

Ants: Communicating, Navigating, and Foraging

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04/16/2017

Introduction:

Although they are simple creatures, ants exhibit a highly complex and organized social dynamic known as eusociality. Eusocial animals exhibit four basic characteristics: Adults live in groups, care for the young is a cooperative effort among the whole colony, reproductive labor is divided (some individuals cannot reproduce), and there are overlapping generations (Plowes 2010).

Cooperation for the good of the system is a necessary component of eusociality. In keeping with this form, ants exhibit far more concern for the collective than for the individual. A number of ants have been found to exhibit self-destructive behaviors for the benefit of the colony. For example, *Camponotus saundersi*, the “Malaysian Exploding Ant”, has the ability to detonate itself in order to defend the colony from predators (Jowers et al, 2013).

Individuals in eusocial groups will often sacrifice their reproductive ability, food resources, and even their life, for the benefit of their nestmates. Self-destructive defensive behavior has evolved independently in a number of social insect species in response to different natural enemies. (Jowers et al, 2013, pg. 1)

Eusocial insect colonies are often colloquially referred to as “hive minds”, but this nomenclature is not entirely accurate. The colony in and of itself does not have a singular mind, but the behaviors of the individuals are so explicitly group-oriented that the colony acts as a single composite structure. There are a plethora of methods that ants use to communicate when foraging for food which arise out of this organizational structure. In this essay, we will outline a number of social techniques ants use to forage, navigate, and communicate. We will also discuss ants that do not make use of social foraging methods, and how they are able to navigate the environment and retrieve food without a method of communicating with other foragers.

I. Social Foraging:**1. Overview:**

Many ant species use social foraging, where information about a discovered food source is shared among nestmates. In this case, foraging information is shared by two means: chemical trail laying and antenna communication.

Chemical trail laying is more prevalent, since it allows for the simultaneous recruitment of a large number of foragers. Chemical trails are usually made of pheromone, which is signalling chemical secreted by the organism to alter other's behavior, contains a volatile compound, making the trail decays over time (Oudenhove, Billoir, Boulay, Bernstein, & Cerda, 2011). Foragers deposit different amounts of pheromone depending on various factors to reinforce or diminish the trail. Such factors include crowding on the route and the availability of food in the source (Czaczkes, Grüter, & Ratnieks, 2014). Wandering foragers use the concentration of pheromone on the trail as a factor for route choice, while they also contribute to the trail network by laying down more pheromone, turning the network into a dynamic "external repository of information for the colony" (Robinson, Green, Jenner, Holcombe, & Ratnieks, 2008). The established network makes the base for the mass recruitment of nestmates, which is one possible model of massive recruitment followed by group foraging ants (Cerdá, Angulo, Boulay, & Lenoir, 2009).

Social foragers use one of the following recruitment models: mass recruitment, group recruitment and tandem running. Mass recruitment happens when individual ants find their way to the source food based on the established network of pheromone, whereas group recruitment requires a single ant to lead a group of its nestmates to the food location down the trail. Group recruitment is generally more precise but smaller in scale than mass recruitment, since the leader ant can take ten individuals on average in every trip (Mashaly, Ahmed, Al-Abdullah, & Al-Khalifa, 2011). Another recruiting process even smaller in scale is known as tandem running. This recruitment technique involves one scout ant leading a single nestmate to the food location. In this scenario, the information is shared mainly by antenna contact, although some studies have shown that pheromone communication is also present, serving functions such as keeping a proper distance between the ants (Mashaly et al, 2011).

While shared information is an important parameter for determining target location, individuals, especially experienced foragers, take into account their own experience when foraging with the group (Evison, Petchey, Beckerman, & Ratnieks, 2008). The individual information possessed by ants comes in the form of stored images of the foraging area, used

sometimes to shortcut the pheromone trail, walk around unexpected obstacles, or even build the path back to the nest based on surrounding landmarks and memory.

Subspecies differ in combining personal and shared information depending on their own physiological and social structures. For instance, ants with better vision rely more heavily on landmarks (Evison et al, 2008) whereas visually unfavored subspecies use pheromone to regulate foraging behavior in a more complex way. One example of the latter type is *Pharaoh's* ants, which uses more than three types of pheromones: a long-lasting repellent pheromone, and two attractive pheromones (Robinson et al, 2008). In general, depositing different types of pheromone gives more detailed information about the route. By the same principle, small colonies favor tandem running over pheromone trails, since their trail network is not easily reinforced and maintained due to the small number of foragers. In this case, tandem running is much more accurate and reliable in getting the naive nestmate to the feeding site (Basari, Laird-Hopkins, Sendova-Franks, & Franks, 2014).

