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**Foraging and Nesting Behavior of Leafcutter Ants (*Atta cephalotes*)
in a Tropical Secondary Forest**

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ABSTRACT

La Calandria Forest is a coffee plantation-turned-reforestation project located in Los Llanos, Monteverde, Costa Rica. One of the species that seems to be successful in this forest is *Atta cephalotes* leaf cutter ants (Hymenoptera: Formicidae). I studied *A. cephalotes* foraging and nesting behavior to better understand their ecological relationships within a tropical forest ecosystem. I recorded the location of *A. cephalotes* nests and foraging sites with a GPS, and then identified plant species that these leaf cutter ants foraged from. After collecting data for two weeks: I created a map of *A. cephalotes* nests and their corresponding foraging sites, calculated foraging distances for each nest, calculated the nest density of an 11-hectare segment of La Calandria, and analyzed the foraged plant species composition. I concluded that: 1) Most *A. cephalotes* nests resided either in clearings or along the forest edge. 2) Different ant colonies never crossed paths, and avoided foraging in each other's territory. 3) La Calandria had an *A. cephalotes* nest density of 1.55 nests/ha. This is higher than values commonly found for tropical primary forest, but lower than the nest densities of forests adjacent to agriculture. 4) *A. cephalotes* foraged from a variety of plant species, but *Inga punctata* comprised 26.4% of the targeted forage sites. 5) On average, larger nests (33m) traveled farther than smaller nests (18m) to forage from plants.

**Asentamiento de colonias y comportamiento de forrajeo de hormigas cortadoras de
hojas (*Atta cephalotes*) en un bosque tropical secundario**

RESUMEN

El bosque de La Calandria es un proyecto de reforestación de una antigua plantación de café ubicada en Los Llanos, Monteverde, Costa Rica. Una de las especies que parece tener éxito en este bosque son las hormigas cortadoras de hojas *Atta cephalotes* (Hymenoptera: Formicidae). Estudié el comportamiento de forrajeo y asentamiento de colonias de *A. cephalotes* para comprender mejor sus relaciones ecológicas dentro de un ecosistema de bosque tropical. Con un GPS, registré la ubicación de los nidos de *A. cephalotes* y la ubicación de las plantas de donde forrajean e identifiqué las especies de plantas de las cuales forrajean. Después de recopilar datos durante dos semanas, creé un mapa de nidos de *A. cephalotes* y sus sitios de forrajeo correspondientes, calculé las distancias totales de forrajeo para cada nido, calculé la densidad de nidos de un segmento de 11 hectareas de La Calandria y analicé la composición de las especies de plantas que las hormigas forrajean. Llegué a la conclusión de que: 1) La mayoría de los nidos de *A. cephalotes* se ubican en claros o a lo largo del borde del bosque. 2) Las diferentes colonias de hormigas nunca se cruzaron, y evitaron buscar alimento en el territorio de cada una. 3) La Calandria tenía una densidad de nidos de *A. cephalotes* de 1.55 nidos / ha. Esto es más alto que los valores comúnmente encontrados para los bosques primarios tropicales, pero más bajos que las densidades de nidos de bosques adyacentes terrenos de agricultura. 4) *A. cephalotes* se

alimentaron de una gran variedad de especies de plantas, pero *Inga punctata* comprendió el 26,4% del total de plantas forrajeadas. 5) En promedio, los nidos más grandes viajaron más lejos (33 m) que los nidos más pequeños (18 m) para forrajear de las plantas.

Leafcutter ants are the dominant herbivore of the Neotropics, consuming over 12 percent of the tropic's leaf production every year. Instead of eating the leaves, however, leafcutter ants use the leaves as a substrate to grow fungus within their nest. One leafcutter ant of particular interest to the Monteverde region is *Atta cephalotes*. This leafcutter ant has the widest distribution of all the leafcutter ants, located all the way from Brazil and Ecuador to the southern portion of Mexico. *A. cephalotes* feed from a wide variety of crops throughout the region, making them a worrisome pest to farmers throughout South and Central America (Hölldobler & Wilson, 1990).

