

# Foraging ecology of the night-active bull ant *Myrmecia pyriformis*

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**Abstract.** Here we report on the nocturnal bull ant *Myrmecia pyriformis*, a species whose activity to and from the nest is mainly restricted to the dawn and dusk twilight respectively. Recent research on *M. pyriformis* has focussed on its visual system, the timing of activity patterns, and the navigational strategies employed by individuals while foraging. There is, however, a lack of basic ecological information about this species. The present study describes the behaviour and foraging ecology of wild populations of *M. pyriformis*. We find that most foragers make only one foraging journey per night, leaving the nest at dusk twilight and returning during dawn twilight. Individuals who make multiple trips typically return with prey. We provide evidence that foragers imbibe liquid food while abroad and likely share these resources via trophallaxis once within the nest. Activity during the night varies with moon illumination, and we postulate that this is due to changes in light levels, which influence navigation to and from the nest. This hypothesis is supported by observations of activity during overcast conditions. Finally, we also describe some aspects of colony founding, colony demise and the behaviour of reproductive individuals during the mating season.

**Additional keywords:** activity pattern, moon, *Myrmecia*, nocturnal.

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## Introduction

The ant genus *Myrmecia* provides an excellent study system for investigating the evolution of niche specialisation. This is because closely related species forage in distinct temporal niches, which influences various aspects of their biology and behaviour (Greiner *et al.* 2007; Narendra *et al.* 2010, 2011; Jayatilaka *et al.* 2011; Reid *et al.* 2011). The night-active *Myrmecia pyriformis* (Smith, 1858) is an excellent candidate to elucidate the behavioural and morphological modifications necessary for being active in dim-light conditions. There is, however, a lack of basic ecological information about this species. This paper describes the foraging ecology of this night-active ant.

*Myrmecia* is essentially restricted to Australia, with only two of the 89 known species occurring elsewhere (Clark 1951; Ogata and Taylor 1991). The larger species are commonly called ‘bulldog ants’ due to their aggressiveness and ferocious attack behaviour. During the 1900s *Myrmecia* species were the focus of several ecological studies because they were understood to possess behavioural and morphological traits that were considered ‘primitive’ among ants (Brown 1953; Wilson 1971; Taylor 1988; Ogata 1991; Peeters 1997). While genetic evidence has removed *Myrmecia* from its formerly basal position in ant

phylogeny (Brady *et al.* 2006; Moreau *et al.* 2006; Ward 2007), it is still believed that some of its species might closely resemble the earliest social organisation and behaviour of formicids (Taylor 2007). This is partially because the newly mated dealate queens do not seal the entrances of new nests after establishment, suggesting that they are partially claustral, venturing out to forage for food for themselves and their brood (Freeland 1958).

More recently, research has been devoted to studying the diversity of chromosomes in *Myrmecia*, since they have the broadest range of chromosome numbers amongst the Hymenoptera (Crosland and Crozier 1986; Imai *et al.* 1994; Hirai *et al.* 1996; Goodisman *et al.* 2008). In fact, *Myrmecia* is the most karyologically diverse of all animal genera, with chromosome numbers ranging from the smallest possible,  $2n=2$  to one of the largest known amongst formicids,  $2n=84$  (Crosland and Crozier 1986; Imai *et al.* 1988, 1990).

Colony size can vary widely from below 50 to over 2200 (Gray 1974). Within nests there is very little worker–worker, worker–queen, or worker–larva social interaction (Haskins and Haskins 1950). Trophallaxis (the regurgitation of food to nest mates and larvae) is present in some species, but instead of

being initiated by the receiver, the donor initiates the interaction (Haskins and Whelden 1954). In some species food resources are distributed throughout the colony via trophic egg laying, a process whereby egg material is laid by workers and fed to recipient larvae, queens and other workers (Freeland 1958; Dietemann *et al.* 2002).

Chemical communication in *Myrmecia* is less sophisticated than in many ant species. The workers navigate visually and do not lay scent trails or show evidence of recruitment to food sources. They feed individually on nectar, sap, and homopteran honey dew, and forage for insect prey when larvae are present within the nest (Haskins and Haskins 1950; Freeland 1958; Gray 1971b; Hölldobler and Wilson 1990).

