MULTIPLE NAVIGATION STRATEGIES IN THE BULLET ANT *PARAPONERA CLAVATA*

BRIAN M. LAPPAS, ALANNA H. PURDY, DYLAN D. THOMAS, THOMAS J. LOBBEN, AND ROBERT H. YANKER III

Faculty editor: Matthew P. Ayres

Abstract: Hymnoptera foraging efficiency is contingent upon the collective ability of workers to locate resource patches and then navigate between the patches and the nest. Ant species are known to vary in the extent to which they rely on pheromone and visual cues for orientation. Bullet ants are a neotropical species that lack caste differentiation and are thought to have relatively primitive abilities to employ pheromone foraging trails. On they other hand, these attributes might be adaptive because they are generalist foragers. Although bullet ants were sometimes slow to discover a new resource patch, they showed a rapid learning curve in navigating back and forth from the nest to the patch, and were surprisingly efficient in recruiting new foragers to the recently discovered patch. Manipulations of the trail substrate indicated that the ants were able to opportunistically develop and exploit a pheromone trail, but did not use the pheromone trail to the exclusion of other cues. Bullet ants thus have versatile navigation abilities that probably enhance their ability to harvest small diffuse patches of resources in tropical ecosystems.

Keywords: ant navigation, learning, pheromones, recruitment, travel time

INTRODUCTION

Two important features of ants which contribute to their ecological success are the ability to orient while foraging, and the ability to develop specialized castes which perform different functions. However there is considerable variation in these features among ant species, with some species using different orientation strategies and completely lacking castes. Some species, such as *Iridomyrmex humilis,* have evolved sophisticated pheromone systems that permit efficient foraging by large numbers of workers to and from distant concentrated food sources (Aron et al. 1992). A potential disadvantage is that these species are often totally reliant upon pheromones, and are unable to find the trail if lost or removed from it. Other ants, such *Lasius niger,* rely less on chemical cues and can find their way back to the nest when a pheromone trail has been removed (Aron et al. 1992).

The bullet ant, *Paraponera clavata,* lacks differentiated castes and is thought to resemble the primitive condition of ants with only partial use of pheromones in foraging (Choe and Crespi 1997). These features might constrain their ecological success relative to more derived ant species with well developed castes and highly evolved pheromone systems, and explain their relatively small colony size and total biomass. Alternatively, it might be that these attributes of *P. clavata* make them well suited to their pattern of resource use. Morphological specialization of castes limits the foraging versatility of individuals, thus a homogenous morphology might be optimal for generalist foragers. They do not form large foraging columns, and forage primarily on small diffuse food sources such as insects and nectar sources close to the nest, which could render pheromone trails less cost-effective. It has even been shown that *P. clavata* makes use of other orientation cues such as canopy contrast, and nonpheromonal environmental odors (Ehmer 1999). Thus, rather than being evolutionarily constrained, their homogenous morphotype and reduced pheromone dependency may be optimal for their particular ecological niche.

We tested how well the bullet ants use pheromone trails, and if they are able to orient themselves using other means. We predicted that bullet ants would use the pheromone trail when available, and that recruitment would increase with pheromone strength, but also that the ants would be able to orient themselves after the removal of their pheromone trail via other environmental cues.

METHODS

We studied the behavior of two colonies of *P. clavata* on two separate trees in the arboreum (ca. 500m and 510m on the path SUR) of La Selva Biological Station, Costa Rica on 20-21 February 2008. We created artificial nectaries using a solution of 4 tablespoons sugar, a pack of Electrodex Electrolyte mix, and one Thorne Research Basic Nutrients III Multivitamin (about 0.05 gr.) in 300 mL water, and set up dishes filled with this solution approximately 1 m from each nest. We began recording data when the first ant found the nectar.

Our first treatment monitored the dynamics of recruitment to a food source. We kept a running count of the total number of ant that had left the nectary to return to the nest (referred to as ant #). To track the apparent learning curve of individual ants, we marked the first ant with a white pen, and tracked its time going from the nectary to the nest (referred to as travel time) for its first seven trips. As more ants were recruited to the nectary, we recorded the travel times of randomly selected ants, indexed by ant # (e.g.: ant #, travel time).

Once a strong pheromone trail appeared to be established (indicated by stable travel times), we began our second treatment. In this manipulation we blocked their established pheromone trails placing a bag covered in fresh soil gathered nearby over them. We continued counting ant # and travel times to assess their response.

Once the travel times back to the nest were stable again, we implemented our third treatment, a preference test for the ants at the nectary. To do this, we rotated the pheromone trail so that it led away from the nest (Figure 1).

