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Exploratory behavior of *Lasius pallitarsis* ants encountering novel areas

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Key words: Chemical communication, exploration, *Lasius pallitarsis*, novelty, recruitment.

Summary

Lasius pallitarsis ants were placed in situations where they encountered unfamiliar areas and had to choose between one of two directions for further exploration. Workers advancing onto new ground apparently leave behind some chemical signature to which later ants orient. This orientation occurred under two types of experimental conditions. First, ants show a significant tendency to follow each other as they advance out from their colony into unexplored areas. The same ants transferred into an entirely novel situation, in which there is no obvious “homeward” direction, show similar behavior. When ants are coming from familiar ground, following tends to increase as the number of ants passing the decision point increases. However, following decreases when ants are on entirely novel ground. The results are discussed in relation to models describing foraging responses.

Introduction

One of the more spectacular aspects of ant foraging behavior is mass recruitment of workers to food sources. Less dramatic, but nevertheless of equal or greater importance, is the searching behavior that initially locates food items. This may often require the exploration of unfamiliar ground, which in turn requires ants to keep track of their position relative to the colony. In solving this problem, some species have been shown to orient to visual landmarks or celestial cues (Wehner, 1987), but such methods would have limited resolution on small-scale navigational problems. The use of a complimentary chemical marking system would improve accuracy when ants need to travel only short distances. Further, by leaving chemical signposts, an ant could avoid excessively retracing her own foraging search path in a new area, and could possibly keep track of the location of nestmates.

Lasius neoniger appears to employ such a chemical marking system, in which an ephemeral trail pheromone regulates cooperative prey retrieval, and a more

persistent, colony-specific chemical marker serves as a general orientation guide (Traniello, 1989a). The marks form a matrix of information for rapid navigation of foragers through a territory by minimizing unfamiliarity. However, the borders of a territory must always abut unfamiliar grounds. Also, even durable signposts can disappear over time because of weathering or lack of reinforcement, leading to situations where ants often encounter unmarked and therefore novel ground. The reactions to novel ground are examined here by allowing a series of *L. pallitarsis* foragers to advance onto unfamiliar ground, in order to test whether the direction of travel chosen by one ant may alter the behavior of ants subsequently reaching the same point in space. The propensity of ants to follow each other is examined with respect to the number of ants that have previously crossed the same ground, the length of time between ants, and whether or not the advancing ants have a point of reference as to the location of their home nest.

Methods

Three *L. pallitarsis* colonies were kept in test tubes that were partially filled with water behind a cotton plug. The open end was stoppered so that the only exit was through a 30 cm long plastic tube (3.5 mm interior diameter), at the end of which the colonies could find food. The colonies had continual access to this tube. New ground was provided by connecting another 15 cm tube that opened from underneath to the middle of a dumbbell-shaped platform (cut from thin plastic sheets to be 12 cm long, with the arms being <0.5 cm wide at the narrowest point). Therefore, as workers reached the end of the added 15 cm tube, they had to choose whether to proceed along the narrow right or left arms of the platform. One of the arms had a black spot at the end of it (evident to the observer, but not to ants until they reached it) so that each arm could also be labeled as "black" or "white". Once the ant had moved at least 4 cm along one arm, she was recorded as having made a decision and removed by aspiration from the platform in a manner that minimized the probability of disturbing others still in the plastic tube. Thus, directional preference could not develop because of returning ants.

The data recorded were whether the ant went left or right, along the black or white arm, and after the first ant, whether the next ant took the same or different arm as the previous ant, and the time between successive ants. Before a trial, whether the black arm was on the right or the left was randomly determined and the platform rotated accordingly. A trial itself consisted of a sequence of up to 14 ants exploring the new ground. After a trial, the new length of tubing and the platform were removed and carefully washed with soapy, hot water and air-dried for more than a day. Colonies experienced trials every second or third day.

The above methodology had ants proceeding from familiar ground into novel area. Immediately after removing the ants from the platform, I released them at the base of a T maze made from plastic tubing (3.5 mm diameter). The worker would run the length of the base (20 cm) and then, as in the experiment above, would have to decide whether to continue along the right or left, black or white, arms. Decisions were scored when the ants moved at least 4 cm along one arm. The same data were

collected and the entire apparatus was cleaned after every trial as described above. All ants were returned to their colonies at the end of each trial. The differences from the previous treatment were that the ants were more agitated because they had just been plucked off the platform, and they had no spatial reference – that is, because the entire apparatus was novel, no “homeward” path could have been marked.

