Optimal foraging behavior in desert harvester ants (Veromessor pergandei)

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Optimal foraging behavior is exhibited when individuals in a species maximize their nutritional intake, while minimizing their energy expenditure during the foraging process. In this study, we explored the foraging behavior of Black Harvester Ants (Veromessor pergandei) to assess if their foraging habits coincided with optimal foraging theory. We observed 35 Veromessor colonies in Anza Borrego State Park in a controlled experiment where piles of large and small pumpkin and oat seeds were placed on a foraging path both near and far from the nest. We found that Veromessor preferred small seeds over large, near seeds over far, and pumpkin seeds over oat seeds. These results supported our predictions that Veromessor would collect higher value and lower cost foods, aligning with patterns predicted by optimal foraging theory. Investigating these foraging behaviors allows us to better estimate future patterns of not only Veromessor, but other foragers as well.

Keywords: O.F.T (optimal foraging theory), Veromessor pergandei, foraging cost, food preference, fitness

INTRODUCTION

Optimal foraging theory predicts that animals are adapted to minimize their energy expenditure while simultaneously maximizing their nutrient intake (Orians and Pearson 1979). For example, the bee species Apis mellifera will select flowers with higher sugar concentration rather than lower sugar concentration in order to maximize honey production efficiency (Roubik and Buchmann 1984). Optimal foraging patterns can also be seen in Lepomis macrochirus, a species of fish that aims to optimize foraging time by selecting prey that are of higher abundance and visibility (Werner and Hall 1974). Optimal foraging has been naturally selected for because of the increased fitness of individuals that maximize foraging efficiency (Pyke et al. 1977). Optimal foraging behavior may also be seen in ants as they forage for food to bring back to the colony. This evolutionary behavior increases the overall fitness of the colony, allowing foragers to retrieve a wide range of foods varying from plant seeds to other animals when resources are limited (Cerda 1997).

Although ants are small in size, they have a relatively large ecological impact on their surrounding plant communities. They can shape the structure and composition of soil and plant communities through aeration, seed dispersal, and increased nutrient content in the soil leading to greater fertility (MacMahon et al. 2000). Ants are capable of performing these ecological functions through their unique foraging behaviors.
Many species of ants communicate while foraging by using pheromones notifying other ants of a food source, enabling them to move copious amounts of food from surrounding areas to their nest.

Black harvester ants (*Veromessor pergandei*, hereafter referred to as *Veromessor*), commonly found throughout the Sonoran Desert, is a eusocial polymorphic ant species. In other words, they live in colonies and have individuals of drastically different morph sizes. However, despite this advantageous morphology, there are still questions regarding how these foraging ants are strategically working to obtain their food in order to provide for their colony (Traniello 1989). The forager’s purpose in a *Veromessor* colony is to provide food to the queen, larvae, and other ants, making foraging efficiency crucial. Food size, distance from the nest, and nutritional content is important regarding optimal foraging theory because there may be a preference of smaller and closer foods due to lower foraging costs and higher nutrient foods due to greater metabolic rewards.

In this study, we conducted an experiment to test the effects of foraging cost and food quality on foraging behavior of *Veromessor*. We manipulated food size and distance from the ant nest as a proxy for foraging cost and food type as a proxy for nutritional quality most favorable nutritional content. In this case, foods containing higher fat and protein content are referred to as higher nutrient foods. We hypothesized that *Veromessor* would prefer smaller food sizes, food closer to the ant colony, and food with the highest nutritional content.

### METHODS

#### 2.1 Sampling Design

This study was performed in the Sonoran Desert in San Diego County at the Steele/Burnand Anza-Borrego Reserve (33.2559° N, 116.375° W) located in Borrego Springs, California. This reserve is dominated by creosote bush. We observed 35 ant colonies in total. *Veromessor* are highly abundant throughout the area. The study was conducted from November 2-5, 2019 from 9:30-11:30 and 14:30-16:30, the most active times of day for *Veromessor* colonies.

Food type treatments included small and large oat and pumpkin seed particles (hereafter referred to as seeds). Oats contain 1.4% fat and 2.4% protein whereas pumpkin seeds contain 19% fat and 19% protein. For food size manipulation, a soil sieve was used to separate small and large seeds of both food treatments after manually crushing them into various sizes. Large oat seeds were greater than 2 mm and small oat seeds were between 1 mm - 2 mm. Large pumpkin seeds were greater than 1 mm while small pumpkin seeds were smaller than .5 mm. Treatments were measured this way in order to control for foraging cost due to pumpkin seeds having a higher density than oat seeds.

