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Temporal Variability in Weaver Ant *Oecophylla longinoda* Latreille (Hymenoptera: Formicidae) Nest Characteristics in Selected Host Plants

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Abstract

Weaver ants (*Oecophylla smaragdina* and *O. longinoda*) are famous for their impressive nest constructions, where they weave together living leaves on their host plants. Also, they are known to protect tropical tree crops against insect pests and are thus being utilized for biological control. Nest numbers have been used to track weaver ant abundances in plantations to optimize their use, assuming the number of nests reflects ant numbers. In this study, we compared nest size, the density of ants, and the proportion of workers in nests between three host plants (cashew, citrus, and mango) and between two seasons (rainy and dry). Nest size, ant density, and worker proportion differed between host species, whereas only nest size and worker proportion showed seasonal differences and only on mango and citrus, respectively. On hosts with smaller nests (in increasing size order: cashew, citrus mango), ant densities in the nests were higher, and the proportion of workers in the nests seemed to increase during seasons where food production on host trees decreased or on hosts where more trophobionts were cultured inside nests. These results have implications for developing methods to estimate ant numbers and raise interesting questions about the function of weaver ant nests.

Introduction

Ants significantly influence many habitats due to their high abundance, stable perennial populations, and feeding habits. Habitats such as tree crop plantations and tropical rain forests are dominated by arboreal ant species (Hölldobler, 1983; Parr & Gibb, 2010; Vayssières et al., 2021). The arboreal weaver ants belonging to the genus *Oecophylla* consist of two species – the African weaver ant *Oecophylla longinoda* and the Asian/Australian weaver ant *O. smaragdina* (Lokker, 1990). Weaver ant colonies usually contain a single maternal queen. They are composed of two distinct worker castes: (i) major workers that mainly forage, build nests, and defend colonies, and (ii) minors that usually remain inside the nests where they nurse the queen and brood (Hölldobler & Wilson, 1978). Weaver ants are also characterized by their large polydomous colonies and are famous for nest constructions (Crozier et al., 2009). Weaver ant nests are made of living leaves, pulled together by major workers, and fastened with silk produced by the larvae (Ledoux, 1950; Way, 1954; Holldobler & Wilson,

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1983; Wojtusiak & Godzińska, 1993; Crozier et al., 2009; Devarajan, 2016). Nests are vulnerable to physical damage by storms and heavy rain (Peng et al., 2004; Offenberg, 2014), and old nests are abandoned when leaves wither (Cole et al., 1948; Lokkers, 1990). Suitable host vegetation should, therefore, not be deciduous (Greenslade, 1972), and the leaves of host plants must exceed a certain size and be strong yet flexible (Van Mele & Cuc, 2007; Vayssières et al., 2011). Weaver ants' host species range is broad, but host preference varies depending on foliage morphology and canopy architecture, availability of nectar and honeydew produced by associated trophobionts (Blüthgen & Fiedler, 2002). However, despite weaver ants' remarkable and famous nest construction, little research has been conducted on characterizing nest morphology and use.

Weaver ants are also famous for their predatory ability against various insect pests of tropical trees (Way & Khoo, 1992; Van Mele, 2008; Offenberg, 2015). The ants were recorded as the first biological control agent used by humans at least 1700 years ago in ancient China (Charles Darwin University, 2010), and since they have proven equally or more efficient than chemical pesticides in several crops (Offenberg, 2015). *O. longinoda* (Latreille), for example, has been reported to control pests of (i) coconut, cashew, and mango in East Africa (Way, 1954; Olotu et al., 2013), (ii) mango in Benin (Van Mele et al., 2007), and (iii) cashew in Benin, Ghana and Tanzania (Dwomoh et al., 2009; Anato et al., 2015).

