

Branching angles reflect a trade-off between reducing trail maintenance costs or travel distances in leaf-cutting ants

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Abstract. The design of transport paths in consuming entities that use routes to access food should be under strong selective pressures to reduce costs and increase benefits. We studied the adaptive nature of branching angles in foraging trail networks of the two most abundant tropical leaf-cutting ant species. We mathematically assessed how these angles should reflect the relative weight of the pressure for reducing either trail maintenance effort or traveling distances. Bifurcation angles of ant foraging trails strongly differed depending on the location of the nests. Ant colonies in open areas showed more acute branching angles, which best shorten travel distances but create longer new trail sections to maintain than a perpendicular branch, suggesting that trail maintenance costs are smaller compared to the benefit of reduced traveling distance. Conversely, ant colonies in forest showed less acute branching angles, indicating that maintenance costs are of larger importance relative to the benefits of shortening travel distances. The trail pattern evident in forests may be attributable to huge amounts of litterfall that increase trail maintenance costs, and the abundant canopy cover that reduces traveling costs by mitigating direct sunlight and rain. These results suggest that branching angles represent a trade-off between reducing maintenance work and shortening travel distances, illustrating how animal constructions can adjust to diverse environmental conditions. This idea may help to understand diverse networks systems, including urban travel networks.

Key words: ant behavior; ant foraging; *Atta cephalotes*; *Atta colombica*; Costa Rica; dendritic systems; extended phenotype; foraging trails; Panama; tropical forests.

INTRODUCTION

The physical structures that animals build can reflect how organisms deal with ecological trade-offs. Given that natural selection operates on the builders through the success of the structures that they build, analyzing how these structures vary among conditions with different costs and benefits allows us to better understand the adaptive nature of animal behaviors. Moreover, animal constructions are often easier to examine, manipulate, and measure than the animal actions themselves (Hansell 2005). For these reasons, animal constructions are considered functionally versatile extensions of their phenotype and a straightforward way

to study how organisms adjust to changing environments (Turner 2009).

Leaf-cutting ants (*Atta* and *Acromyrmex*) are an ideal group in which to study the adaptive significance of animal constructions because they build long-lasting, conspicuous structures. These ants cut huge amounts of plant biomass from the surrounding vegetation and carry it back to the nest, where the plant fragments are used as a substrate for a symbiotic fungus that they cultivate inside underground chambers (Wirth et al. 2003). This removal of plant tissue by sessile ant colonies depends on the construction and maintenance of an extensive system of cleared foraging trails that guide foragers to plant sources and facilitate resource monitoring, worker locomotion, information transfer, and leaf transport efficiency (Shepherd 1982, Rockwood and Hubbell 1987, Wirth et al. 2003, Kost et al. 2005, Farji-Brener et al. 2010). Because the way in which organisms explore space in order to discover and retrieve food is

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vital for reproductive success, leaf-cutting ants should design a trail network that maximizes their benefits and minimizes their costs.

The construction of this essential transport network for leaf-cutting ants clearly represents a benefit for the colony, but also entails costs (Burd et al. 2002, Bruce and Burd 2012). As discussed earlier, trunk trails lead foragers to known resources and reduce traveling time (Rockwood and Hubbell 1987). This advantage allows for more round trips per worker, as well as less time exposed to natural enemies, direct sun, and rain, all factors that may reduce the foraging efficiency of ants. However, maintaining this large and permanent trail system free of debris requires time and energy (Lugo et al. 1973; but see Howard 2001). Overall, leafcutters are constantly expanding the foraging trail system by building branches to monitor and collect new plant sources (Kost et al. 2005, Silva et al. 2013), but this expansion also represents investments in trail cleaning to keep the trail network operational.

The building of trail branches generates a conflict between shortening travel distances and reducing trail maintenance work. Leafcutters often explore new food items in the vicinity of established trails (Shepherd 1982, Farji-Brener and Sierra 1993). When a newly discovered patch represents a palatable and a relatively stable food source, ants build a cleared trail branch connecting this patch with the nearest established trail, creating the typical dendritic nature of the trail network (Kost et al. 2005, Silva et al. 2013). However, this connection can be built at different branching angles that minimize either the distance between the food source and the nest, or the length of the new segment (Fig. 1).

For example, if the new trail branch is built at an angle of 90° (perpendicular to the main trail), the ants will clear and maintain the shortest possible new path, but foragers will have to walk a longer distance from the nest to the food source than if the new trail segment were at a more acute angle. Conversely, if the new trail branch is established at an acute angle from the main trail, foragers would walk a shorter distance from the nest to the new food source, but the colony would have to maintain a larger new trail segment than if it were perpendicular to the main trail (Fig. 1). These conflicting alternatives, depicted as changes in the branching angle, are independent of the distance between the main trail and the newly discovered food source (Appendix A). We propose that this trade-off depends on context, and that ants adaptively adjust the angles of the trail bifurcations depending on habitat features that may unequally affect traveling and trail maintenance costs.

