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Moving in Dim Light: Behavioral and Visual Adaptations in Nocturnal Ants

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Synopsis Visual navigation is a benchmark information processing task that can be used to identify the consequence of being active in dim-light environments. Visual navigational information that animals use during the day includes celestial cues such as the sun or the pattern of polarized skylight and terrestrial cues such as the entire panorama, canopy pattern, or significant salient features in the landscape. At night, some of these navigational cues are either unavailable or are significantly dimmer or less conspicuous than during the day. Even under these circumstances, animals navigate between locations of importance. Ants are a tractable system for studying navigation during day and night because the fine scale movement of individual animals can be recorded in high spatial and temporal detail. Ant species range from being strictly diurnal, crepuscular, and nocturnal. In addition, a number of species have the ability to change from a day- to a night-active lifestyle owing to environmental demands. Ants also offer an opportunity to identify the evolution of sensory structures for discrete temporal niches not only between species but also within a single species. Their unique caste system with an exclusive pedestrian mode of locomotion in workers and an exclusive life on the wing in males allows us to disentangle sensory adaptations that cater for different lifestyles. In this article, we review the visual navigational abilities of nocturnal ants and identify the optical and physiological adaptations they have evolved for being efficient visual navigators in dim-light.

Introduction

Efficient navigation is crucial for most daily tasks including foraging, finding mates, establishing territories, and parental care. While the scale of navigation varies between animals (from a few centimeters to several kilometers), the principles of navigation are surprisingly similar (Biro et al. 2007; Wehner 2009). Even what appears to be a relatively simple task of walking in a straight line cannot be achieved without an external visual compass (Cheung et al. 2007). Ants, despite their tiny size, relatively small brains and few neurons, are highly competent visual navigators. Several ant species restrict their activity to brightly lit periods during the day where visual information is reliable. A significant number of ants, however, are active in dimly lit environments that include animals that forage in the dark confines of the leaf-litter, in closed canopy rain forests, or at night. In dim-light habitats, the visual signal-to-noise ratio is

typically low, which makes detecting reliable visual navigational information a challenge (Warrant et al. 2004; Warrant 2017). This is especially true at night, where light intensities can be 11 orders of magnitude lower than during the day (O’Carroll and Warrant 2017). We will here review the behavioral, optical, and physiological adaptations that ants have evolved for being efficient visual navigators in dim-light.

Visually guided behavior in nocturnal ants

A time to forage and a time to fly

An unusual aspect of ant sensory ecology is that each caste in an ant society performs a unique set of visual tasks despite their similar genotypes. Workers are typically sterile females and exclusively pedestrian and carry out all the day-to-day foraging and above-ground nest maintenance activities that

require vision. Alates are the reproductive winged castes of females and males. During the first stage of their life, winged females require vision: they fly out of the nest for mating, following which they shed their wings, and become pedestrian. They then start a new nest and remain in it for the rest of their lives within the dark confines of the nest chambers where vision plays no role. Males exclusively engage in mating, which involves flying out of the nest to mate, visually tracking flying females and competitors and carrying out aerial pursuits.

The earliest evidence that ants react to light came from John Lubbock who exposed the brood of *Lasius flavus* and *Formica fusca* to ultraviolet light (Lubbock 1882). Ants responded by moving their brood to regions beyond the red wavelength. Following this, the effect of light intensity on ants remained less explored, perhaps because surface temperature and humidity were considered the main abiotic factors to regulate ant activity (Eidmann 1935). The focus shifted back to the importance of light cues when it was first demonstrated that ambient light intensity could trigger foraging activity in the day-active leaf-cutter ants *Atta colombica* (Hodgson 1955). Edward Hodgson observed that foraging began earlier on trails that received light first and later on trails that were in the shade. Increasing the light intensity around sunrise caused the animals to become active earlier than under natural conditions and decreasing the light intensity caused a delay in the foraging onset. But increasing the light intensity after the last forager had returned did not trigger activity, indicating that diurnal ants responded to early availability of light only when it occurred close to their natural foraging time. Ambient light intensity also dictates the time at which nocturnal ants depart from the nest. In the nocturnal bull ant *Myrmecia pyriformis*, workers typically begin foraging just after sunset and restrict their nest departures to the evening twilight (Fig. 1A, B) (Narendra et al. 2010). When light intensity around sunset was artificially increased, ants delayed their exit and began foraging only when light intensity was decreased to correspond to the typical ambient evening twilight condition (Fig. 1C). The endogenous rhythm likely brings animals close to the nest entrance, but exiting the nest appears to be controlled by ambient light intensity. Further evidence that light influences ant activity comes from investigation into circadian rhythms. For instance, diurnal workers of *Formica polyctena* that were entrained to alternating light and dark cycles increased their activity toward the end of the dark period as if anticipating dawn and the onset of foraging (Rosengren 1977, 1986). Monitoring

ambient light to trigger activity is crucial for alates since they must synchronize the timing of mating flights between nests to mate at species-specific times (McCluskey 1965, 1992).

Knowing where to go

Ants are traditionally thought to navigate primarily using pheromone trails. Trail pheromones are indeed utilized by several species but typically for recruitment. Even among trail-following species visual information is used by scouts to locate a food source and by experienced individuals that ignore pheromone trails to reach their goal faster (e.g., Hölldobler 1974; Card et al. 2016). To reach a goal of interest, ants require a compass to maintain a heading direction, a strategy to pinpoint a goal once they are close to it, an estimate of distance traveled and a knowledge of where they are. Day-active ants are known to use both celestial and terrestrial cues to accomplish these tasks (e.g., Wehner 2009). Here we will discuss the visual navigational strategies used by nocturnal ants.

Celestial cues

The earliest record of the use of visual information for nocturnal navigation in ants comes from Santschi's observation that *Monomorium salomonis* ants walking in a straight line at night get disoriented when the clouds cover the moon (Santschi 1911; Papi 1960). The role of the moon in providing compass information has been investigated in *F. polyctena* (Jander 1957), *Formica rufa* (Kaul and Kopteva 1982), and *Camponotus pennsylvanicus* (Klotz and Reid 1993). Ants reversed their foraging direction when the position of the moon was mirrored, demonstrating that they can derive compass information from the moon. On nights with bright moonlight (350–5000 lux), even the strictly day-active desert ant, *Cataglyphis bicolor*, relied on the moon to obtain compass information (Wehner and Duelli 1971; Duelli 1972). In the strictly nocturnal *M. pyriformis*, a greater proportion of outbound and inbound activity occurred on full-moon nights when the lunar illumination was 95% compared with that on moonless nights when the lunar illumination was 0% (Reid et al. 2013). Thus, lunar illumination can enhance the salience of navigational cues in dim-light, leading to increased activity.

Similar to day-active ants (Wehner and Wehner 2001), the nocturnal ant *M. pyriformis* derives compass information from the pattern of polarized skylight (Reid et al. 2011). This has been demonstrated by rotating a polarized filter by +45° or –45° relative to the ambient orientation above the ant that is heading toward a particular goal (Fig. 2A). Ants

