Individual foraging patterns of the jack jumper ant *Myrmecia croslandi* (Hymenoptera: Formicidae)

Piyankarie JAYATILAKA, Chloé A. RADERSCHALL, Ajay NARENDRA & Jochen ZEIL

Abstract

In ants, we know most about the foraging patterns at the colony level. We know surprisingly little about the foraging behaviour of individual foragers and how they shape the behaviour of the colony. To identify spatial and temporal variation in foraging behaviour at the individual level, we studied at two nests the solitary foragers of the Australian jack jumper ant *Myrmecia croslandi* TAYLOR, 1991. These ants are strictly diurnal and active only between October and April. Foragers of *Myrmecia croslandi* have a long life span (about a year) and we took advantage of this to determine the variation in their time of activity and foraging paths over a two-year period. By tracking the outbound paths of foraging ants using a Differential GPS we discovered that: (a) individual ants use very different routes to reach the same destination; (b) distance travelled by foragers was longest (up to 15 m) when they travelled to nest-specific eucalypt trees on which they foraged either for prey or tended to sap-sucking insects; (c) and ants made short forays (< 2 m) into non-tree sectors where they exclusively hunted for prey. Individual foragers exhibited temporal fidelity based on their nest departure times, and could be classified as those active (a) all day, (b) only within eight hours after sunrise and (c) only after eight hours after sunrise. By monitoring individual activity for seven consecutive days we show that individual ants carry out up to six trips per day and rarely forage on consecutive days.

Key words: Ants, foraging patterns, spatial foraging, temporal foraging.

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Introduction

The dynamics of an ant colony is largely influenced by its forager force (TRANIELLO 1989, BIESMEIJER & TÓTH 1998). Foragers directly respond to changes both in the external environment and inside the colony and accordingly alter their foraging behaviour, to ensure the colony has sufficient food reserves. Typically, ants forage individually or by following pheromone trails or by following an experienced individual – a strategy known as tandem running (see CARROLL & JANZEN 1973, TRANIELLO 1989). Regardless of the foraging strategy used by ants, all foragers face the same challenge of deciding where to forage and when to forage (SCHMID-HEMPEL 1984, TRANIELLO 1989). In solitary foraging species, this task of deciding on a foraging location and foraging time depends on the individual forager, as there are no chemical trails or other workers to guide ants from and to the nest.

Even though the relationship between an individual forager and the colony is an important one, we have little understanding of individual foraging patterns in social colonies. From honey bees, we know that foragers make individual decisions on where to forage and whether to recruit other bees depending on a range of external and internal factors (reviewed in VON FRISCH 1967, SOMMEIJER & al. 1983, INOUE & al. 1985, SEELEY 1995, BIESMEIJER & TÓTH

1998). These decisions give rise to foraging careers, which are unique to each individual depending on the age of the worker, type of food and the frequency of foraging (BIESMEIJER & TÓTH 1998). In the context of individual foraging careers in ants, we know from a few ant species that individual foragers exhibit sector fidelity, where animals forage in a small sector around their nest within which they gradually increase their foraging distance with experience (*Cataglyphis bicolor*: SCHMID-HEMPEL 1984, PASTEELS & DENEUBOURG 1987, *Melophorus bagoti*: MUSER & al. 2005). The development of sector fidelity is known mostly from desert ants that are scavengers (*Cataglyphis* species: SCHMID-HEMPEL 1987). Foragers leaving the nest for the first time, most likely exit in random directions (DENEUBOURG & al. 1986). If ants become successful in this randomly chosen sector, they continue to repeatedly forage in this sector. If a foraging trip has been unsuccessful, the number of previously successful trips in that particular sector would determine the likelihood of continuing to forage in that sector. Sector fidelity is high from the start of an individual's career in the Australian desert ant (MUSER & al. 2005), whereas in the Saharan desert ant, sector fidelity increases gradually during an ant's life. Being faithful to a particular sector, however, is not a generic trait but appears

to be driven by the food encounter rates. This has been clearly demonstrated in two populations of *Cataglyphis bicolor*, one inhabiting nutritionally-rich habitats in Greece and the other occupying nutritionally-poor saltpan habitats in Tunisia (WEHNER 1987), where colonies with low foraging success or efficiency exhibited low sector fidelity.

