

# Optimal foraging in leafcutter ants (*Atta cephalotes*): selection of leaves based on proximity to the nest

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## ABSTRACT

The foraging tendencies of *Atta cephalotes*, a leaf-cutting ant, have been widely studied. Optimal foraging theory dictates that ants should maximize rate of energy intake while minimizing costs by harvesting from suitable food sources closer to the nest. However, actual foraging patterns are more disparate and do not always reflect optimal strategies. Here I measure harvesting rates and recruitment speeds at different distances from the nest of *A. cephalotes* colonies by offering six leaf disk samples every 15 minutes at 5, 10, and 15 meters from the nest entrance. Harvesting rate was significantly higher closer to the nest, with 54% of leaf disks selected at 5 meters. Recruitment was also faster closer to the nest, as ants selected leaf disks within the first three minutes in 63% of the trials at 5 meters. Communication between workers may determine selection of closer leaf offerings and thus optimize foraging on a colonial level. Other factors, such as nutritional qualities from a plant, can influence foraging choices, but when leaf offering vary solely by distance, *A. cephalotes* exhibit time and distance-maximizing foraging patterns.

## RESUMEN

Las tendencias de forrajeo de *Atta cephalotes*, una hormiga cortadoras de hojas, han sido ampliamente estudiadas. La teoría de forrajeo óptimo dicta que las hormigas pueden maximizar la energía que obtienen mientras minimizan los costos al cultivar de fuentes de alimento adecuados cercanos al nido. Sin embargo, patrones de forrajeo actuales son distintos y no siempre reflejan estrategias óptimas. Aquí yo mido tasas de recolección y velocidades de reclutamiento a diferentes distancias del nido de colonias de *A. cephalotes*, al ofrecer seis muestras de hojas en forma de disco cada 15 minutos a 5, 10 y 15 metros de la entrada del nido. Las tasas de recolección fueron significativamente mayores cerca del nido, con 54% de hojas seleccionadas a 5 metros. También, el reclutamiento fue más rápido cerca del nido, a medida que las hormigas seleccionaron hojas dentro de los primeros tres minutos en 63% de las pruebas a 5 metros. La comunicación entre obreras puede determinar selección de hojas cercanas ofrecidas y por lo tanto optimizar el forrajeo a nivel de colonia. Otros factores, como cualidades nutricionales de la planta, pueden influenciar la escogencia de forrajeo; pero cuando la hoja ofrecida varía solamente por distancia, *A. cephalotes* exhibe patrones de forrajeo maximizados en tiempo y distancia.

## INTRODUCTION

OPTIMAL FORAGING THEORY states that an organism's foraging behavior should maximize net energy intake when searching for and obtaining food (MacArthur & Pianka 1966). Organisms that optimize by gaining the most energy, while minimizing time spent foraging, should be favored by natural selection, as maximizing energetic efficiency can lead to greater fitness. Over evolutionary time, species should refine mechanisms to improve their energy intake to output ratio when foraging. (MacArthur & Pianka 1966). Optimal foraging can apply to an animal's food choice, its choice of which area to feed in, time allocation in different areas, and optimal speed of movements (Pyke *et al.* 1977). Foraging becomes a more complex process in social insect colonies, where both individual and social aspects interact to determine food intake. Not

only must individuals collect and transport food, but they must also transmit information about its source to others (Roces & Hölldobler 1994).

The leaf-cutting ant, *Atta cephalotes* (Formicidae: Myrmicinae), is a social herbivorous insect. Rather than directly consuming vegetation, they harvest leaves from trees to cultivate a fungus upon which they feed, relying on systems of cleared trunk trails leading to resource plants that enhance food intake rate back to the central nest (Traniello 1989, Kost *et al.* 2005). They also exhibit division of labor among size-based castes and remarkable task partitioning for foraging activities (Wilson 1980). Foraging behavior of eusocial leaf-cutting ants can be influenced by many factors, and *A. cephalotes* foraging tends to be quite complex, with the distribution and quantity of selected plant species often varying among colonies (Rockwood 1976, Traniello 1989). Overall, *A. cephalotes* colonies are generalist herbivores, typically sampling a high proportion of tree species within a colony's territory, sampling up to 65-80% of trees in a location (Rockwood 1977). However, colonies seem to focus most of their foraging effort on a limited number of plant species, with one-third of harvested plant species consisting up to of 87% of a colony's diet (Rockwood and Hubbell 1987).

