FORAGING BEHAVIORS OF *CAMPONOTUS PENNSYLVANICUS* UNDER VARYING SOCIAL DENSITY CONDITIONS

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SUMMER 2016

A thesis
submitted in partial fulfillment
of the requirements
for a baccalaureate degree
in Psychology
with honors in Biology and Entomology

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This study examines how foraging behavior of *Camponotus pennsylvanicus* varies depending upon social densities. The two nest areas had a four-fold size difference. Additionally, we studied forager food preference for sucrose solution, protein, or water and whether changes in density would influence preference. Our results showed heightened foraging activity under higher social density. Increased foraging behavior could be explained by an increase in the frequency of worker interactions. Furthermore, the ants significantly preferred the sucrose solution to the protein source. Compared to protein, ants had more visits and spent more time at the sucrose solution. Water feeding events were marginal and not considered relevant to this study. Social density did not influence food preference. Findings from this study provide insight into understanding the functioning and adaptability of animal societies.
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ACKNOWLEDGEMENTS

I want to express my sincerest appreciation to Dr. David Hughes for inviting me to work in his lab and for showing me the invigorating side of research. You have inspired me, taught me more than I can express, and forever changed my outlook on life. I am eternally grateful to you and all of your guidance. I am incredibly thankful for all of the assistance I received from Andreas Modlmeier at each and every step of this project. Thank you a million times over for all of your help. I couldn't have done this without you. Additional thanks to Dr. James Marden and Dr. Michael Saunders for graciously agreeing to mentor me and for providing valuable feedback and insights. Lastly, I would like to thank my dad, my brothers, and my boyfriend, for providing me with endless amounts of love and encouragement.
Chapter 1

Introduction

Ants encompass a significant portion of the global biomass and across all ecosystems engage in behaviors that influence structure and functioning of environments (Vasconcelos, 1998; Wilson, 1987) through their facilitation of cycling nutrients (Petal, 1978) and soil fertilization (Haines, 1978). Within the class Insecta, 12 out of 13 eusocial species are from the order Hymenoptera (Oster and Wilson, 1978). Of those 12 eusocial species, the one of interest to this paper is Camponotus pennsylvanicus. Eusocial insects are distinguishable from other species with the evolution of three specific traits: a reproductive division of labor between a queen and her sterile workers, cooperative care of the brood, and overlapping generations of workers (Oster and Wilson, 1978). As a result of evolutionary driving forces and their sophisticated division of labor, eusocial species have adapted to operate as one highly organized and functional “superorganism” (Hölldobler and Wilson, 2009). By allocating individual ants into differentiated castes, each with a designated task, thousands of ants are able work jointly and utilize their internal organization to communicate and integrate behaviors best suited for the colony (Oster and Wilson, 1978). Foraging, the behavior of leaving the nest in search of food to bring back to the colony, is one of the most crucial roles an ant can assume. Studying the foraging behavior of various ant species has led to important breakthroughs in understanding the inner workings of ant colonies (Gordon, 2002).

C. pennsylvanicus ants are divided into two castes: queen and continuous polymorphic sterile workers (Fowler, 1984; Oster and Wilson, 1978). Ants in polymorphic colonies vary in size and have an evolutionary advantage over monomorphic colonies as their diverse range of body shapes enable them to obtain a wide variety of food sources (Oster and Wilson, 1978). The evolution of polymorphic ants is thought to be a result of decreased interspecies food competition, in turn allowing the foragers to expand their collecting behaviors to include more diverse food sources to bring back to the colony (Oster and
Sterile workers undertake various roles in the colony throughout their life, but in times of colonial stress, their role assignments become transient so they can engage in behaviors that are in the interest of the colony’s survival (Gordon, 2002; Robinson, 1992; Oster and Wilson, 1978). There are various roles ants that work outside the nest assume, including scouts, patrollers, foragers and soldiers (Oster and Wilson, 1978). Moreover, ants that assume work outside the nest are typically older than the workers who remain inside (Hölldobler and Wilson, 1990; Gordon, 2002). Internally, ants are involved with taking care of the brood, helping to maintain the structural integrity of the nest, and ensure the collected food stay protected (Gordon, 2002). Regardless of the specific role an ant takes on at any given time, individual behaviors influence members of all castes, not just the one they work in (Oster and Wilson, 1978). Therefore, the interdependent nature of the division of labor is an essential component to the overall functioning of the colony (Gordon, 1987, 1989, 2002). If an ant is unable to properly perform her task and other ants were unable to take over for her, this could send ripples throughout the colony, potentially putting the whole colony in danger.

