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Foraging Behavior in Atta Leaf-Cutter Ants: A comparison of disturbed versus undisturbed nests

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SIT Study Abroad

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A comparison of disturbed versus undisturbed nests

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Abstract
The genus of ant, *Atta,* is one of the most prolific and ecologically impactful genera in the subfamily of Leaf-Cutter ants. They prefer to build nests and forage in disturbed areas or on the borders between secondary forest and disturbed areas, as much of their prefered harvest is cultivars. Two nests of *Atta* were studied at the La Hesperia Nature Reserve, one an undisturbed nest aged about four years and one a recently disturbed nest aged about seven years. General foraging behaviors were observed and compared for both nests, including peak foraging hours, headwidth of foraging ants, trail length, plants foraged, and percentages of foraged plants. General foraging behaviors differed only in the difference in location and the population of the nests. Peak foraging hours differed greatly between the two nests. The disturbed nest foraged nocturnally while the undisturbed nest foraged diurnally. According to locals, the nest switched from diurnal to nocturnal foraging after the disturbment, indicating that the disturbment may be the cause of the switch. Head width was found to be greater at the disturbed nest, which may support previous studies that when a large amount of the foraging force is removed from the population other castes with slightly larger head widths can switch tasks to foraging.

Resumen
El género de hormigas, *Atta*, es uno de los géneros más prolíficos y ecológicamente importantes de la subfamilia de hormigas que cortan hojas. Prefieren construir nidos y forrajean en áreas perturbadas o en las fronteras entre bosques secundarios y áreas perturbadas, ya que gran parte de su cosecha preferida son cultivares. Dos nidos de *Atta* fueron estudiados en la Reserva Natural de La Hesperia, un nido sin perturbaciones de unos cuatro años y otro un nido recientemente perturbado con una edad de unos siete años. Se observaron comportamientos generales de forrajeo en ambos nidos, incluyendo horas pico de forrajeo, ancho de cabeza de hormigas forrajeras, longitud del sendero, plantas forrajeras y porcentajes de plantas forrajeras. Los comportamientos generales de forrajeo diferían sólo en la diferencia de ubicación y la población de los nidos. Las horas pico de forrajeo diferían mucho entre los dos nidos. El nido perturbado se alimentaba nocturnamente, mientras que el nido no perturbado se alimentaba diurnamente. Según los lugareños, el nido cambió de forrajeo diurno a nocturno después de la perturbación, lo que indica que la perturbación puede ser la causa del cambio. Se encontró que el ancho de la cabeza era mayor en el nido perturbado, lo que puede apoyar estudios previos de que cuando una gran cantidad de la fuerza de forrajeo se elimina de la población, otras castas con anchos de cabeza ligeramente más grandes pueden cambiar las tareas a forrajeo.

Acknowledgements
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Introduction

The genus of ant *Atta* can be found throughout the western hemisphere and is characterized by their mutualistic relationship with some funguses which they grow within their nests as a food source for their larvae (Luisa, 1989). This characteristic is shared by all genera in the subfamily Myrmicinea. The common name Leaf-Cutter Ants is given to the genus *Atta* because they nurture the fungus growing in their nests with leaves, flowers, fruits, seeds, and other plant material found foraging in the surrounding area (Karslake 2015 and Luisa, 1989).

The genus *Atta* is known to be the most prolific and ecologically damaging as its colonies can become extremely large with a worker force in the hundreds of thousands and an overall population of 1 to 7 million individuals (Luisa, 1989 & Rockwood 1976). Though it is unclear how much they contribute to leaf damage in primary tropical forests, their effect on cultivated land can be immense (Luisa, 1989). *Atta* are most commonly found in disturbed areas, where it has been shown that though they may have the option of foraging for plants growing within secondary forests, they prefer plant cultivars (Karslake 2015). It has been estimated that if some species of *Atta* are foraging from the same pastures as cows, they can reduce the pasture carrying capacity for cattle by as much as 30% (Luisa, 1989).

Given *Atta*'s propensity for cultivated agriculture, and their large population they can become pests to tropical farmers very easily. At *La Hesperia Nature Reserve*, a reserve located in the Eastern Ecuadorian Cloud Forest, several large, established colonies exist in the developed areas of the reserve where cultivated plants are prevalent. The inhabited area of the reserve has many cultivated plants, as the reserve is also an active farm with agricultural plots, sheep, goats, and cattle.

About two weeks before the beginning of this study a seven year old nest of *Atta* was disturbed. The colony was situated on the back wall of a building and was growing so large there began to be concern that the foundations of the building were damaged and the building could be prone to collapse. Additionally, a greenhouse was installed in the building which created the added concern that the ants could begin foraging the leaves from the young plants in greenhouse. The disturbment occurred during the day and was an attempt to kill the colony by pouring boiling water and diesel over the nest. Burning plastic was also placed on top of the nest.

Laboratory studies have shown that as a colony grows in population variability in sizes increases (Wilson, 1980, Wilson, 1983). The caste system is much more varied and polymorphic in the *Atta* genus compared to their sister leaf-cutter ant genus *Acromyrmex*. As the colony grows, the variability in size grows as well; this is thought to be advantageous because if one cast is harmed in any way and is suddenly unable to perform their duties, other similarly sized ants can fill in the gap until enough reproductive cycles can replenish the missing caste (Wilson, 1983).

Reproductive cycles in the *Atta* usually lasts around 50 days (Wilson, 1983), so any disrupture of the normal caste distribution which was caused by the disturbment was unchanged when this study began. The objectives of the study were to track the general foraging habits of the disturbed nest and compare these findings to the same general foraging habits of an undisturbed nest in the same area to determine if the disturbment had any effects on their general behavior.

Additionally, as laboratory studies have shown the flexibility of *Atta* workers in their ability to change their task orientation, a further objective of this study is to confirm or reject the findings of the previous studies.

Methods

Study Site

This study was conducted at the *La Hesperia Nature Reserve*, a reserve located in the Eastern Ecuadorian Cloud Forest. Though the altitude ranges from 1,100-2,040 meters above sea level, the areas developed and cultivated for human use are at an altitude of 1,350 meters above sea level (La Hesperia, 2008). These areas consisted of pastures for goats, sheep, and cows, small agricultural areas, as well as paths and buildings for human use and were surrounded by secondary forest.

