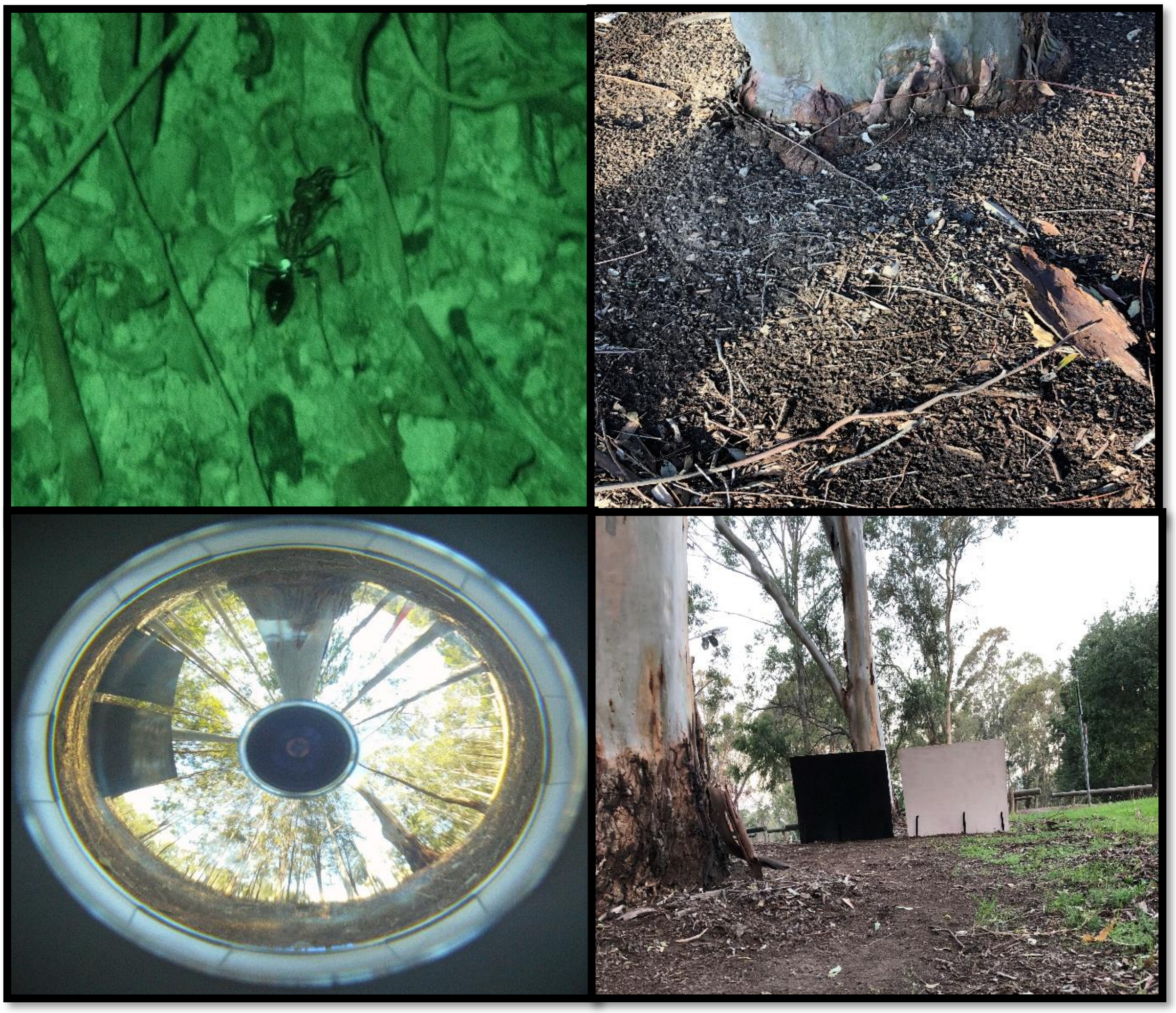
Learning to find a gap: Navigational problem solving in nocturnal bull ants



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Declaration page for the Master of Research thesis

This thesis is written in the form of a journal article from *Behavioural Processes*.

Declaration

I wish to acknowledge the following assistance in the research detailed in this report.

I received assistance from Sudhakar Deeti and Muzahidul Islam in carrying and installing the obstacles on the ants' foraging routes. Sudhakar also helped me to take the panoramic views of the experimental conditions. Professor Ken Cheng provided comments and suggestions on the project and the manuscript.

All other research described in this report is my own original work and the work has not been submitted for a higher degree to any other university or institution.

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Abstract

Solitarily foraging ant species derive compass information from terrestrial landmarks and path integration to navigate. Our test ants, solitary foragers of *Myrmecia midas,* have the added challenge of completing their navigation during evening and morning twilight. The aim of this research was to test bull ants' ability to use edge contrast to find a gap in an obstacle that obstructs their direct path. Ants were individually identified and tested repeatedly on their foraging trip. An artificial obstacle (0.9m by 1.2m wide) with a 10cm gap in it was installed on their foraging route to train them to find the gap. The gap location was unpredictably varied from one run to another so that the ants had to look for it. In training, each nest of ants was given two colour conditions on the obstacles: one with black on one side of the gap and white on the other side (which was easier to spot), one with black on both sides (which was harder to spot). We tested the ants' ability to find the gap and measured the directness of the path. We found that the ants learnt to find the gap in the obstacle after completing several trials. However, we did not find any significant differences in the ants' behaviour in the two colour conditions.

Australian Higher Ed. Graduation Statement Abstract

Solitarily foraging ant species derive compass information from terrestrial landmarks and path integration to navigate. *Myrmecia midas* have the added challenge of completing their navigation during evening and morning twilight when visual cues are less salient. We tested the ants' ability to use edge contrast to locate a gap in an obstacle on their route. We found that bull ants learnt to find the gap in the obstacle after completing several trials although the gap location was unpredictably varied from one run to another. However, we did not find any significant differences in the ants' behaviour for edge contrast.

Highlights:

- **Individuals were able to find gap locations in the obstacle after several trials.**
- **Edge contrast shows no effect on finding the gap location in the obstacle.**

Keywords:

Ants, Navigation, Learn, Obstacle, Gap

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1. Introduction

Insects are clever navigators, and ants, bees, wasps are being used as model organisms to demonstrate insect navigational systems. The fact that insects possess small nervous systems, with a reduced number of neurons, does not constitute a limitation for the production of sophisticated, complex behaviour (Avarguès-Weber et al., 2011; Chittka and Niven, 2009). Besides stereotyped, genetically encoded behaviours, insects exhibit remarkable behavioural plasticity as numerous species learn and memorise different sorts of sensory cues as predictors of reward (Daly and Smith, 2000; Dupuy et al., 2006; Giurfa, 2007; Matsumoto and Mizunami, 2000; Menzel, 1999) or of punishment (Busto et al., 2010; Davis, 2005; Fiala, 2007; Keene and Waddell, 2007; Vergoz et al., 2007) and form memories of such experiences that can be retrieved at different times after learning, from the short-term to long-term range.

Ants (Formicidae) are a globally distributed insect family whose members have adapted to live in a wide range of different environments and ecological niches (Freas and Schultheiss, 2018). They display a wide variety of strategies to forage for food, ranging from entirely solitary, to individuals guided by trunk trails, and group foraging strategies (Beckers et al., 1989; Hölldobler and Wilson, 1990). Individual foragers capitalize on guiding mechanisms by utilising pheromone based chemical trails when they are in a group (Traniello, 1976; Wilson, 1962). Solitarily foraging ants show the ability to utilize visual navigational systems to reach their desired locations as they learn from past experience and they use this memory to navigate from nest to feeders and then find the way back home (Collett and Zeil, 1998). Some solitarily foraging ants use visual cues from their environment for navigation not only on the ground, but also on trees, which they climb to locate resources (Freas et al., 2018). More than a century of research has led to the identification of some key navigational strategies, such as compass navigation, path integration, and route following. Ants have been shown to rely on visual, olfactory, and idiothetic cues for navigational guidance (Freas and Schultheiss, 2018). Current knowledge of landmark use in ants that forage nocturnally is expanding (Freas et al., 2017a,b; Narendra et al., 2017; Narendra and Ramirez-Esquivel, 2017; Reid et al., 2011; Warrant and Dacke, 2011), while landmark based navigation has been widely studied in diurnal ants (Bühlmann et al., 2011; Cheng et al., 2009; Collett, 2010; Freas et al., 2017c; Freas and Cheng, 2017; Fukushi, 2001; Lent et al., 2013; Narendra et al., 2013; Schultheiss et al., 2016; Wehner Wehner, 2003et al., 1996; Wystrach et al., 2011a,b, 2012).

