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Weaver ants shift nest location in response to the selective pressures of habitat disturbance and torrential rain in Sri Lanka

Leonard A. Freed[1] and Dulan R. Vidanapathirana[2]

[1]*Department of Biology, University of Hawaii at Manoa, Honolulu, Hawaii, USA and*
[2]*Herpetological Foundation of Sri Lanka, Wattala, Sri Lanka*

ABSTRACT

Background: Weaver ants in central Sri Lanka endure two monsoon seasons per year and mowing of the understory in coconut palm plantations.

Hypothesis: Mowing of the understory and torrential rain represent selective pressures.

Organisms: Weaver ants (*Oecophylla smaragdina*).

Field sites: Two coconut palm (*Cocos nucifera*) plantations.

Methods: We documented mowing in June as one selective pressure, and torrential rain in October to December as the second selective pressure. One farmer postponed mowing by a month, although he had mowed in June in previous years. We tagged understory plants and trees and counted weaver ant nests.

Results: Weaver ants suffer nest losses on understory plants but not on trees due to torrential rain. We documented movement onto coconut palms the month before mowing even when not mowed. Altogether, 145 out of 326 palms had weaver ants; 60 of these 145 palms had active ant nests less than 2 m away, suggesting polydomy.

Conclusions: Mowing the understory is a human-caused selective pressure. Torrential rain is a natural selective pressure. The movement of the ants under protective foliage in trees protects their nests because trees are not mowed. This movement enables the ants to persist in the plantations.

Keywords: habitat disturbance, switch in nest sites, torrential rain, weaver ants.

INTRODUCTION

Behavioural ecology and evolutionary ecology predict that organisms may experience different selective pressures at different times of the year that require an appropriate behavioural or life-history response (Alcock, 2001; Davies *et al.*, 2012). Multiple selective pressures

Correspondence: L.A. Freed, Department of Biology, University of Hawaii at Manoa, Honolulu, HI 96822, USA. email: lfreed@hawaii.edu

have been documented in diverse organisms (Endler, 1986). However, no sequential selective pressures have been documented, even in specialized texts on natural selection (Sober, 1984; Manly, 1985; Bell, 2008). Yet sequential selective pressures must be widespread. For example, evolutionary biologists recognize that natural selection operates at each life-history stage (Williams, 1966). Larvae or young animals experience different selective pressures than adults (Penchenik, 1999; Greenberg and Marra, 2005; Triplehorn and Johnson, 2005; Wells, 2007; Bone and Moore, 2008), and the leaves of plants fall off and grow anew at different times of the year (Braun, 1950; Lechowicz, 1984).

Weaver ants (*Oecophylla smaragdina*) are important to agriculture because they consume many insect pests (Offenberg and Wiwatwitaya, 2010; Offenberg, 2015). In central Sri Lanka, they live in coconut palm (*Cocos nucifera*) plantations throughout the year. This they do despite the torrential rain that falls during October to December (Gunarathna and Kumari, 2013), and despite the regular mowing of the understory plants in June. The two types of disturbance constitute a sequence of significant habitat changes. We studied their effect on ant behaviour and found that evolutionarily appropriate responses to the two selective pressures enable the ants to live continuously in coconut palm plantations. We also report that changing one of these selective pressures (mowing) for a few generations seems to have evoked a new adaptive response.

The aim of this study was to determine how weaver ants respond to habitat disturbance and torrential rain as different selective pressures occurring at different times of the year.

METHODS

The system

Weaver ants are social insects. In the coconut palm plantations of central Sri Lanka, they build nests in understory plants and trees (Cole and Jones, 1948; Holldobler and Wilson, 1977). They exhibit polydomy – that is, each colony is dispersed into many sub-colonies on the same or different plants (Debout *et al.*, 2007). Each sub-colony must build its own nest and may move that nest if conditions warrant. A single plant may have many active nests. In this study, we measured the behaviour of the ants by treating each plant as a unit and counting the number of active nests observed on each plant over time.