Weaver ant populations should be kept at high and relatively stable levels throughout cropping seasons to control insect pests effectively. According to Peng and Christian (2004), mango trees with abundant weaver ants are less damaged by insect pests than trees with fewer or without weaver ants. Therefore, methods of boosting *Oecophylla* nests in plantations and monitoring their abundance are gaining momentum in crops like cashew (*Ancardium occidentale*), mango (*Mangifera indica*), and citrus (*Citrus* spp).

Ants' abundance is usually estimated indirectly by counting (i) ant trails (Peng et al. 1999), (ii) ants on selected plant parts (Way & Khoo, 1991; Way & Bolton, 1997; Blüthgen et al., 2004), or (iii) ant nests (Peng et al., 1997, Ayenor et al., 2007, Dwomoh et al., 2009, Olotu et al., 2013; Wargui et al., 2015). Nest counts may not always reflect actual ant population levels because counts may include abandoned nests, and nest size (and therefore probably ant numbers) may vary (Lim, 2007). The size of *Oecophylla* nests ranges from a single folded leaf to nests constructed of hundreds of leaves (Way, 1954; Lokker, 1990). Such size differences may depend on leaf age, density, canopy architecture, crop species, and season. For example, young soft foliage is easier to fold and pull than older hardened leaves, and leaf shoots arranged closely in a canopy may allow the inclusion of several shoots in the same nest. Despite intensive research on *Oecophylla* ants, to our knowledge, no studies have looked at factors potentially affecting the nest size nor the density and composition of ants inside the nests. In this study, we tested if *O. longinoda* nest size, the mass of ants, and the proportion of workers inside the nests varied between host tree species (cashew, mango, and citrus) and seasons (rainy and dry) within host species.

Materials and methods

Studies were conducted on a citrus plantation in Tanzania and one cashew and one mango plantation in Benin. In Tanzania, studies conducted in the Tanga region (06°47'12.3" S/ 37°39'01.1" E) dominated by a bimodal rainfall pattern, with a short rainy season (October to December), a long rainy season (mid-March to May) and two dry seasons in between (January to mid-March and June to September). In Benin, the studies were conducted in the Tchaourou region (09°21′30″ N/ 002°37′58″ E), Borgou department, in the Sudanian area, characterized by an unimodal rainfall distribution with a dry (November – May) and a rainy season (June – October).

In Tanzania, weaver ant nests were collected in the citrus plantation from 20 ant colonies from October 2011 to September 2013. We harvested one nest per colony twice a month (mid and end of every month), making 924 nests sampled for two years. Nests were harvested randomly by walking along the field and collecting the first-sighted nest in a colony. In Benin, 20 nests were sampled fortnightly in the cashew and mango plantation from November 2011 to October 2013. However, at each sampling instance, all 20 nests were collected from a single colony in a single orchard. We sampled a different orchard and colony and orchard at each instance, resulting in 300 cashew nests and 600 mango nests. Nests were collected at midday when ants were less active, as reported in Benin (Vayssières et al., 2011) and Australia (Peng et al., 2012). Immediately after harvest, we measured each nest's longest and widest points. We then opened the nest to examine if it was inhabited. Each nest was then sealed in a plastic bag and taken to the laboratory, where it was frozen to allow subsequent counting and weighing of the ants inside. If a sampled nest contained the mother queen of the colony, the nest was returned to the tree where it was sampled to conserve the colony. Nests without ants were considered abandoned and were not included in the study. An abandoned nest was replaced with a new nest until 20 nests were obtained per sampling event.

After freezing, the ants were sorted into two groups: (i) imago workers and (ii) all other castes and developmental stages. Each group's mass (fresh weight) was then measured for each nest. Nest volume was estimated based on the approximate cylindrical shape of the nests by $V = 2\pi r^2 L$, where $r = ½ h$; (r: radius; h: width of nest and L: length of nest) (Lim, 2007).

