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Agent Based Modeling

## An Agent-Based Model of Red Harvester Ant Patrolling and Foraging

### **Summary**

Using agent-based models for exploring harvester ant (*Pogonomrymex*) biology are still relatively rare, though have been successful when used. Here, an agent-based model was created in NetLogo to study the foraging activity of the red harvester ant *Pogonomrymex barbatus*. Simple behavioral rules of deciding when to forage, following a trail, and searching for food mirrored real-world target behavior. The iterative process of simulating complex phenomena manifests itself as a never-finished model: future elements to add include environmental stimuli such as temperature and humidity, calibration of parameters and/or adoption of more complex behavioral rules from published literature, and the extension to multiple colonies to further examine the effects of colony-colony foraging interactions. However, this model is a sufficient building block for starting to create accurate and complex models of red harvester ant foraging behavior.

### **Introduction**

Using agent-based modeling (ABM) for ant foraging is a logical approach: agent-based modeling provides a discrete spatial environment where local, stochastic interactions among ants and between ants and their foodsource dictate the behavior and foraging success of both individuals and the colony as a whole. Multiple agent-based models exist for seed harvester ants of the genus *Pogonomrymex* (see Crist and Haefner, 1994; Haefner and Crist, 1994; Flanagan et al 2011), but relatively little agent-based modeling work has been done on one species, the red harvester ants, *Pogonomrymex barbatus* (though, see Pinter-Wollman et al, 2011). This model was created to simulate the daily foraging activity of red harvester ants in natural, non-laboratory conditions.

There exists much literature, by Gordon and others, quantifying complex relationships against which an ABM could be tested. While much has been elucidated about the biology of these ants, some of the biological complexity was pared away (of necessity) to build a working model. Model validation therefore proceeded with using qualitative descriptions (face-validation) of red harvester ant behavior from Deborah Gordon's two published books, 'Ant Encounters' (2010) and 'Ants at Work' (1999). Information about the biology of the ants presented below is summarized from those two books. Since this model is not at the stage of being used for experiment, the simplifications do not detract from the work done. The flexibility of NetLogo, the platform on which this model was made, ensures modifications to increase the model's accuracy can easily be made.

Harvester ants gather seeds that are individually spatially scattered (not in patches) by wind and flooding. The seeds collected are not seeds produced by local vegetation. Recruitment of ants is rare as the food source is small and easily carried; rather, ants search individually in a large spatial area.

Ants start leaving the nest around sunrise, and are active until about 11, when the heat forces them back inside. Patrollers and nest maintenance workers are the first ants to emerge.

Patrollers walk in a stop-and-start, notably zig-zag pattern with many interactions, first around the nest, and then farther away from it. They choose the 3-5 trails that the foragers will follow that day from the roughly 8 directions the colony may forage. The trails used change from day-to-day, not seeming to reflect any sort of abundant food source from the previous day. Removing patrollers can prevent the whole colony from foraging that day, especially if they are removed early on in the patrolling sequence.

Foragers rush along the trail, slowing down at the searching region of the trail. About 10-20 meters from the nest, they start searching for food. If food, such as a pile of birdseed, is encountered on the trail, foragers will ignore it and continue on to their foraging site (even if seeds are quite limited there). Foraging trips typically take about 20 minutes, and 90% of the ants return successfully with food. Foragers can estimate the density of ants around them by interaction frequency: with fewer interactions per time, they take straighter paths, while a higher interaction density leads to more convoluted paths.

## **Methods**

I originally intended to study the competition for food between multiple colonies located close together, watching how foraging territory and trail shape changed due to direct interactions (meeting and fighting of non-nestmates), and indirect interaction (the taking of a shared food-source). However, in order to test those questions, I needed an accurate representation of how foraging actually proceeded. This model includes only one foraging colony and only one foraging round, but it is hopefully more realistic in what it attempts to model. As mentioned below in the future results, the goal is to be able to extend this to multiple colonies over multiple rounds of foraging.

## **Model structure**

### **Observer**

The user, or ‘observer’ in NetLogo, dictates how many foragers, seeds, and patrollers to create. The user can draw trails for foragers to follow via the trail-draw button and can draw seeds via the food-draw button. These are a vestige of the debugging process, but were interesting and useful enough to keep in the model.

