous species of harvestmen, mating occurs at day roosts, and eggs are deposited on the cave walls and guarded by the parents (Gnaspini 1995, 1996; Machado and Oliveira 1998; Machado 2002). We observed copulations at the *Prionostemma* aggregation sites, but did not see egg-laying or parental care during our study. As noted above, the site-labeling scent might have evolved as a sexual attractant pheromone. In this regard, it would be informative to determine whether production of the scent is sex-limited and/or varies with an individual's reproductive state.

For a more complete treatment of the theoretically possible functions of harvestmen roosting aggregations, see Grether and Donaldson (2006).

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