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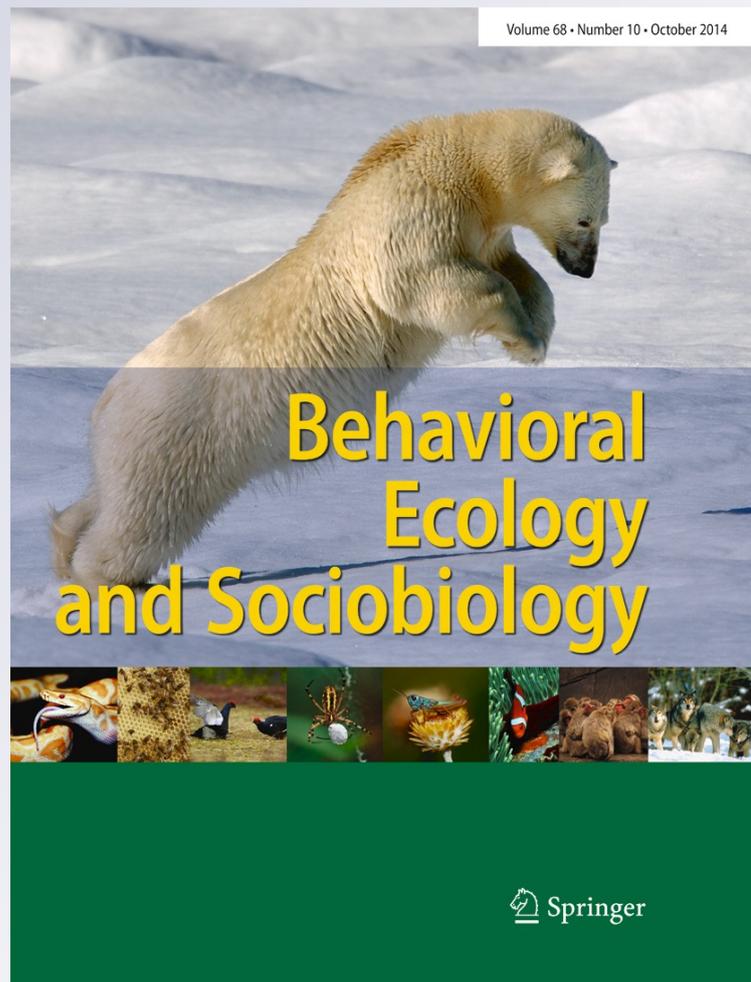
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Communal roosting sites are potential ecological traps: experimental evidence in a Neotropical harvestman

Gregory F. Grether · Abrahm Levi · Carmen Antaky · Debra M. Shier

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Abstract Situations in which animals preferentially settle in low-quality habitat are referred to as ecological traps, and species that aggregate in response to conspecific cues, such as scent marks, that persist after the animals leave the area may be especially vulnerable. We tested this hypothesis on harvestmen (*Prionostemma* sp.) that roost communally in the rainforest understory. Based on evidence that these animals preferentially settle in sites marked with conspecific scent, we predicted that established aggregation sites would continue to attract new recruits even if the animals roosting there perished. To test this prediction, we simulated intense predation by repeatedly removing all individuals from 10 established roosts, and indeed, these sites continued to attract new harvestmen. A more likely reason for an established roost to become unsuitable is a loss of overstory canopy cover caused by treefalls. To investigate this scenario, without felling trees, we established 16 new communal roosts by translocating harvestmen into previously unused sites. Half the release sites were located in intact forest, and half were located in treefall gaps, but canopy cover had no significant effect on the recruitment rate. These results support the inference that communal roost sites are potential ecological traps for species that aggregate in response to conspecific scent.

Keywords Conspecific attraction · Ecological trap · Habitat selection · Traditional site use · Translocation experiment

Introduction

The proximate mechanisms of habitat selection are relevant for predicting how animals will respond to habitat degradation (Farrell et al. 2012; Mihoub et al. 2011; Robertson et al. 2013; Van Dyck 2012). Animals generally do not assess habitat suitability directly but instead rely on indirect cues, which presumably correlated with habitat suitability in the evolutionary past (Robertson and Hutto 2006; Schlaepfer et al. 2002). When the environment changes in ways that decouple such cues from habitat suitability, animals may respond maladaptively and preferentially settle in low-quality habitat. This situation, which likely is becoming more common under human-induced rapid environmental change (Robertson et al. 2013; Sih 2013), is referred to as an ecological trap (Gates and Gysel 1978; Schlaepfer et al. 2002; Battin 2004; Pärt et al. 2007; Robertson and Hutto 2006). In theory, ecological traps can cause rapid population extinction (Delibes et al. 2001; Fletcher et al. 2012).

Communal roosting is a taxonomically widespread behavior in which animals regularly congregate at specific locations (Bijleveld et al. 2010). Communal roosts are often traditional in that they are used primarily because they were used by conspecifics in the past, not because they are necessarily more suitable than alternative sites (reviewed in Grether and Donaldson 2007). Some avian communal roosts have been used for well over a century (Bijleveld et al. 2010). Species that form communal roosts may be especially prone to ecological traps, for two reasons. First, while large roosting aggregations may provide protection against certain types of predators, they may also put large numbers of animals at risk simultaneously if a local roosting site becomes unsuitable.

