

Orientation at the water surface by the carpenter ant *Camponotus pennsylvanicus* (DE GEER, 1773) (Hymenoptera: Formicidae)

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Abstract

Although most terrestrial invertebrates become trapped upon falling into water, workers of many ant species are able to swim to safety. Here we test the hypothesis that workers of *Camponotus pennsylvanicus* (DE GEER, 1773) use visually-based orientation towards lines of contrast to direct their locomotion across the surface of water. We quantified the swimming behavior of field-collected workers by dropping them into an experimental pool in the laboratory. Directed locomotion in *C. pennsylvanicus* is visually-mediated; 97% of ants with vision occluded by paint showed no directionality on the surface and did not escape from the water. When given a choice of white and black emergent targets against a white background, the ants consistently swam towards the black target. Likewise, ants generally swam toward the black background (vs. white) when no targets were present. These results suggest skototaxis; however, when provided with white and black targets against contrasting backgrounds, the ants consistently directed their swimming toward the contrasting target, indicating orientation towards contrasting edges. Trials with two-dimensional and three-dimensional targets suggest that rebounding surface waves are not used as orientation cues by these ants. Collectively, these results indicate that *C. pennsylvanicus* workers use visually-mediated skototaxis and edge orientation to navigate after falling into water and provide a foundation for future investigations into the mechanisms used by terrestrial invertebrates to survive similar circumstances.

Key words: Aquatic, behavior, orientation, skototaxis, swimming.

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Introduction

Active animals depend upon reliable extrinsic information to locomote over or through complex environments. The general characteristics of animal movements (speed, direction, efficiency) result from simultaneous integration of multiple variables, of which directional responses (i.e., taxes) often are fundamental. Animals exhibit a wide variety of taxes (FRAENKEL & GUNN 1961, CAMPAN 1997), but few have been studied specifically in the context of escape from unfamiliar habitats.

Terrestrial arthropods generally are not well equipped for locomotion in aquatic environments. Despite the hydrophobic properties of exoskeleton and cuticular hydrocarbons, arthropods falling into water commonly are entrapped by surface tension forces (VOGEL 1994) and ultimately drown or become food for predators and scavengers (e.g., fish and water striders). However, some terrestrial insects and many spiders exhibit a remarkable ability to escape these circumstances by rapidly treading or swimming across the water surface (MILLER 1972, FRANKLIN & al. 1977, SUTER 2013). Among insects, ants are best studied in this context; various temperate and tropical species locomote

quite well at the water surface, and some use modified gaits to effect forward motion and directional change (e.g., ADIS 1982, DUBOIS & JANDER 1985, BOHN & al. 2012, NARENDRA 2013, YANOVIK & FREDERICK 2014). Here, we examine the role of visual cues in the directionality of swimming in the carpenter ant, *Camponotus pennsylvanicus* (DE GEER, 1773).

Many arthropods rely on visual cues for navigation. Bees, ants, and other central-place foragers variously use information from optical flow and celestial cues to locate resources and return to their nest sites (e.g., WEHNER 2003, EVANGELISTA & al. 2014). Foraging ants also use canopy maps, horizon patterns, local landmarks, and skyline characteristics as orientation cues (e.g., HÖLLDOBLER 1980, KLOTZ 1986, OLIVEIRA & HÖLLDOBLER 1989, GRAHAM & CHENG 2009, BASARI & al. 2014, RODRIGUES & OLIVEIRA 2014). Some aradid bugs and cicindelid beetles orientate specifically towards dark objects (i.e., skototaxis; IRMLER 1973, TAYLOR 1988), and similar behavior was hypothesized for swimming carpenter ants (DUBOIS & JANDER 1985). Contrast is important to any visually-mediated ori-

entation (CAMPAN 1997), and what appears to be skototaxis actually may be orientation towards contrasting edges (i.e., perigrammotaxis; hereafter "edge orientation"; CAMPAN 1997), as shown for gypsy moths (PREISS & KRAMER 1984) and ants (VOSS 1967). However, few studies attempt to distinguish between these different cues.

Some aquatic and riparian arthropods (e.g., gyrenid beetles, spiders) also use waves to locate conspecifics, prey, or other objects at the water surface (BENDELE 1986, BLECKMANN & LOTZ 1987). This suggests that surface waves rebounding from objects protruding above the water surface can be reliable directional cues for an insect treading across the water surface in search of a means for escape. This hypothesis remains untested for ants treading or swimming across the water surface.