### **Environment**

All patches are either brown (soil surface), green (seeds), or purple (ant nest). The patches exist in a 301 x 201 box (no world-wrapping). Ants can reach the edge of the environment and turn back; I saw a method of having agents disappear and continue off-screen but chose to spend the time working on other parts of the model. Patch color and number was occasionally altered, as when trying to match provided pictures for validation.

Seeds are scattered at uniform random across the world, excluding on the nest itself. The seeds are green and the number of seeds is controlled by the user via a slider. When the seed is picked up, the patch turns brown. Currently there is no regeneration or replacement of seeds; this may be added as a future extension.

The nest is a colony of radius 10 patches, larger than the sensing radius of the ants (which I’ve defined as 3 patches). This necessitates the ants response to local interactions, not to that of the colony as a whole. It is roughly centered in the box, but the true location is without much meaning.

## Agents

### Variables

At the beginning of the model-building process, I anticipated having several different colonies of ants. I chose to define my turtles as breeds: a colony 1 breed, colony 2 breed, etc. Later, I simplified the model but kept the breed. Thus, all of my turtle agents are also called colony 1 agents (col-1s).

I chose to keep patrollers and foragers as one breed and not split them, as task allocation is a fluid role in ants. Instead, all agents have a boolean *patroller?* variable that is true for patrollers and false for foragers. This means that all turtles have some variables that more specifically could be patrollers-own variables, such as patrollers-met and patrollers-turn-rate.

Agents have a long list of variables:

```
19 col-1s-own
20 [
21   turn-rate
22   seeds-collected
23
24   inside-nest-timer
25   outside-nest-timer
26   max-time-outside-nest
27   foraging-timer
28
29   carrying-food?
30   looking-food?
31   foraging?
32   in-nest?
33   patroller?
34
35   last-trip-success?
36   last-food-patch? ;;do I have a last food patch?
37   last-food-patch ;;location of last food patch
38
39   patroller-interact-timer
40   patrollers-met
41   pat-foraging?
42
43 ]
44
```

While *looking-food?* and *foraging?* seem to represent the same thing, *foraging?* is used to determine if the ant is moving outside of the nest, while *looking-food?* determines if the ant is currently searching for food.

### Behaviors

Patrollers have only a few behavioral rules, but their behavior shapes the decision of foragers whether to go out and forage or not. Patrollers have a countdown timer of 120 ticks. They need to meet (be within an arc of 3 patches at 120 degrees centered at the front of the patroller) another patroller before the timer reaches 0. If they don't, they start heading back to the nest. When patrollers do meet another patroller, they reset their timer to 120 ticks, increase their turn angles, and add one to their patrollers-met counter.

If each agent's patrollers-met counter is at the threshold or higher, and the countdown timer is above 0, they start returning to the nest and laying a trail. They also set their boolean *pat-foraging?* to true, to indicate to foragers that it is conducive to forage. When patrollers return to the colony, they are asked in NetLogo syntax to disappear (die).

Foragers are more complex in their behavior. Ants wait until a foraging threshold is met, at which point they search for a trail by the nest, follow the trail, search for food, and return straight back to the nest.

The decision to go out to forage is an internal one, relying on local interactions (with the same sensing radius as mentioned above for patrollers) with successful and unsuccessful patrollers (patrollers with pat-foraging? = true are considered successful), and successful and unsuccessful foragers (foragers returning with seeds are successful, foragers returning without food after the maximum time outside the nest are considered unsuccessful). Weights were given to each of these interactions: patroller interactions are twice as influential as other foragers; interactions with successful ants are four times as influential as interactions with unsuccessful ones. Each tick, the timer decreases slightly, making it less likely the ant will go out to forage. Ants that found a seed on the last food trip are more likely to go out and forage again. The mathematics of the decision to forage in *Pogonomyrmex barbatus* is an ongoing subject of work, with recent publications (Davidson et al, 2016; Davidson and Gordon, 2017). Unfortunately, time constraints did not allow for incorporation of their model in this work.