Due to their foraging behavior, *A. cephalotes* possess a strong ecological relationship with the plants in their ecosystem. Active nests lead to a lower biodiversity and a reduced abundance of understory plants near their nest (Garrettson et al. 1998). Additionally, *A. cephalotes* prefer to forage from the high canopies and from newer leaves. (Cherret 1968, T. Lewis et al 1974, and Nichols-Orians and Schultz 1989) They also prefer to forage from leaves high in Nitrogen and Phosphorus, but low in Magnesium and Aluminum, (Berish 1986). Multiple researchers have noted that *A. cephalotes* forage from a wide variety of plant species within their ecosystems (Blanton and Ewel 1985, and Cherrett 1968). These leaf cutter ants prefer to forage from plants close to their nest, but a large proportion of their foraging effort actually occurs between 31.3m and 46.8m away from their nests (Cherrett 1968).

Nest density, measured in nests per hectare, is a common metric to quantitatively evaluate the prevalence of leafcutter ants in a forested area, and may be a good indicator of forest health. Vasconcelos (1995) observed a negative correlation between the maturity of a forest and its leafcutter nest density. In the Brazilian Amazon, he observed that primary forests had the smallest nest density, followed by older secondary forest, while young secondary forest showed the greatest nest density. The nest density of leafcutter ants is extremely high in agricultural areas (Leston 1978 and Jaffe 1986), likely due to the fact that leafcutter ants tend to form nests in open clearings (Jaffe 1989). It appears that many leafcutter ant species, such as *A. cephalotes*, can be considered gap specialists (Hölldobler & Wilson, 1990). Researchers have also observed that *A. Cephalotes* prefer to build their nests on the edge of a forest compared to the center of a forest (Wirth et al. 2007 and Meyer et al. 2009).

In my study, I conducted research on the *A. cephalotes* population of La Calandria Forest in Monteverde, Costa Rica. This coffee plantation-turned-reforestation project now has had some regeneration and reforestation plots growing for over 50 years, while some areas have been growing for less than two years. In my study I aimed to learn more about these leaf cutter ants' foraging preferences and nesting patterns within the context of a secondary Tropical Forest ecosystem.

I produced and analyzed the following four research questions: **1)** Where in La Calandria will *A. cephalotes* nests be the most present? Other research suggests that a forest edge effect increases the presence of *A. cephalotes* colonies, so I hypothesize that I will observe more nests in open areas or on the forest edge. **2)** What will be the nest density of La Calandria, and how will this compare to nest densities researchers have found for primary forest and forested areas adjacent to agriculture? Because La Calandria is a recovering secondary forest, I hypothesize it will hold a greater nest density than primary forests, but hold a lower nest density than agricultural areas. Based on values for nest density found in other studies, I hypothesize that La Calandria will have a nest density between 0.5 and 3 nests/ha. **3)** Which plant species will *A. cephalotes* forage from at La Calandria Forest Reserve, and how will this compare to what *A. cephalotes* forage from in other ecosystems? Other research suggests *A. Cephalotes* forage from a variety of plants, but focus most of their foraging effort on a small subset of species. I hypothesize that I will find a similar trend in my study. I also anticipate that the *A. cephalotes* of La Calandria will forage from different set of plants than the *A. cephalotes* of other ecosystems, likely due to a difference in plant composition of its environment. **4)** Will larger *A. cephalotes* colonies travel a further distance to forage than smaller colonies? Other research suggests this trend (Cherret 1968), and I hypothesized that I would find similar results in my study.

MATERIALS AND METHODS

I conducted my research over a 13-day period from May 7, 2019 to May 19, 2019. The search for foraging sites occurred on a daily basis at various hours between 8:00AM and 11:30 PM.

First, I walked through the trails and understory of La Calandria Forest Reserve to locate *A. cephalotes* nests in the reserve. I recorded nest locations with marking tape and a GPS receiver so that I could later calculate foraging distances for each nest, but also create a map of all forage and nest sites. As I tracked colony locations I took note of their size. I defined a large nest as having a large spoils pile around the nest, while everything else was considered as a small nest.

