Lazy Ants: *Temnothorax Rugatulus* Inactivity

The Effect of Brood Number on Colony and Individual Ant Inactivity

Theodore Jones

Honors First-Year Project: Lab /Field Experience Category

April 15, 2013

In collaboration with Daniel Charbonneau and Anna Dornhaus Ph.D.

Abstract

Ant colonies are examples of highly organized groups and are generally highly efficient. However, high levels of inactivity have been observed in social insects and about 50% of the ants in *Temnothorax rugatulus* colonies are inactive. The cause of this inactivity is unknown. This project investigates possible causes of inactivity, in particular the role that work availability has on colony and individual ant activity levels. We test the hypothesis that observed inactivity is due to inactive ants being idle when work availability is low by testing if colonies with more brood have less inactivity and if activity levels of almost all ants in a colony respond to changes. If a significant number of ants do not respond to changes in brood number, then there may be a substantial group of self-interested ants. The number and type of activity conducted by each ant in four colonies was recorded by video and the amount and type of brood present at each day of filming was measured. An ant was considered inactive for a given measurement day if its level of measured activities was below 25% of the average level for other ants in the same colony during the same day. It was observed that colonies with greater larvae numbers had lower inactivity levels. Additionally, it was found that colonies with greater overall brood number have lower inactivity during the afternoon and under definitions of activity that do not include wandering. To gauge whether almost all individual ants in a colony respond to changes in brood number, or whether some remain inactive, while other ants increase their activity level, we measured the number of individual ants that changed their activity in a significant way when brood numbers changed. We found that between 15 to 23 percent of the ants changed their activity in a significant way. This means there is a substantial subset of ants that do not undergo significant changes in behavior in response to brood number changes, or the data available is insufficient to detect patterns that do exist. The overall results of this experiment suggest that inactivity may be caused by lack of work availability and that larvae may require more work to care for than either eggs or pupae. Observed inactivity is most likely a necessary part of the colony structure to account for changes in brood number. However, the results

of this experiment also leave open the possibility that at least some of the inactive ants are inactive for reasons other than colony benefit.

Introduction

Ant colonies are examples of highly organized groups and are generally highly efficient. However, high levels of inactivity have been observed in social insects. About 50% of the worker ants in *Temnothorax* colonies are inactive[1]. Social insects where similar inactivity has been observed include other ant varieties [2] and honeybees [3] , and inactivity appears to be a common social insect behavior[4]. However, its cause is unknown and few empirical studies have focused on this behavior. *Temnothorax rugatulus* ants are native to Mt. Lemmon and the Chiricahua Mountains. This ant species has a usual colony size of less than 150 individuals. [5] We studied the effect of work availability on inactivity in *Temnothorax rugatulus* by determining the relationship between brood numbers and inactivity level. The goal of this project was to discover the effect that availability of work has on apparent inactivity.

Research Questions

In the first stage of the experiment, we studied four possible relationships between brood and amount of inactivity. The first is that there is no correlation. The second is that colonies with less inactivity could have more brood. The third is that colonies with more inactivity could have more brood. The fourth possibility is that inactivity could vary depending on the type of brood present.

---

1 Anna Dornhaus, Jo-Anne Holley, and Nigel R. Franks, "Larger colonies do not have more specialized workers in the ant Temnothorax albipennis," Behavioral Ecology, 2009

2 J. Retana and X. Cerda, "Behavioural Variability and Development of Cataglyphis cursor Ant Workers," Ethology 89, no. 4 (1991)

3 C. Anderson, "The adaptive value of inactive foragers and the scout-recruit system in honey bee (Apis mellifera) colonies.," Behavioral Ecology 12, no. 1 (2001)

4 P. Schmid-Hempel, "Reproductive competition and the evolution of work load in social insects," American Naturalist, 1990, 501.

5 O. Rüppell, J. Heinze, and B. Hölldobler, "Alternative Reproductive Tactics in the Queen-size-dimorphic Ant Leptothorax Rugatulus (Emery) and Their Consequences for Genetic Population Structure.," Behavioral Ecology and Sociobiology 50, no. 2 (2001)

Inactivity could be different depending on brood composition, the number of eggs, larvae and pupae present.