In addition to sector fidelity, individually foraging ants that navigate using visual landmark information exhibit fidelity towards a particular route (*Neoponera apicalis*: FRESNEAU 1985; *Dinoponera gigantea*: FOURCASSIÉ & OLIVEIRA 2002; *Melophorus bagoti*: KOHLER & WEHNER 2005; *Cataglyphis velox*: MANGAN & WEBB 2012). Ants exhibit route fidelity along both foraging and returning journeys. Among trail following ants, in which distinct trails head off in different directions to the centrally located nest, individual ants exhibit distinct fidelity towards a specific trail (*Formica* spp.: ROSENGREN 1971, *Pogonomyrmex barbatus*: HÖLLDOBLER 1976, *Pheidole militicida*: HÖLLDOBLER & MÖGLICH 1980). Visual route and new landmark memories have been shown to last the entire lifetime in desert ants (*Cataglyphis fortis*: ZIEGLER & WEHNER 1997; *Cataglyphis velox*: MANGAN & WEBB 2012; *Melophorus bagoti*: KOHLER & WEHNER 2005, NARENDRA & al. 2007), whereas visual route memories of trail following ants last for several months over unfavourable weather conditions (*Formica rufa*: ROSENGREN 1977a, ROSENGREN & FORTELIUS 1986a; *Formica* spp.: EBBERS & BARROWS 1980; *Lasius fuliginosus*: QUINET & PASTEELS 1996).

The spatial foraging patterns and especially sector fidelity have so far been addressed in desert ants. In such habitats, the distribution of food resources is typically unpredictable, both spatially and temporally. Therefore, desert ants must scavenge for dead arthropods that have succumbed to high heat (KOHLER & WEHNER 2005). In addition, these ants have a short foraging lifespan of about six days (SCHMID-HEMPEL & SCHMID-HEMPEL 1984). Here, we study the individually foraging Australian jack jumper ant *Myrmecia croslandi* TAYLOR, 1991, that nests in landmark-rich environments. These ants forage at temperatures well below their maximum thermal limits (JAYATILAKA & al. 2011) and have a long foraging lifespan of well over a year in natural conditions. Food resources are abundant in their habitat, with ants from each nest typically visiting nest-specific eucalypt trees on which they forage (NARENDRA & al. 2013a). Given these striking differences in their lifestyle and the phylogenetic importance of the ant genus *Myrmecia* (see CROSLAND & al. 1988, HASEGAWA & CROZIER 2006, WARD & BRADY 2003), here we attempt to describe their spatial foraging patterns and with particular attention to the question whether individuals exhibit fidelity to particular sectors, routes or food sites. The long lifespan of *M. croslandi* provides an opportunity to identify temporal activity patterns at the individual level. In ants, we know very little about "temporal fidelity", i.e., an individual's preference to forage at a particular time of day. Ants are active at different times during the day and within their specific temporal niche, activity is tightly regulated by temperature (e.g., FELLERS 1989, CERDÁ & al. 1998, RUANO & al. 2000, JAYATILAKA & al. 2011), light (CREIGHTON 1953, NARENDRA & al. 2010), competition (SCHOENER 1974, KRONFELD-SCHOR & DAYAN 2003), and predation (WEHNER & al. 1992). However, it is unknown whether individual ants are active at specific times within these temporal niches.
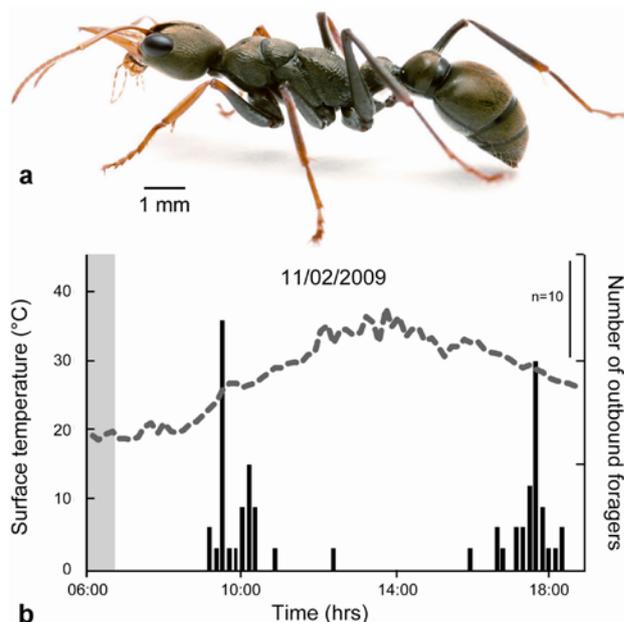

Fig. 1: Study species and typical activity on a warm summer day. (a) A worker of *Myrmecia croslandi*. Photo credit: Ajay Narendra. (b) An example of the daily outbound foraging activity (solid bars) of *Myrmecia croslandi* along with corresponding surface temperature (dashed line). On warm days, ants exhibit a bimodal activity pattern. Modified after JAYATILAKA & al. (2011).