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Second, traditional roosts may continue to be used long after they become unsuitable (Rahaingodrahety et al. 2008; Teng et al. 2012). Protection of roosting habitat is recognized as a conservation priority for many species (Aguirre et al. 2003; Alonso-Mejia et al. 1997; Barclay and Brigham 2001; Brooke et al. 2000; Cardiff et al. 2012; Curtis and Machado 2007; Dellasala et al. 1998; Dennis 2004; Donazar et al. 2002; Fleming et al. 2013; Harms and Eberhard 2003; Kessler et al. 2013; Lambertucci et al. 2008; McGeoch and Samways 1991; Rahaingodrahety et al. 2008; Smith and Racey 2005), but when traditional roosting sites are degraded, the availability of alternative sites is only relevant if the animals will use them (Donazar and Feijoo 2002; Rahaingodrahety et al. 2008). In general, when animals base settlement decisions on the locations of conspecifics, this can lead to the use of suboptimal habitat (Betts et al. 2008; Giraldeau et al. 2002; Miller et al. 2013).

The mechanisms through which roosting aggregations are maintained have a bearing on whether they are likely to become ecological traps. Communal roosts maintained by attraction to persistent conspecific cues, such as scent marks or habitat modifications, may be more likely to become ecological traps than those maintained by the immediate sight, smell, or sound of conspecifics because the presence of conspecifics at least indicates that a site is not lethally unsuitable. To our knowledge, this has not been pointed out previously.

To test the hypothesis that communal roosts are potential ecological traps, we carried out two replicated field experiments on communal roosting harvestmen (Opiliones) at a lowland rainforest site in Nicaragua. We studied a population of *Prionostemma* (not described below the genus level) in which individuals forage solitarily at night and roost in aggregations during the day (Grether and Donaldson 2007), as seen in other species in this genus (Coddington et al. 1990; Wade et al. 2011). Roosting aggregations usually form on the trunks or fronds of spiny palm trees (*Bactris*, *Astrocaryum*) in the forest understory. Spiny palms that are used by the harvestmen do not appear to differ from those that are not used, either in the characteristics of the palms themselves or in microclimate (Grether and Donaldson 2007; Teng et al. 2012). Nevertheless, some spiny palms have been used for over 10 years, while others of the same species have remained unused (Teng et al. 2012). While the locations of the communal roosts are very stable over time, individual harvestmen are not site faithful (Grether and Donaldson 2007). The reason the roosting aggregations form repeatedly in the same locations appears to be that the harvestmen preferentially settle in sites marked with conspecific scent (Donaldson and Grether 2007; Teng et al. 2012).

This mechanism of roost formation, i.e., attraction to conspecific scent, could lead to communal roosts being used long after they became unsuitable, and there is some evidence that this is the case. Harvestmen are very susceptible to desiccation

(Santos 2007), and spiny palms themselves offer little protection from the sun. Roost sites on the edges of clearings or in treefall gaps experience higher daytime air temperatures than do roost sites with intact overstory forest canopies. Spiny palms used as aggregation sites do not differ in forest canopy cover from a random sample of unused spiny palms (Grether and Donaldson 2007), but among used sites, the size of the aggregations correlates positively with canopy cover and negatively with mean air temperature (Teng et al. 2012), which is consistent with the hypothesis that sites with intact overstory canopies are more suitable. *Prionostemma* enter roost sites before dawn and may have no way of sensing whether conditions at a site will be survivable later in the day, but these animals are quite capable of moving during daylight hours (Smith et al. 2012), and would probably leave an exposed roost before succumbing to desiccation. Indeed, on sunny days, harvestmen numbers were observed to decrease sharply between morning and late afternoon at roost sites on the edge of a clearing but not at sites with intact forest canopies (Grether and Donaldson 2007). Leaving an aggregation and traversing the forest floor in search of new roost sites during daylight hours is risky. The spines of the spiny palms provide protection from diurnal predators such as lizards, and the aggregations themselves likely reduce per capita predation risk through dilution and active group defenses (Grether and Donaldson 2007). Thus, roosting in exposed sites and being forced to leave during the day would clearly have negative fitness consequences.

Because conspecific scent appears to be the primary aggregation cue, we predicted that established aggregation sites would continue to attract new recruits even if the animals roosting there consistently left during the day or perished. To test this prediction, we simulated intense predation by removing all of the harvestmen repeatedly from some roosting sites and comparing the size of the aggregations on subsequent days to control sites where harvestmen were counted but not otherwise disturbed. Because removing the harvestmen also removed their ability to deposit chemical attractants, we expected harvestmen numbers to decline gradually at removal sites. No harvestmen were actually killed in this experiment, and it is possible that real predation events leave behind cues, such as body parts or defensive chemical residues, that warn off conspecifics. Nevertheless, this experiment at least served to establish whether aggregations would continue to form at sites where the harvestmen were forced to leave prematurely.

Perhaps the most likely reason for a *Prionostemma* sp. roost site to become unsuitable is a loss of overstory canopy cover caused by natural treefalls or logging (see above). To test the effect of treefalls without felling trees, we took advantage of natural treefall gaps. Previous work showed that new communal roosts can be established by translocating harvestmen to new sites (Teng et al. 2012). We therefore carried out a

translocation experiment in which a random half of harvestmen captured at removal sites was moved to previously unused spiny palms in treefall gaps (gap sites) and the other half was moved to previously unused spiny palms with intact overstory canopies (non-gap sites). Based on the hypothesis that the harvestmen find new aggregation sites by detecting conspecific scent, we predicted that recruitment would not differ between gap and non-gap sites in the short term, even though gaps sites are less suitable.