After I finished locating the colonies, I began to follow the ant trails from their colonies to their respective foraging locations. When explicit visual evidence of leafcutter foraging was observed, I marked the site with flagging tape and recorded its location with a GPS receiver. Explicit visual evidence qualified as either 1) *A. cephalotes* traveling down a plant with organic matter, 2) observing *A. cephalotes* cut leaf pieces from a plant, or 3) observing *A. cephalotes* carry organic matter from the ground to their nest. An expert in plant taxonomy, Eladio Cruz, helped identify the foraged plant species.

With the assistance of Randy Chinchilla, I calculated the distance from each nest to their respective foraging sites using their GPS coordinates. Randy Chinchilla also created a map of La Calandria with all observed colonies and foraging sites. The GPS had a minimum error of 3 meters. This error could cause a high percentage of error for shorter distances. To compensate, I measured foraging distances to the nearest decimeter if the foraging distance was less than 5 meters away or if there was no significant foliage between the nest and its forage site. I excluded the foraging distance data from one nest because I could not locate the nest's precise location, and therefore its GPS marker was inaccurate.

RESULTS

Nesting Location

Within the 11-hectare area of La Calandria I surveyed, I observed 17 *A. cephalotes* nests (**Figure 2**). Nine of the 17 nests resided near the forest edge or within the clearing at the Field Station. It also appears the nests have a reduced presence within the middle of the forest, which includes some of the older secondary plots (**Figure 1**). My results support my hypothesis. Additionally, I observed that *A. cephalotes* avoided other *A. cephalotes* colonies, but they also avoided the paths and foraging sites of other *A. cephalotes* colonies.

Nest Density

I calculated a nest density of 1.55 nests/hectare within this 11-hectare segment of La Calandria (17nests/11hectares). This fragment of forest holds a greater nest density than undisturbed primary forests (**Table 2**). Perfecto and coworkers (1993) found a nest density as high as 0.71 in a tropical primary rainforest in Puerto Viejo, Costa Rica. Meyer found a nest density as low as 2.4 nests per hectare on the forest edge near sugarcane monoculture in Coimbra, Brazil. My nests/ha value of 1.55 does not resemble nest densities found for tropical primary forest, nor does it represent the nest densities of forests near agriculture. I hypothesized I would find a nest density between 0.5 and 3 nests/ha. I conclude that my hypothesis was supported by my data.

Foraging Behavior: Plant Species

I observed 87 foraging sites, 82 of which were plants. *A. cephalotes* foraged from 24 species of trees within 21 different plant families. Three plant species made up 43.6% of the foraged plants in La Calandria. Specifically, they targeted 23 *Inga Punctata* (26.4%), eight *Conostegia xalapensis* (9.2%), and seven *Zanthoxylum fagara* (8.0%) (**Table 1**).

A. cephalotes from La Calandria displayed both differences and similarities to the foraging behavior of *A. cephalotes* in other ecosystems. (**Table 3**). Blanton and Ewel (1985) found that *A. cephalotes* strongly preferred to forage from *Manihot esculenta* in a tropical wet forest of Tuerialba, Costa Rica. Cherret (1968) observed that *A. cephalotes* preferred to forage from *Terminalia amazonica* and *Eschweilera corrugate* within a tropical Wallaba forest of Bartica, Guyana. Both of these other studies also observed that *A. cephalotes* foraged from a variety of plant species, but focused a large proportion of their effort on a small subset of plant species.

Blanton and Ewel (1985) observed *A. cephalotes* foraging *Trema micrantha*, *Cecropia obtusifolia*, and *Croton* spp., three species that *A. cephalotes* also foraged in La Calandria. No mutual foraged plant species occurred between my study and Cherret's (1968) study. I conclude that my data supports my hypothesis.

Foraging Behavior: Foraging Distance

In large colonies, *A. cephalotes* traveled 33 meters on average to their foraging sites. Smaller colonies traveled 18 meters on average to their foraging sites (**Figure 3**). This difference was statistically significant ($T=2.83$, $p=.006$). I conclude that this data supports my hypothesis.