In light of their complex foraging behavior, whether *A. cephalotes* optimally forages is an important question. If optimal foraging theory does apply to an *A. cephalotes* colony, foraging workers should maximize their energy budgets by selecting preferred trees closer to the nest. According to Traniello (1989), leaf-cutters are efficient by cutting trees closer to nests, and optimize their diet by specializing on certain tree species when they are foraging in resource-rich areas and by generalizing on tree species when the quality of resource trees are low. However, other evidence suggests that trees can be selected independently of distance from the nest, and that foraging is not evenly distributed, thus ants are not minimizing retrieval costs (Rockwood 1976). Ants have even been observed to forego resource trees near the nest for an individual of the same species further away (Rockwood and Hubbell 1987). Workers could abandon trees farther from the nest for others closer to the nest if these closer trees, in fact, higher rates of energy return (Roces 2002), in line with optimal foraging theory.

Colony foraging is further complicated when taking into account its individual components. If colonies are foraging optimally as a collective sum of its parts, then individuals should optimize performance. Workers face a trade-off between time spent harvesting and time invested to recruiting nestmates to a new food source (Roces and Hölldobler 1994). Caste-divided systems where specific workers have specific tasks, in theory, allow workers to more efficiently partition leaf harvesting based on body size, as larger workers harvest larger loads (Rudolph 1986, Wetterer 1990). However, it has been shown that workers do not maximize individual foraging efficiency, typically taking suboptimal leaf fragment sizes (Rudolph 1986, Burd 2000).

Previous research has been inconclusive in determining whether energetic optimization applies to leafcutter foraging strategies. In this study I examine whether *A. cephalotes* optimally forage on equally-sized leaf fragment samples based on distance from the nest, using tree species harvested by the colony. If the ants maximize foraging efficiency, then palatable leaf fragments closer to the nest entrance should be selected more often than similar fragments further away. Additionally, if the theory applies, recruitment to leaf samples may be faster closer to the nest as well.

## **METHODS**

### **Study Sites and Leaf Selection**

Three ant colonies near Cerro Plano, Costa Rica were observed between April 17<sup>th</sup> and May 3<sup>rd</sup> 2011, in secondary, premontane moist forest. Two colonies were located in Valle Escondido, at about 1350 meters above sea level (masl), and one at the property of Frank Joyce, at about 1380 masl. Experiments at the two Valle Escondido colonies occurred after 1700 hours when the colonies were active and foraging, while the colony at Joyce's property, which was active both day and night, was tested in the afternoon. Trail segments where experimental procedure occurred tended to be in human-made clearings with relatively little surrounding undergrowth and leaf litter.

Ant foraging trails were followed to determine which tree individuals the ants were foraging from, and one tree individual for each colony was selected for leaf samples. Selected trees were identified to species by Willow Zuchowski and Bill Haber. Leaves were obtained from the approximately the same area of the tree.

### **Experimental Trials**

Leaf disks 1 cm in diameter were made from sample leaves using a hole puncher. Disks were offered to the ants at approximately 5, 10, and 15 meters from the nest entrance, on the same trail that led to the tree used for samples. For each trial, six disks were placed several centimeters apart in a column parallel to the trail. Disks were placed far enough from the center of the trail to avoid interference with ants, but still within the flow of traffic on the trail. After 15 minutes, the number of leaves taken at each distance was recorded and any remaining leaf disks were removed. Six more leaf discs were subsequently placed along the trail at each site, and the 15-minute trial was repeated. To determine differences in recruitment, every trial in which at least one leaf disk was taken within the first three minutes was recorded for each distance. Occasionally, ants were observed to purposely move leaf disks away from the trail to the leaf litter edge; because they were not being taken to the nest they were not counted as removed leaf disks. This behavior was recorded every time it occurred at each distance.