There is a great degree of polymorphism in *Myrmecia*. Several species have workers that vary significantly in size (Haskins and Haskins 1950; Freeland 1958; Gray 1974; Higashi and Peeters 1990; Dietemann *et al.* 2002). Such species usually display bimodal size distribution among workers, with differences in the tasks performed by each class. Small workers remain within the nests and tend to the brood, while larger workers forage for food and inhabit the upper galleries of the nests (Haskins and Haskins 1950; Gray 1974; Higashi and Peeters 1990; Dietemann *et al.* 2002). Finally, *Myrmecia* workers are well known for their large eyes, good visual acuity and aggressive response to movement (Haskins and Haskins 1950; Via 1977; Eriksson 1985; Greiner *et al.* 2007; Narendra *et al.* 2011).

The focus of this study is *M. pyriformis*, a species mentioned only in passing in previous literature. It is found across south-eastern Australia (<http://anic.ento.csiro.au/ants/>), with colony sizes varying from 200 to over 1400 individuals (Barker 1903; Gray 1971a, 1974). Foragers show bimodal size distribution, ranging in length from 9 to 30 mm (Haskins and Haskins 1950; Clark 1951; Dietemann *et al.* 2002, 2004; Greiner *et al.* 2007). The smaller of the two classes resides in the lower parts of the nest (generally where most of the brood is situated) while larger workers reside near the top of the nest (Gray 1974). The workers are thought to secondarily distribute food resources throughout the colony by trophallaxis (Crosland *et al.* 1988). *M. pyriformis* workers forage nocturnally (Brown 1953; Greiner *et al.* 2007; Narendra *et al.* 2010), and possess a potent sting, which is used to subdue prey (McGain and Winkel 2002). Mating flights take place during the day in late summer and early autumn (Tepper 1882; Crosland *et al.* 1988; Narendra *et al.* 2011). Gamergates (a class of workers capable of mating and reproduction) have been reported in *M. pyriformis* (Dietemann *et al.* 2004), and have been recorded to survive for three years in the laboratory, slightly longer than workers of other *Myrmecia* species (Haskins and Haskins 1980; Dietemann *et al.* 2004). When fully developed the nests have two or three main shafts with side chambers linked either directly or via short galleries (Gray 1974).

Recent research on *M. pyriformis* has focussed on its visual system, the timing of activity patterns, and the navigational strategies employed by individuals while foraging (Greiner *et al.* 2007; Narendra *et al.* 2010, 2011; Jayatilaka *et al.* 2011; Reid *et al.* 2011). These studies have shown that *M. pyriformis* foragers are visually well adapted to low light levels, with structural modifications to the compound eyes that increase sensitivity 27-fold when compared with closely related day-active species (Greiner *et al.* 2007; Narendra *et al.* 2011). This

increased sensitivity facilitates accurate and swift navigation to and from foraging sites at dusk and dawn twilight, since foraging individuals rely heavily on visual landmark information for navigation (Reid *et al.* 2011; Narendra *et al.* 2013). In comparison with many other ant species in which out-of-nest activity is thought to depend primarily on temperature, the onset of nest-departure in *M. pyriformis* during evening twilight is determined by the ambient light conditions at sunset (Narendra *et al.* 2010; Jayatilaka *et al.* 2011).

Despite these studies there is still a lack of information on the basic biology and foraging ecology of *M. pyriformis*. Such information is vital to correctly interpret the species' behaviour, morphology and neural organisation. The present study aims to describe the behaviour and foraging ecology of wild populations of *M. pyriformis*.

## Material and methods

### Study site and study species

Observations were carried out on a regular basis from January 2007 to December 2012 on five nests of *M. pyriformis* located close to one another in the Campus Field Station at The Australian National University, Canberra (35°16'50"S, 149°06'43"E) (Fig. 1). Three nests were used for in-depth analysis of foraging activity (termed Nest 1, Nest 2 and Nest 3).

### Field activity data

A head torch fitted with a red filter was used for nocturnal observations on colonies at the field site. This did not appear to disturb the ants. To confirm the 24-h activity pattern of *M. pyriformis* (Greiner *et al.* 2007; Narendra *et al.* 2010), foraging activity at Nest 2 was recorded by monitoring forager traffic across a 30-cm-radius reference circle centred on its entrance on 3 November 2009 (austral spring). The numbers of incoming and outgoing foragers were recorded in 10-min bins.

