



Multisensory homing in the neotropical understory twig-nesting ant *Pseudomyrmex boopis* (Hymenoptera: Formicidae)

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Abstract

Organisms integrate information from a variety of cues to sense their surroundings, but the relative importance of specific sensory modalities is context-dependent. Ants inhabiting the tropical rainforest understory should bias investment in sensory systems that match the selective pressures of a physically complex, low-light habitat. We examined the role of visual and olfactory cues in the homing behavior (returning to a nest site) of *Pseudomyrmex boopis* (ROGER, 1863), a diurnal, understory, twig-nesting ant with large compound eyes. We measured homing success (entering the nest) and efficiency (duration of homing) after displacement in a field experiment with three sensory manipulations: occluded compound eyes (CE), occluded ocelli (O), ablated antennae (deantennated; A), and combinations thereof. Ant workers in all CE treatments could not home successfully, while workers in O and A treatments homed as well as controls. The O treatment reduced homing efficiency (i.e., increased the time lag between discovering and entering a nest). Workers without antennae took longer to get home and were less efficient. Compound eyes are essential for avoiding predation – nearly a quarter of workers in CE treatments were killed by heterospecific ants or spiders. The results of this study show that *P. boopis*, a species occupying a much dimmer environment than its arboreal relatives, has multisensory homing behavior that is primarily driven by input to its large compound eyes. This work contributes to our understanding of the relative importance of sensory cues during multimodal homing in an understudied, natural setting.

Key words: Behavior, leaf litter, multimodal navigation, tropical forest, vision.

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Introduction

Behavior is derived from the integration of information by various sensory modalities. Sensory systems should prioritize the most relevant cues in the environment and reflect a biased investment in the traits that function well against selection pressures within a habitat (ENDLER 1992). The diversity of sensory adaptations across the tree of life demonstrates the many ways in which the challenges an organism faces in its habitat influence the morphology, physiology, and performance of sensory structures. These systems are essential in basic functions, like resource acquisition, interacting with other individuals, and avoiding danger (STEVENS 2013). For many animals, homing (returning to a nest site) is a major component of these activities. Effective homing often requires the integration of sensory input to multiple modalities in complex environments (HEINZE & al. 2018, BUEHLMANN & al. 2020).

We have a limited understanding of how these processes play out in a natural setting.

The sensory ecology of animal navigation and homing is well-studied across a variety of animal taxa (NEVITT 2008, WIEGMANN & al. 2016, HEINZE 2017). Many senses can be involved in the navigational capacity of an animal, including olfaction, vision, magnetoreception, and idiothetic cues (STEVENS 2013). However, energetic investment in different sensory tissues often is constrained (NIVEN & LAUGHLIN 2008), resulting in trade-offs and the filtering of specific information (ENDLER 1992). The senses used in homing can vary across spatial scales; an individual must continually identify relevant cues to avoid maladaptive orientation decisions after displacement (WEHNER & al. 1996, CANNICCI & al. 1999, BUEHLMANN & al. 2012, WYSTRACH & SCHWARZ 2013, HEBETS & al. 2014, ZEIL & al. 2014a,

KNADEN & GRAHAM 2016, BINGMAN & al. 2017, NARENDRA & RAMIREZ-ESQUIVEL 2017, MIDDLETON & al. 2018).

Homing success is particularly important for social insects like ants (Hymenoptera: Formicidae). Ant workers that become lost during foraging or defense are costly to their colony. Ants commonly use their antennae to gain chemical and tactile information during behaviors like foraging and homing (STECK 2012, DRAFT & al. 2018), but many also use well-developed vision via their compound eyes and ocelli (FENT & WEHNER 1985, HARRISON & al. 1989, SCHWARZ & al. 2011a, b, ZEIL & al. 2014b, GRAHAM & PHILIPPIDES 2017). Ants have diverse ecologies, from a subterranean lifestyle to living in the tops of tree crowns. Additionally, within this range of habitats, ants occupy distinct temporal niches. Thus, responses to selective pressures have caused the gain, alteration, and loss of certain sensory structures over evolutionary time (GREINER & al. 2007, NARENDRA & al. 2011, BULOVA & al. 2016, SCHOFIELD & al. 2016, NARENDRA & al. 2017, PENMETCHA & al. 2021). Structurally complex habitats present unique challenges for insect navigation (ROSENGREN 1977, BEUGNON & al. 2005, CHENG & al. 2009, NARENDRA & al. 2013b), and understanding the sensory modalities involved in successfully homing in the physical complexity of tropical rainforests is relevant to understanding patterns of diversity and coexistence.

