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Foraging preferences of *Camponotus spp.* are shaped by sun exposure and food type

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ABSTRACT

Animal foraging behaviors are shaped by their nutritional needs as well as risk mitigation. Understanding how animals balance these trade-offs can provide insights into how they prioritize different survival needs. Carpenter ants are an extremely diverse genus of ants, with much unknown about the behaviors and preferences of many species. We studied the foraging preference of two species of carpenter ant (*Camponotus modoc* and *Camponotus laevissimus*) based on sun exposure and food types. We offered choice trials between a protein-rich (grasshopper) and sugar-rich (jelly) food type. Between trials, each food type was presented in either sun or shade. We hypothesized that shaded sites would have lower discovery time and higher recruitment, especially when the protein-rich grasshopper was combined with shade. Mean discovery times were lower for all jelly options. Recruitment was higher on the grasshopper meals, especially in shaded conditions. Ants were better able to detect the wet, sugary jelly and thus discovered it faster in both the sun and shade but preferred to recruit to the more valuable grasshopper. Foragers may accept risk while foraging for the colony but minimize it while feeding by choosing safer conditions.

Keywords: Carpenter ant *(Camponotus spp.)*, sun exposure, food preference, optimal foraging theory, resource discovery

INTRODUCTION

When selecting foraging sites, animals face trade-offs between maximization of food rewards and minimization of cost or risk (Cowlishaw 1997, Maurer 1990). They may select sites with poorer food resources if there is less likelihood of predation or physical stress compared to richer foraging grounds (Hassel and Southwood 1978, Mason et al. 2017). The specific trade-off between risk and reward can vary between animals. Some common minnows (*Phoxinus phoxinus*), for example, are reward maximizers; they are willing to forage in areas with predators present if there is more food there than in safer habitats (Pitcher et al. 1988). On the other hand, Darwin's leaf-eared mice (*Phyllotis darwini*) will sometimes sacrifice food rewards in exchange for a minimization of risk; on full moon nights with a higher chance of predation, mice may employ less efficient foraging strategies that keep them closer to the nest (Vásquez 1994). A forager's preference also depends on their nutritional

needs; they seek out nutrients they need and avoid nutrients that they have in excess, presenting another kind of trade-off (Simpson et al. 2004).

Insects, like any other animal, display preferential foraging in areas with less risk. For example, grasshoppers (*Melanoplus femurrubrum*) in areas with high predation will eat a nutrient-poor diet if it means spending more time on vigilance (Rothley et al. 1997). Furthermore, fly maggots will feed more in areas with less extreme heat, avoiding food items at high temperatures even when starved (Podhorna et al. 2018). Insects are also able to select food types to hit a target ratio of nutrients: locust (*Locusta migratoria*) nymphs given pairs of protein and carbohydrate feeds of varying concentrations managed to hit the same target ratio across treatments (Chambers et al. 1995).

These kinds of trade-offs between food types and environmental conditions have been studied extensively in ants (Bestelmeyer 2000). Their widespread abundance and quick response to environmental changes allow for many opportunities for experimental and observational studies (Guzman-Mendoza and Castano-Meneses 2007). One such study looked at the interaction between thermal tolerance and interspecific competition on foraging behavior (Wittman et al. 2010). Species with a lower thermal tolerance can forage more efficiently in shaded areas, contributing to colony fitness. Another important factor in foraging success is the needs of the colony an ant belongs to. The nutrients an ant chooses to forage reflects both colony and individual needs (Pyke and Starr 2020). Protein-rich foods are highly valued during brooding season in order to support egg production and larval growth (Renyard 2024, Lach et al. 2010). Sugars are essential for worker ant activity, while also contributing to brood success. Since adult ants cannot eat solid food, they depend on liquids for sustenance. Solid food items with needed nutrients are brought back to the colony to feed the queen and other ants via trophallaxis (Renyard 2024).