Ants that decide to forage find a trail, and then follow it away from the nest. Identifying a simple rule for ants to follow the trail was a challenge, but the successful implementation is really just one line of code:

```

313 to ant-follow-trail
314 if not any? patches in-cone 3 120 with [chemical > 0]
315 [stop]
316
317 face max-one-of [patches in-cone 3 120 with [chemical > 0]] [distancexy col-1-nest-x col-1-nest-y]
318 end

```

Foragers search for and then face a trail patch in a cone of radius 3 patches and an arc of 120 degrees in front of them. In this way, they utilize a greedy algorithm to continuously distance themselves from the nest. Once there is no trail patch that takes them farther away, they begin searching for food.

The search for food is affected by interactions the foragers have with other ants also looking for food. Foragers were given a minimum and maximum turn angle. Ants with lower density prefer straighter routes; ants in high density take more convoluted paths (eg see the path shapes in the results) and this was implemented by starting the ants at the minimum turn angle, then increasing the turn angle after interactions, and decreasing it when not having any interactions. This can lead to a zigzag shape.

When ants find food, they turn green, and return straight to the nest. The color change is not significant; it is just there to make them easier to see. The foraging timer starts at 0 again, and the foragers wait to see if enough local interactions conspire them to forage.

### Model testing: verification and validation

Much of the model testing was done iteratively upon adding a new feature or making significant tweaks to the code that would affect how the model behaved. Boundary conditions were tested, and retested when they did not act as expected. Foragers do not go out unless there are patrollers who give the go-ahead; likewise, absent any food to collect, foragers return to the nest and stay there.

Significant amounts of verification (debugging) were done by using agent labels to display the current state of a variable (turn-rate, patrollers met, time outside the nest, seeds collected) or by changing the color of the agent (foragers carrying food turn green; for a while, successful patrollers turned blue). Likewise, the pen-down command was used to ensure the path shapes were corresponding to the turn-angle and ant density. Model runs were also slowed down and individual ants were watched or followed to ensure intended behavior. Monitors and plots

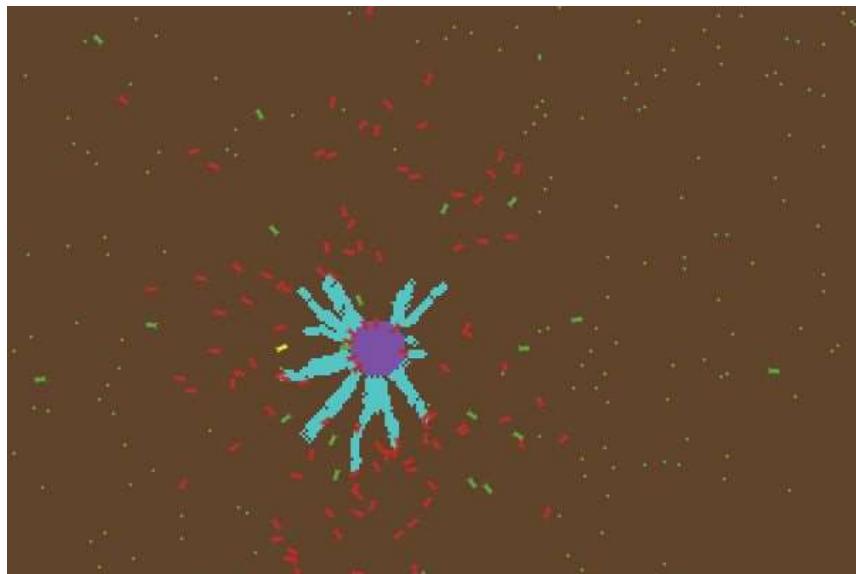
were used to confirm that the seed count of the colony increased appropriately, and that trips were correctly being labeled successful or unsuccessful.

Sensitivity analysis was quite difficult to perform and was not formally done. Though the number of foragers in a colony is about 2,000 (Adler and Gordon, 2003), model runs were typically done using fewer than 100 foragers. Since the model is on the order of  $O(n^2)$  when each ant is checking every other ant near it to update its foraging timer, using 2000 agents for repeated trials to ensure the model is functioning was not appropriate for testing. Additionally, there can be complex interactions between two variables that make sensitivity analysis harder. The number of patrollers in the simulation and patroller-met-threshold have a complex nonlinear relationship (the more patrollers in the simulation, the easier it is to find patrollers to interact with, making foraging much more likely). Ten patrollers having to meet other patrollers 10 times typically produced foraging behavior, but 20 patrollers having to meet other patrollers 20 times typically did not (about 30 simulated patrollers were necessary).