Methods

Study area and species

We conducted this study at Refugio Bartola, a lowland tropical rainforest site in southeastern Nicaragua (10.973°N, 84.339°W; for additional site information, see Cody 2000) near the beginning of the dry season (February 2–20, 2013). Approximately 69 mm of rain fell during the study period. At least two undescribed species of *Prionostemma* (Eupnoi: Sclerosomatidae: Gagrellinae) harvestmen occur at Refugio Bartola, but only the species that we refer to here regularly roosts in spiny palms.

Site selection

Spiny palms tend to grow in clusters and the harvestmen are often found in multiple trees within a cluster. We considered all spiny palms with trunks within 1 m of each other to belong to the same site. *Bactris* sp. are the most abundant spiny palms at Refugio Bartola and only *Bactris* sites were used in our experiments. For the removal experiment, we found 18 communal roosting sites with at least 20 harvestmen present and randomly assigned them to serve as removal ($N=10$) or control sites ($N=8$). Sites in the different treatments were interspersed (Supp. Fig. 1). The mean (\pm SD) minimum within-treatment distance between sites was 164.9 ± 100.6 m ($N=13$ unique minimum distances) while the mean minimum between-treatment distance was 80.6 ± 42.9 m ($N=13$). Removal sites also served as source sites for the translocation experiment. Initially, removal sites did not differ significantly from control sites in aggregation size (Mann-Whitney test $U=47$, $N_1=8$, $N_2=10$, $P=0.57$). For the translocation experiment, we found 20 *Bactris* sites that were not initially being used by the harvestmen. Sites located in treefall gaps served as “gap” release sites ($N=8$), and sites located in intact forest served either as “non-gap” release sites ($N=8$) or control sites where no harvestmen were released ($N=4$). All 20 sites were checked on two consecutive days to verify that they were not being used by harvestmen prior to the experiment.

Removal experiment

We captured and removed all of the harvestmen from 10 roost sites and counted the number present on the following day. This procedure was repeated on at least four consecutive days and up to six consecutive days if the site continued to attract harvestmen. Harvestmen were captured by hand and held temporarily in a wire and mesh cage (Bioquip Products). Harvestmen that were not initially within reach were chased down with a wooden pole. On average, 98.9 harvestmen were removed per site (range, 37–224). For logistical reasons, the time of day at which removals were conducted varied considerably, from 0713 to 1715. To estimate the length of time harvestmen were on the roost prior to removal, we assumed that they entered the roost at 0600. On the last day of the experiment, a final visual count was made at all 10 removal sites. Before and during the experiment, harvestmen were counted, but not captured, at the eight control communal roost sites.

We expected aggregations to decrease in size at removal sites because removing the harvestmen prevents them from depositing additional chemical scent. If so, the timing of the removal ought to affect the number of harvestmen attracted on the next day. To test for this, we constructed a random-effects negative binomial regression model with the number of harvestmen present on the day after removal as the dependent variable (N_{i+1} , where i refers to the day in the series of removals), the length of time in hours that the harvestmen were on the roost prior to removal (*time on roost*) and the number of harvestmen removed (N_i) as continuous predictor variables, and a categorical variable representing the day in the series of removals (*treatment day*).

Translocation experiment

We translocated harvestmen to 16 previously unused sites, half of which were in treefall gaps. Gap and non-gap release sites were paired such that sites within a pair received approximately equal numbers of harvestmen from the same source sites on the same days. Harvestmen were transported to the release sites in a polyester/nylon netting cage (Bioquip Products, Rancho Dominguez, CA, USA), marked on the dorsal surface of the abdomen with small dots of paint (Marvy Decocolor, Uchida of America, Torrance, CA), and released, one at a time, on the trunk of a spiny palm. The paint marks enabled us to distinguish returning harvestmen from new recruits; the color combinations used identified both the site where a harvestman was captured and the site where it was released. On the day after the initial translocation, we counted the harvestmen present and then released additional harvestmen as a supplementary translocation (to increase the likelihood that the translocations would result in the establishment of new communal roosting sites). On the day after the

supplementary translocation, we counted the harvestmen present in the morning (0700–1000), midday (1000–1400), and afternoon (1400–1800). A final count was made near the end of the study, 5–14 days after the initial translocation. To verify that the translocation affected recruitment, we also monitored four non-gap control sites. Each control site was checked for harvestmen on 2–3 days during the experiment. On average, we released 34.6 harvestmen per release site in the initial translocation (range, 16–71) and 22.3 in the supplementary translocation (range, 18–31). In total, 912 harvestmen were translocated. There were no significant differences between gap and non-gap sites in the number of harvestmen released during the initial translocation (Wilcoxon signed-rank test $T=8$, $N=8$, $P=0.19$) or the supplementary translocation ($T=14$, $N=8$, 2 ties, $P=0.72$).

Site monitoring

To characterize the consistency of roost site use over different time scales, we made repeated visual counts of the number of harvestmen present at the same sites after intervals ranging from hours to years. At control sites in the removal experiment, we took counts in the morning (0700–1000), midday (1000–1400), and afternoon (1400–1800) on the first day and once per day on two subsequent days spaced 1–10 days apart. We also revisited sites where communal roosts had been recorded in previous visits to Refugio Bartola (April–May 2001, 2003; January–February 2011) and counted the harvestmen on 2 or 3 days at intervals of one or more days (interval range, 1–15 days). Repeat counts were averaged for between-year analyses.

