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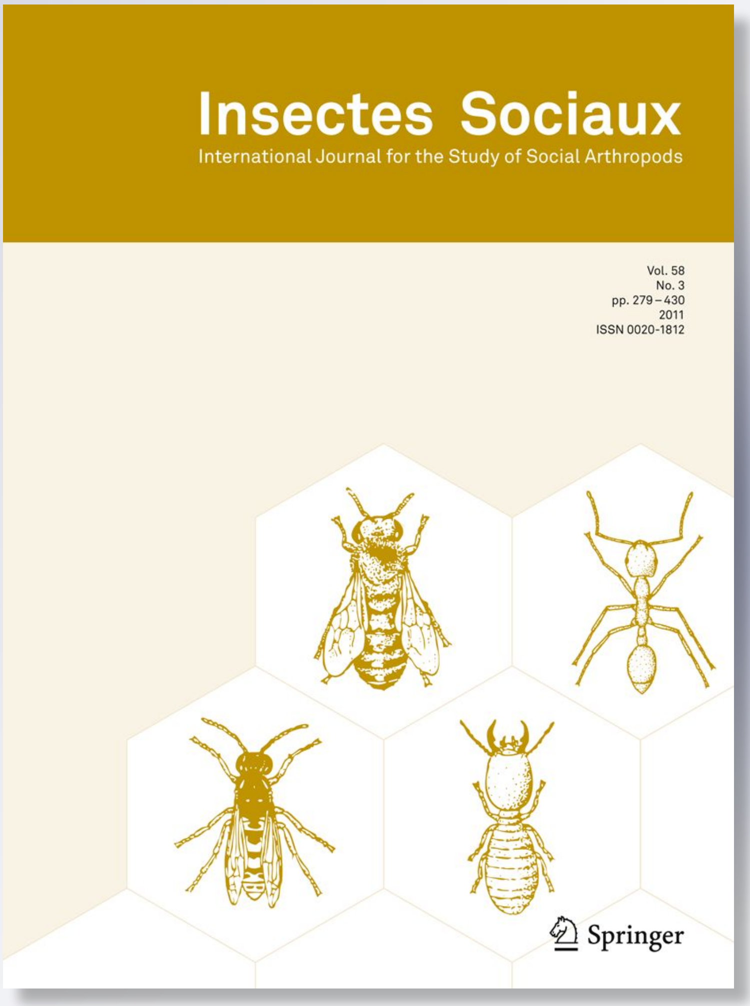

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RESEARCH ARTICLE

Leaf-cutting ants as road engineers: the width of trails at branching points in *Atta cephalotes*

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Abstract We used a simple engineering principle, which suggests that the width of a road needed for a smooth traffic flow is proportional to the peak traffic volume ("engineering hypothesis"), to analyze the adaptive significance of trail width at branching points in the leaf-cutting ant *Atta cephalotes*. Since the flow of outgoing ants splits at trail bifurcations and merges when ants return to the nest through the same paths, the sum of branch widths should equal the width of the trail section upstream of the bifurcation. We measured the width of branches and their preceding trail section and also performed field measurements and manipulations to analyze ant flow, number of collisions, and ant speed in different trail sectors. Contrary to the prediction of the "engineering hypothesis", the sum of branch widths was larger than the width of the trail immediately before the bifurcation. Our data contradict the "trail addition hypothesis" and support the "border effect hypothesis" to explain this pattern. First, the width of the widest branch was smaller than the width of the trail upstream of the bifurcation, an unexpected result if one branch is merely the continuation of the basal trail. Second, ants collided with obstacles more often in the margin than in the central portion of the trail, relocated ants from central to margin trail sectors reduced their speed, and ant flow was higher in the central sections of the trail. Since the delaying effect of trail margins increases as the trail width decreases, ants may build branches wider than expected to reduce the border effect. The delaying effect of trail margins should be included in the analysis of costs and benefits to fully understand the adaptive value of the design of ant trail networks.

Keywords Ants · Building behavior · Costa Rica · Foraging trails · Trail design

Introduction

Many animals produce a range of structures to modify their surroundings adaptively and control the flow of energy and matter between them and their environment (Turner, 2000). These structures may vary within a species in shape, form, and design, affecting their efficiency. Since natural selection operates on the builders through the success of the structures that they build, the constructions of animals are considered functionally versatile extensions of their phenotype (Hansell, 2005). Therefore, the study of animal-built structures is often a simple and integrative way to understand the adaptive behavior of organisms.