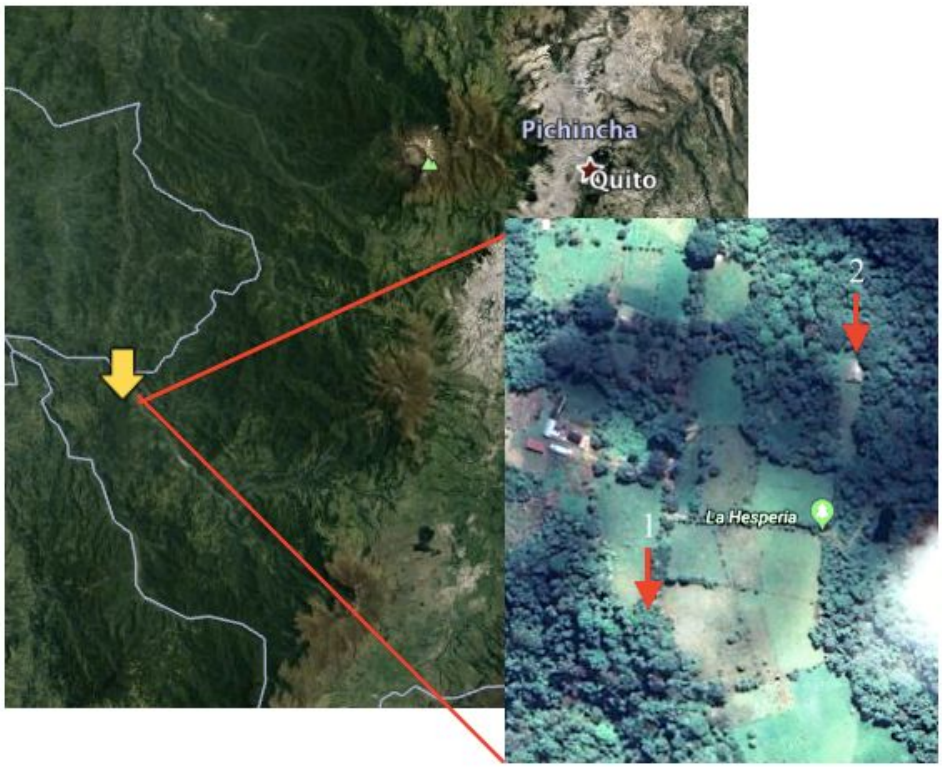

Figure 1: Location of La Hesperia within Ecuador indicated by a yellow arrow and locations of the Undisturbed Nest (1) and Disturbed Nest (2) indicated by red arrows within the reserve (satellite image generated by by Google Earth, 2019)

Before data collection began, a study of three undisturbed nests of *Atta* known to the local workers was performed in order to elect which nest would be used to compare with the disturbed nest. The disturbed nest was located in an open disturbed area and was judged by locals to have been established for approximately seven years before being disturbedby the locals. The nest itself was approximately five meters wide, though most of the activity was centered in a two meter by two meter section of the nest.

Each of the three undisturbed nests were judged by locals to have been established for three to four years. The undisturbed nest chosen was located in the border area between secondary forest and distubed area. Immediately bordering the nest was pasture, secondary forest, and a well-traveled path. This nest was chosen to compare with the disturbed nest as secondary forest and disturbed areas were comparably available as with the disturbed nest, as seen in Figure 1.

Data Collection

Data collection began by determining the peak foraging hours for each nest. For each nest, data was taken every 2 hours from 6:00AM to 12:00AM (Orr, 1992 and Hart, 2002). As seen in Figure 2, loaded ants which crossed a chosen marked line along the trail were counted for one minute. Loaded ants were considered any ant carrying a harvested organic material. This was repeated three times for each entrance to calculate an average (Orr, 1992 & Rockwood, 1976). Data was collected from five entrances from the undisturbed nest, though one entrance was inaccessible during the night, therefore data was not collected during hours of darkness. Data was collected from two points from the disturbed nest. Though there were three entrances, two of the entrances were less than a quarter meter away from each other and the loaded ants came from the same pathway. Therefore, data was collected from this point of convergence. A second day of data collection occurred for the disturbed nest because a secondary entry point was discovered on the opposite side of the nest after the initial survey was conducted.

Figure 2: Entrance *c* of the undisturbed nest marked as an example of the methods for counting loaded ants for forage rates

After peak foraging hours were determined, data was collected based on these time frames. During peak foraging time an initial map of each trail leading from each nest was made, marking what type of environment the trails passed though (disturbed, pasture, shrubs, or forest). Approximations were made on the length of the trails, and the environment of each material foraged was recorded and plants were marked with a plastic tie and given a number for later identification. It was observed during this initial survey period that capuchin monkeys regularly visited the trees above the undisturbed nest as the trail next to the nest was bordered by mandarine fruit trees. Each day capuchins were observed in the trees above the nest was marked. Each day the nest was visited trails were followed and any changes in foraged materials or trails was marked. Though yellow, brown, and green leaves were forged from the ground no attempt was made to identify these leaves because they differed too greatly.

At both nests, when peak foraging began, head widths were measured from the same points at which foraging rate data was collected. Data was collected on head widths for five consecutive days. From the same point at each location a single loaded ant was picked from the trail. The ant's head width was approximated with a standard 10 cm ruler. For each location fifteen ant's head widths were measured. While it was not possible to observe whether the ants foraged young leaves versus mature leaves from observing the act of harvesting, *Hypoxis hirsuta* and *Arachis repens* harvests were compared in size and color to mature and young leaves to determine whether they were mature.

To determine the percentages of different types of foraged material and to observe any difference in foraging rate over time, videos were taken at the same locations as the initial foraging rate survey and head width data collection. At the beginning of peak foraging, videos were taken for three minutes using a phone camera in order to take an average following the same procedures as the initial foraging rate survey. The disturbed nest was observed to be sensitive to light and loaded ants were observed to double back on their trails and walk in a confused manner compared to their usual straight path when the light was shined on them for long (longer than forty-five seconds to a minute) periods of time. For this reason, videos of the undisturbed nest were taken in one minute sections with breaks between recordings, whereas the undisturbed nest was recorded in three consecutive minutes. The attempt was made to collect data daily, however, when it rained heavily the ants dropped their leaves and stopped their activity making it impossible to collect data.

Additionally, each hole, excluding the entrances where loaded ants entered with foraged material, was marked using a stick and plastic marker. The number of active holes was recorded both during the peak foraging period and the less active foraging period. Activity was measured not by the number of ants present at the hole, but rather the presence of ants at the hole.