Benefits and costs might vary with changes in habitat characteristics. In particular, the relative importance of reducing travel distances and trail maintenance effort may depend on the environment through which leaf-cutter ant trails pass. Forests may impose higher trail maintenance costs compared to open areas because litter is constantly falling onto the forest ground. For

example, in leaf-cutting ants, the estimated cost of removing a kilogram of litter from trails is ~ 4000 ant-hours. Annually, this work requires $\sim 10\,000$ ant-days of work per year by trail clearers in forest colonies (Howard 2001). Conversely, shortening travel distances could be more relevant in open areas than in closed forest, because foragers are exposed to direct sunlight and rain, which decrease foraging activity (Whitford and Ettershank 1975, Mintzer 1979, Hart et al. 2002, van Oudenhove et al. 2011, Ribeiro et al. 2012). Directly quantifying the costs and benefits that forest and open areas impose on leaf-cutting ants by measuring the production of sexual individuals or colony growth is a very difficult task to achieve using mature colonies in natural conditions (Hölldobler and Wilson 2010). However, costs and benefits may be indirectly and easily compared from changes in the design of foraging trails.

The branching angles of trails in the forest and in open areas could indirectly indicate which factor has a larger effect on the trail construction process. We will explain the mathematical rationale and show the function to assess the benefits of reducing the distance from the nest to the food source when a new trail section is built at an acute angle rather than perpendicular to the main trail. Consider a new food source located at a site N , at a minimum distance m from a main trail, i.e., at 90° (Fig. 1). Let d be the distance between M (the intersection point of the perpendicular straight line that connects the main trail with N) and the bifurcation point B where the new trail leaves the established trail. The length of new trail that the ants build and maintain when using angles lower than 90° is $\sqrt{m^2 + d^2}$, or h , the hypotenuse of the triangle (Fig. 1). Then we have an efficiency function

$$b(d) = m + d - h \quad (1)$$

that measures the net benefit (reduction in distance units) of building at a certain angle compared to a perpendicular branch m . Here, $b(d)$ is equivalent to NP (net profit) in Fig. 1. Similarly, we can calculate a function for the cost (c) of maintaining a longer new trail section at a certain angle relative to the minimum length of the new trail (the perpendicular branch m) as:

$$c(d) = h - m. \quad (2)$$

This function measures the additional distance built (in distance units) compared to the minimum trail length they could have built at 90° . A trade-off function takes the traveling benefits (Eq. 1) and subtracts the maintenance costs (Eq. 2) multiplied by a factor α that weights the importance of the costs relative to the benefits in determining the branching angle:

$$\begin{aligned} f(d) &= b(d) - \alpha c(d) = (m + d - h) - \alpha(h - m) \\ &= (m - \sqrt{m^2 + d^2})(1 + \alpha) + d. \end{aligned} \quad (3)$$

The distance d and the corresponding angle that maximizes $f(d)$ would be the angle that provides the