1.1 Path Integration- Visual Navigation (Landmarks)

Ants are efficient navigators, guided by path integration and visual landmarks. Path integration is used to keep track of the straight-line distance direction and direction from the starting point, operates continuously in the background, and can be called upon as necessary, or relied on in habitats in which no useful visual cues are available (Cheng, 2012). It is the primary strategy in landmark-poor habitats, but landmarks are readily used when available (Narendra et al., 2013). Night active bull ants use both terrestrial landmarks and celestial cues to navigate to and from their nest location. These cues persist even as light levels drop during the twilight/night (Freas et al., 2017a,b). Freas et al. (2017a) showed that *Myrmecia midas* forager ants were unable to orient to the nest direction and their heading directions were randomly distributed when the visual landmarks at the local displacement site were blocked. Moreover, foragers were unable to orient towards the nest after small lateral displacements away from the nest when they were collected on the nest tree during evening twilight. The diurnal desert ant species *Melophorus bagoti* inhabits a cluttered semi-arid environment filled with bushes, trees, and grass tussocks (Cheng et al., 2009, 2014). It also employs path integration to return to the nest when landmarks are not available (Narendra et al., 2007). Cheng et al. (2009) found that *M. bagoti* used the terrestrial panorama for navigation. Ants are thought to learn landmark information through a carefully constructed series of learning walks carried out in multiple directions around a goal (Narendra and Ramirez-Esquivel, 2017). Ants look back to the nest entrance during pirouettes, which is when the ants frequently stop and gaze back in the direction of the nest entrance for the longest stopping phases; most probably they use the technique of taking snapshots to memorize their surroundings (Fleischmann et al., 2017). However, learning of a visual landmark panorama around a goal is a gradual rather than an instantaneous process (Fleischman et al., 2016).

1.2 Path Integration- Celestial Compass

Ants' successful navigation always faces two challenges: the first one is to come out from the nest and find the way towards the destination; and the most important second one is to follow the right route to come back to the nest again. The navigational strategy of path integration is the ability to maintain a direction and vector distance pointing from the individual's current position to the nest site (Wehner, 2003). Path integration employs a celestial compass, which differentiates distinct patterns in polarised light to successfully recall the home vector after completing foraging. Ants have a specialized group of receptors in the dorsal region of the eye (the dorsal rim) which helps them to perceive polarised directions in UV light (Wehner, 1997). The celestial compass employs the polarisation of scattered skylight and the position of the sun itself, which allows the ant to compensate for the inherent two-fold ambiguity associated with polarised light (Duelli and Wehner, 1973; Rossel and Wehner, 1986; Wehner, 1984, 1987). Nocturnal bull ants have the added challenge of completing their navigation during the evening and morning twilight when visual cues are less salient compared to those used by diurnal species of ants (Narendra et al., 2017). To increase their optical sensitivity, most nocturnal insects have superposition eyes (e.g., moths), where light from several lenses is superimposed on to a single photosensitive structure, the rhabdom (Land and Fernald, 1992; Land and Nilsson, 2002; McIntyre and Gaveney, 1998; Warrant and Dacke, 2011). However, nocturnal hymenopteran insects (e.g., ants, bees, wasps) have apposition eyes, where light reaches the rhabdom through a single lens, thus being less sensitive compared to superposition eyes. To overcome this reduced sensitivity, nocturnal hymenopterans increase their optical sensitivity by having larger lenses and wider photoreceptors compared to their diurnal relatives (Greiner, 2006; Greiner et al., 2007; Moser et al., 2004; Warrant and Dacke, 2011; Narendra et al., 2011; Somanathan et al., 2009; Warrant, 1999, 2008).

1.3 Panoramas

During learned panorama-based navigation, the specific cues in use remain debated, as which visual cues and aspects of the panorama are used for directional guidance remain uncertain (Freas and Schultheiss, 2018). Most prevalent models involve view-based matching, where foragers compare stored views with their current view to direct them to their goal (Möller, 2012; Zeil et al., 2003). Research has also found evidence for the use of the skyline pattern/height as navigational cues (Graham and Cheng, 2009). The desert ant *Melophorus bagoti* has been shown to have the ability to use skyline cues through the presence of the UV contrast between the sky and ground to orient successfully as well as retaining skyline cues over long periods (Freas, et al., 2017c; Schultheiss et al., 2016). Another view-based strategy of current interest consists of ants' use of the fractional position of mass of the visual scene when comparing stored views and current views (Lent et al., 2013). Here, ants acquire the fraction of the terrestrial scene to the left and right while facing the goal, comparing these stored views to their current view while navigating. When only a single terrestrial object is visible, foragers appear to learn the position of the object's centre of mass within stored views and attempt to place this centre of mass in the same retinal position when navigating (Buehlmann et al., 2016; Woodgate et al., 2016).

1.4 Bull Ant Species

Nocturnal bull ant species are found in the *Myrmecia* genus and are among the most primitive of all known living ants (Gibb and Cunningham, 2011). Ants of the genus are considered specialist predators (Andersen, 1990). Almost all species in the genus *Myrmecia* are found in Australia and its coastal islands (John, 1951). Ants of this genus prefer to inhabit grasslands, forests, heath, urban areas and woodland. Nests are found in *Callitris* forests, dry marri forests, *Eucalyptus* woodlands and forests, mallee scrub, in paddocks, riparian woodlands, and wet and dry sclerophyll forests (Shattuck and Barnett, 2010). Nests can be found in debris, decaying tree stumps, rotten logs, rocks, sand, and soil, and under stones (John, 1951; Shattuck and Barnett, 2010). Some species construct dome-shaped mounds containing a single entrance, but some nests have numerous holes that are constantly used and can extend several metres underground (John, 1951). Sometimes, these mounds can be 0.5 m (20 in) high (Whinam and Hope, 2005). Workers decorate these nests with a variety of items, including charcoal, leaves, plant fragments, pebbles, and twigs (John, 1951; Shattuck and Barnett, 2010). Unlike most ants, workers are solitary hunters, and do not lay pheromone trails; nor do they recruit others to food (Wilson, 2000). Most bull ant species are diurnal, and forage on the ground or on low vegetation in search of food, but a few are nocturnal and only forage at night (Shattuck and Barnett, 2010). Most *Myrmecia* ants are active during the warmer months, and are dormant during winter (Jayatilaka et al., 2011). However, *M. pyriformis* is a nocturnal species that is active throughout the whole year. *M. pyriformis* also has a unique foraging schedule (Narendra et al., 2010); 65% of individuals that went out to forage left the nest in 40–60 minutes, while 60% of workers would return to the nest in the same duration of time at dawn. Foraging *Myrmecia croslandi* workers rely on landmarks for navigation back home (Narendra et al., 2013). If displaced a short distance, *M. midas* will scan their surroundings, and then rapidly move in the direction of the nest (Freas et al., 2017a).

Solitarily foraging nocturnal bull ant species are dependent upon cues in their environments to find food and return accurately to their nest. They need an external compass reference to walk in a straight line (Cheung et al., 2007). Solitarily foraging bull ants and other solitarily foraging ant species derive compass information from terrestrial landmarks and path integration to head towards their goal (Collett, 2012; Collett et al., 2006; Schultheiss et al., 2016; Wehner, 2003). To obtain compass information from landmarks, ants first acquire visual information around the goal (Baddeley et al., 2011; Fleishmann et al., 2016; Narendra et al., 2007; Nicholson et al., 1999; Zeil et al., 2014) through a carefully orchestrated series of learning walks that occur in different compass directions around the goal. While returning to the goal, ants move to match their current view to the memorized nest-oriented image to head toward the goal (Collett et al., 2001; Graham and Cheng, 2009; Narendra et al., 2013a; Wehner et al., 1996; Wystrach et al., 2011a; Zeil 2012). Ants also obtain compass information from multiple celestial cues, most notably the pattern of polarised skylight derived from the sun (Zeil et al., 2014). The polarisation information is acquired through a specialized dorsal region of the ant's eyes (Narendra et al., 2016; Zeil et al., 2014) and is processed via polarization sensitive optic lobe neurons (Schmitt et al., 2015). This directional information is coupled with distance information the ant accumulates as it travels away from the nest (Wittlinger et al., 2006). To return home, ants integrate these two sources of information and compute the shortest home vector (Collett and Collett, 2000; Wehner and Srinivasan, 2003).

1.5 Learning in Myrmecia midas

Learning is a cognitive process that involves a change in behaviour as a result of experience relevant to the behaviour (Papaj and Prokopy, 1989; Shettleworth, 2001). Most of the research on insect learning and memory has focused on associative learning such as Pavlovian and operant conditioning. In the former, animals learn an association between a conditioned stimulus and an unconditioned, biologically relevant stimulus (Pavlov and Anrep, 1927). In the latter, they learn to associate a behavioural action with the reinforcement resulting from that action (Skinner, 1938). Ants use panorama-based navigation for acquiring the cues around the nest through multiple pre-foraging learning walks (Baddeley et al., 2011; Fleischmann et al., 2016, 2017; Nicholson et al., 1999; Zeil et al., 2014), while *C. noda* uses geomagnetic cues on its first learning walks (Fleischmann et al., 2018). During these walks, foragers meander near the nest entrance, likely learning the panorama makeup around the nest (Wehner et al., 2004). Learning walks using have been well studied in *Cataglyphis noda*, a desert ant species living in environments containing few panorama cues and evidence shows clear improvement about the panorama after 3-7 walks before foraging with some artificial landmarks (Fleischmann et al., 2016, 2018). *C. noda*, during the learning walk, the novices take nest-centred views from various directions around the nest (Fleischmann et al., 2018). Although learning walks have not been studied yet in *M. midas*, learning walks appear to be mediated by the environment, as species inhabiting landmark-rich environments will occasionally 'pirouette' and turn back to the nest, likely learning panorama cues (Fleischmann et al., 2017). These pirouettes are observed in some barren-habitat species like *Ocymyrmex robustior* (Müller and Wehner, 2010), while pirouettes are not found in *C. fortis*, which inhibits a visually barren habitat of salt plans (Fleischmann et al., 2017). Learning either about the cues of the panorama or other navigational strategies based on learning walks is a ripe topic for future research.