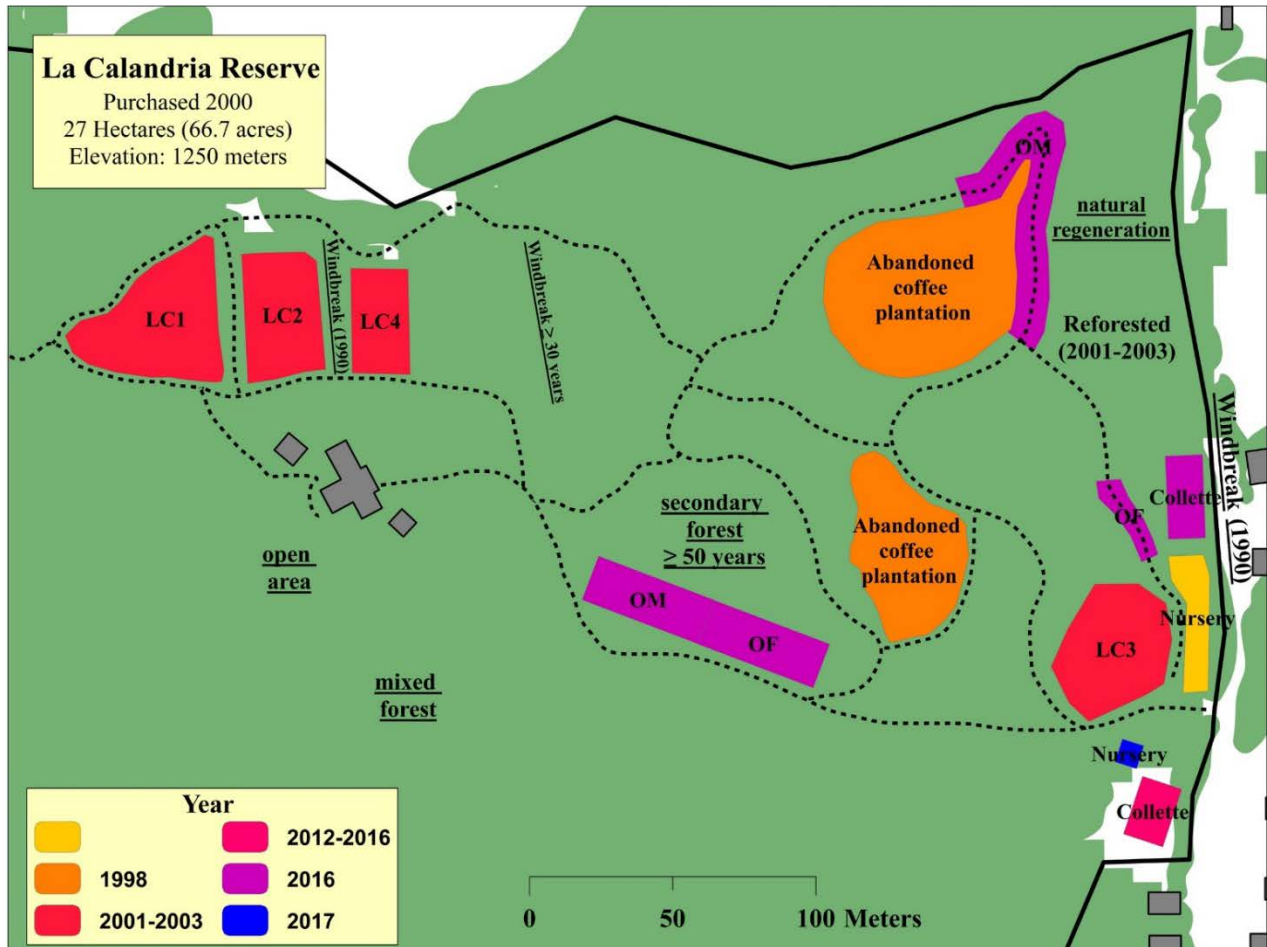


Fig. 1: Map of the 11 hectare study site. The grey boxes (middle left) represent the field station. Black dashes represent hiking trails.