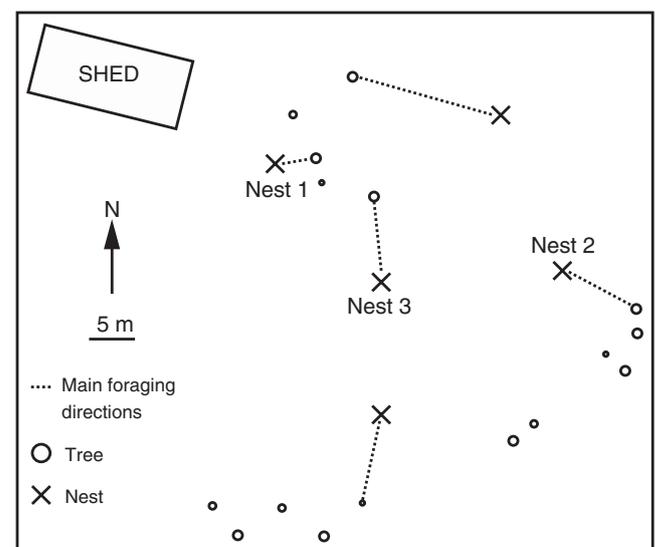


Fig. 1. The study site. All nests were within 35 m of one another and located near *Eucalyptus* trees.

To investigate individual foraging times, ants at Nest 2 were marked on the mesosoma and gaster with water-based acrylic paint (Citadel Colour, Games Workshop, England) to allow individual identification. Three 24-h observation sessions were carried out at the subject nest during November 2009 (austral summer) to record the number of trips by each forager each night, the duration of each trip and the level of success in prey capture.

In order to determine whether individuals imbibe liquid food while foraging, individually marked ants at Nest 2 were collected in the evening twilight as they left for foraging. Within 10 min of being captured, they were brought to a nearby laboratory and weighed on a microbalance (Sartorius LE26P, Precision Weighing Balances, MA, USA). Ants were taken back to the field and released at the base of the tree on which they were known to forage. These same ants were caught close to the nest entrance while they were returning during morning twilight and weighed once more. Data were analysed with a paired *t*-test.

As light levels influence activity times in *M. pyriformis* (Narendra *et al.* 2010), we postulated that the phase of the moon (with resulting changes in ambient light conditions) might influence activity. To investigate this possible effect we recorded 24-h activity patterns during different lunar phases at Nest 1 and Nest 2. Lunar phase is expressed as the percentage of illuminated moon surface. At Nest 1, activity was recorded during February 2006 (austral summer) when the lunar illumination value was 0.0% and 95.0%. At Nest 2, activity was recorded during November 2009 (austral summer) when lunar illumination values were 3.8% and 99.1%. An additional recording was made at Nest 2 on a completely overcast night. Apart from this, all monitoring took place on clear nights with relatively little cloud cover. Light levels were recorded in radiometric units using a SHD033 detector (Warsash Scientific: ILT 1700) at Nest 2 and values were logged every 0.5 s for the entire recording period.

Data on moon-phase and activity patterns were analysed by comparing the number of foragers active during the night with those active during dusk and dawn twilight. Differences between these two groups were analysed using Fisher's Exact test.

#### *Astronomical data*

Astronomical data (sunset, sunrise, moonset, moonrise, twilight, moon phase and lunar illumination) were obtained from Geoscience Australia (<http://www.ga.gov.au>). Sunset and sunrise are defined as the time when the upper edge of the solar disk coincides with the ideal horizon. The end of astronomical

twilight after sunset and the beginning of astronomical twilight before sunrise are defined as the points when the centre of the sun is 18° below the ideal horizon. The period between sunset and the end of evening astronomical twilight is referred to as 'dusk twilight' and that between the start of dawn astronomical twilight and sunrise as 'dawn twilight' (see also Cronin *et al.* 2006). The period following dusk astronomical twilight and preceding dawn astronomical twilight is referred to as 'night'.