1.6 Other ant models for navigational studies

Myrmecia midas remains active during summer months when the temperature is high, but begins to reduce activity as temperatures lower during April and May, which is then followed by a winter long dormancy period (Clark, 1951). *Melophorus bagoti*, which similarly relies on visual cues for successful navigation, has a shorter period of activity.

M. bagoti are solitarily foraging ground nesting ants and are found in desert soil. Their surroundings are dominated by buffel-grass, tussocks, rocks and trees (Muser et al., 2005); and indeed they occur in the deserts in Australia where many landmark-based cues are salient (Cheng et al., 2009). Another solitarily foraging ant species is *Cataglyphis fortis*; their habitat in North African salt plans is barren and the nest entrance a tiny hole in the ground that is almost invisible. Natural landmarks are scarce and the ants mainly depend on path integration for returning to the starting point. However, this ant species can also learn to use landmarks successfully to navigate through their largely featureless habitat (Fleischmann et al., 2016; Wehner and Räber, 1979). Namibian desert ants, *Ocymyrmex robustior* when learning new landmarks in the neighbourhood of the goal, acquire this landmark information when they cannot see the goal (Müller and Wehner, 2010). Unlike *M. midas*, *M. bagoti*, *C. fortis* and *O. robuster* ants live in a hot climate and they are diurnal thermophilic scavengers that feed mainly on dead insects (Muser et al., 2005; Wehner, 1987). All of the model ant species are diurnal and their thermophilic lifestyle with individual foraging activity make them interesting subject for studies. They are also seen as prime candidates for the navigational studies of ants.

1.7 Obstacle Navigation

To properly negotiate obstacles in their path, animals typically need to alter their behaviour. For instance, an animal that is walking in a straight line and encounters an obstacle may respond to it by initiating any of a number of behaviours, such as climbing, tunnelling, jumping, escaping or turning (Harley et al., 2009). However, the animal may first have to evaluate the object to determine the appropriate response. These objects may be predators (Comer et al., 2003), prey items (Catania and Kaas, 1997; Dehnhardt et al., 2001), tall obstacles (Watson et al., 2002) or walls (Camhi and Johnson, 1999; Cowan et al., 2006; Wiesel and Hubel, 1963). To respond appropriately, the animal must detect and extract specific properties of the objects it encounters. While this is often thought of as a visual process, many insects and vertebrates use mechanosensory information for navigation (Patla et al., 1999). While some invertebrates can use mechanosensors on their front limbs to sense obstacles (Blaesing and Cruse, 2004; Pick and Strauss, 2005), they can also gain mechanosensory information from the antennae (Camhi and Johnson, 1999; Dürr and Krause, 2001; Horseman et al., 1997; Pelletier and McLoed, 1994).

Obstacle navigation in ants has been studied in group foragers rather than solitary foragers. A recent set of experiments by McCreery et al. (2016) looked at the obstacle-navigation strategy of groups of crazy ants, *Paratrechina longicornis*, a species that is highly effective at group transport. The ants were presented with multiple challenges, including a concave obstacle; concave obstacles pose a special challenge as they require the ants to move away from the direction of their nest. These experiments suggest that this ant species employs a stochastic but time-adaptive strategy for complex tasks that enables successful navigation of concave obstacles. McCreery et al. (2016) concluded that these groups start with a relatively simple strategy, using nest direction information, and incorporate increasing levels of stochastic behaviour into their strategy over time, moving farther away from their goal they longer they are stuck.

In another study by Ron et al. (2018) the dynamics of cooperative transport was investigated, when the motion of the ants was frustrated by a linear obstacle that obstructed the motion of the cargo. The obstacle contained a narrow opening that served as the only available passage to the nest, and through which single ants could pass but not with the cargo. The ant-cargo system was provided an analytical model in the constrained environment. Ron et al. (2018) concluded that the system exhibits spontaneous transitions between two modes of motion either by attempting to pass through the opening, or take large excursions to circumvent the obstacle due to fluctuations in the applied force on the cargo.

However, our test ant species, the night active Australian bull ant, *Myrmecia midas*, is a solitarily foraging species (Freas et al., 2017a) and each forager heads out every night to a single foraging tree, the same tree night after night. Obstacle navigation in this particular species has never been studied. In regard to the study of obstacle navigation, utilisation of an artificial obstacle that obstructs their direct path towards their goal in their natural environment provides a unique opportunity to study how well they learn the unpredictable location of the gap on each night. Solitarily foraging ants use all visual cues critical for successful navigation, including the celestial compass, landmarks, and the surrounding panorama (Freas et al., 2017a), and we expect that they will use all these means to pass through the gap. This study can enhance our understanding about obstacle navigation in solitary foraging ants.

1.8 Research Objective

As stated above, solitarily foraging ant species derive compass information from terrestrial landmarks and path integration. Night active *M. midas* head out every night to a single foraging tree, the same tree night after night. This solitary foraging ant species does not follow pheromone trails like group foraging ants. Moreover, they complete their foraging activity within the evening and morning twilight. The visual cues are not so salient compared to those used by diurnal species of ants. This sets the context for posing a problem for them to learn. Their navigation towards obstacles and their learning capabilities have yet not been studied.

The goal of the current project was to test how well bull ants can learn to find a gap in an obstacle that obstructs their direct path, with different colours signalling the gap. In tests, each ant was individually identified and tested repeatedly on their foraging trip for each night. We hypothesize that after completing several trials night active bull ants will learn to seek out the gap in the obstacles while high edge contrast will help them to locate the gap.

We tested the ants' ability to use edge contrast to locate the gap while we measured the directness of the path to the gap. Our final aim was to examine whether they learnt to look for the gap at all.

2. Methods

2.1 Study animals

The experiments were done with Australian night active bull ants, *Myrmecia midas*. This ant species forages from the evening to morning twilight. They are solitary foragers and they head out every night from their nest to forage in a single foraging tree. However, each forager goes to a single foraging tree while different foragers may go to different foraging trees. Bull ants are active during the summer months but their activity can also be observed in late June. However, all the experiments were conducted from January to May 2018 on two different nests of bull ants. The nests were located on the northern side of the Macquarie University North Ryde campus in Sydney, Australia (33°46′11″ S, 151°06′40″E). *M. midas* nests were found in habitats consisting of stands of *Eucalyptus* trees with mostly barren understoreys with the nest entrance located near the base of a tree. Individuals were collected and tested from three different foraging routes of those two selected nests of the ant species. Research in ants does not require animal ethical approval in Australia.

2.2 Experimental design and set up

In a bull ant nest two types of foragers can be found on the basis of their foraging tree selection. One group selects the nest tree for foraging and another group selects other trees than the nest tree for foraging and those trees can be called foraging trees. The nest tree foragers just come out from their nest and climb on the same tree where the nest is situated at the base of that tree. The other forager group comes out from their nest and travels some distance on the ground and climbs on the foraging trees. Regular observation and marking the experimental ants determine either the ants were nest tree foragers or foraging trees foragers. As nest tree foragers do not travel on the ground, it was not possible to place any obstacle on the ground for them. So, our entire research project was done only on the foraging tree foragers.

Two nests were selected and they were identified as Nest A and Nest B and they were tested in succession, one nest at a time. Nest A had two suitable routes for the experiments and Nest B had only one suitable route. For Nest A, the two foraging routes were indicated as Route 1 and Route 2. The distance between the nest tree and the foraging tree in Route 1 was 8.5m and in Route 2 it was 4.3m. The distance between the nest tree and the foraging tree in Nest B was 3.9m. Ants regularly travel the whole distance for foraging and a particular ant never changes its foraging route, thus making them suitable routes for experimentation. Experimentation started before sunset and continued for 3-4 hours. At first, some initial obstacles were installed at the middle of the foraging routes and ants' behaviour was observed as some pilot tests. The obstacles were made of wooden boards and there was no coloration on those boards. In these pilot tests we found that some ants climbed on the obstacles and passed it that way as they blocked the direct path between nest and foraging tree; some searched for alternative ways by going around the obstacles to go to the foraging tree and avoided the obstacles; and only a few ants came back to the nest rather than foraging on that day. After a week when they were used to the obstacles then the final experiments were started. On every route two artificial obstacles were installed (each 0.9m by 1.2m wide) with a 10cm gap in it, in the middle of the foraging route. The obstacles were provided in two colour conditions: one with black on one side of the gap and white on the other side (which is easier to spot), one with black on both sides (which is harder to spot). For installing the obstacles two wooden boards were used and they were placed on the ground using large plastic pins which secured them from falling. Two colour conditions were made by colouring the wooden boards using spray paints which became odourless once they dried out. The obstacles were placed 4.25m away from the nest tree on Route 1 and 2.15m away from the nest tree on Route 2 for Nest A, while in Nest B the obstacles were placed 1.95m away from the nest tree towards the foraging tree (Figure 1A). Terrestrial views of the experimental sites were also taken before (Figure 1B) and after (Figure 1C) the installation of the obstacles.

