ants approaching the sugared and non sugared sponges (paired t-test, df=5, P = 0.91). Also, there was no significant difference between "ant time" spent upon the sugared and non sugared sponges (paired t-test, df=4, P= 0.84).

Due to time constraints we made post-trial observations of only two of the five trees treated. We observed significantly more feeding behavior upon the sugared sponge, and was exclusively aggressive behavior directed towards the non-sugared sponge (Table 1). These differences in ant behavioral response to sugared vs. non sugared sponges were significantly different (G test, G=13.917, df=17, P=0.0002).

Opportunistic observations during the trial revealed that in addition to those feeding directly on the sugared sponges, there were a total of 45 ants feeding upon sugar solution spilled upon the branches in the vicinity of the foreign bodies.

Table 1: Post-trial observations of the total number of ants exhibiting either feeding or aggressive behavior on the sugared and non-sugared sponges. Data from both trees are combined.

Behavior	sugar	non-sugar
feeding	10	0
aggressive	2	10

Discussion

Ants clearly fed on the sugar treatment and exhibited aggressive behavior towards the foreign object with no sugar treatment. These observations support our hypothesis that ant aggressive behavior will change to feeding behavior when confronted with a foreign body that also supplies food. In spite of these qualitative differences in ant behavior between the sugar and non sugar treatments, the activity level of the ants and the time ants spent on the foreign bodies did not differ between the two treatments. This is probably because the initial disturbance of placing the objects may have been interpreted by the ants as identical, and thus they recruited equally in the two treatments. The similar time ants spent on the two foreign bodies may be explained by noting that this estimate only measured time on the foreign body, not ant behavior on the foreign body. In fact, as stated earlier, ant behavior differed greatly on the two treated sponges. The observation that ants fed on spilled sugar water near the foreign body also lends support to the hypothesis that ants will exploit a food source, even when associated with a foreign body.

The accepted theory of acacia ant behavioral patterns is that the ants will attack any object disturbing the host tree. (Janzen 1983) The observed behavioral shift from aggression to feeding contradicts this notion, suggesting that the ants' number of aggressive responses to a disturbance is not absolute. Our results therefore indicate that ant behavior is not rigid in the defense of the host acacia tree. Evolutionarily, this behavioral plasticity would have allowed the ants to feed not only on the tree nectaries, but additional food sources. It may be that the lack of absolute aggression by the ants allows, for example, for the presence of Streak-backed Oriole (*Icterus pustulatus*) and Rufous-naped Wren (*Campylorhyncus rufinucha*) nests in the host acacia tree. The means by which these birds avoid eliciting aggressive defense from the ants, however, remains unknown (Hang et al., 1997).

In interpreting the results, it is important to note that one of the tested non-sugar branches may have been effectively larger and thus contained more ants than the comparative sugared branch. In this case, the branch with the non-sugar sponge was in contact with a nearby branch, increasing the effective size of the branch and possibly confounding the data. If this non-sugar branch was larger and contained more ants than the sugared branch to which it was compared, the ant activity levels would be artificially higher on the non-sugar branch.

In the future, it would be useful to examine ant behavior during the experiments. We observed that initial ant behavior on the sugar-containing sponge was aggressive but seemed to shift to feeding over time, suggesting a temporal shift in behavior. This may be important in understanding ant responses because it could demonstrate a shift in ant behavior due to a disturbance which offers the ants a nutritional benefit.

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POSSIBLE MECHANISMS FOR DIFFERENCE IN AGGRESSION OF *PSEUDOMYRMEX SPINICOLA* AND *P. FLAVICORNIS* COLONIES ON ACACIA TREES

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Abstract. Pseudomyrmex spinicola has been reported to be more aggressive than *P. flavicornis* in defending their host acacia trees. We predicted that this difference in aggressiveness between the two species could occur due (i) to faster recruitment to the site of the disturbance, (ii) to differences in colony size, or (iii) to differences in individual ant aggressiveness. Our results suggested that *P. flavicornis* had increased activity and recruitment after disturbance while *P. spinicola* activity and recruitment levels remained fairly constant, although none of these differences were statistically significant. It may be that *P. flavicornis* requires a greater increase in recruitment and activity from basal levels to efficient response levels than does *P. spinicola*. We found no significant difference in colony size between *P. spinicola* and *P. flavicornis*. Methodological problems prevented us from comparing individual ant aggressiveness. Studies with a larger sample size or an improved method for quantifying individual ant aggressiveness could potentially uncover a mechanism explaining the reported higher *P. spinicola* aggressiveness.