2. Dealing with Trail Bifurcations:

In their foraging expeditions, ants will also frequently be confronted with splits in the road. The decisions they make under these circumstances are determined by a variety of factors. In their paper *Effect of Trail Bifurcation Asymmetry and Pheromone Presence or Absence on Trail Choice by Lasius niger Ants*, Antonia Forster et al. (2014) outlined a number of experiments they performed in order to study how ants deal with trail bifurcation. Their findings showed that ants place a great deal of importance on social information. In the experiments, ants were placed in a straight pathway and approached a fork in the trail. Every time the test was run, the angle of the fork was rotated 15 degrees to the right.

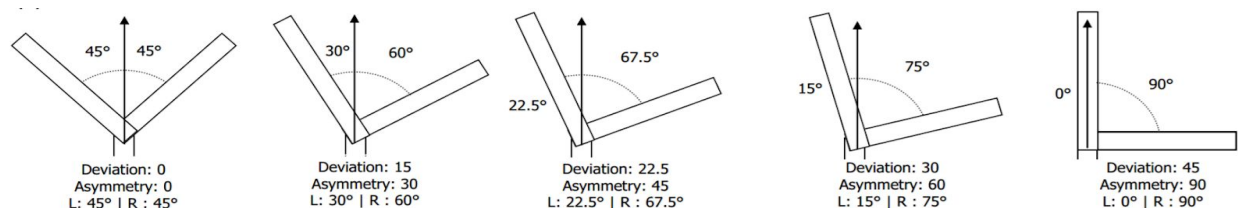


Figure 1: Rotation angles of the bifurcation (Forster, et al, 2014, pg. 2). Adapted from (2014). *Effect of trail bifurcation asymmetry and pheromone presence or absence on trail choice by Lasius niger ants* by Forster, A., Czaczkes, T. J., Warner, E., Woodall, T., Martin, E., & Ratnieks, F. L.W. International Journal of Behavioural Biology, 120(8).

In the first experiment, the two branches of the trail were coated in equal amounts of pheromone. As the bifurcation angle shifted, ants became more and more likely to choose the less deviating path. This showed that in their pathfinding decisions, ants generally preferred straighter paths over more complex routes. The second experiment coated only one of the branches with pheromone. Across all bifurcation angles, ants were more likely to choose the pheromone-marked branch. Ants were also more likely to choose the pheromone-coated branch the less it deviated. (Forster et al, 2014)

Overall... there is an effect of asymmetry as the preference of ants for the pheromone-marked branch over the unmarked branch is reduced from 65%, when it is the less deviating branch, to 53%, when it is the more deviating branch. These results demonstrate that trail asymmetry influences ant decision-making at bifurcations and that this information interacts with trail pheromone presence in a non-hierarchical manner. (Forster et al, 2014, pg.1)

These experiments showed that while pheromone trails are the primary means of directing ant trail choice, ants also prefer to move in a 'path of least resistance', which becomes most relevant when no pheromone trails are present (Forster et al, 2014).

3.Path Optimization:

Ants impressive foraging skills do not stop at the level of tracing a path to the food source. In fact, throughout the food transportation phase, ants work collaboratively on optimizing their route, based on linearity and distance. The paper *Chaos–order transition in foraging behavior of ants* offers an interesting way to tackle the optimization behavior of ants. It is in fact presented as a gradual development from chaotic to periodic behavior (Li, Peng, Kurths, Yang, & Schellnhuber, 2014, p. 8393). Following this model, ants' optimization behavior can be described as follows, assuming an environment with a single food source for simplicity's sake. Initially, "scout ants" are sent out by the colony to look for food sources. These preliminary foragers look for food pseudo-randomly, since no factors in their environments are strongly influencing their search direction/behavior. This results in a chaotic navigation of the colony. As

soon as the food-source is found, ants lay pheromone trails to communicate to the rest of the colony the location of food. This communication is also referred to as “recruitment” since the scout ants are recruiting other ants to help with the transportation of food. As soon as the new recruits enter the field, optimization begins (Li, Peng, Kurths, Yang, & Schellnhuber, 2014, p. 8393).