## Results

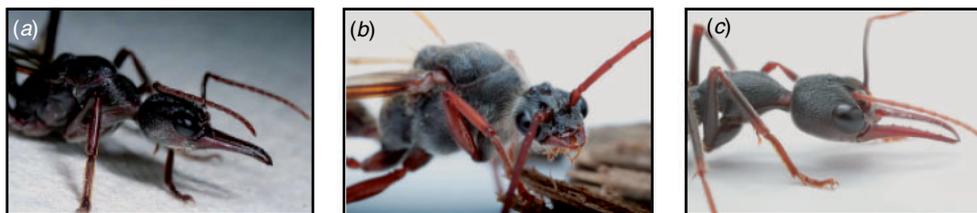
### *Reproduction*

Reproductive *M. pyriformis* males and females were seen at nest entrances from early February to mid-April (austral summer to autumn). Both sexes can be easily identified by the presence of wings (Fig. 2*a, b*). Males can be distinguished by several features, the most notable of which are reduced mandibles, small head size, reduced antennal scape, large ocelli and a slender gaster. Queens resemble workers in almost all features but have slightly larger mesosoma, gaster and ocelli (Fig. 2*a, c*). Both males and queens were found at the nest entrance during the day, dusk twilight and early parts of the night. When observed after sunset both males and queens, independent of one another, would often emerge from the nest to walk very slowly around the nest entrance and return to the nest. They were often accompanied by a small number of workers that moved agitatedly around these alates. On 4 March and 5 March 2012, males of *M. pyriformis* left the nest (Nest 2) at 1100 hours. Mating in *M. pyriformis* was observed on hilltops on two occasions, immediately after rainy days (3 February 2011, Mt Ainslie; 8 January 2012, Mt Majura) in the morning between 1030 and 1230 hours.

On two other occasions dealate females were observed moving through the environment at night. One was found during February 2008 (austral summer) and another in March 2010 (austral autumn) climbing a tree during dusk twilight. The second individual was partially dealate with one wing attached. On both occasions the weather was warm and calm and there had been heavy rain during several previous days.

### *Establishment*

During observations in the field we noticed two nests in 2007 that were absent earlier and were most likely relatively new, young colonies. One nest was found in the spring of 2007 near a previously established *M. pyriformis* nest. This new nest did not survive for long. Foragers from the established nest patrolled the new nest area and attacked its workers as they emerged to forage. This occurred every night until foraging from the new



**Fig. 2.** Reproductive and worker castes in *M. pyriformis*. (a) Reproductive female, (b) reproductive male, and (c) worker. Photos by Ajay Narendra.

nest ceased. No foragers were seen at this site again and the nest entrance was soon covered with soil. Similar behaviours of suppressing apparently competitive non-conspecific nests were observed at Mt Majura Nature Reserve, Canberra. At the start of activity each evening two or three *M. pyriformis* foragers would patrol the nest entrance of a diurnal-crepuscular bulldog ant species, *Myrmecia tarsata* (Smith, 1858), and attack returning foragers. Workers of *M. pyriformis* carried/dragged *M. tarsata* ants individually up to 15–20 cm away from the nest, dropped them after extensive biting and stinging and returned back to the nest of *M. tarsata* to capture more individuals. Injured *M. tarsata* slowly attempted to return to the nest.

The second 'new' nest of *M. pyriformis* that we observed, first in the spring of 2008, remained active and free of competitive interference (Nest 3). Evening departure activity began up to 20 min earlier than at other nearby, well established nests. This pattern of relatively early departure continued until early April (austral autumn), at which point the colony sealed its nest entrance for hibernation. The entrance remained sealed until the following spring when foraging resumed, with foragers first seen in late October. Observation continued across the following winter, during which the nest entrance this time remained continuously open with workers leaving to forage. At all other nests we monitored during this study foraging continued throughout each of the winter periods.

#### The end of the colony

The longest surviving colony known to us was first encountered in February 2006 when 437 foragers were recorded departing the nest (Campus Field Station, ANU, Canberra). It remained functional with a large force when last checked (28 April 2013). Its forager force was large enough when first observed to imply a colony-age of at least three years (in evidence, another observed colony known to be two years old had a much lower forager number of ~30). The forager force of the colony was still large (numbering over 100) in April 2013 and the colony did not appear to be at risk, as relatively large workers were numerous and constituted most of the foraging force. This may be taken in *M. pyriformis* as an indication of good colony health (Freeland 1958; Gray 1974; Dietemann *et al.* 2002) and suggests that *M. pyriformis* colonies can persist in nature for at least 10 years.

During the period of observations one colony went into obvious decline, eventually dying. Initial signs of decline were first noted when forager numbers during winter (2009) were unusually low in comparison to nearby nests, with only five individuals leaving the nest to forage. The nest entrance of the declining colony remained extremely small (<1 cm diameter) as the weather warmed. The nest entrance continued to shrink until it finally disappeared in April 2010 (austral autumn). In *M. pyriformis* the size of the nest entrance appears to change with forager numbers. Typically, during summer the entrance is large (3–5 cm diameter) and kept clear of debris and plant material. During winter it becomes narrower, presumably as a result of reduced forager traffic. Over the preceding summer at the declining colony, foragers were relatively few and all were small, minor workers. When this nest was healthy, foragers ranged in size from 15 to 30 mm, with most of the foraging force consisting of larger individuals. Towards February 2010

(austral summer), foraging essentially ceased and the few workers present remained near the nest entrance during the foraging period. Eventually, they also disappeared and the nest entrance closed completely.