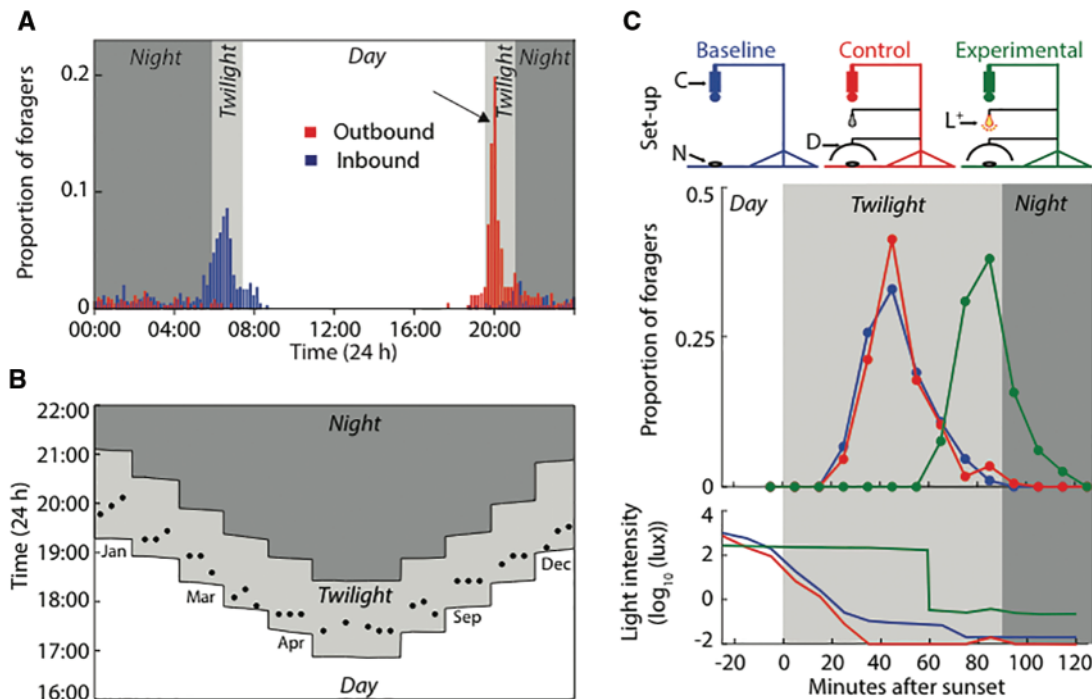


Fig. 1 Ambient light intensity triggers foraging in a nocturnal ant, *Myrmecia pyriformis*. **(A)** Daily activity schedule on a single summer day shows that a majority of the individuals leave the nest in the evening twilight and return in the morning twilight. Arrow indicates the peak foraging in the evening twilight. **(B)** Peak foraging activity occurs strictly during the evening twilight over the entire year. The time of peak outbound activity (indicated by an arrow in **1A**) was determined by monitoring activity pattern at a single nest throughout the year. Observations were done in blocks of three consecutive days and repeated at every 30-min change in sunset time throughout the year. Each filled circle refers to the peak-activity time on a single day. There was no activity on one day in May when surface temperatures at sunset was $<7^{\circ}\text{C}$. **(C)** Ambient light intensity triggers the foraging onset. Foraging activity above the nest and ambient light intensity was filmed on three different days. Baseline: activity was filmed with a camera (C) from above the nest (N); Control: activity was filmed with a diffuser (D) placed above the nest; Experimental: activity was filmed with a light source (L) ON for 60 min after sunset and then switched OFF. Activity and light intensity in the three conditions are shown. Figures modified from Narendra et al. (2010).

that encountered such a change in the polarization pattern modified their orientation according to the rotation of the polarized filter. Upon exiting, they encountered the ambient polarized skylight and reoriented appropriately. Although the exit-orientation of ants was in the expected direction, the extent to which they changed their orientation was weak. The reason for this has become clear from another nocturnal species, *Myrmecia midas* (Freas et al. 2017b). The extent to which individual ants rely on the pattern of polarized skylight is dependent on the distance traveled and on their foraging state (i.e., outbound: to find food; inbound: returning to the nest). Inbound ants responded more to the change in the orientation of the polarization pattern compared with the outbound ants (Freas et al. 2017b). In addition, the greater the distance the animals traveled, the stronger their response to a change in the pattern of the polarized skylight (Freas et al. 2017b). This variation in the magnitude of response is most likely because *Myrmecia* ants rely predominantly on terrestrial

visual cues for navigation (Narendra and Ramirez-Esquivel 2017).

Terrestrial cues

Similar to their day-active relatives, nocturnal ants rely on terrestrial landmarks in their dim-light environment to obtain compass information, to establish routes, and to pinpoint goals. The first evidence that ants orient using visual landmark information came from the trail-following ant *L. flavus* (Lubbock 1882). Ants trained to travel toward a distant candle changed their heading direction by 180° when rotated on a turntable by the same degree. One of the landmark features that ants use to obtain compass information is the overhead canopy pattern. For the short excursions that ants carry out, canopy patterns detected through the UV–green gradient can generate sufficient contrast in dim-light to provide directional information (Warrant and Dacke 2010). Canopy orientation in ants was first demonstrated in a day-active ant *Paltothyreus tarsatus* that operates in forested habitats where it has little access to direct