Many ant species forage in trees, and will occasionally fall into puddles or flooded forest understory (YANOVIK & FREDERICK 2014). Here we explore how workers of a common Nearctic forest ant, *Camponotus pennsylvanicus*, respond to visual cues while swimming. Specifically, we address three questions related to their behavior. First, do *C. pennsylvanicus* workers use their eyes to orient while swimming? Second, do these ants exhibit skototaxis and/or orientation towards edges? Finally, to determine if the ants were guided by waves reflected from protruding objects, we asked whether ants preferentially orient towards a three-dimensional target.

Methods

Ants used for this project were obtained from Iroquois Park in Louisville, Kentucky, USA (38.1674° N, 85.8147° W), during June and July of 2015. Iroquois Park is a ca. 300 ha urban park dominated by oak-hickory-maple woodland. We collected workers and partial nests of *Camponotus pennsylvanicus* ants from dead woody debris and transported them to the lab at the University of Louisville. The ants were identified using the keys of CREIGHTON (1950). We specifically chose *C. pennsylvanicus* as the focal species for this study because it is very common in forests and suburban woodlands of eastern North America (e.g., CREIGHTON 1950, ELLISON & al. 2012), it is easily recognized, and it consistently exhibited swimming behavior during preliminary trials. Plastic containers (ca. 15 × 15 × 30 cm) containing a small amount of soil and wood fragments from the nest site served as housing for the ants in the lab. A band of Fluon® PTFE-30 (BioQuip Products, Inc., Gardena, CA, USA) applied around the inside top margin of each container prevented ant escape. Ants were fed honey and were provided with ad lib water via a vial stoppered with a cotton wick. New nest fragments were collected approximately weekly and experiments were organized so that each set of trials included ants from multiple nests.

Experimental arena: Swimming trials were conducted in a white, circular, vinyl pool (Fig. 1, diameter = 152 cm, height = 25 cm; Intex Recreation Corp, Long Beach, CA, USA) containing tap water to a depth of 3 - 5 cm. The pool was housed in a laboratory room separate from the cages in which the ants were housed, thus removing the potential confounding effects of celestial cues and short-term memory of local landmarks (e.g., DURIER & al. 2003). Also, to negate the effects of skyline cues (GRAHAM & CHENG 2009), we homogenized the visual environment around the pool by erecting a curtain of either white cotton

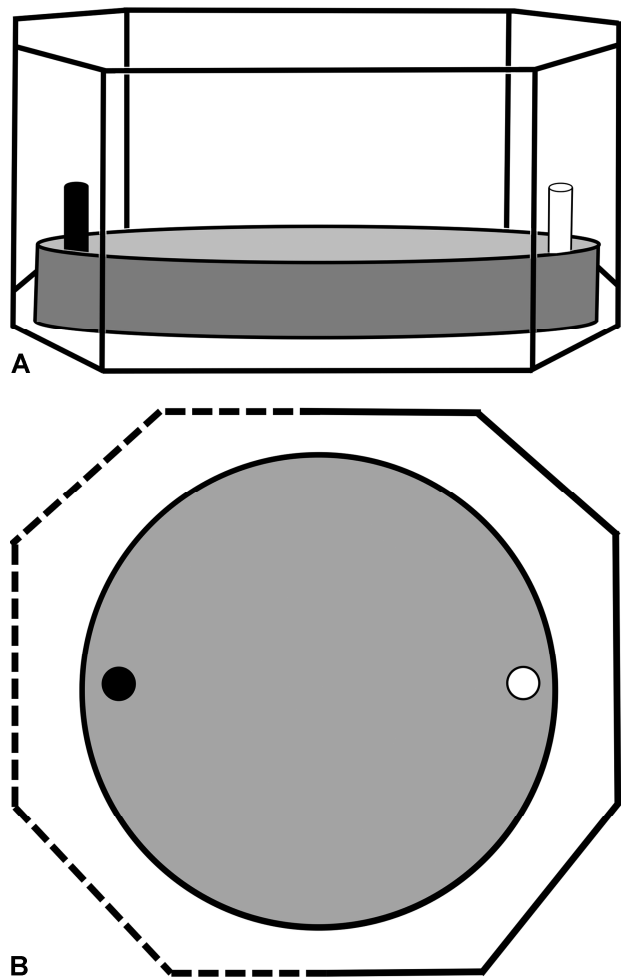


Fig. 1: Side view (A) and top view (B) of the experimental arena used to conduct swimming trials. The arena consisted of an octagonal PVC pipe frame surrounding a circular vinyl pool (shaded). Targets were placed within the pool as shown by the black and white cylinders (A) or circles (B). The top-down view depicts the most complex experimental setup used in this study. The right half of the PVC frame supported a black background (solid line) whereas the left half of the frame supported a white background (dashed line). The two target poles were placed at cardinal directions and centered in front of the background of opposite color. This combination of backgrounds and targets was variously modified depending on the objectives of the experiment, as explained in the text.

or black polyester cloth, depending on the experiment. The curtain was supported by an octagonal frame of 2 cm diameter PVC pipe (height = 182 cm, width = 200 cm) surrounding the pool. We lit the arena with two compact florescent lights (14W, 800 lumens each) housed in aluminum reflective shades attached to opposite sides of the top margin of the PVC frame. Both lamps were directed toward the water surface at an oblique angle.