Upon finding a food source, the new foragers continue on the chaotic exploration of their environment for a while. In fact, scout ants might leave multiple trails leading to the same source of food. Recruits in this case randomly decide on a pheromone path to follow and reinforce it by laying more pheromone as they go back and forth between the food source and the nest. Path optimization emerges over time, and relies heavily on the nature of pheromone. Ant trail pheromone is an evaporative substance. Therefore, the longer the path, the more time it takes for a single ant to traverse it and compensate for the evaporation for the previously laid pheromone. On the other hand, shorter paths benefit from multiple back-and-forth travels in shorter periods of time, which results in continuous reinforcement of pheromone deposits. Since foragers show a tendency to pick strong pheromone paths over weak or nonexistent ones, eventually, the whole foraging group starts using the optimal road. Therefore, the colony moves from a chaotic movement/behavior, to a periodic and organized one, which displays the group intelligence that ants are famous for (Li, Peng, Kurths, Yang, & Schellnhuber, 2014, p. 8394).

Another study conducted in UCLA by doctors Nonacs and Yates showed that linearity was an important criteria in path selection for ants. The said study created a foraging environment with a single source food and three pathways varying in turns but equal in length. The subspecies studied was *Linepithema humile*, a group-foraging subspecies adopting the model of mass recruitment. The ants, 2400-2600 in total divided into 14 groups, were collected in UCLA's campus in Westwood California. An artificial foraging area was built in the model shown in figure 2 (Yates & Nonacs, 2016, p. 502).

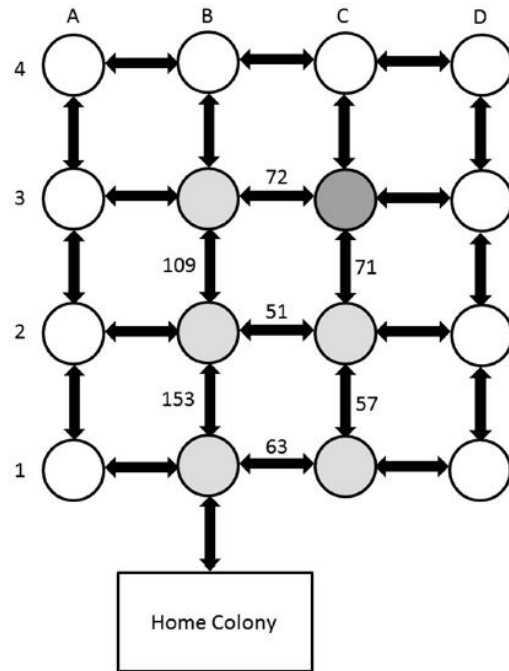


Figure 2: Artificial foraging area used in a UCLA experiment to test effects of linearity on ants' optimization skills. Adapted from "Preference for straight-line paths in recruitment trail formation of the Argentine ant, *Linepithema humile*," by Yates, A. A., & Nonacs, P., 2016, *Proceedings of the National Academy of Sciences of the United States of America PNAS*, 502.

The grid is built of plastic cups connected by transparent tubing. The diameter of each cup is 5 cm, and the distance between the centers of every two cups is 11.4 cm. The home colony, which is a plaster container coated with Fluon, is connected to Cup B1 whereas the food source was set to be cup C3. The numbers next to the tube segment show the mean numbers of ants taking that path. The numbers prove a clear preference for path B1-B2-B3-C3, which is the path with the least *initial* number of turns. In other words, the ant colony showed a preference for linearity whenever faced with a trail bifurcation (Yates & Nonacs, 2016, p. 503).

Finally, ants have inspired a great deal of computer algorithms. The most well-known is probably ACO (Ant Colony Optimization), an algorithm inspired by ant's trail-laying technique, used to find the shortest path in combinatorial optimisation problems. ACO follows the model of group-foraging ants: virtual 'ants' are set free in a net and programmed to deposit pheromone at every visited edge. The amount of pheromone "evaporates" gradually after each tour, make the

amount deposited inversely proportional to the distance traversed. This ensures that the shortest path prevails eventually.