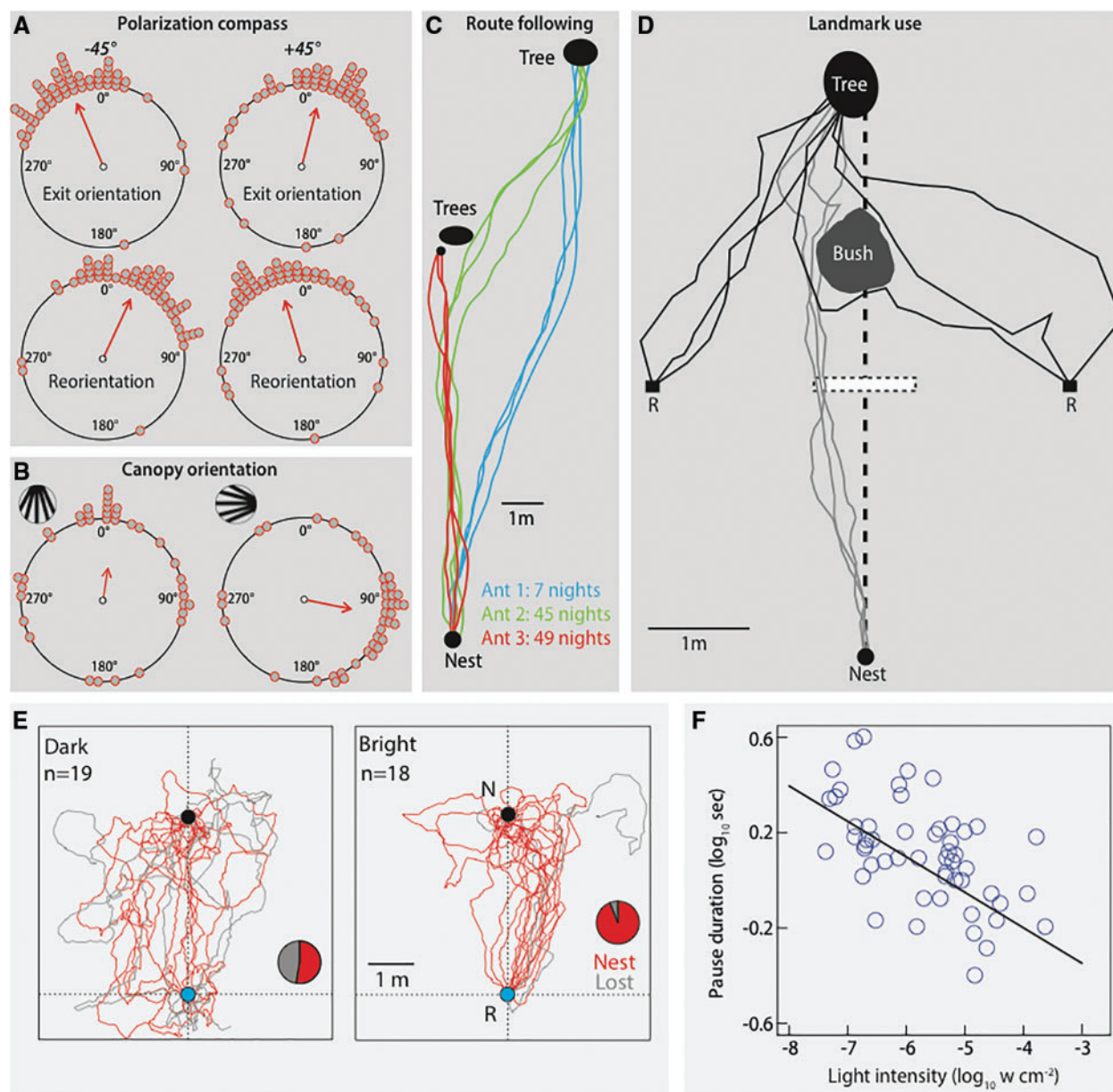


Fig. 2 Navigational strategies used by nocturnal ants. **(A)** Nocturnal *M. pyrifomis* foragers derive compass information from the pattern of polarized skylight. A polarization filter placed above a foraging ant was rotated either -45° (left column) or $+45^\circ$ (right column) relative to the ambient pattern of polarized skylight. Ants respond predictably by exiting the polarization filter in the appropriate direction (Exit orientations) and reorienting when they experienced the ambient skylight polarization pattern (Reorientation). Data for each circular plot are pooled from two nests and modified from Reid et al. (2011). **(B)** The trap jaw ant *Odontomachus hastatus* obtains compass information from the canopy pattern. Ants trained to a striped canopy pattern (left inset) were well oriented in the control condition (left). When the striped pattern was rotated by 90° (right), ants also modified their heading direction accordingly. Mean direction and length of the mean vector are indicated by an arrow in each circular plot. Figure modified with permission from Rodrigues and Oliveira (2014). **(C)** Idiosyncratic routes of three nocturnal ants, *M. pyrifomis* over 7 nights, 45 nights, and 49 nights showing fidelity toward route and foraging trees (Reid 2010). **(D)** Use of landmarks by a nocturnal ant, *M. pyrifomis*. Typical foraging paths from nest to the tree are shown. Six ants were captured at the halfway mark (white rectangular box) and displaced by 2m either toward the left or right of the nest-tree line. Displaced ants either orient immediately toward the tree or head toward a conspicuous bush and detour around it to reach the tree. Adapted from Reid et al. (2011). **(E)** Homing efficiency of nocturnal *M. pyrifomis* decreases at low light levels. Homing paths of ants released at the base of the foraging tree (R, blue circle) as they head toward the nest (N, black circle) in dark (60–120 min before sunrise) and bright (60–120 min after sunrise) light conditions. Pie graphs show the proportion of ants that reached the nest within the recording duration of 50 min. Nest: ants that successfully returned to the nest; Lost: ants that did not return to the nest. **(F)** The nocturnal worker ant *M. pyrifomis* pause for longer durations as light level drops, a behavioral strategy to improve photon capture in low light. Modified from Narendra et al. (2013d).

sun or polarized skylight (Hölldobler 1980). It is only recently that canopy orientation has been demonstrated in a crepuscular–nocturnal ant, *Odontomachus hastatus* (Rodrigues and Oliveira 2014). Ants were trained to find food in an arena with a striped pattern as the roof. Ants tested with the canopy pattern rotated by 90° changed their orientation accordingly, demonstrating that ants derive compass information from the canopy pattern (Fig. 2B). Even trail-following ants such as the nocturnal *C. pennsylvanicus* orient using the canopy pattern (Klotz and Reid 1993). At present, it is unknown how and when ants learn the canopy pattern and whether different moonlight intensities affect the use of this information.

Nocturnal *M. pyriformis* ants use terrestrial landmarks to establish individualistic routes to specific *Eucalyptus* trees in their dimly lit habitats (Fig. 2C). They adhere to these routes for several weeks (Reid 2010). Slight modifications to the landmark panorama (removal of three dead trees) appear to create a significant mismatch to the ants between their previously learnt views and their current retinotopic view, disrupting their typical navigational behavior (Narendra and Ramirez-Esquivel 2017). Image difference analysis revealed very little difference between the before and after tree removal scenes. However, on the first encounter of the modified scene, the proportion of ants foraging reduced dramatically, and most individuals stayed close to the nest carrying out re-learning walks before heading out to forage on subsequent nights. It remains to be determined whether ants extract specific features from the landmark panorama or use the information from the entire panorama.

Path integration

Path integration is the ability to integrate distances traveled and angles steered on the outbound journey to compute the shortest vector home, a strategy that is well known in several day-active ant species (Müller and Wehner 1988; Beugnon et al. 2005; Narendra 2007; Narendra et al. 2013b, 2013c). Among nocturnal ants the ability to path integrate is known only in the genus *Myrmecia*. Foragers of both *M. midas* and *M. pyriformis* that had a home vector >10 m when displaced to unfamiliar locations relied on their path integrator. These ants typically traveled for a short distance before beginning a search (Narendra et al. 2013d; Freas et al. 2017a). Perhaps, ants travel for a short distance relying on the path integrator because they detect sufficient mismatch in the visual scene between the familiar and the displacement site, a

behavior often seen in ants that occupy landmark rich habitats (e.g., Cheung et al. 2012).

Navigational knowledge

Very few studies have attempted to map the navigational knowledge of night-active ants. Such a demonstration has been done in the day-active ants by capturing animals returning home close to their nest and displacing them to locations where they have never been. In such experiments, the diurnal desert ant *Cataglyphis fortis* searches extensively around the release location and then heads directly home (Wehner et al. 1996). After being released in an unfamiliar location, another diurnal ant *Myrmecia croslandi* briefly scans the world and heads directly home without engaging in a search (Narendra et al. 2013b). In the nocturnal *M. pyriformis*, ants leaving the nest were captured about half-way from their food source and displaced by 2m toward the left or the right of the nest-tree line (Fig. 2D) (Reid et al. 2011). A majority of the displaced ants headed directly to the tree, while some detoured around a familiar bush and then headed to the tree. Even during homing, *M. pyriformis* ants captured at a food source and displaced to a location 12m lateral to their foraging corridor were able to return home (Narendra et al. 2013d). Thus, nocturnal ants also can reach a goal from locations they have not previously visited. It is unlikely that ants use a map (Cruse and Wehner 2011; Cheung et al. 2014), but they must have a familiar catchment zone within which they can find a goal through well-directed paths from novel locations. The extent of this catchment zone is likely to be dictated by the area covered during the learning walks and the landmark density in the habitat (Narendra et al. 2013b).

Navigational competence in dim-light

It is clear that night-active species rely on navigational strategies similar to their diurnal counterparts. However, are nocturnal navigators as efficient as their diurnal relatives? There is growing evidence to suggest that navigating at night is less efficient than during the day. The best evidence for this comes from comparing the navigational competence of a nocturnal ant species at different light intensities (Narendra et al. 2013d). Ants heading home in the dark at least an hour before sunrise had the least straight paths, the lowest success rate in finding home and the longest homing duration compared to ants returning home in bright conditions an hour after sunrise (Fig. 2E). Further, in the dark condition, homing ants that reached the nest vicinity

searched longer for the nest entrance, indicating that pinpointing goals in dim-light may be difficult for ants. These differences in navigational efficiency between the bright and dark conditions suggest that pheromones may not aide in either route navigation or in pinpointing the nest.

Behavioral evidence suggests that accessing visual navigational information in the dark is also difficult. This is evident from experiments carried out on nocturnal *M. pyriformis*, where ants were captured at a food source and displaced to locations near the nest (~12m). Ants displaced in bright conditions just before sunset were able to find home by well-directed paths, however, a majority of the ants displaced after sunset in the dark searched close to the release location. Accessing terrestrial visual information is also difficult when ants cannot maintain a stable head position. To match their current views to previously memorized views, maintaining a stable head position is critical. Head movements in ants around both the roll (Raderschall et al. 2016) and pitch axes (Ardin et al. 2015) can adversely affect visual navigation. Substantial changes in the head pitch or head roll occur when individual ants carry large pieces of food items or when they walk on uneven surfaces. Nocturnal ants compensated for 30–100% of their body roll when forced to walk on a twisted band (Raderschall et al. 2016). However, their ability to compensate for body roll deteriorated as light levels dropped, demonstrating that ants use visual information to stabilize head roll. It appears that the inefficiency of navigating at night and the difficulty of accessing reliable visual information has led to the nocturnal *Myrmecia* restricting their navigational tasks to the twilight period. To navigate efficiently in the dimly lit twilight periods, nocturnal ants have evolved a behavioral strategy to improve photon capture: they pause frequently and for longer durations as light levels drop (Fig. 2F) (Narendra et al. 2013d). This adaptation allows the eye to capture a brighter view of the world by increasing integration periods. Such behavioral adaptations are seen not only in nocturnal ants (Fourcassié et al. 1999; Narendra et al. 2013d), but also in bumblebees (Reber et al. 2015) and spiders (Nørgaard et al. 2008).

Optical adaptations for dim-light conditions

With few exceptions, ants have a pair of apposition compound eyes (Fig. 3), which is an eye design typical for insects active in bright light conditions. In an apposition eye, each eye contains several ommatidial units, and each ommatidium has its own lens, which

captures light, and a crystalline cone that funnels light onto a photosensitive structure called a rhabdom (Fig. 3A). Each rhabdom is made up of microvilli from 8 to 9 retinula cells and contains the pigment rhodopsin that absorbs light and converts it into electrical neural signal (Warrant and Dacke, 2010; Tierney et al. 2017; Warrant 2017). Screening pigments ensheath each ommatidium, which ensures light travels within each ommatidium and is not shared between neighboring ommatidia (e.g., Narendra et al. 2016a). This organization limits the optical sensitivity of the eye. The “truly” nocturnal insects such as moths have superposition eyes where each rhabdom captures light from multiple facets, increasing their optical sensitivity (Land 1981). Nevertheless, ants active in dim-light conditions are competent visual navigators and it is hence essential to identify the optical and physiological adaptations they have evolved, which we discuss below.

