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Swimming Behavior in Temperate Forest Ants

By

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Submitted in partial fulfillment for the requirements for Graduation (*summa
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Swimming behavior in temperate forest ants

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Undergraduate thesis

Abstract

Most terrestrial arthropods are helpless in water, and falling from a tree into a flooded forest understory should be especially problematic for small, cursorial organisms like ants. Whereas many species of tropical arboreal ants can tread across the water surface (i.e., swim), less is known of this behavior in temperate forest ants. I tested for swimming ability in various ant species collected from tree trunks in Kentucky. Results show that *Camponotus pennsylvanicus*, and *C. nearcticus*, are strong swimmers (operationally defined as directed motion at speeds > 3 body lengths per sec.), while *Crematogaster ashmeadi*, and *Monomorium minimum* tend to struggle and become trapped at the water surface. Laboratory studies suggest that the ants direct their swimming toward dark objects (i.e., skototaxis), presumably to locate tree trunks or other emergent structures. Collectively, these results suggest that living and foraging well above the ground poses special challenges for cursorial animals.

Introduction

Ant colonies function as a social unit (Gordon, 2010). There is a hierarchy system, and each caste is vital to the survival of the colony as a whole. A caste is defined as a specific level in the colony hierarchy (Gordon, 2010). Taking care of young, maintaining the nest, foraging, and defense are examples of different tasks. Workers, the small females that do not reproduce, are responsible for taking care of the young and also for foraging for supplies to sustain the rest of the colony (Delgado, 2000). Ants colonize on the ground, as well as in the trees. Some species forage both on land and in trees, and navigate easily between the two habitats. Certain ant species like *Camponotus*, otherwise known as the carpenter ant, place their nests and also forage high in the canopy of trees in the tropical rainforests of Central and South America, with no need to come down from the tree to the forest floor (Baader, 1996).

Arboreal ant species spend all of their time in the tree. However, there are circumstances beyond the ant's control. For example, winds moving the branches high in the canopy where these ants are commonly found may cause them to lose their connection with the tree and plummet to the forest floor. Likewise, when birds or mammals forage in the tree, the movement of the branches causes ants to fall to the ground below (Haemig, 1997). In the tropical rain forests of South America, the ants could potentially land in the leaf litter, a great distance from their nest with a low likelihood of returning (Yanoviak et al, 2005). During the wet season however, the forest floor is usually covered in water. Aquatic insects like the water striders (family Gerridae), are an example of an aquatic surface dwelling species that would have no trouble falling onto a rain covered forest floor (Milne and Milne, 1978). Unlike terrestrial land species, striders are capable of navigating successfully across the water without being trapped. This neustonic behavior is possible because their legs do not sink down into the water, but manage to stay on the surface, enabling them to maneuver, change direction and transport themselves on the forest floor when it is covered.

In contrast to water striders, moths, bees, butterflies and various other small, terrestrial creatures are trapped by the water. Water's basic property of

surface tension prevents their escape. Moths and bees as well as butterflies find that their wings are trapped; while others simply struggle and lack forward motion or directionality. They are eventually caught by underwater predators (Small et al, 2013) or die by drowning. Some spiders, however, have mastered the ability to navigate on the water's surface without being entrapped. Certain species of land spiders like those found in the Agelenidae family are able to remain dry and move on the water's surface similar to how they maneuver on land (Stratton et al, 2004). Ants are a terrestrial surprise, in that they too possess the ability to evade almost certain death that comes with falling into the waters below. Certain ant species in the tropics bypass falling into the leaf litter or onto the water's surface entirely by displaying directed aerial descent, or gliding behavior (Yanoviak et al, 2005). Most species of the Pseudomyrmecinae family and *Cephalotes* genus in South America display this gliding behavior. These ants will glide not only when dislodged from the tree, but also to avoid predators as well.

Not every ant species possesses the ability to glide; some ant species display behaviors similar to that of the aquatic dwelling water strider. Certain arboreal ant species actually swim when they land on the water surface. South American ant species in the families Dolichoderinae and Formicinae displayed strong swimming behavior on the surface of the water (Yanoviak and Frederick, 2014). Certain species have better success than others, and that is correlated to ant size. Larger ants have greater success at navigating on the water surface without being affected by surface tension (DuBois & Jander, 1985). Smaller ant species like *Monomorium minimum* struggle with the tension effects and end up flailing at the water surface (DuBois & Jander, 1985). In contrast, when other ant species, like *Camponotus pennsylvanicus*, hit the surface of the water, they almost immediately begin moving (swimming) towards a nearby object, such as the base of a nearby tree.