Key Words: acacia, acacia-ants, aggression, Pseudomyrmex

Introduction

Acacia collinsii trees at Palo Verde National Wildlife Refuge, Costa Rica are commonly inhabited by either *Pseudomyrmex spinicola* (red) or *Pseudomyrmex flavicornis* (black) aggressive ant colonies. The relationship is an example of a co-evolved mutualism in which the tree provides the ants with food and shelter, and the ants protect the tree by repelling and removing potential invaders (Howe and Westley 1988). Past studies have shown that red ants defend their host tree more aggressively than do black ants (Gilmartin et al. 1991; Cook et al. 1993). We examined possible mechanisms that could account for the higher aggression of red ants. We hypothesized that red ants are more aggressive than black ants because: (i) they recruit faster to the disturbance site, (ii) they have larger colonies, and/or (iii) they have higher individual ant aggressiveness.

Methods

On 10 January 1997 in Palo Verde National Wildlife Refuge, Costa Rica, we sampled four pairs of red and black ant inhabited acacia trees. We chose individual black ant acacias by randomly assigning a distance along the road near the OTS field station and a direction from the road at which we were going to begin our search. We then systematically chose the nearest red ant tree of similar size and physical condition. No pair of trees were greater than 10 m apart. All trees were 2-4 m tall.

To observe ant activity and recruitment in response to a disturbance, we repeatedly tapped the end of a secondary branch for four minutes. We monitored ant movement: (i) at the disturbance, (ii) at the base of the primary branch on which the disturbance occurred, (iii) on a secondary branch of this primary branch, and (iv) at the base of a different primary branch. At each of these positions, we first counted the number of ants that moved toward and away from the site of disturbance for two minutes before initiating the disturbance. We then repeated the procedure during the last two minutes of the disturbance.

Ant activity was measured as the total number of ants moving past each of the four monitoring points per minute. Recruitment was measured as net flux (no. ants toward - no. ants away) of ants moving toward the disturbance site per minute.

To estimate colony size, we first counted the total number of branches per tree. On six randomly selected branches, we counted the total number of ants that were on each branch and the number that arrived on the branch in one minute. Ants arriving on the branch were counted to estimate the number of ants on the stem. We then counted the number of thorns on each of the six branches. On each branch we removed one randomly selected thorn and counted the number of ants it contained. Colony size was estimated as (no. branches x no. thorns x no. ants/thorn) + (no. branches x no. ants/branch).

To estimate individual ant aggressiveness we first isolated 10 ants to a section of branch using Tanglefoot™, a sticky material. We then placed a foreign

piece of plant leaf 4 cm2 in area on the isolated region of the branch and measured the time required for the ants to remove it. This procedure, however, had to be abandoned because the Tanglefoot™ created a larger disturbance than the introduced foreign piece of leaf.

RESULTS

Red ant activity did not increase after the disturbance (52.4 + 22.0 ants/minute pre-disturbance vs. 51.3 + 23.5 ants/minute post-disturbance), while that for black ants increased from 29.3 + 12.0 ants/minute to 83.9 + 30.0 ants/minute (Fig. 1). Neither of these differences was statistically significant (red: paired t-test, t=0.059, df=3, P=0.96; black: paired t-test, t=2.69, df=3, P=0.074), although that for the black ants approached significance and was influenced by an extremely high variance.