A division of labor ensures, when faced with environmental stressors, the colony can act promptly and with a summation of force by functioning as a unit and delegating tasks to efficiently address any environmental stressors (Gordon, 2002) such as predation (Munger 1984; Nonacs, 1990; Hölldobler, 1981; Adams, 1990) and fluctuations in food availability (Oster and Wilson, 1978). A major benefit to having an integrated caste system is fast and efficient communication within the colony through parallel operations (Oster and Wilson, 1978). Much like the interior organs and systems in the human body have various feedback mechanisms to facilitate communication with each other, it is in the best interest of an ant colony to have various ways for individual ants to stay interconnected with each other so they are all continuously aware of the activities in and around the nest (Oster and Wilson, 1978). Parallel pathways of communication act as security systems and prevent colonies from experiencing detrimental outcomes in the event one of the systems of information is rendered inefficient (Oster and Wilson, 1978).
One means of communication that is of particular importance to a colony is recruitment behavior of foragers (Gordon, 2002). Despite poor visible capabilities (Gordon, 1995), ants use various methods to recruit foragers. The specific recruitment behaviors C. pennsylvanicus engage in are referred to as mass recruitment (Beckers et al., 1989) and communication (Traniello, 1977). After leaving the nest, scouts create a “trunk trail” (Oster and Wilson, 1978, p. 250) composed of hindgut material and formic acid, which helps orient stimulated ants to food sources (Hartwick et al., 1997; Traniello, 1977). When C. pennsylvanicus scouts return to the nest, they communicate with inactive foragers by antennal contact and rapid body movements to alert them to the location of nearby food (Traniello, 1977). The degree of scouts vacating the nest and subsequently interacting with other workers in the nest upon their arrival, directly influences the number of recruited foragers and amount of food brought into the colony (Traniello, 1997).

When trying to establish a complete picture of recruitment behavior, the rate, locality, and contextual implications of antennal contact are important to consider (Gordon, 1993). Furthermore, Gordon (2002) later demonstrated that a popular nest location for ants to exchange information is located at the entrance and exits of nests. Here, outside workers have the ability to communicate and interact with several ants who have tasks inside the colony, thus allowing a stream of information to freely flow so both inside and outside workers are constantly aware of the state of the nest. Even though chemical communication is a component of the antennal interactions, ants do not instruct each other to perform a task via chemical signaling (Gordon, 2002). Much like the human equivalent to “dropping hints”, the ant “knows” a task needs to be completed through the rate of interactions with other ants. The degree and frequency of the antennal interactions, not the chemical component, are the main driving forces that will influence the behaviors an ant takes on after an encounter with another ant (Adler and Gordon, 1992; Albert and Barabasi, 2002). The interactions can be thought of as a conditional statement. For example, if I am a forager, then I will most likely seek food sources when I interact with a specific number of patrollers/other foragers in a given time frame. Simply put, a forager’s behaviors are largely influenced by its interactions with other foragers, scouts, and patrollers (Gordon, 1991, 2002).
Little is known about the changes in foraging activity *C. pennsylvanicus* ants undergo when the size of their nesting area is altered. To better understand how social density (total number of ants divided by nest area) influences foraging activity, specifically food source preference, this study aimed to address two research questions: (1) Do foragers prefer sugar, protein, or water sources, and does social density dictate the food source preference? and (2) Will there be altered foraging activity in high versus low density? Based on studies using *Temnothroax rugatulus* (Cao, 2013), we predict ants exposed to high density will engage in more scouting and foraging activities than ants exposed to low density. Furthermore, based on previous literature (Tobin, 1993; Gotwald, 1968; Traniello, 1977; Fowler and Roberts, 1980) we predict ants will demonstrate a preference for the 10% sucrose solution over the protein and water sources during foraging activities. Investigating the effect social density has on group dynamics, specifically the foraging behaviors of *C. pennsylvanicus*, will help us to better understand that factors that guide division of labor, which made ants one of the most ecologically successful groups (Wilson, 1978).
Chapter 2
Methods