Leaf-cutting ants (*Atta* and *Acromyrmex*) are an ideal group to study the adaptive significance of the constructions

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of animals due to their enormous colony size and the conspicuous structures that they build. Leaf-cutters form the largest colonies known among social insects, with up to several million workers occupying a single nest (Fowler et al., 1986). These ants cut tissue from the surrounding vegetation and carry it back to their nest, where the plant fragments are used as a substrate for a symbiotic fungus that they cultivate inside underground chambers. Hence, leaf-cutters build structures that are far larger than the individual workers, such as sophisticated nests and extensive trail networks. Several studies show that nest architecture plays a key role in the control of internal climate, affecting ant survival and reproduction (Bollazzi and Roces, 2007; 2010 and references therein). This suggests that nest structures function as an extension of the colony phenotype itself (Turner, 2000). However, there are relatively few studies that have analyzed the trunk trail system as extended phenotypes of the ant colony (Burd et al., 2002; Burd, 2006; Fourcassié et al., 2010). Here, we employ some simple ideas from traffic engineering to analyze the width of trails at branching points and discuss their adaptive significance in the leaf-cutting ant *Atta cephalotes*.

In the process of construction and maintenance of foraging trails, leaf-cutting ants confront the same problems as road engineers: paths should allow a smooth traffic flow at the lowest possible cost for the society as a whole. Leaf-cutters construct persistent trails to enhance the flow of resources and information, minimizing travel time to and from food sources (Rockwood and Hubbell, 1987; Roces and Bollazzi, 2009; Farji-Brener et al., 2010). The construction and maintenance of this large and permanent trail system is time and energy demanding because nearby plants are constantly invading cleared trails and litter is regularly falling on the forest floor (Shepherd, 1982; Howard, 2001; Kost et al., 2005). If trails are costly to build and maintain (Shepherd, 1982, but see Howard, 2001), they should be designed to maximize the rates of traffic flow to and from foraging sites. Engineering principles suggest that the width of a road necessary to ensure a smooth traffic flow is proportional to the peak traffic volume (Smeed, 1967, 1968). A narrow trail involves lower costs for construction and maintenance, but may cause heavy traffic congestions in periods of maximum flow, decreasing worker speed, and thus reducing the overall food intake of the colony. In contrast, a wider trail allows ants to proceed at their preferred speed. This may be desirable from the perspective of the individual, but from the colony's viewpoint each unit of trail width is used inefficiently because it implies extra construction and maintenance costs (Burd et al., 2002). Hence, if ants behave optimally, they should adjust the width of their trails so that their capacity is close to the maximum flow of foragers.

The trade-off between costs and benefits that determines the optimal width of a trail is particularly relevant at branching points, where the ant flow necessarily splits through the branches. A typical leaf-cutting ant trail system consists of a persistent, dendritic network radiating out to food sources (Kost et al., 2005). The building of trail bifurcations is a frequent event in the development of a trail network; a mature *Atta* nest may show up to 50 trail bifurcations (Kost et al., 2005). Since trail branches are not interconnected (i.e., there are no loops or road bypasses), ants must converge at the same main trail both to depart from and return to the nest entrance. If ants build and maintain the width of a trail proportionally to the peak traffic volume, the sum of branch widths should equal the width of the trail section upstream of the bifurcation (Burd et al., 2002). As previously discussed, branches that are narrower in conjunction than the preceding main trail section may cause traffic congestions at the peak of ant flow, and branches that are wider than the preceding main trail section may entail extra costs for construction and maintenance. We test this additive-width morphology idea ("engineering hypothesis") in the trail system of the leaf-cutting ant *A. cephalotes*, and discuss the adaptive significance of possible deviations from this theoretical engineering rule.

Methods

We conducted this study at La Selva Biological Station of the Organization for Tropical Studies (10°26′N, 83°59′W) in the Atlantic lowlands of Costa Rica, between January and February 2011. The area is a lowland wet forest that receives a mean annual rainfall of 4 m (see McDade et al., 1994 for a full site description). *A. cephalotes* is the most common leaf-cutting ant species in La Selva, and shows an extensive and permanent trail system (Farji-Brener, 2001; Kost et al., 2005).