If colonies with less inactivity have more brood, this could support the possibility that the nest's increased activity is due to increased workload. It could also support the possibility that some observed inactivity is due to the inactive ants being on standby for when more work is available. If colonies with more inactivity have more brood, the inactivity may be related to workers laying eggs, although other causes are possible. This is because an increase in worker egg laying may result in more total eggs and brood in the colony. If the inactivity varies based on the type of brood present, this could mean that caring for certain types of brood is more labor intensive than caring for other types of brood.

In the second stage of the experiment, we studied whether all individual ants in a colony respond to changes in brood number, or whether some remain inactive, while other ants increase their activity level. We measured the number of individual ants that changed their activity in a significant way when brood numbers changed.

Methods and Procedures

Four colonies were used to study the relationship between brood number and inactivity. The colonies used for this experiment will be referred to as A12_1, M12_1, A12_2, and M12_6. All colonies used in this project were wild caught on Mt. Lemmon. Experimental ant colonies were kept in enclosures that were filmed for five-minute periods. Video was taken at 8:00 a.m., 12:00 p.m., 4:00 p.m., 8:00 p.m., 12:00 a.m., and 4:00 a.m. The colonies were filmed between May and October of 2012. The number and type of activities conducted by each ant in the videos was then recorded. Using the footage taken between May and August, analysis was completed for all time-points for all colonies. But for footage taken after August, analysis has only been completed for the 4 p.m. time-point for A12_1 and A12_2 . The activities recorded were foraging, nest construction, feeding and grooming, and trophallaxis, along with time spent wandering both inside and outside the nest. Inactivity was measured using observations of the percentage of ants engaged in these activities. Overall inactivity levels were measured that both included and exuded wandering. Additionally, the number and type of brood (egg, larvae, pupae) visible in each video was counted. The total brood numbers for each day of observation were taken as the average of brood numbers observed during each day of observation. In the colonies under study, changes in brood population were the main source of work availability variation. The effect of work availability changes not relating to brood care on total inactivity should be minimal. This is because the ants were kept in a controlled and stable environment with regular feeding. No significant changes to the ant enclosures were made during the experiment. An ant was considered inactive for a given measurement day if its amount of time spent in activity was below 25% of the average level for other ants in the same colony during the same day. Although multiple videos were taken on each day of measurement, inactivity was calculated on the scale of each measurement day, not for each video.

Comparisons of the number of brood present to the level of inactivity were made and used as the basis of statistical analysis for correlation. Plots of the inactivity/ brood number data were made and linear regressions were taken for the brood/ inactivity data. Data sets used were: total brood number/ inactivity, larvae number/ inactivity, pupae number/ inactivity and egg number/ inactivity. For all three, separate plots were made for inactivity with, and without, wandering inside considered inactive. R squared and ANOVA P values were then taken to test the level of correlation and its significance. The R squared value is the percent of the observed inactivity that can be explained by shifts in brood number. The P value is the likelihood that the observation is significant and not due to random error.

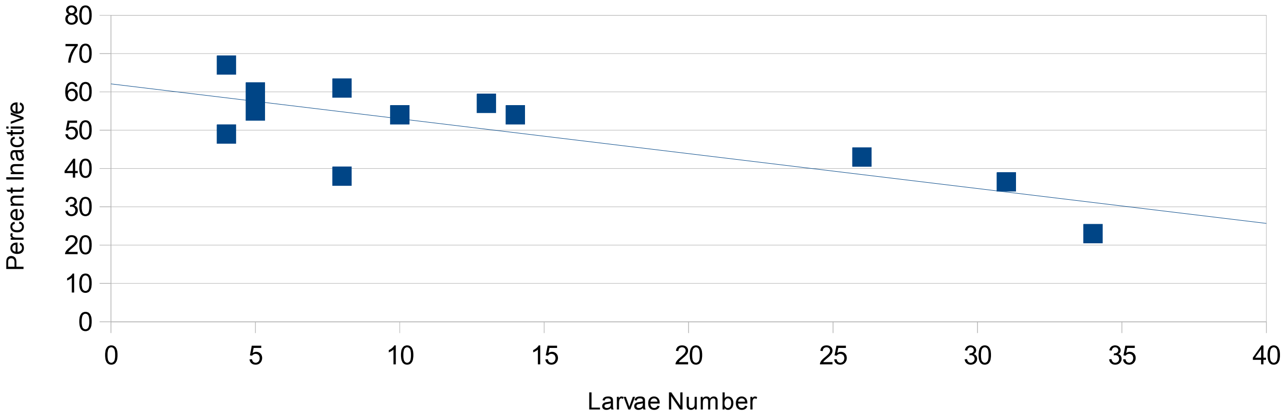
To gauge whether almost all individual ants in a colony respond to changes in brood number, we measured the number of ants that changed their activity in a significant way when brood numbers changed. For each ant monitored in colonies A12_1 and A12_2 an ANOVA for the ant activity/brood number data for that ant was taken. The percentage of ants showing significant change in activity (p value 0.05 or better) was recorded.