This directionality displayed by ants in both North and South America is possibly linked to skototaxis. Skototaxis is defined as the ability to navigate to darker objects that contrast with the overall background (DuBois & Jander, 1985). Several different terrestrial and aquatic species are known to exhibit this

behavior. Beetles that live in the leaf litter use skototaxis to help navigate to tree trunks during the flooding that occurs seasonally in the Amazon (Irmiler, 1973). Adults of three different flat bug species also showed positive orientation towards dark objects (Taylor, 1988). Skototaxis behavior is beneficial for terrestrial species, like ants, that do not possess gliding capabilities. When the ant first hits the water, it is a prey item for underwater predators. Swimming to the nearest dark object will potentially provide the ant with an avenue for escape, as long as the ant can swim quickly. This behavior allows them to survive in foreign habitats, and presumably assists them in evading predators while they return to the base of the tree.

Neustonic qualities are present in tropical ant species, and the same is true of some species of arboreal ants in North America (DuBois & Jander, 1985). Nothing is known about Kentucky species of ants in terms of swimming ability or directionality. Many genera of ants are found both here and in tropical rain forests (e.g., *Camponotus*, *Crematogaster*; Yanoviak, 2006), but few studies have compared their behaviors. Although most tree-dwelling ants in Kentucky are unlikely to land in a body of water filled with predators, the same can not be said for all North American ants. The general goal of my research was to explore swimming behavior in local arboreal ants. Within that goal, I focused on the following questions: 1) which ant species exhibit swimming behavior?, 2) how fast do they swim?, 3) does swimming speed change with body size?, and 4) which swimming species exhibit skototaxis? I predicted that the two species of *Camponotus*: *C. nearticus* and *C. pennsylvanicus* would both exhibit strong swimming behaviors and show skototaxis behavior. These predictions were based on the previous work of Yanoviak & Frederick (2014) and DuBois & Jander (1985).

Methods

This research was conducted in Louisville, Kentucky. All ants were taken from campus trees at the University of Louisville, which is located about two miles south of the city center. The campus is set in an urban environment, with

over 2,000 trees of varying types. The city of Louisville averages 31 degrees C during the summer months-- i.e., when my samples were being collected. Only trees with ant activity were surveyed, and all ants were collected on warm, mostly clear days because ants were not active during rain.

My first objective was to determine which ant species exhibit swimming capabilities. These trials were conducted in the field. A small, rectangular pan about 25 mm deep was used as a swimming arena. The water depth in the pan was about 13 millimeters. Worker ants were collected by placing baits (tuna mixed with honey) on tree trunks about 1.5 m above the ground. Foraging ants were captured with an aspirator, or with tweezers depending on the ant's size. An aspirator (Figure 1) uses mouth suction to draw an ant through a tube that ends at a vial. This vial was then stoppered until the ant could be tested. Extreme care was taken to ensure that the ant was not damaged during the capture. This was done to guarantee their swimming ability was not adversely affected. After the ant was captured, it was transferred to a vial coated in Teflon. The Teflon creates a non-stick surface to prevent escape. This coating also enabled me to simulate a natural fall by simply inverting the vial over the white pan and allowing the ant to fall into the water.

Once an ant hit the water surface, its swimming abilities were measured and categorized into one of the three groups: strong, weak, or non-swimming. Following Yanoviak and Frederick (2014), strong swimmers were classified as having directed movements reaching speeds >3 body lengths per second. Weak swimmers were described as displaying relatively slow but directed movement in the water, and non-swimmers made no swimming motion or appeared to be struggling, with no organized use of the legs. Twenty five ants of each species were collected and tested, and the ants came from a minimum of three different colonies on separate trees. This was to ensure that observed behaviors were consistent among colonies.

Once I had determined which ant species possessed strong swimming abilities, I moved my research into the lab. A small vinyl pool (1.8 m diameter) was placed in the middle of the lab on the floor (Figure 2). The lining of the pool

was white on the sides. An octagonal structure was built around the pool out of PVC pipe. The structure reached 1.7 meters in height and strips of white cloth were placed over the sides all around to block out any external shapes that created shadows on the water's surface. There were two long PVC strips crossing over the top of the pool and four work lights with 14 watt compact fluorescent bulbs were set over the pool which created an equal light source. All ceiling lights were turned off, and the window in the room was also blocked with blinds and covered with black cloth.

All trials were recorded with a video camera to determine the speed of the ants in the water. I used iMovie and NIH ImageJ software to convert the video to a series of frame-by-frame images (resulting in 30 images per second). These image sequences were analyzed and measured to determine the distance an ant traveled during a 2-4 second interval (i.e., 80-120 images, depending on the length of the video). The images were then reviewed to find a series of images where the ant traveled in a straight line. The first and last images in that straight segment of the ant's trajectory were then measured using the ImageJ line tool to determine the distance traveled per second. The speed of eight *Camponotus pennsylvanicus* and eight *Camponotus nearcticus* was calculated.