Two important aspects of foraging in ants are how quickly they find a food source, and how many ants are recruited to it. The discovery time of a food source could reflect what environment an ant prefers to forage in. If an ant species prefers to forage in cooler temperatures, for example, they are more likely to find a food source in that environmental condition, as there will be more foragers present (Pearce-Duvet and Feener 2011). The maximum number of ants on a food source reflects value of the food, in terms of individual or colony needs. Ants will recruit more help to food they find as higher value (Carroll and Janzen 1973). This higher value may align with brooding season or individual needs, as sugars help with worker sustenance while protein is required to raise new eggs. If the food source is solid, however, this can almost certainly be attributed to value for brood/colony needs, as worker ants cannot consume solid food themselves.

Carpenter ants (*Camponotus spp.*) are the most abundant genus of ants globally (Wheeler 1911). With this abundance and diversity comes variety in preferences for specific foraging conditions and nutrients. Many species of carpenter ants are nocturnal (Rossi and Feldhaar 2020). Generally, carpenter ants prefer to forage in cooler temperatures or under less direct sun to avoid desiccation (Lach et al. 2010). Brood rearing periods peak in summer, which is associated with a foraging preference for

protein-rich foods (Sanders 1972). Ants have been found to preferentially discover these protein-rich foods, which are generally considered more valuable (Pearce-Duvet and Feener 2010).

We tested the effects of sun exposure and food type on ant foraging preference. We used discovery time and maximum number of ants on a given food as metrics of preference. Knowing that carpenter ants generally prefer to forage in cooler temperatures or shade, we decided to set up a paired design experiment with two plates: one in the sun and one in the shade. The two food types we used were solid protein-rich food (a grasshopper) and wet sugar-rich food (strawberry jelly). A "treatment" was a pair of two plates in front of a colony, each with a food item, with one plate in the sun and one in the shade. The combinations of food and shade yielded four treatments: grasshopper sun / jelly shade, jelly sun / grasshopper shade, grasshopper sun / grasshopper shade, and jelly sun / jelly shade.

We expected the discovery time for the shaded plates to be lower than the discovery time for the sun plates, regardless of food treatment. Additionally, we predicted that shaded plates would have a greater maximum number of ants compared to sun plates. We also expected the magnitude of the maximum number of ants per treatment to vary depending on the food treatment with *a)* greatest proportional difference between jelly sun / grasshopper shade, *b)* intermediate difference between grasshopper sun / grasshopper shade and jelly sun / jelly shade, and *c)* no difference in maximum number of ants between grasshopper sun / jelly shade.

METHODS

2.1 Study System

Our study was carried out at Sagehen Creek Field Station, California (39.4325 N, 120.2369 W) from July 31, 2026, to August 2, 2026. Sagehen is a natural reserve located on the eastern side of the Sierra Nevada in California, USA. It has an elevation of approximately 1,950 m and is dominated by mixed coniferous forests and meadows (UC Nature). Sagehen is characterized by a Mediterranean climate with hot dry summers and cold wet winters. The three-day sampling period was mostly sunny, with average daily temperatures up to 31°C in the afternoons and down to 2°C in the early morning. Within our study system, carpenter ants live in soil beneath rocks, living plants, and dead wood (Rossi and Feldhaar 2019). Grasshoppers were commonly seen throughout the meadows during the day. Common species of plants in the meadow included grasses (Gramineae) and sedges (Cyperaceae).

Carpenter ants are abundant across the landscape in summer. There are four common species of carpenter ants present in Sagehen. The two species our study focused on were *Camponotus modoc* and *Camponotus laevissimus*. *Camponotus modoc* foraging activity peaks from May to August, while *Camponotus laevissimus* has a slightly longer activity period from April to October (Hansen 1985, Mackay 2019). After these summer activity peaks, both species' activity starts to diminish and ceases in winter, when they go into hibernation (Sanders 1972). During our observation period from late July to early August, we noticed that both species were foraging

around their colonies when the sun was directly above.

Carpenter ants are omnivorous. They have a wide-ranging diet, including both insects and honeydew produced from aphids (Hansen 1985). Studies have found that they especially prefer nitrogen- and sugar-rich foods (Cannon 1998). During rapid larval growth periods in the summer, workers forage extensively for protein to feed their queen for egg production and brood rearing (Sanders 1972, Cannon and Fell 2002, Renyard 2024). Insects are ants' primary source of nitrogen and protein. Additionally, workers collect sugar (or carbohydrates) year-round to sustain themselves energetically.