The foraging timer is an important part of the model that could have used sensitivity analysis, but the search space of parameters is enormous. The foraging timer changes in six different ways. Patrollers and foragers have different effects on the timer: patrollers were given twice the decision weight. Successfully returning patrollers and foragers bring the timer closer to its threshold, while unsuccessful ones decrease it. The unsuccessful agents decrease the timer by a quarter the value that successful ones increase it. The foraging timer also varies if an ant was previously successful at finding food or not. Each tick, the foraging timer decreases slightly. This was a straightforward solution to ensuring that not every ant is constantly foraging, but rather responds to food availability information provided by other foragers, but may decidedly miss some real-world complexity.

## **Results**

The simulated environment is displayed mid-run below. The background brown patches roughly simulate soil, the green patches are seeds, the blue patches are patroller trails, and the purple patches are the nest mound of the colony. The red agents are foragers, green agents are foragers returning with food, and there is one remaining patroller (yellow).



View of the ants mid-simulation. Green patches are the food source and blue patches are the trails. Foragers are red, successful foragers returning to the colony are green. One patroller (yellow) remains outside the nest.

Patrollers are the first ants to leave the nest, and the frequency and number of local interactions between patrollers are assumed to dictate whether the colony will forage that day. Patrollers typically lay trails of variable length in 3-8 directions. These trails are typically linear and of a fixed width; the trails may become fan shaped due to overlap between trails lain by multiple patrollers. Even the longest trails extend only partially into the environment, and ants begin foraging immediately off the trail. These trails do not diffuse or disappear over the run of the model.

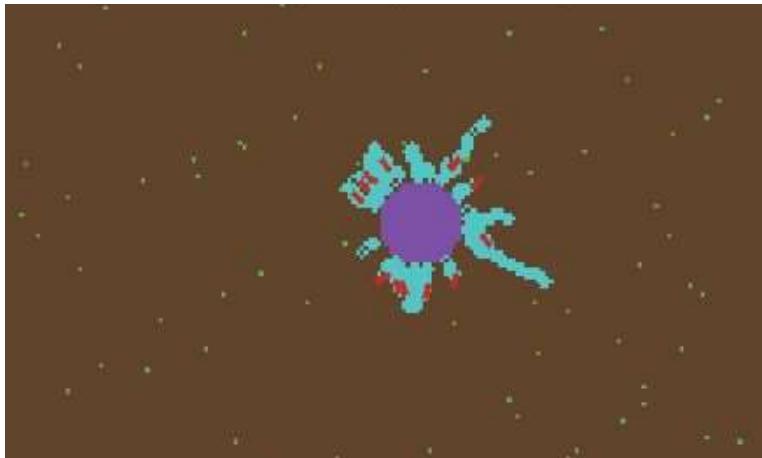
Not all simulated rounds produce foraging, though all do include patrollers leaving the nest. The choice of certain combinations of parameters produce quite interesting behavior. With a small number of patrollers and a high number of patrollers necessary to meet, there are few (or zero) trails drawn by patrollers. These trails also tend to be closer to the nest. Though there are trails available to follow for foraging, and some successful patrollers have returned, each forager is not stimulated enough to forage, and the colony as a whole does not forage. Increasing the number of patrollers, or decreasing the number of patrollers necessary to meet, robustly stimulates foraging activity. Trails tend to be longer, and the colony as a whole almost always forages. These results in trail shape are from the interplay of the number of patrollers and the number of interactions that each patroller needs to be successful. Additional parameters that are likely to influence trail formation are the minimum and maximum turn rate for patrollers, as well as the timer for how frequently each patroller needs to interact with another before it starts returning to the nest. These were not tinkered with.