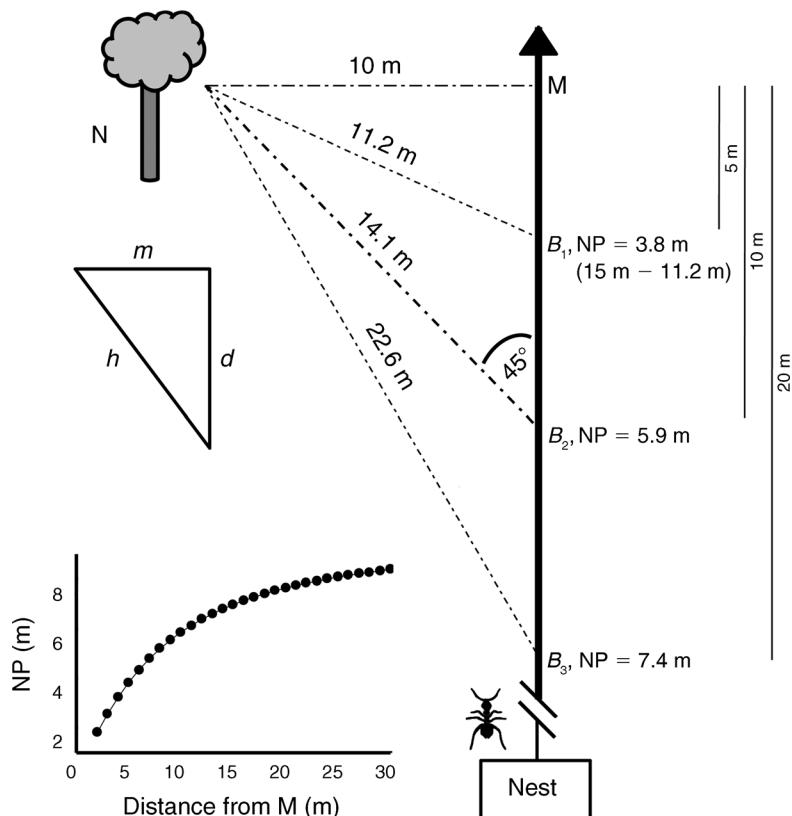


FIG. 1. This example illustrates the conflict for leaf-cutting ants between shortening travel distances and reducing trail maintenance work. The diagram shows different connection routes (h) between an established foraging trail and a recently discovered, fixed-point food source (N). Building new trail branches perpendicular to N (here, at fixed point M on the main trail) entails the lowest trail maintenance effort, even though this is the worst option for reducing overall travel distance by foragers. In the example, a branching angle of 90° (at point M with minimum (i.e., perpendicular) distance m between N and the main trail) requires maintaining 10 m of new trail, but traveling 15 m with respect to the bifurcation point (B_1) of the first shortcut (5 m + 10 m). At B_1 , the length of the new trail is 11.2 m, 1.2 m longer than the 90° branch at M, but the overall distance that foragers should walk is shortened by 3.8 m (net profit, NP). The second option at B_2 illustrates a shortcut at 45° . This alternative generates a trail branch 4.1 m longer than the branch at 90° (14.1 m – 10 m), and a net reduction in the overall travel distance (NP) of 5.9 m (20 m – 14.1 m). The third alternative at B_3 illustrates a branch with a bifurcation angle $< 45^\circ$, where the new trail section would be 12.6 m longer than the branch at 90° (22.6 m – 10 m), but the overall travel distance is reduced (NP) by 7.4 m (30 m – 22.6 m). Hence, new trail branches established at an acute angle from the main trail shorten the distance from the nest to the new food source, but create larger new trail segments to maintain than a branch perpendicular to the main trail. The triangle formed by the distance (d) along the main trail between the new branch trail at B and point M perpendicular to new food source N, the perpendicular branch distance (m) and the hypothetical shortcut distance (h). The graph inset shows how the net profit (NP) varies with the distance between a branching angle of 90° (at M) or smaller branching angles, B (shortcut distances, h). See the mathematical rationale in Appendix A.

largest net benefit. That optimal angle depends on how important the costs are relative to the benefits, i.e., it depends on the weight of each factor on the colony performance as given by α in the trade-off Eq. 3. Now, it is simple to find the distance d that maximizes the net benefit. Setting the derivative equal to zero and solving for d yields:

$$f'(d) = 1 - \frac{(1 + \alpha)d}{\sqrt{m^2 + d^2}} = 0 \rightarrow d = \frac{m}{\sqrt{(1 + \alpha)^2 - 1}}. \quad (4)$$

This distance corresponds to an optimal branching angle (see Appendix A) of

$$\theta = \text{atan}\left(\sqrt{(1 + \alpha)^2 - 1}\right) \quad (5)$$

where atan represents the arctangent. Therefore, the optimal branching angle depends only on α ; that is, the weight of the costs relative to the benefits. For instance, if α tends to 0 (i.e., when the additional maintenance costs relative to a perpendicular branch are negligible compared to the relative savings in traveling distance for the foragers), d tends to ∞ , and the angle that maximizes the equation tends to zero. In other words, if trail maintenance had no costs, going directly from the nest to the new food source is more beneficial than building a branch from a main trail. Conversely, if α tends to ∞ , d tends to 0, and the branching angle tends to 90° . That is,