Both carpenter ant species have different foraging behaviors. *C. modoc* is nocturnal and prefers to forage from 8 pm to 4 am when the temperature is cooler (Hansen 1985, Palladini et al. 2007). On the other hand, *C. laevissimus* is diurnal and is more active in the afternoons, when the temperature is usually warmer (Mackay 2019). The difference in heat tolerance and foraging periods between *C. modoc* and *C. laevissimus* might be driven by their strategies to minimize risks, just like *C. martensi,* another carpenter ant species that avoids mortality risk in high temperatures by prioritizing staying in cooler environments (Cerdá et al. 1998).

2.2 Colony Selection

To find study colonies, we surveyed the area along Sagehen Road looking for wood that appeared occupied by carpenter ants. We noted frass, entry holes, and visible ants in the area. We marked each site that seemed to be a colony with a flag. We baited the flagged sites with jelly and grasshoppers and returned after one hour to see if ants were feeding on the bait. If ants were feeding on either bait, we considered the site to be active and included it in our study. Otherwise, we excluded the sites that were either inactive or were shaded throughout the whole day. We sampled nine ant colonies in total: five belonged to *C. laevissimus* and four belonged to *C. modoc*. Seven of the nine colonies were in the open meadow with sunlight all day, and the other two were on the edge of pine forests, having partial sunlight throughout the day.

2.3 Treatments and Measurements

We experimented with two food types: Smucker's strawberry jelly (12 g sugar per tablespoon) and dead grasshoppers (mostly *Camnula pellucida* and *Pseudochorthippus curtipennis*). Jelly represented a sugar-rich food and grasshoppers represented a protein-rich food. Each food type was tested in both sun and shade, for a total of four paired treatment types in the sun and shade respectively: 1) grasshopper sun / jelly shade, 2) jelly sun / grasshopper shade, 3) grasshopper sun / grasshopper shade, and 4) jelly sun / jelly shade.

We used a matched-pair design. Each of the colonies was assigned one of the four treatments, which were rotated over the study period to make sure each colony received each treatment at least once. Foods were placed on paper plates—we spread one tablespoon of jelly or taped down one grasshopper per plate. Plates were placed around 30 cm from the colony and around 60 cm apart from each other. Treatments were carried out in the mornings (10 am to 1 pm) and afternoons (1 pm to 5 pm). Shade was created by placing a folding chair over

one plate, and ensuring the shade stayed on the plate as needed.

We observed each colony for two hours, recording the number of ants on each plate every five minutes in the first hour and every 15 minutes in the second hour, as preliminary trials showed a peak in activity around 40 minutes after treatment applications. For each observation interval (either every five or 15 minutes), the plate was observed for one minute to determine the maximum number of ants present on the food item. We used two metrics for measuring carpenter ant food preference: discovery time (in minutes) and maximum number of ants. Discovery time measured how long it took the first ant to notice and begin to feed from the bait after placement. This could potentially show a preference of smell for one food type over another. We also recorded the maximum number of ants that were observed feeding from the bait at once during the two-hour observation period, which shows recruitment and value of a food source for individual or colony needs.

2.3 Statistical Tests

A t-test was used to ensure no confounding effect of species or time of day on discovery time or maximum number of ants. We ran paired t-tests of discovery time and maximum number of ants for each of the four treatments (grasshopper sun / jelly shade, jelly sun / grasshopper shade, grasshopper sun / grasshopper shade, jelly sun / jelly shade). All statistical analyses were done using JMP (2026 JMP® Version 18. JMP Statistical Discovery LLC, Cary, NC.)