For 19 large nests of *A. cephalotes* in different successional stages of forest, we randomly selected 30 trail sections at branching points (experimental units, see Fig. 1). These sections (40 cm long) were located on different trunk trails and at variable distances from the nests, and included 20 cm of a main trail and the subsequent 20 cm of each of the trail branches. We measured (in cm) the width of the main trail (T_1) and its subsequent branches ($B_{1.1}$ and $B_{1.2}$) five times at different nearby points, and used their mean value for statistical analyses. We tested whether the sum of branch widths was equal to, lower or higher than the width of the preceding main trail (i.e., $\mathrm{T}_1 = \mathrm{B}_{1.1} + \mathrm{B}_{1.2}$; $\mathrm{T}_1 > \mathrm{B}_{1.1} + \mathrm{B}_{1.2}$, and $\mathrm{T}_1 < \mathrm{B}_{1.1} + \mathrm{B}_{1.2}$, respectively) in two ways. First, we used a simple regression model to assess whether the width of the branches depends on the width of

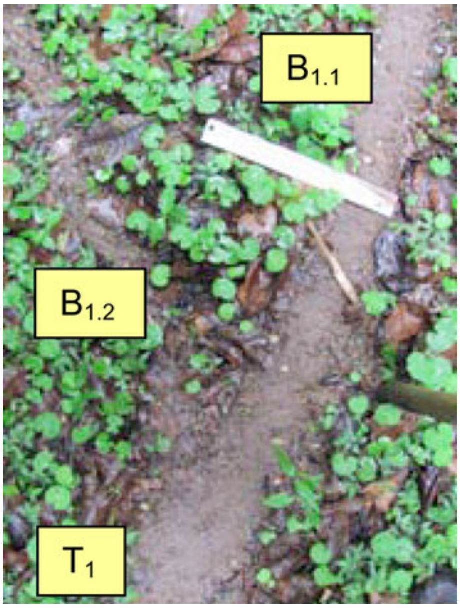

Fig. 1 Branching section in a foraging trail of the leaf-cutting ant *Atta cephalotes*. T_1 trail section before bifurcation, $B_{1.2}$ and $B_{1.1}$ trail branches. Note that although $B_{1.1}$ appears to be the prolongation of the main trail, its width is lower than T_1. Note also how nearby vegetation overhangs the trail margins

the preceding main trail. Since a regression with an intercept = 0 and a slope $b = 1$ is expected if the sum of branch widths equals the width of the trail section upstream of the bifurcation, we tested both the slope and intercept against zero. Different scenarios are feasible. A slope b significantly greater than unity but an intercept = 0 means that the excess of $B_{1.1} + B_{1.2}$ relative to T_1 increases with increasing T_1 (and the opposite trend if $b < 1$). An intercept significantly greater than zero also implies $B_{1.1} + B_{1.2} > T_1$, but the amount by which the sum of branch widths exceeds the basal trail width decreases, is constant or increases throughout the range of basal trail widths depending on whether b is less than, equal to or greater than unity, respectively. Second, we compared the sum of branch widths versus the width of the preceding main trail using a paired *t* test.

Since the sum of branch widths was greater than the width of the preceding main trail (see "Results"), we performed additional field measurements and experiments to test alternative explanations for this pattern. First, to test whether this result was just the consequence of connecting a branch to the main trail (hereafter, "branch addition hypothesis"), we compared the width of the widest branch with the width of the preceding main trail using a paired *t* test. If one of the branches was really the prolongation of the main trail, we expected both widths to be identical (i. e., $B_{1.1} = T_1$, and therefore, always $B_{1.1} + B_{1.2} > T_1$). Second, to test whether the discovered pattern was caused by the fact that trail borders represent less active trail sections because of nearby vegetation delaying ant walking (hereafter, "border effect hypothesis"), we (a) recorded the traffic flow at the border and center sections of trails (b) measured the number of ant collisions with obstacles in each section, and (c) relocated loaded ants from the trail center to the trail border (controlling for the handling effect) and measured their speed before and after the manipulation.

