Foraging Behavior of Tetramorium Caespitum in an Urban Environment: the Effect of Food Quality on Foraging

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Abstract
Animals' foraging strategies are directly related to their fitness. Proposed models of optimal foraging assume that animals strategize in terms of maximizing benefits over the cost of acquiring resources. Ants are social insects that are comparable in biomass to humans inhabiting the plant. As such, it is crucial to understand the foraging strategies of such an influential member of the ecosystem. With the ever-increasing rate of urbanization and human encroachment, it is even more important to consider the foraging patterns of species inhabiting urban areas. In this study we investigate optimal foraging strategies in the pavement ant, Tetramorium caespitum. Specifically, our study examined if pavement ant colonies would alter their foraging behavior so as to maximize benefits and minimize costs. To do this, we exposed the ants to food of two varying nutritional qualities to test how they allocated foragers across these two resources. Food quantity, distance to the food source and terrain were the same in both types of resources. Across a two day period, we saw that T. caespitum colonies increased ant recruitment when food quality increased and decreased ant recruitment when food quality decreased. Our control treatments where food quality did not change also did not see a change in ant recruitment. This study shows that species that live in urban areas, such as T. caespitum, can adapt to forage optimally. Studies like this can be used to make predictions about survival of species that are newly associated with urban environments.

Keywords
Optimal foraging, Tetramorium caespitum, urban areas, ant recruitment

Disciplines
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Foraging behavior of *Tetramorium caespitum* in an urban environment: the effect of food quality on foraging

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INTRODUCTION

Foraging strategies are directly relevant to survival and reproduction. Proposed models of optimal foraging theory assume that animals strategize in terms of maximizing benefits over the cost of acquiring resources. Social insects, especially ants, are extremely abundant and can be comparable in biomass to humans inhabiting the planet (Hölldobler and Wilson 1990). Because of this, understanding the foraging strategies of such a strong member of the ecosystem is an important topic of behavioral ecology. Many studies have analyzed the rules that shape resource use in these insects across wild ecosystems, however, fewer studies look at insects associated with urban environments. This is important because with an increase in urbanization and human encroachment, we expect more species to be located in urban environments. Understanding how species forage in urban areas will allow us to make predictions about how species newly associated with urban areas will forage and survive. In our study, we investigate optimal foraging in a highly urban species, the pavement ant, *Tetramorium caespitum*. We also examined whether optimal foraging was repeatable in *T. caespitum* across days.

In social insects such as bees, wasps, ants, and termites, colony fitness is affected by the amount of food brought back by foragers. In fire ants, after the examination of food, the individual’s interpretation of it is formulated into chemical signals released on a trail and other forms of communication are passed within a colony (Wilson 1962). Recruitment velocity in forest ants, *Lasius pallitarsis*, depends on the information passed down by the ant recruiter to the other members of its colony. The ants travel faster to food when the recruiter ant provides positive information about food quality (Roces and Nuñez 1993). Pavement ants are a good species to use in our study because they have been living in urban environments for a long time and because it is easy to quantify their investment in a resource by counting the number of ants present.
A study determined that food trail path is also a factor that influences foraging behavior in harvester ants, *Pogonomyrmex occidentalis* (Fewell 1988). These ants are more likely to forage on clear pathways rather than vegetated pathways because it is less energetically costly (Fewell 1988). Foraging tactics are also influenced by predation risk. Species in urban habitats are usually at high predation risk and are more likely to abandon risky locations and continue searching for food in an area that is most effective for both themselves and their colony (Nonacs and Dill 1990).

Specifically, this study examines whether pavement ant colonies alter their foraging behavior in an economical manner. We expose the ants to food of varying nutritional qualities to test how they allocate foragers across resources. We hypothesize that pavement ants will forage optimally even though they are associated with urban environments. We expect optimal foraging strategies to be maintained across a wide variety of environments because of their tight association with survival and fitness of species. If pavement ants forage optimally, then they will allocate greater numbers of foragers when exposed to higher quality food than when exposed to lower quality food, all else equal. We also hypothesize that optimal foraging in pavement ants will be repeatable across days. As an important part of survival and fitness, optimal foraging should be a constant strategy in pavement ants and not a random act. If this is the case, then we predict a similar number of ants recruited to similar food source qualities across days.

**METHODS**

*Measuring Ant Foraging*

We worked with a colony of *Tetramorium caespitum* located in a grassy area next to a sidewalk for our experiment. We conducted the experiment on Tuesday, September 20th and
Wednesday, September 21st. We exposed the ants to two food qualities: The Hill's Science Diet Kitten Liver & Chicken Entrée (1.34 cal/g) wet cat food served as the high quality food source, while Hill's Science Diet Light Liver & Chicken Entrée (0.88 cal/g) wet cat food served as the low quality food source.