## **RESULTS**

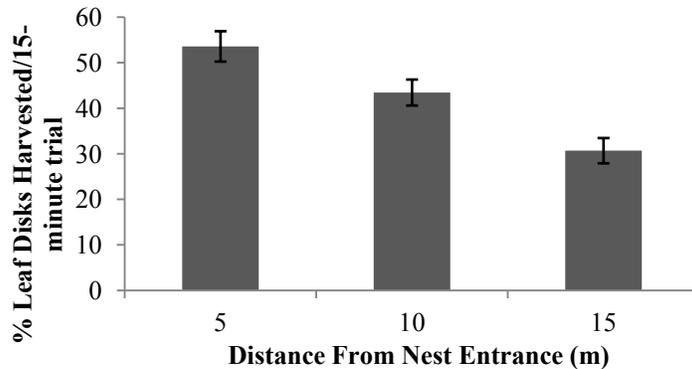
### **Species Identities of Leaf Samples**

Leaves from a different tree species were used for each colony. One colony at Valle Escondido was offered leaves from a *Viburnum costaricanum* (Caprifoliaceae) individual 26m from the nest, and the other *Oreopanax xalapensis* (Araliaceae), from an individual 35m away. The colony on Frank Joyce's property was offered *Symphonia globulifera* (Clusiaceae), from an individual 52m from the nest.

### **Harvesting Rate**

Overall, 107 15-minute trials were run at each distance from the nest, for a total of 320 trials. There were differences in leaf disk extraction rate among the different colonies; Valle Escondido

colony 1 had the highest pickup rates. However, all colonies picked up the greatest percentage of disks 5 m from the nest entrance. Distance from the nest had a significant effect on leaf extraction (One-Way ANOVA,  $F_{2, 320} = 14.7$ ,  $P < 0.0001$ ). For each trial, ants 5 meters from the nest entrance took  $53.6\% \pm 3.3$  of leaf disks on average (Figure 1). At 10 meters from the nest, ants removed  $43.4\% \pm 2.8$  of leaf disks were per trial, while at a distance of 15 meters, only  $30.7\% \pm 2.8$  of leaf disks were removed. Post-hoc tests revealed the pickup rates of disks were significantly different at each distance (Tukey-Kramer HSD,  $P < 0.05$ ).



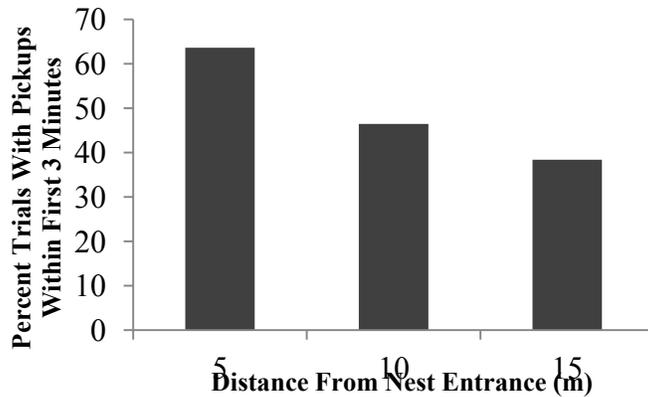
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FIGURE 1. Harvesting rate of *A. cephalotes* at three distances from the nest entrance, represented by mean percent leaf disks picked up per 15-minute trial ( $n = 107$  trials at each distance, 6 disks offered per trial). Data were recorded at three different colonies near Cerro Plano, two at Valle Escondido and one on Frank Joyce's property. Percentage of leaf pickups per 15-minute trial varied significantly among distances, with highest pickup rates occurring closest to the nest. Error bars represent  $\pm$  one standard error of the mean.

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### Recruitment Speed

Distance also had a significant effect on the recruitment speed of ants (Chi-squared Goodness of Fit,  $\chi^2 = 6.65$ ,  $df = 2$ ,  $P = 0.036$ ), as ants tended to recruit faster to disks closer to the nest. At 5 meters from the nest entrance, leaf disks were extracted within three minutes of placement  $63.3\%$  of the time (Figure 2). At a distance of 10 meters, leaf disks were taken within three minutes  $46.5\%$  of the time, while 15 meters from the nest, leaf disks were taken within three minutes only  $38.4\%$  of the time.



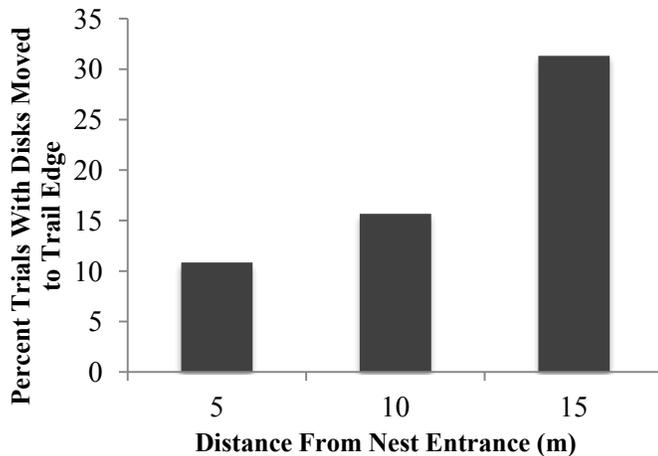
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FIGURE 2. Recruitment speed of *A. cephalotes* at three distances from the nest entrances represented by percentage of trials in which leaf disks were picked up within the first three minutes ( $n = 99$  trials at each distance). Data were recorded at three different colonies, two at Valle Escondido and one on Frank Joyce's property near Cerro Plano. Recruitment speed varied among distances, with leaf removal occurring within the first three minutes most frequently closest to the nest.