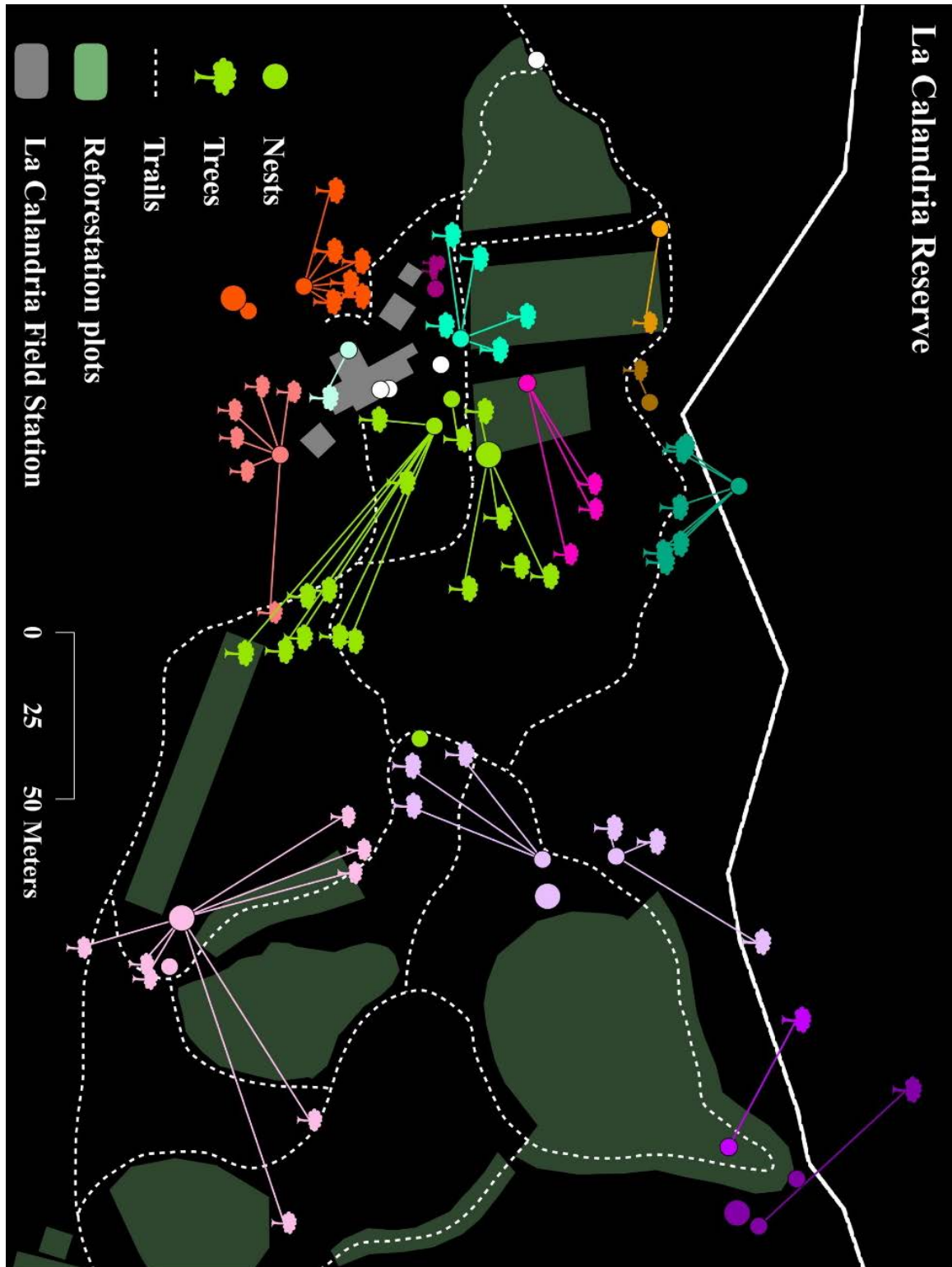


Fig. 2: Map of surveyed area with nest locations and foraged trees. Each dot represents an *A. cephalotes* nest. Each tree icon represents a foraging site. Nests are color coded to correspond with their respective foraging sites and to differentiate themselves from other nests. This image does not include the 19 foraging sites that had their distances measured by hand. White nest have no foraging sites recorded with GPS. I excluded the orange nest (top left) from the forage distance calculations.