Results

Irrespective of whether ants were advancing from known or unknown ground, workers were significantly more likely to choose the direction traveled by the previous ant (Tab. 1). Overall, the propensity to follow was similar in the two situations: 60.0% followed when advancing from familiar ground versus 58.8% when advancing over entirely novel ground. These results cannot be explained by innate directional preference, as ants did not go left or right significantly more often. Nor did ants develop any notable affinities for particular sides of the platform or T maze: black or white arms were not significantly preferred. The results were similar across the three colonies tested. Because each colony was tested several times, many ants were probably recorded more than once, but a minimum of 42 workers must have been used (14 ants per trial across 3 colonies). Finally, ants did not appear to be running in tandem (cf. Möglich et al., 1974) in that following did not require close proximity. Following did not decline significantly for pairs of ants separated for 1–10 minutes.

When ants advanced from a known area, the propensity to follow increased as the number of ants (2–14) passing the decision point increased ($y = 49.5 + 1.4x$), but

Table 1. The decisions made by ants when they were advancing from familiar or new areas. Ants were able to take a combination of left (L) or right (R) and black (B) or white (W) arms, which would be the same (S) or different (D) choice as the previous ant. (* = $p < 0.005$, for chi square comparisons to random choice)

<i>Familiar</i>						
Colony	L	R	B	W	S	D
1	86	99	91	94	106	65
2	13	23	17	19	20	13
3	79	68	67	80	78	58
Total	178	190	175	193	204	136
$\chi^2 =$		0.39		0.88		13.60*
<i>New</i>						
1	84	98	100	82	101	67
2	18	19	15	22	19	15
3	67	79	78	68	78	57
Total	169	196	193	172	198	139
$\chi^2 =$		2.00		1.21		10.33*
<i>Familiar + New</i>						
Grand total	347	386	—	—	402	275
$\chi^2 =$		2.08				23.82*

when they were agitated and advancing from a novel area, the propensity to follow decreased ($y = 69.0 - 1.4x$). The slopes of the two regressions are significantly different ($F_{1,22} = 4.33$, $p < 0.05$).

Discussion

As *Lasius pallitarsis* workers explore new areas, they apparently leave behind a chemical signature. Uses for such orientation cues could be to allow the marking ant to retreat homeward rapidly if she were to encounter a dangerous situation, and to reduce the redundancy of purely random search. The marks also have a meaning for other ants, as shown by their significant following tendency. However, a sizeable proportion of ants choose to go in the opposite direction from the previous ant, even when the two are less than a minute apart. This suggests that the marking mechanism, although durable, is either often missed or not a compelling releaser of behavior.

A system that results in weak following behavior, in the absence of any indication that the lead ant has located a specific item, may be advantageous to species with mass recruitment to prey items. Because the most profitable food items cannot be retrieved alone, a foraging strategy that tends to clump workers may make them more effective in locating each other than one that disperses them evenly (Traniello, 1989b). Conversely, species that are solitary foragers might be expected to be more likely to avoid nestmates and therefore distribute their efforts evenly across their territory. *Cataglyphis bicolor* do forage solitarily, and workers show almost no tendency to follow others (Schmid-Hempel, 1987).

Ants may mark their routes in several ways. One mechanism could be to modulate recruitment pheromones to serve as signposts in new areas. Such a system appears to be used by *Myrmica rubra* (Cammaerts et al., 1977) and *Iridomyrmex humilis* (Aron et al., 1989). *L. pallitarsis* workers, however, were not seen to drag their gasters, as reported for the previous species, and as they themselves do when mass recruiting to food sources (Nonacs, 1990). Hölldobler and Palmer (1989) found tarsal glands in *Amblyopone australis* which appear to function for trailmarking, but whether they are found in the genus *Lasius* is not known. Finally, the marks could be molecules that are sloughed off the exoskeleton simply as a consequence of walking. Therefore, ants may be following a general odor trail left by all *L. pallitarsis* workers. It is not known whether the behavior in this experiment was a response to any ant or whether workers could specifically recognize that a nestmate had recently passed, although in *L. neoniger*, trail pheromones do seem to be colony-specific (Traniello, 1980).

Following in *L. pallitarsis* does seem to be partially context-dependent. When ants advance from familiar ground, the later ants in a sequence are more likely to follow than are the earlier ants. The reverse occurs when agitated ants are on entirely unfamiliar ground. Such exploration by ants has been modeled as a self-organizing process, in which a few simple rules for movement, that require little more than ants leaving and responding to marks, simulate complex patterns of group movement and habitat exploitation (Deneubourg and Goss, 1989). This study explicitly shows that individual *L. pallitarsis* are clearly aware of where nestmates have gone before, and use that information in determining their own movements. The results, however, also

show that the rules ants use can change as their motivational state changes. Excited ants on unfamiliar ground seemed to use slightly different rules. This is consistent with predation risk having a large impact on optimal foraging behavior and patch use (Nonacs and Dill, 1990) and being communicated amongst foragers in a manner that adaptively inhibits recruitment responses (Nonacs, 1990). Including functional considerations of the goals and the recent experiences of the foragers should lead to self-organization models that not only describe the foraging process, but are predictive across a wide array of colony states.

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