Foraged material was identified with the help of locals who knew the common names of plants. These common names were then identified by their scientific names (Gentry 1993). When possible the plant was identified to the species, however in some cases identification to the genera was the most specificity possible. Locals helped inform whether species were native or introduced.

Analysis

Peak forging was graphed as the average foraging rate per minute every two hours for eighteen consecutive hours for both nests. The mean and mode were calculated for the head widths of both nests and a two tailed unpaired T-test with equal variance was performed using $\alpha = .05$ to determine whether the size differences between nests was significant. Additionally, a two tailed T-test with unequal variance was performed using $\alpha = .05$ to determine whether the foraging rates were significantly different between the two nests.

An ANOVA was attempted to analyze the changes in activity between night and day between the undisturbed and disturbed nests, however, the software used provided inconsistent and incongruent values. In place of the ANOVA several two tailed T-test with unequal variance using $\alpha = .05$ were performed to get a general idea of significance. These calculations were made using percentages of active entrances excluding foraging entrances.

Results

Peak Foraging Hours

As seen in Figure 3, peak foraging in the disturbed nest was found to begin between 21:00 and 23:00, making the foraging nocturnal. Peak foraging in the undisturbed nest was found to begin between 10:00 and 12:00 and last until between 19:00 and 21:00, as shown in Figure 4, making the foraging behavior of the undisturbed nest diurnal.

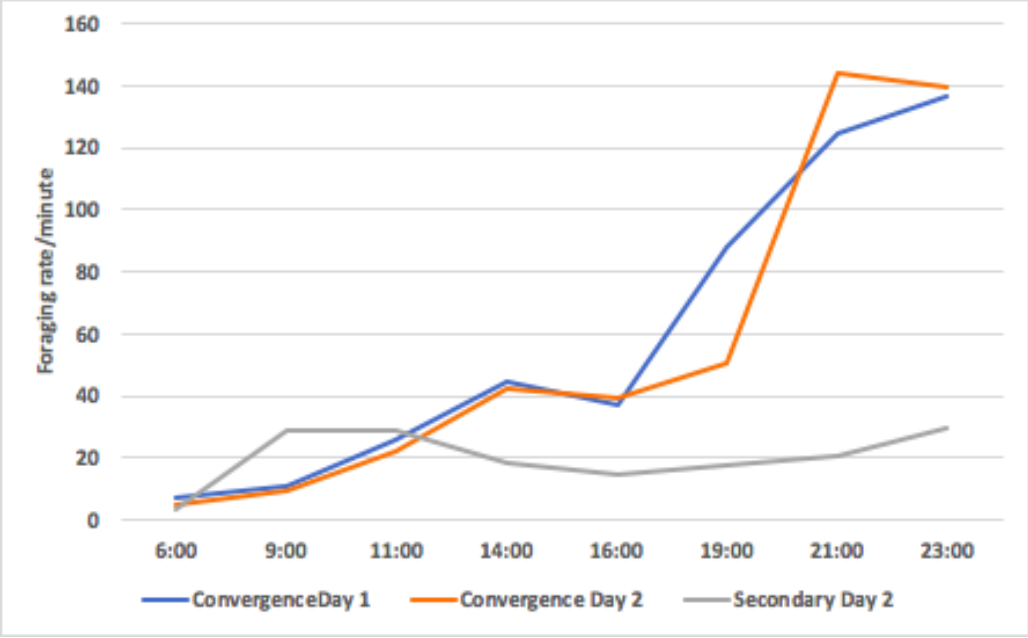

Figure 3: Average foraging rate per minute of each entrance of the disturbed nest.

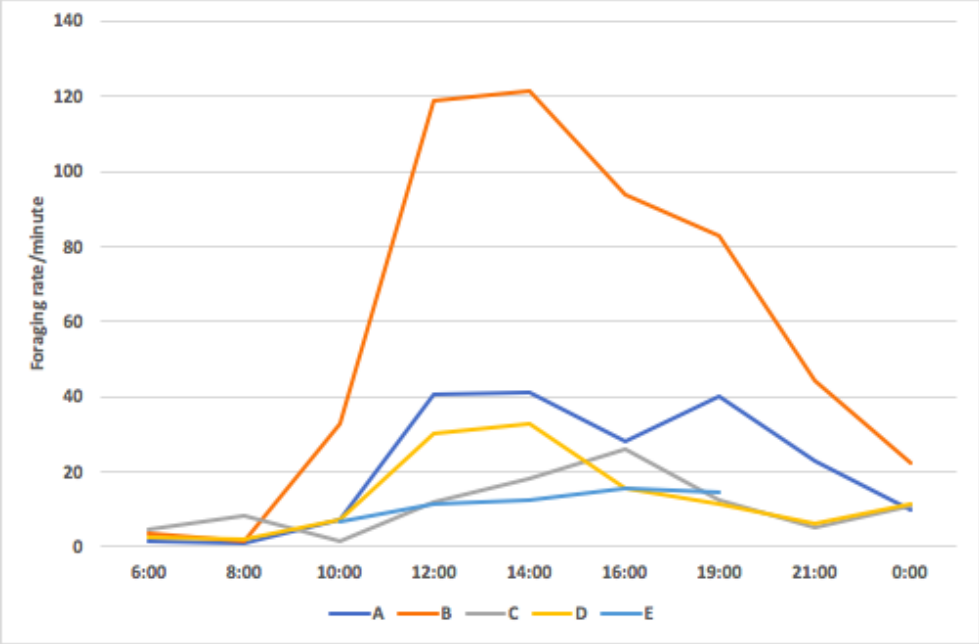

Figure 4: Average foraging rate per minute of each entrance of the undisturbed nest.

Comparison of Head Widths between Nests

As shown in Table 1, though the mean head width was found to be different between the two nests, the mode was found to be the same. An equal variance T-test was used as the variance was found to be similar, 0.23 for the undisturbed nest and 0.26 for the disturbed nest.The absolute value of the calculated *t* value 10.278 exceeded the critical value of 1.96 (df=521, α=.05), indicating that the difference between the mean head width of the undisturbed nest and disturbed nest was significant.

Table 1: Mean and mode head widths measured in mm of loaded ants in undisturbed versus distubed nests.