Despite the success and popularity of ACO, professors Reid, Sumpter and Beekman (2011) from the university of Sydney argue that it does not explore the full optimization potential of group-foraging ants, especially in dynamic environments. Instead, the researchers proposed an experiment that they believed would fill in the missing holes in the study of ants' behavior. In this experiment, the ant colony would be challenged to solve Towers of Hanoi. Simply described, Towers of Hanoi is a computer science problem consisting of three pegs and a certain number of discs of varying diameters. The discs are initially all in one peg in decreasing order of parameters. The goal is to move them all from one peg to another in the smallest number of moves, while respecting the following rules: the player cannot move more than one disc at a time, the disc moved should be from the top of the stack, and no disc can be stacked on top of one of smaller diameter. The optimal solution currently known to this problem uses a recursive algorithm with a time complexity of $2^n - 1$, where n is the number of discs in the game (Reid, Sumpter, & Beekman, 2011, p. 51).

In order to test the optimization capabilities of ants, the set of possible moves in the problem was used to generate an undirected graph, which was turned into a maze with a single entry and exit points (nest and food source), as shown in Figure 2 (Reid, Sumpter, & Beekman, 2011, p. 51).

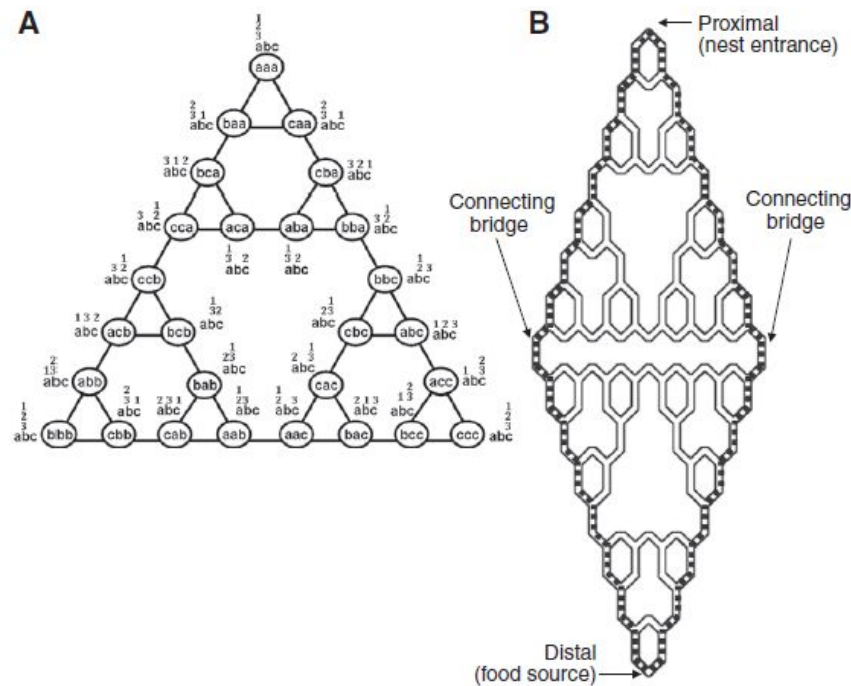


Figure 3: Tower of Hanoi Maze. Adapted from “Title of Article,” by Reid, C. R et al., 2010, The Journal of Experimental Biology, 51.

Around 60 colonies of Argentine ants were used in the experiment, 30 of which were pre-exposed to the maze before the trials. The results showed that 93.3% of the colonies familiar with the foraging ground managed to find a minimal path within one hour, and 90% to 93.3% of the same category were able to re-build a minimal path when their initial solution was obstructed. On the other hand, only 43% of the ants unexposed to the foraging terrain prior to the trials managed to build a minimal path with one hour, and only 73.3% to 78.6% of them were able to reconstruct an optimal solution when the initial one was lost. Both categories were nonetheless impressive in their optimization and navigation skills. With such a level of efficiency and adaptation, ants have a lot to teach us when it comes to optimization problems (Reid, Sumpter, & Beekman, 2011, p. 53).

Part II: Individual Foraging

1. Overview:

Earlier we discussed how an ant colony is a composite structure made up of individual ants working together under a eusocial paradigm. This composite and group-oriented structure can be seen in foraging behavior as well. We have already looked at methods such as trail pheromone and tandem running that allow ants to communicate while foraging. Although these are powerful and commonplace means to navigate, some ants lean on the use of personal information over social information. Ants are compelled by their eusocial nature to act instinctively for the good of the colony, so there is no need for a social or communicative structure to motivate them to work. If a species of ant can find enough food without a communication method, there is no evolutionary incentive to develop one. Due to this, several ant species do not even require the use of communication when foraging at all.