The effects of host species and season on nest size, ant biomass, ant density (ant mass per nest volume), and worker proportion (imago worker mass/total ant mass) were tested by two-way ANOVAs and *Post Hoc* Tukey HSD. Nest size, total ant biomass, and ant density were log10 transformed, and worker proportion arcsine square root was transformed before analyses to normalize residuals. All analyses were performed using JMP 11.

Variations in nest volume and ant total fresh weight per nest by season and crop were analyzed using the Wilcoxon test. A non-parametric correlation using the Spearman test was done to compare the relationship between the nest volumes and total fresh weight. All analysis was performed using JMP 11.

Results

Large and significant nest size differences were found between host species (ANOVA: $F_{2,1818} = 490.5$, $p < 0.0001$) and seasons (ANOVA: $F_{1,1818} = 7.3$, $p = 0.007$) with a significant interaction between the two (ANOVA: $F_{2,1818} = 4.0$, $p = 0.018$) (Table 1). Mango had the largest nests (mean ± S.E. = 2.82 ± 0.07 l), followed by citrus (mean ± S.E. = 1.46 ± 0.04 l). The smallest nests were found in cashew trees (mean ± S.E. = 0.49 ± 0.02 l) (Fig 1). The interaction effect was based on a seasonal difference in nest size in mango (Tukey HSD: t-ratio = -4.17; p = 0.0004), whereas the two other hosts did not differ between seasons (Tukey HSD: cashew; t-ratio = 0.11; p = 1.0, citrus; t-ratio = -1.41, p = 0.72). In mango, nests were 21 % smaller on average in the dry season (mean ± S.E. = 2.47 ± 0.10 l) compared to the rainy season (mean ± S.E. = 3.12 ± 0.10 l) (Fig 1).

The average (± S.E.) ant biomass per nest in citrus, mango, and cashew was 8.01 ± 0.27, 7.57 ± 0.21, and 5.85 g ± 0.21, respectively. The density of ants in the nests showed a pattern opposite to nest sizes (Fig 2), as densities were highest on the trees with smaller nests. Cashew had the highest density (mean ± SE = 14.55 ± 0.52 g/l) followed by citrus (mean ± SE = 7.22 ± 0.27 g/l) and lastly mango (mean ± SE = 3.60 ±0.11 g/l) (ANOVA: $F_{2,1818} = 86.5$, $p < 0.0001$). In none of the host trees did ant densities differ between seasons (ANOVA: $F_{1,1818} = 0.8$, $p = 0.36$) (Table 1).

Table 1. Mean ± S.E. of nest ant densities and nest size in different host plants and seasons.

Host plant	Ant densities (g/l)		Nest size (l)	
	Mean ± SE	Two-way ANOVA	Mean ± SE	Two-way ANOVA
Mango	3.60 ± 0.11	$F_{2,1818} = 86.5$ $p < 0.0001$	2.82 ± 0.07	$F_{2,1818} = 490.5$ $p < 0.0001$
Cashew	14.55 ± 0.52		0.49 ± 0.02	
Citrus	7 ± 0.27		1.46 ± 0.041	
Season effect		$F_{1,1818} = 0.8$ $p = 0.36$		$F_{1,1818} = 7.3$ $p = 0.007$