Tropical rainforests comprise diverse habitat types along the vertical gradient from the canopy to the ground. In the forest understory, light is diffuse and relatively dim (CHAZDON & al. 1996, RICHARDS & COLEY 2007). Vegetation and debris provide structural complexity. These features influence sensory system evolution and potentially affect the utility of certain sensory modalities. Here, we test the hypothesis that understory ants have sensory structures that are biased toward chemical detection versus visual perception. We explore this possibility in the neotropical twig-nesting ant *Pseudomyrmex boopis* (ROGER, 1863), a species that has undergone a secondary transition from life in the canopy to dwelling in the understory (WARD & DOWNIE 2005). *Pseudomyrmex boopis* are diurnal, solitary foragers that nest on or near the ground in the cavities of dead twigs and branches (WARD 1993). Their large eyes and responsiveness to visual stimuli (D.C. Prince, unpubl.) suggest that they rely primarily on visually-guided behavior. The main goal of this study is to determine the relative importance of olfactory versus visual cues in the homing behavior of *P. boopis*. Secondly, we explore the relevance of different sensory systems to predator avoidance.

Material and methods

Study site

Field work for this study was conducted in seasonally moist lowland tropical forest on Barro Colorado Island (BCI), Panama (9° 8' 59" N, 79° 51' 21" W). Field data were collected during various months of the wet seasons (May - December) of 2017, 2018, and 2019. This site is described in detail by LEIGH & al. (1996).

Focal species

Pseudomyrmex boopis is a neotropical ant found in rainforest and tropical moist forest (WARD 1993), and is common in the understory of BCI (Fig. S1, as digital supplementary material to this article, at the journal's web pages). They are polydomous – colonies typically occupy several cavities in dead twigs on the forest floor or suspended near the forest floor. Workers are active from sunrise to sunset (D.C. Prince, unpubl.). Homing trials were conducted at 27 nest twigs from 23 *P. boopis* colonies, from which 246 workers were collected for sensory manipulations. At least 24 hours after marking a focal nest, up to six uninjured *P. boopis* workers were collected as they exited. Species identity was confirmed using the key in WARD (1993). Voucher specimens were deposited at the University of Louisville and the Fairchild Invertebrate Museum at the University of Panama.

Sensory manipulations







Each collected *Pseudomyrmex boopis* worker was painted with small spots on its gaster and / or pronotum in a unique color combination so that individuals could be tracked (Fig. S2). Marked workers were divided among six groups, and each group was assigned up to three sensory manipulations (Tab. 1). Ants in the control group (C) were marked with paint but otherwise unmanipulated. Treatments included occlusion of all three ocelli (O), both compound eyes (CE), ocelli and compound eyes (O + CE), ablation of both antennae at their base (A), or combined visual occlusion with deantennation (A + O + CE). Workers were anesthetized on ice for a few minutes prior to and during the manipulation. Ocelli and compound eyes were occluded by applying a small amount of white enamel paint. All ants were held at ambient temperature for at least 60 minutes prior to the start of a homing trial. Within a given treatment, no more than nine ants were from a single colony, and the majority of treatments had fewer than five ants from the same colony. Pilot studies were conducted with marked workers to confirm that manipulated individuals will return to their colonies and forage normally for several days, at which point the paint markings were largely gone.

Homing success trials

Trials designed to measure homing success began by returning workers to their focal nest 45 - 90 minutes prior to sunset, when workers consistently cease foraging and enter the nest for the night (D.C. Prince, unpubl.). After being transported from the laboratory area to the nest vicinity, ants were released individually from petri dishes, positioned in an arc approximately 35 centimeters from the base of the focal nest twig (Fig. S3) in a relatively flat area that was not obscured by vegetation and where workers from the same colony had been observed previously. This release location was always closer to the focal nest twig than to other twigs occupied by the same colony.

The timing of each trial began when dishes were uncovered and ants were allowed to roam freely. If an ant did

Tab. 1: Description of sensory manipulation treatment groups and diagrams showing the location of paint on a dorsal head view of *Pseudomyrmex boopis*. Head of specimen CASENT0915326 photographed by Zach Lieberman, from www.antweb.org.