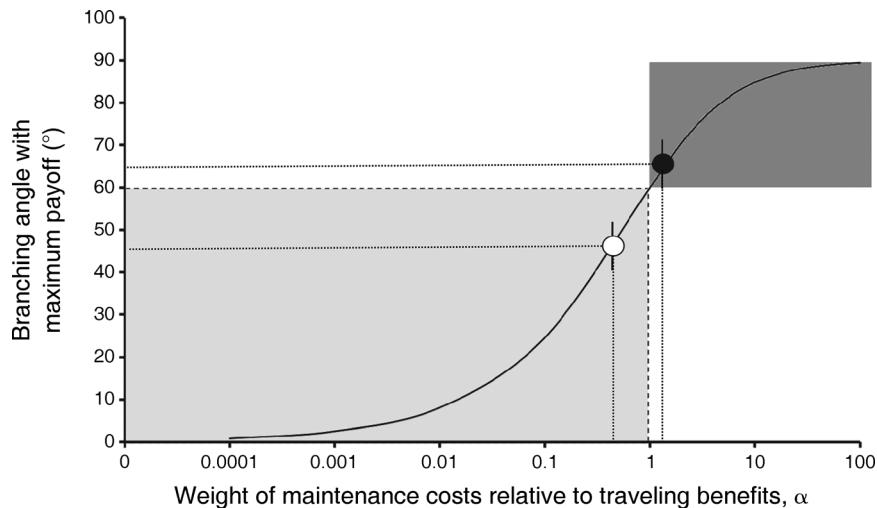


FIG. 2. Optimized trade-off function (solid line) showing the branching angles (y -axis) that yield the maximum payoff depending on a factor α , which weights the importance of the costs of maintaining a larger new trail segment relative to the benefits of walking shorter distances from the nest (x -axis, log scale). The angle with the highest payoff depends on the balance between costs and benefits: at $\alpha = 1$, trail maintenance costs are of equal importance to the benefits of shortening travel distances in determining trail design, and the trade-off function yields a maximum payoff when branches are at 60° (dashed line); $\alpha < 1$ implies that trail maintenance costs are relatively less important than shortening travel distances, and maximum payoffs are obtained with branching angles $< 60^\circ$ (light gray area); $\alpha > 1$ means that trail maintenance costs are relatively more important than shortening travel distances, where maximum payoffs are obtained with branching angles $> 60^\circ$ (dark gray area). The circles represent the mean branching angle (error bars show SE) found in forest ant colonies (black) and in open-area ant colonies (white). The mathematical rationale of this trade-off function is explained in Appendix A.

if the cost of trail maintenance were much larger than the benefit of walking shorter distances, ants should build trail branches perpendicular to the main trail. For each weight (α) there is an angle that yields a maximum gain for the trade-off function (Fig. 2). Accordingly, we expect branching angles $> 60^\circ$ to be found in forest colonies (i.e., where trail maintenance costs are relatively more important than shortening travel distances, $\alpha > 1$), and branching angles $< 60^\circ$ in colonies located in open areas (i.e., where shortening travel distances are relatively more important than trail maintenance costs, $\alpha < 1$; Fig. 2). We tested this idea by measuring branching angles for a large number of *Atta* colonies inhabiting contrasting tropical habitats.

METHODS

Study area

Fieldwork was conducted during 2011, 2012, and 2013, in tropical wet forests and open habitats of Costa Rica (10° N, 83° W) and Panamá (9° N, 79° W). In Costa Rica, the majority of nests were sampled at La Selva Biological Station (LS), in the Caribbean lowlands of Costa Rica. La Selva is a field station operated by the Organization for Tropical Studies (OTS) and has ~ 4000 mm of rain annually. A complete description of this site is available in McDade (1994). We also sampled ant nests in Monteverde cloud forests and in a transitional dry-wet forest belt in the Cacao-Maritza biological corridor near the Nicaraguan border. In Panamá, the majority of nests were sampled at Barro Colorado

Island (BCI), a field station of the Smithsonian Tropical Research Institute (STRI), and around Pipeland Road (Gamboa), Soberanía National Park. These sites receive ~ 2600 mm rain annually. A full flora and habitat description of these sites are available in Croat (1978) and Leigh et al. (1982).

Ant species and methodology

In these areas we searched for nests of *Atta cephalotes* and *Atta colombica*, the most common leaf-cutting ant species in Central America (Hölldobler and Wilson 2010). These species build conspicuous, long-lasting trail networks that are free of debris. Trunk trails can reach up to 100 m long, and a trail network of a mature nest might have several branching points (Silva et al. 2013). Both ant species inhabit wet forests, but can also be found in disturbed, open areas (Farji-Brener 2001). We sampled a total of 79 trail bifurcations from 40 mature *Atta* nests (64 from *A. cephalotes* and 15 from *A. colombica*), 40 in forests and 39 in open areas. Nests located in forest were randomly selected while walking in primary and secondary forests of the biological reserves, and those in open areas were mainly located around research facilities and nearby disturbed habitats. Both habitats were near each other in both the Costa Rica and Panama sampling sites. In all sites, the sampling procedure was the same. In each nest, we selected about three main trails and used a protractor to carefully measure the branching angle of one randomly selected bifurcation per trail. The direction of the main



FIG. 3. Two foraging trails from nests of the leaf-cutting *Atta cephalotes* located in forest (left) and open areas (right) of Costa Rica. Note the amount of litterfall around the cleared trail in the forest colony, and its absence around the cleared trail in the open area colony. Photo credit: A. G. Farji-Brener.

trail was considered the “North” (i.e., 0° degrees) and was used as reference to measure the branching angle. Trail branches were normally located at 5–40 m from the nest. We considered bifurcations from different trails as independent samples because the discovery of a new food source and the subsequent building of a new trail branch in different trails of the same nest are often performed by different ant workers (Farji-Brener and Sierra 1998, Elizalde and Farji-Brener 2012). Nest location was characterized by the presence or absence of tree cover and litterfall on the ground. This categorization (i.e., forests vs. open areas) was clear-cut; open areas normally were dominated by an herbaceous layer without trees, exposed to direct sun and rain, and lacked tree litterfall on the ground. Conversely, forest understory was characterized by low direct sunlight and rainfall, and had large amounts of litter on the ground (Fig. 3). To compare the branching angles between nests in open areas and forest, we used a two-way ANOVA. Habitat type (open areas vs. forest) and ant species (*A. cephalotes* vs. *A. colombica*) were both considered as fixed factors. Branching angle was the response variable. The data met the ANOVA assumptions and no transformation was needed.