Eye design of a nocturnal ant

The most significant limitation for nocturnal visual navigators is the number of available photons. Some elements of the compound eye can be modified to increase light capture. What elements of the compound eye predict a nocturnal lifestyle? We compiled existing data to analyze the relationship of eye morphology (facet numbers, largest facet diameter, and rhabdom width) with activity time in ants (Fig. 3D), using a standardized major axis regression with the program (S)MATR (Warton et al. 2006). We used head width as a measure of body size, which has been used widely in ant literature (e.g., Kaspari and Weiser 1999; Ramirez-Esquivel et al. 2017). Our current knowledge of ant activity time is inadequate (Table 1). Hence, for this analysis we have classified diurnal animals as those that are exclusively active during the day and nocturnal animals as those that exhibit activity after sunset anytime in the year. Our classification of nocturnal animals thus includes crepuscular and nocturnal species and also those that switch from a diurnal to a nocturnal lifestyle. Studies on optical parameters of ants are also limited, which makes it difficult to trace eye traits across the ant phylogeny. But even in the limited dataset there are clear trends: both nocturnal and diurnal species had similar scaling slopes for facet numbers, facet diameters, and rhabdom widths ($P_s > 0.1$; Fig. 3D). While more facets were found in visual hunters (e.g., *Gigantiops*, *Harpegnathos*, *Myrmecia*) that benefit from improved spatial resolution, facet number did not show a significant relationship with temporal niche ($W^2 = 2.21$, $P = 0.14$,

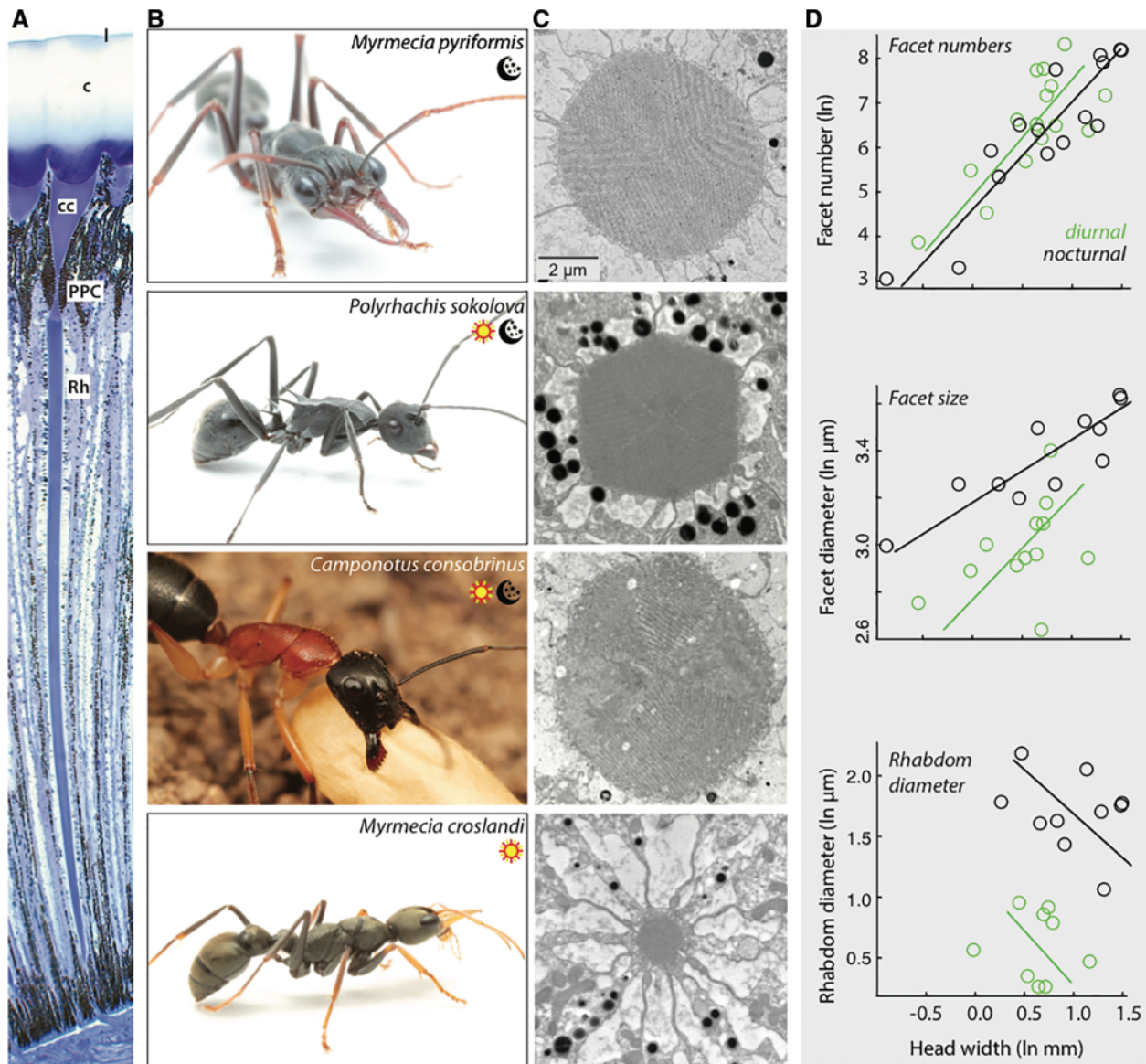


Fig. 3 The eyes of nocturnal ants. (A) Longitudinal section of the ommatidium of *M. pyriformis* showing lens (l), cornea (c), crystalline cone (cc), primary pigment cell (ppc), and rhabdom (rh). (B) Illustration of an exclusively nocturnal ant (top row), ants active during both day and night (second and third row) and an exclusively diurnal ant (bottom row). (C) Cross-section of rhabdoms as a transmission electron micrograph of species in (B). Scale bar for all cross-sections is shown in top panel. (D) Scatter plots of the best-fit standardized major axis regression lines of the relationship between head width and facet number (top), facet diameter (middle), and rhabdom diameter (bottom) in diurnal and nocturnal ants. Data compiled from Bernstein and Finn (1971); Menzel and Blakers (1975); Menzi (1987); Klotz et al. (1992); Baker and Ma (2006); Greiner et al. (2007); Gronenberg (2008); Narendra et al. (2011); Schwarz et al. (2011); Ramirez-Esquivel (2012); Narendra et al. (2013a); A. Narendra, unpublished data, and R. Nettimi, unpublished data). See also Table 1.

Fig. 3D). Both, facet size and rhabdom diameter were significantly larger in the nocturnal species (facet size: $W^2 = 22.46$, $P < 0.001$; rhabdom diameter: $W^2 = 48.15$, $P < 0.001$; Fig. 3D). Thus, the facet size and rhabdom diameter, both of which modulate light capture, are good predictors of the temporal niche that an ant species occupies. Such visual adaptations are found even in congeneric species

(*Myrmecia* species in Fig. 3B, C). For instance, the nocturnal *M. pyriformis* has large facets (37.5 μm) and wide rhabdoms (5.9 μm), compared with their diurnal relative *M. croslandi* (facet size: 22 μm; rhabdom width: 1.3 μm; Greiner et al. 2007; Fig. 3C and Table 1). In addition, the nocturnal ants have longer rhabdoms, which together results in a 27-fold increase in the optical sensitivity, S (μm²sr), compared

Table 1 Summary of known facet numbers, facet diameters, and rhabdom diameters of ant species relative to their head width and activity time