Experiment Set-up

One colony of *C. pennsylvanicus* ants was collected from the Pennsylvania State Game Lands no. 176, located in Centre County, PA, during the spring of 2015 (Appendix, Figure 1). From the original colony collected, we selected 1 queen, 75 workers, and 15 larvae for the experiment. The ants were fed 10% sucrose solution and a protein mix made from 3 frozen crickets that were homogenized using a tissue layer (Qiagen, Valencia, CA, USA). The room in which they were kept was about 76 degrees Fahrenheit with at least 40% humidity. The length of the experiment spanned a total of 14 days and was conducted from August 29th to September 11th 2015. Before the experiment started, each ant had a unique barcode, and corresponding number, assigned to them as a form of identification. Barcodes approximately 3 mm x 3 mm. were glued to the ant’s gaster using Cyanoacrylate glue (Maxi-Cure TM, Hobbytown USA). In an attempt to simulate a natural environment for the colony, after the glue had completely dried, the ants were then placed into a constructed nest box (6.5 cm x 4 cm; 26 cm2) made out of wood (Appendix, Figure 2). A total of 4 wooden boxes were constructed for the experiment (Appendix, Figure 3).

To monitor and record the activity of the ants within the nest regions, cameras were placed in the built up portion of the wooden nest (Appendix, Figure 4). The camera located in the first nest region is referred to as camera 1, with camera 2 and 3 referring to the middle nests and camera 4 (Appendix, Figure 5) referring to the nest region that feeds into the foraging area. The camera located above the three food sources (protein, water, and 10% sucrose solution) is referred to as the outside camera and was used to monitor the preference for food throughout the experiment (Appendix, Figure 6). The distance between camera 4 and the outside camera is roughly 188 cm (Appendix, Figure 7). Wooden sticks supported the
suspended yarn that enabled ants to travel between the nest boxes and the food sources as a way to simulate a more natural foraging environment and to differentiate between foragers and workers who left the nest (i.e. scouts, patrollers, etc.). Camera types varied dependent upon which region of the experiment they were in; GoPro Hero 2 was used for the outside camera whereas GoPro Hero 3 and GoPro Hero3+ (RageCams, Sparta, MI) were used for the nest regions. All cameras were modified to include infrared filters so nocturnal behavior would be recorded without disturbing their activities. To mimic light and dark periods of the natural world as close to possible, the colony was exposed to about 14 hours of light and 10 hours of darkness.

We simulated “high density” environment during the first half of the experiment by providing the ants with only one nest box, referred to as camera 1. The nest box associated with camera 1 had an area of 26cm2 and we allowed them a 6-day habituation period so they could adapt to the size of the enclosure. After the initial habitation period, ant activity in the camera 1 region, as well as the outside camera region, were recorded for 3 consecutive days. Next, we simulated the “low density” environment by adding 3 more nest boxes (respectively camera 2, camera 3, and camera 4), thus quadrupling the nest area available to 104cm2. The ants were given 6 days to habituate to the newly expanded nest area. For both density conditions, we recorded ant activity in the camera box that lead to the foraging arena (camera 1 for high density and camera 4 in low density). We also recorded the feeding activity using the outside camera footage. The total amount of footage analyzed from the outside camera for high density was 164,686 seconds, and 164,490 seconds for low density.

In and out Behavior

Using the recorded video footage, entrance and exiting of the nest regions were recorded in both camera 1 (high density) and camera 4 (low density). An ant was classified as “in” when her entire body was in the nest area. Ants were classified as “out” when her entire body had left the exit portion of the
nest and no part of her was visible. Time stamps of each entrance and exit were recorded. Data collection took approximately 65 hours for camera 1 and 85 hours for camera 4.

Foraging Behavior

When ants began feeding on protein, water, or the sucrose solution, the corresponding times were noted. The ants were understood to be feeding when their mandibles oscillated rapidly and their antennae were not moving. Data collection took approximately 120 hours for outside camera.
Chapter 3

Results

Foraging Behavior

Ants had significantly more feeding events during the high density treatment (2,019 events) than the low density treatment (638 events) (Yates Chi Square Test= 383.86; df= 1; p< 0.0001). In high density, 53 out of the 75 workers left the colony (Figure 1). Of the 53 ants that left (71%), 8 (15.1%) of them traveled to the outside camera area and had at least one feeding event. Therefore, roughly 11% of all workers in high density foraged. In low density, 46 workers left the colony (61%), and of those, 4 (8.7%) had at least one feeding event. Therefore, roughly 5% of all workers in low density foraged.