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### Rejection Frequency

Ants were also observed to purposely move leaf disks away from the trail to the edge of leaf litter in some cases, and the frequency of this rejection varied significantly by distance (Chi-squared Goodness of Fit,  $\chi^2 = 19.77$ ,  $df = 2$ ,  $P < 0.0001$ ), as ants further from the nest were more likely to do this. Ants at a distance of 5 meters and 10 meters from the nest entrance moved disks away from the trail for only 10.8% and 15.7% of the trials, respectively (Figure 3). However, at a distance of 15 m, disks were moved to trail margins 31.3% of the time.




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FIGURE 3. Rejection frequency *A. cephalotes* at three distances from the nest entrance, represented by percentage of trials in which leaf disks were purposely moved to the sides of the trail by ants (n = 83 trials at each distance). Data were recorded at three different colonies, two at Valle Escondido and one on Frank Joyce's property at Cerro Plano. Rejection frequency varied among distances, with leaf disks moved to trail margins more frequently farther from the nest.

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### Additional Observations

Each colony tended to have several trunk trails, and harvested trees tended to be between about 10-100 meters from the nest; the majority of resource trees were within 60 meters of the nest. The observed foraging area and distance of resource trees from the nest agreed with previous observations (Rockwood 1976, 1977). Leaf disks were always removed by the smallest workers on the trail, the minors, consistent with studies of caste-partitioned foraging (Rudolph 1986, Wetterer 1990), as the leaf disks were smaller than cut leaf fragments carried by larger workers. Additionally, the first ants to encounter leaf disks would not pick them up, but appeared to inspect them, before other ants arrived to remove the disks.

## DISCUSSION

With higher leaf pickup rate as well as faster recruitment closer to the nest, *A. cephalotes* colonies favored leaf samples in close proximity to the nest. These preferences reflect an optimal foraging strategy, as selecting nearby food sources minimizes search time and travel distance, and thus is more energy-efficient for the colony. Maximizing foraging strategy in this way agrees with the optimal foraging hypothesis proposed by Traniello (1989). That the relatively small leaf disks were always harvested by smaller ants reflects evidence of efficient partitioning of foraging tasks based on caste size (Rudolph 1986, Wetterer 1990). Previous research typically has explored optimal foraging patterns on a larger-scale level examining host-plant selection. However, holding constants of leaf size, leaf species, and other factors equal, we see that ants exhibit a preference for harvesting leaves based on proximity from the nest.

It should be noted that leaf samples were offered much closer to the nest than the actual resource tree from which they were obtained. If workers searching for foraging material are distributed evenly throughout the trunk trail, it would seem that leaf samples should be selected at the same rate regardless of distance. Foragers could select leaves when they happened upon them; it would be energetically optimal on an individual level (Roces and Hölldobler 1994). Perhaps forager traffic was less dense as far as 10-15 meters from the nest, explaining foraging preference at 5 meters, but ants encountered leaf disks soon after placement regardless of distance. The results indicate that there is a more complicated foraging dynamic within the colonies.

*Atta cephalotes*, like many social insects, rely on pheromones for communication, which can be used to transmit information about food sources and recruit workers to resource trees (Jaffe and Howse 1979, Traniello 1989, Farji-Brener *et al.* 2010). The number of workers recruited to a food source depends on its quality, and by varying pheromone output ants can regulate forager density on trunk trails, and thus foraging efficiency (Jaffe and Howse 1979, Farji-Brener *et al.* 2010). Because suitable resource trees can be widely dispersed, time spent searching for new food sources limits potential for optimizing foraging efficiency (Rockwood and Hubbell 1987). Thus, when leaf samples are offered along the trunk trail near the nest, foragers have quick access to food information than more distant food sources. The closer the food is to the nest, the faster information exchange and recruitment to the new food source can occur faster. Research indicates that workers are more likely to harvest a leaf the sooner they arrive to it (Shepherd 1982), and that outbound ants are more likely to find and select food after colliding into a returning worker with the same type of food (Farji-Brener *et al.* 2010). These can explain higher selection rates and recruitment closest to the nest, as ants would have encountered the most leaf-disk carrying workers in the first five meters of the trail. Though ants may not optimize as individuals, pheromone-signaled recruitment can enable more efficient foraging on a colony level by directing more ants to the nearest food source in order to minimize foraging time. Additionally, further from the nest, it may have been more energetically valuable for an ant to continue to and harvest from the actual food source (the tree), then to select a relatively small food item.