Experimental visual targets added to the pool included a black PVC pole, a white PVC pole, and a stripe of black polyester cloth. The white and black poles were identical in size (i.e., height = 61 cm, diameter = 6 cm), and the black stripe had the same two-dimensional profile as the poles (61 cm × 6 cm). The poles stood just inside the

edge of the pool and the black stripe was attached to the inside of the pool.

General experimental procedures: All experiments employed the same basic procedure of dropping ants onto the water surface. We placed ant workers individually into a 15 ml plastic vial coated with Fluon. The vial was then inverted above the approximate center of the pool from a height of ca. 10 cm. Dropping ants onto the water in this manner generally had one of two outcomes: 1) the ant swam to the edge of the pool or an experimental target within 3 min (Video S1, as digital supplementary material to this article, at the journal's web pages), or 2) the ant struggled at the water surface or swam in an undirected manner and did not reach the pool edge within 3 min. We recorded the azimuth at which each ant exited the pool to the nearest 5 degrees. When ants did not escape the pool within 3 min (scenario 2 above), they were removed from the arena and recorded as "no exit". Each ant was used only once.

Vision occlusion experiment: We tested the prediction that ants use visual cues to orient while swimming by occluding the vision of 32 *Camponotus pennsylvanicus* workers and dropping them into the experimental pool as described above. Following methods used in previous ant studies (YANOVIK & al. 2005, 2011), we occluded the ants' vision by painting over their compound eyes with white enamel fingernail polish applied with the tip of an insect pin (Fig. S1, as digital supplementary material to this article, at the journal's web pages). To control for potentially confounding effects of the fingernail polish, we painted a similarly sized area between the eyes of 32 different workers (Fig. S2, as digital supplementary material to this article, at the journal's web pages). To facilitate painting under a stereoscope, ants first were anesthetized by cooling in a refrigerator (2°C) for 20 minutes, then transferred to a cold stage (i.e., a petri dish containing ice and covered with a thin plastic film). Additionally, as a negative control for directional bias caused by shadows or other subtle characteristics of the arena, ten ants were tested before a target was added. All experimental and control ants were allowed to warm to ambient lab temperature (23°C) for at least 20 min, then individually tested in the pool.

Skototaxis and edge orientation experiments: We used a series of experiments combining contrasting (i.e., white and black) targets and backgrounds to determine if swimming workers of *Camponotus pennsylvanicus* direct their motion towards dark objects (i.e., skototaxis) or to lines of contrast (i.e., edge orientation). Unlike the vision occlusion experiments, ants were not cooled or otherwise manipulated before these trials. First, we tested for skototaxis by giving ants a choice between a black pole and a white pole on opposite sides of an entirely white arena. Equal numbers of trials (N = 11 for each direction) were run with the poles in all four combinations of cardinal directions (i.e., the black pole at North and the white pole at South, the black pole at South and the white pole at North, etc.). We then tested for edge orientation by presenting the ants with a white pole against a black background. Specifically, we replaced the white background with the black background and repeated the same series of trials (N = 12 for each direction) described above. Both experiments were preceded by a series of control trials (i.e., either a white or black background with no targets present) to account