#### Daily activity pattern

We observed foraging activity in detail at Nest 2 (3 November 2009) to confirm the 24-h activity pattern described in previous studies. A total of 140 foragers left the nest on a single day. Activity began just before sunset (Fig. 3), with foragers exiting the nest and moving directly to nearby *Eucalyptus* trees, which they scaled. The number of departing foragers increased steadily to peak 20 min after sunset, with 33 individuals exiting the nest in that particular 10-min bin. In total, 1.4% of the foragers left the nest before sunset, 87.9% left during dusk twilight, and 10.7% after twilight.

The behaviour of foragers as they left the nest changed as the ambient light waned. Close to sunset ants began to gather at the nest entrance, but did not immediately set off towards the trees, often waiting for several minutes before departure. Some individuals that had partially emerged from the nest promptly turned and re-entered. This behaviour was often repeated several times before foragers left the vicinity of the nest. During dusk twilight this behaviour changed and foragers left the nest without hesitation. During the night (i.e. after dusk twilight) many individuals exited the nest and wandered close to the entrance for 1–10 min before re-entering. In contrast to those that had exited earlier, most did not later re-emerge to forage. The resulting reduction in activity is seen in the rapid decline of outgoing forager numbers towards the end of the dusk twilight period (Fig. 3).

After leaving the nest, foragers walked towards and climbed nearby *Eucalyptus* trees. Most spent the entire night on the trees (see following section) and returned to the nest during dawn twilight. In total, 135 foragers returned to the nest: 13.3% before dawn twilight, 56.3% during dawn twilight, and 30.4% after sunrise. The behaviour of the returning foragers at the nest entrance again differed with time of day. Those returning during the night generally began to search for the nest within 50 cm of the entrance. On a few occasions, the search lasted for 1 h until the entrance was located. Foragers returning during dawn twilight

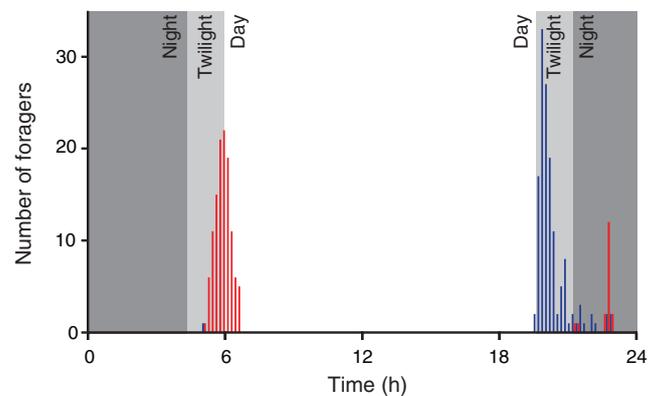


Fig. 3. Daily activity pattern. Bars indicate outbound (blue,  $n = 140$ ) and inbound (red,  $n = 135$ ) forager traffic, recorded in 10-min bins.

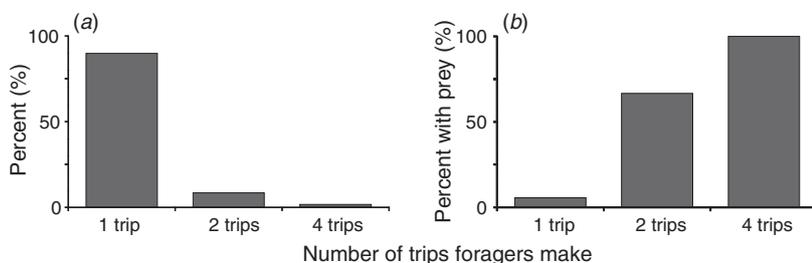
also searched for the nest entrance, but for a much shorter period. Those returning after sunrise only needed to perform minimal search to locate the entrance. This was also observed when foragers were released at the base their foraging tree at bright light intensities around sunrise time. These individuals were immediately oriented to the nest and entered without searching (see also Narendra et al. 2013).