	Undisturbed Nest	Disturbed Nest
Mean	1.86mm	2.34mm
Mode	2mm	2mm

Comparison of Foraging Trails, Plants Harvested, and Foraging Patterns

As shown in Figure 6, three of the five foraging entrances lead directly onto the human made path. These trails largely followed the human path, which was traversed daily by cows, humans, and occasionally cars. The trail leading from entrance *a* traversed along the border between forest and cleared pasture.Though entrance *a* and *e* traveled through forest, no trees were foraged from the forest. As shown in Table 2, all foraged trees except Tree 4, *Monimiaceae,* were planted

intentionally along the border of the human path. During the period of this survey both Tree 1, *Citrus,* and Tree 3, *Persea caerulea*, were abandoned on Day 3 and Day 10 data collection of foraging percentages respectively. Tree 1, *Citrus,* was abandoned two days after *Citrus* and *Ficus citrifolia* fruit fell to the ground 1 m away. The trails leading into the pasture, as seen in Figure 6, are each harvesting *Hypoxis hirsuta*, an invasive plant not planted intentionally in the pasture. Where other red arrows indicate ground harvest, *Ficus citrifolia*, *Citrus,* and fallen leaves were foraged. These were also foraged along the trail, not exclusively at the terminus of the trail, if fruit was present within 30-50cm of the trail. The furthest foraged was Tree 4, *Monimiaceae*, at approximately 157m from entrance *a*, while the furthest foraged material was approximately 184m away from entrance *a* where many *Citrus* fruits were fallen on the ground. Trails did not extend more than approximately 40 meters down from the nest (according to the orientation of the map in Figure 6). The trails of a different colony were present approximately 50m from the nest, meaning the trails of each nest never crossed.

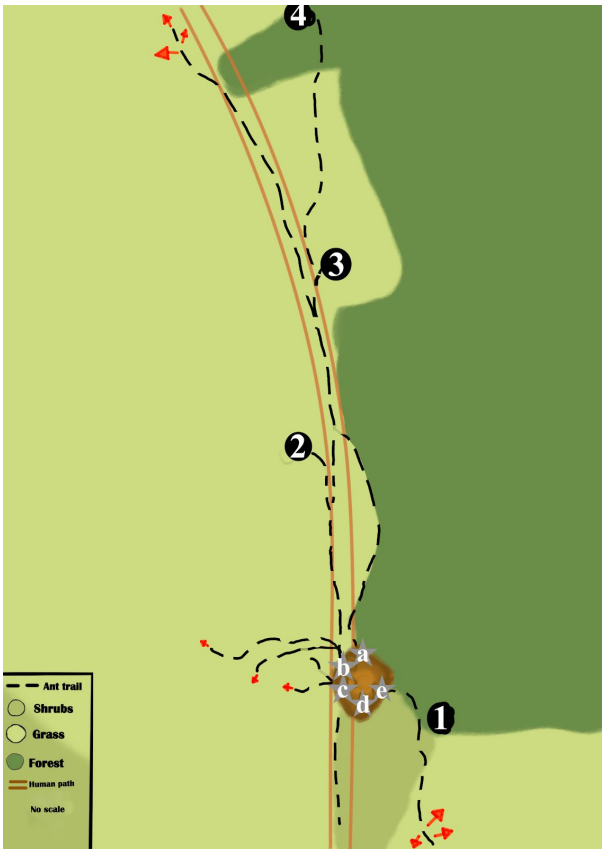

Figure 6: Map not to scale of the undisturbed nest and foraging trails. Entrances marked as *a-e* and foraged trees marked as 1-4. Red arrows indicate ground foraging where trails branch to individual leaves or fruit.

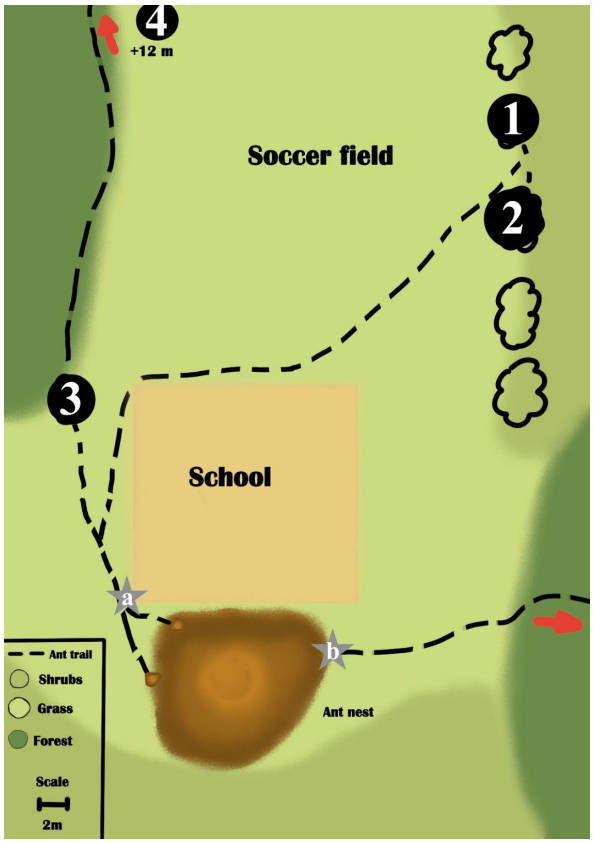

Figure 7: Map of the disturbed nest and foraging trails, with scale indicated on the map. Entrances marked as *a* and *b* and foraged trees marked as 1-4. Red arrows indicate where trails exceed the bounds of the map, unless otherwise indicated the distance from the edge of the map is unknown.

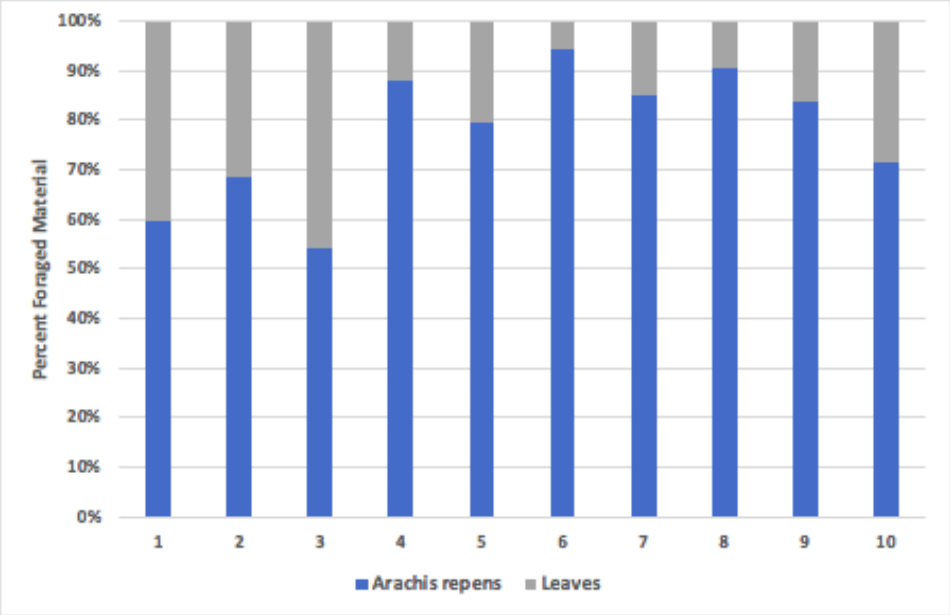

Figure 5: Percent foraged materials for each observation day from entrance *b* of the disturbed nest.