In a selected subset of trails, we confirmed whether the measured branching angle correctly pointed to the food source location. In 20 randomly selected trail bifurcations (10 in open areas and 10 in closed forests; 12 of *A. cephalotes* and 8 of *A. colombica*), we followed the trail branch from the bifurcation point to the harvested food source. Subsequently, with the help of a compass, we connected both points in a straight line with a tape measure on the ground. We measured the angle formed by the intersection of this line and the main trail (LA, angle *in line* with the food source) and compared it with the measured branching angle (BA). If the trail branch pointed properly to the location of the food source, we expected both angles to be similar (i.e., $LA - BA \approx 0$). We tested whether the subtraction between these two angles was different from zero using a *t* test for a single sample ($n = 20$).

RESULTS

Branching angles of both ant species showed high variability. Overall, the lowest bifurcation angle found was 21° (for *A. cephalotes* in open areas) and the straightest was 90° (for both species in forest habitats). Branching angles were affected by habitat type ($F_{1,75} = 21.7$, $P < 0.0001$), but not by ant species ($F_{1,75} = 0.94$, $P = 0.36$) or the interaction between them ($F_{1,75} = 0.72$, $P = 0.40$; Fig. 4). For both ant species, branching angles were consistently smaller in open areas ($43^\circ \pm 4^\circ$, mean \pm SE; 95% CI = $[35^\circ, 51^\circ]$) than in forests ($65^\circ \pm 2^\circ$, $[60.3\text{--}69.5]$; Fig. 2). We found the same trend when using each ant colony as replicate (see Appendix B for ANOVA tables). Branching angles often properly pointed to the position of the food source. The mean angle generated by $LA - BA$ (0.6°) was statistically indistinguishable from zero ($t = 0.8$, $df = 19$, $P = 0.40$; $[-0.9^\circ, 2^\circ]$). Although sometimes the trail branch was not connected to the food source by a straight line (i.e., the branch was winding to avoid physical obstacles), initial branching angles at the bifurcation with the main trail

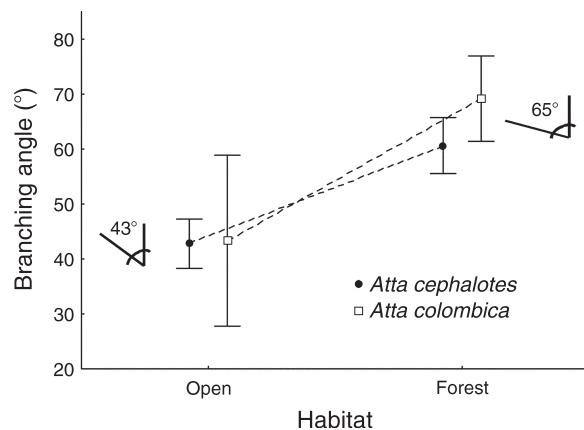


FIG. 4. Branching angles (mean with 95% CI) found in foraging trails of the leaf-cutting ants *Atta cephalotes* and *Atta colombica* in open areas and forests.

almost always pointed directly to the position of the food source.

DISCUSSION

The architecture of transport paths can affect the rate of food input in consuming entities that use routes to access food, including super organisms such as leaf-cutting ant nests (Bruce and Burd 2012). Therefore, the design of foraging trail networks should be under strong selective pressure to reduce costs and maximize benefits. We found that, in both leaf-cutting ant species, the bifurcation angles of trails strongly differ depending on the location of the ant colony. These results support the predictions of our mathematical model, suggesting that the branching angles of leaf-cutting ants reflect a trade-off between reducing trail maintenance costs and shortening travel distances, costs that vary in their relative importance in different habitats.