Study sites

The two study sites were located in coconut palm plantations in an agricultural district near Nochchiyagama in central Sri Lanka, about 27 km east of Anuradhapura. One site, the main site (290 × 130 m), was bounded on the west by an irrigation ditch, on the south by a cornfield, on the east by a row of teak trees (*Tectona grandis*), and on the north by a road (Fig. 1A). We used 17 rows of palms totalling 326 trees and the understory plants dispersed among the palms. Ants built nests in 21 species of trees, shrubs, vines, and forbs in the plantation (Table 1). The main site was studied from early March through July 2015 and again during June–July 2016. This site was not mowed in June 2015.

The second site, the minor site, was a smaller plantation with 18 coconut palms. We studied ants there from November 2014 through June 2015. This site was mowed as usual in June. We inspected both sites in late April and June to determine whether present or past mowing resulted in predicted nest-plant shifts.

Fig. 1. (A) Coconut palm plantation where weaver ants constructed nests in understory plants as well as trees. (B) Mowed plantation where most nests were in tall trees.

Rainfall

We measured rain daily for a year (December 2014 to December 2015) in a site located 5 km from the two coconut palm plantations. We totalled the rain that fell each month. Gunarathna and Kumari (2013) document rainfall from 1975 to 2010 and we compared their data with our own measurements of rainfall. We also measured torrential rains in May 2016.

Survey of ant nests

We surveyed ant nests at the minor site in November and December 2014, and then again during late April and June 2015. We surveyed the main site each month from March until

Table 1. Plant species on which weaver ants located their nests

Plant species	Plant family
Trees	
Cocos nucifera	Arecaceae
Tectona grandis	Lamiaceae
Mangifora indica	Anacardiaceae
Lannea cormandelica	Anacardiaceae
Azadirachta indica	Meliaceae
Psidium guajava	Myrtoideae
Limonica acidissima	Rutaceae
Citrus medica	Rutaceae
Syzygium cumini	Myrtaceae
Cassia fistula	Fabaceae
Cordia dichotoma	Boraginaceae
Lepisanthes phylla	Sapindaceae
Nauclea orientalis	Rubiaceae
Shrubs, small trees, vines, and forbs	
Gmelina asiatic	Verbenaceae
Stachytarpheta urticaefolia	Verbenaceae
Calotropis gigantea	Asclepiadaceae
Morinda coreia	Rubiaceae
Coccineus grandis	Cucurbitaceae
Securinega leucopyrus	Phyllanthaceae
Tinospora cordifolia	Menispermaceae
Hemiparasitic plant	
Dendrophthoe falcata	Loranthaceae

late July 2015. We tagged each plant that had nests. Surveys consisted of inspecting every tree and understory plant and counting weaver ant nests. Active nests on understory plants were identified by observing ants on the surface of the nest or by tapping lightly on the nest with a pencil and observing workers move onto the nest. Active nests in trees were inspected through binoculars. Ants on the exterior of nests in trees indicated active nests.

Effect of rain on ant nests

We determined the effect of rain on weaver ant nests. At the main site, there were 10 understory plants and 11 trees with weaver ant nests that we inspected at least twice before 31 March 2015. Torrential rain fell on that date and on 1 April. An additional 25 understory plants and 16 trees were inspected once before and shortly after the rains. We used a logistic regression to model the decrease in nests. Decrease in nests was assessed in relation to type of plant and presence or absence of torrential rain. The model included plant (understory or tree), rain (light or torrential), and their interaction.

Effect of mowing on ants

The farmer who owned the main site postponed mowing until late July (Fig. 1b). He had mowed during June in previous years, thus the ants had been exposed to elimination of the understory plants on that site. We began surveying weaver ants on the 326 coconut palms in late April. Using binoculars, we determined whether the ants occurred at the base of the palm, 1 or 2 m above the base, on the lower half of the trunk, or the upper half of the trunk

We completed the first survey by 10 May. We resurveyed during the last two weeks in May. Then, using a sign test, we compared the number of palms within rows with weaver ants and without weaver ants during the two surveys. More palms within rows with ants were considered a 'success'. The main site was mowed as usual during June 2016, so we investigated the number of understory plants with nests.