Data

Figure 1-- Brood Number/ Inactivity Data Table 1--A data table showing all brood number versus inactivity data-points is as follows for the days when data-points for 8:00 a.m., 12:00 p.m., 4:00 p.m., 8:00 p.m., 12:00a.m., and 4:00 a.m. were all available, and where time spent wandering inside is considered inactive.

Colony	Date	Total Brood	Egg	Larvae	Pupae	Percent Inactive
A12_1	08/14/12	12	8	4	0	49
A12_1	08/17/12	10	1	4	5	67
A12_1	08/26/12	8	0	5	3	60
A12_2	08/17/2012	54	41	8	5	38
A12_2	08/26/2012	31	21	5	5	55
A12_2	08/14/12	54	41	8	5	61
M12_1	05/31/12	52	7	31	14	36.5
M12_1	05/22/12	45	8	34	3	23
M12_1	05/10/12	30	4	26	0	43
M12_6	07/04/12	54	38	10	6	54
M12_6	07/07/12	47	29	14	4	54
M12_6	07/14/12	66	49	13	4	57

Figure 2-- Graphs, R squared, and ANOVA P values of total brood number versus inactivity, and larvae versus inactivity for the above data-set are as follows.



The R squared value for this data-set is 0.62 and the ANOVA P value is 0.00244.

The R squared value is 0.091 and the P value is 0.34.

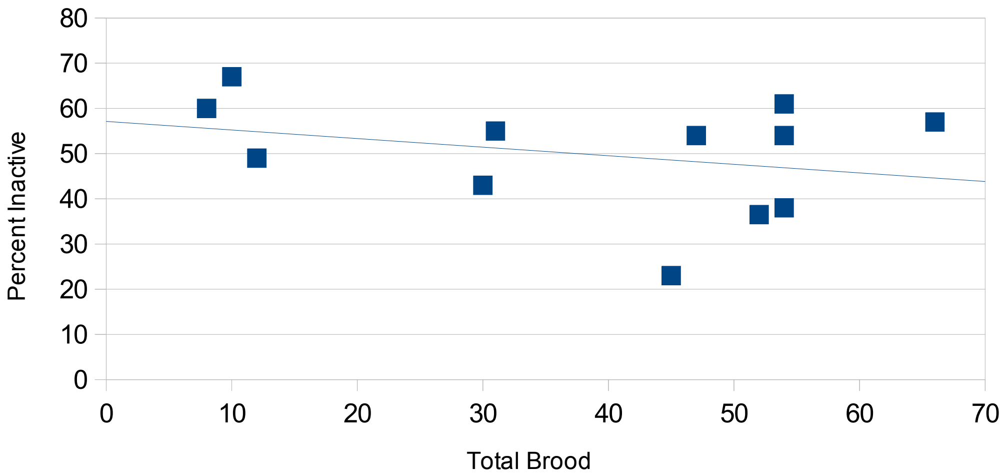
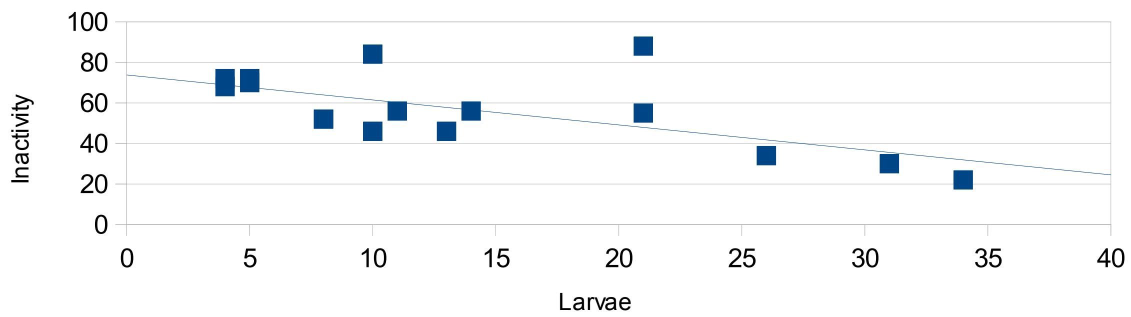


