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Cover Photograph: Workers of the topical leafcutter ant *Atta colombica* transporting flower petals to their nest in Gamboa, Panama in June 2018. Photograph © Kaitlin Baudier.

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Variation in Reflective Flow Explains Speed of Obstruction Circumnavigation on *Atta colombica* Foraging Trails

Catherine T. Prendergast[1], Jon F. Harrison[1], and Kaitlin M. Baudier[1,2,*]

Abstract – Many species follow networked trails. When such trails are blocked, obstructions must be circumnavigated or traffic redirected, but the strategies used by insects to cope with such trail blockages are variable. In a short field experiment, we obstructed foraging trails of a single nest of the tropical leaf-cutting ant *Atta colombica* and tested several hypothesized factors that might affect obstacle circumnavigation time. Nestward traveling ants solved the obstacle problem more quickly than outward bound ants. Traffic rate and terrain difficulty were not related to solving speed. More than half of the ants were reflected by the obstacle (reversing direction), with outbound ants much more likely to be reflected than nestward traveling ants. A lower proportion of reflected ants was associated with faster solving speed, both comparing nestward versus outbound ants and variation across obstructions. While further studies with greater colony-level replication will be required to test the generality of these findings, this preliminary study suggests that nestward- and outbound-traveling ants have different strategies when encountering trail obstacles.

Introduction

Efficient traffic flow is important for many social organisms, including ants. Leaf-cutting ants clear trunk trails (networked trails that lead from the nest to foraging sites) of debris, which allows foragers to travel on the forest floor 2.6 to 10 times faster than on uncleared paths (Bouchebti et al. 2019, H**ö**lldobler and Wilson 2011, Shepherd 1982, Steadman et al. 2020), enhancing efficiency in a manner similar to highway systems. Previous study of strategies these ants use to detect, breakdown, and remove small obstructions have yielded interesting findings for the field of collective behavior (Caldato et al. 2016). However, trunk trails can sometimes become blocked by objects too large to be removed such as large branch falls or displaced rocks. Trunk-trails then become vulnerable to cascading failure, wherein the blockage of the foraging trail leads to a lapse in foraging traffic as ants are unable to navigate the trail system for a period of time, leading to a reduction in food intake at the colony level (Howard 2001). In this behavioral note, we investigated the responses of one colony of *Atta colombica* Guérin-Méneville (Colombian Leafcutter Ant) to the presence of seven immovable obstructions that completely blocked trunk trails.

Leaf-cutting ants are ecosystem engineers that strip plants of their leaves in order to feed their massive, farmed fungus gardens underground (H**ö**lldobler and Wilson 2011). The large size of leaf-cutting ant colonies coupled with their multi-modal navigational foraging make them interesting species to study in terms of how they navigate obstructions to the smoothed trails they create to efficiently traverse the forest floor (Hölldobler and Roces 2001, Hölldobler and Wilson 2011, Riveros and Srygley 2008). A large obstruction not only disrupts the continuous pheromone trail, but also the visual geometry of the trail and communication between outbound and nestward ants, all vital methods of information-gathering (Czaczkes et al. 2015) that affect foraging efficiency (Bouchebti et al. 2015). To circum-

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navigate, ants need to navigate through the surrounding vegetation and back to the cleared trail on the other side. The primary aim of this study was to investigate how quickly ants circumnavigate large trail obstructions, and what factors influence circumnavigation time. We also examined how quickly the ants restored traffic flow after obstruction removal.

There is precedent for nestward and outbound ants to differ in their capacity or motivation to solve object circumnavigation problems. Nestward ants use different strategies for travelling on foraging trails than outbound ants due to the higher cost of leaf-carrying (Dussutour et al. 2009b). Because outbound ants can return to the nest and have more alternate pathways to complete their task, we hypothesized that outbound ants might more readily be reflected by the obstacle, returning to the nest when faced with an obstruction, or be recruited to a different trail and resource via U-turns, which serve an important, understudied role in ant navigation (Beckers et al. 1992, Dussutour et al. 2009a, Reid et al. 2012). In contrast, nestward ants carrying leaves must deliver loads to the nest to complete their task. We therefore predicted that nestward ants would be less likely to be reflected by the obstacle and would circumnavigate obstructions faster than outbound ants. We also asked whether higher traffic rates were associated with quicker problem-solving, as is sometimes but not always observed (Kao and Couzin 2014, Kao et al. 2014). Higher traffic rates might allow quicker circumnavigation due to the presence of more ants searching for routes. However, interactions among ants encountering obstructions could impede problem-solving via increased physical interactions, time costs of information exchange, or introduction of conflicting information.