Figure 1. (A) Installed obstacles with a gap in it on the foraging routes of the ants. (B) Terrestrial view of the location around the nest before installation of the obstacles on the foraging Route 1 in Nest A. (C) Terrestrial view of the location around the nest after installation of the obstacles on the foraging routes in Nest B. Terrestrial images were taken using a bloggie camera that takes a 360º view of the area and then the images were converted into cylindrical views by using PlayMemories Home software (all the images were taken during the day time so not under the experimental conditions).

The experiment was done on 42 ants. Some of the ants were not regular foragers, so that final results were based on 20 ants. We excluded those ants for our analysis that appeared only once or twice after being selected for experimentation. In training each ant was marked with individual paint markers after it had successfully passed through the gap in the artificial obstacles on their first trial in order to identify ants on subsequent nights. The unsuccessful ants were not painted and they were excluded from the experiment. For marking the ants, they were captured after passing the obstacles through the gap and were placed inside separate transparent plastic containers. The opening of the container was closed using cotton, and then the containers were placed inside an ice-box for 2-3 minutes to cool the ants. When the movement of the ants ceased then separate Citadel ant paint markers were used to mark each of the ants separately. The paint markers lasted throughout the whole experimental period. After painting we waited for the ants to warm up and then they were released at their nest entrances. We confirmed from watching them that they all went back inside the nest.

After their first trial, ants were trained each day to pass through the gap and training continued until each ant had performed four practice trials including the first trial so that some ants had more training trials. In training trials, obstacles were always placed in one spot, exactly along the line connecting the nest and the foraging tree. After that, different conditions of the experiment were conducted. In test trials, when the painted ants came out from their nest they were followed until they passed through the obstacles either using the gap in it or going around them to go to the foraging trees. During test trials, the gap locations were varied unpredictably from one run to another. The gap location was moved from in 25 cm increments, thus 25 cm, 50 cm, 75 cm, or 100 cm to the left or right randomly. As the experiment was done after evening, red-filtered headlamps were used to observe the ants (Freas et al., 2017). While following the ants, their foraging paths were recorded on gridded papers only during the test phases for further analysis. For recording the paths, we placed a 8×8 m grid of 1m squares made with thread. The grid was made by sticking tent pegs into the ground and winding string around the pegs. The set-up allowed us to record the paths of the ants on gridded paper but offered few unnatural obstructions to the ants, although they walked across the strings. The experiments were continued until most of the ants performed ten experimental trials, while some of the ants performed more than ten trials and a few of them performed fewer than ten trials as they were not regular foragers and some of them stopped appearing during the test conditions. In experiments, we presented the black-white colour condition on both the routes of Nest A and the black-black colour condition to Nest B.

2.3 Statistical Analysis

Foraging paths of each ant in test trials were recorded on gridded paper and for analysis the paths on paper were scanned into digital format. The paths were digitized using the GraphClick software (www.arizona-software.ch/graphclick). The points were converted into *x*-*y* coordinates with the *x*-axis representing left-right travel (negative to the left), the *y*-axis representing the foraging direction towards the obstacles, and (0, 0) being the start point from the nest. The path characteristics analysed were path length and *x*-axis span, both relativized by the distance from the nest to the gap location. Path length was defined as the distance of travel by the ant from the nest entrance to the line at which the obstacles were located, while *x*-axis span was defined as the maximum left-right distance in the path, that is, the difference between the highest and the lowest *x*-values in the transcribed paths. For both path length and *x*-axis span, the dependent measure was divided by the distance from the nest to the gap. An analysis of variance was done on each dependent measure (path length, *x*-axis span) in R, with colour condition as a between-subjects factor and trial number as a within-subjects factor or repeated measure.

We also compared the proportion of ants going through the gap during the test phase. The trials were aggregated to look for learning effects. For each ant one measure for the first half of the tests, and a repeated measure for the second half of the tests were calculated. The ten trials were divided into two blocks of five, and we compared the two blocks to look for the learning effects. The statistical analysis of variance contained colour condition as a between-subjects factor and block (first half of the test vs. second half of the test) as a within-subjects or repeated-measure factor.

3. Results

As individual ants came out from their nest and headed towards the obstacles in the test trials, they searched for the gap location in the obstacles; in total 42 individuals found it and passed through it and some individuals avoided the obstacles completely and passed them on the right or left side. However, 2 ants came back home after finding obstacles on their way on their first trials during the test trials and 3 ants tried to climb the obstacles on their third, sixth and tenth trials separately throughout the total test trials and we did not consider those runs as passing through the gap.

For the analysis of data in test phase, we restricted trial numbers to the first 10 and selected 20 ants. 10 ants completed their 10 trials in black-white colour conditions and another 10 ants completed their 10 trials in black-black colour conditions. We excluded four other ants from black-white colour conditions and another one ant from black-black colour conditions from this analysis to make balanced number of animals in the two colour conditions as they performed fewer than 10 trials. For these 10 trials we analysed the two dependent measures of relativized path length and *x*-axis span, path length and *x*-axis span divided by the distance from the nest to the middle of the gap in the obstacles based on the trial-by-trial data with two colour conditions.

Figure 2 shows the distribution of path lengths in each trial for both the colour conditions. It shows improvement over trials as the path lengths were decreasing in both the colour conditions. The analysis of variance confirmed this, revealing significant main effect of trials, with paths becoming more efficient (smaller path length) over successive trials (F-test, F = 19.27, $p < 0.05$). However, the colour condition did not show any significant main effect (F-test, F = 2.17, $p = 0.175$). The interaction between colour condition and trial number also did not show any significant effect (F-test, F = 1.21, $p = 0.230$).

Figure 3 shows the distribution of *x*-axis spans in each trial in both the colour conditions. It also shows improvement over successive trials. The *x*-axis span is decreased over trials. In inferential statistics, the analysis of variance showed a significant main effect of trials (F-test, F = 22.17, $p < 0.05$). Again, colour condition did not show any significant main effect (F-test, F = 3.44, $p = 0.097$). The interaction between colour condition and trial numbers also did not show any significant effect (F-test, F = 1.97, $p = 0.194$).

Figure 4 shows the proportion of ants going through the gap in the test phase. We aggregated trials to look for learning effects. We measured the first half of the tests and a repeated measure for the second half of the tests for each ant that had performed 10 trials during the test phase. The analysis of variance showed that the block main effect (difference between the first half of trials and the second half of trials) was not significant (F-test, F = 7.82, p = 0.219). The colour conditions also did not differ significantly (F-test, F = 1.13, p = 0.481). The interaction between these two factors also did not show any significant effects (F-test, F = 0.74, p = 0.548).

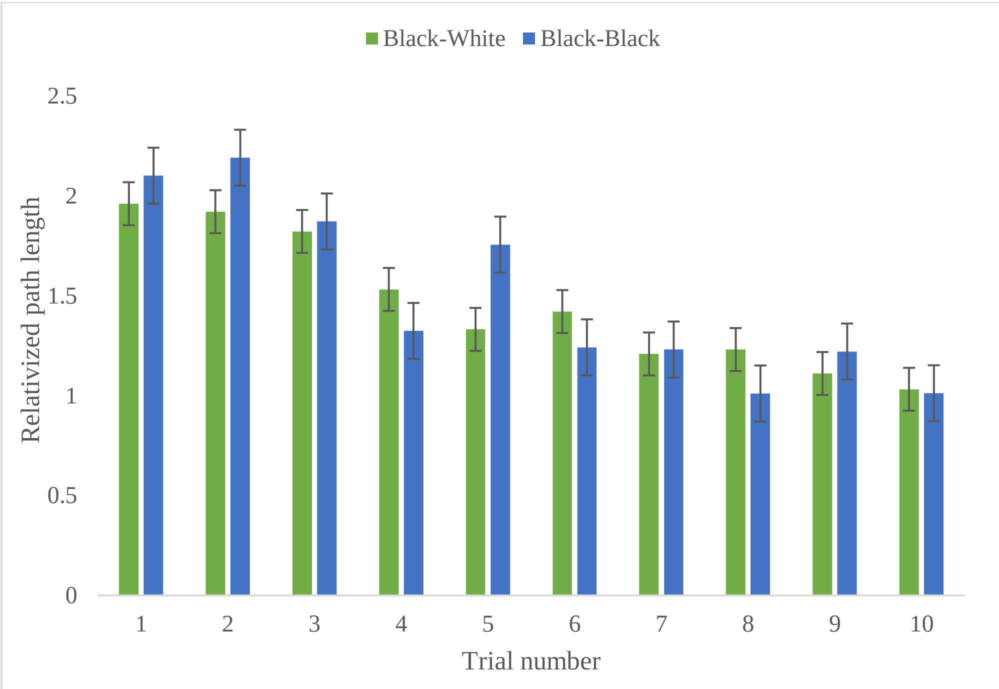

Figure 2. Data from the first 10 trials in both the colour conditions. The x-axis represents trial number while the y-axis represents the relativized path length, which is the path length divided by the distance from the nest entrance to the gap in the obstacles. Error bars indicates 95% confidence intervals about the mean.