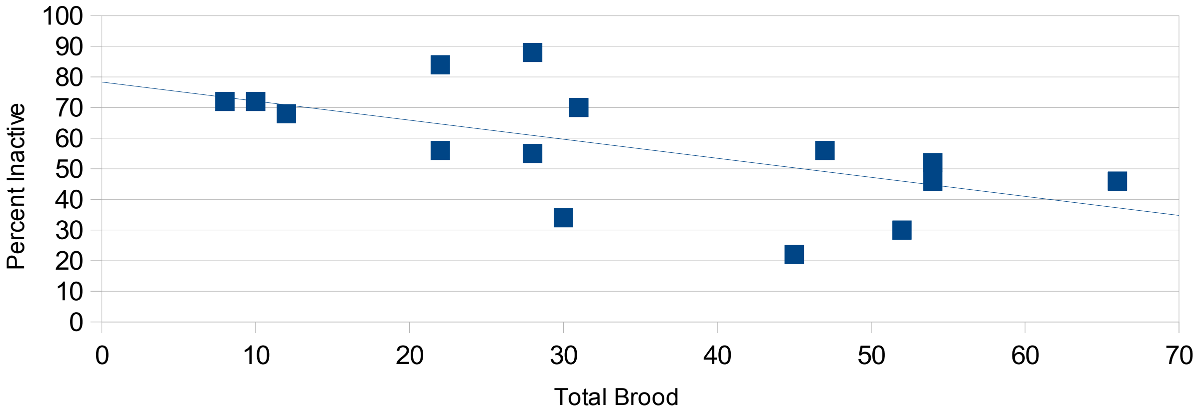
Figure 3-- Brood Number/ Inactivity Data Table 2--A data table showing all brood number versus inactivity data-points is as follows for all data-points at 4:00 pm and where time spent wandering inside is considered inactive.

Colony	Date	Total Brood	Egg	Larvae	Pupae	Percent Inactive
A12_1	08/14/12	12	8	4	0	68
A12_1	08/17/12	10	1	4	5	72
A12_1	08/26/12	8	0	5	3	72
A12_1	10/13/12	22	8	11	3	56
A12_1	10/14/12	22	9	10	3	84
A12_2	08.17.2012	54	41	8	5	52
A12_2	08.26.2012	31	21	5	5	70
A12_2	08/14/12	54	41	8	5	52
A12_2	10/13/12	28	7	21	0	55
A12_2	10/15/12	28	7	21	0	88
M12_1	05/31/12	52	7	31	14	30
M12_1	05/22/12	45	8	34	3	22
M12_1	05/10/12	30	4	26	0	34
M12_6	07/04/12	54	38	10	6	46
M12_6	07/07/12	47	29	14	4	56
M12_6	07/14/12	66	49	13	4	46

Figure 4-- Graphs, R squared and ANOVA P values of total brood number versus inactivity, and larvae versus inactivity for the above data-set are as follows.



The R squared value is 0.41 and the P value is 0.0075.

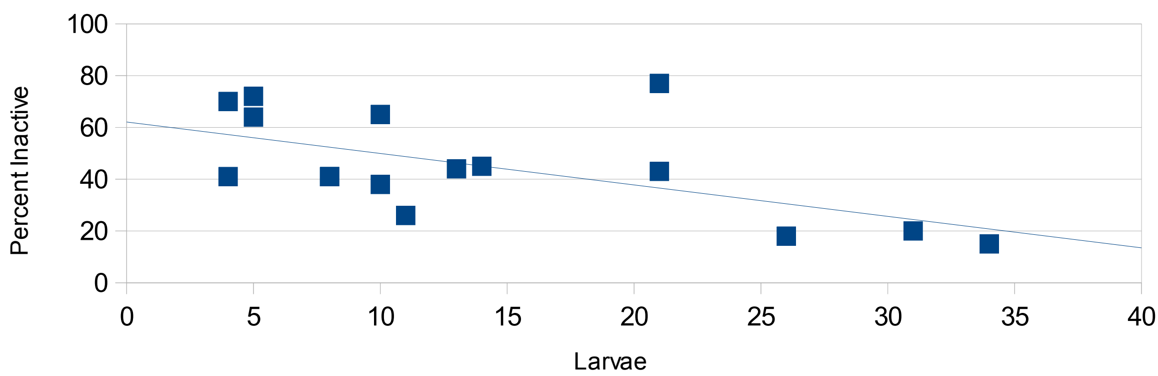


The R squared value is 0.37 and the P value is 0.012.