Materials and Methods

In June 2018, we observed responses to seven metal trail obstructions at different points along two major foraging trunk trails radiating from the nest of a single *A. colombica* colony in Gamboa, Panama. Data were collected over two days while ants were foraging, from 07:00–14:00. Because we wished to examine effects of traffic level on obstacle circumnavigation independently of time of day or temperature, we selected obstruction locations that differed widely in traffic rate when observed at the same time upon an initial survey of the area. All sites where observations were made remained in near complete canopy shade for the duration of all observations.

We mounted a cell phone video camera above the trail, recording trail traffic 14 cm to either side of obstructions. The obstruction was an 8.5 cm diameter smooth metal cylinder, pushed into the soil so ants could not climb over or dig underneath it. Average pre-obstruction nestward and outbound traffic rates were calculated from 20 sequential counts of ants passing a centroid reference point per minute. The obstruction was then placed, and we filmed for another 20 minutes. We filmed for an additional 5 minutes following obstruction removal to capture the return of foraging columns to their original path.

We collected behavioral data from the videos of each obstruction (Fig. 1). We measured the time at which the first nestward and first outbound ant from each obstruction successfully navigated around the obstruction (i.e., circumnavigated it and continued along the trail on the other side, leaving the frame of the video without turning back), hereafter ‘time to first pass.’ We recorded the time at which the first nestward and outbound ant reused the ‘original’ trail (the central segment of the trail which had previously been obstructed) after obstacle removal, hereafter ‘time to first reuse.’ We tracked the paths taken by a subset of ants for each obstruction. We observed 10 nestward and 10 outbound ants per obstruction during the second minute after obstruction placement. Ants that traveled back in the direc-

tion they came and exited the frame of the video after encountering the obstruction were defined as 'reflected ants.' To test for effects of traffic rate and directionality of movement (nestward versus outbound) on the speed with which each group circumnavigated the obstruction, we fitted a linear model with time to first pass as a response variable and with traffic rate and direction (nestward or outbound) as fixed factors. Significance of factors was assessed using a Type II likelihood ratio test. A linear regression tested whether number of reflected ants (out of 10 observed per each direction at each obstruction) had an effect on time to first pass or time to first reuse. A t-test compared number of reflected ants between outbound and nestward groups.

Forager speed can vary more than twofold based on how much clearing a trunk trail has received (Bouchebti et al. 2019). For this reason, we measured trail width (width that was cleared of vegetation), distance from nest, and a metric of relative trail difficulty (see "Index of environmental impenetrability" or env_I in Supplemental File 1, available online at https://eaglehill.us/neononline/suppl-files/neon-017-Baudier-s1.pdf) to test for correlations between any of these potential factors and our main variables of interest. Trail widths at obstructions ranged from 5.03–10.2 cm, and distances from the nest entrance ranged from 1.43–21.7 m. We used a correlation matrix (Pearson correlations) to explore these factors and their relationship to the main variables of interest more in-depth (Fig. S1). All analyses were performed in R version 4.0.0 (R Core Team, 2019).

