then 20 ants while all other trails included > 60 ants. We claculated proportion of ants choosing each path bifurcation (a vs. b and c vs. d) and estimated 95% confidence intervals using the binomial probability distribution.

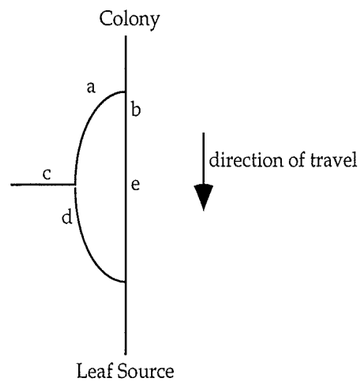

FIG. 1. Experimental setup: a-c-d represents a paper-pheromone trail which we constructed and b-e represents the original ant trail. The proportion of ants following trail: a = 0.42, b = 0.58, c = 0.50, d = 0.50 (the c/d bifurcation only applies to ants that choose a).

RESULTS

Leaf-cutter ants heading away from the nest chose their former trail , cleared of pheromone, 58% of the time (95% confidence interval = 30 to 75 %, n = 3108), and a paper pheromone trail leading in a different direction 42% (95 % confidence interval = 18 to 62 %, n = 3108; gates a vs. b in Fig, 1). Of those ants who chose the paper-pheromone trail, equal proportions chose a path leading back to the original trail (50 %, 95 % confidence interval = 23 to 69 %, n = 769)and one leading in the opposite direction (50 %, 95 % confidence interval = 24 to 69 %, n = 769; gates c vs. d in Fig. 1). Among 9 trails, ants choosing path A over B ranged from 18 - 77%, and those choosing C over D ranged from 28 - 77%.

DISCUSSION

Ants leaving the nest to forage apparently use a combination of directional information and pheromones to locate leaf resources. Leaf-cutter ants followed the paper-pheromone trail in the manner described by Hangartner (1967), clearly indicating that pheromone trails play a role in the direction choice of outgoing ants. However, 58% of the ants remained on the original trail. It is possible that all ant pheromone was not eliminated via our sweeping, leaving a faint trail which outgoing ants could still follow. A combination of sweeping and washing the original trail with water might more completely eliminate the pheromone trail.

An alternative explanation for the behavior we observed is that returning ants provide visual, tactile, and/or chemical cues to outgoing ants. If so then outgoing ants which do not encounter their leaf-carrying counterparts might not have a reliable cue, resulting in the haphazard path selection which we observed. This could be examined in future studies by a similar experimental design that also contorls for returning ants on the ant trail. This would allow analysis of the relative importance of direct ant-ant communication as well as that of pheromone trail adn directional control in influencing the decision of outgoing ants.

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TRAIL RE-ESTABLISHMENT FOLLOWING DISTURBANCE IN *ATTA COLUMBICA*

DUSTIN R. RUBENSTEIN

Abstract. Trail disturbances result in a loss of foraging time and a reduction in leaf acquisition for leaf cutter ant colonies. The more productive the trail, the greater the cost. Thus, it should be adaptive for ants on productive trails to reestablish their trails faster than ants on less productive trails. It may also be adaptive for ants on productive trails to drop their leaves more readily following disturbances to allow rapid re-establishment of the trail. Although more productive trails had greater expected losses, trail re-establishment times were not related to trail productivity, the number of leaves dropped, or the number of ants along the trail. Consequently, trails with the highest productivity suffered the greatest losses. This suggests that leaf cutter ant responses to trail disturbances are not influenced by trail productivity and may be largely a matter of chance.

Key words: cost, leaf biomass, leaf cutter ants, trail productivity, pheromones

INTRODUCTION

Leaf cutter ants (*Atta columbica*) are eusocial insects with at least three specialized castes: minima, media workers, and maxima soldiers (Dyhrman et. al 1993). Nests can contain as many as 5 million ants, with the majority being media workers (Stevens 1983). Media workers cut tiny pieces of leaves from trees and carry them back to the nest along trails marked by pheromones. The leaf pieces are used to culture a fungus that provides the major food source for the colony (Stevens 1983).

Trail disturbances result in a loss of foraging time and a reduction in leaf acquisition by the colony. The more productive the trail, the greater the cost. Thus, it should be adaptive for ants on productive trails to reestablish their trails faster than ants on less productive trails. Some ants drop their leaves in response to a trail disturbance. This behavior presumably helps them reestablish the trail faster because ants not carrying leaves are most responsible for reestablishing trails (Dyhrman et. al 1993). Although they incur an immediate cost by dropping leaves, the eventual savings in time (and future dropped leaves) may translate into a smaller overall loss in leaf biomass. Thus, it may be adaptive for ants on productive trails to drop their leaves more readily in order (to help reestablish the trail) than ants on less productive trails.