Habitat and microclimate measurements

The only factor known to predict harvestman presence is the number of spiny palms; sites with more spiny palms are more likely to contain harvestmen (Grether and Donaldson 2007). Among sites used by the harvestmen, however, several factors have been found to correlate with aggregation size: crown height, spine density, canopy cover, and air temperature (Teng et al. 2012). Crown height was measured with a measuring tape and pole, and trunk diameter was measured with a ruler, on all of the spiny palms at a site. Spine density was measured by placing a 4-cm² wire quadrat on the trunk of the palms and counting all spines originating within the quadrat. The quadrat was placed at three different heights above the ground (0.8, 1.15, and 1.55 m) in the four cardinal directions around the trunk. If a site had more than five spiny palms, we measured spine density on a random half of them. Canopy cover was measured with a concave spherical densiometer (Forestry Suppliers Inc, Jackson, MS, USA). The same observer made all measurements of a particular type. Only spiny palms with crown heights ≥ 2 m were counted or measured because the

harvestmen are rarely found on smaller trees (Grether and Donaldson 2007). Site averages were used in the analysis.

We placed data loggers (EL-USB-2 Lascar Electronics Inc., Erie PA) at all of the release sites and the monitored roost sites (i.e., control sites in the removal experiment) to obtain temperature and humidity readings every 5 min for at least one 24-h cycle (mean \pm SD=2.8 \pm 1.7, range 1–6, $N=21$). From the data logger files, we obtained the temperature and humidity ranges for each site. Due to a data logger launching error, however, we failed to obtain temperature and humidity records for one of the gap release sites and two of the monitored roost sites. We did not have enough data loggers to place them at all of the sites simultaneously, but paired sites in the translocation experiment were monitored on the same days.

Statistics

Stata 12.1 (StataCorp, College Station, TX, USA) was used for most of the computations. Harvestmen counts in the removal and translocation experiments were analyzed using count-based negative binomial regression models (xtnbreg), with site entered as a random-effects panel variable to account for the repeated measures design of the experiments. Negative binomial regression was used because the data were overdispersed relative to a Poisson process. At sites where more than four removals were carried out, only data from the first four removals were included in the analysis. Exact P values for Mann-Whitney tests and for Spearman rank correlations with $N < 17$ were calculated by permutation. Exact P values for Wilcoxon signed-rank tests were obtained from Daniel (1990). All reported P values are two-tailed.

Results

Removal experiment

Harvestmen aggregations continued to form at removal sites, and all but one of the sites were still attracting harvestmen up to the end of the study period (last count mean \pm SD=5.9 \pm 5.4, range 0–17, $N=10$). Over the course of the experiment, at least 521 harvestmen roosted in these sites after the first removal, which is nearly as many as were present at the time of the first removal ($N=527$). The size of the aggregations tended to decrease with each successive removal, while at control sites, the aggregations remained relatively stable (Fig. 1), resulting in a significant interaction between time and treatment (random-effects negative binomial regression, chi-sq.=33.53, $df=2$, $P < 0.0001$). Compared with the initial aggregation size, the mean \pm SD aggregation size at removal sites declined to 45.5 \pm 38.7 % by the second day (range 20.0–151.6 %; $N=10$), to 26.8 \pm 24.7 % by the third day (range 0.0–80.6 %; $N=10$), and to 15.9 \pm 11.2 % by the fourth day

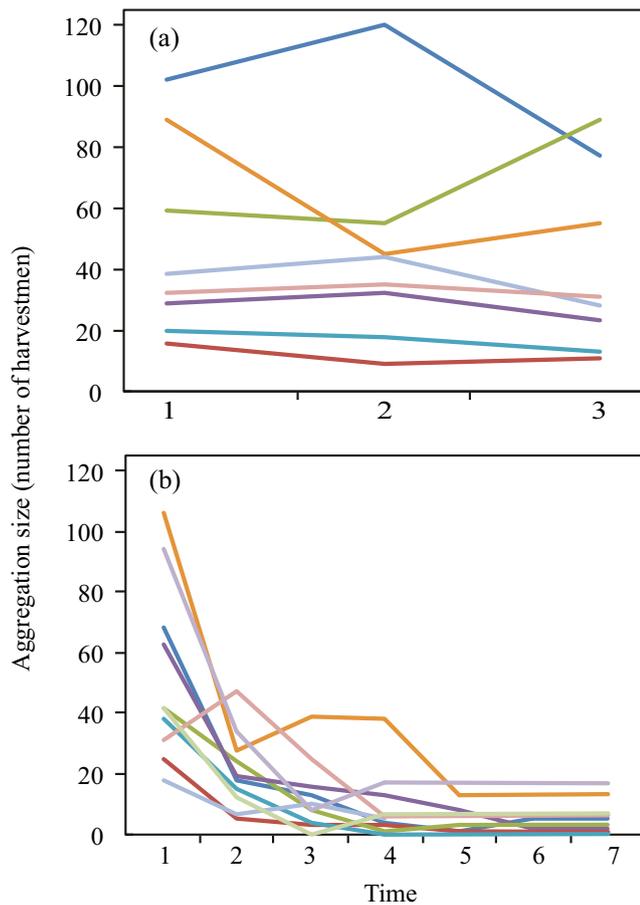


Fig. 1 Effects of major disturbance on harvestmen recruitment. At control sites (a), harvestmen were counted but not captured on 3 days during the experiment at irregular intervals (1–4 days between times 1 and 2; 1–10 days between times 2 and 3). At removal sites (b), all harvestmen were removed on 4–6 consecutive days and a final count was made at the end of the study (time 7). The range of start dates (time 1) was identical for control and removal sites (5–15 February 2013). Each colored line represents a different roosting site. See text for statistical results

(range 0.0–35.8 %; $N=10$). Significant decreases in aggregation size occurred at removal sites between days 1 and 2 ($z=-5.01$; $P<0.001$) and between days 2 and 3 ($z=-2.45$, $P=0.01$) but not between days 3 and 4 ($z=-1.14$, $P=0.26$). At control sites, there was no significant change in aggregation size between days 1 and 2 ($z=-0.65$, $P=0.52$) or between days 2 and 3 ($z=-0.63$, $P=0.53$).