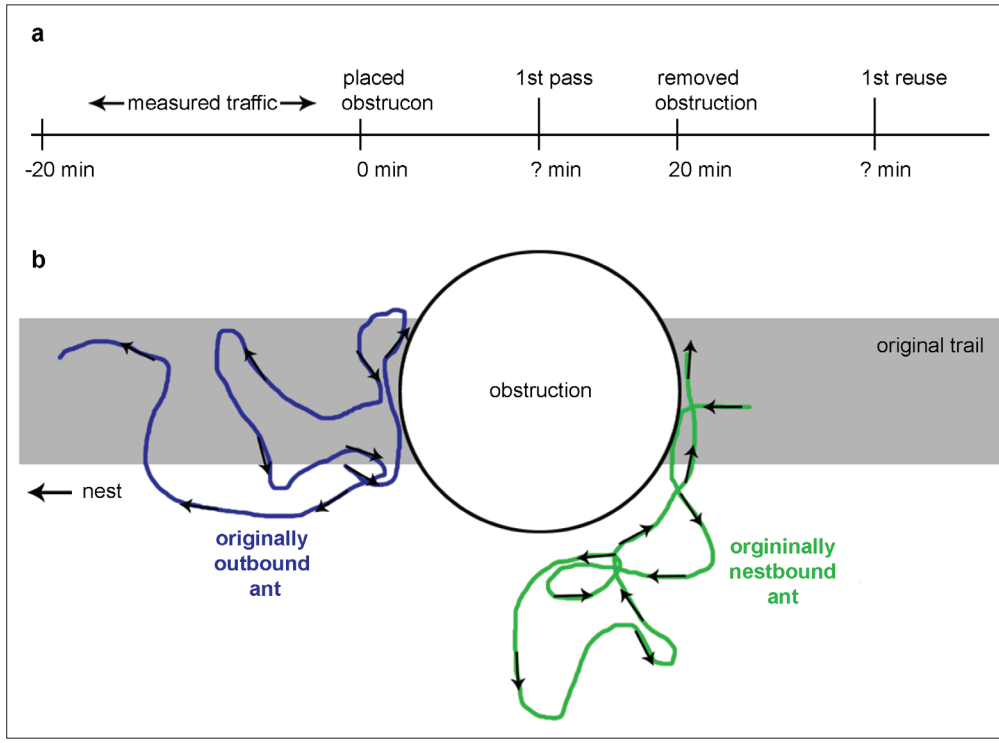

Figure 1. (a) Visualization of the timeline followed while recording the experiment. (b) Example traces of the paths of a single outbound ant and a single nestward ant relative to the obstruction over a one-minute timeframe in the second minute following trail obstruction. Orientation of each ant is shown by arrows (point of the arrow corresponds to the head of the ant). Space between arrows represents distance traveled by the ant over 5 seconds.

Results

Pre-obstruction traffic rate had a marginally non-significant effect on time until the first ant circumnavigated the obstruction (trend toward a negative relationship; Fig. 2a; Table 1), but nestward ants circumnavigated obstacles significantly faster than outbound ants (Fig. 2b; Table 1). Groups where fewer ants were reflected achieved a faster time to first pass (Fig. 3a). Twice as many outbound as nestward ants were reflected by obstructions (Fig. 3b). However, time to first reuse was not significantly predicted by the number of reflected ants (linear regression: F = 2.31, p = 0.154, R^2 = 0.162; Fig. S2).

Pearson's correlations revealed a strong positive correlation between time to first pass and time to first reuse, and a moderate negative correlation between percentage of leaf carriers and both time to first pass and time to first reuse (Fig. S1). However, distance to nest, env_l (terrain difficulty) and trail width showed little correlation (positive or negative) with time to first pass or time to first reuse and were weakly correlated with each other (Fig. S1).

