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Sisters or strangers: How does relatedness affect foraging in carpenter ants?

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ABSTRACT

Optimal foraging theory (OFT) states that animals will forage in a way that maximizes energy intake while minimizing energy expenditure. Eusocial insects are examples of species that exhibit OFT. One type of eusocial insect is the carpenter ant *(Camponotus).* Carpenter ants use pheromone trails as a form of communication. In using chemical cues to communicate with one another, carpenter ants fulfill OFT by maximizing energy rewards and minimizing energy spent searching for resources. We conducted choice trials with different sugar water concentrations and observed how relatedness between ants affected foraging behavior. We tested if carpenter ants would act according to OFT and forage from the resource with the highest energy reward or if the presence of non-related ants would influence their behavior. We collected ants at Mclaughlin Natural Reserve in California and placed them in an arena with four different sugar water concentrations either with ants of the same colony (sisters; intracolonial) or ants of a different colony (strangers; intercolonial). Our findings supported our hypothesis that the presence of ants from different colonies affects foraging preferences. Intracolonial ants took less time to visit concentrations and made more visits to higher concentrations in comparison to ants in intercolonial trials. We theorize that this may be due to the chemical cues used to distinguish between ants of the same colony and to communicate the presence of sugar water. We also observed that ants had a strong preference for the highest concentration of sugar water, supporting our second hypothesis that ants prefer higher quality resources. We speculate that this is due to optimal foraging theory, where animals seek to maximize their energy intake while minimizing their energy expenditure. The findings of this study highlight the complexities of animal foraging behavior and communication between members of the same species.

Keywords: optimal foraging theory, carpenter ants, Hymenoptera, eusocial, pheromones

INTRODUCTION

Optimal foraging theory (OFT) states that animals will forage for food in a way that maximizes energy intake while minimizing energy expenditure (Morehead & Feener, 1998). OFT has two branches: classical OFT which applies to solitary foragers and foraging game theory which applies to social species (Pyke and Starr, 2020). Foraging game theory is distinguished from classical OFT in that individuals respond directly to the behavior of others.

Eusocial insects are one example of a group of organisms that exhibit foraging game theory. Eusocial insects include organisms within *hymenoptera* like ants, wasps, and bees. These organisms are all insects that live in highly dense, self-organizing systems (Boomsma and Franks, 2006). The two main characteristics of eusociality are overlapping generations in which adults take care of the young and a caste system where kings and queens are distinguished from workers (Hölldobler and Wilson, 1980). Eusocial insects have haplodiploidy, meaning they are 75% related to one another and are almost all female, therefore eusocial colonies are composed almost exclusively of sisters (Detrain and Deneubourg, 2006).

For eusocial insects to maintain their complex societal organization, efficient communication and cooperation between individuals must occur. One way eusocial insects communicate is through body language. The western honey bee communicates the location of a food resource by moving its abdomen in a "dance" (von Frisch, 1967). Chemical cues are also a means of communication. Ants create pheromone trails that lead nestmates to food sources (Renyard et al., 2019) and even in the presence of multiple pheromone trails from different ant species, individual ants can recognize their colony-specific scent (Chalissery et al., 2019). Both ant pheromone trails and honey bee dances are forms of communication that enable foraging game theory within OFT; in leading nestmates directly to high-quality food sources, eusocial insects reduce overall time spent searching for food, therefore minimizing energy expenditure and maximizing energy reward.

One food resource that offers particularly high energy rewards for foraging insects is sugar water. Previous research establishes that ants, bees, and wasps are attracted to sugar water (Nyamukondiwa and Addison, 2014) (Couvillon, 2019) (Lioy et al., 2020). For our study we conducted choice trails using sugar water and carpenter ants (*Camponotus essigi*). We ran trials between sister ants (of the same colony; intracolonial) and between strangers (ants from different colonies; intercolonial) to explore whether carpenter ants would act in line with OFT and forage for the food with the highest energy reward (i.e. highest concentration of sugar) or if their foraging would be influenced by the pheromone trails of their nestmates. We hypothesized that overall, ants from intracolonial and intercolonial trials would both prefer the highest sugar concentration as opposed to other treatments. We also sought to explore the difference between intercolonial and intracolonial trials in the context of pheromone trails and the disruptive presence of non-nestmates. In a previous study, carpenter ants placed in a laboratory setting were able to identify nestmates from non-nestmates even after two months of isolation from their colony (Zweden et al., 2008). Given carpenter ants' strong ability to identify nestmates, we hypothesized that ant visitation in intercolonial trials would be less than intracolonial trials because ant communication would be disrupted by the distracting presence of non-nestmates.

METHODS

2.1 Study Site

Research was conducted at McLaughlin Natural Reserve in Lower Lake, California from February 22 to February 26 of 2021. McLaughlin Reserve consists of serpentine soils, grassland, chaparral, and oak woodland habitats. McLaughlin is home to 27 species of ant including the carpenter ant (Fisher, 1997). This study focuses on the *Camponotus* genus of carpenter ants.