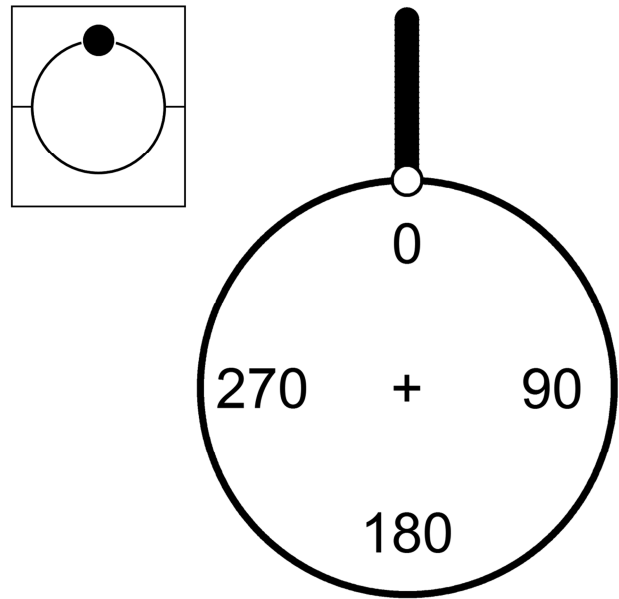


Fig. 2: A circular histogram of ant swimming directions in the vision occlusion experiment. The histogram shows the frequency of successful escape at a given azimuth ($\pm 5^\circ$). Many ants exited at a single azimuth in this experiment (i.e., 32 ants with only painted heads exited at 0°) and these points are stacked so that they appear as a bar that is proportional in length to the number of ants that chose this exit point. Filled points = control, i.e., ants with heads painted but eyes exposed (N = 32 trials); open point = treatment, i.e., ants with vision occluded by paint (N = 32 trials). Ants were provided with a black pole target against a white background. The target was moved to different cardinal points of the pool for different trials; the plotted results were normalized so that the black pole is always at 0° . The inset figure depicts the experimental design: The large circle represents the experimental pool, the small circle represents the black pole, and the two rectangular sections represent the color of the background (i.e., white).

for any effects of the arena that could have caused a directional bias.

We further explored the possibility that ants exhibit edge orientation behavior by presenting them with two contrasting sections of background in the same arena. The first of these experiments provided two contrasting edges by changing the experimental pool background to half black and half white and excluding targets. The contrasting edges of the background sections intersected at opposite cardinal directions (Fig. 1). We rotated the halves of the background to cumulatively occupy all four possible directions for ten trials each, similar to the rotation of targets among cardinal directions described above.

The final edge orientation experiment tested whether ants preferentially oriented towards contrasting objects rather than individual edges. For this test, we conducted the same trials as the previous experiment, except that the black and white poles were now centered in front of the background section of the opposite color (i.e., the black pole in front of the white background and vice versa). As in previous experiments, we frequently rotated these targets and backgrounds such that they ultimately occupied each cardinal direction for a similar number of trials (i.e.,