RESULTS

Forty-five treatment replicates were obtained from the nine colonies. Of these, only 32 were usable for discovery time as the remaining 13 had zero visits. Time of day (morning or afternoon) did not affect discovery time ($N_{morning}$ = 16, $N_{afternoon}$ = 16, t = 0.15, p = 0.88) or maximum number of ants ($N_{morning}$ = 26, $N_{afternoon}$ = 19, t = -0.49, p = 0.63). Moreover, there was no effect of ant species on discovery time (N_{modoc} = 12, $N_{laevissimus}$ = 20, t = -0.27, p = 0.79) or maximum number of ants (N_{modoc} = 18, $N_{laevissimus}$ = 27, t = 0.54, p= 0.30) either.

3.1 Discovery Time

The ants took longer to discover the grasshopper in the sun than the grasshopper in the shade (Table 1, Fig. 1). For the rest of the treatments (grasshopper sun / jelly shade, jelly sun / grasshopper shade, jelly sun / jelly shade), the discovery time was approximately the same in the sun and the shade. Grasshopper plates had a higher mean discovery time than jelly plates, regardless of if they were in the sun or the shade (Fig.1).

3.2 Maximum Number of Ants

A higher maximum number of ants visited the shade than the sun in the grasshopper sun / grasshopper shade treatment and the jelly sun / grasshopper shade treatment (Table 1, Fig. 2). Of these two treatments, the jelly sun / grasshopper shade treatment yielded the largest proportional difference in maximum ants, while the grasshopper sun / grasshopper shade treatment yielded a smaller proportional difference in maximum ants (Fig. 2). However, for the grasshopper sun / jelly shade treatment and the jelly sun

Table 1. Paired t-test results for ant discovery time and maximum number across treatments. T-test results for discovery time (time for ants to find the food object) and maximum number of carpenter ants on food baits. Data was collected in Sagehen Creek Field Station, Truckee, California, from July 31 to August 2, 2026.

Treatment	N	T-Ratio	P-Value	Difference
Discovery time (min)				
Grasshopper sun/ Grasshopper shade	9	2.76	0.025	sun > shade
Grasshopper sun/ Jelly shade	7	1.65	0.15	sun = shade
Jelly sun/ Grasshopper shade	9	0.78	0.46	sun = shade
Jelly sun/ Jelly shade	7	0.84	0.43	sun = shade
Maximum number of ants in a sampling period				
Grasshopper sun/ Grasshopper shade	11	2.76	0.020	sun < shade
Grasshopper sun/ Jelly shade	11	0.25	0.81	sun = shade
Jelly sun/ Grasshopper shade	12	3.71	0.0034	sun < shade
Jelly sun/ Jelly shade	11	1.54	0.15	sun = shade

/ jelly shade treatment, approximately the same maximum number of ants visited the shade and the sun (Table 1, Fig. 2).

DISCUSSION

We found that sun exposure and food type influenced the foraging preference of carpenter ants. However, we found that the time of day or ant species did not affect carpenter ant foraging preference. This is interesting, as *Camponotus laevissimus* is diurnal (Mackay 2019), while *Camponotus modoc* is nocturnal (Hansen 1985). The lack of effect of species on foraging preference could be attributed to the fact that neither *Camponotus laevissimus* nor *Camponotus modoc* were observed to co-occur at our sampling sites, which means that competition between them was unlikely. Moreover, habitat characteristics such as resource availability are known to affect ant foraging strategies (Segev et al. 2021). Since both *Camponotus laevissimus* and *Camponotus modoc* live in the same general habitat, their foraging strategies could also be similar. The reason we found no effect of time of day on our results could be due to