*Foraging behaviour*

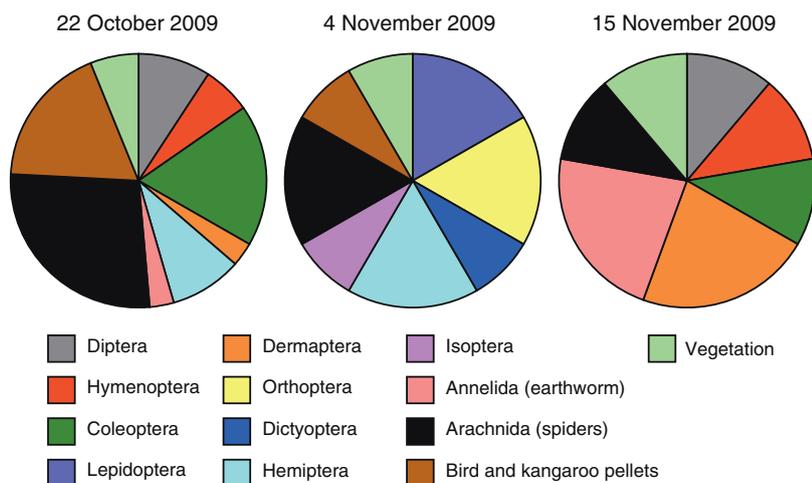
The foraging times of individual ants were recorded on three separate days at Nest 2 (22 October 2009, 4 November 2009, 15 November 2009). These observations took place on evenings with little to no cloud cover. Of the 177 individually marked ants observed, most of them (89.8%) made only one foraging trip per night (Fig. 4a). A trip generally began during dusk twilight, lasted 8 h 41 min ± 9 min (mean ± s.e) and ended during dawn twilight. Two foraging trips per night, each lasting, on average, 4 h 5 min ± 32 min were made by 8.5% of the ants, and four foraging trips, each lasting, on average, 1 h 42 min ± 33 min were made by 1.7% of the ants. Most of those making multiple foraging trips returned with prey: of those making two trips per night, 66.6% returned with prey, and of

those making four trips, 100% had prey (Fig. 4b). Most of those making two trips returned with prey on the first trip only (70%), while two returned with prey on both trips (20%), and one returned with prey on the second trip only (10%). Of those making four foraging trips, two returned with prey on all four occasions, while one forager returned with prey on only one foraging trip. We observed that individuals who made multiple trips were foraging on the same trees used by ants that made only one trip, indicating that these *M. pyriformis* individuals were able to navigate to and from the nest during the night when light levels were markedly lower than during the twilight period.

In total, 12.4% of the marked foragers returned with prey, closely matching the 13.2% foraging success of the colony when both marked and unmarked ants are considered together. Note that this success rate refers only to the collection of prey gathered to provide larval nourishment. The prey varied and included other ant species (notably *Camponotus* species), beetles, slaters, earwigs, scale insects, spiders, moths, earthworms, flies, caterpillars and cockroaches (Fig. 5). The more unusual items collected by foragers included grass seeds, grass fragments, leaves, possum faeces and kangaroo faeces.



**Fig. 4.** Foraging behaviour of individually marked ants ( $n = 177$ ). (a) Several foraging trips of individual ants. (b) The percentage that return with prey, depending on trip number. Most foragers make only one foraging journey per night.



**Fig. 5.** Proportion of prey and other additional items that workers of *Myrmecia pyriformis* from a single nest returned with on three different days.

On two occasions workers with extremely distended gasters, presumably carrying liquid food, were observed returning to the nest. After less than 20 min they each exited the nest and set out on another foraging trip, no longer with distended gasters (we assume that the putative liquid food had been deposited or passed-on, perhaps by trophallaxis, to other colony members). To determine whether foragers do indeed return to the nest with liquid food we weighed individual ants at Nest 2 before and after foraging. The average weight before foraging was  $94.1 \pm 11.3$  mg (mean  $\pm$  s.d.,  $n=15$ ). In comparison, the average weight upon returning to the nest was  $107.1 \pm 8.8$  mg ( $n=15$ ). This average increase of  $13.1 \pm 5.9$  mg represents a significant difference in weight before and after foraging (paired  $t$ -test:  $t=8.6$ , d.f.=14,  $P < 0.001$ ), indicating that foragers imbibe liquid food when abroad. The weight of two of the 15 ants increased by more than 20 mg when they were measured upon return.

#### The influence of lunar phase on foraging behaviour

While most of the navigational tasks, i.e. heading to the tree and returning to the nest, in *M. pyriformis* occur during dusk and dawn twilight a sizeable proportion of the activity takes place during the night (Greiner *et al.* 2007). Ambient light levels play a major role in the onset of foraging in this species (Narendra *et al.* 2010), with the navigational efficiency of individuals reducing at low light (Narendra *et al.* 2013). It is hence reasonable to propose that the intensity of lunar illumination might influence their foraging activity. Therefore we compared the activity levels during the night (i.e. after dusk twilight and before dawn twilight) at different lunar phases (Nest 1: 11 February 2006, 28 February 2006; Nest 2: 4 November 2009, 15 November 2009).