Treatment (sample size)	Abbreviation	Diagram	Manipulated sensory structure		
			Ocelli painted	Compound eyes painted	Antennae ablated
Control (n = 43)	C				
Antennal ablation (n = 40)	A				×
Ocelli occluded (n = 44)	O		×		
Compound eyes occluded (n = 48)	CE			×	
Ocelli and compound eyes occluded (n = 41)	O+CE		×	×	
Ocelli and compound eyes occluded with antennal ablations (n = 30)	A+O+CE		×	×	×

not leave the petri dish within five minutes, the side of the dish was gently tapped to encourage movement out of the dish. Dishes were then removed from the area. Ambient temperature, relative humidity, and cloud cover were recorded during each trial. The focal nest entrance was monitored and the following events were systematically noted: a worker reaching the nest entrance, entering the nest twig, or interacting with another animal. The general path and behavior of each ant was recorded to the best of the observer's ability. A trial ended when the worker entered the nest or was killed by a predator, or at sunset. If a worker was no longer visible, the last known position was recorded, and it was marked as a homing failure. *Pseudomyrmex boopis* workers do not forage during heavy rain and typically do not exit the nest after a storm until leaf surfaces are dry (D.C. Prince, unpubl.), so all homing trials were conducted during dry periods within 30 hours of collection.

Homing success trials after reversal of visual occlusion

A subset (n = 21) of unsuccessful CE or O + CE individuals were collected to test their homing ability the following day with their visual occlusion reversed. These ants were kept at ambient temperature in the lab overnight. The following day, paint was removed from their compound eyes and ocelli with fine forceps. The ants were then returned to their nest twig and observed for 60 minutes.

Statistical analyses

The effect of treatment on the homing success of workers was tested using a generalized linear model (R version 3.5.2; R CORE TEAM 2022). Homing success was a binary response variable, and treatment, number of minutes from release time to sunset, and their interaction, were fixed effects. To account for complete separation in the data (i.e., treatments without variation in response), Firth's bias-reduction method was used to fit a generalized linear model (package *brglm*). Tukey's honestly significant difference (HSD) post hoc tests were used to identify differences between all treatments (package *multcomp*).

To determine the effect of treatments on homing efficiency, a linear mixed-effects model (LMM) was fit with total trial time as the response variable. Three measures of homing efficiency related to trial time were tested separately: number of minutes from release to entering the nest (successful homing trials), number of minutes to discover the nest entrance (if that occurred during a trial), and number of minutes from nest discovery to entering (successes only). All time-based results were log-transformed to fit a normal distribution. Treatment, time to sunset, and their interaction were included as fixed effects; nest was included as a random effect (package *lme4*). The date, environmental variables, and time to sunset did not contribute to any LMM and were dropped using stepwise Akaike information criterion model reduction, leaving a linear model with treatment as the remaining term.

The model with time to discover the nest as the response variable included treatment and a random nest effect. As above, Tukey's HSD test was used to test for differences between treatments.

The proportions of ants in each treatment that were preyed upon during trials were compared using Fisher's Exact Test, with post hoc pairwise comparisons (package rstatix). The average total time taken to reenter the nest among control ants and ants that had visual occlusion treatments reversed was compared using a t-test. Time was log-transformed, and the Bonferroni method was used to correct for multiple comparisons.

Binomial confidence intervals (95%) were calculated for the proportions of homing success and predation using the Clopper-Pearson method for binary data, which uses the binomial distribution to return asymmetrical lower and upper limits that indicate a range of 95% confidence around a proportion. These confidence intervals are reported on figures with proportions, while standard error is reported for all durations (minutes).

Results

Homing success

Ants with occluded compound eyes (CE; $n = 48$) were significantly less successful at homing (locating and entering their nest twigs) than groups with unmanipulated compound eyes ($F_{5,240} = 54.05$, $p < 0.001$; Fig. 1). Six (12.5%) CE ants homed successfully, while O + CE ($n = 41$) and A + O + CE ($n = 30$) ants never located the nest entrance. Workers in the C ($n = 43$), A ($n = 40$), and O ($n = 44$) treatments had the highest homing success rates.