2.2 Intercolonial and Intracolonial Conditions

An intracolonial trial contained 8 sister ants collected from the same site. Intercolonial trials contained stranger ants (four from two different colonies), totaling eight ants. To ensure the ants were from different colonies, we standardized the distance between collection sites by walking at least 200 meters from one collection site to the next (Carroll and Janzen, 1973). Each set of unrelated stranger ants were placed into the same 18cmx18cmx5.9cm container for choice trials. Ants were taken to the McLaughlin lab after collection to begin choice trials.

2.3 Choice Trials

In order to test the preferences of sugar water concentrations in carpenter ants, the ants were placed in containers with four leaves that each had two droplets of one kind of sugar water concentration. The concentrations were: 10%, 18%, 30%, or 60%. These concentrations were achieved by diluting the 60% concentration into 30%, diluting 30% into 18% and so on. Sugar concentrations were measured with a refractometer. Leaves were placed in a square formation at the bottom of the container and were rotated after each trial so that no bias toward a certain direction or placement occurred. Plastic wrap was secured with tape over the container to ensure observer visibility and to prevent ants from escaping. We monitored ants for 30 minutes and recorded each time an ant visited a droplet. A visit was a direct contact between an ant's head and the droplet for longer than one second. In addition, we recorded the time of day the ants were tested and how long they were in containment before being tested. Data was organized into ten 3-minute time intervals.

2.4 Statistical Analysis

Data was analyzed using JMP v.14 for statistical analysis and visualization. We used a chi-squared test to examine the relationship between the concentration that was first visited and the concentration with the most visitation. We also tested whether total sips of different sugar concentrations were affected by the relatedness of the ants in the trial via an ANOVA test.

RESULTS

We conducted a total of 35 trials: 16 intercolonial and 19 intracolonial. Intercolonial trials overall had less visits, at an average of 14.3 visits per trial, while the intracolonial trials had an average of 19.2 visits. Whether ants were foraging with sisters or with strangers, the average time to make the first visit to a droplet was relatively similar at around 260-310 seconds. The intercolonial trials had more variation in visitation than the intracolonial trials. We observed that whether the trial was intercolonial or intracolonial had a significant effect on sugar water concentration preference: ants foraging with their sisters had stronger preferences. Intracolonial ants were more specialized and preferred 60% sugar concentration while intercolonial ants were less specialized and consumed relatively similar amounts of each of the concentrations (p=0.02, Figure 1). Furthermore, the first concentration that was visited tended to be the most popular concentration in each trial. About 67% of the trials had a strong preference for the droplet concentration that was first visited (p=0.01).

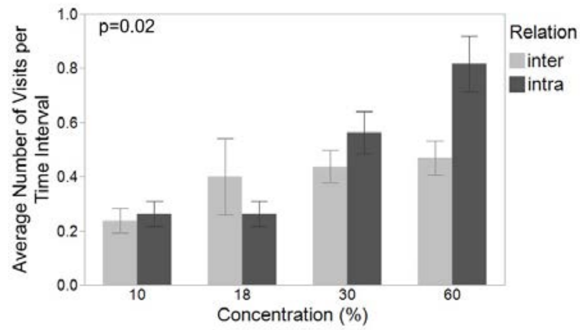

Figure 1. Visits to each sugar water concentration within intercolonial and intracolonial conditions. Carpenter ants placed in trials with their sisters (intracolonial) showed a stronger preference for higher sugar concentrations. Ants in trials with strangers (intercolonial) conditions showed less distinct preferences. Visits are the number of times an ant made direct contact with a sugar water droplet for more than one second. Additionally, ants foraging with their sisters made fewer visits to the sugar water than the ants foraging with strangers. We speculate that this is due to disrupted communication between members of the same colonies.

DISCUSSION

This study aimed to explore the foraging behavior of carpenter ants and how their foraging may differ when they feed with their sisters or among strangers. We also wanted to investigate the sugar content preferences of ants and how optimal foraging theory may play into it. Our findings supported our first hypothesis that the presence of ants from different colonies affects foraging preferences. Ants in intercolonial trials made fewer visits overall to all the sugar concentrations (Figure 1). The ants foraging with strangers also showed a weaker preference for higher concentrations as opposed to the sister ant trials. We speculate that this is due to impaired communication between ants of different colonies and the distraction of being with non-nestmates. The observed preference for the highest concentration of sugar water (Figure 1) also supported our second hypothesis that predicted ants would prefer higher quality resources. We believe this may be connected to OFT since ants would select the concentration that would provide the greatest energy reward. Although the carpenter ants showed partial preference toward higher concentrations, we also found that they strongly favor whichever resource they visited first, regardless of concentration. We speculate that this may be driven by the chemical cues and pheromone trails left by the ants. Despite this effect, a general preference for higher concentrations was seen in both intercolonial and intracolonial trials.

There is still much to explore about optimal foraging theory. There may be heritable traits within a population that cause offspring to forage in the same manner as their parents, or there may be fitness benefits that come with certain foraging behaviors (Pyke 2000). The foraging behavior of organisms shapes the way they interact with their environment, competitors, and food sources. Our study further explored this relationship and offers important implications on how eusocial organisms may communicate with each other. Future research should be conducted on the location and composition of ant pheromone trails to better understand the chemical cues carpenter ants use to communicate.

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