Occasionally, workers went out of their way to clear introduced leaf disks from the trail off to the edge of the leaf litter. This form of rejection must be considered. That workers would spend time and energy moving a suitable food item away from the trail seems counterintuitive from an efficiency standpoint. An explanation pertinent to optimal foraging theory may reflect communication between workers. Ants further away may receive information about food available closer to the nest and forgo harvesting, and thus remove unneeded leaf disks from the trail. If unneeded, removing these disks may have been a behavior done to clear the trails of obstructions to maintain efficient traffic flow to and from food sources (Roces and Hölldobler 1994, Howard 2001). Trails also tended to be narrower at sites 15 m from the nest entrance than the sites closer, so keeping clear pathways may have been more important where traffic is constrained. However, the leaf disks were relatively small, and would not seem to be an impediment to the ants. Evidence indicates leafcutters will remove trail obstacles as small as 0.02 g, and that doing so only incurs low energetic cost (Howard 2001). Unused leaf disks may not have been significant obstructions, but ants would not compromise efficiency in removing them either.

The foraging strategy for the colony as a whole often involves other factors that cannot be entirely explained by experimental studies; actual patterns are more complex. *Atta cephalotes*

often forage in patchy environments, where high-quality resources can be sparsely distributed (Kost *et al.* 2005). Preferences for certain plants may be influenced by more than just distance, as some studies indicate leafcutters occasionally avoid apparently suitable trees close to the nest (Rockwood and Hubbell 1987). Rather than optimize efficiency by minimizing foraging time at nearby trees, they may be selecting leaves to maximize nutritional benefits, especially for fungal growth. Leaf preference can be influenced by levels of secondary chemistry, water content, leaf toughness, nutritional payoffs, and even salt content within the foliage (Hubbell *et al.* 1984, Berish 1986, Howard 1987, Nichols-Orians & Schultz 1989, Farji-Brenner 2001, O'Donnell *et al.* 2010). Taking into account such qualities can help explain foraging strategy on the colonial level in a varied habitat. Another hypothesis explains that ants may avoid closer trees to conserve resources (Cherrett 1983), reflecting longer-term optimization over the lifetime of a colony (Shepherd 1982).

Applying optimal foraging models to *A. cephalotes* is further complicated by behavioral limitations unpredictable resource distribution. Some models assume that forager knowledge of resource base is required for optimal strategy, but individual leafcutters typically have limited knowledge of food sources (Traniello 1989). It is difficult to be optimal when many potential resource plants are unknown. Even mechanisms like trunk trails, which improve leaf transport efficiency, have trade-offs in that they restrict ability to search for new food sources (Traniello 1989).

Though this study did not consider larger-scale environmental foraging patterns, it reveals aspects of optimal foraging on a smaller scale, independent of the availability and distribution of resource trees in a colony's territory. Leafcutters may discriminate between plants due to nutritional qualities or other demands, but we see definitive foraging trends when variations in leaf type, size, and ease of extraction are constant. When offered equivalent selections of leaves, *A. cephalotes* exhibit a preference determined by proximity to the nest. This behavior is not necessarily the most efficient on an individual level, but reflects an optimization-oriented foraging strategy for the colony as a whole.

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## LITERATURE CITED

- BERISH, C.W. 1986. Leaf-cutting ants select nitrogen-rich forage. *American Midland Naturalist*. 115: 268-276.
- BURD, M. 2000. Foraging behavior of *Atta cephalotes* (leaf-cutting ants): an examination of two predictions for load selection. *Animal Behaviour*. 60: 781-788.
- CHERRETT J.M. 1983. Resource conservation by the leaf-cutting ant *Atta cephalotes* in tropical rainforest. In S.L.Sutton, T.C. Whitmore, and A.C. Chadwick (eds.). *Tropical Rain Forest: Ecology and Management*, pp. 253-263. Blackwell Scientific Publications, Oxford, UK.