The true shape of the foraging trails (left, from *Ants at Work*) can be roughly simulated by the simple behavioral rules for patrollers, but sometimes these same rules provide an amorphous blob. The color scheme was changed to more accurately mimic the target image

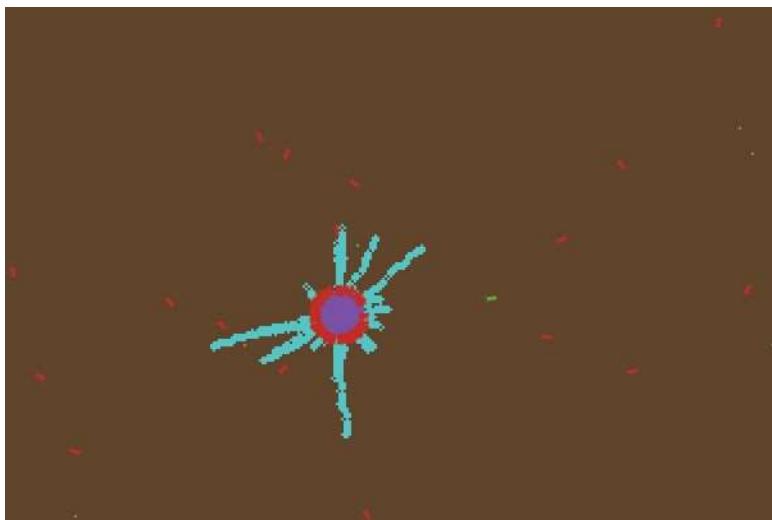
Each forager has an individual foraging timer updated by local interactions with other ants. When the timer reaches the threshold, the ant decides to forage. It finds a trail leading away from the nest and follows it, then starts looking for food once the trail is finished. Ants that previously found food are more likely to go out and forage than ants that were unsuccessful. The threshold value to forage is set at the same value for each ant, and once the threshold is met, the ant nearly always forages (the ant may not go out to forage if in the process of finding a trail it meets enough unsuccessful ants). Foragers follow the trails lain by patrollers away from the

colony and then start searching for seeds. Foragers will not pick up seeds on the trail, even if they walk right over them.



Foragers (red) following the trails lain by patrollers (blue).

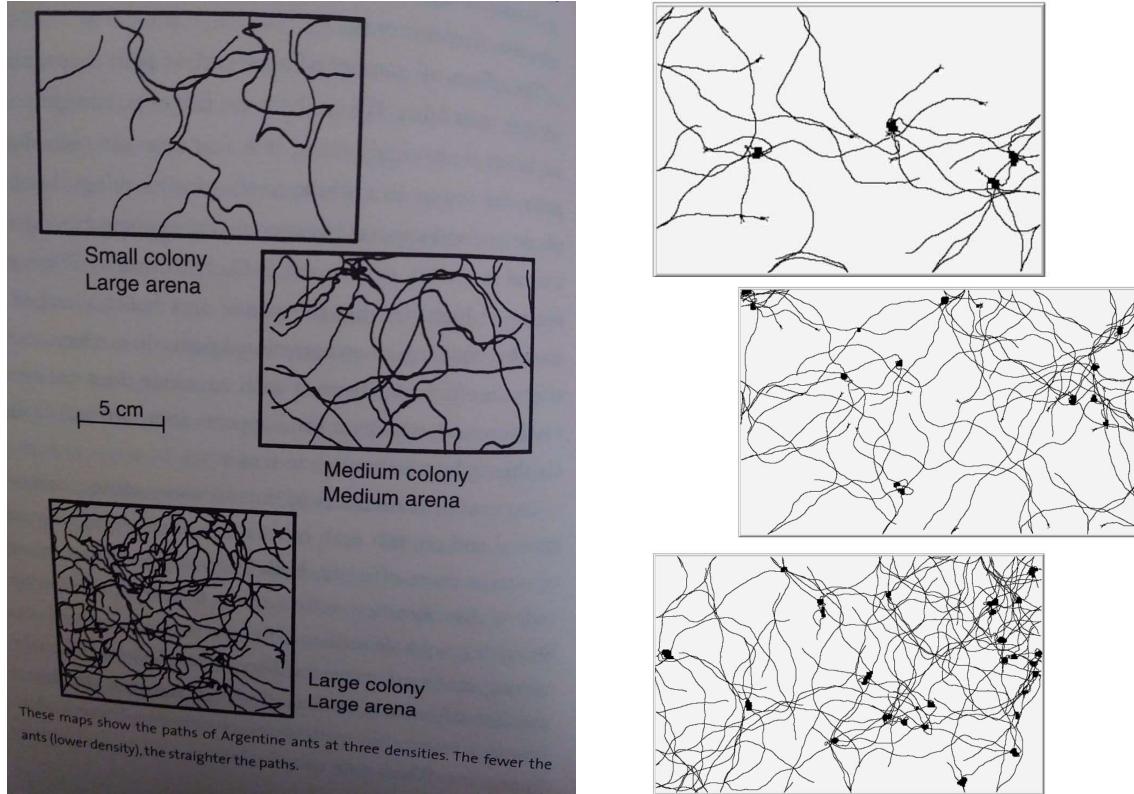
The colony as a whole responds to seed availability. When few seeds are being brought in, the majority of foragers are waiting inside the nest. Near the end of the simulated round, only a few ants are out foraging at a time. The return of successful ants to the nest produces nonlinear effects on waiting foragers: successful foragers may each stimulate 0, 1, 2, or more nearby foragers. Unsuccessful foragers return to the nest after 1,200 ticks (based on a foraging time of 20 minutes, at one tick per second). Unsuccessful foragers never stimulate more foraging activity.