On Tuesday’s session one, two identical scoops of high quality food were placed 4 cm away from the entrance of the ant nest in opposite directions (8 cm apart from each other). After the first ant placed its antenna on a particular scoop of food, we recorded the number of ants foraging on that scoop every minute for 45 minutes. To conclude session one, the two food sources were cautiously removed as to not kill any of the ants, and there was no food present for one minute. Session two included the same procedure, however, one of the scoops was high quality food and other scoop was low quality food.

On Wednesday, we used the same procedure, except session one included two scoops of low quality food, while session two had one high quality scoop and one low quality scoop. The treatments that remained the same throughout both sessions, high quality on Tuesday and low quality on Wednesday, served as controls. These treatments created a baseline to ensure that the time of day and the order of food presentation did not have an effect on the number of ants recruited to forage. The sessions that contained the same quality food source, session one on Tuesday and session two on Wednesday, created a baseline for location. This was to make sure that one location did not attract more ants than the other.

Data Analysis

To create a recruitment curve, we used Microsoft Excel to collapse the number of ants into cumulative five-minute bins and we plotted the number of ants present at each food source. This curve displayed the number of ants recruited to each treatment of food, with respect to time.
It allowed for a visual comparison of the ant activity before and after their food was manipulated. The Statistical Package for the Social Science (SPSS) was used to perform a two-way ANOVA, histograms, interaction plots, and a Wilcoxon Signed Rank Test. The two-way ANOVA was performed on data collected in the last 15 minutes of each session. It tested to see if there was a significant difference in the number of foragers in between the sessions, the treatments, and the interaction between the sessions and the treatments. A two-way ANOVA assumes normality of the data, so histograms of the number of ants observed during the last 15 minutes of each session and treatment were created to test the normality (Figure 1A and 1B). Based on the fact that only Wednesday’s session two of the low-high treatment histogram appeared normal to visual inspect, we should have used a nonparametric test (Figure 1B). However, based on the context of our experiment, we proceeded with the parametric two-way ANOVA instead. A plot of the mean number of ants observed per minute during the final 15 minutes of study for each treatment and session was created to analyze the interaction between sessions and treatments. This assisted in interpreting the two-way ANOVA results because it is based on the same subset of data used for the ANOVA. The final statistical test performed was the Wilcoxon Signed Rank Test. This was used to see if there was a significant difference in the number of ants recruited on Tuesday than on Wednesday. It compared the number of ants observed at the high quality food source in the last 15 minutes of the second session of both days.

RESULTS

On Tuesday, our recruitment graphs show that all treatments on both sessions asymptote to a stable number of ants (Figure 2A). We found that session one had a significantly higher mean number of ants recruited than session two overall (two-way ANOVA: p < 0.01, n=30, 30,
F = 507.555). The two treatments also differed significantly. Overall, the HH treatment had a significantly higher mean than that of the HL treatment (two-way ANOVA: p < 0.01, n=30. 30, F = 2081.108). We also see a significant interaction where the number of ants decreased significantly from the high quality treatment to the low quality treatment between session one and session two, and the high quality treatment stayed the same between both sessions (two-way ANOVA: p < 0.01, n=, F = 810.078, Figure 3A).

On Wednesday, our recruitments curves showed that all but one treatment reached an asymptote and leveled off. The LH treatment on Wednesday showed a slight dip at the end of session two (Figures 2A and 2B). Session one had a significantly lower mean number of ants recruited than session two overall (two-way ANOVA: p < 0.01, df = 1, F = 153.489). Additionally, the overall mean number of ants in the LL treatment was significantly lower than in the LH treatment (two-way ANOVA: p < 0.01, n=30 l, F = 179.571). There was also a significant interaction between treatment and session where the number of ants increased from session one to session two on the LH treatment and remained the same from session one to session two for the LL treatment (two-way ANOVA: p < 0.01, df = 1, F = 193.379, Figure 3B).

Finally, our wilcoxon signed rank results show a significantly larger number of ants recruited to the second session’s high quality food source on Tuesday than on Wednesday (Wilcoxon: n=15, p < 0.01, Figure 4).

DISCUSSION

The results of our study show that pavements ants foraged optimally. We are confident in our two-way ANOVA data analyses because all but one of our recruitment curves stabilized during the last 15 minutes. The only curve that did not stabilize well was the LH treatment on Wednesday, which showed a slight dip at the end of session two (Figures 2A and 2B). This
means that our colony reached a decision as to how many ants they were going to recruit to each food source for both days.