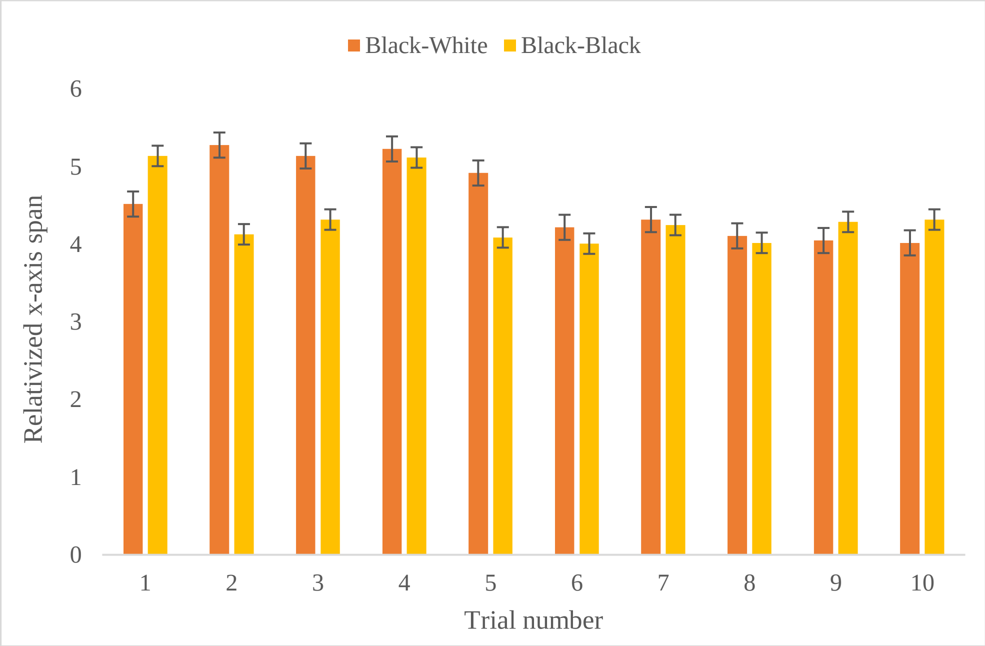

Figure 3. Data from the first 10 trials in both the colour conditions. The *x*-axis represents the trial number while the *y*-axis represents the relativized *x*-axis span. Error bars indicates 95% confidence intervals about the mean.

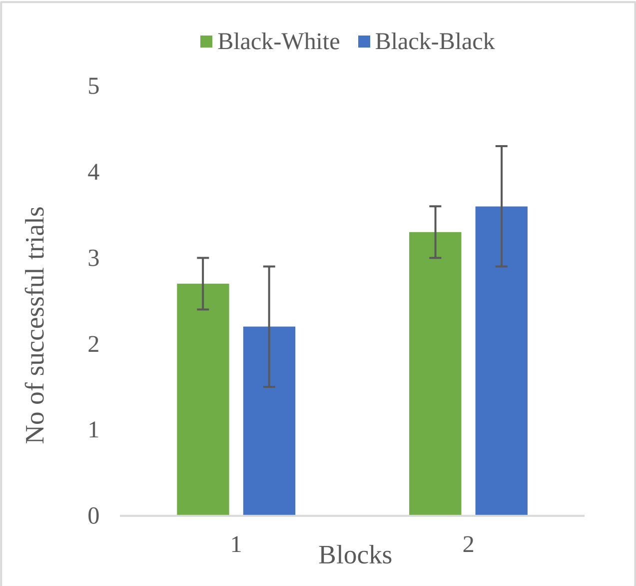

Figure 4. Data from aggregating the first half of the tests and the second half of the tests for two colour conditions. The *x*-axis represents the trial number while the *y*-axis represents the number of successful trials as going through the gap of each ant. The first two bars show the first half of the tests and second two bars show the second half of the tests. Error bars indicate 95% confidence intervals about the mean.

Recorded paths of a single individual ant are given in the supplementary section where its foraging paths in the test phase are shown with the unpredictable movements of the gap location in the obstacles.

4. Discussion

The main aim of the present study was to examine the learning strategies of nocturnal bull ants during obstacle navigation. We have shown that *M. midas* learns to find a gap in an obstacle that obstructs their direct paths after several trials.

For testing the ants' ability to find a gap in an obstacle we selected two different nests within the same environment. Both of these nests were surrounded by landmarks, which are used by this and other species of bull ants to navigate from the nest to the foraging trees (Freas et al., 2017a,b; Narendra et al., 2017; Narendra and Ramirez-Esquivel, 2017; Warrant and Dacke, 2011). The artificial obstacles that were placed on the ground acted like new landmarks and ants had to find the suitable way to go to their foraging tree using the new landmarks. Image analysis showed that the change in the overall panorama following the installation of the obstacles was considerable. To deal with new landmarks ants often learn through a carefully constructed series of learning walks carried out in multiple orientations (Fleischmann et al., 2016; Jayatilaka et al., 2013). Experienced ants also do some scanning behaviour at the start of the day (Wystrach et al., 2014). Typically, ants leaving the nest are well oriented towards their foraging trees and do not turn back and look elsewhere. When our tested ants first encountered the change in their visual panorama, a number of animals turned back and looked towards the nest direction and also looked around. It is during the learning walks (or learning flights in bees (Collett et al., 1993; Dittmar et al., 2011; Zeil and Kelber, 1996;) and wasps (Collett et al., 1993; Stürzl et al., 2016)) that insect are thought to develop a visual representation of the goal environment which they recall during trip to pinpoint home (Stürzl et al., 2016). However, it was not clear from our results how many learning walks were enough to learn about the change of the landmarks. The situation in the experimental problem is complicated by the fact that the gap location changes from night to night. After completing four successful trials less than half ants still failed to find the gap location in the obstacles. Some, however, avoided the obstacles and passed around it on the sides to go to the foraging trees.

Scanning behaviour is another useful strategy in navigating by the use of the surrounding visual scene (Wystrach et al., 2014; Zeil et al., 2014). Ants perform more scans when their familiar surroundings have been altered or when the direction provided by terrestrial cues conflict with celestial cues (Wystrach et al., 2014). In the current study, we showed that ants learnt about the change in their landmarks and panorama after several trials. This behaviour must rely on the use of learnt visual cues. It has recently been shown that while on their foraging route, members of *M. pyriformis*, another nocturnal *Myrmecia* species that relies heavily on the visual scene (Reid et al., 2011), attempt to stabilise their head horizontally while travelling on route on an uneven surface, as view similarity drops markedly as the view is rotated around the roll axis (Raderschall et al., 2016). This species has also been shown to perform extensive scanning behaviours during learning walks around the nest, indicating that scan behaviours are part of the nocturnal ant's navigational repertoire (Narendra and Ramirez-Esquivel, 2017). Similar behaviours seem to apply for obstacle navigational strategies in *M. midas*. The same visual memories and strategies may be used when foraging both on ground and on trees (Freas et al., 2018). Narendra and Ramirez-Esquivel (2017) showed in their studies that *M. pyriformis* is highly sensitive to panorama changes. When several trees were removed, resulting in small changes to the nest panorama, foragers showed major disruptions in their navigational efficiency, walking slower and in a less directed fashion. Furthermore, these behavioural changes persisted over multiple nights before returning to pre-change levels, suggesting a period of learning the new panorama. However, there appears to be a range of flexibility, in that some ants may learn new panoramas after only one exposure (Freas and Cheng, 2017, 2018) and can successfully orient to both new and old panoramas for multiple days after a change occurs (Freas et al., 2017c). Fernandes et al. (2018) showed that visual cues learnt by wood ants through Pavlovian conditioning are retained for at least 1 h. They suggest that memory retention is dependent upon the ants' performance during training and ants can form visual associative memories when restrained. Our test ant species, *Myrmecia midas*, also showed visual associative learning after completing several trials in the current experiment.

Fleischmann et al. (2016) showed that the desert ant species *Cataglyphis fortis* locates their goal more accurately and precisely with increasing experience. In most cases, experienced foragers pick up a food item, run straight into the middle of the landmark array and center their search on the test field around the fictive nest entrance (Cheng et al., 2014; Wehner and Räber, 1979; Wehner et al., 1996). In contrast newly foraging ants search at the release point. Faced with an artificial landmark array consisting of four cylinders, the Australian desert ant *M. bagoti* gradually increased its search performance for the nest on a test field when trained with a different number of trials over different numbers of days (Narendra et al., 2007). Buehlmann et al. (2016) have shown that wood ants trained to different shapes in the panorama, use the centre of mass of each salient feature for guidance. Our study lends support to these studies by showing that many experienced foragers were able to locate the gap in the obstacles.