Methods

Study species: Workers of *Myrmecia croslandi* are monomorphic and are approximately 11 mm in body length (Fig. 1a). Colonies typically have a workforce of about 100 - 200 foragers (P. Jayatilaka, unpubl.). The ants are strictly diurnal and are active only from Austral spring to Austral autumn (October - April) (GREINER & al. 2007, JAYATILAKA & al. 2011). During this period, on days when surface temperature exceeds 35°C, ants exhibit a bimodal activity, avoiding the warmest part of the day (Fig. 1b). The ants are solitary foragers and show no evidence of relying on recruitment or pheromones for finding food.

Workers of *Myrmecia croslandi* feed on tree sap and hunt on both trees and on the ground for live prey, which they carry back to the nest. We studied two nests, nest A and nest B located in the Campus Field Station at the Australian National University in Canberra, Australia (35° 16' 49.87" S and 149° 06' 43.74" E). The nests were about 60 m apart from each other. The vegetation in the area consisted of eucalypt trees such as *Eucalyptus macrorhyncha* and *E. viminalis* with very little undergrowth (JAYATILAKA & al. 2011).

Recording duration: Nest A was studied between October 2011 and April 2012 with 53 days of observation. Nest B was observed between January 2011 and March 2011 and September 2011 and February 2012 with 33 and 34 days of observation, respectively. All ants that left the nest during this period were individually marked (Nest A: 43 ants; Nest B: 37) with a water-soluble acrylic paint (Citadel Colours, France). Observations were carried out throughout the day: from when the first forager left the nest until no more ants left the nest. No observations were made on rainy and overcast days. Ants were considered to

have commenced a foraging trip when they crossed a reference circle of 60 cm diameter around the nest entrance. The final foraging destinations (e.g., trees) and where possible, type of prey collected were noted for each ant upon their return to the nest.

Nest exit times were monitored either by an observer at the nest or by a video camera (Canon HD Legria HFS 10) looking down at the nest. Video recordings were played back frame-by-frame in VirtualDub (Free Software Foundation Inc, Cambridge, USA) to identify individuals and their exit times.

Sector fidelity: To identify whether ants from the two nests foraged in particular sectors or visited particular sites, we opportunistically selected and tracked 32 ants from Nest A and 31 ants from Nest B. To determine at the individual level whether ants were faithful to a particular sector, we recorded three to five outbound foraging tracks for each marked individual. While tracks were obtained over consecutive days of recording, these may not necessarily be the consecutive foraging paths of individuals. Given several ants did only one or two trips and some were caught by spiders we were able to record three outbound paths for 21 ants (Nest A: 8; Nest B: 13). We determined the foraging direction on the first recorded trip for each ant and compared this to the foraging directions of the second and third recorded trips. Ants that foraged within 60° of the first foraging direction during two consecutive trips were considered to exhibit sector fidelity. By recording whether individuals were successful in acquiring prey during a foraging trip, we determined whether the success of capturing prey on the first trip increased fidelity to that sector during subsequent trips. We used a Generalised Linear Mixed Model in GenStat (VSN International Ltd, HP1 1ES, UK) to determine this relationship. Typically, foragers of *Myrmecia croslandi* head to nest-specific trees on which they forage (NARENDRA & al. 2013a). By determining the distance travelled by ants on the three outbound trips, we identified whether individual ants travelled distances equal to or greater than the nest-tree distance in other spatial directions. We used a two sample, unpaired t-test to analyse this relationship in GenStat (VSN International Ltd, HP1 1ES, UK). Using a Generalised Linear Model, we also tested whether ants that visited trees continued to do so, on the second and third trips. In desert ants it has been shown that as ants gain experience they travel further from the nest (PASTEELS & DENEUBOURG 1987, MUSER & al. 2005). We hence tested whether the distance travelled by individuals in the 1st, 2nd and 3rd foraging trips differed by a one-way ANOVA test in GenStat (VSN International Ltd, HP1 1ES, UK).

