

A RESPONSE THRESHOLD MODEL FOR ANT COLONIES

BYRON HEERSINK

1. INTRODUCTION

Division of labor in social insects has been a widely studied topic in entomology. A number of models have been developed in order to explain how insects perform various tasks to fulfill the needs of their colony. One particular model that was introduced by Robinson and Page [2] is the response threshold model, in which individual insects perceive colony needs through certain stimuli they encounter in their environment which encourage the performance of a task. To each task, an individual worker has an associated threshold, which is a measure of resistance to the task. A worker will perform a given task if it encounters a stimulus associated to the task which exceeds the worker's threshold. Thus workers with a low threshold associated to a particular task are likely to perform the task while workers with a high threshold are not. The response threshold model was given a mathematical framework by Bonabeau, Theraulaz, and Deneubourg [1], and has been given experimental evidence by, for example, Weidenmüller, Kleineidam, and Tautz [3].

The goal of this project was to program a simulation of an ant colony which makes use of the response threshold mechanism to model the behavior of each ant. In addition, unlike some previous models, it takes into account the spatial organization of colony needs and different tasks which have varying natures in terms of the time, effort, and actions that must be taken in order to perform them, which is accomplished through a physical emulation of the ant colony. I then analyzed the behavior of the program to examine the different worker patterns, as well as the colony's ability to handle its task needs, which resulted from various conditions set on the colony. In particular, I saw how the parameters affecting the thresholds of the workers and the stimuli generated in the colony affected colony behavior.

2. THE MODEL

The ant colony model consists of a nest, an outside area, and a tunnel connecting the two, and an initial population of eggs, larvae, pupae, and adult workers. The majority of the area of the nest is used to contain the eggs, larvae, and pupae. The nest also contains an area where workers rest, and a food storage area. The outside area consists of food sources from which the colony can forage, as well as occasional enemy insects. The program moves forward in short, discrete time segments, considered as seconds. Over time, the eggs, larvae, and pupae transition to their next life stage, the workers move according to the task they are performing, dirt accumulates on the larvae and workers and in the nest, and the workers and larvae get hungry.

By default, the workers perform no particular task and randomly walk inside and outside the nest, perceiving stimuli associated to the following tasks: larvae cleaning, worker cleaning, nest cleaning, larvae feeding, foraging, and patrolling. To each of these tasks, every worker is given a threshold, a

fixed numerical value quantifying the worker’s resistance to performing the task. In all simulations, the thresholds are independently sampled from a random variable of the form $\max\{N(\mu, \sigma), 1\}$, where $N(\mu, \sigma)$ is a normally-distributed random variable with mean μ and standard deviation σ (the maximum preventing worker response to a task that is not needed). To each task is also associated a stimulus level that can be detected by the workers. The stimuli associated with cleaning are simply the dirt levels accumulated on the larvae and workers and in the nest, the feeding stimulus is the hunger level of the larvae, and the foraging and patrolling stimulus levels are functions inversely related to the amount of food in storage, and the number of current patrollers, respectively.

To make the program more realistic and spatially restrain individual workers’ perception of the colony’s task needs, the nest (the outside area, respectively) is divided into a 10-by-10 (50-by-50, respectively) grid of zones. Then the stimuli associated to the cleaning and feeding tasks that the workers perceive is restricted to the zone they are in. So, for example, a worker can detect the dirt accumulation and the hunger of only the larvae in their zone. On the other hand, the foraging and patrolling stimuli are “globally perceived”, i.e., workers who walk by the food storage know the whole colony’s need for foraging, and those who go to the patrolling area know the colony’s need for patrolling.

At points in time regularly spaced by 30 seconds, each worker with no task checks the stimuli it perceives, and if a stimulus level exceeds its corresponding threshold, it will start performing the associated task. At the same points in time, workers who are performing a task will, with a small probability, decide to stop their tasks. These probabilities are set so that on average, a cleaning task will take 10 minutes, a larvae feeding task 15 minutes, and foraging and patrolling tasks 2 hours.

3. RESULTS

I began by establishing a baseline simulation, in which the stimulus increase rates, i.e., the dirt accumulation and hunger rates, were set at reasonable values, the threshold values for all workers and all tasks were sampled from the random variable $\max\{N(\mu, \sigma), 1\}$ with $\mu = 35$ and $\sigma = 10$, and the initial population of workers, eggs, larvae, and pupae were set at 200, 140, 140, and 140, respectively. The other simulations were then given by changes to this baseline simulation in terms of the stimulus increase rates, thresholds, and initial population. All simulations were given a time length of one day. The primary statistics gathered and examined were the stimulus levels over time, which measure how well the colony is controlling task needs; the average number of workers engaged in each task over time; and division of labor measures, one being the average number of task types a worker engages in, i.e., the average repertoire size, and the other being the total number of workers that have engaged in each task at least once, i.e., the work group sizes.