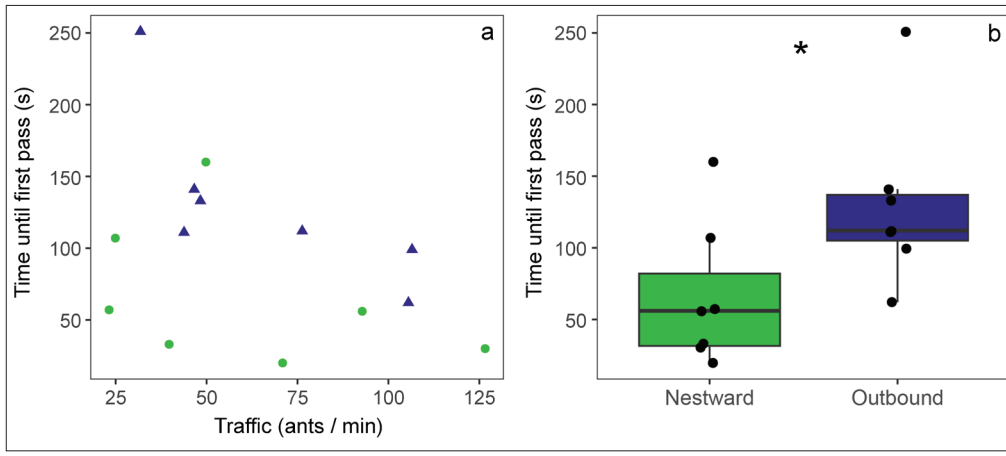

Figure 2. Type II analysis of a linear model (structure: Time_first_pass ~ Traffic + Direction, adjusted R2 = 0.42) showed a marginally nonsignificant effect of traffic rate (a, F1,11 = 4.21, p = 0.065) but a significant effect of traffic direction (b, F1,11 = 7.02, p = 0.023) on solving time (n = 14; groups of ants traveling either nestward or outbound on each of the seven observed trails) (Table 1). Data for outbound ants shown in indigo (triangles in panel a), nestward traveling ants shown in green (circles in panel a).

Table 1. Statistical output of Type II analysis of a fitted linear model (Time_first_pass ~ Traffic + Direction).

	df	Sum Sq	Mean Sq	*F*	*p*
Traffic	1	9556.4	9556.4	4.2112	0.06474
Direction	1	15929.7	15929.7	7.0198	0.02261*
Residuals	11	24961.9	2269.3		

Discussion

Trail obstructions due to events such as fallen tree limbs are common in the rainforest environment of *A. colombica* (van der Meer and Bongers 1996). Perhaps not surprisingly, we report that ants found their way around these relatively small artificial blockages quickly: on average, within 5 minutes. However, the time it took trails of ants to solve obstacle problems varied by a factor of 10, and was not significantly related to traffic level or local terrain difficulty. The significant factors we do report in this brief study of one nest help form testable hypotheses for the behavioral tactics this ecologically dominant tropical ant species uses to respond to interruptions in foraging. These findings of flexible responses of leafcutter ants to trail obstacles also suggest some previously unrecognized aspects of ant foraging strategies.

Perhaps the most striking observation was that large fractions, averaging 80% of outbound ants, were reflected by obstacles. Reflected ants turned around and traveled back toward either the nest or other foraging areas. This was not apparent until we tracked individuals in the videos, because there were typically many ants moving quickly near the obstacle after the trail was blocked. When more ants were reflected and fewer remained in the vicinity of the obstacle, circumnavigation occurred more slowly (Fig. 3a). Nestward ants engaged in less of this reflective flow than outbound ants (Fig. 3b). Solving was also faster for ants traveling nestward than for those traveling outbound (b). This could be evidence of a temporary directional division of labor, wherein nestward ants solve obstructions and outbound ants move out of the way. Because leafcutter ant trails are all connected to the nest, it would be relatively easy for an outbound ant to return to the nest and find a different, unobstructed trunk trail to traverse. Time and energy may be saved if the outbound ant returns to the nest and leaves again on a different foraging trail. It is more difficult to understand why 40% of nestward ants were reflected, especially those carrying leaves, as in most cases it was not apparent that there was another trunk trail