Tracking foragers: Outbound, marked ants were selected opportunistically and tracked using coloured flags and a Differential Global Positioning System (DGPS, NovAtel Inc, Canada; see also NARENDRA & al. 2013a, b). The flags were placed on the ground, behind an ant as she walked across the ground. The pin-marked trail was subsequently recorded by moving the rover antenna of a DGPS system along it. DGPS consists of a stationary base station receiver (NovAtel, FLEXPAK-V2-L1L2-G GPS plus GLONASS RT-2) with a base station antenna (NovAtel, GPS-702-GG-L1/L2, GPS plus GLONASS) and a rover receiver (OEMV-2-RT2-G GPS plus GLONASS) with a rover antenna (NovAtel, ANT-A72GLA-TW-N 532-C). The stati-
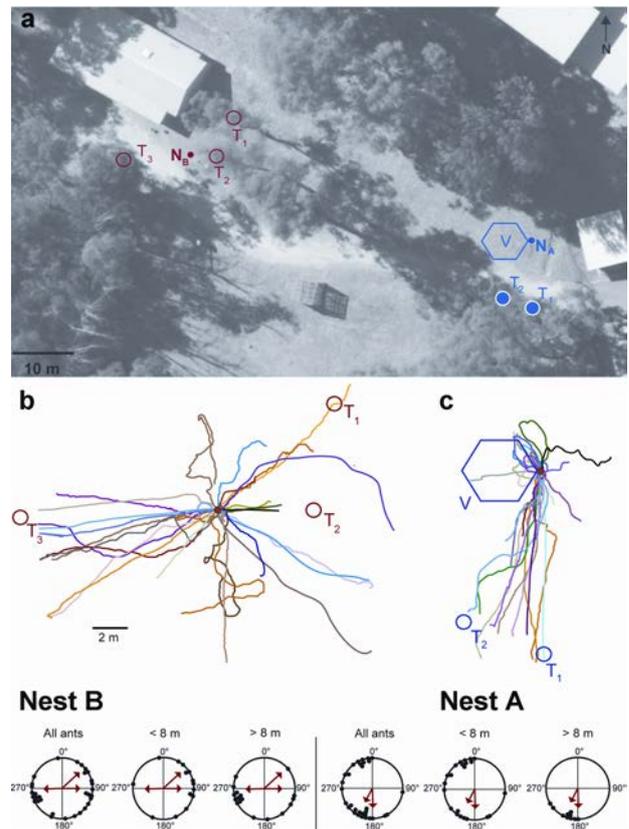

Fig. 2: Sector fidelity at the colony level in *Myrmecia croslandi*. (a) Nest A (N_A), Nest B (N_B) and the trees (T_1, T_2, T_3) and vegetation patch (V) ants visit are overlaid on an aerial photograph. Outbound paths and circular histograms of ants from (b) Nest B and (c) Nest A are shown with only one path for each individual. Nest position is indicated by a red circle. Circular histograms show bearing for: all ants (Nest A: ø = 241.34°, r = 0.41 , n = 32; Nest B: ø = 155.55°, r = 0.15 , n = 31); ants that travelled less than 8 m (Nest A: ø = 288.23°, r = 0.37 , n = 22; Nest B: ø = 80.16°, r = 0.54 , n = 14); ants that travelled greater than 8 m (Nest A: ø = 202.23°, r = 0.95, n = 10; Nest B: ø = 225.42°, r = 0.46 , n = 17). Red arrows indicate directions towards the main foraging trees.