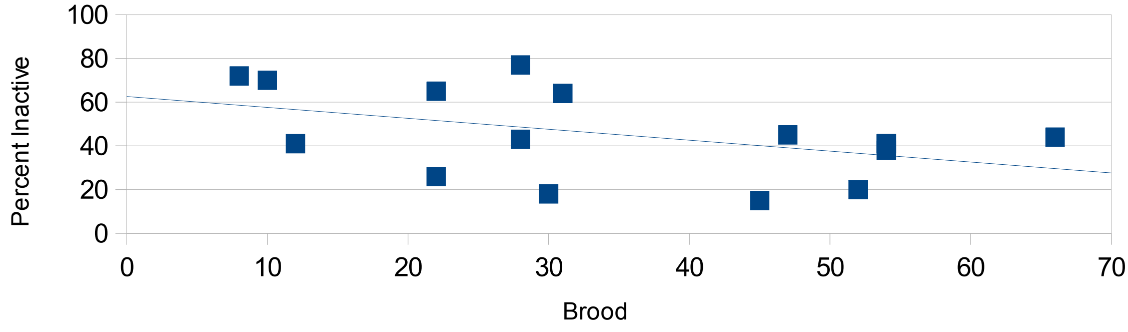
Figure 5-- Brood Number/ Inactivity Data Table 3 A data table showing all brood number versus inactivity data-points is as follows for all data-points at 4:00 pm and where time spent wandering inside is not considered inactive.

Colony	Date	Total Brood	Egg	Larvae	Pupae	Percent Inactive
A12_1	08/14/12	12	8	4	0	41
A12_1	08/17/12	10	1	4	5	70
A12_1	08/26/12	8	0	5	3	72
A12_1	10/13/12	22	8	11	3	26
A12_1	10/14/12	22	9	10	3	65
A12_2	08.17.2012	54	41	8	5	41
A12_2	08.26.2012	31	21	5	5	64
A12_2	08/14/12	54	41	8	5	41
A12_2	10/13/12	28	7	21	0	43
A12_2	10/15/12	28	7	21	0	77
M12_1	05/31/12	52	7	31	14	20
M12_1	05/22/12	45	8	34	3	15
M12_1	05/10/12	30	4	26	0	18
M12_6	07/04/12	54	38	10	6	38
M12_6	07/07/12	47	29	14	4	45
M12_6	07/14/12	66	49	13	4	44

Figure 6--Graphs, R squared and ANOVA P values of total brood number versus inactivity, and larvae versus inactivity for the above data-set are as follows.



The R squared value is 0.35 and the P value is 0.014.



The R squared value is 0.21 and the P value is 0.073.

Fifteen percent of the ants in A12_1 and A12_2 showed significant change in activity in response to changes in larvae number and 23% showed significant change in activity in response to changes in overall brood number.

Conclusions

A significant correlation between larvae number and inactivity was observed. All inactivity versus larvae number data-sets showed a significant correlation with P values of 0.00244, 0.0075 and 0.014. Therefore, it was observed that colonies with more larvae had less inactivity (Figures 2, 4, 6). The correlation between inactivity and larvae number was stronger when data from all times was analyzed, not just the late afternoon 4:00 p.m. time-point. Additionally, it was found that colonies with greater overall brood number had lower inactivity during the afternoon and under definitions of activity that do not include wandering (Figure 4). This correlation had a significant P value of 0.012. However, no significant correlation between pupae number and inactivity was observed (Figures 2, 4, 6). This result suggests that inactivity may be caused by lack of work availability in the colony and that larvae may require more work to care for than either eggs or pupae. This supports the possibility that the observed inactivity is due to fluctuations in work availability and that this inactivity is most likely a necessary part of the colony structure to account for changes in larvae number.

In the second stage of the study, focusing on individual ants, we found that between 15 to 23 percent of individual ants changed their activity in a significant way. This means there is a substantial subset of ants that do not undergo significant changes in behavior in response to brood number changes, or the data available is insufficient to detect patterns that do exist. This result leaves open the possibility that at least some of the inactive ants are inactive for reasons other than colony benefit.