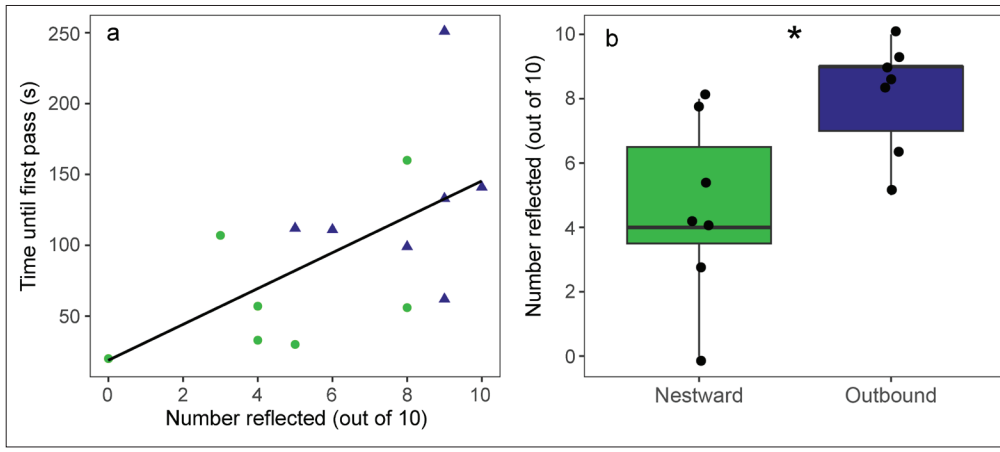

Figure 3. (a) Time to first pass increased with proportion (number out of ten observed) of reflected ants ($F_{1,12} = 6.33$, $p = 0.027$, $R^2 = 0.345$). (b) Number of ants per obstruction (n = 7 obstructions) that were reflected (turned and reversed direction) was higher for outbound ants ($F_{1,12} = 7.29$, $p = 0.019$). Data for outbound ants shown in indigo (triangles in panel a), nestward traveling ants shown in green (circles in panel a).

available to return from the foraging area to the nest. It may be that this behavior reduces crowding at the obstacle that might attract predators or impede solving the obstacle problem. While we found a marginally non-significant effect of traffic level measured before the obstacle placement on solving time, there was a trend toward higher traffic slowing obstacle solution. It is possible that reflected ants returning to the nest communicate information about blockages to nestmates, potentially stimulating traffic redirection away from the site of the obstacle. This was not investigated in our study. However, there is precedent for the adaptive use of similar tactics in other species and contexts. In *Linepithema humile* (Mayr) (Argentine Ant), for instance, a greater number of foraging ants U-turn and lay trail pheromone on routes to high-value food sources, with higher U-turn contacts to outbound ants signaling higher recruitment (Reid et al. 2012).

Reflectance in response to obstructions is a little-investigated behavior but is reported to be common in *Pheidole megacephala* (Fabricius) (African Big-headed Ant) (Dussutour et al. 2009a). Reflection responses likely differ according to the type of obstruction, however, because *A. colombica* are not reported to engage in frequent U-turns when faced with low overhead clearance (a covered bridge) (Dussutour et al. 2009c). More generally, reflectance illustrates a general principle of problem-solving: sometimes it may be more efficient to give up on obstacles. One practical example of this concept is the methodology that guides navigation apps to reroute cars around high-traffic areas.

Why there was so much variation in the proportion of reflected ants across the different obstacle tests remains an interesting question. Possible explanations include that some foraging sites are linked by other routes, that outbound ants perceive differing levels of productivity for different foraging sites, or that some trails have higher recruitment or persistence. This topic merits further exploration.

Temperature and time of day can significantly affect the walking speeds and leaf intake of *A. colombica* at this site (Welch et al. 2020). It is unlikely that temperature or time of day affected the observed differences between nestward and outbound ants, as these were paired measures made at the same time at each site. However, temperature or time of day may have influenced the observed cross-site variation. In our data set, there was no significant connection between traffic rate (a strongly temperature- and time-of-day driven factor) and any of our focal metrics of obstacle solving ability. However, proportion of ants carrying leaves, a factor known to vary with time of day (Welch et al. 2020), did show a negative correlation with obstacle circumnavigation time. As such, future investigations of the relationship between temperature and obstruction circumnavigation remain an interesting prospect.

The ants that solved obstacle problems were not reflected, but instead found routes through the vegetation, around the obstacle and back to the trail on the other side. Ants use a variety of strategies to navigate while foraging (Wehner 2020), including a magnetic compass (Riveros and Srygley 2008), visual information (Ribeiro et al. 2009), trail pheromones (H**ö**lldobler and Wilson 2011), and also egocentric information (Bisch-Knaden and Wehner 2001). The observation that for some, but not all obstacles, ants were able to solve the problem quickly, may also be due to some of these observation locations having stronger visual or olfactory cues that could be used by ants to find their way. These results merit further studies exploring the generalizability of these findings in this species and beyond.

Data Availability

The data used to support the findings of this study are included within Supplemental File 1, available online at https://eaglehill.us/neononline/suppl-files/neon-017-Baudier-s1.pdf.

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Author contributions

Catherine Prendergast collected all field data during an ASU Study Abroad Course at STRI in Panama, with oversight from Baudier and Harrison. Prendergast and Baudier conducted the statistical analysis, with input from Harrison. Prendergast wrote the first draft, and Prendergast, Baudier and Harrison edited and revised the document.

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