The observed outcomes of the homing trials fell into two categories (Fig. 2). Workers with occluded compound eyes (CE treatments) typically wandered in apparent confusion around the release site. In most cases, they initiated stereotypic hiding behaviors such as climbing vegetation or "entering" holes in leaves. Some ants wandered into leaf litter and were not visible at the end of the trial, while others were visibly killed by predators. A few visually intact workers that did not enter the focal nest entered alternate nest twigs occupied by the same colony. Most were not visible at the end of the trials, but none wandered or hid in the same manner as ants in CE groups at any point.

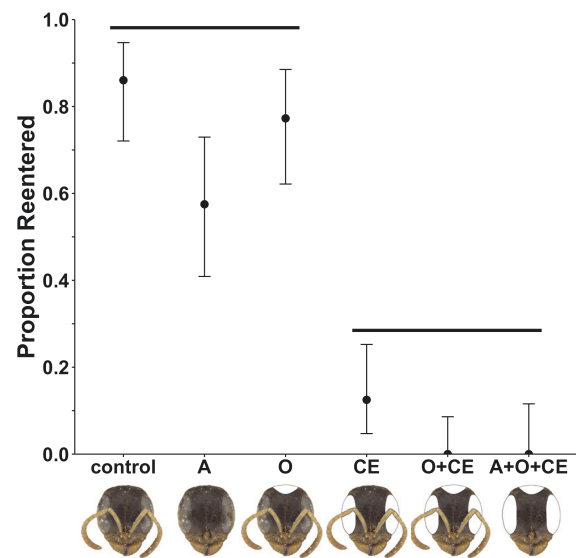


Fig. 1: Proportion of ants that successfully returned to and entered the focal nest entrance. Vertical bars around the proportion indicate 95% confidence intervals based on the binomial distribution (Clopper-Pearson method) for binary data, indicating 95% confidence that the proportion is within that range. Horizontal bars connect means that do not differ. Homing success was tested with 246 ants: control ($n = 43$), A ($n = 40$), O ($n = 44$), CE ($n = 48$), O + CE ($n = 41$), A + O + CE ($n = 30$). Head of specimen CASENT0915326 photographed by Zach Lieberman, from www.antweb.org.

Homing efficiency

Experimental treatment was the best predictor of the total trial time from release to entering the nest twig ($F_{3,96} = 11.03$, $p < 0.001$; Fig. 3). Specifically, deantennated (A) workers had a significantly longer trial time than C and O ants (Fig. 3). The C and O ants entered between 1 - 54 minutes after release. The time taken by CE workers to enter the nest did not differ significantly from other treatments.

The time required to discover the nest twig was longer for A ants than O ants ($F_{4,77} = 3.5$, $p = 0.012$), but ants in both A and O treatments took the same amount of time to enter after arriving ($F_{1,19} = 0.22$, $p = 0.647$). Some A workers ($n = 16$) were delayed after locating the nest twig and took up to 40 minutes to

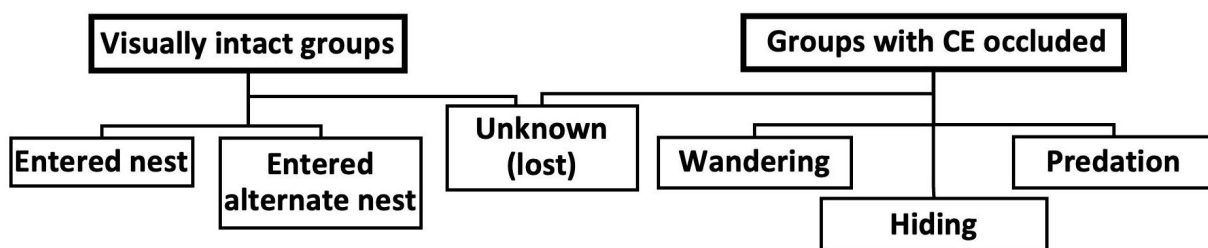


Fig. 2: Observed outcomes of homing trials in visually intact groups and compound eye-occluded groups. Visually intact workers either entered the focal nest or entered another nest twig used by the same colony. Workers with compound eyes occluded either wandered, hid, or were preyed upon. Some in each group had an unknown outcome (considered lost).