To determine ant swimming direction and skototactic behavior, I marked the principal coordinates (N, S, E, W) on the floor of the lab near the perimeter of the pool. Along with these coordinates, three more specific compass points between each were marked to get an accurate estimate of which direction the ants were swimming (within ca. 10 degrees). Ants were collected using the same process as described above, and then brought inside to test for directionality. As a control to establish that the ants were not swimming in any consistent direction in the lab pool, I tested twenty five ants from at least three different colonies in the pool with no experimental targets added. Each ant was dropped from the Teflon coated vial and given up to two minutes of swim time. Once the ant hit the water surface, the initial direction as well as every direction change was noted.

I then used a black pole and a white pole as experimental targets to assess skototaxis. Both the black and white poles were about 0.5 m in height

with a diameter of about 50 mm (Figure 3). The attractiveness of the two poles was tested separately, beginning with the white pole, which was placed first at the North compass mark. Twenty five ants were tested individually with the pole in this position. The white pole was then placed at East, then West and finally South. At each direction an additional twenty five ants were tested with the prediction that the result would be the same as the control. After these trials, the black pole was used in the same manner as the white. The prediction was that the ants exhibiting skototaxis would swim to the black pole (i.e. in the northern direction) when the black pole was placed there because there would be a contrast between the pole and the white pool lining.

Results

Several ant species were tested to determine which Kentucky ants can swim (Table 1). The strong swimmers were *Camponotus pennsylvanicus* and *Camponotus nearcticus* as predicted. *Monomorium minimum* and *Crematogaster ashmeadi* were classified as non-swimmers, and two different *Lasius* species were identified as weak swimmers. The rest of the experiments were conducted using only the two strong swimmers.

There was no relationship between ant size and ant swimming speed for either *C. pennsylvanicus* or *C. nearcticus* (Figure 4). Linear regressions for both species were non-significant ($p > 0.70$ in both cases). *Camponotus pennsylvanicus* workers were larger than *C. nearcticus* workers (t-test $p < 0.0001$), but there was no difference in average swimming speed between species (t-test $p = 0.15$).

During the control treatment in the skototaxis experiment, ants dropped into a pool with no pole swam in various directions and never reached the edge. The white pole experiments gave the same results as the control group. It was clear that the ants were not attracted to the pole. However, the black pole provided very different results from the control and white pole groups (Figure 5). When the black pole was present, the ants reached the side of the pool at the

black pole over 50% of the time for each species. This outcome was consistent regardless of the position of the pole in the pool.

Discussion

Yanoviak et al. (2005) showed that certain ants possess gliding abilities to prevent landing on flooded forest floor during a fall. This behavior enabled tree dwelling ants to evade the predators and drowning risks that water would generally bring to terrestrial insects. Yanoviak and Frederick (2014) subsequently showed that non-gliding ants often could swim when landing in a flooded understory. Here, I have shown similar behavior in two common species of arboreal ants in Kentucky. I also showed that strong swimmers use skototaxis potentially to avoid death. Overall, these results were as expected, based on previous studies of swimming in North American ants (Dubois & Jander, 1985).

The lack of relationship between ant size and swimming speed was not expected. I predicted that ant mass would negatively correlate with swimming speed: smaller ants would be quicker on the water surface than their heavier counterparts. Although there was no obvious effect of body size for the two fastest swimmers, *Monomorium minimum*, the smallest species that I tested, was found to be a non-swimmer. They exhibited no swimming movements and appeared to be stuck by the surface tension of the water. However, my results are based on relatively small sample sizes. If I could repeat this experiment, I would record and measure more ant trials.

The results of the skototaxis experiment were as I predicted. The strongest swimming ants displayed clear skototaxis behavior when dropped into a pool with a dark pole as a target. All control trials were unsuccessful (Figure 5). Each ant was dropped into the center of the pool with no pole attached to the pool's edge. Their swimming direction was sporadic. The ants would start out going one direction, then would double back and start going another direction. They would continue doing this erratic swimming behavior until they either lost the strength to continue or I removed them from the pool. Both species displayed the same behaviors.

Considering that a circle has 360 different possible azimuths, the fact that the ants swam to the black pole in over 50% of trials is strong evidence for skototaxis. The only instances in which an ant did not reach the pole were due to complications when hitting the water. For example, one ant became trapped in the water when it hit the surface and it was unable to correct itself. Another ant landed on its side and was not able to right itself to maneuver properly. The specimens struggled to find the black pole only when it was at the North position, and this could be the result of some shadow effects created by a bookshelf located on the south side of the room. Regardless, the ants still had a > 50% success rate with the pole at this location.