Species	Head width (mm)	Facet number	Facet size (μm)	Rhabdom diameter (μm)	Activity	References
<i>Camponotus consobrinus</i> (major worker)	3.1	798	34	7.8	Nocturnal	Narendra et al. (2016b)
<i>Camponotus detritus</i>	3.79	1300	—	—	Diurnal	Menzi (1987)
<i>Camponotus irritans</i>	2.11	350	—	—	Nocturnal	Menzi (1987)
<i>Camponotus ligniperda</i>	2.48	450	—	—	Nocturnal	Menzi (1987)
<i>Camponotus pennsylvanicus</i> (minor worker)	1.2	375	—	—	Nocturnal	Klotz et al. (1992)
<i>Camponotus pennsylvanicus</i> (major worker)	3.5	658	—	—	Nocturnal	Klotz et al. (1992)
<i>Camponotus sericeiventris</i> (major worker)	2.3	660	—	—	Diurnal	R. Nettimi (2017, personal communication)
<i>Cataglyphis bicolor</i> (major worker)	2.1	1300	24	2.5	Diurnal	Menzi (1987)
<i>Formica integroides</i>	1.9	680	19.3	—	Diurnal	Bernstein and Finn (1971)
<i>Formica polyctena</i>	1.56	750	18.4	2.6	Diurnal	Menzel and Blakers (1975)
<i>Gigantiops destructor</i>	2.52	4100	—	—	Diurnal	Gronenberg (2008)
<i>Harpegnathos saltator</i>	2.2	1600	30	2.2	Diurnal	A. Narendra (2016, personal observation)
<i>Iridomyrmex purpureus</i>	2	496	14	2.3	Diurnal	Ramirez-Esquivel (2012)
<i>Melophorus bagoti</i> (major worker)	3.2	590	19	1.6	Diurnal	Schwarz et al. (2011)
<i>Melophorus hirsutus</i> (major worker)	1.7	296	19	1.4	Diurnal	Ramirez-Esquivel (2012)
<i>Melophorus hirsutus</i> (minor worker)	0.98	241	18	1.7	Diurnal	Ramirez-Esquivel (2012)
<i>Myrmecia croslandi</i>	2.04	2363	22	1.3	Diurnal	Narendra et al. (2011)
<i>Myrmecia desertorum</i> (major worker)	4.4	3625	38	5.8	Nocturnal	A. Narendra (2016, personal observation)
<i>Myrmecia nigriceps</i> (major worker)	3.6	3210	32.9	5.5	Nocturnal	Narendra et al. (2011)
<i>Myrmecia piliventris</i>	1.9	2288	22	1.3	Diurnal	A. Narendra (2016, personal observation)
<i>Myrmecia pyriformis</i> (major worker)	4.45	3593	37.5	5.9	Nocturnal	Narendra et al. (2011)
<i>Myrmecia pyriformis</i> (small worker)	2.3	2320	26	5.1	Nocturnal	Greiner et al. (2007)
<i>Myrmecia tarsata</i> (major worker)	3.7	2724	28.7	2.9	Nocturnal	Narendra et al. (2011)
<i>Nothomyrmecia macrops</i>	1.6	670	24.5	8.9	Nocturnal	A. Narendra (2016, personal observation)
<i>Notoncus ectatommoides</i>	1.3	209	26	5.9	Nocturnal	Ramirez-Esquivel (2012)
<i>Pheidole</i> sp. (major worker)	0.87	27	26	—	Nocturnal	Ramirez-Esquivel (2012)
<i>Pheidole</i> sp. (minor worker)	0.42	21	20	—	Nocturnal	Ramirez-Esquivel (2012)
<i>Polyrhachis sokolova</i>	1.93	596	33	5.0	Nocturnal	Narendra et al. (2013a)
<i>Solenopsis invicta</i> (major worker)	1.15	92.65	20.1	—	Diurnal	Baker and Ma (2006)
<i>Solenopsis invicta</i> (minor worker)	0.58	48	15.7	—	Diurnal	Baker and Ma (2006)

Exclusively day-active animals are classified as diurnal; exclusively nocturnal, crepuscular, and species that are active both during and night are classified as nocturnal.

with their diurnal relatives. Optical sensitivity is calculated as,

$$S = \left(\frac{\pi}{4}\right)^2 A^2 \left(\frac{d}{f}\right)^2 \left(\frac{kl}{2.3 + kl}\right),$$

(Land 1981; Warrant and Nilsson 1998)

where A = largest facet diameter (μm); d = diameter of the rhabdom (μm); f = focal length, determined

by the distance from the center of curvature of the inner corneal lens surface (as an estimate for the position of the nodal point) to the tip of the rhabdom; l = the rhabdom length; k = absorption coefficient assumed to be $0.0067 \mu\text{m}^{-1}$.

Regulating light flux to occupy wider temporal niches

Very few ants are exclusively nocturnal. A majority of them switch activity from day to night based on

their temperature preference (e.g., Duncan and Crewe 1994) or tidal patterns (Narendra et al. 2013a). These ants, similar to the exclusively nocturnal ants, have large facets and wide rhabdoms (Narendra et al. 2013a). How do they cope with changes in light intensity? Even the strictly nocturnal ants have to cope with such changes in light intensity when their nests are disturbed during the day and workers have to rush out to defend their nest. Ants that encounter a wide range of light intensities regulate the amount of light that reaches the rhabdom through a pupillary mechanism (Menzi 1987; Narendra et al. 2013a, 2016a). When exposed to bright light, these ants have a variable primary pigment cell that constricts the crystalline cone to form a narrow cone tract ($<1\ \mu\text{m}$ in diameter) to control light flux (Fig. 4). When the eye is dark-adapted the primary pigment cells move away from the crystalline cone, increasing the diameter of the proximal crystalline cone to $>5\ \mu\text{m}$. While the constriction is light dependent, the opening of the aperture in the dark is controlled by an endogenous rhythm (Narendra et al. 2016a). This primary pigment cell-driven pupillary mechanism is absent in the strictly day-active ants such as *C. bicolor*, *F. polystena*, and *M. croslandi* (Brunnert and Wehner 1973; Menzel and Knaut 1973; Menzi 1987; Narendra et al. 2016a). In these day-active ants, as a response to bright light, only the retinula cell pigment granules migrate radially toward the rhabdom in the light-adapted state and they move away from the rhabdom in the dark-adapted state. Thus, the pupillary mechanisms allow ants to modify their optical sensitivity to be active in a wide range of light intensities.

Investigating the visual system of ants is further rewarding due to differences in locomotion and activity time within a single species. Workers of *M. pyriformis* restrict their activity to the dim-light periods of twilight and night, whereas alates fly out of the nest in the day to mate (Narendra et al. 2011). Following mating, the now inseminated female establishes a nest of her own and forages during the early evening for a brief period of her life. The nocturnal workers have a visual system designed for dim-light, diurnal males have a visual system designed for life on the wing and for diurnal activity, and winged females have an intermediate visual system best suited for diurnal flying and pedestrian foraging in dim-light (Narendra et al. 2011). In leaf cutter ants (*Atta* spp.), the nocturnal alates have significantly larger facets compared with the diurnal alates (Moser et al. 2004). Thus, both between and within species, visual systems have

evolved to suit specific light environments. Such intraspecific visual adaptations are also found in bees and wasps (Greiner 2006; Somanathan et al. 2009). These adaptations alone, however, are not sufficient to explain the visually guided behavior of insects at light intensities that are up to 11 orders of magnitude dimmer than those during the day. To further suppress noise and to improve the visual signal, insects have developed physiological means of improving optical sensitivity by sacrificing spatial and temporal resolution (Warrant et al. 1996; Warrant 1999, 2008, 2017; Warrant and Dacke 2010, 2016; Stöckl et al. 2016a).

How fast are photoreceptors of nocturnal ants?

Temporal resolution is the ability of an eye to detect fast moving objects and is typically identified by the impulse response, the photoreceptor response time to a brief flash of light. In ants, photoreceptor response times have been studied not according to the light levels that animals experience but in the context of walking speeds. The fast moving *Pseudomyrmex phyllophilus* has faster responses (ca. 15 ms) to a 300 ms flash of light compared with the slow-moving *Camponotus rufipes* and *Atta sexdens* (de Souza and Ventura 1989). In bees, the nocturnal *Megalopta genalis* encodes less information at both bright and dim-light levels compared with the diurnal *Lassioglossum leucozonium* (Frederiksen et al. 2008). This difference is because their photoreceptors have a low signal-to-noise ratio and thus a higher optical sensitivity, which is a clear visual adaptation among nocturnal insects. Nocturnal ants, in addition, have slow UV photoreceptors (Ogawa et al. 2015). UV sensitivity (average sensitivity between 350 and 400 nm) dropped by 42.2% when the stimulation frequency increased from 10 to 30 Hz. This reduced sensitivity at short wavelengths in response to higher stimulation frequency was also present in diurnal ants, but the effect was much smaller. UV receptors in nocturnal ants are thus comparatively slow, which might selectively increase sensitivity to short wavelengths. Indeed, the ratio of the spectral sensitivity at short wavelengths to peak sensitivity is relatively high in the nocturnal ants. This might be an adaptation to ensure the UV signal is reliable at low light intensities which is crucial for visual navigation as it increases the contrast between the sky and the ground in the visual panorama (Wilson 1978; Moller 2002; Schultheiss et al. 2016). The UV range is also used to obtain reliable compass information from the pattern of polarized skylight (Zeil et al. 2014).

