Dietary preference of *Formica obscuripes* depends on role not time

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ABSTRACT

Resource management is necessary for the success of a species. Optimal foraging theory states that a species will attempt to minimize the energy spent obtaining resources, whilst maximizing the resources collected. Optimal foraging theory can be examined through the lens of ant colony behavior. *Formica obscuripes* utilizes role specialization and resource partitioning in each colony to minimize its energy use while maximizing its nutrient reserve. However, nutrient preferences within roles have been largely unstudied. In this study, we examine foraging *F. obscuripes* to determine their resource foraging preference, and thus their contribution to colony nutritional needs. We performed choice trails at forty colonies between liquid lipids and simple carbohydrates between aphid-tending ants and mound-building ants to test their preferences. We found that at both locations ants chose simple carbohydrates over lipids, however, mound-building ants have a higher tendency to forage lipids than aphid-tending ants. *Formica* mound-building ants require more lipids because they perform high-energy tasks such as colony construction and defense. Lipids are conserved within mounds to limit the risk of losing valuable resources to predation or dehydration. Aphid-tending ants may consume fewer lipids due to their high mortality rates and prefer simple carbohydrates because of their ability to metabolize them quickly.

Keywords: ants, optimal foraging theory, role specialization, dietary preference

INTRODUCTION

Social species often depend on communal foraging to develop and prosper. Optimal foraging theory attempts to explain this behavior by stating that animals will minimize the energy used to acquire resources (MacArthur and Pianka 1966). These resources are not equally distributed in nature which may impact how a species forages. To maximize energetic trade-offs, foragers must take into account food availability, food distribution, foraging risk, and specific colony needs (Emlen 1966). Food choice is also of paramount concern to foraging species since nutrient types differ greatly in metabolic rates. Nutrients such as lipids, proteins, and carbohydrates comprise every species diet. Lipids provide more than twice the amount of energy per gram than carbohydrates, optimizing energy obtained for foragers (Ahern and Rajagopal 2018).
However, lipids take longer to metabolize than carbohydrates making them less optimal for instantaneous energy absorption. Lipids are less abundant than carbohydrates resulting in greater energy required to obtain them. This results in a foraging trade-off between energetic value and expense.

Living organisms depend on locally available resources for survival, and ants are no exception. Ant foraging success is particularly sensitive to what nutrients are readily available (Bestelmeyer and Wiens 2003). They depend on the resources around them to build their colonies and to collect food. Thus, local resources may impact how ants establish and grow. Ants are also ubiquitous and voracious beings that can drastically alter the distribution and abundance of local vegetation (Beattie and Culver 1977). The creation of their mounds not only kills the parent plant but increases the heterogeneity of surrounding vegetative communities (Cole 1932, Beattie and Culver 1977). Ants also increase nutrients in local soils (Frouz 2008). With such environmentally changing behaviors, ants must use a variety of foraging techniques to meet their energetic demands.

*Formica obscuripes*, hereafter referred to as *Formica*, are morphologically separated into three working castes: minima, media, majora (Weber 1935). Each caste can perform any of the four main roles: nursing, foraging, aphid-tending, and mound-building. The minima caste generally forage and care for larvae while the media predominantly works as aphid-tenders (Weber 1935). And the majora caste tend to perform mound-building and protection of the colony (Weber 1935). *Formica* receive nutrients according to their role in the colony. It may increase the colony’s fitness to distribute fewer nutrients to ants traveling farther from the mound since they have a higher risk of depredation and dehydration (Nonacs 2002). However, the extent to which aphid-tenders and mound-builders prefer these resources is largely unknown (Kay 2002).

An ant’s ability to acquire and distribute food is vital for the whole colony’s success, two of the strategies used to achieve this are gathering and regurgitation. *Formica obscuripes* is a genus in the formicidae family easily distinguished by their unique mounds, composed of small twigs and bark, and their aphid farming activities (Cole 1932). Mutualistic interactions between ants and aphids have been widely studied, showing that both parties greatly benefit from each other (Stadler and Dixon 1998). Ants acquire an easily accessible energy source from aphids (honeydew: an aphid excretion mainly composed of simple carbohydrates), while aphids can form larger colonies and are protected by the ants. To take advantage of this energy source, *Formica* heavily depend on regurgitation for distribution.