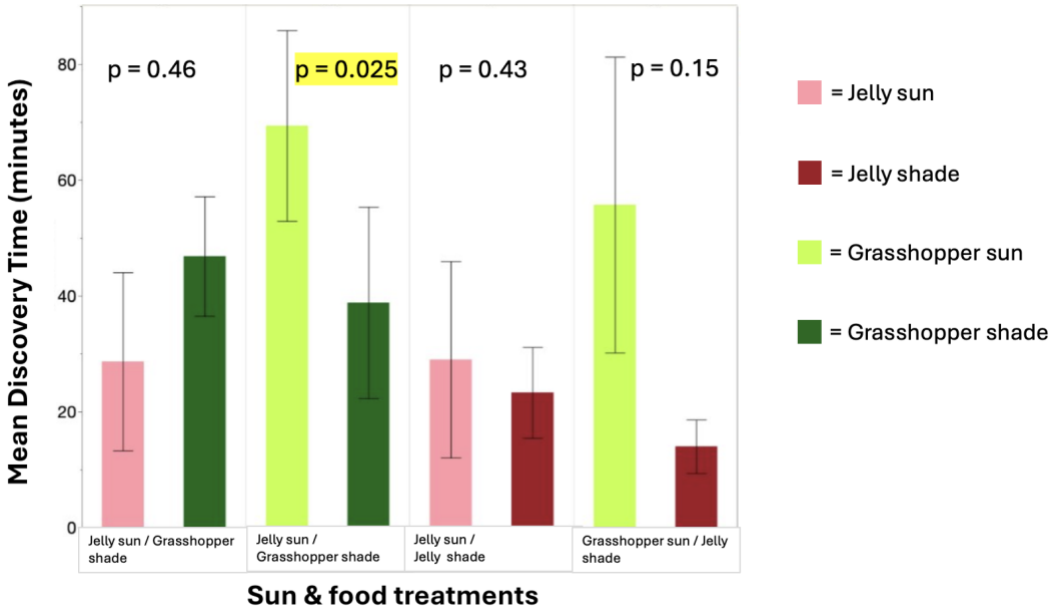


Figure 1. **Food type and sun exposure mean time for *Camponotus spp.* to discover grasshopper and jelly baits (in minutes).** Dead grasshopper and jelly baits were placed on paper plates 30 cm from *C. modoc* and *C. laevissimus* colonies. Each colony received two plates of food, one in the sun and one in the shade. Food items were watched for 2 hours and time between food placement and commencement of feeding by a worker was recorded. Error bars represent one standard error from the mean. Data was collected in Sagehen Creek Field Station, Truckee, California, from July 31 to August 2, 2026.

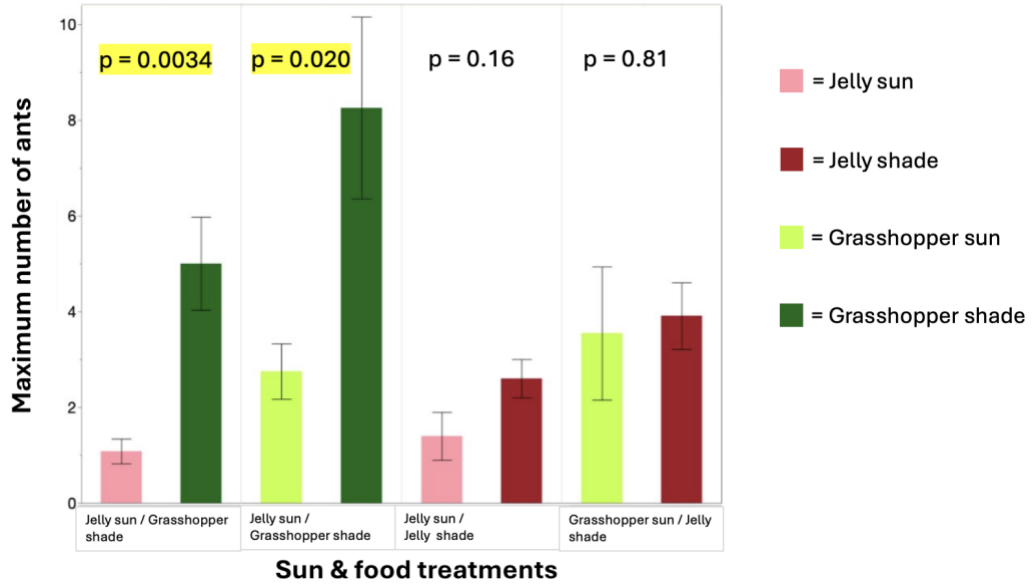


Figure 2. **Food type and sun exposure affect the maximum number of *Camponotus spp.* workers recruited.** Maximum number of *Camponotus spp.* workers during a two-hour feeding period on grasshopper or jelly meals placed near the nest. Combinations of food items were varied, with one always in the shade and one in the sun. Error bars represent one standard error from the mean. Data was collected in Sagehen Creek Field Station, Truckee, California, from July 31 to August 2, 2026.

our broad categorization of times into "morning" or "afternoon." Species-specific foraging patterns could vary on a smaller scale of resolution than our methods measured.