Oftentimes these ants exist in areas where food sources are smaller and more spread out. This is because social information methods such as pheromones are necessary to allow a large number of ants to converge on a single source of food, but when food is scarce and small, a single ant is sufficient to transport it back to the nest. The Sahara Desert Ant, *Cataglyphis Bicolor*, exhibits this behavior. *Cataglyphis* forages within a very small time interval for insects killed by the hot sun, and then returns to the nest. Because *Cataglyphis* scavenges for individual dead insects and not large food sources, it does not require a pheromone trail system to lead other members of the colony to food. It is also difficult for a pheromone system to work in a desert environment. In the desert, the sand moves so much that the environment is constantly changing. Leaving a pheromone trail to mark food is not a viable option because the trails would likely be swept away.

2. Navigational tools for Cataglyphis ants: Path integration

In the absence of pheromone trails, scavenger ants rely on other navigational tools to guide their foraging journey. One such tool is path integration. Intuitively, the word path integration can be thought of in reference to the mathematical concept of integrals, which is basically a summation in a continuous domain. In light of this definition, path integration can be

seen as the building of a path by means of addition of its discrete chunks. This navigational technique is also called ‘dead-reckoning’ and was used by sailors for a long time before it was discovered in animals (Muller & Wehner, 1988, p. 5287).

The formal definition of path integration does not deviate too much from its intuitive description. Muller and Wehner define this technique as ants’ ability to “integrate their tortuous outbound routes and return home along straight (inbound) routes” (Muller & Wehner, 1988, p. 5287). Whereas artificial navigational systems use advanced vector summation techniques in path integration, ants use a simple yet sufficient approximation to linearize their path. Despite this, in observing the navigational behavior of *Cataglyphis* ants it has been noted that scavengers appear to deviate significantly from their homeward path when lacking the support of visual landmarks (i.e, left to rely on path integration alone) (Muller & Wehner, 1988, p. 5287).

Muller and Whener advance three reasons to explain why such a flawed estimation is sufficient for the navigational purposes of ants. First, based on the researchers’ experiments, ants deviate too much only when they perform u-turns, which they usually avoid in real-life foraging scenarios. Second, ants’ deviation is directionally unbiased, meaning that if an ant deviates by 80° to the left of the intended trajectory, it is likely to deviate again by the same degree to the right at some point in its journey, which makes the errors cancel out eventually. Finally, in the rare cases where ants cannot avoid U-turns or simply deviate by a bigger angle than they can make up for, they can always take advantage of backup strategies, such as landmarks and efficient search strategies (Muller & Wehner, 1988, p. 5289).

It is also interesting to note that ants’ path integration, and navigation in general, makes use of different compasses, namely sun, wind and skylight polarization. The following section discusses how these different compasses affect ants’ path-building capabilities.

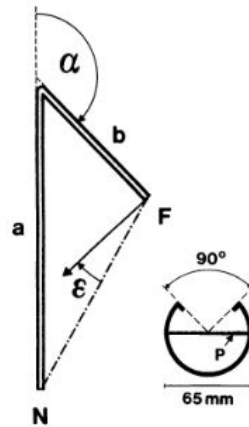


Figure 3: Two-leg path. Adapted from “Path integration in desert ants, *Cataglyphis fortis*,” by Muller, M., & Wehner, R. P., 1988, *Proceedings of the National Academy of Sciences of the United States of America PNAS*, 5287.

3. Navigational tools for *Cataglyphis* ants: Polarization, sun and wind

Scavenger ants make use of three different factors (or compasses) to locate themselves while they're out hunting for food: polarization, sun's position and wind force. Each of these compasses can define the angular position necessary for the path integration technique discussed earlier. Different subspecies show different preferences for a compass over the other. The following paragraphs discuss *Cataglyphis* preferences with regards to every compass (Muller & Wehner, 2007, p. 1).

Cataglyphis relies heavily on polarization. These desert ants actually possess a visual system capable of sensing polarized skylight from the ants' environment, called the Dorsal Rim Area. This allows ants to see color structures in the sky that are invisible to us, providing them with visual landmarks. Specific neural properties also seem to be supporting the visual system, which allows ants to make full use of skylight polarization in their navigational behavior (Muller & Wehner, 2007, p. 1).