The acute branching angles of ant colonies in open areas ($\sim 43^\circ$) suggest that construction of new trail sections is largely driven by reducing traveling distance to the nest. According to our mathematical model, this branching angle suggests that trail maintenance costs are half as important as shortening travel distances ($\alpha = 0.5$; Fig. 2). The reduced amount of litterfall could make trails less costly to maintain in open areas, but foragers are directly exposed to sun and rain, which would favor the construction of a new segment that reduces traveling distance, even when ants have to maintain a larger section. Direct sunlight exposure may limit ant foraging (Whitford and Ettershank 1975, Mintzer 1979) by (1) affecting oxygen consumption and water loss, thus increasing costs in ant transport (Lighton and Feener 1989); (2) increasing the desiccation rate of the leaf fragments, thus negatively affecting fungal growth (Bowers and Porter 1981); and (3) accelerating pheromone evaporation, thus reducing trail-following behavior and ant recruitment intensity (van Oudenhove et al. 2011). Field observations confirm the negative effect of high temperatures on ant foraging; at noon, colonies in open areas showed no foraging activity, whereas those located in the darkest forest understory usually had foraging activity. Additionally, ants suffer stronger negative effects of direct rain in open areas than in forests because of the absence of a canopy that intercepts rainfall. In fact, leaf-cutting ants stop foraging and abandon the leaf fragments during rain (Hart et al. 2002). In other words, walking in open areas might be more costly than walking in the forest understory for leaf-cutting ants. These abiotic restrictions on foraging and the absence of litterfall probably explain why reducing walking distance is the main driver of trail branching design in open areas.

Conversely, ant colonies in forests built trail branches at angles that shortened the length of new trail sections, but that were not perpendicular to the main trail ($\sim 65^\circ$), which suggests that maintenance costs in forest are of greater importance than the benefits of shortening travel

distances, but that traveling costs are not negligible. Precisely, the mean branching angle found in forest corresponds to maintenance costs being an additional 50% more important than traveling benefits in determining branching angles ($\alpha = 1.5$; Fig. 2). This could be (1) because maintenance costs are higher in forest than in open areas, or (2) because the benefits of shortened traveling distances are relatively small in forest compared to open areas, or (3) a combination of both. Foraging trails in forest receive huge amounts of litterfall, which must be constantly removed to maintain the trail system in operational condition. Trails without maintenance are completely covered by litter in a few days (Howard 2001, Evison et al. 2008; A. G. Farji-Brener, *personal observations*). On the other hand, the forest understory receives considerably less direct sunlight and rain compared to the ground of open areas. Hence, it is logical to hypothesize that colonies located in forests experience less selective pressure to shorten travel distances, but higher selective pressure to reduce the length of new trail sections (i.e., minimizing trail maintenance work) compared to colonies located in open areas.

A potential criticism to our interpretation is that the difference in branching angles between open areas and forests might be a consequence of restrictions in the use of certain orientation cues. For example, if ants are guided visually by celestial and terrestrial cues, they might orient themselves better in open areas (with more visual access to the sky and to isolated trees as stable landmarks) than in forests. Consequently, ants might be able to build better shortcuts in open areas than in the forest understory. However, this appears not to be the case. Leaf-cutting ants can use a variety of directional cues (Vilela et al. 1987), but they often orient themselves using the earth's magnetic field (Banks and Srygley 2003, Riveros and Srygley 2008). Moreover, leafcutters often forage at night, when visual cues are trivial. Hence, changes in the ability of ants to build adequate shortcuts do not satisfactorily explain the different branching angles between open areas and forests, a pattern that we believe is best explained by a compromise between shortening travel distances and reducing trail maintenance costs. Another potential flaw of this work is that we could not monitor the formation of trails to demonstrate our hypothesis (our experiment was unsuccessful; see Appendix C). Nonetheless, we consider that the examination of trail building is not essential to test our idea. It is the angle that trails finally achieve, regardless of what early stages of branch formation they go through, that will determine the costs and benefits over the long run of harvesting from a source.

Other studies have also considered the design of ant foraging trails to be the result of optimization processes. Branching angles have been interpreted as a compromise between (1) finding the shortest way to the main trail or to the nest (Acosta et al. 1993); (2) maximizing food intake of known resources and exploring for novel food

patches (Jackson et al. 2004); and (3) establishing trails that provide efficient access to high-quality resources (Kost et al. 2005, Buhl et al. 2009). Branching design often tends to maximize acquisition of food, because trail branching normally directs ants to areas with highly palatable resources. For example, seed-eating ants and leaf-cutting ants branch the trunk trails in areas with high abundance of seed sources (López et al. 1993) and high abundance of palatable plant species (Silva et al. 2012, 2013), respectively. Nevertheless, as far as we know, this work is the first that explain why branching angles may differ between colonies, and to use this simple measure to understand the compromise between the need for reducing trail maintenance work and reducing travel distances. The integration of these selective forces with the others discussed previously may help to better understand the nature of branching design of ant trail networks and other biological ramified structures.