At removal sites, the length of time the harvestmen were on the roost prior to removal was the only significant predictor of the aggregation size on the next day N_{i+1} (full model Log likelihood = -100.37, Wald chi-sq. = 26.84; $P<0.0001$; time on roost coefficient \pm SE = 1.145 \pm 0.056, $z=2.77$, $P=0.006$; N_i coefficient \pm SE = 1.012 \pm 0.007, $z=1.79$, $P=0.07$; treatment day chi-sq. = 1.57, $df=2$, $P=0.45$). The magnitude of the time on roost coefficient indicates that for each hour the harvestmen remained on the roost, the aggregation on the next day was 14.5 % larger. We also examined models with one or more

variables removed. The treatment day term was significant if and only if N_i was removed from the model (with both time on roost and N_i removed, treatment day chi-sq. = 14.99, $df=2$, $P=0.0006$). Thus, it appears that the length of time the harvestmen were on the roost before being removed was the main determinant of the aggregation size on the next day, but the number of harvestmen removed also had an influence, and together, these factors accounted for the decrease in aggregation size over time caused by the removal treatment.

Habitat characteristics and microclimate

By design, gap and non-gap sites in the translocation experiment differed significantly in canopy cover (Mann-Whitney test, $U=96$, $N_1=8$, $N_2=12$, $P=0.00002$) but not in any other habitat characteristics (number of spiny palms $U=50$, $N_1=8$, $N_2=12$, $P=0.91$; mean crown height $U=51$, $N_1=8$, $N_2=12$, $P=0.85$; mean trunk diameter $U=53$, $N_1=8$, $N_2=12$, $P=0.73$; mean spine density $U=48$, $N_1=8$, $N_2=12$, $P=1$). The mean \pm SD canopy cover at gap sites was 67.27 \pm 10.16 versus 87.25 \pm 3.09 % at non-gap sites, for an average difference between gap and non-gap sites of 20.0 %.

Maximum air temperature correlated negatively with canopy cover across all sites for which we obtained 24-h temperature and humidity readings (Spearman rank correlation $r_s=-0.53$, $N=21$, $P=0.014$). All gap release sites reached higher air temperatures than any non-gap release sites (Mann-Whitney test $U=56$, $N_1=7$, $N_2=8$, $P=0.0003$; for representative examples, see Fig. 2). The mean \pm SD maximum air temperature at gap sites was 30.9 \pm 1.3 $^{\circ}$ C (range 29.5–32.5 $^{\circ}$ C, $N=7$) versus 28.1 \pm 0.7 $^{\circ}$ C (range 27–29 $^{\circ}$ C, $N=8$) at non-gap sites. On an average day, the air temperature first peaked at 12:05 \pm 1:27 h (mean \pm SD; range 08:41–15:21, $N=21$) and last peaked at 13:23 \pm 1:56 h (range 09:55–16:39; $N=21$). Minimum humidity was not significantly correlated with canopy cover ($r_s=0.16$, $N=21$, $P=0.49$), but sites that reached higher temperatures also reached lower humidities ($r_s=-0.71$, $N=21$, $P=0.0003$), and gap sites tended to reach lower humidities than non-gap sites ($U=12$, $N_1=7$, $N_2=8$, $P=0.07$; for representative examples, see Fig. 2). The mean \pm SD minimum relative humidity at gap sites was 67.2 \pm 8.6 % (range 58–83 %, $N=7$) versus 73.8 \pm 3.8 % at non-gap sites (range 67.5–78.5 %, $N=8$).

Translocation experiment

The experimental translocations were successful in attracting harvestmen to previously unused spiny palms (Fig. 3). Harvestmen were found in 14 of 16 release sites on the first day post-release and in all release sites by the second day post-release. By comparison, no harvestmen were found in any of the release sites on 2 days prior to the translocation or in the four non-gap control sites for the duration of the experiment.