We also inspected weaver ant movement onto palms in the minor site. The minor site was mowed during June, as it had been in previous years. This site was surveyed during late April and then again in June after mowing. We determined whether the ants showed the same shifts in nest location in the two sites.

In the main site, we examined the relationship between weaver ants on each palm during the last two weeks in May and active weaver ant nests on the closest plants to each palm regardless of location of the plant (up to 20 m). For each of the 326 palms, we documented whether the palm had weaver ants or not, and the nearest distance to an active weaver ant nest. We averaged the distances to palms with ants and then without ants in a particular row. Then we compared the two distances in the 17 rows with a paired t-test. The rows were independent because the distance to closest plants was generally less than the distance between comparable trees in rows.

We also detected two smaller ant species (*Paratrechina* and *Crematogaster*) ascending the palms in the main site. We compared the presence of these ant species with weaver ants in the upper half of palm trunks during the last two weeks in May with a test of proportions. This was done to determine whether the ascent to palms was a general phenomenon, as well as which species were observed first on them.

We observed other coconut palm plantations while travelling in Sri Lanka in July. To examine the generality of mowing, we noted whether nine of them had been mowed.

RESULTS

At the minor site in February, we found two understory plants with nests, along with 154 nests in two trees. In the main site in early March, we also found weaver ant nests in both understory plants and in trees. These are months with low rainfall (Fig. 2).

Rainfall

Figure 2 shows daily rainfall averaged by month between December 2014 and December 2015. The rain for the two Decembers will be dealt with separately below. During the last three months of the year, an average of 850 mm of rain fell per month compared with an average 344 mm during March through May ($t_4 = 5.3$, $P = 0.006$). However, during 2016, rainfall in May totalled 1082 mm, much greater than during the same month in 2015 ($t_1 = 176.8$, $P = 0.0036$). The heavier rains in May 2016 and October–December 2015 caused widespread flooding and landslides. However, this was inconsequential to the ants, which

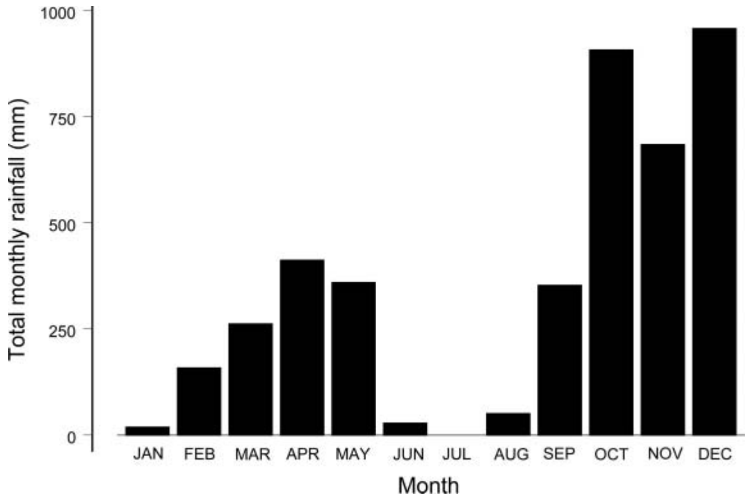

Fig. 2. Mean monthly rainfall measured at a distance of 5 km to the two coconut palm plantations. Rain was summed over each 24-hour period, and then totalled for each month.

were protected by palm fronds while colonizing the palms. Ant nests in understory plants first appeared after the torrential rain that fell in December.

Monthly rainfall (Fig. 2) was highly correlated with average rainfall from 1975 to 2010 (Gunarathna and Kumari, 2013) at a location 27 km distant from our study sites (Pearson correlation = 0.91, $t_{10} = 6.7$, $P = 0.0001$). Rainfall during June, July, and August was consistent with these months being the driest continuous months of the year in both datasets. Thus our single-year rain measurements were not unusual. Three months in the long-term dataset (January, March, and May) had standard deviations that were approximately equal to the means.