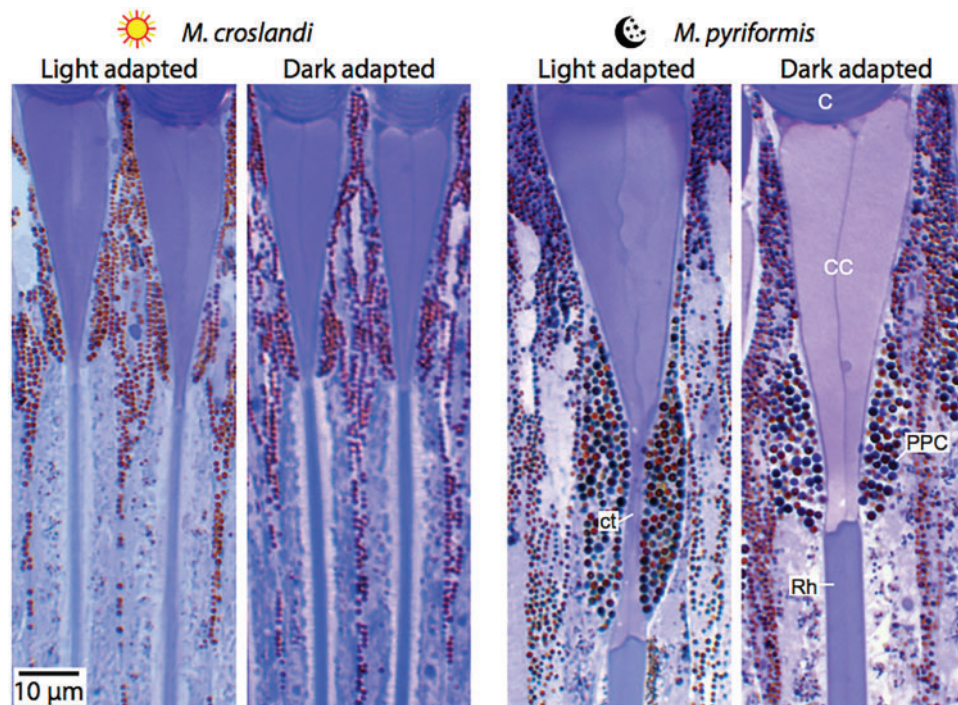


Fig. 4 Longitudinal sections of ommatidia show that a light-dependent pupillary mechanism is present in nocturnal ants. Eyes of the day- (left) and night-active ants (right) were light-adapted (300 lux from 3 h after sunrise for 24 h) or dark-adapted (stored in light-tight container from 3 h after sunset for 24 h). In the night-active species the primary pigment cell pupil constricts the crystalline cone to form a narrow cone tract of 1.6 μm in diameter in the light-adapted state. In the dark-adapted state, the primary pigment cell pupil moves away from the crystalline cone increasing the diameter of the proximal crystalline cone to 5.3 μm . Such migration of the primary pigment cells does not occur in the day-active species. Modified from Narendra et al. (2016a). Cornea (C), crystalline cone (CC), primary pigment cell (PPC), crystalline cone tract (ct), and rhabdom (Rh) are shown.

Ants have long been considered unique among hymenopterans in being dichromats (sensitive to UV and green wavelengths) (Menzel and Knaut 1973; Lieke 1981; Labhart 1986; Cammaerts 2007). Recent evidence suggests that both diurnal and nocturnal ants have the molecular (Yilmaz et al. 2016) and physiological basis (Ogawa et al. 2015) for trichromacy. Intracellular recordings in nocturnal bull ants *Myrmecodia vindex* have shown that their compound eye is sensitive to UV, blue, and green regions of the spectrum. Why do ants need color vision? We know color vision is useful for reliable object discrimination because it is not affected by shifts in intensity or ambient light conditions (Johnsen et al. 2006; Somanathan et al. 2008; Kinoshita and Arikawa 2014). However, at present there is no clear behavioral evidence to demonstrate the function of color vision in ants. Since many hymenopterans rely on pollen and nectar offered by plants, it is tempting to assume that insect visual sensory system is adapted to detect floral patterns. However, trichromacy in arthropods predates the evolution of angiosperms (Chittka 1996), suggesting that color vision may have evolved for object detection, which is an integral part of navigation (Ogawa et al. 2015).

Both behavioral and physiological investigation are needed to elucidate the function of color vision in ants.

Spatial summation

There is growing evidence in several insects that spatial summation occurs in the lamina, the first visual processing neuropil (e.g., Greiner et al. 2004; Stöckl et al. 2016a, 2016b). The retinal axons of a single ommatidium project to one cartridge in the lamina where the cartridges are retinotopically organized. In addition to the short and long visual fibers, the lamina contains relay neurons, the laminar monopolar cells (LMCs), that receive input from photoreceptor axons. In nocturnal insects, the dendrites of the LMCs extend into neighboring cartridges whereas in the diurnal insects they are confined to their own cartridge. Such dendritic branching is thought to improve spatial summation in insects active in dimly lit habitats. Differences in dendritic branching have been documented in nocturnal and diurnal bees (Greiner et al. 2005) and hawkmoths (Stöckl et al. 2016b). In ants, the extent of branching has been documented only in a day-active ant *C. bicolor*

(Ribi 1975), in which LMCs are confined to their own cartridge. To the best of our knowledge, this has not been investigated or characterized in nocturnal ants.

Conclusion

Ants occupy a wide range of niches, from the dimmest to the brightest terrestrial habitats. Ants active in dimly lit habitats use navigational strategies similar to diurnal ants such as deriving visual compass information from both celestial and terrestrial cues. Nocturnal ants use both local and distant terrestrial landmark information to navigate through their cluttered world. Even in low light conditions, their visual system is sensitive enough to detect subtle changes in their familiar landmark panorama. However, as light intensity decreases during the night accessing visual navigational information becomes difficult and the navigational competence of ants also decreases. Hence, visually guided nocturnal ants carry out a majority of their navigational tasks during the twilight period. To improve the visual reliability in low light conditions they have evolved distinct optical adaptations that include large facets and wide rhabdoms together with slow photoreceptor response time. Studies of the investment patterns in brain regions involved in visual processing would further elucidate adaptations for dim-light activity.