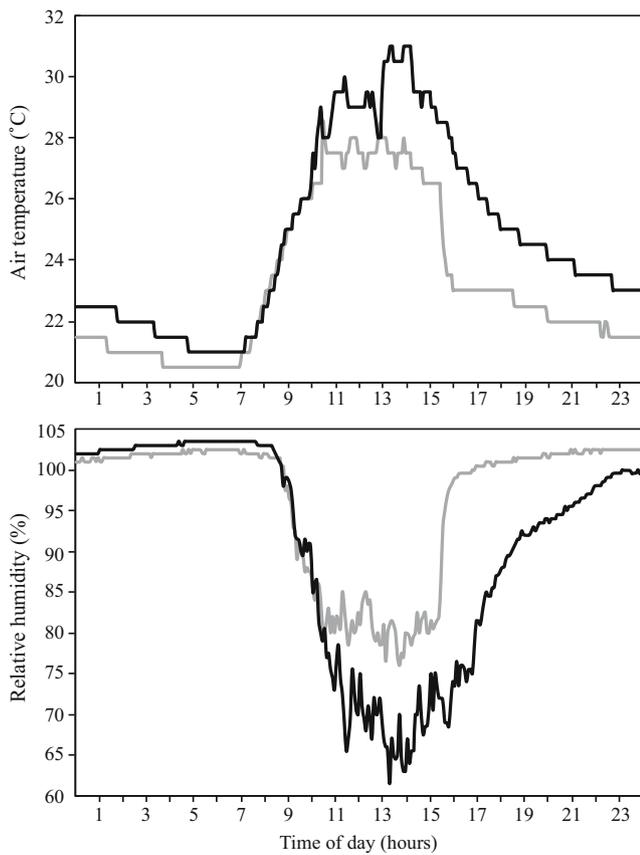


Fig. 2 Representative temperature and humidity profiles for gap and non-gap release sites in the translocation experiment. In the gap site profile (black line), air temperature peaks at 31.0 °C, which is close to the gap site mean maximum temperature of 30.9 °C. In the non-gap site profile (grey line), air temperature peaks at 28.5 °C, which is close to the non-gap site mean maximum temperature of 28.1 °C. Temperature and humidity are plotted every 5 min for one 24-h period per site starting at midnight. These profiles were chosen for the figure because their peak air temperatures came closest to the mean peak temperatures recorded at gap and non-gap release sites. These are not matched sites in the experiment and the profiles were recorded on different days. A statistical comparison of the mean maximum temperatures and minimum humidities is presented in the text

Restricting the analysis to unmarked harvestmen (i.e., only new recruits), significantly, more were found at release sites than at control sites (Mann-Whitney test $U=56$, $N_1=4$, $N_2=16$, $P=0.005$).

Most release sites only attracted small numbers of harvestmen, but there were two noteworthy exceptions. One gap site attracted 15 harvestmen (12 unmarked) on the first day, 32 harvestmen (31 unmarked) on the second day, and 27 harvestmen (all unmarked) on the last (eighth) day. One non-gap site attracted 22 on the first day, 16 on the second day, and 17 on the last (fifth) day (all unmarked). Overall, at least 103 different individuals (81 % unmarked) were found at release sites.

Despite the differences between gap and non-gap release sites in microclimate, there was no significant difference in the number of harvestmen recruited (random-effects negative

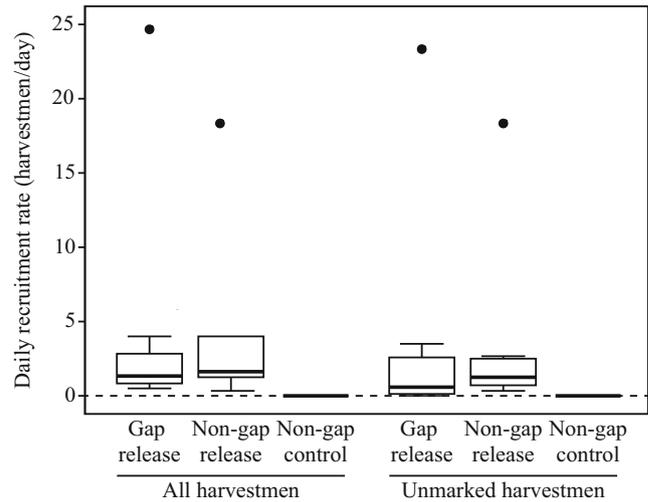


Fig. 3 Translocation experiment results. Daily recruitment rate (harvestmen per day) at gap release sites, non-gap release sites, and non-gap control sites. Box plots depict the median (thick horizontal line), interquartile range (box), upper and lower adjacent values (error bars), and outside values (points). $N=8$ release sites of each type and $N=4$ non-gap control sites. See text for statistical comparison

binomial regression, $z=0.13$, $P=0.90$). On the day after the initial translocation, we found 4.2 ± 5.0 harvestmen (mean \pm SD; range 0–15, $N=8$) at gap release sites and 4.5 ± 7.2 harvestmen (range 0–22, $N=8$) at non-gap release sites. On the day after the supplementary translocation, we found 4.9 ± 11.0 harvestmen (range 0–32) at gap sites and 4.4 ± 5.3 (range 0–16) at non-gap sites. At the last count, 8.9 ± 3.4 days (range 5–14, $N=16$) after the initial translocation, gap sites had 4.4 ± 9.3 harvestmen (range 0–27) and non-gap sites had 3.2 ± 5.9 harvestmen (range 0–17). There was no significant change in aggregation size over time (chi-sq.=2.70, $df=2$, $P=0.26$) and no significant time by treatment interaction (chi-sq.=1.29, $df=2$, $P=0.5245$), although it should be noted that the interval between the second and final roost census was variable (3–11 days) and relatively short.