The colony also feeds on lipids as a secondary energy source, lipids are higher in energy but take longer to metabolize. Lipids increase reproductive success and allow ants to feed larvae and perform high energy activities such as mound-building and defense (Kay 2002). Ants usually obtain lipids from seeds and small insects. Solid lipids cannot be regurgitated and therefore are exclusively brought and distributed at the mound (Brian 1973). Worker ants primarily distribute lipids to the queen, larvae and mound workers. Liquid lipids are more easily distributed to the colony because they can be regurgitated. Even though liquid lipids are not widely available in nature, one study by Howard and
Tschinkel (1981) showed that liquid lipids can be distributed in the colony using isotope tracing. Foraging of both simple carbohydrates and lipid resources depend on the immediate needs of the colony. Ants will spend more time looking for resources that are quickly depleted within the colony, and thus simple carbohydrate foraging is expected to be a larger part of the total foraging than lipids (Kay 2002).

In this study, we tested how ants performing different roles respond to the presence of lipids and simple carbohydrates. We predicted more ant activity in the morning than in the evening since we observed more mound-building in the afternoon and foraging activity is temporally dependent (Gordon 1999). Our second hypothesis predicted that there would be higher visitation to both nutrients from aphid-tenders than mound-builders. Mound-building ants are less likely to forage for resources since they are occupied with mound-building (Herbers 1977). Our final hypothesis predicted that mound-building ants would consume more lipids than simple carbohydrates, while aphid-tenders would consume more simple carbohydrates than lipids. Lipids provide mound-building ants with high-energy nutrients needed for mound-building and defense.

METHODS

2.1 Study Area

Our experiment was conducted between July 31 and August 4, 2019 at the Inyo National Forest in Mammoth Lakes, California (37°36'42.8"N 118°49'53.6"W). The landscape of our study area is a Great Basin sagebrush steppe dominated by sagebrush (Artemisia spp.), bitterbrush (Purshia tridentata), and rabbitbrush (Chrysothamnus spp.). We selected forty Formica obscuripes ant mounds that were active and varied in size to account for the natural distribution of colony sizes.

2.2 Experimental Design

We implemented choice trials at distances of zero and one meter from each mound of forty ant colonies to determine feeding preferences of mound-building and aphid-tending Formica. No mounds were within 12 meters from one another. Choice trials were conducted during observational periods in the morning (8 AM to 10 AM) and evening (7 PM to 9 PM) when ants are the most active (McIver, J.D. and Yandell, K., 1998). We surveyed twenty colonies during the morning and twenty during the evening. The length, width, and height of each ant colony were recorded at the time of the surveys. During a ten minute observation, we counted the number of ant visits to the simple carbohydrates and lipids at each mound. We recorded the activity for each colony at separate times.

Distance from the mound was used as a proxy for ant role since it was previously observed that mound-builders were located at the mound and aphid-tending ants forming trails from the mound (McIver and Loomis 1993). Selecting trails that led to an actively farmed sagebrush one-meter away from the mound allowed us to control for ant role, and to increase the probability to attract mound-builders we placed the bait next to the mound and away from any established trails. We used a simple syrup made of six-parts water and one-part sugar to act as a substitute for honeydew, Formica’s main food resource. We used olive oil as a lipid alternative to the simple
carbohydrates because it has similar physical properties to the simple syrup. Carbohydrates and lipids were placed one meter away from the edge of the mound along pre-existing foraging trails and at the edge of the mound.

2.3 Statistical Analysis

To test for temporal and role differences in ant activity, we performed a two-way ANOVA test on total visits in relation to role, time of day, and their interaction. Mean total visits was logarithmically transformed to create a normal distribution for statistical analyses. In order to test for the preferred nutrient type between aphid-tending ants and mound-building ants, we performed two-way ANOVA test on visits between nutrient types and roles. Lastly, to further test for differences in foraging preferences between the two roles of ants, we performed a t-test between percent sugar visits for aphid-tending ants and mound-building ants. We used the percentage of simple carbohydrate visits to the total visits as the site’s preference for simple carbohydrates.