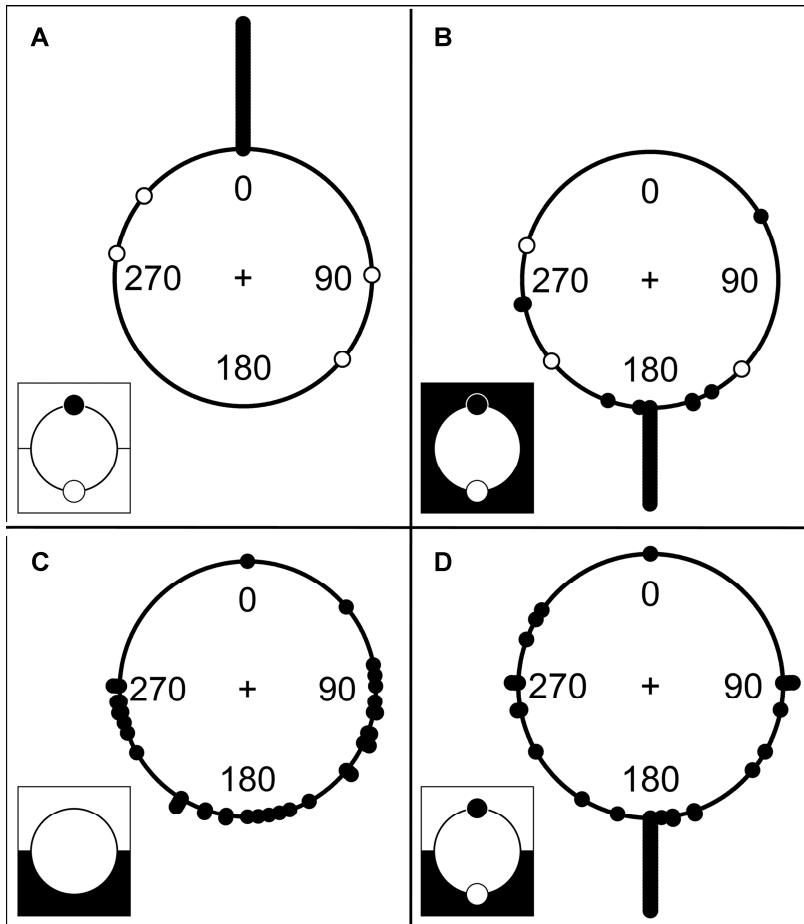


Fig. 3: Circular histograms depicting the distribution of swimming directions relative to different targets in an experimental pool. Points stacked on the rim of the circle represent the frequency of successful escape at a given azimuth ($\pm 5^\circ$). When large numbers of individuals exit at the same location, the stacked points appear as a bar proportional in length to the number ants exiting at a single location. The largest bars in panels A, B, and D represent a total of 40, 32, and 29 ants, respectively. Filled points = treatment, i.e., ants dropped into the arena with black and white poles (panel A: $N = 40$ trials, panel B: $N = 41$ trials, panel C: $N = 40$ trials, and panel D: $N = 54$ trials); open points = control, i.e., ants dropped into the arena with no targets (panel A: $N = 30$ trials; panel B: $N = 10$ trials). The data are normalized so that the black pole is always at 0° in A, B, and D. When no poles were included (C), the white background was centered at 0° . The inset figure in each panel depicts the experimental design as in Figure 2.

12 trials with the black pole at South and 14 trials for each other direction).

Emergent object preference: Finally, to determine if ants differentially swim towards three-dimensional versus two-dimensional targets, we gave them a choice between a black pole and a black stripe of cloth with similar dimensions. The black pole conspicuously emerged from the water on one side of the arena whereas the black stripe was appressed against the opposite side of the pool. The background was white for all of these trials. To test for any pre-existing directional bias, ten control trials were conducted in the white arena before the targets were added.

Statistical analyses: We used the Rayleigh test of uniformity to assess directional bias during swimming (FISHER 1993). We performed these analyses and plotted the results using the *circular* and *CircStats* packages of the R statistical program (R DEVELOPMENT CORE TEAM 2014). We normalized the position of the black pole or the black background (when the pole was not present) at zero degrees for each trial used in analyses. Statistical tests of directional bias were not performed on negative controls (i.e., solid backgrounds with no targets) or the vision occlusion experiment because escape failure was near 100% in these tests (i.e., ants dropped into the pool with no targets showed no consistent directionality and only rarely swam to the edge within 3 min). Additionally, 12 ants were excluded from the remaining experiments because they failed to swim to the edge of the pool. This included ca. 10% and 15%

of the edge orientation trials conducted with homogenous white and black backgrounds, respectively, but less than 3% of trials for the remaining experiments.

Results

Workers of *Camponotus pennsylvanicus* ants clearly used visual cues to orient while swimming across the surface of water. Most (97%) of ants with occluded vision failed to swim to the edge of the pool, whereas control ants (with painted heads, but exposed eyes) successfully escaped from the arena in 100% of trials (Fig. 2; $N = 32$, $r = 1.0$, $p < 0.001$). In each successful trial, the ants swam in a directed manner towards a black pole placed at the edge of the arena. By contrast, the ants with occluded vision either remained still in the middle of the pool or appeared to swim aimlessly in circles. None of the negative control ants (used to test for bias in the arena) successfully exited the experimental pool.

Edge orientation experiments: Different combinations of backgrounds and targets dramatically changed the orientation behavior of swimming *Camponotus pennsylvanicus* workers. When given a choice between a black or a white pole in front of a white background, 100% of ants swam to the black pole (Fig. 3A, $N = 40$, $r = 1.0$, $p < 0.001$). By contrast, when ants were presented with white and black poles in front of a black background, 78% of ants swam to the white pole (Fig. 3B, $N = 41$, $r = 0.90$, $p < 0.001$). In both experiments, no ants swam to the pole that matched the background.

The characteristics of the experimental arena did not affect ant orientation when targets were absent. In 30 trials with a white background and no targets, only four ants exited the arena, and their exit points showed no directional bias (i.e., 90, 130, 280, and 310 degrees). The results were similar with an entirely black background. In these ten trials, seven ants swam aimlessly and three exited at scattered locations: 135, 230, and 285 degrees.

Ants exhibited skototaxis and a tendency to navigate towards edges when given the option between black or white backgrounds with no targets. Only 10% of ants swam to the white half of the background, whereas 80% of the ants exited via the black background (Fig. 3C, $N = 40$, $r = 0.43$, $p < 0.001$). Although contrasting edges were $< 3\%$ of the potential exit points, 10% of ants exited at the black / white interface and an additional 28% exited on a section of the black background within 20 degrees of this interface. Moreover, many of the individuals that exited near the line of contrast initially swam towards a central section of the black background before abruptly changing course and accelerating towards the interface between the background sections. Collectively, these results indicate that the swimming direction chosen by 38% ($N = 15$) of the individuals was influenced by the line of contrast between the white and black backgrounds.