METHODS

On 2 February 1998, I examined leaf cutter ant trails in Corcavado National Park, Costa Rica. I calculated the productivity for ten randomly chosen trails by measuring the rate at which ants carried plant parts towards the colony. I also calculated the rate at which all ants moving towards the colony passed a fixed point to get an estimate of the number of ants per trail per unit time. I made three consecutive replicate counts for each rate and averaged these values for mean trail productivity and density. I disturbed a flat portion of each trail and recorded the time it took ants to reestablish the trail. I cleared a 30 cm patch of all leaves, debris, and sand with my feet out to ~ 15 cm on either side to ensure ants could not find trace pheromones in the cleared debris. I considered the trails to be reestablished when the transport rate reached > 80% of the initial values. I also recorded the number of leaves that the ants dropped while trying to reestablish the trail.

I calculated the average proportion of ants with leaves from proportions calculated for each individual trail. Regression analyses were used to test the relationship between trail productivity and (1) trail re-establishment time and (2) the probability of dropping leaves. I estimated costs in loss of leaf biomass during trail re-establishment by multiplying initial trail productivity (leaves/sec) by the time it took to reestablish the trail, and regressed these values against trail productivities.

RESULTS

Ant behavior following a disturbance was highly variable. Ants along both sides of the disturbance helped to reconnect the trail, and, contrary to Dyhrman et. al (1993), it appeared that both workers carrying leaves and workers without leaves took part in trail re-establishment. The proportion of ants carrying leaves was quite constant across trails at ~ 0.85. Directly following the disturbance, tens to hundreds of ants milled around the edge of the disturbance while a few individuals fanned out in all directions. The original trails were partially reestablished (> 80% of the initial leaf transport rate) within 3 - 7 minutes, and completely reestablished within 15 - 30 minutes in all ten trials (mean ± SD = 265 sec ± 82 sec). Some ants dropped the leaves they were carrying while attempting to reestablish the trail. A few of these leaves were examined by other ants once the trail had been reestablished, but most were left on the ground untouched.

Following a disturbance, ants on more productive trails did not reestablish trails faster than ants on less productive trails ($F_{1,8} = 0.02$, $P = 0.88$), and the probability of ants dropping their leaves did not increase with increasing trail productivity ($F_{1,8} = 0.06$, $P = 0.81$). Because they did not reestablish trails more quickly, productive trails suffered the greatest costs from trail disturbance ($F_{1,8} = 12.30$, $P = 0.008$; Fig. 1).

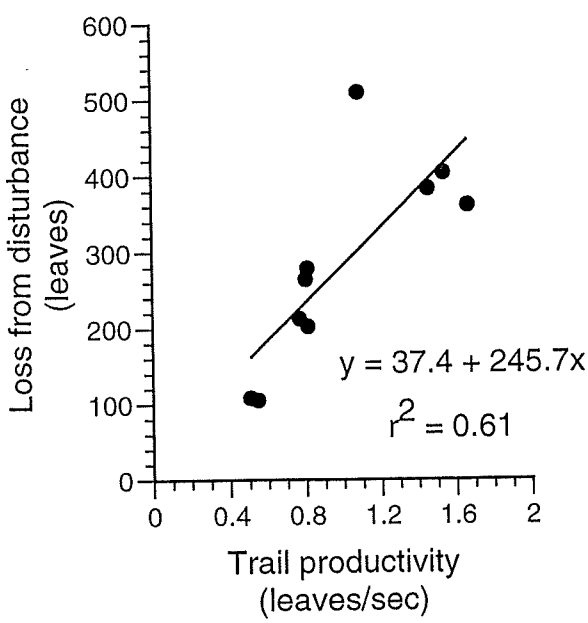

FIG. 1. Estimated loss from disturbance vs. trail productivity prior to disturbance (n = 10).

DISCUSSION

Despite greater potential losses, ants on more productive trails did not reestablish their trails faster than ants on less productive trails. Trail re-establishment time did not seem to be related to the number of ants on the trail, nor to the number of leaves dropped. Consequently, trails with an initial productivity that was four-fold higher suffered losses from trail disturbance that were about four-fold higher. Thus, leaf cutter ant responses to trail disturbances do not seem to be influenced by trail productivity, and because these responses were quite variable, they may be largely a matter of chance. I only disturbed each trail one time, which did not permit a test for variance among trails. If time until trail establishment is due to chance discovery of the lost trail ends, and not due to systematic differences in social behavior, trails should not differ in the average time until trail re-establishment. Alternatively, trails may differ in the speed of re-establishment, but due to factors other than trail productivity.

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