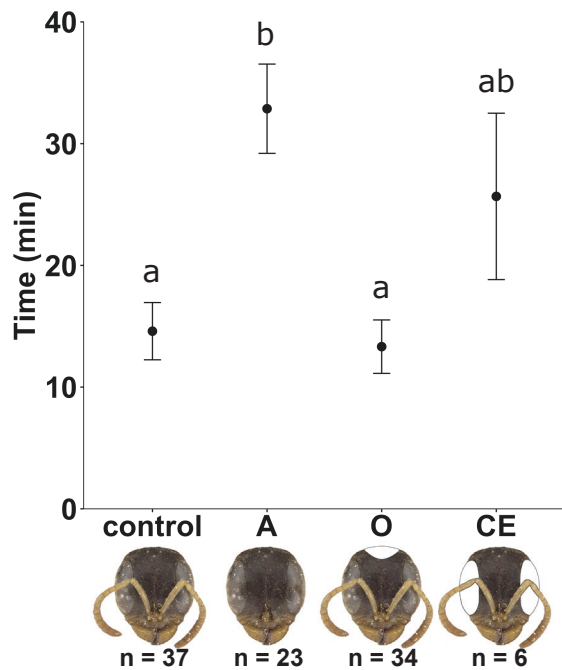


Fig. 3: Average time (minutes) taken to home successfully after release. Bars indicate standard error. Head of specimen CASENT0915326 photographed by Zach Lieberman, from www.antweb.org.

enter the nest (mean \pm SE = 13.3 \pm 3.0 min; n = 17). Ants in the C and O treatments generally entered the nest almost immediately (between 0 - 1 minutes) after locating the twig. Some O workers displayed difficulty in orienting their bodies to enter the nest cavity, although this did not always cause a conspicuous delay (mean \pm SE = 11.8 \pm 8.1 min; n = 4).

Predation

Workers were preyed upon in 28 of the 246 homing trials. Overall, 23% of workers in groups with occluded compound eyes (CE, O + CE, or A + O + CE) were preyed upon during a trial. Workers in these groups were preyed upon significantly more frequently than workers with uncovered compound eyes ($X^2 = 29.38$, df = 1, $p < 0.001$). A larger proportion of O + CE and A + O + CE workers were preyed upon than those in the A group (Fisher's Exact Test $p \leq 0.020$; Fig. 4), whereas CE workers did not differ from the other groups (Fig. 4).

All predation events involved occluded compound eyes, except for one deantennated worker that was attacked during a trial by the trap-jaw ant *Odontomachus bauri* EMERY, 1892. *Odontomachus bauri* was the most frequent predator (n = 16) of *Pseudomyrmex boopis*, followed by *Ectatomma ruidum* (ROGER, 1860) (n = 11), and one encounter with an ant-specialist salticid spider in the genus *Corythalia* (Araneae: Salticidae) (EDWARDS & al. 1974; Fig. S4). There were no significant differences in the amount of time from release to predation events among treatments ($F_{3,24} = 0.94$, $p = 0.435$; Fig. 5).

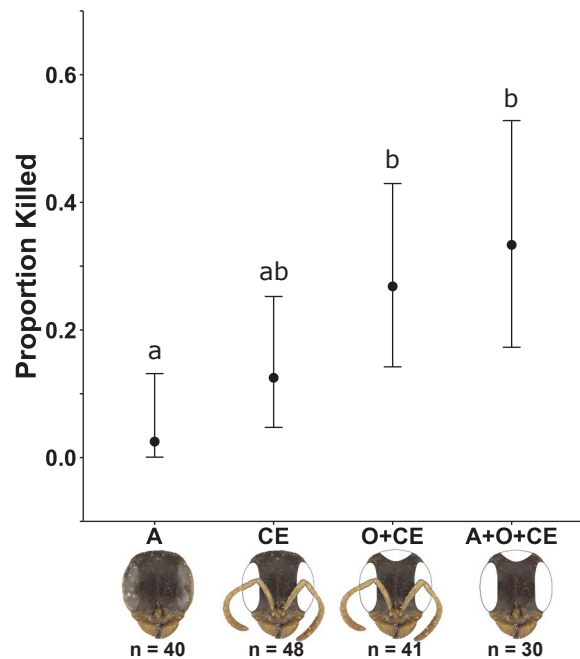


Fig. 4: Proportion of ants that were preyed upon during homing trials. Vertical bars around the proportion are 95% confidence intervals based on the binomial distribution (Clopper-Pearson method) for binary data, indicating 95% confidence that the proportion is within that range. Different letters indicate significant differences among treatments.