Effect of rain on ant nests

On 31 March and 1 April 2015, 233 mm of rain fell. Logistic regression, through the highly significant interaction term in Table 2, showed the differential effect of amount of rain on nests in understory plants versus nests in trees (Fig. 3). The 10 plants in the understory lost no nests in light rain before 31 March, but the 25 understory plants saw the greatest losses during torrential rain. Nests in trees suffered minor losses with light or torrential rain.

Table 2. Analysis of deviance table for logistic regression of weaver ant nest losses before and during rain on 31 March and 1 April 2015

Factor	d.f.	Deviance	Residual d.f.	Residual deviance	$Pr(\chi^2)$
NULL	3	17.35			
Type of plant	1	1.71	2	15.64	0.19
Type of rain	1	8.01	1	7.63	0.005
Plant × rain	1	7.63	1	0	0.006

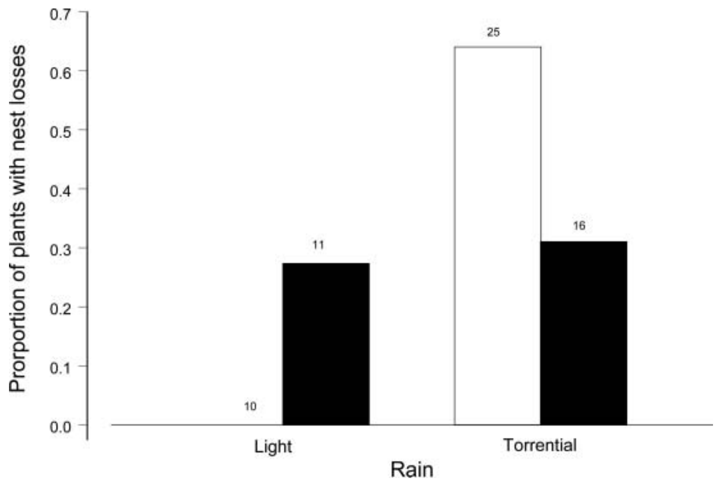

Fig. 3. Weaver ant nest losses under different rainfall amounts (light and torrential) and in understory plants (□) and trees (■) at the main site. The analysis of deviance table from logistic regression is shown in Table 2. Sample sizes are indicated above the bars.

These losses could have resulted from *Dinopium* woodpecker foraging, which during this time was observed exclusively in trees. Net losses from the torrential rains included three nests from trees and 36 nests from understory plants. Twenty per cent of the understory plants lost all nests and never recovered. Thereafter, until early June in the main site without mowing, 16 of 18 trees (89%) saw increases compared with 25 of 59 (42%) understory plants (test of proportions, $\chi_1^2 = 10.19$, $P = 0.0014$).

Movement of ants onto palm trees

Movement of ants onto palm trees was first observed in late April at the main site. An increase in the number of palms with ascending weaver ants was observed between late April and 10 May and again between 15 and 30 May (sign test, $P < 0.0001$; Fig. 4a). Altogether, 145 of the 326 palms had weaver ants. Furthermore, the period between 15 and 30 May saw a higher prevalence of ants in the upper half of the trunk (10 vs. 38 of 326 palms; $\chi_1^2 = 16.39$, $P < 0.0001$). The closest distances of active ant nests to a focal palm with ants were much less than in palms without ants (paired *t*-test, $t_{16} = 7.99$, $P < 0.0001$; Fig. 4b). In fact, 60 of the 145 palms with weaver ants (41%) had active weaver ant nests less than 2 m away. We observed an exodus of ants from the understory plants to the palm in three cases. This suggests polydomy in movement from understory plants to palms.

The ants switched nest sites in the absence of mowing in the main site and in the minor site that was mowed in June. May was the month of movement in both sites before mowing. At the minor site, ants moved onto coconut palms in 4 of 18 trees. The two tagged understory plants with nests were cut down by mowing. The main site still retained 30 understory plants with active nests that would also have been cut down if mowed. No trees were cut down. During late June 2016, when the main site was mowed, we could find only two understory plants with ant nests. This compares with 59 ant nests documented to have had ant nests earlier in June the previous year.