Bifurcations are observed widely in nature, such as in dendrites and axons of neurons, tracheal or vascular systems, corals, and plants (Turcotte et al. 1998). In all of these systems, the maintenance costs, as well as the need to reduce distances between the bifurcation and the target point, are highly dependent on context, allowing for the formation of different branching angles. For example, bifurcation angles of roots and tree branches may differ in contexts that strongly diverge in resource availability or competition level. When a general scarcity of resources imposes high maintenance costs for plants, branching angles should be close to 90° to reduce the length of new structures. Conversely, when nearby plants strongly compete via roots for transient water or soil nutrients (Rajaniemi 2007), or via branching for light after a tree-fall gap (Vepakomma et al. 2010), branching structures should be more acute in order to access those resources as quickly as possible. Similar parallels might be expected in vascular systems or neuronal networks (Cuntz et al. 2007, Huo et al. 2012). Finally, the knowledge of this trade-off could also lead to a better travel network design in human cities (Guihaire and Hao 2008). For example, secondary roads should be built with angles near 90° in areas with high probability of road damage, to diminish the maintenance work required. Conversely, bifurcations should be built at more acute angles in situations where shorter travel distances are critical, such as hospital accesses. Moreover, our conceptual framework (Fig. 2) may guide the building of bifurcations according to the a priori knowledge of the relative importance of maintenance costs and the benefits of shorter distances (i.e., α value). Overall, the idea that branching angles reflect a trade-off between the reductions in maintenance costs and reductions in travel distances illustrates well how animal constructions adjust to diverse environmental conditions. This working hypothesis may be useful for understanding a diversity of network systems, and could offer some practical implications for urban planning.

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LITERATURE CITED

- Acosta, F., F. López, and M. Serrano. 1993. Branching angles of ant trunk trails as an optimization cue. *Journal of Theoretical Biology* 160:297–310.
- Banks, A. N., and R. B. Srygley. 2003. Orientation by magnetic field in leaf-cutter ants, *Atta colombica* (Hymenoptera: Formicidae). *Ethology* 109:835–846.
- Bowers, M., and S. Porter. 1981. Effect on foraging distance on water content of substrates harvested by *Atta colombica*. *Ecology* 62:273–275.
- Bruce, A. I., and M. Burd. 2012. Allometric scaling of foraging rate with trail dimensions in leaf-cutting ants. *Proceedings of the Royal Society B* 279:2442–2447.
- Buhl, J., K. Hicks, E. R. Miller, S. Persey, O. Alinvi, and D. Sumpter. 2009. Shape and efficiency of wood ant foraging networks. *Behavioral Ecology and Sociobiology* 63:451–460.
- Burd, M., D. Archer, N. Aranwela, and D. J. Stradling. 2002. Traffic dynamics of the leaf-cutting ant, *Atta cephalotes*. *American Naturalist* 159:283–293.
- Croat, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Redwood City, California, USA.
- Cuntz, H., A. Borst, and I. Segev. 2007. Optimization principles of dendritic structure. *Theoretical Biology and Medical Modeling* 4:21.
- Elizalde, L., and A. G. Farji-Brener. 2012. To be or not to be faithful: flexible fidelity to foraging trails in the leaf-cutting ant *Acromyrmex lobicornis*. *Ecological Entomology* 37:370–376.
- Evison, S., A. G. Hart, and D. E. Jackson. 2008. Minor workers have a major role in the maintenance of leafcutter ant pheromone trails. *Animal Behavior* 75:963–969.
- Farji-Brener, A. G. 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. *Oikos* 92:169–177.
- Farji-Brener, A. G., S. Amador-Vargas, F. Chinchilla, S. Escobar, S. Cabrera, M. Herrera, and C. Sandoval. 2010. Information transfer in head-on encounters between leaf-cutting ant workers: food, trail condition or orientation cues? *Animal Behavior* 79:343–349.
- Farji-Brener, A. G., and C. Sierra. 1993. Distribution of attacked plants along trails in leaf-cutting ants: consequences in territorial strategies. *Revista de Biología Tropical* 41:555–560.
- Farji-Brener, A. G., and C. Sierra. 1998. The role of trunk trails in the scouting activity of the leaf-cutting ant *Atta cephalotes*. *Ecoscience* 5:271–274.
- Guihaire, V., and J. K. Hao. 2008. Transit network design and scheduling: A global review. *Transportation Research Part A: Policy and Practice* 42:1251–1273.
- Hansell, M. H. 2005. *Animal architecture*. Oxford University Press, Oxford, UK.
- Hart, A., C. Anderson, and F. Ratnieks. 2002. Task partitioning in leaf-cutting ants. *Acta Ethologica* 5:1–11.
- Hölldobler, B., and E. O. Wilson. 2010. *The leafcutter ants: civilization by instinct*. W. W. Norton, New York, New York, USA.
- Howard, J. J. 2001. Costs of trail construction and maintenance in the leaf-cutting ant *Atta colombica*. *Behavioral Ecology and Sociobiology* 49:348–356.