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References

- Ardin P, Mangan M, Wystrach A, Webb B. 2015. How variation in head pitch could affect image matching algorithms for ant navigation. *J Comp Physiol A* 201:585–97.
- Baker G, Ma P. 2006. Morphology and number of ommatidia in the compound eyes of *Solenopsis invicta*, *Solenopsis richteri*, and their hybrid (Hymenoptera: Formicidae). *Zool Anz* 245:121–5.
- Bernstein S, Finn C. 1971. Ant compound eye: size-related ommatidium differences within a single wood ant nest. *Cell Mol Life Sci* 27:708–10.
- Beugnon G, Lachaud J-P, Chagné P. 2005. Use of long-term stored vector information in the neotropical ant *Gigantiops destructor*. *J Insect Behav* 18:415–32.
- Biro D, Freeman R, Meade J, Roberts S, Guilford T. 2007. Pigeons combine compass and landmark guidance in familiar route navigation. *Proc Natl Acad Sci U S A* 104:7471–6.
- Brunnert A, Wehner R. 1973. Fine structure of light- and dark-adapted eyes of desert ants, *Cataglyphis bicolor* (Formicidae, Hymenoptera). *J Morphol* 140:15–29.
- Cammaerts M. 2007. Colour vision in the ant *Myrmica sabuleti* Meinert, 1861 (Hymenoptera: Formicidae). *Myrmecol News* 10:41–50.
- Card A, McDermott C, Narendra A. 2016. Multiple orientation cues in the trunk trail forming ant, *Iridomyrmex purpureus*. *Aust J Zool* 64:227–32.
- Cheung A, Collett M, Collett TS, Dewar A, Dyer F, Graham P, Mangan M, Narendra A, Philippides A, Stürzl W, et al. 2014. Still no convincing evidence for cognitive map use by honeybees. *Proc Natl Acad Sci U S A* 111:4396–7.
- Cheung A, Hiby L, Narendra A. 2012. Ant navigation: fractional use of the home vector. *PLoS One* 7:e50451.
- Cheung A, Zhang S, Stricker C, Srinivasan MV. 2007. Animal navigation: the difficulty of moving in a straight line. *Biol Cybern* 97:47–61.
- Chittka L. 1996. Does bee color vision predate the evolution of flower color? *Naturwissenschaften* 83:136–8.
- Cruse H, Wehner R. 2011. No need for a cognitive map: decentralized memory for insect navigation. *PLoS Comput Biol* 7:e1002009.
- de Souza JM, Ventura DF. 1989. Comparative study of temporal summation and response form in hymenopterian photoreceptors. *J Comp Physiol A* 165:237–45.
- Duelli P. 1972. The relation of astromenotactic and anemomenotactic orientation mechanisms in desert ants, *Cataglyphis bicolor* (Formicidae, Hymenoptera). In: Wehner R, editor. *Information processing in the visual systems of arthropods*. Berlin, Heidelberg: Springer. p. 281–86.
- Duncan FD, Crewe RM. 1994. Field study on the foraging characteristics of a ponerine ant, *Hagensia havilandi* Forel. *Insectes Soc* 41:85–98.
- Eidmann H. 1935. Zur Kenntnis der Blattschneiderameise *Atta sexdens* L., insbesondere ihrer Ökologie. *Z Angew Entomol* 22:185–436.
- Fourcassie V, Henriques A, Fontella C. 1999. Route fidelity and spatial orientation in the ant *Dinoponera gigantea* (Hymenoptera: Formicidae) in a primary forest: a preliminary study. *Sociobiology* 34:505–24.
- Freas CA, Narendra A, Cheng K. 2017a. Compass cues used by a nocturnal bull ant, *Myrmecia midas*. *J Exp Biol* 220:1578–85.
- Freas CA, Narendra A, Lemesle C, Cheng K. 2017b. Polarized light use in the nocturnal bull ant, *Myrmecia midas*. *R Soc Open Sci* (doi:10.1098/rsos.170598).

- Frederiksen R, Wcislo WT, Warrant EJ. 2008. Visual reliability and information rate in the retina of a nocturnal bee. *Curr Biol* 18:349–53.
- Greiner B. 2006. Visual adaptations in the night-active wasp *Apoica pallens*. *J Comp Neurol* 495:255–62.
- Greiner B, Narendra A, Reid SF, Dacke M, Ribi WA, Zeil J. 2007. Eye structure correlates with distinct foraging-bout timing in primitive ants. *Curr Biol* 17:R879–80.
- Greiner B, Ribi WA, Warrant EJ. 2005. A neural network to improve dim-light vision? Dendritic fields of first-order interneurons in the nocturnal bee *Megalopta genalis*. *Cell Tissue Res* 322:313–20.
- Greiner B, Ribi WA, Wcislo WT, Warrant EJ. 2004. Neural organisation in the first optic ganglion of the nocturnal bee *Megalopta genalis*. *Cell Tissue Res* 318:429–37.
- Gronenberg W. 2008. Structure and function of ant (Hymenoptera: Formicidae) brains: strength in numbers. *Myrmecol News* 11:25–36.
- Hodgson ES. 1955. An ecological study of the behavior of the leaf-cutting ant *Atta cephalotes*. *Ecology* 36:293–304.
- Hölldobler B. 1974. Home range orientation and territoriality in harvesting ants. *Proc Natl Acad Sci U S A* 71:3274–7.
- Hölldobler B. 1980. Canopy orientation: a new kind of orientation in ants. *Science* 210:86–8.
- Jander R. 1957. Die optische Richtungsorientierung der Roten Waldameise (*Formica rufa* L.). *Z Vgl Physiol* 40:162–238.
- Johnsen S, Kelber A, Warrant EJ, Sweeney A, Widder EA, Lee RL, Hernandez-Andres J. 2006. Crepuscular and nocturnal illumination and its effects on color perception by the nocturnal hawkmoth *Deilephila elpenor*. *J Exp Biol* 209:789–800.
- Kaspari M, Weiser M. 1999. The size–grain hypothesis and interspecific scaling in ants. *Funct Ecol* 13:530–8.
- Kaul RM, Kopteva GA. 1982. Night orientation of ants *Formica rufa* (Hymenoptera, Formicidae) during movement along paths. *Zool Zhurnal* 61:1351–8.
- Kinoshita M, Arikawa K. 2014. Color and polarization vision in foraging *Papilio*. *J Comp Physiol A* 200:513–26.
- Klotz JH, Reid BL. 1993. Nocturnal orientation in the black carpenter ant *Camponotus pennsylvanicus* (DeGeer) (Hymenoptera: Formicidae). *Insectes Soc* 40:95–106.
- Klotz JH, Reid BL, Gordon WC. 1992. Variation of ommatidia number as a function of worker size in *Camponotus pennsylvanicus* (DeGeer) (Hymenoptera: Formicidae). *Insectes Soc* 39:233–6.
- Labhart T. 1986. The electrophysiology of photoreceptors in different eye regions of the desert ant, *Cataglyphis bicolor*. *J Comp Physiol A* 158:1–7.
- Land MF. 1981. Optics and vision in invertebrates. In: Autrum H, editor. *Handbook of sensory physiology*, Vol. VII/6B. Berlin: Springer. p. 472–592.
- Lieke E. 1981. Graded and discrete receptor potentials in the compound eye of the Australian Bulldog-ant (*Myrmecia gulosa*). *Biol Cybern* 40:151–6.
- Lubbock J. 1882. *Ants, bees, and wasps: a record of observations on the habits of the social Hymenoptera*. New York (NY): Appleton and Company.
- McCluskey ES. 1965. Circadian rhythms in male ants of five diverse species. *Science* 150:1037–9.
- McCluskey ES. 1992. Periodicity and diversity in ant mating flights. *Comp Biochem Physiol* 103A:241–3.
- Menzel R, Blakers M. 1975. Functional organisation of an insect ommatidium with fused rhabdom. *Cytobiologie* 11:279–98.
- Menzel R, Knaut R. 1973. Pigment movement during light and chromatic adaptation in the retinula cells of *Formica polyctena* (Hymenoptera, Formicidae). *J Comp Physiol A* 86:125–38.
- Menzi U. 1987. Visual adaptation in nocturnal and diurnal ants. *J Comp Physiol A* 160:11–21.
- Moller R. 2002. Insects could exploit UV–Green contrast for landmark navigation. *J Theor Biol* 214:619–31.
- Moser J, Reeve J, Bento J, Lucia TMCD, Cameron S, Heck NH. 2004. Eye size and behaviour of day- and night-flying leafcutting ant alates. *J Zool* 264:69–75.
- Müller M, Wehner R. 1988. Path integration in desert ants, *Cataglyphis fortis*. *Proc Natl Acad Sci U S A* 85:5297–0.
- Narendra A. 2007. Homing strategies of the Australian desert ant *Melophorus bagoti*. I. Proportional path-integration takes the ant half-way home. *J Exp Biol* 210:1798–803.
- Narendra A, Alkaladi A, Raderschall CA, Robson SKA, Ribi WA. 2013a. Compound eye adaptations for diurnal and nocturnal lifestyle in the intertidal ant, *Polyrhachis sokolova*. *PLoS One* 8:e76015.
- Narendra A, Gourmaud S, Zeil J. 2013b. Mapping the navigational knowledge of individually foraging ants, *Myrmecia croslandi*. *Proc R Soc Lond B Biol Sci* 280 published online (doi: 10.1098/rspb.2013.0683).
- Narendra A, Ramirez-Esquivel F. 2017. Subtle changes in the landmark panorama disrupt visual navigation in a nocturnal bull ant. *Philos Trans R Soc Lond B Biol Sci* 372 published online (doi: 10.1098/rstb.2016.0068).
- Narendra A, Greiner B, Ribi WA, Zeil J. 2016a. Light and dark adaptation mechanisms in the compound eyes of *Myrmecia* ants that occupy discrete temporal niches. *J Exp Biol* 219:2435–42.
- Narendra A, Raderschall CA, Robson SKA. 2013c. Homing abilities of the Australian intertidal ant, *Polyrhachis sokolova*. *J Exp Biol* 216:3674–81.
- Narendra A, Ramirez-Esquivel F, Ribi WA. 2016b. Compound eye and ocellar structure for walking and flying modes of locomotion in the Australian ant, *Camponotus consobrinus*. *Sci Rep* 6:22331.
- Narendra A, Reid SF, Greiner B, Peters RA, Hemmi JM, Ribi WA, Zeil J. 2011. Caste-specific visual adaptations to distinct daily activity schedules in Australian *Myrmecia* ants. *Proc R Soc Lond B Biol Sci* 278:1141–9.
- Narendra A, Reid SF, Hemmi JM. 2010. The twilight zone: ambient light levels trigger activity in primitive ants. *Proc R Soc Lond B Biol Sci* 277:1531–8.
- Narendra A, Reid SF, Raderschall CA. 2013d. Navigational efficiency of nocturnal *Myrmecia* ants suffers at low light levels. *PLoS One* 8:e58801.
- Nørgaard T, Nilsson D-E, Henschel JR, Garm A, Wehner R. 2008. Vision in the nocturnal wandering spider *Leucorchestris arenicola* (Araneae: Sparassidae). *J Exp Biol* 211:816–23.
- O'Carroll DC, Warrant EJ. 2017. Vision in dim light: highlights and challenges. *Philos Trans R Soc Lond B Biol Sci* 372 published online (doi: 10.1098/rstb.2016.0079).
- Ogawa Y, Falkowski M, Narendra A, Zeil J, Hemmi JM. 2015. Three spectrally distinct photoreceptors in diurnal and