Abandoned roost sites

In our resurvey of 17 roost sites that were last checked in February 2011, all but two of the sites were still being used by the study species in February 2013. The two exceptions are the only sites that no longer had intact overstory canopies—a pattern that is unlikely to arise by chance (Fisher's exact test, $P=0.007$). These are the only sites that the harvestmen are known to have abandoned since site monitoring first began in April 2001. At one of the abandoned sites (R17), a large upper canopy tree fell sometime after the 2011 study period, leaving the spiny palms exposed to direct sunlight at midday (G. Grether pers. obs). The other abandoned site (Y0a) is on the west-facing edge of a forest clearing, which has existed since at least 2001, and receives direct sunlight only in the

afternoon. Grether and Donaldson (2007) observed that the aggregation at this site decreased in size between the morning and afternoon counts on sunny days (e.g., from 101 to 31 animals) in April–May 2003. Small numbers of harvestmen were still roosting at this site in April–May 2007 (G.F. Grether pers. obs.) and in January–February 2011 (Teng et al. 2012), but not in February 2013.

Temporal repeatability of aggregation size

The visual counts taken at established roost sites (some of which also served as controls in the removal experiment) showed that the repeatability of aggregation size was high over short-time scales and eroded gradually over time, as expected based on the hypothesized mechanism of roost site formation (i.e., chemically mediated conspecific attraction). Aggregation size varied even within days, but not in a consistent direction in relation to the time of day (Fig. 4; Skillings-Mack test comparing morning, midday, and afternoon counts, $SM=1.562$, $N=8$, $P=0.45$). Nevertheless, repeat counts taken at different times on the same days were very strongly correlated across sites (Spearman rank correlations: morning vs. midday $r_s=0.96$, $P=0.001$; midday vs. afternoon $r_s=0.99$, $P=0.0001$; morning vs. afternoon $r_s=0.97$, $P=0.0005$; all $N=8$). The between-days analysis showed that, on a time scale of 1–15 days (mean \pm SD = 5.0 ± 4.4 days), the correlation between repeat counts was highly significant but smaller in magnitude than the within-day correlations ($r_s=0.81$, $N=23$,

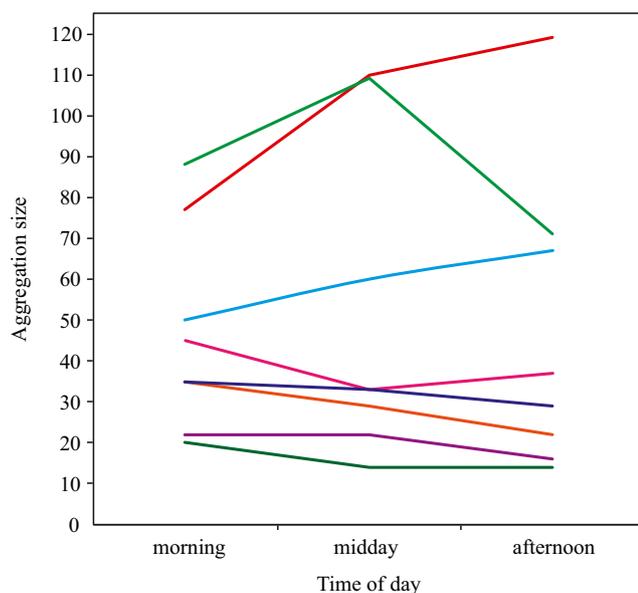


Fig. 4 Within-day variation in aggregation size. The larger changes exceed what could plausibly be attributed to measurement error, which implies that harvestmen come and go throughout the day. Each colored line represents a control site in the removal experiment on a single day. Morning counts were made between 0700 and 1000, midday counts were made between 1000 and 1400, and afternoon counts were made between 1400 and 1800

$P=0.000002$), and the longer the time interval between counts, the greater the change in harvestman numbers ($r_s=0.46$, $N=23$, $P=0.028$). In the between-years analysis, the correlation between repeat counts was marginally significant over an interval of 2 years (2013 vs. 2011 $r_s=0.48$, $N=17$, $P=0.05$) but not over an interval of 10 years (2013 vs. 2003 $r_s=0.17$, $N=13$, $P=0.58$). Thus, the overall pattern is that the correlation between repeated site counts declined over time and became statistically indistinguishable from zero after about 2 years (Fig. 5).

Discussion

We carried out two replicated field experiments to test the hypothesis that communal roosting behavior makes harvestmen susceptible to ecological traps. Our removal experiment demonstrated that the tradition of roosting at a particular site would continue for some time even if all of the individuals roosting there perished (no animals were actually killed). Our translocation experiment showed that the rate of recruitment to new aggregation sites is not affected by whether the sites have intact overstory canopies (Fig. 3), which is thought to be a major determinant of habitat suitability (see “Introduction”). An earlier study showed that harvestmen will continue using spiny palms from which the protective spines have been removed (Donaldson and Grether 2007). In combination, the results of these experiments leave little doubt that established aggregation sites would continue to be used for some time even after they became significantly degraded. To our

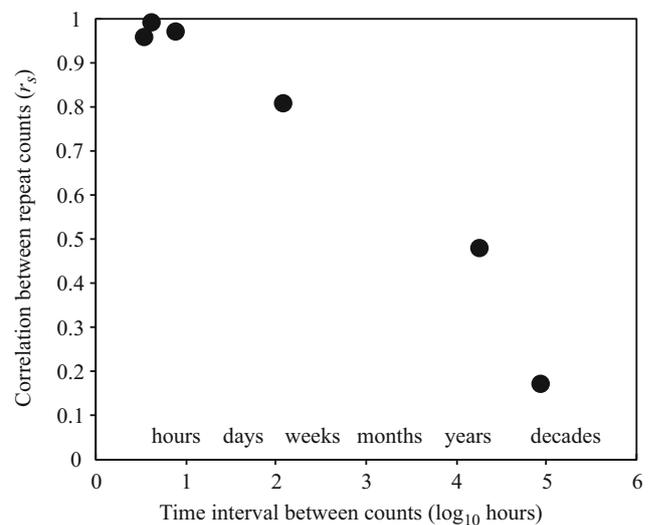


Fig. 5 Repeatability of aggregation size over multiple time scales. Each point represents the Spearman rank correlation between harvestmen counts taken at two different times at the same roost sites. The time interval between counts is shown on the horizontal axis (\log_{10} scale). See text for further details and statistical tests

knowledge, this is the first experimental evidence that roosting sites are potential ecological traps.