#### 2.2 Experimental Design

To manipulate distance, seeds were placed 1 meter (near) and 2 meters (far) away from the ant nest. At each colony, half a teaspoon of each treatment was measured and placed in a randomized order at both distances, perpendicular to the foraging path (Figure 1). We placed the
food treatments approximately three centimeters away from each other to avoid any cross-contamination between ants gathering food. Each colony was observed for 10 minutes immediately after all the seeds were placed. A hit was recorded each time an ant picked up a seed to bring back to the nest.

**RESULTS**

Overall *Veromessor* ants preferred smaller seeds over larger seeds for both food types (N = 35, t = 6.26, p < 0.0001, Figure 2). Ants collected more seeds that were near the colonies than from far (N = 35, t = 2.92, p = 0.003, Figure 3). Ants preferred pumpkin seeds over oat seeds (N = 35, t = 7.93, p < 0.0001, Figure 4). There were no interactions between the effects of food size, distance, or type.

![Figure 1. Placement of food treatments.](image)

*Figure 1. Placement of food treatments.* We conducted this experiment in the Sonoran Desert in San Diego County at the Steele/Burnand Anza-Borrego Reserve from November 2–5. Four different treatments of food were placed at one meter and two meters away from the colony perpendicular to the *Veromessor* foraging path. Bolded circles indicate the larger sized seeds. Shaded circles indicate pumpkin seeds. Non-shaded circles indicate oat seeds.

![Figure 2. Number of seeds collected vs. seed size.](image)

*Figure 2. Number of seeds collected vs. seed size.* Bars represent the average number of small and large seeds collected. For both food types, ants collected a greater number of small seeds than large seeds. Error bars represent ± 1 SEM. (N = 35, t = 6.26, p < 0.0001). Numbers of hits were log-transformed to normalize data.
DISCUSSION

Our study supported the phenomena that ants exhibit optimal foraging behavior. All variables measured portrayed independent effects on ant foraging behavior. *Veromessor* selected more small seeds overall compared to large seeds, indicating their preference for lower foraging cost. Carrying a smaller seed requires less energy expenditure than bringing a larger seed back to the colony (Crist and MacMahon 1992, Tomer 2012). Our seed size results were consistent with past studies in which a different species of harvester ants, *Pogonomyrmex*, generally favored smaller seeds over larger seeds also due to their lower foraging cost (Pirk and Casenave 2009).

*Veromessor* ants also exemplified foraging behavior through the distance and food type manipulations. There were steady patterns seen with the selection of seeds collected closer to their nest as well a greater selection of pumpkin seeds. Pumpkin seeds have almost twenty times more protein and fat content than oat seeds, making them higher in nutrients ultimately leading to the higher preference shown by *Veromessor*. A related study was conducted on *Veromessor* and found that they also preferred seeds with higher protein and fat content (Gordon 1980). This pattern was also seen in previous patterns observed in *Pogonomyrmex* sp. where there were greater preferences for seeds with higher nutritional content (Crist and MacMahon, 1992).

Throughout all trials, *Veromessor* consistently exhibited strategies aligning with the optimal foraging theory. *Veromessor* optimized their nutrient intake while also minimizing foraging costs by

**Figure 3. Number of seeds collected vs. distance from colony.** Bars represent the average number of near and far seeds collected. Ants took more seeds from near treatments than from far treatments. Error bars represent ± 1 SEM. (N = 35, t = 2.92, p = 0.0038). Numbers of hits were log-transformed to normalize data.

**Figure 4. Number of seeds collected vs. seed type.** Bars represent the average number of pumpkin and oat seeds collected. Ants took more pumpkin seeds than oat seeds. Error bars represent ± 1 SEM. (N = 35, t = 7.93, p < 0.0001). Numbers of hits were log-transformed to normalize data.
collecting smaller sized pumpkin seeds closer to their colony compared to any other seed treatment. These optimal foraging patterns of *Veromessor* may be an indication of their level of fitness. Maintaining an abundance of substantial nutrients, such as protein or fats, provides a longer future for the colony. To further understand how adaptations of *Veromessor* might evolve over time, a future study may be conducted using obstacles in their foraging path. This manipulation will assess their learning curve according to the predictions of foragers consistently aiming to optimize their efficiency. Investigating these foraging behaviors allows us to improve our comprehension of *Veromessor* fitness and strengthen predictions of the optimal foraging theory.

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**REFERENCES**