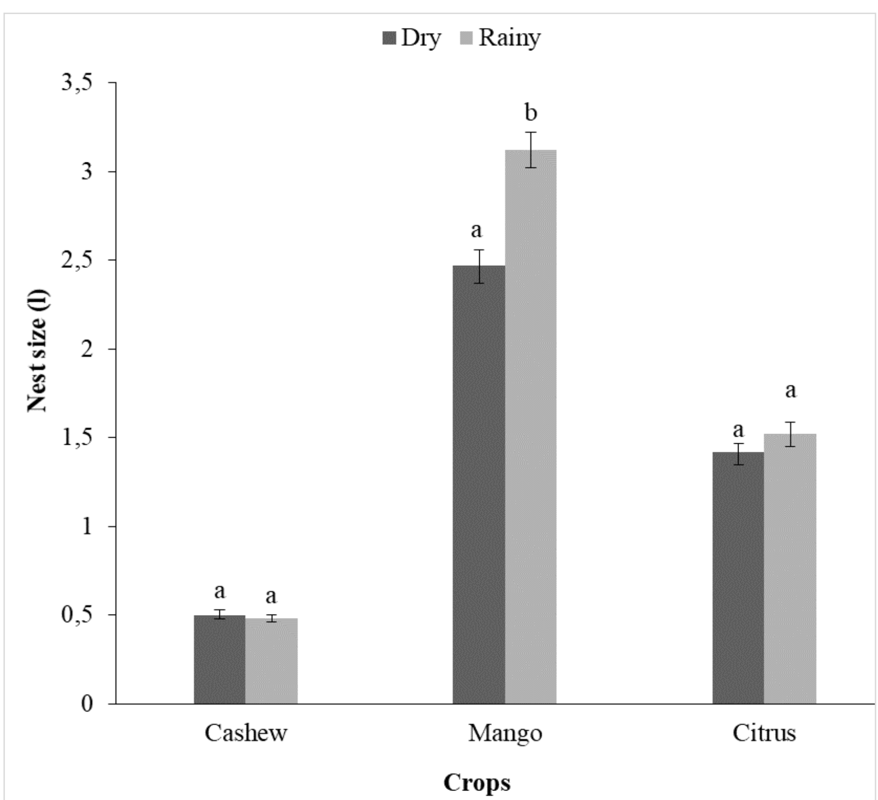

Fig 1. Average nest volume (± S.E.) by host plant species and season. Different letters within each crop show significant differences at the 5 % level.

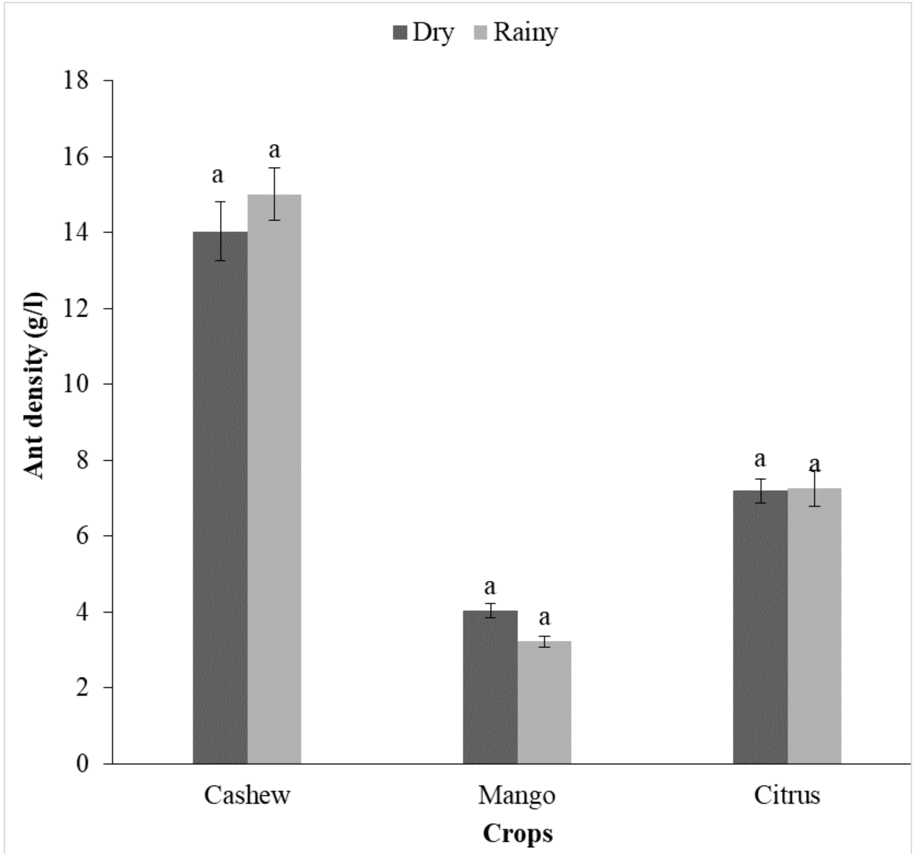

Fig 2. Average (± S.E.) density of ants per nest (g of fresh weight per litter) by crop and season. Different letters within each crop show significant differences at the 5 % level.