The disturbed nest was using trails that appeared well established, indicating that the trails were present before the disturbance. Additionally at least two abandoned trails were observed that appeared to have been previously highly trafficked. The trail which crossed the soccer field was 10cm wide at its widest point and completely clear of any grass along the path. As seen in Figure 7 and Table 3, each foraged tree was present on the border between secondary forest and disturbed area or in disturbed area. Each foraged tree was planted intentionally as natural borders between forest or pasture and areas with human activity. During observation no foraged trees were abandoned and foraging from each tree was consistent throughout the survey period. As seen in Figure 7, the trail extending from entrance *b* lead into thick shrubs making it difficult to follow the trail to the source of the foraged material. However, as seen in Figure 5, the majority of the harvested material was able to be identified by the characteristic leaves of *Arachis repens.* The furthest harvest tree was Tree 4, a non-native *Fraxinus*, at approximately 64m away from entrance *a*. Though secondary forest was available to the colony, and the trail leading from Tree 3 to Tree 4 made its way through the forest about 1m from the edge, no trees within the forest were harvested.

Hypoxis hirsuta and *Arachis repens* were found to be exclusively young leaves. Additionally, the leaves of *Acacia* were observed to be very young, though they were not compared to mature leaves as a sample of a branch was not able to be obtained. When *Citrus* was foraged as a tree only the leaves were takes, however when the fruit of *Citrus* had fallen to the ground every part of the fruit was harvested including the peel, the flesh, and the seed. While *Ficus citrifolia* fell to the ground regardless of the presence of capuchin monkeys, fresh *Citrus* was only observed to fall to the ground with their presence. Capuchin monkeys were observed every day until Day 3 of data collection of foraging percentages. They returned briefly on Day 6 and were absent for the remainder of the survey.

Table 2: Foraged material from the undisturbed nest.

	Common Name	Scientific Name		
Tree 1	Mandarina Acido	*Citrus*	Non-native	Planted
Tree 2		*Acacia*	Non-native	Planted
Tree 3	Aguacatillo	*Persea caerulea*	Native	Planted
Tree 4		*Monimiaceae*	Non-native	Wild grown
Grass	Yellow Star Grass	*Hypoxis hirsuta*	Non-native	Wild Grown
Ground Harvest	Mandarina Acido	*Citrus*	Non-native	Planted
Ground Harvest	Strangler Fig	*Ficus citrifolia*	Native	Wild Grown
Ground Harvest	Gualicon	*Macleania pentaptera*	Native	Wild Grown

Table 3: Foraged material from the disturbed nest.

	Common Name	Scientific Name		
Tree 1	Ash	*Fraxinus*	Non-native	Planted
Tree 2	Aguacatillo	*Persea caerulea*	Native	Planted
Tree 3	Mandarina Acido	*Citrus*	Non-native	Planted
Tree 4	Ash	*Fraxinus*	Non-native	Planted
Ground Harvest	Manifora	*Arachis repens*	Non-native	Planted
Ground Harvest	Gualicon	*Macleania pentaptera*	Native	Wild Grown

As shown in Table 4, the mean of the foraging rates between the undisturbed and disturbed nests are different. An unequal variance T-test was used to determine if this difference was significant. The absolute value of the calculated *t* value 7.8 exceeded the critical value of 2.1 (df=18, $\alpha = .05$), indicating that the difference between the mean foraging rate of the undisturbed nest and disturbed nest was significant.

Table 4: Mean foraging rates in the disturbed versus undisturbed nests.

Undisturbed Nest	Disturbed Nest
152.7/minute	98.1/minute

Yellow and brown leaves were foraged from the ground as shown in Figure 8. These were only observed foraged from places where fruit was additionally being cut and foraged. Yellow and brown leaves were not foraged when the ground harvest was a green plant such as *Arachis repens* and *Hypoxis hirsuta.*

Figure 8: Foraging ants cutting a fallen yellow leaf.

As seen in Figure 9 and Figure 10, the percentages of green leaves (including grass leaves) increased when the percentage of *Citrus* decreased. The change can be seen when entrance *d* is isolated in Figure 11. As the *Citrus* began to become fewer and more dried out the foraging ants switched to foraging fallen green leaves. Flower petals and whole flowers were foraged along the trails when they had fallen to the ground.

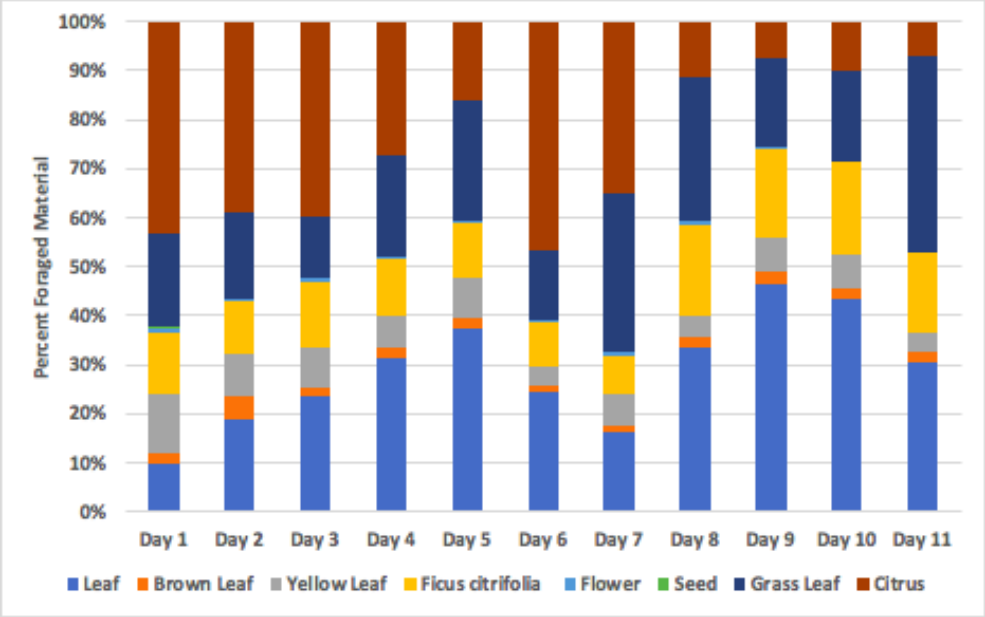

Figure 9: Percentages of foraged materials from the undisturbed nest.