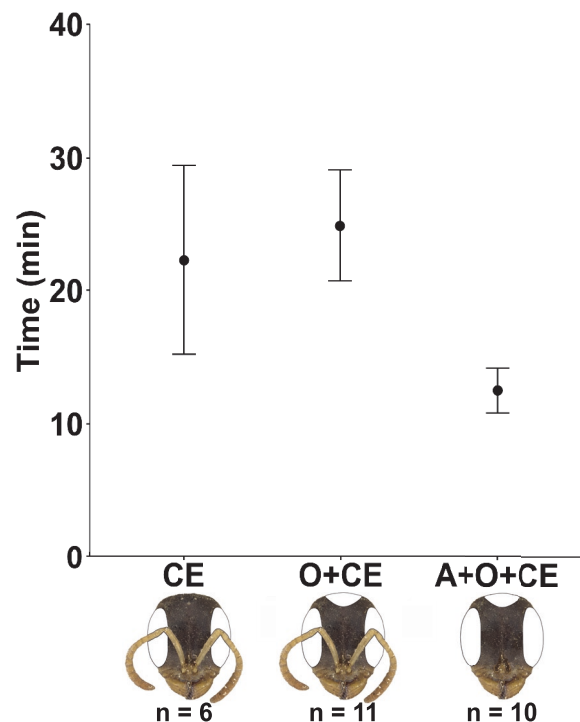


Fig. 5: Average duration (minutes) of trials involving compound eye occluded ants that ended in a predation event. Error bars indicate standard error. Head of specimen CASENT0915326 photographed by Zach Lieberman, from www.antweb.org.

Homings success following reversal of visual occlusion

One day after their homing trials, we released 21 ants (3 O + CE and 18 CE) with visual occlusion treatments reversed and recorded their homing success. These ants were from eight different colonies. During a 60-minute observation period, 15 (71.4%) successfully entered their nest twig. The mean \pm SE time taken to return to the nest was 19.3 ± 3.8 minutes. This duration did not differ significantly from the total trial time of C ants in the initial homing trials ($t = -1.31$, $df = 26.5$, $p = 0.295$). Individuals that did not enter their nest either wandered away from the twig, never initiated homing behavior, or were deterred from approaching the nest area due to the presence of *Odontomachus bauri*.

Discussion

The results of this study support the hypothesis that the homing behavior of *Pseudomyrmex boopis* is primarily visually guided. Their compound eyes, but not the ocelli or antennae, are essential for successful homing. This species has large apposition compound eyes, which function well under abundant light (CRONIN & al. 2014), but have also adapted to dim light conditions (WARRANT & al. 2004, WARRANT 2008, WARRANT & DACKE 2010, NARENDRA & al. 2011, 2013a, WARRANT & DACKE 2016, NARENDRA & al. 2017, O'CARROLL & WARRANT 2017, WARRANT 2017). Workers of *P. boopis* spend much of their time on low vegetation and in the leaf litter (D.C. Prince, unpubl.), but also occur in tree fall gaps (FEENER & SCHUPP 1998) where ambient light is often relatively intense and like the habitats of their more arboreal congeners. A comparison between the eye structures of *P. boopis* and other closely related species may reveal sensory trade-offs associated with life in different forest habitats. Occlusion of the ocelli did not influence the success or efficiency of a *P. boopis* homing trial. YANOVIK & al. (2011) found that occlusion of the ocelli of *Pseudomyrmex gracilis* (FABRICIUS, 1804) similarly did not affect directed aerial descent performance, a behavior that facilitates reorientation towards their starting point after a fall from the canopy. This further suggests that any cues ocelli perceive (e.g., celestial cues) are not involved in orientation or homing near the nest, leaving the function of ocelli in *Pseudomyrmex* workers unknown. Future studies that examine homing at greater distances from the nest, where other visual cues could be influential, may reveal their relevance.