We counted the number of ants at the nectary before Treatment 3, and compared the number of ants which followed the old trail (pheromone) with the number of ants which appeared to be taking other paths and presumably using other forms of navigation (e.g., visual memory, terrain usage, magnetic orientation). We ended the experiment when all of the ants that were at the dish left (to guard against effects of establishment of a new pheromone trail).

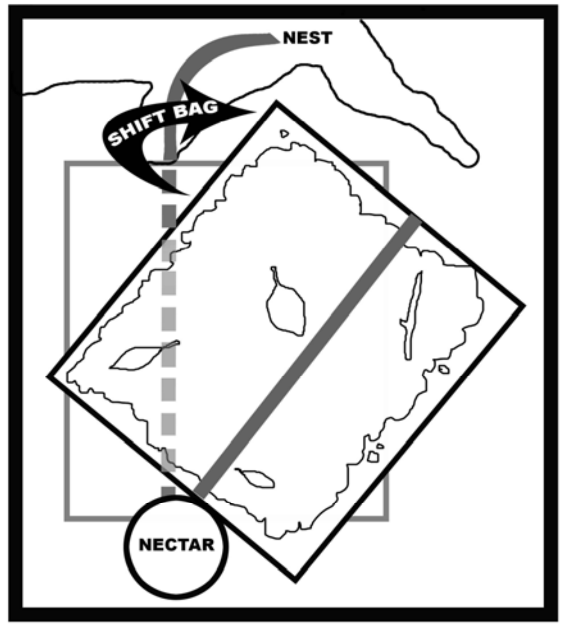

FIGURE 1. Experimental setup for manipulations of bullet ants in the arboreum of La Selva, Costa Rica. The gray rectangle represents a garbage bag covered in dirt which we placed over the path of ants going from the nectar to the nest. After a new pheromone trail had been established over the garbage bag, we rotated it away from the nest and assessed the proportion of ants following the pheromone trail (gray line) versus going straight back to the nest (dashed line).

RESULTS

In all experiments, the first trip back to the nest required the longest time, and subsequent return times decreased non-linearly until reaching a minimum by an individual's 3rd or 4th trip to the nectar (Figure 2). Apparently, individual ants became increasingly proficient at retuning to the nest, due to the pheromone trail becoming stronger, improved use of other cues, or both. Travel duration of all foragers was quickly minimized once a strong pheromone trail was established to the nectar (Figure 3).

After removing the pheromone trail with a plastic bag, the ants became disoriented and stridulated frequently. However, the ants cautiously established a new pheromone trail over the dirt on the bag, and back to the nest. Right after this treatment, trip duration first increased dramatically, and then quickly decreased to pre-treatment times after ca. 10 foragers had re-established the route. In two of the four experiments, the average trip time after the treatment was longer than the average trip time before it was applied, which was likely due to more difficult terrain (sticks, leaves) laying over the initial pheromone trail. We inferred from the slope of the curve in Figure 5 that there was roughly the same number of foragers before and after the experimental manipulation.

To assess the importance of pheromones for navigation, we presented the ants with conflicting pheromone and visual cues by creating a pheromone trail that pointed away from their intended destination. Before the rotation of the bag, 100% of the ants followed the putative pheromone trail upon leaving the nectar dish. After the rotation, the ants did not randomly disperse from the nectary, for all of the ants either headed either along the new direction indicated by the pheromone trail, or in the correct direction towards the nest. Contrary to expected if bullet ants were completely reliant on pheromones, a significant fraction of the ants at the nectary went in the correct direction, and did not follow the pheromone trail. In the first tree, only 15 out of the 27 ants at the dish followed the pheromone trail. Thus, the direction in which ants headed upon leaving the nectary after the treatment was significantly different compared to before the treatment (Fisher's exact test, $p < 0.0001$). In the second tree, only 1 of the 6 ants took the pheromone trail, and the remaining 5 headed straight to the nest; this also significantly different than before the treatment (Fisher's exact test, $p < 0.0001$).

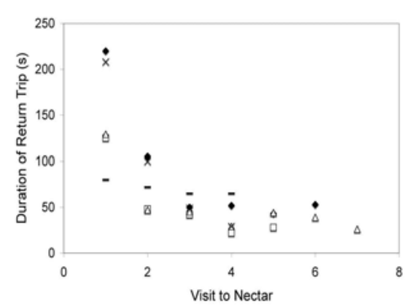

FIGURE 2. Relationship between the return trip duration of the first ant to find the nectary and its number of visits to it at La Selva, Costa Rica. Symbols differentiate first foragers from six separate experiments.