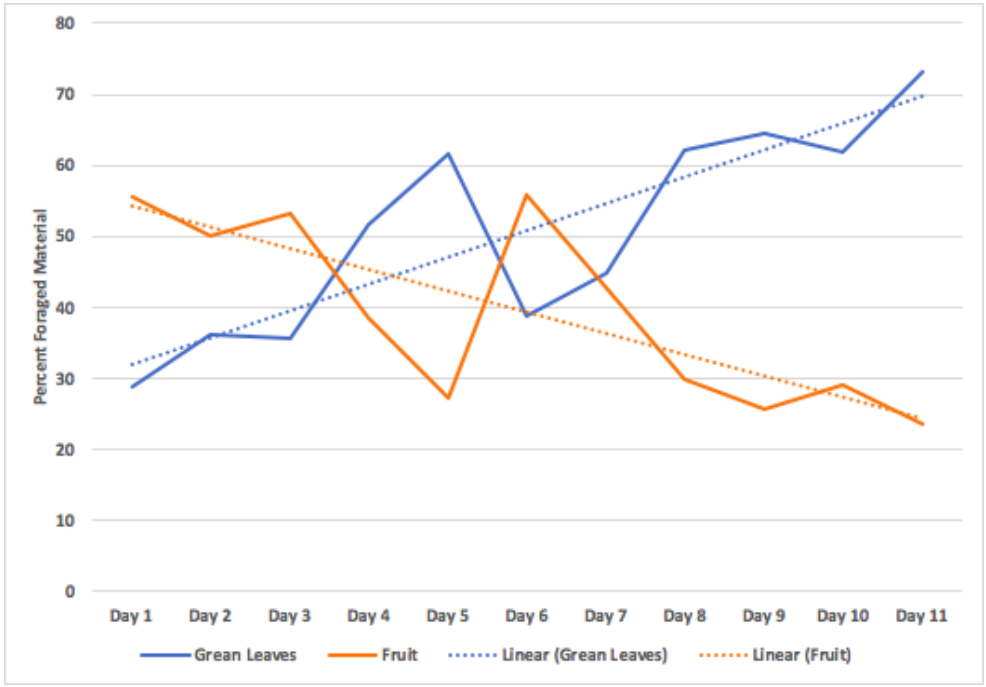

Figure 10: Percent foraged of fruit (*Citrus* and *Ficus citrifolia*) versus green leaves (all harvested trees, green leaves fallen to the ground, and *Hypoxis hirsuta*).

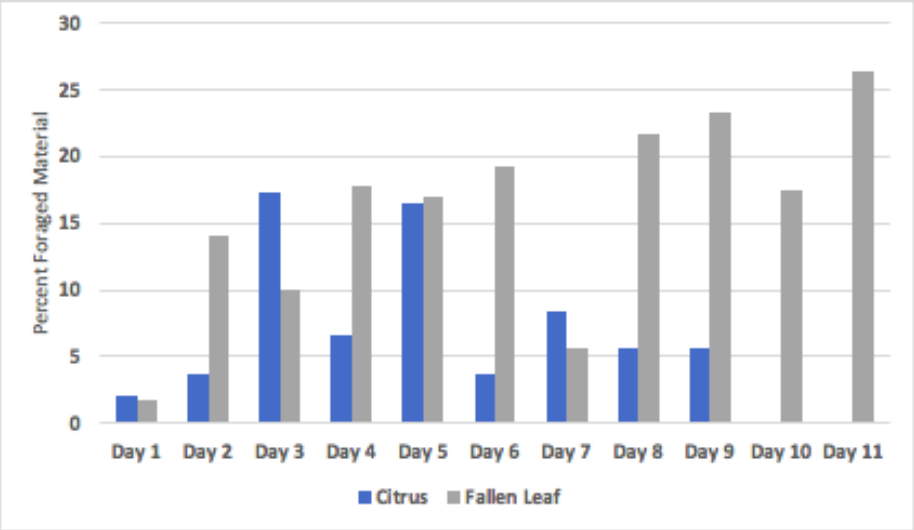

Figure 11: Percent Foraged *Citrus* vs Fallen Green Leaves of entrance *d* of the undisturbed nest.

As seen in Figure 12, the disturbed nest had little variability in its foraged materials. On day one a mandarine peel was left on the trail that crossed the soccer field, likely left by a child after a soccer game. The foraging ants foraged the entire mandarine peel, taking three days to completely cut it and bring it into the nest. As shown in Figure 13, and observed in the undisturbed nest, brown and yellow leaves were foraged from the ground when the *Citrus* was also harvested, however when the *Citrus* no longer present yellow and brown leaves were no longer foraged.

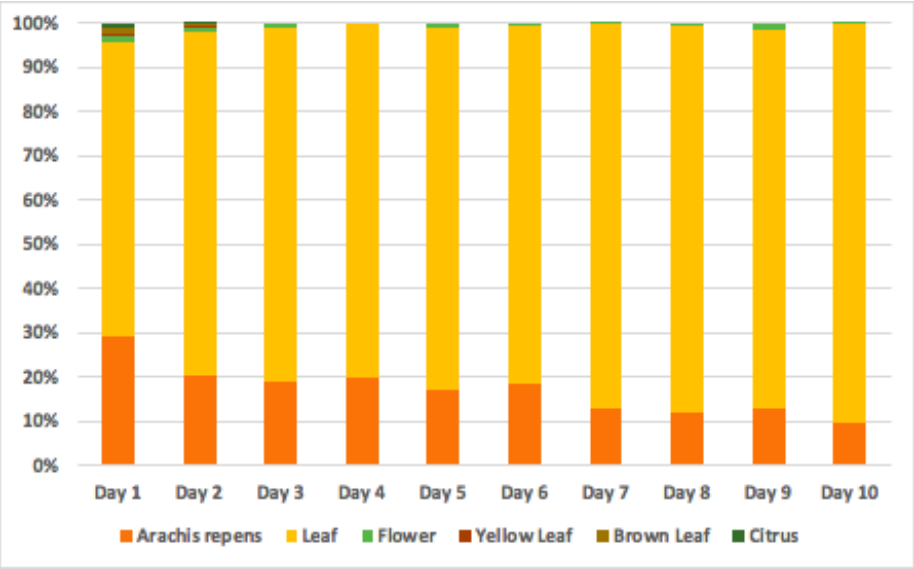

Figure 12: Percentages of foraged materials from the undisturbed nest.