In our final test of edge orientation behavior, the diverse set of potential targets for orientation caused the ants to choose a variety of exit points (Fig. 3D). In 54 trials, 29 ants (54%) swam to the white pole in front of the black background, 13 ants (24%) exited at some section of the black background, seven ants (13%) exited at the interface between the two background colors, and four ants (8%) either exited along the white background, or had no exit point at all. Contrary to our expectations, only one of the ants exited the arena at the black pole in front of a white background. Overall, the swimming ants in this experiment exhibited a strong directional bias towards the white pole contrasted against the black background ($\bar{Y} = 0.67$, $p < 0.001$).

Emergent object orientation test: Workers of *Camponotus pennsylvanicus* ants were similarly attracted to the three-dimensional target (black pole) and the two-dimensional target (black stripe) when presented simultaneously against a white background and opposite each other in the pool. Specifically, 58% of ants swam to the black pole and 42% chose the black stripe, suggesting no bias towards emergent three-dimensional objects (Fig. 4). Despite the strong trend, we caution that there was insufficient statistical power to adequately test the hypothesis of no difference in attraction to the pole or stripe. None of the ants swam to the pool edge in the ten control trials conducted before we added the targets.

Discussion

Animals use a variety of mechanisms to escape unfamiliar habitats or potentially dangerous circumstances. For insects, this most often occurs via winged flight; however, cursorial taxa like ants generally are constrained to running or jumping. These mechanisms often are ineffective against the surface tension forces of water, and few ants will voluntarily tread on or through water (but see BOHN & al. 2012, NARENDRA 2013, YANOVIK & FREDERICK 2014). However, many ants have a remarkable ability to survive

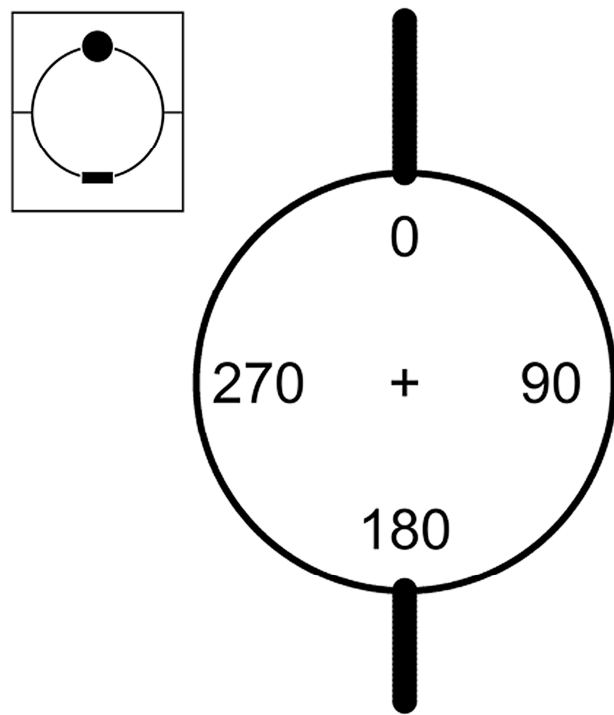


Fig. 4: The distribution of ant exit points when introduced to an experimental pool with a black cloth (normalized at 180°) and a black emergent object (normalized at 0° , $N = 52$). No control ants exited ($N = 10$ trials), so no control points are depicted. The black bars are proportional to the number of ants that exited at the black pole and black cloth stripe (i.e., 30 and 22, respectively). The inset figure depicts the experimental design as in Figure 2.

falling into puddles and similar aquatic settings by directing their movements (i.e., swimming) toward the relative safety of the shoreline or emergent objects (DUBOIS & JANDER 1985, YANOVIK & FREDERICK 2014). Here, we explored the role of vision and the visual cues used by workers of *Camponotus pennsylvanicus* to direct their swimming (Video S3).

Ants use a variety of navigational tools when foraging on the ground, including short-term memory, odometry, landmarks, celestial cues, and skyline characteristics (e.g., KLOTZ 1986, GRAHAM & CHENG 2009, BASARI & al. 2014, RODRIGUES & OLIVEIRA 2014). The relevance of these tools for ants landing in an aquatic setting remains largely unexplored, although some swimming ants clearly orient towards dark objects (i.e., skototaxis; DUBOIS & JANDER 1985, YANOVIK & FREDERICK 2014). We similarly observed strong skototaxis in swimming *Camponotus pennsylvanicus* workers in this study.