At Nest 1, night activity was recorded on a 'new moon' (illumination 0%; no. of foragers = 561) and a 'full moon' day (illumination 95.0%; no. of foragers = 439). A significantly greater proportion of outbound (Fisher's Exact Test:  $P=0.014$ ) and inbound (Fisher's Exact Test:  $P<0.0001$ ) activity took place during the night of the 'full moon' observations (Fig. 6a).

At Nest 2, night activity was recorded with moon illumination at 3.8% (no. of foragers = 140) and 99.1% (no. of foragers = 161) (Fig. 6b). A significantly greater proportion of outbound activity took place during the night on the full moon observation (Fisher's

Exact test:  $P=0.0009$ ). However, in contrast to Nest 1, moon illumination did not result in an increase in inbound activity (Fig. 6b), with no significant differences between the two observations (Fisher's Exact Test:  $P=0.53$ ). During the full moon observation light levels at 170 min after sunset were higher than on the 3.8% moon illumination night (Fig. 6c). Several large trees and buildings surrounding the foraging area blocked the light for some time after moonrise and the increase in light level did not take effect until 70 min after moonrise. The differences in ambient light intensity during these different lunar phases were less dramatic than expected (Fig. 6c). Nonetheless, the following observations during an overcast evening suggest that increased light levels do indeed facilitate increased foraging activity.

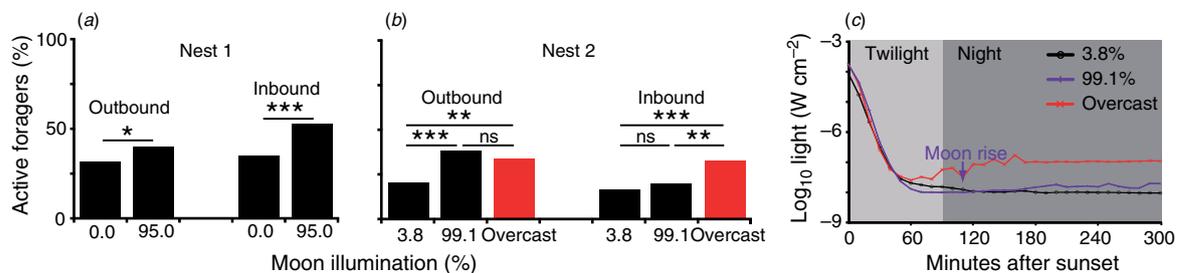
#### Foraging activity on overcast evenings

We recorded a 24-h activity pattern at Nest 2 on a completely overcast evening and report the number of active foragers at night (Fig. 6b, red bars). Light levels during the overcast evening were, in fact, greater than on all other observational periods (Fig. 6c), as the field site is only 1.5 km from Canberra's well lit Central Business District. As a result significant light from the city is reflected down from the cloud-cover on overcast evenings.

The effect of this increased light may explain the high levels of outbound and inbound forager traffic observed during the night (Fig. 6b; no. of foragers = 290). During the overcast night, 34.5% of foragers left the nest after twilight, which was significantly greater than the 20.0% observed when moon illumination was 3.8% (Fisher's Exact Test:  $P=0.002$ ). There was no significant difference in forager traffic between the overcast recording and when moon illumination was 99.1% (Fisher's Exact Test:  $P=0.47$ ). However, 33.4% of inbound foragers returned during the night in overcast conditions, which was significantly greater than the 16.5% and 20% that returned during the 3.8% and 99.1% moon illumination recordings, respectively (Fisher's Exact Test:  $P<0.001$  (3.8% moon illumination),  $P=0.003$  (99.1% moon illumination)).