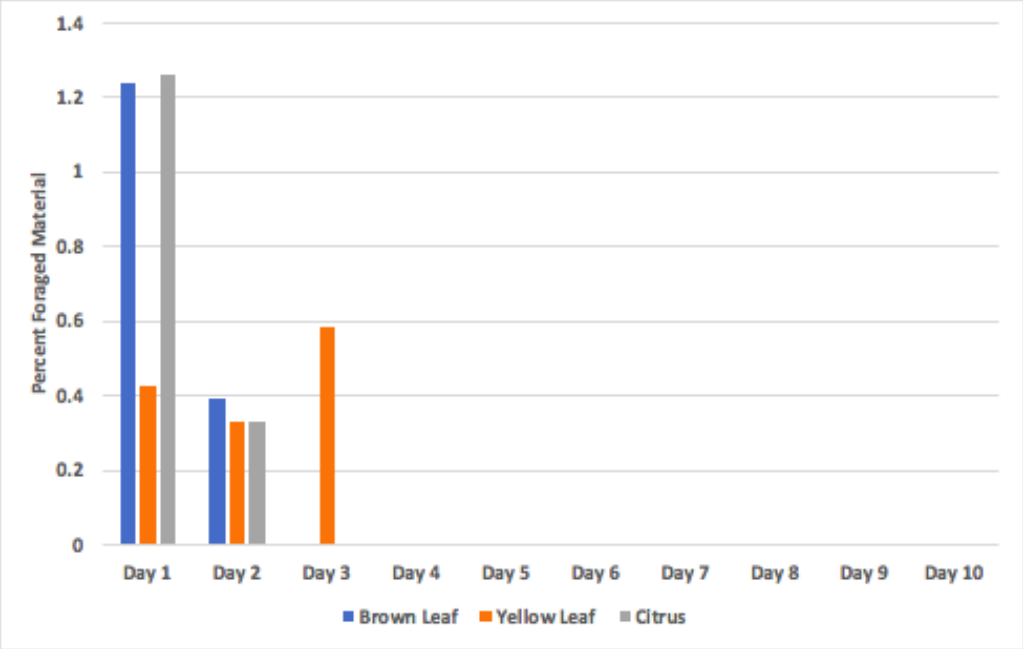

Figure 13: Percent Foraged *Citrus*, yellow leaf, and brown leaf of the disturbed nest.

Other Activity

Entrance holes for both the undisturbed and disturbed nest changed daily as new holes were built and established holes were destroyed by rain or other outside influence. The disturbed nest had more holes than the undisturbed nest, as seen in Table 5.

Table 5: Mean number of entrances (excluding foraging entrance) at both nests.

Undisturbed Nest	Distrubed Nest
23	54

Though data was collected based on peak foraging time, it was observed that the activity of the holes was not related to foraging period, but instead to time of day, as shown in Table 6. An equal variance T-test was used to determine if this difference between nocturnal activity and diurnal activity was significant for both nests. For the undisturbed nest, the absolute value of the calculated t value 2.33 exceeded the critical value of 2.08 ($df=20$, $\alpha=.05$), indicating that the difference was significant. For the undisturbed nest, the absolute value of the calculated t value 5.87 exceeded the critical value of 2.08 ($df=20$, $\alpha=.05$), indicating that the difference was significant.

Table 6: Mean active entrance percentages (excluding foraging entrance) at both nests.

	Undisturbed Nest	Disturbed Nest
Day	59%	76%
Night	76%	83%

As seen in Table 6, the percent of active entrances was larger in the disturbed nest. An equal variance T-test was used to determine if this difference between disturbed and undisturbed nests was significant. For diurnal activity, the absolute value of the calculated *t* value 2.49 exceeded the critical value of 2.08 ($df=20, \alpha=.05$), indicating that the difference was significant. For nocturnal activity, the absolute value of the calculated *t* value 2.12 exceeded the critical value of 2.08 ($df=20, \alpha=.05$), indicating that the difference was significant.

Discussion

Peak Foraging Hours

The peak foraging hours were found to be significantly different between the undisturbed and disturbed nests. The undisturbed nest had a diurnal foraging period, which is the normal period of foraging, while the disturbed nest had a nocturnal foraging period. Locals anecdotally reported that before the disturbance foraging occurred diurnally. As stated in the introduction, the disturbment occurred during the day. The switch to nocturnal foraging may be in response to the disturbment. Orr showed in a study that in *Atta cephalotes* foraging period and labor division within castes was affected by the presence of parasitic flies (1992). However in a study by Tonhasca, in 1996, the presence of parasitic flies had no effect on the foraging period of *Atta sexdens*. Additionally he stated that nocturnal foraging is not uncommon in the species as the species is sensitive to hot (over 30 degrees Celsius) dry climates (Tonhasca, 1996). The trails of the disturbed nest were in majority open areas where they would be more susceptible to changes in temperature by direct sunlight, whereas the trails of the undisturbed nest were majority in the shade. Though *Atta sexdens* has been observed in Ecuador and *Atta cephalotes* has not (Ziegler, Narula, & Janicki, 2018), the switch from diurnal foraging to nocturnal foraging after the disturbance conflicts with the reasons for nocturnal foraging stated by Tonhasca. Additionally, the max temperature during the study was 27.5 degrees Celsius, with an average max temperature of 25 degrees Celsius, which is far below the untolerated 30 degrees Celsius. The ant's sensitivity to light also indicates that the switch to nocturnal foraging is not only related to temperature and humidity.