The sun compass is mostly used as a support system, when *Cataglyphis* ants fail to make proper use of polarized light (if the sky is obscured in an experimental setting for instance). A study conducted by Muller and Wehner in 2006 explains this preference as follows. Apparently, desert ants consider sunlight to be part of the polarized skylight spectrum. Therefore, its

information is incorporated as part of a composite if it appears to be in accordance with the information received from the rest of the sky. However, if the rest of the sky is obscured, it becomes relevant for navigation in and of itself. Despite this, the neural channels for processing the sunlight and polarized light information seem to be independent. This finding was revealed when studying interocular transfer in ants, i.e their ability to transfer data collected from one eye to the other. This transfer seems to be only possible for polarization, whereas sunlight information, regardless of the magnitude of its impact, seems to be localized in each eye (Muller & Wehner, 2007, p. 2).

Wind also plays an important role in providing ants with cues about their angular position. In fact, *Cataglyphis* ants seem to be taking into consideration the wind direction when choosing their path, and can go as far as to modify their initial direction downwind if wind cues are explicit enough in their environment (i.e, strong and persistent wind over a long period of time). However, wind data is secondary compared to celestial cues. Desert ants only rely on wind when they do not have access to celestial information (usually in experimental settings) or when the sun had risen to a high position in the sky. However, when compared with sunlight data alone, wind information seems to prevail (Muller & Wehner, 2007, p. 2).

Part III: Suggested Model

After researching the behaviors and foraging methods of several different ants, we decided that it would be best to model that of the *Cataglyphis* desert ant. We picked this species because the EV3 technology provides us with limited sensory capabilities. Because of this, we wanted to move away from ants that rely heavily on visual markers or pheromone trails. These forms of communication would be difficult and problematic for us to model without adequate sensory capabilities in our robot. *Cataglyphis* is a good option because one of the only constant landmark that is available to this ant is the sun. They use this as a reference point in navigation, which we can more easily model.

In our implementation, we intend for our robot to be able to leave the nest, moving in a zig-zag pattern. It will periodically stop and look around, checking its position in reference to the 'sun'. It will keep running and checking the sun until it senses 'food'. Then it will grab the food

and drag it in a straight line back to the nest. It will navigate back to the nest by summing how far it went in each direction compared to the sun to calculate the net change of position from nest to food. It can then use that information to go straight back.

Our robot will have mandibles run by either one or two motors for the purpose of grabbing food. In between the mandibles, there will be a color sensor meant to emulate a sense of smell. The food will be represented by an LED light, so when the robot is close enough, it will sense the food through the color sensor as if it had smelled it. It will have two motors driving wheels in order to move. The sun will be represented as an infrared beacon in a fixed location. The robot will have an IR sensor so it is able to sense its angle in reference to the beacon. The head of the bot will also have an ultrasonic distance sensor to represent enough eyesight for the robot to not bump into things as it is wandering. If the robot meets an obstacle as it is navigating, it will divert its path to avoid it. If it meets an obstacle when returning home, it will go around the obstacle and return to its direct path to home.

The code will be structured into three main layers. We will be implementing a subsumption architecture solution, using the lejos subsumption package in order to achieve this. The first layer is seeking food. The bot will loop within this state until it has sensed food with its color sensor. In the seeking food state, the robot will drive for a random distance within a relatively small range. Then it will turn a random distance between approximately 30 and 60 degrees alternating positive and negative angle changes. Each time the ant bot moves, the direction and distance will be recorded and added to the sum of previous movements. This will keep a running sum so the path home is always known. Once the robot gets close enough to the LED food source to sense it, the random behavior is abandoned. The bot will then move into the second state of having found food. In this layer it moves in a more direct path towards the food. When the Brightness surpasses the threshold, the robot will know that it is close enough and grab the food with its mandibles. Once it has the food, it will enter its third and final layer, return home. Using the position calculations from the previous layers, the ant bot will turn around and move in a direct path home.

Conclusion:

Both social and individual foraging ant species exhibit some extraordinary behaviors in their food collecting process by utilizing information from their environment. In social foraging species, the individuals contribute to gradually build the pheromone network which is a collective information for all members in the colony. They can use this in combination with their own knowledge to find the optimal path. Individual foraging species perform techniques such as path integration - the process that uses polarization, sun position and wind force as reference for their angular position to navigate themselves without help from other colony members about the food location. Everything they do is meant to make the commute between the feeding sites and nest as efficient as possible hence maximizing the energy intake of the colony as a whole. We will be attempting to model the desert ant *Cataglyphis* which works individually in the food collecting process. It will be responsible for its own navigation by keeping track of its position in relation to the sun while searching for food to take back to the nest.

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