Conclusion

Through these experiments I was able to obtain a general list of swimming ants found on campus at the University of Louisville that coincided with previous research (Dubois & Jander, 1985). I was also able to discover that skototaxis behaviors are utilized when ants found themselves on the water surface. This behavior is useful for avoiding predators that may be present in the water, and also their swimming ability allows them to navigate on the waters surface without being trapped by surface tension. If I were to continue my research on this topic, I would test ant species collected at other locations in Louisville and throughout the region to determine if the behavior depends on the collection site. I would also like to see if the size of the pole used for skototaxis experiments affects the success rate (i.e., Would ant navigation be altered by a smaller target?). I would also change the size of the pool to see if a larger experimental arena could cause different outcomes (i.e., Would the distance from the target affect ant escape success?). Finally, I would explore the role of other variables, such as surface tension or the presence of predators, in determining ant swimming ability.

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Figures



Figure 1. The aspirator used to collect ants in the field.



Figure 2. The pool used for the lab experiments (shown without water in this case)



Figure 3. The black and white poles used for the experiments in the pool

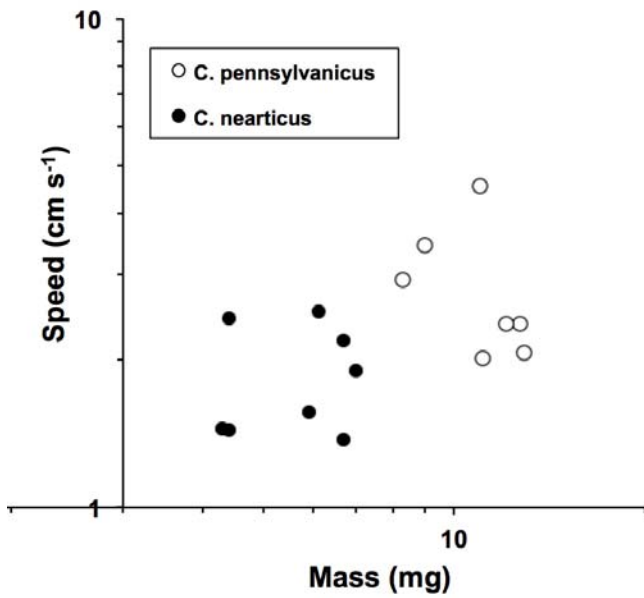


Figure 4. The relationship between ant mass and swimming speed for workers of the two fastest swimming ant species. N = 8 for each species.

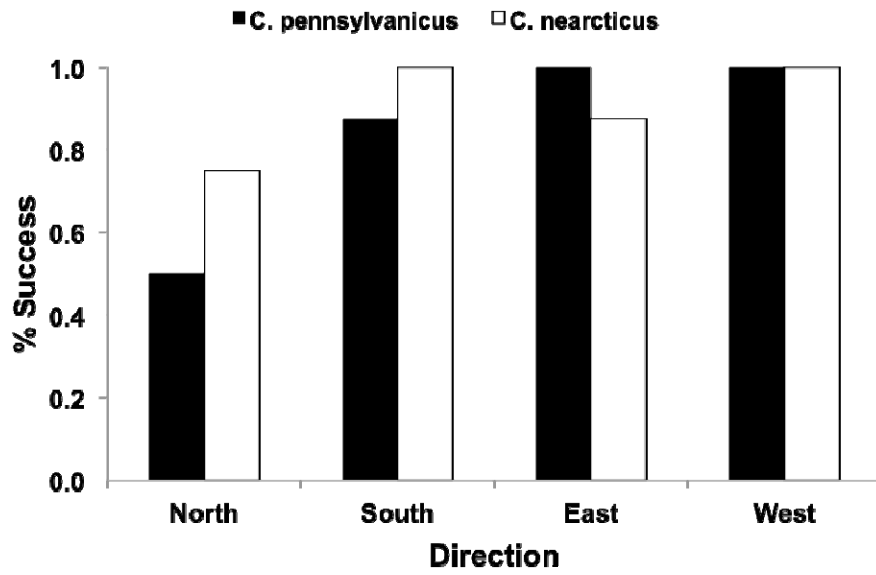


Figure 5. The success rate for each pole location in the skototaxis experiment. N = 8 ants for each species at each cardinal position.

Ant Species	Average mass (g)	Mass SD	Average Speed (cm/sec)	Speed SD	Swimming ability
<i>Camponotus nearcticus</i>	0.00548	0.00107	1.86	0.467	Strong
<i>Camponotus pennsylvanicus</i>	0.01078	0.00188	2.59	1.0596	Strong
<i>Lasius alienus</i>	0.00098	0.00052	N/A	N/A	Weak
<i>Crematogaster ashmeadi</i>	0.00096	0.00048	N/A	N/A	None
<i>Monomorium minimum</i>	0.00001	N/A	N/A	N/A	None

Table 1. Ant species that were tested in the field for swimming abilities. Average mass and standard deviation (SD) were calculated for all ants. Average velocity with standard deviation was calculated only for strong swimmers. Average mass for *Monomorium minimum* was determined by division.