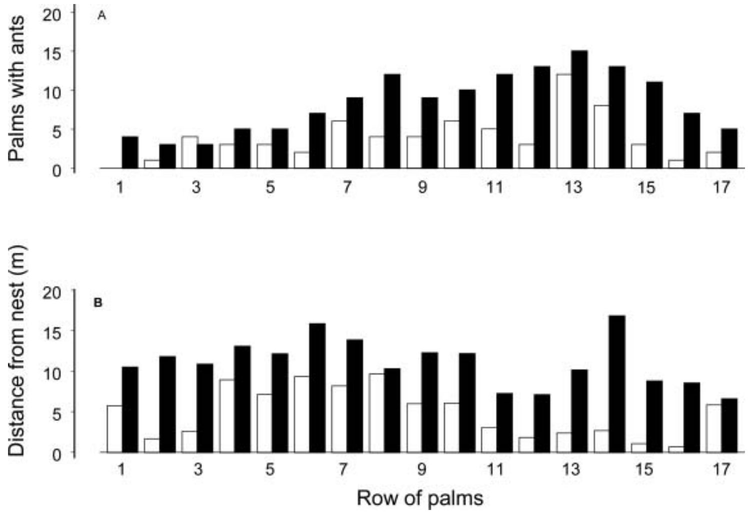

Fig. 4. (A) Increase in the number of palms with weaver ants during two time periods at the main site: late April to early May (□), and late May (■). (B) Averaged distance to active weaver ant nests from individual palms within rows of trees with weaver ants (□) and palms without weaver ants (■).

At the main site, nests were observed connecting contiguous leaflets with silk on the underside of lower palm fronds. These fronds sloped down so that rain would be guided away from the nests. In addition, fronds higher up protected the lower fronds. We also observed weaver ants ascending teak trees and mango trees (*Mangifora indica*); these nests received protection from branches with leaves higher up. Nest placement in trees protected most nests from mowing and the very heavy rains in October–December 2015 (Fig. 2). This movement occurred while nests in the unmowed understory were increasing. But during July, understory plants with nests decreased in number from 29 to 22. By mid-July, the understory had become increasingly brown because of little rain, and active nests in understory plants declined further.

Vertical movement of nests was observed initially in weaver ants. Only 6 of 121 (5%) palms were observed to have the other two species of ants on the upper half of their trunks compared with 39 of 145 (27%) palms with weaver ants ($\chi^2_1 = 21.1$, $P < 0.0001$). However, this shows the generality of ant movement with respect to mowing as a selective pressure.

Rainfall in December differed between 2014 and 2015. Furthermore, during December 2014 there were two sets of two days during which the amount of rain that fell exceeded the total amount in March/April 2015 (267 and 275 vs. 233 mm), which caused nest failure during the period 31 March to 1 April 2015. There were no consecutive days in December 2015 that experienced more than 233 mm of rain. This shows annual variation in December rainfall. However, the ants on palms were protected from vertical rain by leaves higher up and could travel on the other side of the palm that had less vertical rain.

DISCUSSION

We noted two factors operating at different times of the year that together caused weaver ants to shift location of their nests. The first is the mowing that takes place in June, which destroys understory plants with nests. The second is the torrential rains during October–December, which, based on late March and early April 2015, destroy up to 12 times as many nests located on understory plants than those in trees. The movement onto palm trees with protective foliage helped guard against the mowing in June, and also guarded against the heavy rains that fell during October–December 2015. By climbing palm trees in May, the ants were protected from both selective pressures. Ant nests remain in trees from May through December, although two-way movement was identified on dry days. Here we analyse the selective pressures of rain and mowing.

Conversations with farmers indicated that mowing the understory of coconut palm plantations started in 1996, when the government gave farmers weedwhackers (strimmers) so the palm trees could gain exclusive access to the limited rain that fell during the three-month dry season of June, July, and August. A minority of farmers do not cut plants with weaver ant nests for religious reasons. However, the majority of farmers cut all understory plants around the coconut palms because coconuts are a major source of income. This type of mowing occurs widely in Sri Lanka, as we saw while travelling. This selective pressure is responsible for the shift in nest sites to trees before mowing because it eliminates nests on understory plants.