Traffic flow (ants/100 $\text{cm}^2\ \text{s}^{-1}$) in border and center trail sections was recorded in 19 trunk trails (10–20 cm wide) from 19 nests (one per nest) using a digital video camera positioned directly above the trail surface. The camera focal length was set to allow an entire 30 cm of the trail to be filmed. For each trail, 30 s of traffic at different times of the day that differed in their foraging activity were analyzed. Each trail was recorded once ($N = 19$). The trail border was predetermined as the wide section overhung by vegetation ($\sim$1.5 cm from both trail limits toward the center, independently of trail width); the center section was considered as the remaining trail lane. The field manipulation was performed removing 15 randomly selected loaded ants from the trail center to the border section by collecting them with a forceps by the leaf fragment they were carrying. This field experiment was performed in 15 different trails (one ant per trail). Manipulated ants were slightly forced to keep walking along the border section of the trail by placing 5-cm high walls of transparent plastic. Ants that were disturbed by this plastic wall were not considered in the analysis. To control for handling, another 15 laden ants were removed from the trail center and deposited in the same trail section after 10 s. Ant speed was calculated in both the relocated and control treatments as the time needed by an ant to walk along 30 cm of trail before and after the manipulation. Paired *t* tests were used in all the comparisons. Finally, a simple regression model was used to determine whether ant flow in the trail border section depended on the ant flow in the trail center section. All response variables were examined to meet parametric assumptions and transformed when necessary. Analyses were performed using the software Statistica 7.0®.

Results

Trails and branches showed a remarkable variation in their widths. Typically, both decreased their widths with increasing distance from the nest. The width of trail sections upstream of a bifurcation ranged between 6 and 18 cm, and the width of individual branches between 4 and 13 cm. The sum of branch widths depended on the width of the preceding main trail section (linear regression, $R^2 = 0.50$). At branching points, wider trails always showed wider branches. The slope of the regression model was significantly different from zero ($b = 0.88$, $F_{1,\,28} = 27.1$, $P < 0.0001$),

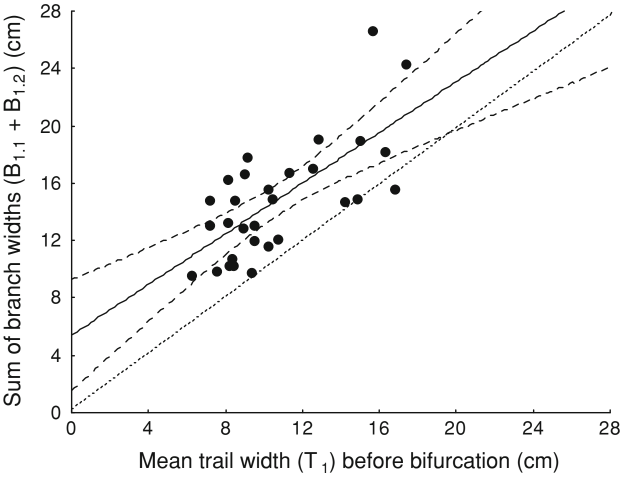

Fig. 2 Regression model (with 95 % of confidence limits) showing that the sum of branch widths increases as the width of the preceding section of trail increases, with a slope $b \approx 1$ ($b = 0.88$, 0.54–1.24, 95 % confidence limits) and an intercept significantly different from zero (5.41, 1.5–9.3, 95 % confidence limits). Thus, $B_{1.1} + B_{1.2} > T_1$, but the amount by which the sum of branch widths exceeds the basal trail width is relatively constant throughout the range of basal trail width. A regression with $b = 1$ is illustrated by a *dashed line*

but not significantly different from unity (0.54–1.24, 95% confidence limits). On the other hand, the intercept was significantly different from zero (5.41, 1.5–9.3, 95 % confidence limits, $F_{1,\,28} = 8.2$, $P < 0.008$, Fig. 2). The sum of branch widths was on average 40 % greater than the width of the trail section before the bifurcation (14.9 ± 0.7 vs. 10.7 ± 0.6 cm, respectively, mean ± 1 SE, $t = 7.9$, $N = 30$, $P < 0.0001$). Overall, the amount by which the sum of branch widths exceeded the basal trail (i.e., ~5 cm) appeared to be constant throughout the range of measured basal trail widths (because $b \approx 1$ and intercept different from zero).