One set of simulations tested the effects of changes in the initial population sizes of the ant colony. The worker to egg, larva, and pupa populations were kept at a 10 to 7 ratio, and the worker population was set to various values from 50 to 1000. The main noteworthy observation is that the average repertoire size was mostly stable or fluctuated without a clear trend as population size increased. This is contrary to the expectation that as population size increases, there is a higher division of labor. As population size increases, there are more workers with very low thresholds

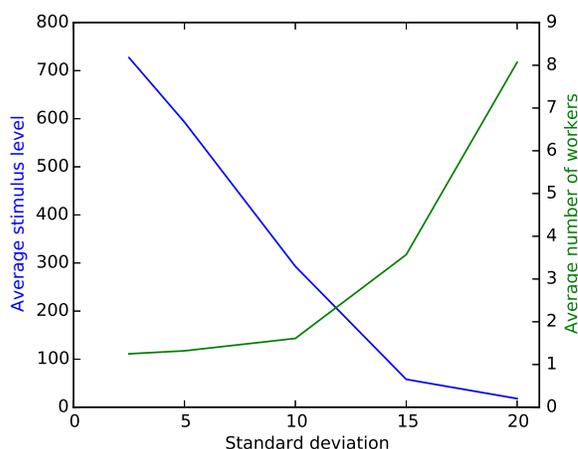


FIGURE 1. Threshold standard deviation vs. average stimulus level and number of workers for the larvae cleaning task

which take over each task, which is expected to cause an increased task specialization and thus lowering the average repertoire size.

In another set of simulations, the mean μ of the threshold of a single task was set to values from 15 to 55, while the thresholds for the other tasks were kept at 35. In other words, the workers' overall sensitivity to a particular task was changed. (The changes were made to each task independently.) The results of these simulations were generally as expected. For example, the stimulus level of this task increased with the threshold mean, reflecting the fact that the workers' reduced sensitivity to the task allowed the associated colony need to build up before worker responses. Also as expected, the average number of workers performing the task declined as the threshold increased.

I also considered changes in the standard deviation σ to a single task, ranging from 2.5 to 20. As expected, increasing the standard deviation generally resulted in a decrease in the corresponding stimulus level and an increase in the average number of workers performing the task, reflecting the fact that the lowest thresholds of the colony decrease away from the mean 35. (See Figure 1.) Counterintuitively, in many cases the work group size engaging in the task decreased as the standard deviation increased. This could reflect the fact that the thresholds of the workers are more clustered, and so there are more workers with similar, low thresholds which can respond to the task at a given time.

As demonstrated by these simulations testing the changes in the thresholds, an important factor determining how the colony will handle a given task need under normal circumstances is the collection of lowest threshold values the workers in the colony have. In some cases, this dependence on lowest thresholds can be quite sensitive. Figures 2 and 3 show the actual distributions of worker thresholds corresponding to nest cleaning in two baseline simulations. Simulation 1 resulted in a corresponding average stimulus level of 133 and an average number of workers of 1.24, while simulation 2 resulted in an average stimulus level and number of workers of 46 and 1.89, respectively. Thus a shift downward in a few worker thresholds resulted in a much better control on the nest dirt buildup.

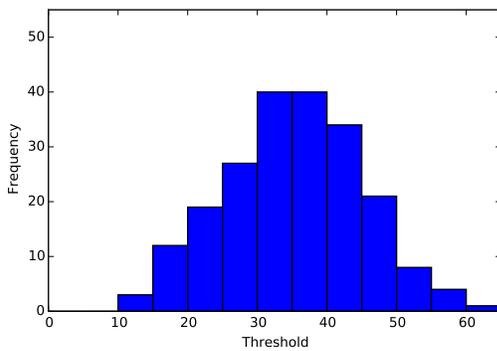


FIGURE 2. Simulation 1 histogram of nest cleaning thresholds

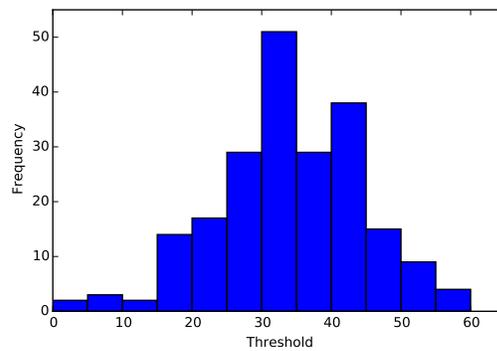


FIGURE 3. Simulation 2 histogram of nest cleaning thresholds

Lastly, the stimulus increase rates were changed, collectively as well as individually, ranging between 0.5 and, in some cases, 720 times the baseline rates. The results generally met expectations: higher stimulus rates yielded greater stimulus levels and average number of workers performing the task (or tasks) over time, which in turn caused the workers to perform more types of tasks, yielding a higher average repertoire size. These were the only changes which had a significant impact on the division of labor.

4. FUTURE WORK

Due to the run time of the program, the time length of all simulations were set to one day, and as a result, long term well being and growth of the colony was unable to be evaluated. So one direction of future work is to examine longer term simulations and to measure what factors contribute the colony's success and growth. Another direction is to change the way the thresholds of workers are chosen. Instead of making them all independent, they could be coupled together in some way; for example, a worker having one very low threshold would cause the others to be high. This coupling could reflect the idea that each worker has limited abilities, or that certain types of workers are inherently more able to perform certain tasks than others.

Acknowledgements. I thank Samuel Beshers for his guidance in this project and acknowledge support from National Science Foundation grant DMS 1345032 “MCTP: PI4: Program for Interdisciplinary and Industrial Internships at Illinois.”

REFERENCES

- [1] E. Bonabeau, G. Theraulaz, J.L. Deneubourg. *Fixed response thresholds and the regulation of division of labor in insect societies*. Bull. Math. Biol. 60 (1998), 753–807.
- [2] G.E. Robinson, R.E.J. Page. *Genetic basis for division of labor in an insect society*, in: The Genetics of Social Evolution, ed. M.D. Breed, R.E.J. Page, Boulder, CO: Westview (1989), 61–80.
- [3] A. Weidenmüller, C. Kleineidam, J. Tautz. *Collective control of nest climate parameters in bumblebee colonies*, Animal Behaviour 63 (2002), 1063–1071.