To test the ants' detection of edge contrast we used two colour conditions in two separate nests. The black and white colour condition provided sharp edge contrast to detect the gap location, which was easier to spot. In contrast, the black and black colour conditions did not provide any edge contrast to detect the gap location, which was harder to spot. However, the results did not show any significant differences between the learning of these two groups. Möller (2002) proposed that insects are able to detect the skyline by distinguishing the ultraviolet/green contrast between the ground and the sky. The sky has a much higher proportion of UV light relative to green wavelengths, compared to the relative amount of UV light being reflected from vegetation and other objects below the skyline (Chittka et al., 1994). The ratio of UV to green may be perceived by ants and other insects through the use of UV and green receptors in their eyes (Mote and Wehner, 1980). Möller (2002) suggests that the UV/green contrast creates a reliable discrimination mechanism between ground objects and the sky that is superior to detection based only on the UV contrast due to the fixed threshold in the UV/green contrast. Additionally, the results of Möller (2002) suggest that skyline detection would be impossible by only using green receptors due to overlap between ground objects and the sky in the green colour range. A UV/green contrast mechanism for skyline detection could not be utilised by individuals in the obstacles due to lack of UV cues in the sky after providing the colour conditions on the obstacles.

Now the question arises: how were the ants able to find the gap location in the obstacles? The experiments were done in the ants' natural environments and about 75m away from the test ground there were a lot of street lights as well as a car parking field around it. As the colour conditions did not help the ants to locate the gap but still they were successful in finding it, there was a chance that the street lights were passing through the gap to allow ants to identify the location of the gap.

Future Directions

Individual ants oriented correctly during the test phase after completing several successive trials and trial-by-trial improvement was also observed. Nocturnal ants always face challenges in their navigation as the visual cues are less salient compared to those used by diurnal species of ants (Narendra et al., 2017). This gap-finding test can be also tested on other species of nocturnal ants. Although diurnal ants are easy alternatives to study, nocturnal ants are less well studied. In our test it seemed quite easy for the ants to pass around the obstacles on their far sides, so the obstacle test could be made more difficult for the ants to circumnavigate in future projects. We could create wider obstacles to prevent or reduce navigation around the obstacles. Another future project would be to also place an artificial food source for the ants at the gap, to examine the effects on learning of an immediate reward. As we did our test only on the individuals who were travelling out to for forage, those ants coming back to their nests after completing foraging could also be tested in gap finding.

We did not find any significant effects of the colour conditions we provided during our tests. This negative result calls for replications comparing colour contrasts under different conditions.

Another possible future direction for our study would be to use a high-quality global-positioning system (GPS) device to track the movements of the ants much more accurately. The best GPS systems now have accuracies in the range of centimetres.

In future we would like to develop software that allows us to analyse the walking paths of the individuals during testing more accurately. Due to time constraints the current project was designed to test ants' ability to find the gap while in future we can analyse their strategies of overcoming the obstacles in more detail.

Conclusions

Foraging ants have been key to the study of navigational strategies such as path integration, panorama-based guidance, and the use of olfactory, visual and idiothetic cue sets. Although the learning and neurobiological mechanisms are unclear, we have shown that nocturnal bull ants, a majority anyway, can find a 10cm gap in an obstacle. The findings from this research add significant knowledge about the learning in invertebrates, specially in ants, while training has proved that ants gradually improve the tasks they have been assigned for.

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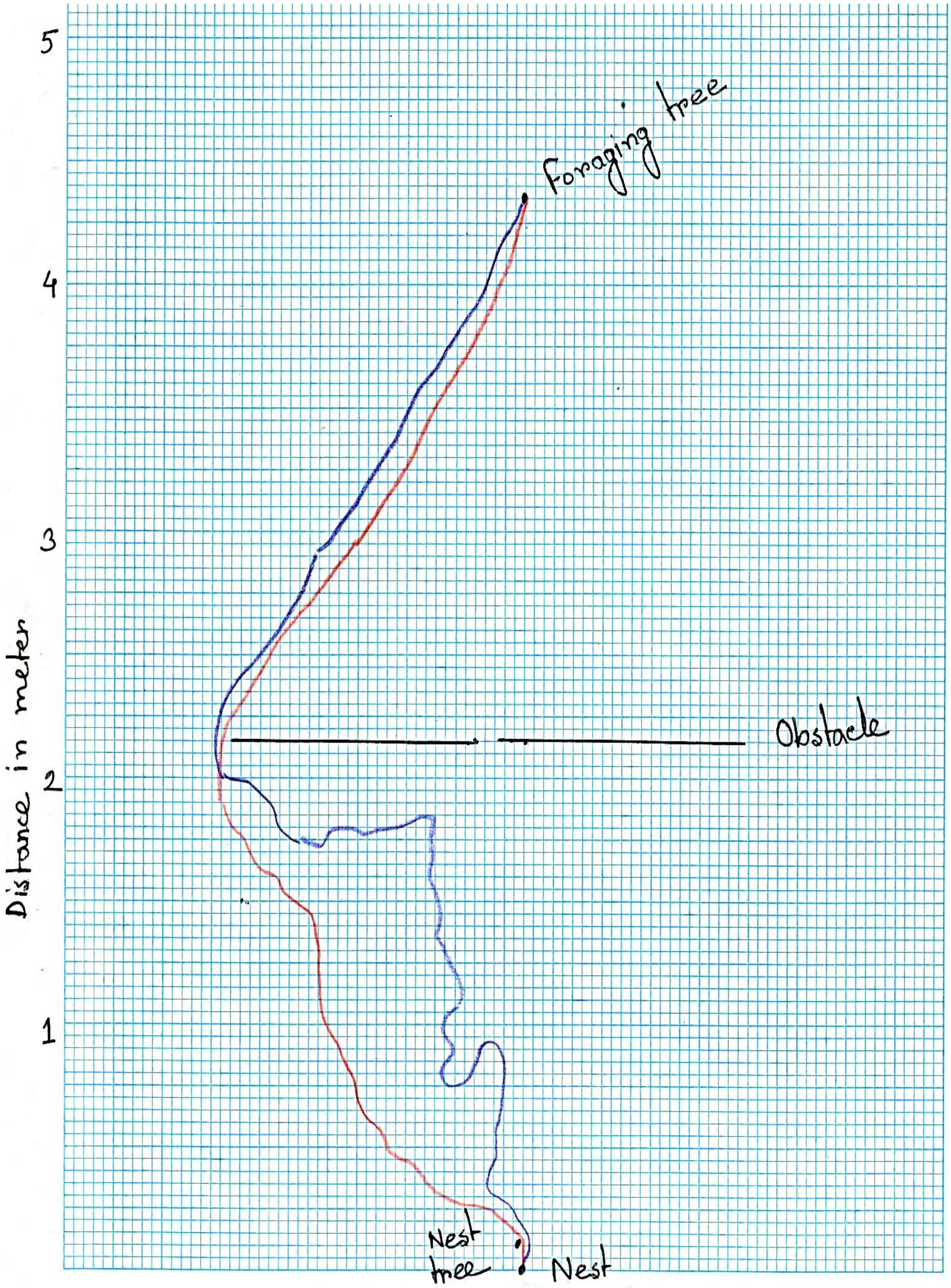