The widest branch was always narrower than the trail just before the bifurcation (8.4 ± 0.4 vs. 10.7 ± 0.6 cm, respectively, mean ± 1 SE, $t = 5.03$, $N = 30$, $P < 0.0001$). Traffic flow was higher in the center than in the border section of a trail (2 ± 0.4 vs. 1 ± 0.2 ants/100 cm^2 s^{-1}, $N = 19$, $t = 4.2$, $P < 0.001$). Loaded ants collided with obstacles more frequently in the border than in the center trail section (4.3 ± 0.9 vs. 2.6 ± 0.7 collisions (mean ± 1 SE) along 30 cm, respectively, $N = 15$, $t = 4.7$, $P < 0.001$). In general, this higher number of collisions was a consequence of the presence of protruding nearby vegetation and fallen twigs on the trail borders. Accordingly, ants walked more slowly when they were moved from the center to the border section of a trail (1.7 ± 0.2 vs. 1.4 ± 0.1 cm s^{-1}, center vs. border speed, respectively, mean ± 1 SE, $t = 2.4$, $N = 15$, $P < 0.03$). Handling per se did not affect ant speed; ants removed from and returned to center trail sections showed similar speed before and after the manipulation (1.54 ± 0.2 vs. 1.56 ± 0.2 cm s^{-1}, before and after the manipulation, respectively, mean ± 1 SE, $t = 0.3$, $N = 15$, $P < 0.79$). Lastly, ant flow in border sections increased with increments in ant flow at trail centers ($R^2 = 0.72$, $N = 19$, $P < 0.001$).

Discussion

Leaf-cutting ant trails provide a good model system for studying the value of extended phenotypes, because they play an essential role in resource acquisition and information transfer, are easy to measure, and feasible to manipulate (Burd et al., 2002, Fourcassié et al., 2010). Here, we used a simple engineering principle, which proposes that the width of road necessary for a smooth traffic flow is proportional to the peak traffic volume, to analyze the adaptive significance of the trail width at branching points in the leaf-cutting ant *A. cephalotes*. Since an outgoing ant flow must split into two active branches (or, for returning ant flow, converge into a main trail), we expected the sum of branch widths to equal that of the preceding section of the main trail. However, the sum of branch widths was, on average, 40 % higher than the width of the trail just before the bifurcation. Our results are not in accordance with the trail addition hypothesis; instead, they support the "border effect hypothesis" to explain this exception to the proposed engineering rule.

The "branch addition hypothesis" proposes that the sum of branch widths will be higher than the width of the preceding trail section if one branch is merely an addition to a main trail ($B_{1.1} = T_1$ and thus, always $B_{1.1} + B_{1.2} > T_1$). If this is the case, one branch should in fact be the continuation of the main trail. However, the widest branch was always narrower than the preceding portion of the trail, contrary to the expectations of this hypothesis. Trails are not merely pheromone-defined paths over existing substrates but physical corridors made by ants by cutting vegetation and clearing debris along paths to their foraging sites (Howard, 2001; Evison et al., 2008). Hence, trails and branches are not temporally static and their widths depend on the activity of ants. Workers can widen trail sections harvesting nearby vegetation and removing obstacles, but reductions in these clearing activities decrease trail width noticeably (see Fig. 1). Consequently, the connection of a new branch to a main trail may eventually explain only initial differences between the width of branches and their previous trail section, but not the maintenance of these differences through time.

The "border effect hypothesis" proposes that not all trail sectors are equivalent to each other for foraging ants. As discussed earlier, trunk trails minimize travel time to and from food sources. However, trail margins may represent "slow lanes", because nearby vegetation often overhangs cleared trails and reduces ant speed (see Fig. 1), particularly of loaded workers. Since borders are of a fixed area, their detrimental effect on ant speed increases as the width of a trail decreases (i.e., trail margins take up relatively more area in narrow than in wide trails). Therefore, ants can build branches wider than expected by an engineering rule to minimize the border effect. Several lines of evidence support this hypothesis. First, ants collide more frequently when walking along the border than on central sections of a trail. Second, our field manipulation demonstrated that, as a consequence, ants decrease their speed by 20 % if they walk along trail margins. Accordingly, ant flow was twice as large in the center compared to the border sections of trails, although the difference in ant flow between these two sectors decreased as overall ant flow increased. This suggests that loaded ants prefer to walk along the central sector of trails, because they meet fewer obstacles and can walk faster, while they move to trail margins only in situations of high ant flow, probably to reduce high traffic congestions. Other leaf-cutting ant species also show a higher ant flow in central than in border portions of trails (Dussutour et al., 2004). Finally, if border areas are removed from the calculations, the sum of the central lanes from the branches equals the width of the main trail just before the bifurcation (10.9 ± 0.7 vs. 10.7 ± 0.6 cm, respectively, $t = 0.3$, $N = 29$, $P = 0.76$). Overall, these findings demonstrate that trail margins function like “slow lanes”, supporting the “border effect hypothesis” as the reason why the sum of branch widths is often wider than their preceding trail section.