Figure 1. Distribution of ants remaining in the colony, leaving the colony, and actively foraging

Of the 9 active foragers, only 3 were engaging in feeding events in both treatments. For example, ant 703 was only active during the low density treatment, whereas ant 594 was active during both treatments (Table 1; Figure 2).
Table 1. Distribution of feeding events for foraging ants in high and low density

<table>
<thead>
<tr>
<th>Ant ID</th>
<th>High Density Feeding Events</th>
<th>Low Density Feeding Events</th>
</tr>
</thead>
<tbody>
<tr>
<td>528</td>
<td>252</td>
<td>0</td>
</tr>
<tr>
<td>594</td>
<td>184</td>
<td>161</td>
</tr>
<tr>
<td>598</td>
<td>112</td>
<td>0</td>
</tr>
<tr>
<td>631</td>
<td>126</td>
<td>0</td>
</tr>
<tr>
<td>643</td>
<td>25</td>
<td>56</td>
</tr>
<tr>
<td>646</td>
<td>418</td>
<td>0</td>
</tr>
<tr>
<td>666</td>
<td>500</td>
<td>417</td>
</tr>
<tr>
<td>698</td>
<td>402</td>
<td>0</td>
</tr>
<tr>
<td>703</td>
<td>0</td>
<td>4</td>
</tr>
</tbody>
</table>

Figure 2. Number of feeding events individual ants engaged in during high and low density treatments
Food Source Preference

Ants significantly preferred the sucrose solution over protein in high density (Yates Chi Square= 621.9, df= 1, p < 0.0001) and in low density (Yates Chi Square= 47.13, df= 1, p < 0.0001). Water drinking events were not taken into consideration as the degree in which they were observed were very rare and indicated the ants were only sampling the source momentarily. Comparing the mean duration of sugar and protein’s feeding events in both high and low density, the mean duration of their water drinking suggest their lack of interest in the feeding source (Table 2; Figure 3).

Table 2. Average duration of feeding event at each food source for high and low density

<table>
<thead>
<tr>
<th>Food Source</th>
<th>Mean Duration of Feeding (sec)</th>
<th>Mean Duration of Feeding (sec)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>High Density</td>
<td>Low Density</td>
</tr>
<tr>
<td>Sugar</td>
<td>111.95</td>
<td>64.31</td>
</tr>
<tr>
<td>Protein</td>
<td>96.92</td>
<td>68.35</td>
</tr>
<tr>
<td>Water</td>
<td>15.87</td>
<td>2.29</td>
</tr>
</tbody>
</table>

Figure 3. Comparing the mean feeding durations at food sources in high and low density treatments
Out of the three food sources, there was an overwhelming preference for the sucrose solution regardless of social density (Table 3; Figure 4).

Table 3. Number of feeding events per food source in high and low density

<table>
<thead>
<tr>
<th>Density</th>
<th>Number of Feeding Events: Sugar</th>
<th>Number of Feeding Events: Protein</th>
<th>Number of Feeding Events: Water</th>
<th>Total Number of Feeding Events</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>1726</td>
<td>262</td>
<td>31</td>
<td>2019</td>
</tr>
<tr>
<td>Low</td>
<td>432</td>
<td>192</td>
<td>14</td>
<td>638</td>
</tr>
</tbody>
</table>

Figure 4. Percentage of total feeding events occurring at each food source for (a) high and (b) low density treatments

Furthermore, of the total time spent feeding at all sources, ants in both density treatments spent the majority of their time collecting sucrose solution, followed by protein and then water (Table 4; Figure 5).
Table 4. Total feeding duration at each food source for the high and low density treatments

<table>
<thead>
<tr>
<th>Density</th>
<th>Feeding Duration:</th>
<th>Feeding Duration:</th>
<th>Feeding Duration:</th>
<th>Total Feeding</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sugar (sec)</td>
<td>Protein (sec)</td>
<td>Water (sec)</td>
<td>Duration (sec)</td>
</tr>
<tr>
<td>High</td>
<td>193,218</td>
<td>24,392</td>
<td>492</td>
<td>219,102</td>
</tr>
<tr>
<td>Low</td>
<td>27,780</td>
<td>13,124</td>
<td>32</td>
<td>40,936</td>
</tr>
</tbody>
</table>