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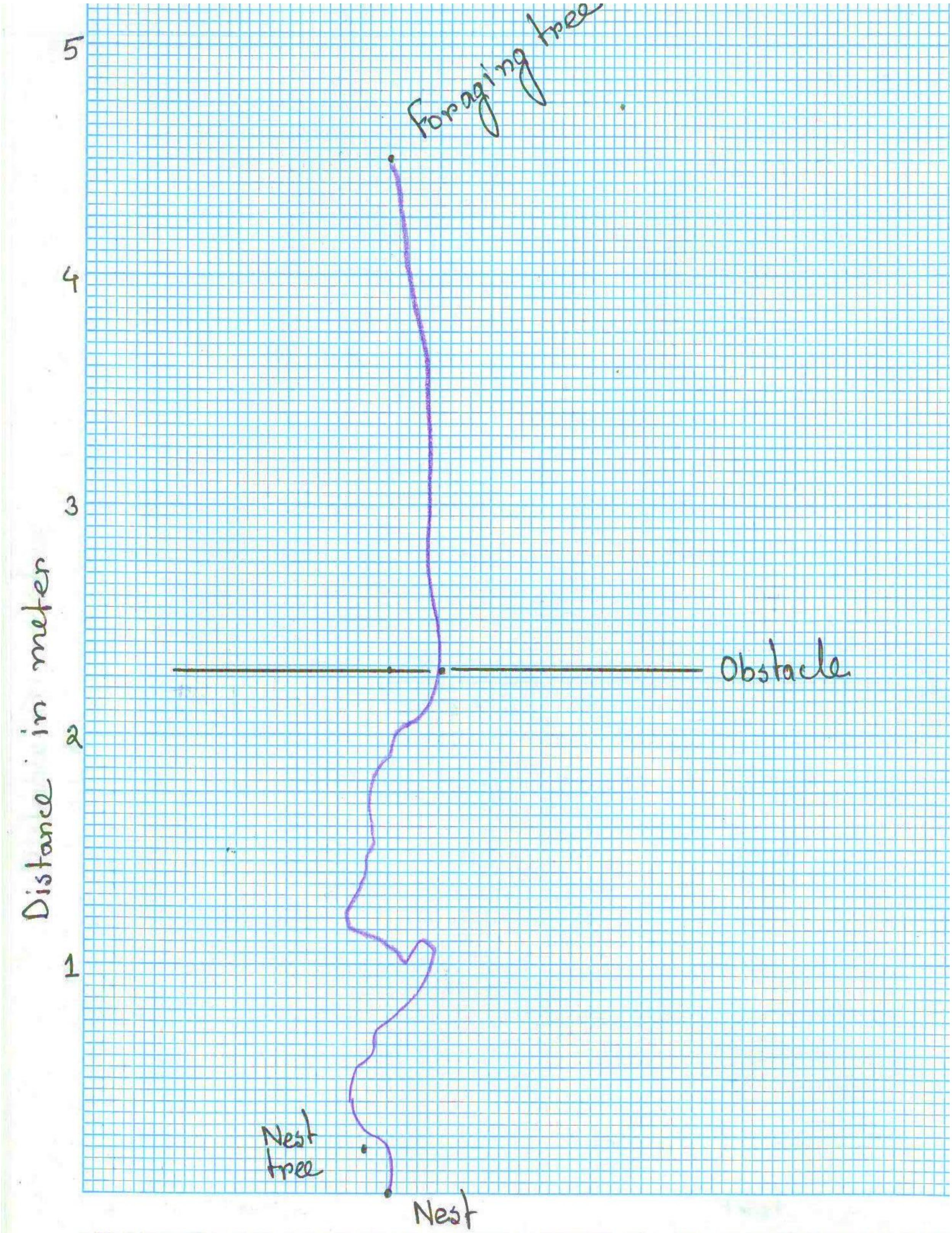

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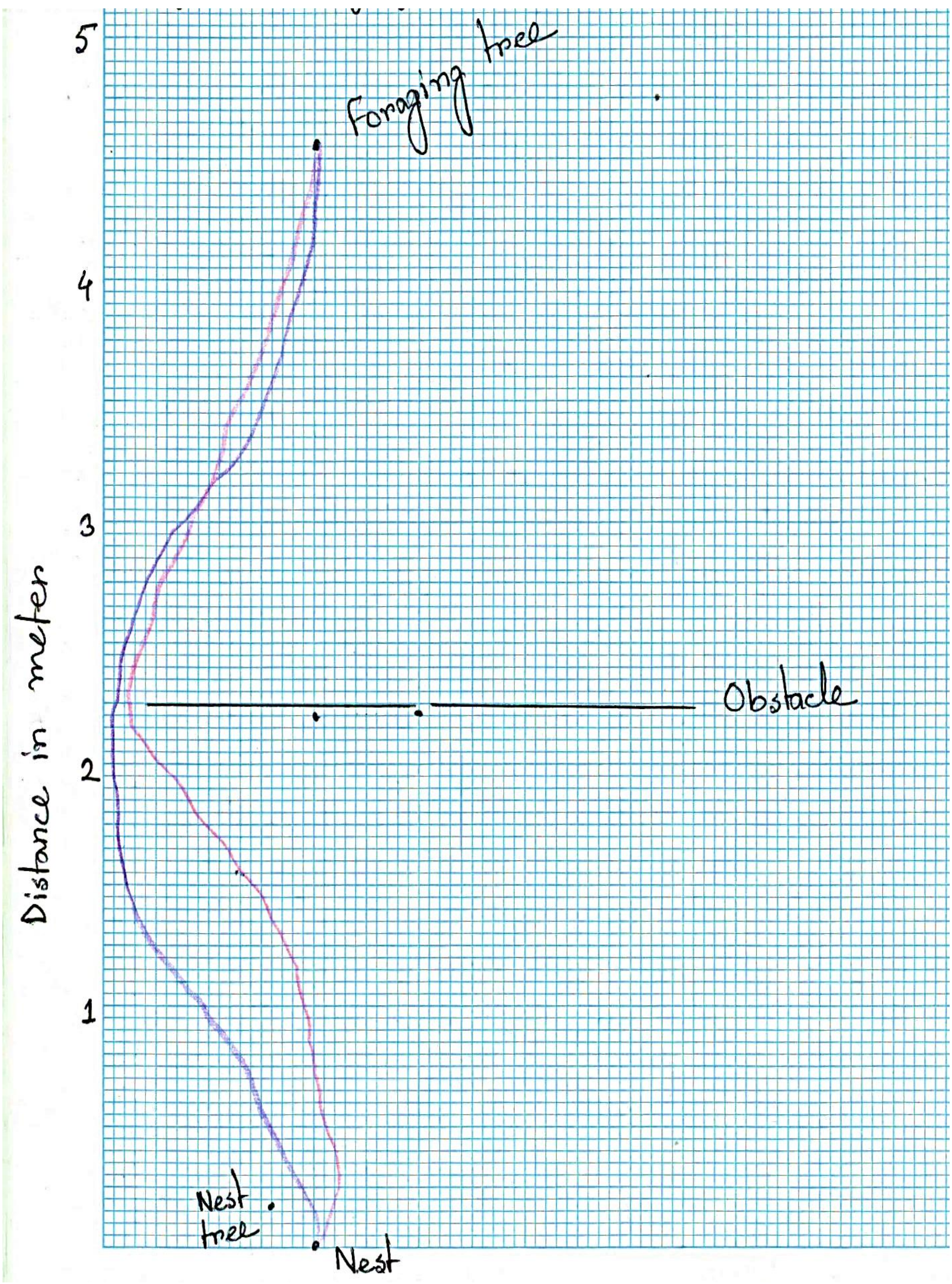

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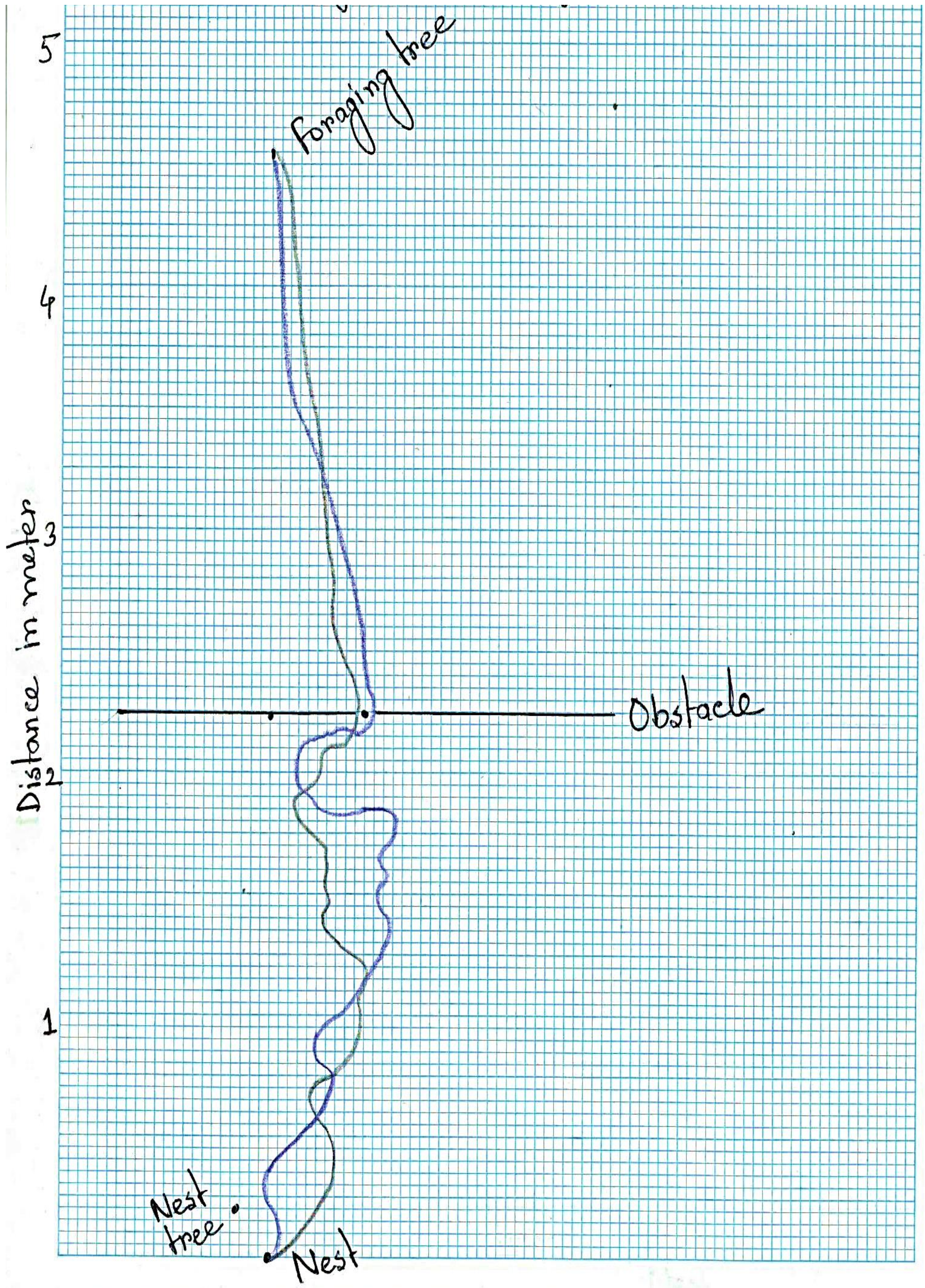