On Tuesday, we found a higher number of ants on treatment HH versus treatment HL overall, and a higher number of ants on session one versus session two overall. We also found that the number of ants did not change from session one to session two on HH treatment but decreased significantly from session one to session two on the HL treatment. These results agree with our predictions that pavement ants will recruit more ants to the high quality food source and supports our hypothesis that they forage optimally.

On Wednesday, there was a lower number of ants on the LL treatment than on the LH treatment overall, and a lower number of ants in session one than in session two overall. There was a significant increase in number of ants from session one to session two on the LH treatment, and there was no change in the number of ants between session one and session two on the LL treatment. This coincides with our prediction that ants will allocate more foragers to high quality food sources and provides additional support for our hypothesis that the pavement ants would forage optimally.

The wilcoxon signed rank test showed that the number of ants recruited to the high quality treatment was significantly higher on Tuesday than on Wednesday. However, the interaction curves show that the ants consistently recruited more workers to the high quality food source compared to the low quality food source, regardless of the day. The increased number of ants on Tuesday could be due to the fact that there were more favorable conditions: it was not raining, it was less windy, and it was a higher temperature. Tuesday was much sunnier and therefore the increased sunlight may have made it easier to count the number of ants more accurately than on Wednesday when there was less sunlight. Reliability of the method in which
ants were counted could have also been the source of this error. Perhaps for future studies multiple pictures can be taken of each food source to improve accuracy of each scan count and eliminate human error. Even though ants did not recruit the consistent numbers across days, they were still foraging optimally on both Tuesday and Wednesday. Therefore, this still supports our hypothesis that optimally foraging would be repeatable, regardless of the day.

Our results ultimately supported our hypothesis that pavement ants would forage optimally, despite their urban habitat. Our conclusions coincide with the findings of Collignon and Detrain (2009) who found that a *Tetramorium caespitum* colony will allocate more ants to forage a food source that contains a higher caloric content (2009).

Although the exact mechanism behind group foraging behaviors is unknown, its presence in other animals, including wasps, is well documented (Lozada et al. 2016). Our results can also help to propose foraging models for other animals. Often these foraging habits include not only communication between members of the same species, but also communication between species. In a study of five ant species, the more dominant species used chemical and pheromone trails to indicate their presence to less dominant species, including *Tetramorium caespitum* (Binz et al. 2014). Evolutionarily, our findings show that overtime, *Tetramorium caespitum* have optimized foraging in a way that is energetically beneficial to the formation, growth, and reproduction of their colony, even though they are in an urban environment.

Further research can determine the mechanism of how these foraging tactics have evolved or have been maintained in other species that live in urban areas. It would also be notable to test whether isolating ant colonies in low quality food environments versus high quality food environments would cause a shift in colony size. This would help us prove whether
or not the food sources we chose for our experiment could indeed influence colony growth, reproduction and survival in *Tetramorium caespitum*.

Our study shows that urban species can forage optimally and is among a few other studies that indicate that species are capable of thriving and using foraging strategies in urban settings. A study on Eastern Red Bats, they adapted to foraging urban areas by changing wing morphology. Their wings were shorter and broader as the areas they foraged at were smaller but had more resources (Brianne *et al.* 2007). A different study on gray squirrels, *Sciurus carolinensis*, showed that they were able to thrive in an urban setting despite limited food because there is less predation (Bowers and Breland 1996). Studies like ours can be used to give us critical insights into how species that live in urban areas will adapt to forage and it can help us make prediction about survival of species that are newly associated with urban environments.


TABLES AND FIGURES

Figure 1A. Normality plots for all 4 combinations of Tuesday’s sessions, 1 and 2, and treatment groups, HH and HL.

Figure 1B. Normality plots for all 4 combinations of Wednesday’s sessions, one and two, and for treatment groups, LL and LH.

Figure 2A. Recruitment curve of the number of ants present at the high quality food source and low quality food source in session one and two of Tuesday’s study.
Figure 2B. Recruitment curve of the number of ants present at the high quality food source and low quality food source in session one and two of Wednesday’s study.

Figure 3A. Interaction plot of the mean number of ants present in session one and two of Tuesday’s study. HH: high quality to high quality treatment. HL: high quality to low quality treatment.
Figure 3B. Interaction plot of the mean number of ants present in session one and two of Wednesday’s study. HH: high quality to high quality treatment. HL: high quality to low quality treatment.

Figure 4. Comparison of the overall number of ants in both sessions and treatments on Tuesday and Wednesday.