Although skototaxis was apparent, the ants also consistently swam toward a white target placed before a black background, suggesting strong orientation to contrasting edges. Moreover, the reverse arrangement (a black pole in front of a white background), despite being an obvious target in previous experiments, was essentially ignored when presented across from the white pole in front of a black background. Many ants that reached the white pole or the black / white background interface initially swam towards the black background before re-orienting. This pattern suggests that the large background section is a relatively weak

stimulus that is then superseded by a stronger tendency to orient towards edges. Regardless, the results indicate that edges of contrast are important orientation cues for these ants, and perhaps supersede simple skototaxis in some cases. This interpretation is further complicated by the observation that the ants were more strongly attracted to discrete contrasting targets than to a single vertical line of contrast (i.e., the vertical edge separating the white and black backgrounds), and additional experimentation is necessary to improve our understanding of this decision-making process. Ultimately, these varied outcomes indicate that differences in the directional cues used by swimming *Camponotus pennsylvanicus* are subtle and context-dependent, with primary tendency for skototaxis and secondary orientation towards edges (e.g., when the background is homogenous). This interpretation is similar to the different "visual detector mechanisms" proposed for *Formica* ants by VOSS (1967).

Our experimental results clearly show that directional swimming in *Camponotus pennsylvanicus* is visually-based, as expected from field observations and the results of similar studies (e.g., VOSS 1967, YANOVIK & FREDERICK 2014). The specific anatomical and neurological mechanisms that effect such strong directionality are potentially interesting topics for further study, but were beyond the scope of this project. Likewise, the very artificial setting for our experiments, although necessary to remove potentially confounding variables, ignored the large number of skyline and landmark cues available to ants in nature. Thus, it is possible that ants do not employ dark objects or lines of contrast as primary cues in the field. The simple design of our test arena could be easily modified or moved outdoors to experimentally add such components (e.g., GRAHAM & CHENG 2009). Although our data lacked sufficient power for a definitive test, we did not find clear evidence that non-visual cues unique to three-dimensional objects, such as rebounding surface waves (BENDELE 1986), are important to *C. pennsylvanicus* orientation. Cumulatively, our results suggest that these ants identify two-dimensional profiles that contrast with the background environment as potential escape routes.

Escape tactics are key targets for natural selection (SOUTHWOOD 1988), and visually-based orientation is important for ants to reach the relative safety of the shore or an emergent object following a fall into water. The results of this study suggest at least three topics for future research. First, a similar survey of escape behaviors across the ant phylogeny would potentially reveal patterns in the evolution of orientation behaviors. Second, manipulating anatomical structures used for swimming (e.g., external hairs or individual legs) and their properties (e.g., hydrophobicity or surface area) would provide mechanistic information about adaptations for swimming by terrestrial invertebrates. Finally, quantification of variation in swimming vectors for individual ants during protracted escape efforts would improve our understanding of the temporal dynamics of the behavior.

