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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.

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 cm^2 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