When few ants are successfully returning with food (colored green), the majority of the ants are inside the nest.

As mentioned in the methods section, the path shape of foragers responded to the density of ants present. The simple rule for adjusting turning angle by a fixed amount for each interaction produced a similar response to what has been experimentally derived (below). The

color scheme was changed to more accurately mimic the target image, and instead of being localized in a colony to begin with, foragers were distributed uniformly across the arena. Their paths taken are in black; black patches correspond to locations where ants interacted (and thus path shapes changed significantly).



Ant path shapes responding to ant density in the arena. The image on the left is from *Ants at Work*, while the images on the right are replications in the agent-based model of the results with simple behavioral rules given to the ants. Ants have a minimum and maximum turn rate, and their current turn rate depends on the rate of interaction with other ants. The black patches in my figures are where two ants were close enough to potentially interact.

## Discussion

Using simple agent variables and behavioral rules can produce similar qualitative behavior between the agent-base model and a simplified reference pattern in real-world harvester ant foraging behavior.

One strength of using an agent-based model for complex systems is that built-in stochasticity can be used to incorporate (or even explain) uncertainty. Given a set of parameters, the colony may forage some days and not on others. Predicting whether the colony will forage in the next round is not possible, but summary statistics can identify the likelihood that it occurs. Real-world observations show that not all colonies forage every day, but also that some colonies are more likely to forage on a given day than others. The self-organized colony-level decision of whether to forage depend on exogenous circumstances such as colony food level, ambient temperature, and cloud cover or be due to the inheritance of behavior through evolutionary processes. This work shows, however, that the difference in parameters guiding simple

behavioral rules (the number of patrollers met, the frequency with which fellow patrollers need to be met, reaction of path shape to patroller density) between colonies could explain some of the variability seen in their foraging.

The downside of creating an ABM for a system that is already well-studied is that it is immediately obvious where the shortcomings of the model are; it cannot be used, in many cases, for theory creation when the underlying theory already exists and is well explained.

Building a model is by nature an iterative process with no clear end: it is constantly possible to add on more features, more complexity, and hopefully more accuracy.

The first extension would be calibrating spatial and temporal boundaries. Foragers can travel up to 30 m from the nest, so patches representing the border of the simulation would need to be located farther away. Meanwhile, patroller trails only extend about 20 cm. This requires further thought about the resolution of the environment as well: increasing the number of patches would introduce more computational needs into the model. Since the sensing radius of ants is fairly limited, creating a logical spatial scale could be a challenge.

Temporal boundaries would be critical as well: if defining a model tick as a second would require calibrating the distance the agents can move during each tick. Likewise, the maximum time outside of the nest timer deserves some consideration: while the average foraging duration is about 20 minutes (1200 seconds, or 1200 ticks), some trips may take upwards of two hours. Perhaps an outside-nest-timer is not even strictly necessary.

The next extension would be a calibration of the parameters and complexifying behavioral rules in the model to results from current literature. Adler and Gordon (2003) calculate and estimate several parameters, including the resource renewal rate of seeds (0.1/min), the number of foragers in a mature colony (1,890 ants), and their speed (2.5 meters/min). More recent work suggests that returning ants may walk at a different speed than others (Davidson and Gordon 2017). Likewise, the mathematics of the decision to forage is apt to be more complicated than a simple timer with a deterministic go-forage result when a threshold is met as was used in this model. Davidson et al (2016) suggest a logistic regression model.