Unlike ecological traps caused by human-made attractants, such as artificial sources of light (Horváth et al. 2009), which may persist indefinitely, ecological traps caused by conspecific attraction are not likely to persist for long periods. Nevertheless, even temporary ecological traps may hamper the recovery of endangered species. If established communal roosting sites can become ecological traps, merely protecting alternative roosting habitat might not be an adequate conservation measure. Interventions that prevent existing communal roosts from becoming degraded, or that result in the establishment of new communal roosts, may be required to reduce extinction risk for vulnerable populations. The behavioral mechanisms of roost site selection are relevant for predicting how quickly degraded sites will be abandoned. All else being equal, species that rely on direct visual or auditory detection of conspecifics for roost settlement would be expected to abandon degraded roost sites more quickly than species that settle in response to persistent chemical cues or physical modifications of the habitat. Chemical communication is found across taxa (Wyatt 2010) and is the primary signaling modality in arthropods and mammals (Breithaupt and Thiel 2011; Brown and Macdonald 1985; Carde and Millar 2004; Stoddart 1976; Wyatt 2010). Understanding and exploiting target species chemical signals has been shown to facilitate species recovery (Campbell-Palmer and Rosell 2011). Our results offer a novel mechanism and add to a growing body of research that links olfactory communication to conservation.

Our results make it clear that *Prionostemma* sp. do not abandon degraded roost sites quickly. What is not clear yet is how this affects population growth. The precise fitness consequences of roosting at degraded sites would be difficult to measure because individuals are not bound to specific roost sites and therefore cannot be classified as inhabiting low- or high-quality habitat. As already noted, harvestmen are quite capable of moving during daylight hours (Smith et al. 2012) and would probably leave a roost site before succumbing to heat stress or desiccation. But leaving the roost and moving across the forest floor during the day must increase predation risk (this could be tested experimentally). The existing evidence that overstorey canopy cover affects the suitability of roost sites is that aggregation size correlates negatively with canopy cover among established sites (Teng et al. 2012) and that roost sites in treefall gaps and clearings are eventually abandoned (see Results).

While there was no significant difference in the size of the aggregations at gap and non-gap release sites during our study, we predict that gap sites will be abandoned sooner than non-gap sites, for the following reason. Whether through mortality or dispersal, fewer harvestmen will last through sunny days at gap sites, leading to a reduction in the amount of scent

deposited and a reduction in the size of the next aggregation, in a positive feedback loop, until the sites are abandoned. The removal experiment generated such a feedback loop, as shown by the result that removing harvestmen earlier in the day resulted in a smaller aggregation on the following day.

Only one removal site was abandoned during our study, but the size of the aggregations decreased significantly (Fig. 1). A reduction in aggregation size was expected simply because removing the harvestmen prevents them from depositing additional chemical cues at the roost sites. The removals might also have caused temporary depletion of the local harvestman recruitment pool. While these animals can move up to 0.2 km in a single night, most movement is more localized. In a study on individually marked harvestmen, the maximum daily return of individuals to the site where they were marked ranged from 15 to 26 % per site (Grether and Donaldson 2007). Thus, the decrease in aggregation size at removal sites may have been caused not just by a reduction in the amount of scent deposited but also by a reduction in the local recruitment pool. Roost site disturbances that increase the mortality rate of the harvestmen would be expected to have the same two effects but would not be expected to cause such rapid reductions in aggregation size as wholesale removals. Indeed, it took at least 10 years for harvestmen to abandon a roost site on the edge of a forest clearing even though the aggregations there shrank on sunny afternoons (see “Results”). Some combination of local recruitment pool effects and chemical conspecific attraction may also be responsible for the correlation between repeated site counts eroding over time (Fig. 5).

Another possible explanation for the decline in aggregation size in the removal experiment is that the captured harvestmen left repulsive chemicals at the roost sites. We cannot rule this out, but this mechanism alone would not explain why removing the harvestmen earlier in the day caused a larger reduction in the size of the aggregation on the following day (the reverse would be expected).

Most known examples of ecological traps come from avian studies (reviewed by Battin 2004; Robertson and Hutto 2006; Schlaepfer et al. 2002; Robertson et al. 2013), but arthropods, which often have more specialized sensory capabilities than birds, may be even more prone to making habitat selection errors in the context of human-induced rapid environmental change (e.g., Hedin et al. 2008; Horváth et al. 2009; Horváth et al. 2007; Kriska et al. 2006; Ries and Fagan 2003) and can serve as valuable indicators of disturbance (Uehara-Prado et al. 2009). Harvestmen are among the most abundant arthropods in tropical forests (Wade et al. 2011) and are strongly affected by habitat fragmentation and other anthropogenic disturbances (Bragagnolo et al. 2007). Our results highlight a new mechanism—chemically mediated conspecific attraction—that may cause degraded habitat to become an ecological trap.

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