The proportion of workers in the nests (based on mass) was significantly higher in mango (mean ± S.E. = 0.71 ± 0.008) compared to the other two hosts (mean ± SE and Tukey HSD, cashew: 0.67 ± 0.01, t-ratio = -4.32, $p < 0.0001$; citrus: 0.68 ± 0.006, t-ratio = -4.66, $p < 0.0001$), whereas cashew and citrus did not differ significantly (Tukey HSD: t-ratio = -0.87, p = 0.66). Only citrus showed a difference in workers' proportion between seasons (Tukey HSD: t-ratio = 3.98, p = 0.001), with more workers in the nests during the dry season (mean ± S.E. = 0.71 ± 0.008) compared to the rainy (mean ± S.E. = 0.65 ± 0.01).

Discussion

Nest sizes differed significantly between the three different host plant species. In cashew, nests were much smaller than in the two other hosts. Leaf shoots of cashews are far apart compared to mango and citrus, and this distance could limit the ants' ability to tie together multiple leaf shoots (I. Ouagoussounon, unpublished data). As a result, their nests in cashews usually only include the leaves from a single shoot, and nests are limited to the size that can be supported by one shoot. In contrast, the foliage and shoot density was higher in mango and citrus. In these trees, ant nests often included more than a single shoot; therefore, some nests are larger than in cashews. It follows that the canopy structure of host plant species shapes the morphology of weaver ants' nests and possibly also the preference and suitability of host species. One result was an inverse relationship between ants' density and the nests' size. A higher density of ants was recorded in hosts with smaller nests. The current study could not determine whether the higher density in smaller nests was disadvantageous to the ants. However, it was recently concluded that *O. longinoda* performs less in cashews than mango monocrops in Benin (Wargui et al., 2018). The sampling design employed in the current study (sampling the first nest found) was possibly biased towards larger, oversampled nests. Thus, the average nest volume reported may be slightly overestimated, although care was taken to minimize this effect. Also, high-hanging nests at the top of the canopy would be underrepresented with this sampling design as some would be difficult to see.

In mango, nests were smaller during the dry compared to the rainy season (Wargui et al., 20215). Mango trees are most physiologically active during the dry season, thus producing flowers and fruits attractive to ant-attended trophobionts (Peng et al., 2005; Vayssières et al., 2021). During this period, the ants disperse their colonies and build many small nests around aggregations of attended homopterans on flowers and fruits. This dispersion contributes to seasonal differences in nest sizes in mango. Therefore, the records of nests cannot be used as a reliable measure of ant abundance in trees, as there were differences in nest size between seasons but no difference in ant density. Thus, for mango, an average nest was larger and held more ants in the rainy season compared to the dry season.

Similarly, Wargui et al. (2015) found more, and possibly smaller, nests in Beninese mango in the dry season than in the rainy season. The authors further suggested that nest numbers were a poor measure of ant abundance and that nest size needs to be considered to reflect ant numbers better. Likewise, Lokkers (1990) also found more and smaller nests of *O. smaragdina* when host trees were more physiologically active during leaf, flower, and fruit development.

The uniformity of ant densities across seasons makes it easier to estimate ant abundance using nest volume/size, as suggested in several studies (Lim, 2007; Verghese et al., 2013; Pinkalski et al., 2015). Within crops, the ant density was stable over the season; thus, nest size was a predictable measure of the number of ants in the nests. Thus, models using nest sizes to estimate ant abundances do not need to be calibrated differently between seasons. The same model parameters can track ant numbers throughout the year. On the other hand, there were differences in ant density between host species. Therefore, model parameters should be adjusted according to species when using a model on different host species.