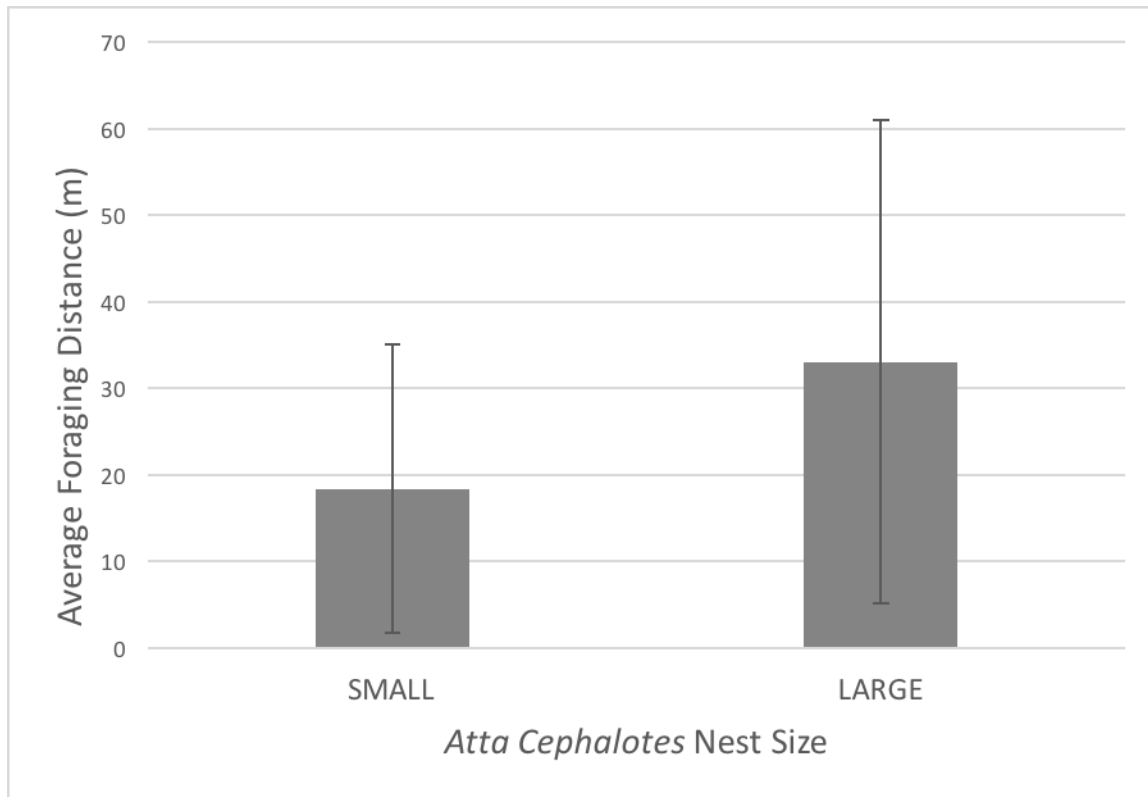


Fig. 3: *A. cephalotes* nest size vs the average distance traveled in meters for observed foraging sites. This difference was statistically significant ($T=2.83$, $p=.006$).

Table 1: List of foraged plant species with corresponding plant family. Also included is the number of individual foraged plants in each species by raw count and by percentage.

**A. cephalotes* foraged items from the ground at five foraging sites. These items included white flower petals, dead leaves, twigs, and tree bark.