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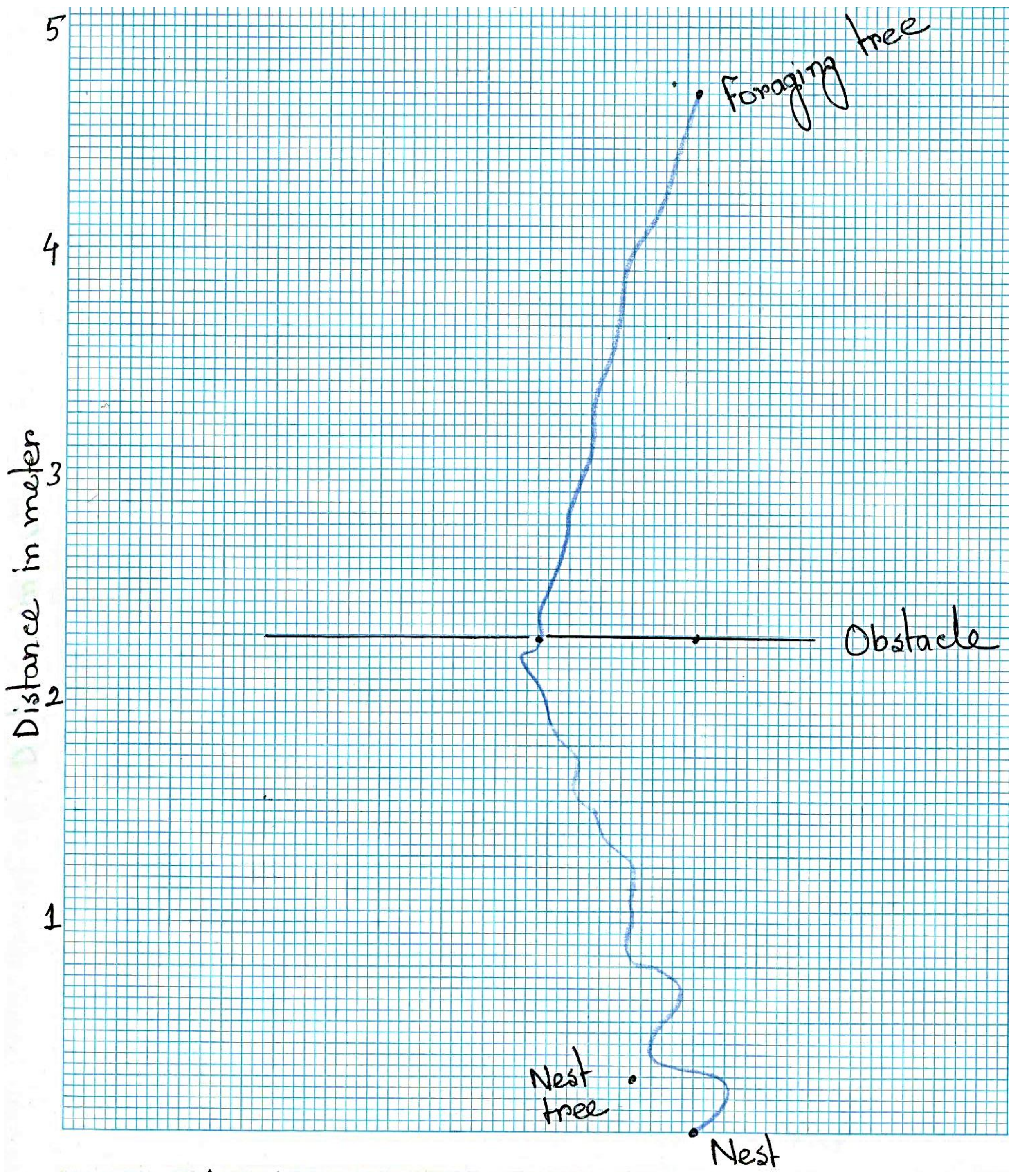

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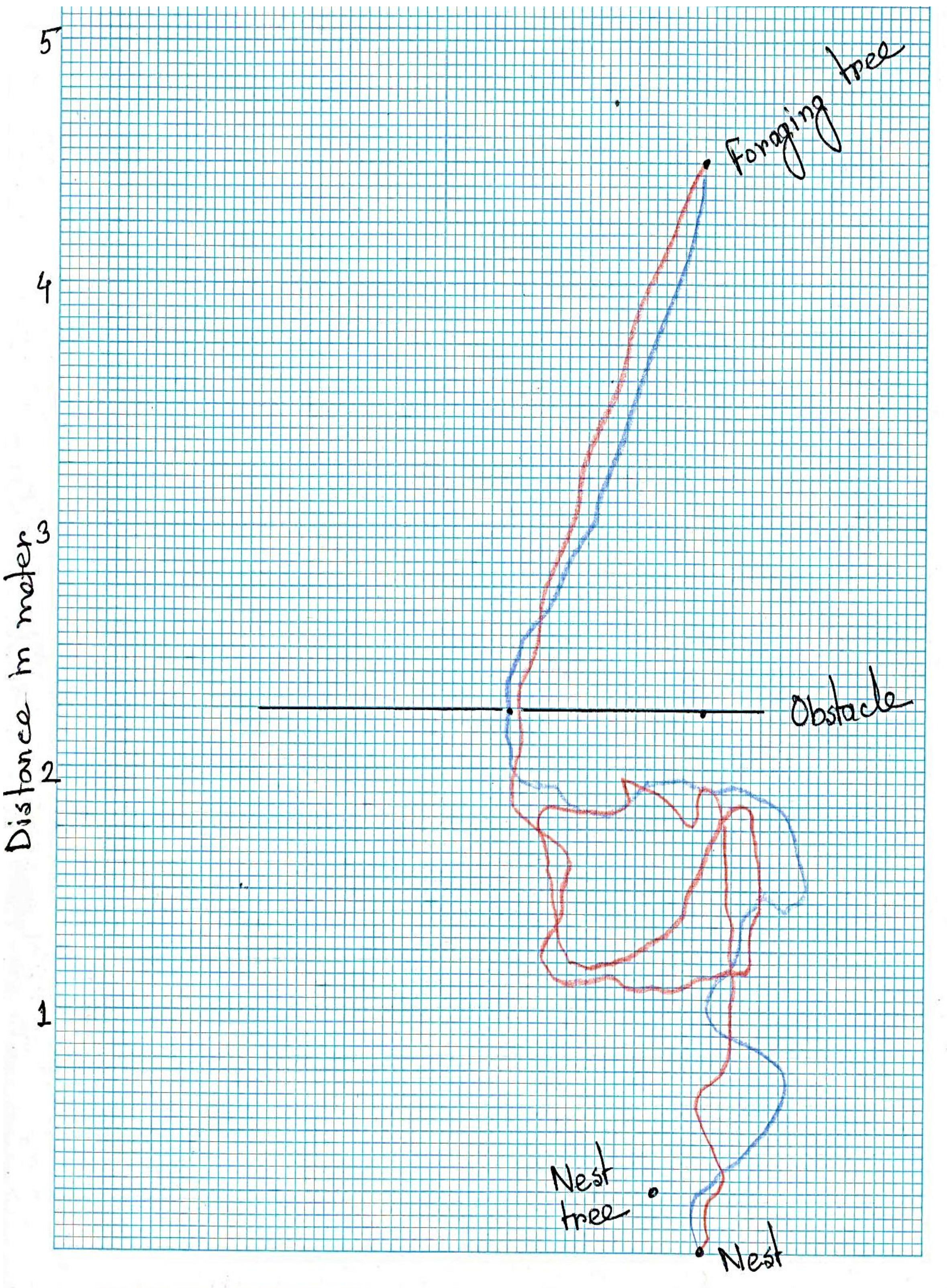

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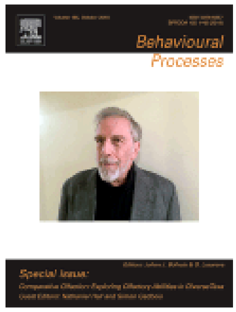

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• Number the illustrations according to their sequence in the text.
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Cancer Research UK, 1975. Cancer statistics reports for the UK. http://www.cancerresearchuk.org/aboutcancer/statistics/cancerstatsreport/ (accessed 13 March 2003).
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