When homing, *Pseudomyrmex boopis* requires the integration of visual and olfactory cues near the nest entrance to maximize success and efficiency. Unmanipulated (C) workers that immediately homed and entered the nest entrance upon release set the standard for efficiency. The lack of difference among treatments in the time taken to find the nest twig was likely due to the tendency of C and O ants to resume normal foraging behavior on nearby vegetation after being released. Similar behavior was observed in *Gigantiops destructor* (FABRICIUS, 1804) (BEUGNON &

al. 2005) and *Cataglyphis fortis* (FOREL, 1902) (WEHNER & al. 1996).

While workers with intact vision likely used visual cues to home successfully, the results of this study indicate that olfactory or tactile cues perceived by the antennae become important close to the nest entrance. The function of ocelli in the workers of this species remains unclear, but our observations suggest that ocelli can be involved in positioning the body when entering the twig cavity entrance hole. Workers with ocelli occluded or antennae ablated had difficulty with this task – the latter were delayed up to 40 minutes. Most *Pseudomyrmex boopis* workers enter the nest head-first unless they are carrying a load, in which case they guide their body into the nest by inserting their gaster after first antennating the nest entrance (D.C. Prince, unpubl.). So, the deantennated workers may lose the benefit of first detecting olfactory cues emanating from within the nest (STECK 2012). Additionally, mechanoreceptors on the sensilla of the antennae could sense tactile cues that aid in maneuverability in tight spaces like nest openings.

The results of this study raise multiple questions about the mechanism of visual homing in *Pseudomyrmex boopis*. Specifically, what local and global visual cues does *P. boopis* use to find their nest, and is there variation at different spatial scales? Do the ocelli contribute to homing at other spatial scales? We did not quantify the paths of the homing ants or manipulate their visual environment, and as such, we are unable to report navigational methods used by this species. Ants in closed canopy forests rely in part on canopy patterns, vertical landmarks, and motor memories for navigation (OLIVEIRA & HÖLLDOBLER 1989, BAADER 1996, EHMER 1999, BEUGNON & al. 2005, MACQUART & al. 2006). *Pseudomyrmex boopis* workers regularly traverse a three-dimensional landscape amongst low vegetation and leaf litter covered with woody debris. They often forage for > 60 min while leaping between leaves or from vegetation to the ground from up to 15 cm, as does their sister species *Pseudomyrmex tenuis* (FABRICIUS, 1804) (DEJEAN & al. 2014). Another big-eyed species in the *tenuis* group of *Pseudomyrmex*, the ground-nesting *P. termitarius* (SMITH, 1855) orients with a “kinesthetic sense” and did not rely on visual or chemical cues when homing through a maze (JAFFE & al. 1990). Workers that had visual occlusion reversed homed normally and retained memory of visual cues near the nest 24 hours after anesthesia and displacement. Similar memory retention occurs in other ants, including *Myrmecia croslandi* TAYLOR, 1991 and *Cataglyphis fortis* (see ZIEGLER & WEHNER 1997, COLLETT & al. 2013, NARENDRA & al. 2013b, PISOKAS & al. 2022).

Predation is a strong selective pressure that shapes the sensory biases of organisms. Workers of *Pseudomyrmex boopis* with occluded compound eyes are at greater risk of predation, do not forage, and often engage in stereotypic hiding behavior. Losing workers to predation is particularly detrimental to polydomous species, like *P. boopis*, that support relatively few workers in a nest twig at any

given time (D.C. Prince, unpubl.). After release, workers with occluded vision would walk until they encountered a vertical structure, climb it, and ultimately stay hidden above the leaf litter. The compound eyes of *P. boopis* otherwise readily detect movement, allowing workers to escape into the leaf litter or onto nearby vegetation when predators approach.

In summary, the results of this study contribute to our understanding of the sensory cues involved at different stages of homing in ants. Here, we show that an understorey-dwelling ant that is active until sunset relies on its compound eyes to home effectively in the dark understorey. Furthermore, the homing behavior of *Pseudomyrmex boopis* is multisensory, with use of the antennae increasingly important with increasing proximity to the nest entrance. *Pseudomyrmex* would be a good subject for future studies investigating evolutionary transitions, energetic trade-offs, and how photic conditions are related to morphology and physiology (TIERNEY & al. 2017). A better understanding of how sensory systems vary between closely related species occupying contrasting habitats can ultimately help to address major questions in biology about the relationship between habitat, behavior, and brain evolution.

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Contributions of authors

DCP designed and conducted the research, and wrote the manuscript; SPY assisted with experimental design and logistics, edited the manuscript, and funded the research.

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