Plant Species	Plant Family	Number of Individual Plants Foraged	Proportion of Individual Plants Foraged
<i>Asteraceae 1</i>	Asteraceae	3	3.4%
<i>Asteraceae 2</i>	Asteraceae	2	2.3%
<i>Cana india</i>	Cannaceae	1	1.1%
<i>Cecropia obtusifolia</i>	Urticaceae	3	3.4%
<i>Citrus Limon</i>	Rutaceae	1	1.1%
<i>Conostegia xalapensis</i>	Melastomataceae	8	9.2%
<i>Croton niveus</i>	Euphorbiaceae	4	4.6%
<i>Danopsis Americanus</i>	Timeliaceae	1	1.2%
<i>Dyphysa Americana</i>	Fabaceae	2	2.3%
<i>Ficus costarricana</i>	Moraceae	2	2.3%
<i>Hamelia Patens</i>	Rubiaceae	3	3.6%
<i>Inga punctata</i>	Fabaceae	23	26.4%
<i>Malvaviscus arboreus</i>	Malvaceae	1	1.1%
<i>Mangifera indica</i>	Anacardiaceae	1	1.1%
<i>Matayba opositifolia</i>	Sapindaceae	2	2.3%
<i>Meliosma spp.</i>	Sabiaceae	2	2.3%
<i>Monstera deliciosa</i>	Araceae	1	1.1%
<i>Myrciantes spp. "black"</i>	Myrtaceae	1	1.1%
<i>Myrsine coriacea</i>	Myrsinaceae	3	3.4%
<i>Stenotaphrum secundatum</i>	Poaceae	1	1.1%
<i>Syzygium jambos</i>	Myrtaceae	2	2.3%
<i>Tecoma stans</i>	Bignoniaceae	2	2.3%
<i>Trema micrantha</i>	Cannabaceae	6	6.9%
<i>Zanthoxylum Fagara</i>	Rutaceae	7	8.0%
Other*	Ground Items*	5	5.7%
Total		87	100%

Table 2: Ecosystems, locations, and nest densities of six studies, including my own.

	Carson, 2019	Meyer, et al. 2009	Vasconcelos et al. 1995	Jaffe, Vilela, 1989	Wirth et al. 2007	Perfecto et al. 1993
Location	La Calandria Forest, Costa Rica	Coimbra, Brazil	Fazendas Dimona, Brazil	Orinoco Amazon Basin	Coimbra, Brazil	Puerto Viejo, Costa Rica
Ecosystem	Secondary Tropical Rainforest	Atlantic Lower Montane Rain Forest	Primary Tropical Evergreen Forest	Primary Tropical Rainforest	Atlantic Lower Montane Rain Forest	Primary Tropical Rain Forest, Caribbean Lowlands
Nest Density in Nests/ha	1.55	2.4-3.6 near mono culture 0.2-0.34 in primary forest	0.03	0.045	0.33 in primary forest, 2.79 near monoculture	0.5-0.71

Table 3: Location, ecosystem, proportion of plant species foraged, mutual foraged plants, and preferred plant species for three forage behavior studies, including my own.

	Carson, 2019	Blanton and Ewel, 1985	Cherret, 1968
Location	La Calandria Forest, Costa Rica	Tuerialba, Costa Rica	Bartica, Guyana
Ecosystem	Secondary Tropical Rainforest	Tropical Premontane Wet Forest	Wallaba Forest, Tropical Rain Forest
Number of Foraged Plant Species/Total Plant Species Available	23/NA	17/332	36/72
Mutual Foraged Plants with Carson, 2019	NA	<i>T. micrantha</i> , <i>C. obtusifolia</i> , and <i>Croton</i> spp.	None
Preferred Plant Species Foraged	<i>Inga Punctata</i>	<i>Manihot esculenta</i>	<i>Terminalia amazonica</i> and <i>Eschweilera corrugate</i>

DISCUSSION

Nest Location

There are a few possible explanations why *A. cephalotes* prefer to build nests in open areas and forest edges. One leading theory is that *A. cephalotes* build more nests in these areas due to a greater abundance of pioneer plant species (Silva et al. 2013). *A. cephalotes* find pioneer plant species more desirable to forage because they tend to lack chemical defenses and have favorable nutritional content (Coley, 1983). It's also possible there are more nests on forest edges and clearings because *A. cephalotes* queens attempt to build nests in open areas more often than covered forest. *A. cephalotes* queens are clumsy flyers (Jack Longino, pers. comm.). It is possible they avoid flying through dense canopies, and as a result, are more likely to land in an open clearing to build their nest.

Colonies avoided the foraging sites and paths of other leafcutter colonies, which could be a byproduct of their territorial behavior (Salzemann and Jaffe, 1990). *A. cephalotes* contain a territorial pheromone that is colony-specific (Jaffe et al., 1979), and when different ant colonies infringe on each other's territory they can react violently (Carlin and Hölldobler 1986, and Salzemann et al., 1992). *A. cephalotes* may be avoiding the pheromone trails from different *A. cephalotes* colonies, hence the lack of overlapping trails and lack of shared forage sites between the different colonies.