Ongoing Work

Additional work to test the effect of temperature on inactivity is planned. To test the effect that temperature has on movement, we will measure movement levels using optical flow data and test how this correlates with temperature. We will also measure inactivity levels. Four colonies (different than the ones used in the inactivity versus brood number observations) have been collected and will be placed in a temperature-controlled environment and filmed. Inactivity and movement levels will be observed as temperature is varied from 10C to 30C in 5C increments-- two measurements each week, each measurement at a different temperature. Inactivity will be measured in the same way as in the inactivity/ brood number observations

Movement levels in the colonies, as measured by optical flow data, could be higher when temperatures are higher. This could be because the higher temperature could increase metabolic rate and therefore movement level. Higher temperature usually result in higher metabolic rates in other ant species. [6] It is also possible that there is not a significant correlation between movement levels and temperature, or that movement levels are lower when temperatures are higher. These

---

[6] John R.B Lighton, "Discontinuous CO2 Emission in a Small Insect, the Formicine Ant *Campoxotus Vicixus*," *The Journal of Experimental Biology*, no. 134 (July 21, 1987): [Page 367-368], accessed March 2, 2013

possibilities will be analyzed by using a t-test/ANOVA test to tell if there is a significant correlation between movement and temperature. Inactivity could be lower when the temperature is higher. However, research on other ant species shows that ants often forage less when the temperatures are higher, or shift their foraging to the night.[7] [8] There could also be no relation between inactivity and temperature, or inactivity could be higher when temperature is higher. At the time of writing, there are no results on these issues.

---

[7] George J. Gamboa, "Effects of Temperature on the Surface Activity of the Desert Leaf-cutter Ant, *Acromyrmex Versicolor* Versicolor (Pergande) (Hymenoptera: Formicidae)," American Midland Naturalist 95, no. 2 (April 1976): [Page 485], accessed March 2, 2013, http://www.jstor.org.ezproxy1.library.arizona.edu/stable/2424417?seq=1.

[8]T. Shivashankar, H. C. Sharathchandra, and G. K. Veeresh, "Foraging activity and temperature relations in the ponerine ant Harpegnathos saltator Jerdon (Formicidae)," Proceedings: Animal Sciences 98, no. 5 (September 1989): , accessed March 2, 2013,

Bibliography

Anderson, C. “The adaptive value of inactive foragers and the scout-recruit system in honey bee (Apis mellifera) colonies.” *Behavioral Ecology* 12, no. 1 (2001): 111-19.

Dornhaus, Anna, Jo-Anne Holley, and Nigel R. Franks. “Larger colonies do not have more specialized workers in the ant Temnothorax albipennis.” *Behavioral Ecology*, 2009.

Gamboa, George J. “Effects of Temperature on the Surface Activity of the Desert Leaf-cutter Ant, Acromyrmex Versicolor Versicolor (Pergande) (Hymenoptera: Formicidae).” *American Midland Naturalist* 95, no. 2 (April 1976): 485-91. Accessed March 2, 2013. http://www.jstor.org.ezproxy1.library.arizona.edu/stable/2424417?seq=1.

Lighton, John R.B. “Discontinuous CO2 Emission in a Small Insect, the Formicine Ant Campoxotus Vicixus.” *The Journal of Experimental Biology*, no. 134 (July 21, 1987): 363-76. Accessed March 2, 2013. http://jeb.biologists.org/content/134/1/363.short.

Retana, J., and X. Cerda. “Behavioural Variability and Development of Cataglyphis cursor Ant Workers.” *Ethology* 89, no. 4 (1991): 275-86.

Rüppell, O., J. Heinze, and B. Hölldobler. “Alternative Reproductive Tactics in the Queen-size-dimorphic Ant Leptothorax Rugatulus (Emery) and Their Consequences for Genetic Population Structure.” *Behavioral Ecology and Sociobiology* 50, no. 2 (2001): 189-97.

Schmid-Hempel, P. “Reproductive competition and the evolution of work load in social insects.” *American Naturalist*, 1990, 501-26.

Shivashankar, T., H. C. Sharathchandra, and G. K. Veeresh. “Foraging activity and temperature relations in the ponerine antHarpegnathos saltator Jerdon (Formicidae).” *Proceedings: Animal Sciences* 98, no. 5 (September 1989): 367-72. Accessed March 2, 2013. http://link.springer.com/article/10.1007%2FBF03179963.