Comparison of Head Widths between Nests

The modal head width between the undisturbed nest and the disturbed nest were equal with a head width of 2 mm. Wilson, in 1980, showed that the modal head width for the median workers, the foragers of *Atta sexdens* was 2.2 mm. The finding of the modal head width therefore is consistent with previous literature of the most frequent size of the foraging caste. However, the

median head width sizes were found to be significantly different between the two nests, with the disturbed nest having a larger head width on average compared to the undisturbed nest. This confirms Wilson's finding in 1983 in a laboratory setting that when workers are removed other size castes are able to fill in the foraging force. Wilson also showed that the remaining ants in the normal foraging force increase their activity up to 5 times compared to normal (1983). This may explain why the mode for both nests is the same while the average head width is different. The literature additionally suggests that when *Atta cephalotes* is being parasitized larger ants forage at night compared to the day in order to fight off the parasitic flies (Yackulic & Lewis 2007). This may be an alternative reason for the difference in average head size.

Comparison of Foraging Trails, Plants Harvested, and Foraging Patterns

Though the disturbed nest was located in a more open area, the disturbed and undisturbed nests had similar patterns of foraging trails. Though each nest had access to secondary forest neither of the foraging forces foraged plant material from inside the forest. This finding is supported by the literature, which states that *Atta* prefer to forage from disturbed areas. Each nest had a trail which traversed along the border of the forest as well as trails which crossed open areas. In the case of the disturbed nest the trail crossed the soccer field, While the undisturbed nest had trails which crossed the human path. This is counter intuitive given that there is daily activity on the human path which cases momentary disruptions of the trail. The variety of environments of the main trails may provide a diverse set of options for foraging to maximize the types of foraging plants available. For instance the capuchin monkeys only every dropped *Citrus* on or around the human path as the *Citrus* trees were planted on the border of the path. The ants were in a prime location to exploit the fallen *Citrus,* and once the fruit had dried they had no problems finding new foraging material, as seen in Figures 9, 10, and 11. These Figures also demonstrate that there is a relationship between abandonment of foraging for green leaves and the foraging of fruit. In the undisturbed nest, Tree 1, *Citrus,* was abandoned after *Citrus* and *Ficus citrifolia* fell to the ground nearby. This shows a preference for fallen fruit over leaves.

While the maturity of every foraged material was not able to be determined, both the disturbed and undisturbed nests were seen to harvest young leaves. This preference is supported by the literature. One reason put forth for this preference for younger leaves is that they have higher concentrations of P and K (Mundim, Costa & Vasconcelos 2009), which is beneficial for the fungus growing within their nests. An interesting finding shown particularly well in Figure 13, demonstrates that when there is a presence of fruit on the ground, foraging ants will harvest not only the fruit but yellow and brown leaves found on the ground as well. This was observed along the trails of the undisturbed nest, but is shown particularly well in the data of the disturbed nest given there was only one *Citrus* present over the survey period.

Rockwood in 1976 stated that foraging trails are usually found within 60 m of the nest but can extend up to 80 m. The majority of the trails extending from the undisturbed nest did stay within 60 m, however the furthest foraged material extended much further than 80 m. The furthest foraged material was approximately 184 m away from the nest and there were other foraged trees further than 80 m from the nest. This is more consistent with a study by Lewis, Pollard, & Dibley in 1974 which found that trails can lead as much as 235 m from the nest. This same study cited Cherrett (1968), which found that trails which lead through secondary forests can extend up to

320 m from the nest. This may provide insight into why the genus prefer to forage in disturbed areas— it takes less effort and distance to reach their preferred plant. Long term studies have shown that *Atta* will ignore other foraging material in order to reach a preferred plant (Berish 1986).

The undisturbed nest had a higher foraging rate compared to the disturbed nest's foraging rate, meaning more foraged material was cultivated by the undisturbed nest. The attempted destruction of the disturbed nest occurred soon enough to the beginning of the study that a full cycle of larval maturation had not yet occurred. The population of the disturbed nest was therefore lower than that of the undisturbed nest.

Other Activity

Data was taken on activity of every entrance of each of the nests at peak vs not peak foraging period. However, the activity was not dictated by when foraging period occurred, but rather time of day. Activity around entrances was much more prominent at night for both nests. Additionally, the disturbed nest was significantly more active than the undisturbed nest both during the day and the night. This seems to indicate that more nest construction or maintenance was occuring at the disturbed nest rather than the undisturbed nest. While more entrances were observed at the disturbed nest, this may be due to the age of the nest before the disturbance, as it was three years older than the undisturbed nest.

Further Study

When it began raining forcefully, on several occasions loaded ants would heavily prefer the trail that led along the forest border at the undisturbed nest rather than the trail that lead down the middle of the human path. Further study should be done to explore how foraging behaviors change in regards to heavy rains of short duration. Additionally, weather foraging behaviors change during the rainy season, perhaps so that trails lead into the forest to avoid the direct rain. Additionally, the phenomena of preference for fruit rather than leaves is interesting and should be explored more, as well as the foraging of leaf litter in conjunction with fallen fruit. Understanding the behavior, patterns, and preferences of *Atta* is important not only to understand a major pest for cultivars, but also to understand their place in the ecosystem for conservation efforts. *Atta* may be important to secondary forest regrowth preparing the soil through nutrient enrichment and tilling (Moutinho, Nepstad, & Davidson, 2003).

Limitations

The ruler used to measure head widths left anything less than a millimeter up to approximation. Head widths are therefore not measured to exact numbers. Additionally, data was not collected consecutively every day. When the rain came down forcefully, especially at night, the ants dropped their leaves and stopped foraging. For this reason days are numbered as Day 1, Day 2, Day 3 rather than by the calendar dates. This was more of an obstacle for the disturbed nest, whose peak foraging hours were during the night when it would rain the hardest. There is one less day of data for the disturbed nest for this reason. Lastly, the software used to calculate the ANOVA to compare the activity of entrances between day and night and disturbed and undisturbed nests had a bug and I was unable to use the output. This meant I had to use multiple T-tests, which are not the ideal statistical test for this data.

Conclusion

There was no discernible difference between foraging patterns in the disturbed and undisturbed nests. The undisturbed nest had a larger foraging harvest, a wider range, and a greater diversity of foraged material, however this could be attributed to the location of the nest and its larger population. In both nests fruit was harvested when made available by outside influence as ground harvest. Both nests showed a higher rate of activity around entrances which were not foraging entrances at night rather than during the day, and the disturbed nest had more activity at these entrances overall compared to the undisturbed nest, indicating construction was occurring inside the nest. The two main differences in foraging behavior were the difference in peak foraging hours (nocturnal at the disturbed nest, diurnal at the undisturbed nest) and the mean head width, which was larger at the disturbed nest. The nocturnal foraging of the disturbed nest seemed to be a product of the disturbment itself. The larger head width at the disturbed nest indicates support for previous laboratory studies of the flexibility within castes for task change.

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