Nest Density

The plots of young secondary forest, clearing near the field station, and prominent forest edge near the field station likely contribute to the high nest density of La Calandria. La Calandria holds a nest density greater than values commonly found for primary tropical rainforest, suggesting La Calandria may need more time to recover until its nest density resembles that of a healthy primary forest. However, it is encouraging to see that this forest segment holds a lower nest density than the nest densities found in agriculture areas, suggesting the reforestation project at La Calandria has made reasonable progress.

It's important to consider the ecological consequences an increased presence of *A. cephalotes* could have on a tropical forest ecosystem. Maybe an increased population of leaf cutter ants leads to an increase in its predator populations, such as *Nomamyrex esenbeckli*, an army ant (Swartz 1998). The biodiversity and abundance of understory plants decreases near *A. cephalotes* nests (Garrettson et al. 1998). Additionally, these leafcutter ants can reduce nutrient availability for plants by removing leaf litter near their nest (Meyer et al., 2013). *A. cephalotes* also forage heavily from seedlings that are close to their nest (Meyer et al. 2010). Some or all of these ecological effects could become more prominent in secondary forests with elevated nest densities, such as La Calandria.

Foraging Behavior: Plant Species

The foraged plant species composition at La Calandria differs significantly than the foraged plant species composition of other ecosystems, highlighting these creatures' ability to

forage from a variety of plant species. Blanton and Ewel (1985) studied foraging behavior of *A. cephalotes* on the Caribbean slope of Costa Rica at a lower elevation than La Calandria, which likely explains why their foraged plant composition differed significantly to my study. The capability for *A. cephalotes* to forage from a variety of plant species may allow them to easily adapt to changing plant distributions and biodiversity due to climate change (Randin et al. 2009).

There are a few possible explanations for why *I. punctata*, *C.a xalapensis*, and *Z.fagara* comprised nearly half of the observed foraged plants in La Calandria. One possible theory is these plant species existed in greater abundance than other plant species of La Calandria. I did not record biodiversity data, so I cannot confirm nor deny this notion. It's also possible *A. cephalotes* preferred to forage from these three plants because they lacked plant defenses. *I. punctata* produces nectar from its extrafloral nectaries to attract ants to itself, which then defend the plant from potential herbivores. However, this mutualism is less effective at higher elevations, likely due to a reduced abundance of these mutualistic ants at higher elevations (Koptur, 1985). Researchers observed that *Azteca instabilis*, an Azteca ant, defended *C. xalapensis* against flea beetles (Gonthier et al. 2010). La Calandria rests at 1250m, while *A. instabilis* do not typically reside above elevations of 500m (Longino, 2007), so they could not have been present at La Calandria. Marr and Tang (1992) observed that other plants of the *Zanthoxylum* genus contained pesticidal chemicals in their leaves. However, it's unclear if this is also holds true specifically for *Z. fagara*.

Foraging Behavior: Foraging distance

On average, larger *A. cephalotes* nests traveled 15m farther than smaller nests to forage from plants. One possible explanation for this result is that smaller nests do not have enough ants to maintain a pheromone trail over long distances. The pheromones that leafcutter ants leave evaporate rather quickly (Riley et al. 1974). At longer distances, it's possible that smaller colonies may not have enough ants to generate pheromone trails faster than their rate of evaporation. Another possible theory is that smaller ant colonies don't have enough ants to clear trails over longer distances. Worker ants have a variety of tasks, and some of them are dedicated to clearing debris from foraging trails (Howard 2001). Smaller ant colonies may not have enough workers to simultaneously a) maintain and clear a long foraging trail and b) travel long distances to forage from plants.

Conclusion

The nest density of La Calandria suggests that this reforestation project has made progress, but needs more time until its nest density resembles that of a primary forest. The nesting patterns of *A. cephalotes* confirmed that these leafcutter ants tend to build nests on clearings and the forest edge, but also provided further evidence of their territorial behavior. Additionally, *A. cephalotes* exhibit an extensive pallet when foraging from plants, which may allow them to adapt well to altering plant biodiversity and distributions.

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