#### Discussion

We report here some novel aspects of the foraging ecology of the night-active *M. pyriformis*. Most foragers made one nest



**Fig. 6.** The influence of moon illumination and cloud cover on night-time activity. (a) Nest 1 (forager numbers: 0% = 561, 95% = 439). (b) Nest 2 (forager numbers: 3.8% = 140, 99.1% = 161, Overcast = 290). (c) Light levels at Nest 2. The proportion of activity taking place during the night (after dusk twilight and before dawn twilight) increased as moon illumination increased. Light levels are substantially greater on overcast evenings due to light pollution (c), which may result in the greater proportion of activity that takes place during the night at Nest 2 on overcast evenings (b, red bars). Light levels were logged every 0.5 s in radiometric units. \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

departure at dusk and returned to the nest at dawn. The high proportion of foragers making only one foraging trip could be explained by difficulties encountered when navigating to and from the nest during the night. As *M. pyriformis* relies primarily on visual cues for navigation (Reid *et al.* 2011), and visual cues degrade as light levels fall, navigation becomes more difficult (Narendra *et al.* 2013). This in turn may restrict movement to and from the nest to periods of dim light (discussed in the following paragraph). However, we did observe that some foragers made two or more foraging forays per night. In most cases these foragers returned to the nest during the night with prey. Returns may well be triggered by success in prey collection and the need to deliver this prey fresh to larvae (Haskins and Haskins 1950; Gray 1971b). However, these night-time returns come at a cost, as individuals take far longer to locate the nest entrance compared with those that return during or after dawn twilight (see also Narendra *et al.* 2013).

Bursts of outbound and inbound forager traffic in *M. pyriformis* are tightly synchronised with dusk and dawn twilight. The timing of outbound foraging is known to be initiated by ambient light conditions (Narendra *et al.* 2010). Narendra *et al.* (2010) showed that foragers actively monitor ambient light around sunset time and depart the nest to forage only when conditions are ideal. This is supported by our observations that departing foragers waited at the nest entrance close to sunset, or even re-entered the nest before ultimate departure. We confirm that foragers committed to departure only during a small time window at twilight. Foragers that left the nest later, after twilight, stayed close to the nest before re-entering without foraging, presumably because light levels were by then insufficient to navigate to specific *Eucalyptus* trees.

A further indication of the importance of light levels comes from the observation that activity varies with moon phase. As the illuminated portion of the moon (and thus ambient light levels) increased, a greater number of inbound and outbound foragers were active during the night. The increased lunar illumination at night appears to provide additional navigational information for ants to travel, with perhaps the moon itself being a compass cue (Klotz and Reid 1993). The observation that night-time activity also increased on bright overcast nights suggests that ambient light levels, and thus the amount of light available for landmark navigation, influences activity.

As light levels have such a large influence on movements to and from the nest (i.e. on periods of navigation), why is activity not shifted towards brighter light conditions? One reason may be predation. During the period of our studies we observed artamid and corcoracid birds – Australian magpies (*Cracticus tibicen*), white winged choughs (*Corcorax melanorhamphos*) and black currawongs (*Strepera versicolor*) – preying upon the ants as they were travelling from foraging trees back to the nest (S. Reid, pers. obs.). While relatively few individuals were taken, all attacks occurred during the late dawn period. Furthermore, a resident possum observed at one nest began activity during dusk twilight and was observed feeding on foragers as they moved towards the trees (A. Narendra, pers. obs.). Because of such pressures, *M. pyriformis* workers might avoid predation because their movements to and from the trees are timed relative to the low light conditions of twilight.

However, there could also be an element of competition with other ants that also influences foraging timing. A hint comes from our observation that a newly established colony was susceptible to attack from nearby conspecific nests, and, in apparent response, initiated foraging activity up to 20 min earlier than surrounding colonies. This nest was also observed to hibernate over winter, unlike more mature nests that regularly dispatched small foraging forces throughout that season.

Lastly, our observations on colony demise suggest a division of labour in *M. pyriformis*, as large numbers of small workers (which do not normally leave the nest) began foraging towards the end of colony life. Freeland (1958) observed a similar situation in a diseased nest of *Myrmecia forceps* Roger.

## Conclusion

Many aspects of the biology of *M. pyriformis* are similar to those of other *Myrmecia* species. We confirm that nuptial flights take place in daylight in this species during late summer and early autumn, and that foraging workers are active in evening twilight and at night (Tepper 1882; Crosland *et al.* 1988; Narendra *et al.* 2011). Our records of dealate females outside their nests confirm that queens of this species are partially claustral during colony foundation (Freeland 1958). There is also some evidence that resources are distributed within the colonies by trophallaxis (see also Crosland *et al.* 1988). However, some features of *M. pyriformis* behaviour, especially regarding foraging patterns and foraging ecology, set this species apart as an excellent candidate for future studies that seek to elucidate the cues initiating activity, the navigational strategies employed by foragers, and the neurobiology of these behaviours. The ecological observations recorded here provide a context in which the relationship between behaviour, environment and sensory systems can be more adequately explored.

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