Figure 5. Food preference based on total feeding duration at each food source for the high density (a) and low density (b) treatments.
Chapter 4
Discussion

In support of the work done by Cao (2013) and our prediction regarding the effect manipulating social densities would have on ant behavior, specifically foraging activities, we found an observable difference in the degree of foraging activity between the social density treatments. There were a greater percentage of workers leaving and subsequently foraging for food in high density than in low density (Figure 1). Additionally, ants in high density had significantly more feeding events (2,019 events) than in low density (638 events). Different degrees of recruitment activity and subsequent foraging behavior could be explained by changes in colony needs during the high and low density treatments (Gordon, 2002a). In high density, the ants presumably determined more foragers were necessary to combat the structural limitations of a tightly packed nest, and as a result, roles were reassigned and more ants assumed the task of foraging (Gordon, 2002a). When the nest area expanded in the low density treatment, the colony was no longer under stress and the need for enlisting foragers decreased (Gordon, 2002a). Another potential explanation for the difference in foraging activity is scout-forager and forager-forager encounter rates (Cao, 2013). Due to the limited nest area available to the ants in high density, scouts and foragers experienced an increase in encounter frequency. This increase in encounters corresponded with an increase in antennal interactions, which enabled scouts to more effectively communicate with and recruit large amounts of foragers in a short amount of time at entrance and exit nest locations (Gordon, 2002a). According to Gordon (2002a), when interaction rates between scouts and foragers decrease, recruitment activity is limited and consequentially, foraging behavior is reduced. Therefore, when we quadrupled the nest size, the ants were able to spread out over a larger area, most likely leading to a reduction in the encounter rates and overall foraging activity.

Furthermore, differences in the number of foraging activity for individual ants during high and low density conditions provided supporting evidence of social density’s influence on ant foraging behaviors (Table 1; Figure 2). These variances could be explained by the “foraging-for-work” hypothesis
This hypothesis asserts that ant task allocation can be influenced by the geographical location an ant is at in the nest at a specific time (Gordon, 1966, 2002a). For example, if ant A is near the entrance and ant B, a scout, has recently come back, ant A could be recruited to forage simply because she is in close proximity to ant B. In high density, more workers were compressed near the nest entrance/exit and thus were more likely to be recruited to forage simply because they were able to come into contact and communicate easily with returning scouts and foragers. In low density, fewer ants were clustered around the entrance/exit as a result of the increase in available nest area, in turn reducing the likelihood for large amounts of workers to be recruited to forage. Alternatively, the ants may have become tired throughout the length of the experiment, thus resulting in the reduced amount of foraging activity observed in low density. However, the ants had previously spent approximately three months living in our research laboratory with ad libitum food, indicating that there wouldn’t be a valid reason or circumstance for them to suddenly become worn-out during the experiment. Further studies are necessary to better determine the reasons behind the decrease in foraging activity when nest area is increased.

Consistent with previous literature (Tobin, 1993; Gotwald, 1968; Cannon and Fell, 2002) and our prediction regarding food preference, we concluded C. pennsylvanicus ants significantly preferred the carbohydrate-rich 10% sucrose solution to the protein source. For both social density treatments, the greatest number of foraging visits occurred at the sucrose solution (Table 3; Figure 4). The ants further demonstrated their food preferences through the average length of each visit to the sucrose solution (Table 2; Figure 3) and the total amount of time spent collecting the sugar water (Table 4; Figure 5) being greater than the respective time values for protein, in both high and low densities. Moreover, we did not take water collecting events into consideration, as the degree in which they were observed were very rare and indicated the ants were only sampling the source momentarily. Fowler and Roberts (1980) attributed the bias foragers display towards consuming carbohydrate-rich foods to an evolutionary preference favoring sources that will provide them with ample energy to forage. Furthermore, feeding on the sucrose solution proves beneficial to the colony because the liquid source allows foragers to share the nutrients
with the greatest amount of nest mates in a limited amount of time (Oswalt, 2007). Traniello (1977) discovered *C. pennsylvanicus* foragers were able to unload roughly 98% of their retrieved liquid to 62% of other workers in 10 minutes. Studies with *Myrmica rubra* found that, despite foragers freely transferring liquid sources throughout the colony, they only share protein sources with specific nest mates (Lange, 1967; Brian and Abbot, 1977). Further studies are necessary to determine if the same selectivity of sharing food crops extends to *C. pennsylvanicus* as well.