- CHERRETT, J. M. 1989. Leaf-cutting ants, biogeographical and ecological studies. In H. Lieth and M. Werger (Eds.). *Ecosystem of the World* 14b, Tropical Rain Forest Ecosystems, pp. 473-488. Elsevier, Amsterdam, NL.
- FARJI-BRENER, A. 2001. Why are leaf-cutting ants more common in secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos*. 92: 169-177.
- FARJI-BRENER, A., S. AMADOR-VARGAS, F. CHINCHILLA, S. ESCOBAR, S. CABRERA, M.I. HERRERA AND C. SANDOVAL. 2010. Information transfer in head-on encounters between leaf-cutting workers: food, trail condition or orientation cues? *Animal Behavior*. 79: 343-349.
- HOWARD, J.J. 1987. Leafcutting ant diet selection: the role of nutrients, water, and secondary chemistry. *Ecology*. 68:503-515.
- HOWARD, J.J. 2001. Costs of trail construction and maintenance in the leaf-cutting ant *Atta colombica*. *Behavioral Ecology and Sociobiology*. 49: 348-356.
- HUBBELL, S.P., J.T. HOWARD, AND D.F. WIEMER. 1984. Chemical leaf repellency to an attine ant: seasonal distribution among potential host plant species. *Ecology*, 65: 1067-1076.
- KOST C., E.G. DE OLIVEIRA, T.A. KNOCH, AND R. WIRTH. 2005. Spatial-temporal permanence and plasticity of foraging trails in young and mature leaf-cutting ant colonies (*Atta* spp.). *Journal of Tropical Ecology*. 21: 677-688
- JAFFE K., AND P. E. HOWSE. 1979. The mass recruitment system of the leaf cutting ant, *Atta cephalotes*. *Animal Behavior*. 27: 930-939.
- MACARTHUR, R. H. AND E. R. PIANKA. 1966. On optimal use of a patchy environment. *The American Naturalist*. 100: 603-609.
- NICHOLS-ORIAN, C.M. AND J.C. SCHULTZ. 1989. Leaf toughness affects leaf harvesting by the leaf cutter ant, *Atta cephalotes*. *Biotropica*. 21: 80-83.
- O'DONNELL, S., J.M. GARCÍA, J. BEARD, T. CHIWOCHA, D. LEWIS, C. LIU, H. PHILLIPS, AND T. WILLIAMS. 2010. Leaf cutter ants (*Atta cephalotes*) harvest baits offering sodium chloride rewards. *Insectes Sociaux*. 57: 205-208.
- PYKE, G. H., H.R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology*. 52: 137-154.
- ROCES F. 2002. Individual complexity and self-organization in foraging by leaf-cutting ants. *The Biological Bulletin*. 202: 306-313.
- ROCES F., AND B. HÖLLDOBLER. 1994. Leaf density and a trade-off between load-size selection and recruitment behavior in the ant *Atta cephalotes*. *Oecologia*. 97: 1-8.
- ROCKWOOD, L. 1976. Plant selection and foraging patterns in two species of leaf-cutting ants (*Atta*). *Ecology*. 57: 48-61.
- ROCKWOOD, L. 1977. Foraging patterns and plant selection in Costa Rican leaf cutting ants. *Journal of the New York Entomological Society*. 85: 222-233.
- ROCKWOOD L., AND S.P. HUBBELL. 1987. Host-plant selection, diet diversity, and optimal foraging in a tropical leafcutting ant. *Oecologia*. 74: 55-61.
- RUDOLPH, S.G. AND C. LOUDON. 1986. Load size selection by foraging leaf-cutter (*Atta cephalotes*). *Ecological Entomology*. 11: 401-410.
- SHEPERD, J. D. 1982. Trunk trails and the searching strategy of a leaf-cutter ant, *Atta colombica*. *Behavioral Ecology and Sociobiology*. 11: 77-84.
- TRANIELLO, J. 1989. Foraging strategies of ants. *Annual Review of Entomology*. 34:191-210.
- WETTERER, J.K. 1990. Load-size determination in the leaf-cutting ant, *Atta cephalotes*. *Behavioral Ecology*. 1: 95-101.
- WILSON, E.O. 1980. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). *Behavioral Ecology and Sociobiology*. 7: 143-156.