Other untested hypotheses may also explain the existence of branches that are wider than expected from engineering rules. First, trail branches may show temporal plasticity in their use. Suitable resources for leaf-cutting ants, such as young leaves, fruits or flowers, commonly show drastic and rapid seasonal changes in their availability (Fowler and Stiles, 1980). If different trail branches direct foragers to resources that fluctuate in their availability over time, it is plausible that the flow of workers on each trail branch will show drastic seasonal changes associated with the occurrence of these resources. Therefore, the two branches may be wider than expected because both direct a high number of foragers, but at different time periods. Second, if trails have low costs of construction and maintenance as proposed by Howard (2001), the costs to maintain branches wider than expected under engineering principles could be smaller than their benefits by reducing the probability of traffic congestions. Both hypotheses deserve more detailed studies.

As discussed above, the width of trails depends on ant activity. However, the mechanisms through which ants widen their trails remain elusive. One possibility is a “passive” erosion of trail margins at higher ant flows. This mechanism would provide a self-organization of the optimal trail construction, since no ant needs to perceive or recognize the most favorable width (Burd et al., 2002). However, an “active” mechanism is also feasible. For e.g., there is strong evidence that *Atta* workers actively maintain trail clearance (Shepherd, 1982; Howard, 2001), including the existence of ants particularly dedicated to trail maintenance (Hart and Jackson, 2006; Evison et al., 2008). We also observed ants cutting the nearby vegetation and depositing the fragments next to the trail, a behavior consistent with an active clearing function. Thus, it is possible that both mechanisms, passive and active, play a role in the widening of trail branches.

Transport networks are essential for the economies of human civilizations and also for the economies of many insect societies, like ants. Therefore, their design should be under selective pressure to maximize their benefits and reduce their costs. The width of foraging trails could not only be analyzed in terms of building and maintenance costs, but also in terms of foraging efficiency. Other factors, rather than the ant flow per se suggested by engineering principles, may affect foraging efficiency and thus determine the width of foraging trails. For e.g., ants may build trails narrower than expected to enhance the information transfer that occurs when outbound and laden returning ants collide (Farji-Brener et al., 2010; Bollazzi and Roces, 2011). In this case, a trail that is too wide could lead to a lower rate of food return to the nests because of reduced ant contacts, decreasing foraging efficiency (Burd et al., 2002; Dussutour et al., 2007). However, a trail that is too narrow would have the same negative effect as a wider trail if it promotes an excessive number of collisions and traffic congestions (Burd and Aranwela, 2003; Farji-Brener et al., 2011). Here, we found an additional factor that may affect foraging efficiency and, in turn, the width of trails: the border effect. Under this context, ant trail networks may operate like vascular tubes, rivers or close dirt roads, where sectors close to the margins represent slow-moving zones, rather than like human-made paved highways (Burd, 2006). In particular, this hypothesis has a correspondence in fluid dynamics; laminar flow of a fluid through a tube varies as the fourth power of the radius of the tube, for a given tube length and pressure drop (Poiseuille′s law; the fourth-power effect). Thus, small changes in the radius have vast consequences on the flow rate because of frictional resistance between the tube walls and the fluid. Since the wall section relative to the center rapidly increases as the radius of the tube decreases, small tubes have a disproportionally great resistance to flow compared to wider ones. The tube wall and friction are obviously analogous to the border of an open trail and ant collisions with protruding vegetation along the border. If this is true, the delaying effect of trail margins should be included into the analysis of costs and benefits to fully understand the adaptive value of the design of ant trail networks.

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