We found that discovery time was not determined solely by sun exposure, which contrasts with our hypothesis that light would be the only determining factor. While ants took longer to discover the grasshopper in the sun than the grasshopper in the shade, there was no difference between discovery time in the sun and the shade for the rest of the treatments (grasshopper sun / jelly shade, jelly sun / grasshopper shade, jelly sun / jelly shade). On the contrary, food type had a more notable impact on the discovery time. Across all treatments, grasshopper plates had a higher mean discovery time than jelly plates, regardless of if they were in the sun or the shade. The carpenter ants likely found the jelly faster for two reasons: (1) the jelly was liquid, making the odor easier to detect than the grasshopper, (2) the jelly had more surface area than the grasshopper did during the experiment, which means that ants are more likely to run into it if randomly moving around (Pearce-Duvet and Feener 2010). Future studies could address how exactly the physical state of the food (liquid or solid) or the surface area of the food affects ant discovery time.

Both sun exposure and food type played a role in the maximum number of carpenter ants in each treatment. Overall, the carpenter ants recruited more to plates that were shaded (low risk) or contained grasshoppers (protein-rich; high reward) than to plates that were unshaded (high risk) or contained jelly (sugar-rich; low reward). The carpenter ants recruited more to protein-rich grasshoppers because they were foraging during their breeding season and prefer protein-rich sources to rear their young (Renyard 2024, Lach et al. 2010). The carpenter ants recruited more to the shaded treatment because they were avoiding the desiccation risk in the sun (Lach et al. 2010). The effects of food treatment and sun exposure appeared to be additive, with the largest proportional difference between options in the jelly sun / grasshopper shade treatment. Furthermore, an intermediate proportional difference was observed in the grasshopper sun / grasshopper shade treatment, and no difference was observed in the grasshopper sun / jelly shade treatment.

The jelly sun / grasshopper shade treatment had the largest proportional difference because the jelly sun portion lies on the unfavorable extreme with low reward and high risk, while the grasshopper shade portion lies on the favorable extreme with high reward and low risk. These two extremes combine to form a relatively large difference. On the other hand, the grasshopper sun / grasshopper shade treatment contains the grasshopper sun portion with high reward and high risk, and the grasshopper shade portion with high reward and low risk. Since the grasshopper food type was the same in both portions of this treatment, the only real effect that is seen is the effect of shading, which is weaker than the effect of both shading and food type that was seen in the jelly sun / grasshopper shade treatment. Lastly, the grasshopper sun / jelly shade treatment had no difference in maximum ants because the sun exposure and the food type were opposing each other; the grasshopper sun portion was high reward and high risk, while the jelly shade treatment was low reward and low risk. All in all, the maximum number of ants present for the jelly sun /

grasshopper shade, grasshopper shade / grasshopper sun, grasshopper sun/jelly shade treatments matched our hypothesis, but the proportional difference between maximum ants for the jelly sun / jelly shade treatment did not match. We found no difference in maximum ants between the jelly in the sun and the jelly in the shade, while we predicted that there would be an intermediate difference between them. This could be perhaps attributed to the density of the ants on the jelly being generally low.

Overall, we found that ants were willing to search in less favorable environments, but less willing to stay in them and recruit others. The more valuable grasshopper was able to draw more ants out into the sun than the less valuable jelly, but ants still preferred to stay in the shade when they could. We found evidence that foragers are willing to search and eat in risky areas, but that the risk of the area affects the value of the food. A valuable food item in a less favorable environment will become measurably less preferable than an identical food item in a favorable environment. Both food type and environmental risk play a role in foraging, with food type affecting discovery and environmental risk determining if the animal chooses to stay. Though animals must always balance risk and reward, they are not always reward maximizers or risk minimizers. Risk may be accepted when foraging but minimized during more vulnerable feeding periods.

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