Another extension would be to enable multi-round foraging. The current model only supports one foraging round each time the model is run. Patrollers returning to the nest are sent underground (in NetLogo, the turtles are asked to die), so there is not currently any possibility of multi-round foraging. In the real-world, patrollers continue their role for multiple days, and they tend to lay trails in similar directions day-to-day. Colonies have 3-8 foraging trails lain by patrollers; there is fidelity in these directions, so the model would need to have patrollers remember the locations they were in. Patrollers are currently asked to die so they don't continuously influence the ants to forage; a mechanism would need to be developed where the patroller agents are kept but the patrollers are no longer influential to the foragers.

Accurately extending the temporal aspect would introduce significant complexity to the model. Temperature and humidity vary during the day but both are influential in starting and ending the morning and/or afternoon foraging rounds. This would obviate the need for having a global foraging timer that enables the ants to forage for only a set period of time; it would also provide a different method for starting multi-round foraging (ie foraging when the temperature variable is between certain values, instead of starting foraging at a certain modulo base).

A sinusoidally changing variable could be implemented to the model for the daily temperature change. Then, a seasonal variable could be added to adjust season-specific foraging behavior.

The current model assumes a uniformly flat and unobstructed surface where all patches are equally likely to contain food or be visited by an ant. This may be true of a simulated ant colony in the lab, but this is not the case in the actual study-site. Outside of the roughly 2-meter cleared mound area, there is sometimes dense vegetation through which trunk trails pass. This vegetation could be modeled, for example, using similar logic as the ‘Line of Sight Example’ in the NetLogo models library. The primary difficulty would lie in creating an accurate model topography based on the patterns of vegetation; a potentially useful approach would be to take an overhead photo and import it into NetLogo, using color as a proxy for elevation.

## **References**

- Adler, Frederick R., and Deborah M. Gordon. “Optimization, Conflict, and Nonoverlapping Foraging Ranges in Ants.” *The American Naturalist*, vol. 162, no. 5, pp. 529–543.
- Crist, and Haefner. “Spatial Model of Movement and Foraging in Harvester Ants (Pogonomyrmex) (II): The Roles of Environment and Seed Dispersion.” *Journal of Theoretical Biology*, vol. 166, no. 3, 1994, pp. 315–323.
- Davidson, Jacob D, and Deborah M Gordon. “Spatial Organization and Interactions of Harvester Ants during Foraging Activity.” *Journal of the Royal Society, Interface*, vol. 14, no. 135, 2017, pp. Journal of the Royal Society, Interface, October 2017, Vol.14(135).
- Davidson, Jacob D., et al. “Effect of Interactions between Harvester Ants on Forager Decisions.” *Frontiers in Ecology and Evolution*, vol. 4, 2016, Article 15. Frontiers in Ecology and Evolution, Oct 5, 2016.
- Gordon, Deborah. “The Spatial Scale of Seed Collection by Harvester Ants.” *Oecologia*, vol. 95, no. 4, 1993, pp. 479–487.
- Gordon, Deborah. *Ants at Work : How an Insect Society Is Organized*. New York, NY, Free Press, 1999.
- Gordon, Deborah. *Ant Encounters: Interaction Networks and Colony Behavior*. Princeton, N.J., Princeton University Press, 2010.
- Haefner, and Crist. “Spatial Model of Movement and Foraging in Harvester Ants (Pogonomyrmex) (I): The Roles of Memory and Communication.” *Journal of Theoretical Biology*, vol. 166, no. 3, 1994, pp. 299–313.
- Paz Flanagan, Tatiana, et al. “How Ants Turn Information into Food.” *Artificial Life (ALIFE), 2011 IEEE Symposium On*, 2011, pp. 178–185.
- Pinter-Wollman, Noa, et al. “The Effect of Individual Variation on the Structure and Function of Interaction Networks in Harvester Ants.” *Journal Of The Royal Society Interface*, vol. 8, no. 64, 2011, pp. 1562–1573.