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References

- ADIS, J. 1982: Eco-entomological observations from the Amazon: III. How do leafcutting ants of inundation-forests survive flooding? – *Acta Amazonica* 12: 839-840.
- BASARI, N., BRUENDL, A.C., HEMINGWAY, C.E., ROBERTS, N.W., SENDOVA-FRANKS, A.B. & FRANKS, N.R. 2014: Landmarks and ant search strategies after interrupted tandem runs. – *Journal of Experimental Biology* 217: 944-954.
- BENDELE, H. 1986: Mechanosensory cues control chasing behaviour of whirligig beetles (Coleoptera, Gyrinidae). – *Journal of Comparative Physiology A* 158: 405-411.
- BLECKMANN, H. & LOTZ, T. 1987: The vertebrate-catching behaviour of the fishing spider *Dolomedes triton* (Araneae, Pisauridae). – *Animal Behaviour* 35: 641-651.
- BOHN, H.F., THORNHAM, D.G. & FEDERLE, W. 2012: Ants swimming in pitcher plants: kinematics of aquatic and terrestrial locomotion in *Camponotus schmitzi*. – *Journal of Comparative Physiology A* 198: 465-476.
- CAMPAN, R. 1997: Tactic components in orientation. In: LEHRER, M. (Ed.): *Orientation and communication in arthropods*. – Birkhäuser, Basel, pp. 1-40.
- CREIGHTON, W.S. 1950: *Ants of North America*. – Museum of Comparative Zoology, Cambridge, MA, 585 pp + 557 plates.
- DUBOIS, M.B. & JANDER, R. 1985: Leg coordination and swimming in an ant, *Camponotus americanus*. – *Physiological Entomology* 10: 267-270.
- DURIER, V., GRAHAM, P. & COLLETT, T.S. 2003: Snapshot memories and landmark guidance in wood ants. – *Current Biology* 13: 1614-1618.
- ELLISON, A.M., GOTELLI, N.J., FARNSWORTH, E.J. & ALPERT, G.D. 2012: *A field guide to the ants of New England*. – Yale University Press, New Haven, CT, 416 pp.
- EVANGELISTA, C., KRAFT, P., DACKE, M., LABHART, T. & SRINIVASAN, M.V. 2014: Honeybee navigation: critically examining the role of the polarization compass. – *Philosophical Transactions of the Royal Society B-Biological Sciences* 369: art. 20130037.
- FISHER, N.I. 1993: *Statistical analysis of circular data*. – Cambridge University Press, Cambridge, UK, 277 pp.
- FRAENKEL, G.S. & GUNN, D.L. 1961: *The orientation of animals: kineses, taxes and compass reactions*. – Dover Publications, New York, NY, 376 pp.
- FRANKLIN, R., JANDER, R. & ELE, K. 1977: The coordination, mechanics and evolution of swimming by a grasshopper, *Melanoplus differentialis* (Orthoptera: Acrididae). – *Journal of the Kansas Entomological Society* 50: 189-199.
- GRAHAM, P. & CHENG, K. 2009: Ants use the panoramic skyline as a visual cue during navigation. – *Current Biology* 19: R935-R937.
- HÖLLDOBLER, B. 1980: Canopy orientation: a new kind of orientation in ants. – *Science* 210: 86-88.
- IRMLER, U. 1973: Population-dynamic and physiological adaptation of *Pentacomia egregia* CHAUD. (Col. Cicindelidae) to the Amazonian inundation forest. – *Amazoniana* 4: 219-227.
- KLOTZ, J.H. 1986: Topographic orientation in two species of ants (Hymenoptera: Formicidae). – *Insectes Sociaux* 34: 236-251.
- MILLER, P.L. 1972: Swimming in mantids. – *Journal of Entomology (A)* 46: 91-97.
- NARENDRA, A. 2013: Homing abilities of the Australian intertidal ant *Polyrhachis sokolova*. – *Journal of Experimental Biology* 216: 3674-3681.

- OLIVEIRA, P.S. & HÖLLDOBLER, B. 1989: Orientation and communication in the Neotropical ant *Odontomachus bauri* EMERY (Hymenoptera: Formicidae, Ponerinae). – *Ethology* 83: 154-166.
- PREISS, R. & KRAMER, E. 1984: The interaction of edge-fixation and negative phototaxis in the orientation of walking gypsy moths, *Lymantria dispar*. – *Journal of Comparative Physiology A* 154: 493-498.
- R DEVELOPMENT CORE TEAM 2014: R: a language and environment for statistical computing. Version. 3.1.1. – R Foundation for Statistical Computing, Vienna, Austria.
- RODRIGUES, P.A.P. & OLIVEIRA, P.S. 2014: Visual navigation in the Neotropical ant *Odontomachus hastatus* (Formicidae, Ponerinae), a predominantly nocturnal, canopy-dwelling predator of the Atlantic rainforest. – *Behavioural Processes* 109: 48-57.
- SOUTHWOOD, T.R.E. 1988: Tactics, strategies and templets. – *Oikos* 52: 3-18.
- SUTER, R.B. 2013: Spider locomotion on the water surface: biomechanics and diversity. – *Journal of Arachnology* 41: 93-101.
- TAYLOR, S.J. 1988: Skototaxis in three species of flat bugs (Heteroptera: Aradidae). – *Annals of the Entomological Society of America* 81: 537-538.
- VOGEL, S. 1994: *Life in moving fluids: the physical biology of flow*. – Princeton University Press, Princeton, NJ, 488 pp.
- VOSS, C. 1967: Über das Formensehen der roten Waldameise (*Formica rufa*-Gruppe). – *Zeitschrift für vergleichende Physiologie* 55: 225-254.
- WEHNER, R. 2003: Desert ant navigation: how miniature brains solve complex tasks. – *Journal of Comparative Physiology A* 189: 579-588.
- YANOVIK, S.P., DUDLEY, R. & KASPARI, M. 2005: Directed aerial descent in canopy ants. – *Nature* 433: 624-626.
- YANOVIK, S.P. & FREDERICK, D.N. 2014: Water surface locomotion in tropical canopy ants. – *Journal of Experimental Biology* 217: 2163-2170.
- YANOVIK, S.P., MUNK, Y. & DUDLEY, R. 2011: Evolution and ecology of directed aerial descent in arboreal ants. – *Integrative and Comparative Biology* 51: 944-956.