In summary, our results suggest that social density influences foraging behavior but not food preference. Examining foraging activity, we found the ants engaged in more foraging behavior in high density than in low density. Regarding food preference, the ants significantly preferred the 10% sucrose solution regardless of social density. Studying the dynamics of an ant colony, particularly the mechanisms ants use to communicate and maintain their division of labor, proves to be an important topic when trying to understand human beings. Both human brains and ant colonies function without a “central governing body,” and yet both entities manage to work together as one highly efficient organism, capable of carrying out various tasks simultaneously (Gordon, 2010). By further investigating the behaviors displayed by ant colonies and the environmental factors guiding them, we will be able to gain invaluable insights into the functioning and malleability of our brains.
Appendix

Figure 1. Region in State College, Pennsylvania where *C. pennsylvanicus* ants were collected during spring 2015.
Figure 2. Interior view of a wooden nest box.
Figure 3. Overview of experimental set up with nest boxes. Ants would travel from the A region (camera 1) to the D region (camera 4). The exit location in the D region led to the external foraging area. Regions B and C were intermediate boxes that allowed the ants more room to move.
Figure 4. Interior view of the ants in region A (camera 1) during the high density treatment.
Figure 5. Outside view of a nest box. GoPro cameras (A) were attached to the nest box (C). Infrared lights (B) were inserted into all nest boxes so ant activity could be monitored in the dark.
Figure 6. View of outside camera (A) and foraging area (B) with the 10% sucrose solution (left microtube labeled S), protein (located in the middle), and water (large test tube located to right) sources.
Figure 7. Visual of entire experiment. The GoPro camera (A), which is attached to the nest box (B), monitored ant activity as they left and entered the nest from foraging. After leaving the nest box, ants would traverse the foraging area (C), reaching the food sources (E). All foraging activity was recorded using the outside camera (D). During the night, the infrared light for the outside camera (F) was turned on so ant activity could be monitored in the dark.
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Bachelor of Science in Psychology with a focus in Neuroscience
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Awards/Achievements 2011-2012:
Member of Phi Eta Sigma National Honor Society
President’s Award
Deans List (Fall 2011 and Spring 2012)

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Schreyer’s Honors College Student
Member of Paterno Fellows Honors Program
Member of National Honor Society of Collegiate Scholars
Member of Psi Chi (International Honor Society in Psychology)
Member of Alpha Epsilon Delta (National Health Pre-Professional Honor Society)
Dean’s List (Fall 2012)

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Dean’s List (Spring 2014)

Awards/Achievements 2014-2015:
Dean’s List (Fall 2014 and Spring 2015)

Awards/Achievements 2015-2016:
Dean’s List (Spring 2016)

Experience

Research Assistant
Undergraduate Research Assistant
Dr. Peter Arnett’s Neuropsychology Sports Concussion Lab

Our research investigated changes in cognitive, affective, and behavioral functioning that result from brain injury. In particular, we studied college athletes who have suffered mild traumatic brain injuries (MTBI) due to concussions.

Hospital Volunteer
Mount Nittany Medical Center
As a patient floor volunteer, I discharged patients, transported medical equipment, and took patients to and from diagnostic testing locations throughout the hospital. As an emergency department volunteer, I ensured emergency rooms were fully stocked (with sheets, blankets, towels, and pillows), protect patient’s privacy, and assist nurses with various tasks.

**Research Assistant**  
Fall 2014- Fall 2015  
Undergraduate Research Assistant  
Dr. Melissa Rolls’ Biochemical and Molecular Biology Lab

Our research aimed to better understand the protein pathways using *Drosophila melanogaster* as the model organism. In particular, I researched how microtubule formation occurred at dendritic branch points in a class IV neuron.

**Research Assistant**  
Fall 2015- Present  
Undergraduate Research Assistant  
Dr. David Hughes’ Biology and Entomology Lab

Our research examined the social dynamics of eusocial insects, specifically the *Camponotus pennsylvanicus*. My thesis centered around the alterations in foraging behavior and food preference for a colony when exposed to different social nest densities.

**Skills**

**Computer Skills**

Programs: Microsoft Word, PowerPoint, Excel