- nocturnal Australian ants. *Proc R Soc Lond B Biol Sci* 282 published online (doi: 10.1098/rspb.2015.0673).
- Papi F. 1960. Orientation by night: the moon. *Cold Spring Harb Symp Quant Biol* 25:475–80.
- Raderschall CA, Narendra A, Zeil J. 2016. Head roll stabilisation in the nocturnal bull ant *Myrmecia pyriformis*: implications for visual navigation. *J Exp Biol* 219:1449–57.
- Ramirez-Esquivel F. 2012. From large to small, from day to night: the sensory costs of miniaturisation in ants [Honours thesis]. [Canberra]: The Australian National University. p. 1–45.
- Ramirez-Esquivel F, Leitner NE, Zeil J, Narendra A. 2017. The sensory arrays of the ant, *Temnothorax rugatulus*. *Arthropod Struct Dev* published online (doi:10.1016/j.asd.2017.03.005).
- Reber T, Vähäkainy A, Baird E, Wesckström M, Warrant EJ, Dacke M. 2015. Effect of light intensity on flight control and temporal properties of the photoreceptors in bumblebees. *J Exp Biol* 218:1339–46.
- Reid SF, Narendra A, Hemmi JM, Zeil J. 2011. Polarised skylight and the landmark panorama provide night-active bull ants with compass information during route following. *J Exp Biol* 214:363–70.
- Reid SF. 2010. Life in the dark: vision and navigation in a nocturnal bull ant [PhD thesis]. Canberra: The Australian National University. p. 1–130.
- Reid SF, Narendra A, Taylor RW, Zeil J. 2013. Foraging ecology of the night-active bull ant *Myrmecia pyriformis*. *Aust J Zool* 61:170–7.
- Ribi WA. 1975. Goldi studies in the first optic ganglion of the ant *Cataglyphis bicolor*. *Cell Tissue Res* 160:207–17.
- Rodrigues PAP, Oliveira PS. 2014. Visual navigation in the neotropical ant *Odontomachus hastatus* (Formicidae, Ponerinae), a predominantly nocturnal, canopy-dwelling predator of the Atlantic rainforest. *Behav Processes* 109:48–57.
- Rosengren R. 1977. Foraging strategy of wood ants (*Formica rufa* group). II. Nocturnal orientation and diel periodicity. Helsinki: Societas pro fauna et flora Fennica.
- Rosengren R. 1986. Ortstreue in foraging ants of the *Formica rufa* group—hierarchy of orienting cues and long-term memory. *Insectes Soc* 33:306–37.
- Santschi F. 1911. Observations et remarques critiques sur le mécanisme de l'orientation chez les Fourmis. *Rev Suisse Zool* 19:303–38.
- Schultheiss P, Wystrach A, Schwarz S, Tack A, Delor J, Nooten SS, Bibost AL, Freas CA, Cheng K. 2016. Crucial role of ultraviolet light for desert ants in determining direction from the terrestrial panorama. *Anim Behav* 115:19–28.
- Schwarz S, Narendra A, Zeil J. 2011. The properties of the visual system in the Australian desert ant *Melophorus bagoti*. *Arthropod Struct Dev* 40:128–34.
- Somanathan H, Borges RM, Warrant EJ, Kelber A. 2008. Nocturnal bees learn landmark colours in starlight. *Curr Biol* 18:R996–7.
- Somanathan H, Kelber A, Borges RM, Wallen R, Warrant EJ. 2009. Visual ecology of Indian carpenter bees II: adaptations of eyes and ocelli to nocturnal and diurnal lifestyles. *J Comp Physiol A* 195:571–83.
- Stöckl AL, O'Carroll DC, Warrant EJ. 2016a. Neural summation in the Hawkmoth visual system extends the limits of vision in dim light. *Curr Biol* 26:821–6.
- Stöckl AL, Ribi WA, Warrant EJ. 2016b. Adaptations for nocturnal and diurnal vision in the hawkmoth lamina. *J Comp Neurol* 524:160–75.
- Tierney SM, Friedrich M, Humphreys WH, Jones T, Warrant EJ, Wcislo WT. 2017. Consequences of evolutionary transitions in changing photic environments. *Aust Entomol* 56:23–46.
- Warrant EJ. 1999. Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. *Vis Res* 39:1611–30.
- Warrant EJ. 2008. Seeing in the dark: vision and visual behaviour in nocturnal bees and wasps. *J Exp Biol* 211:1737–46.
- Warrant EJ. 2017. The remarkable visual capacities of nocturnal insects: vision at the limits with small eyes and tiny brains. *Philos Trans R Soc Lond B Biol Sci* 372 published online (doi: 10.1098/rstb.2016.0063).
- Warrant EJ, Dacke M. 2010. Visual orientation and navigation in nocturnal arthropods. *Brain Behav Evol* 75:156–73.
- Warrant EJ, Dacke M. 2016. Visual navigation in nocturnal insects. *Physiology* 31:182–92.
- Warrant EJ, Nilsson D-E. 1998. Absorption of white light in photoreceptors. *Vis Res* 38:195–207.
- Warrant EJ, Kelber A, Gislén A, Greiner B, Ribi WA, Wcislo WT. 2004. Nocturnal vision and landmark orientation in a tropical Halictid bee. *Curr Biol* 14:1309–18.
- Warrant EJ, Porombka T, Kirchner WH. 1996. Neural image enhancement allows honeybees to see at night. *Proc R Soc Lond B Biol Sci* 263:1521–6.
- Warton DI, Wright IJ, Falster DS, Westoby M. 2006. Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–91.
- Wehner R. 2009. The architecture of the desert ant's navigational toolkit (Hymenoptera: Formicidae). *Myrmecol News* 12:85–96.
- Wehner R, Duelli P. 1971. The spatial orientation of desert ants, *Cataglyphis bicolor*, before sunrise and after sunset. *Experientia* 27:1364–6.
- Wehner R, Wehner R. 2001. Polarization vision—a uniform sensory capacity? *J Exp Biol* 204:2589–96.
- Wehner R, Michel B, Antonsen P. 1996. Visual navigation in insects: coupling of egocentric and geocentric information. *J Exp Biol* 199:129–40.
- Wilson M. 1978. The functional organisation of locust ocelli. *J Comp Physiol* 124:297–316.
- Yilmaz A, Lindenberg A, Albert S, Gröbel K, Spaethe J, Rössler W, Groh C. 2016. Age-related and light-induced plasticity in opsin gene expression and in primary and secondary visual centers of the nectar-feeding ant *Camponotus rufipes*. *Dev Neurobiol* 76:1041–57.
- Zeil J, Ribi WA, Narendra A. 2014. Polarisation vision in ants, bees and wasps. In: Horváth G, editor. *Polarized light and polarization vision in animal sciences*. Berlin: Springer. p. 41–60.