Similar results were found for recruitment: red ant recruitment increased from -0.25 + 2.0 ants/minute to 1.25 + 1.6 ants/minute, and black ant recruitment increased from 29.3 + 12.0 ants/minute to 83.9 + 30.0 ants/minute (Fig. 2). Again, however, these differences although in the predicted direction were not statistically significant (red: paired t-test, t=1.04, df=3, P=0.38; black: paired t-test, t=1.83, df=3, P=0.17).

We found no difference between mean size of red (2433.6 + 1680.2 individuals) and black (1919.0 + 442.7 individuals) ant colony size (paired t-test, t=0.30, df=3, P=0.79).

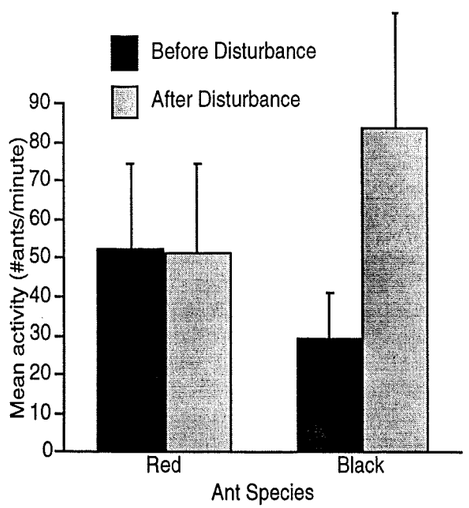

FIG. 1. Red and black ant activity before and after a disturbance on 4 pairs of acacia trees.

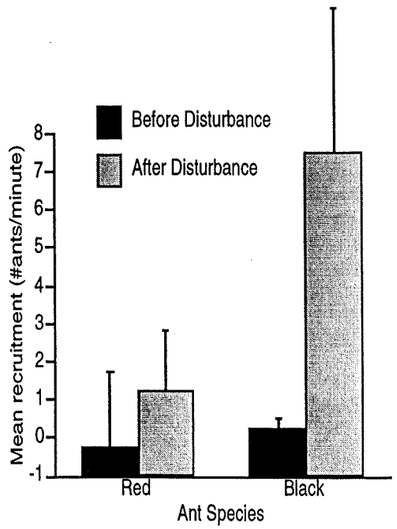

FIG. 2. Recruitment of red and black ants towards a disturbance before and after disturbance on 4 pairs of acacia trees.

DISCUSSION

Although there was no statistically significant increase in ant activity or recruitment after disturbance for either species, the observed trend was that *P. flavicornis* increased activity and recruitment after disturbance while *P. spinicola* activity and recruitment levels remained fairly constant. The data suggest that *P. flavicornis* may require a greater increase in recruitment than *P. spinicola* in order to respond to disturbances, i.e., that *P. spinicola* has a basal activity sufficient to respond effectively to foreign threats, while *P. flavicornis* has a basal activity much lower than that required to respond to disturbances effectively and so must increase activity and recruitment in response to a disturbance. This is supported by ant activity levels before disturbance (see Fig. 1).

One difficulty with the experiment was that tapping affected the entire branch rather than a localized point. Ants may not have been able to determine the source of the disturbance. Furthermore, many ants that arrived on the disturbed branch left after finding

no foreign substance or invader. Measuring activity and recruitment during the first two minutes of the disturbance, rather than the final two minutes, would have allowed us to examine the initial response of the ant colony.

We found no difference in red and black ant colony size, suggesting that aggressiveness is not related to colony size. However, tree health could have been a factor: black ant trees in our sample were less abundant and appeared less healthy than red ant trees. Because we arbitrarily selected red ant trees to be near the black ant trees, the red ant trees in the sample may have been unrepresentative of the population, i.e., not randomly selected. Small sample size may have limited results as well.

The third prediction concerning inherent individual differences in the aggressiveness of the two ant species could not be tested because of a methodological difficulty. Studies with an alternative method for quantifying individual ant aggressiveness and a larger sampling of acacias could potentially uncover a mechanism explaining higher reported *P. spinicola* aggressiveness.

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