- Huo, Y., G. Finet, T. Lefevre, Y. Louvard, I. Moussa, and G. Kassab. 2012. Which diameter and angle rule provides optimal flow patterns in a coronary bifurcation? *Journal of Biomechanics* 45:1273–1279.
- Jackson, D. E., M. Holcombe, and W. Ratnieks. 2004. Trail geometry gives polarity to ant foraging networks. *Nature* 432:907–909.
- Kost, C., E. G. de Oliveira, T. A. Knoch, and R. Wirth. 2005. Spatio-temporal permanence and plasticity of foraging trails in young and mature leaf-cutting ant colonies (*Atta* spp.). *Journal of Tropical Ecology* 21:677–688.
- Leigh, E. G., A. S. Rand, and D. Windsor. 1982. *The ecology of a tropical forest*. Smithsonian Institution, Washington, D.C., USA.
- Lighton, J., and D. H. Feener. 1989. Water-loss rate and cuticular permeability in foragers of the desert ant *Pogonomyrmex rugosus*. *Physiological Zoology* 62:1232–1256.
- López, F., F. J. Acosta, and J. M. Serrano. 1993. Responses of the trunk routes of a harvester ant to plant density. *Oecologia* 93:109–113.
- Lugo, A. E., E. G. Farnworth, D. Pool, P. Jerez, and G. Kaufman. 1973. The impact of the leaf cutter ant *Atta colombica* on the energy flow of a tropical wet forest. *Ecology* 54:1292–1301.
- McDade, L. A., editor 1994. *La Selva: ecology and natural history of a Neotropical rain forest*. University of Chicago Press, Chicago, Illinois, USA.
- Mintzer, A. 1979. Foraging activity of the Mexican leaf-cutting ant *Atta mexicana* in a Sonoran Desert habitat (Hymenoptera, Formicidae). *Insectes Sociaux* 26:364–372.
- Rajaniemi, T. K. 2007. Root foraging traits and competitive ability in heterogeneous soils. *Oecologia* 153:145–152.
- Ribeiro, P. L., A. Camacho, and C. A. Navas. 2012. Considerations for assessing maximum critical temperatures in small ectothermic animals: insights from leaf-cutting ants. *PLoS ONE* 7:e32083.
- Riveros, A. J., and R. B. Srygley. 2008. Do leafcutter ants, *Atta colombica*, orient their path-integrated home vector with a magnetic compass? *Animal Behavior* 75:1273–1281.
- Rockwood, L. L., and S. P. Hubbell. 1987. Host-plant selection, diet diversity, and optimal foraging in a tropical leaf-cutting ant. *Oecologia* 74:55–61.
- Shepherd, J. D. 1982. Trunk trails and the searching strategy of a leaf-cutter ant, *Atta colombica*. *Behavioral Ecology and Sociobiology* 11:77–84.
- Silva, P., A. Bieber, T. A. Knoch, M. Tabarelli, I. R. Leal, and R. Wirth. 2013. Foraging in highly dynamic environments: leaf-cutting ants adjust foraging trail networks to pioneer plant availability. *Entomologia Experimentalis et Applicata* 147:110–119.
- Silva, P., I. R. Leal, R. Wirth, F. P. Melo, and M. Tabarelli. 2012. Leaf-cutting ants alter seedling assemblages across second-growth stands of Brazilian Atlantic forest. *Journal of Tropical Ecology* 28:361–368.
- Turcotte, D. L., J. D. Pelletier, and W. I. Newman. 1998. Networks with side branching in biology. *Journal of Theoretical Biology* 193:577–592.
- Turner, J. S. 2009. *The extended organism: the physiology of animal-built structures*. Harvard University Press, Cambridge, Massachusetts, USA.
- van Oudenhove, L., E. Billoir, R. Boulay, C. Bernstein, and X. Cerdá. 2011. Temperature limits trail following behavior through pheromone decay in ants. *Naturwissenschaften* 98:1009–1017.
- Vepakomma, U., B. St-Onge, and D. Kneeshaw. 2010. Response of a boreal forest to canopy opening: assessing vertical and lateral tree growth with multi-temporal lidar data. *Ecological Applications* 21:99–121.
- Vilela, E. F., K. Jaffě, and P. E. Howse. 1987. Orientation in leaf-cutting ants (Formicidae: Attini). *Animal Behavior* 35:1443–1453.
- Whitford, W. G., and G. Ettershank. 1975. Factors affecting foraging activity in Chihuahuan Desert harvester ants. *Environmental Entomology* 4:689–696.
- Wirth, R., H. Herz, I. Rye, W. Beyschlag, and B. Hölldobler. 2003. *Herbivory of leaf-cutting ants*. Springer-Verlag, Berlin, Germany.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-0220.1.sm>