We found that the proportion of workers was higher in mango nests than in the two other hosts. In mango, weaver ants attend plenty of scale insects on the leaves used to build the nest. As these scales are situated on the inner side of the nest, workers attending these scales will be found in the nests. We observed that fewer scales were attended inside nests in citrus and even fewer in cashew. Nests in mango, to a larger extent, function as “barns” for trophobionts, and a higher proportion of workers stayed inside the nests.

On the contrary, a larger part of the trophobionts may be situated outside the nests on stems and petioles of fruits and flowers in cashew and citrus, possibly explaining the difference observed in worker proportions between seasons in citrus. Fewer workers were found in the nests during the rainy season when trees were more active. Thus, trophobionts were available as they feed on flower and fruit petioles preferentially. As a result, more “outside” works were required during this period, potentially leading to fewer workers observed in the nests.

Attending scale insects in nests could also serve as an alternative explanation for the difference in nest sizes and ant densities between hosts. Furthermore, trophobionts (mainly scale insects) are cultured by the ants inside nests on some hosts (e.g., mango) but not on others (e.g., cashew), implying that nest space is required on hosts with nest trophobionts. In this case, nests functioned only as ant “housing”, whereas, in mango, they functioned both as ant “housing” and as a breeding ground for trophobionts. If nest trophobionts require additional space, it may follow that nests are being constructed with larger volumes and fewer ants. If nests only served as housing, it would be expected that ants constructed fewer nests in mango (as they were larger), keeping total nest volume constant and thus keeping the ant density similar to the ants in cashew. This hypothesis needs further testing by, e.g., analyzing if there is an association between the numbers of nest trophobionts and nest size/ant density across a broader range of host species.

The density of ants found in the nests in this study was considerably lower compared to what was found by Pinkalski et al. (2015) in nests of *O. smaragdina* in Australia. In Australia, average densities in nests of mango ranged from 16 to 31 g fresh weight L^{-1}, according to plantation and sampling events. The density found in mango in the current study was only 4 g L^{-1}, i.e., at least four times lower. The formula used to estimate nest volume tends to produce estimates that are too high. Pinkalski et al. (2015) found that *O. smaragdina* nests, due to their deviations from a true spherical shape, were, on average, 25 % smaller than predicted by the formula.

Furthermore, handling the nests (measuring the size and checking if the brood was inside) meant that worker ants had time to leave the nest before it was sealed in the bag. In Pinkalski et al. (2015), nests were sealed in bags before measurements were taken, thus allowing only a minimal number of ants to escape. However, it has previously been reported that *O. longinoda* nests in Tanzania contained much lower numbers of sexuals compared to *O. smaragdina* in Thailand (Rwegasira et al., 2015; Offenberg & Wiwatwitaya, 2010). Also, the number of ants per nest was much higher in Australian *O. smaragdina* compared to *O. longinoda* in Tanzanian (Lokkers, 1990, Fig 5.22d; Rwegasira et al., 2015, Fig 2 and 4), at least during part of the season. The proportions of workers inside the nests were more similar between Australia and the current study. In Australia, the proportion of workers ranged from 59 to 82% (Pinkalski et al., 2015), whereas they ranged from 65 to 71% in the present study. A higher proportion of workers outside the nests during flowering and fruiting is desirable in biological control. This indicates that more workers are devoted to patrolling and thus protecting against pests when trees are most vulnerable.

In conclusion, the nest volume, the density of ants, and the proportion of workers in a nest varied between host tree species. Still, only nest size and the proportion of workers were affected by season and only on some hosts (on mango and citrus, respectively). Season and host plants have implications for the different methods used to estimate ant numbers, and the results also raise interesting questions about the function of weaver ant nests.

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