Since shortly after 1996, the ants have moved in advance of the annual mow. Before that, they moved to trees to avoid the torrential rains in October through December. Thus the change might have been an earlier ascent onto palms to avoid the mowing during June. Mowing thus represents an extraordinary case of a selective pressure inflicted by humans on other organisms (Palumbi, 2001).

The second selective pressure is the heavy rainfall in October–December. Because of the mowing that takes place, the ants have already shifted the location of their nest sites to trees. Perhaps the reason why they don't return to understory nests during the dry months of July, August, and September is that the understory plants do not recover during the dry months. This is also evident in the loss of understory nests during July at the main site, which was not mowed in June 2015.

We found that nests on understory plants are susceptible to torrential rainfall. Weaver ants are renowned for their cooperative behaviour in constructing nests from folded leaves and use larvae that spin silk to hold the folded leaves together (Holldobler and Wilson, 1977, 2009; Crozier *et al.*, 2010). Ants leave a small circular opening on the side through which they enter and leave the nest. Thus torrential rain might leak through nests on understory plants, as documented during 31 March and 1 April 2015. The rains during October through December are much heavier but the nests were protected by foliage higher up, which blocked the rain.

Other causes of nest failure were minor. Nests were lost due to overgrowth by vines. Nests were also abandoned when a tree defoliated, but when new leaves appeared the tree was re-colonized. In addition, *Dinopium* woodpeckers poke at weaver ant nests and then eat the workers that emerge, perhaps resulting in a shortage of workers and loss of the nest. However, these other causes of nest loss are trivial compared with those that result from mowing and the torrential rain that falls over both study sites.

Mowing was not a proximate factor because the ants moved onto palm trees even when mowing was not undertaken. The switch in nest sites in May is analogous to bird migration where the birds leave with plenty of fuel (Alerstam and Hedenstrom, 1998; Greenberg and Marra, 2005). However, the movement of ants onto coconut palms occurs much earlier due to mowing and the ants remain in trees for five months. In bird migrations, decreasing photoperiod is the proximate factor. Days were becoming longer in Sri Lanka, thus increasing photoperiod may be the proximate factor shaping the movement before mowing.

The two other species of ants may provide an additional explanation for the timing of movement of weaver ant nests. These ants also moved onto coconut palms but did so later than the weaver ants. Nest sites differed among the three species of ants (Way and Bolton, 1997), so competition for nest sites is not a factor. However, weaver ants are carnivorous, so by ascending earlier, the other species of ants could become their prey.

These two causes of habitat disturbance – mowing followed by heavy torrential rains – may involve trade-offs at different times of the year. During the dry season, the ants in palms and other trees must descend to the ground to capture prey. We observed them moving down, and then up onto both palms and other trees. They were seen to carry caterpillars up a tree (Sudd, 1965) and transport a nestling woodpecker, tossed out of the cavity by a common myna (*Acridotheres tristis melanosternus*), along the ground (Wojtusiak *et al.*, 1995). The ants opened up the woodpecker on the ground and carried the pieces up the tree (Yanamoto *et al.*, 2009). This involves more energy per unit of prey because of handling time and transport up the tree compared with an understory plant. This same trade-off occurs during the exceptionally rainy months of October and December. However, during days of little or no rain during October–December, the ants can prey on animals in the understory while it is regenerating. But they must still transport prey to nests in trees. Coping with these trade-offs permits weaver ants to reside in coconut palm plantations throughout the year.

The difference in rainfall during the two Decembers suggests a risk-averse life history. The lower rainfall during December 2015 was still greater than all the other months, and had the highest standard deviation in the 1975–2010 dataset (Gunarathna and Kumari, 2013). However, as the ants are unable to predict the rainfall in December, they must locate nests in protective trees to reduce disaster occurring first from mowing in June and then from potentially heavy rainfall in December.

In summary, we have documented sequential selective pressures on weaver ants. Both selective pressures are physical rather than biological. This may help to make identification of sequential selective pressures simpler. Experimental procedures may be required to infer such selective pressures when they are biological.

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