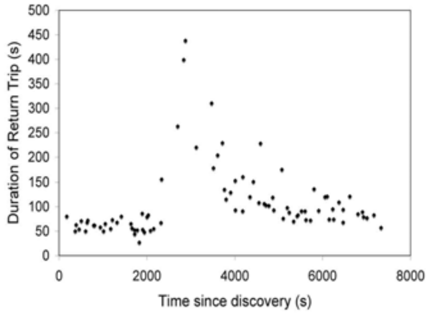

FIGURE 3. Duration of return trips versus total time since first discovery of nectar of bullet ants in La Selva, Costa Rica. The spike in trip time corresponds to an experimental treatment in which we covered their pheromone trail.

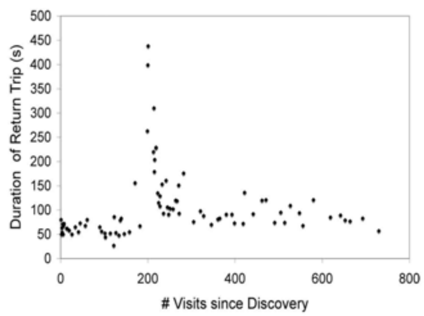

FIGURE 4: Duration of return trips versus the total number of visits to that nectar source by bullet ants in La Selva, Costa Rica. The sudden increase in duration after 200 visits corresponds to an experimental treatment in which we covered their pheromone trail.

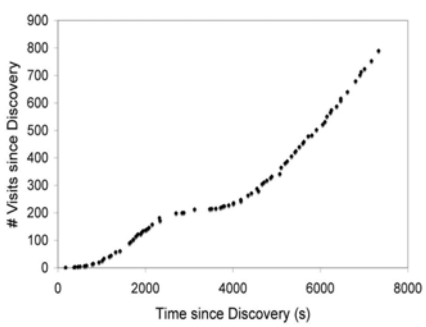

FIGURE 5. Cumulative number of visits to a Petri dish filled with nectar versus time since initial discovery of it for bullet ants in La Selva, Costa Rica. The plateau corresponds to an experimental treatment in which we covered their pheromone trail.

DISCUSSION

Our results argued against the hypothesis that bullet ants are intrinsically poor foragers that lack the orientation abilities of more derived ant groups. Instead, bullet ants can apparently use a flexible combination of pheromones and environmental cues to orient themselves. Although they were sometimes slow to find the artificial nectary (it usually took 15-120 minutes for an ant to discover it), after the first ant returned to the nest, its learning curve was surprisingly fast (Figure 2). Recruitment was also faster than might be expected for ants that are minimally eusocial (Figure 5). Within a few minutes of discovering the resource patch, all of the potential foragers were engaged in harvesting the nectary, and were moving as quickly as the terrain permitted. Our data suggests that as more ants walk to and from the nectary, pheromone strength increases, and consequently trip time decreases to a minimum determined by the distance and terrain (Figure 4).

The choice experiment was particularly telling by showing that the ants do not necessarily blindly follow the pheromone trail, as tends to be the case for leaf-cutter or army ants. This implies that bullet ants can use means other than pheromones to navigate. Having multiple navigation strategies could be an adaptation to small colony size and diffuse resources. If local resources tend to be limited, the colony would benefit more from individualistic foraging of ants, which enhance the chances of locating additional resource patches. Presumably the cost : benefit ratio of establishing a pheromone trail to a local resource patch increases when fewer ants are going to employ the trail before it is depleted. The result that at least as many ants returned to the nectary after the first disturbance suggests that the reward was great enough that it was worthwhile for the ants to invest considerable effort to re-establish the connection between the nest and the nectary.

It is not known exactly how ants navigate in the absence of pheromones. The simplest possibility is that they resort to visual cues, but other possibilities include scents (volatile pheromones or nonphermonal), spatial memory, or even magnetic fields (Banks and Srygley 2003). We hypothesize that vision is important, but it is not obvious what visual cues are being exploited.

LITERATURE CITED

Aron, S., R. Beckers, J.L. Deneubourg and J.M. Pasteels. 1993. Memory and chemical communication in the orientation of two mass-recruiting ant species. Insectes Sociaux 40:369-280.

Banks, A.N., and R.B. Srygley. 2003. Orientation by magnetic fields in leaf-cutter ants, *Atta colombica* (Hymenoptera: Formicidae). Ethology 109:835-846.

Choe J.C., and B.J. Crespi. 1997. Morphologically 'primitive' ants: comparative view of social characters, and the importance of queen-worker dimorphism. Pages 372-391 in Choe J.C., editor. The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge.

Ehmer, B. 1999. Orientation in the Ant *Paraponera Clavata*. Journal of Insect Behavior 12: 711-722.