RESULTS

*Formica* expressed no temporal difference in activity between morning and evening (N=40, F=0.01, p=0.75; Figure 1). Additionally, there was no difference in total *Formica* activity between aphid-tending ants and mound-building ants (N=40, F=0.02, p=0.90; Figure 2). *Formica* consumed simple carbohydrates more than lipids irrespective of role (N=80, F=60.12, p< .0001). However, mound-building ants consumed a larger proportion of lipids than aphid-tending ants (N=80, F=7.17, p=0.01; Figure 2).

**Figure 1. No temporal changes in *Formica* activity.** We surveyed twenty *Formica obscuripes* mounds in the morning and twenty in the evening at Inyo National Forest in Mammoth Lakes, California. We implemented choice trials using simple carbohydrates and lipids, recording visits to each food choice. There was no difference between the mean total activity of *F. obscuripes* between the two observation periods (N=20, F=1.04, p=.31).

**Figure 2. *Formica* role differences in nutrient preferences.** We surveyed twenty *Formica obscuripes* mounds in the morning and twenty in the evening at Inyo National Forest in Mammoth Lakes, California. We implemented choice trials between mound-building ants and aphid-tending ants using simple carbohydrates and lipids and recorded visits to each food choice. There is no difference between the total activity of *Formica* between roles of the colony (N=40, F=1.10, p=.30). Proportion of *Formica* visits to sugar by aphid-tenders were greater than visits by mound-builders. (N=40, F=7.17, p=.01)
DISCUSSION

Our results found no temporal difference in ant activity between morning and evening peak intervals. We also found no difference in ant activity between aphid-tenders and mound-builders. Mound-building ants preferred a higher proportion of lipids than aphid-tending ants, however simple carbohydrates were preferred over lipids for both roles.

We predicted more ant activity in the morning than in the evening since we observed more mound-building in the evening and foraging activity is temporally dependent (Gordon 1999). However, we found no difference in Formica activity between the morning and evening. This indicates that both aphid-tending and mound-building are performed at the same rates during both intervals of peak activity. We can conclude that this temporal constancy solidifies our other findings in role activity rates and dietary preferences.

Our second hypothesis predicted higher visitation rates from aphid-tenders as opposed to mound-builders, since mound-building ants do not regularly forage (Herbers 1977). However, we found no difference in activity between the two roles. This finding supports optimal foraging theory, since both roles foraged for the nutrients that were more readily available than honeydew.

Our final hypothesis predicted that mound-builders would consume more lipids than simple carbohydrates, while aphid-tenders would consume more simple carbohydrates than lipids. Ants from both roles consumed simple carbohydrates more than lipids, however, lipid consumption increased with mound-builders. Higher frequencies of simple carbohydrate visits at the mound could be explained by an intrusion of aphid-tending ants, since aphid-tending ants regularly preferred simple carbohydrates over lipids. In contrast, mound-building ants preferred larger proportions of lipids because they need such nutrients to perform high-energy tasks (Kay 2002). The aphid-tenders regurgitate simple carbohydrates to foragers travelling away from the mound, energizing the exploration of new territories. However, aphid-tending ants experience more mortality than mound-building ants, since depredation and dehydration increase as ants travel farther away from the mound. Thus, lipid reserves acquired by aphid-tending ants are at more risk of being lost. (Nonac 2002). In conclusion, the colony limits the risk of losing valuable lipids and energy through role specialization.

Future studies could conduct choice trials focusing on foraging and nursing Formica. These studies would provide insight on the nutrient needs of the remaining two roles and determine if a certain role is more selective when foraging. Another study could survey food preferences using protein as an additional nutrient type. Formica also forage for insects which provide the colony with protein. Examining choice trails that include proteins could provide for a more accurate representation of colony nutritional requirements.

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REFERENCES

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