onary base station calculates corrections for the mobile rover antenna through a radio link so that the position of the rover antenna can be determined with accuracy better than 10 cm. We monitored error estimates during recording and stopped recording when the error estimates were > 10 cm. The base station was mounted on a tripod and set to integrate antenna position readings for 30 minutes before recording was started. The rover receiver was carried on a back-pack and was connected to the rover antenna at the end of a long hand-held stick that was moved along the pin trails. Data from the DGPS unit were recorded into a text file as Northing, Easting and Height along with standard deviations (in metres) for each coordinate at 1 s intervals using a laptop connected to the base station through a USB port. GPS coordinates and error estimates were extracted with a custom-written MATLAB program (Mathworks, Natick, USA) and converted to .gps files using GPSU File Converter (GPS Utility Limited, www.gpsu.co.uk, United Kingdom). These files were then
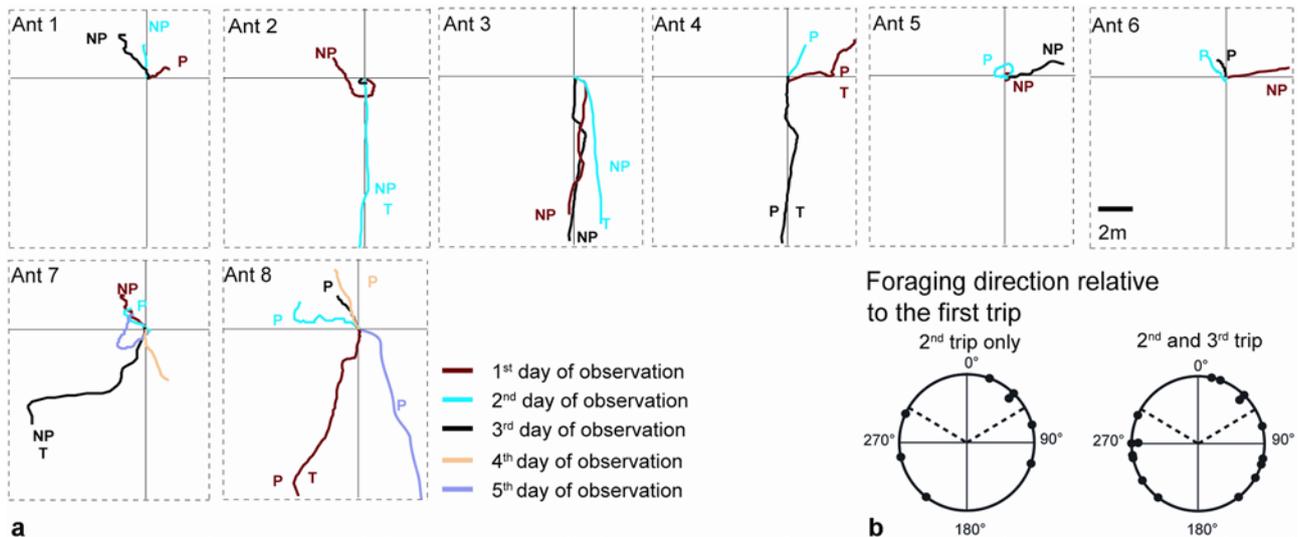
Fig. 3: Sector fidelity at the individual level in *Myrmecia croslandi* at Nest A. (a) Three to five outbound paths of individual ants are shown. Nest position is at the intersection of lines. Labels at the end of each track indicate whether the forager was successful in capturing prey (P), visiting a tree (T) or unsuccessful in capturing prey (NP). (b) Circular histograms indicate bearings of the 2nd trip relative to the 1st trip (ø = 33.53°, r = 0.26, n = 8) and bearings of the 2nd and 3rd trip relative to the 1st trip (ø = 358.28°, r = 0.03, n = 16). First trip = 0°. Ants that foraged within 60° of the first foraging direction (area within the dashed lines) during two consecutive trips were considered to exhibit sector fidelity.

registered with aerial photographs provided by the Australian Capital Territory Planning and Land Authority, ACT, Australia, using GPS Utility (GPS Utility Limited, www.gpsu.co.uk, United Kingdom).

Temporal fidelity: To determine whether ants exhibited fidelity in exiting the nest at specific times, we used ants that we observed to have left the nest at least twice (Nest A: 38, Nest B: 34) and asked whether there were changes in the daily time of forager exit.

Foraging frequency: Given that workers of *Myrmecia croslandi* are long-lived (at least a year), we hypothesised that ants do not make regular trips. To test if this was the case, we determined the number of foraging excursions individual ants made over a period of seven consecutive days (Nest A: 15 ants; Nest B: 15 ants). We used the time of exit as a measure of the number of trips ants made. We determined the foraging frequency of individual ants and also the regularity of foraging over a seven day period (Nest A: 19th January 2011 - 25th January 2011; Nest B: 28th January 2011 - 3rd February 2011). We compared differences in foraging frequency between the two nests using a two-sample unpaired t-test. We also determined the duration of foraging for three trips per ant (Nest A: 8 ants; Nest B: 13 ants). Foraging trip duration was calculated from the time a forager left the 60 cm circle on an outbound trip and returned to the nest. We compared differences in foraging trip duration between the two nests using a two-sample unpaired t-test. We determined whether the foraging duration of individuals that visited trees and individuals that did not visit trees was different by a two-sample unpaired t-test.

Results

Ants from both nests foraged on the ground and on multiple nest-specific eucalypt trees that were between 10.3 and 11.6 m from nest A and between 8.7 and 12.9 m from nest B (Fig. 2). At nest A, foragers visited two trees (T_1 and T_2) South of the nest whereas at nest B, foragers visited trees North-East (T_1), East (T_2) and West (T_3) of the nest. Foragers from nest A regularly returned with prey items such as aphids, spiders, crickets, moths and flies from a patch of vegetation (V) West of the nest (Fig. 2c).

Sector fidelity: At both nests, individuals that visited trees travelled longer distances compared to individuals that hunted for prey on the ground. Individuals that travelled shorter distances foraged in random directions around the nest. Out of 32 ants tracked at nest A, ten ants headed in specific directions to trees and travelled distances greater than 8 m (Fig. 2c, 8.6 ± 1.1 m, mean ± SD) compared to ants that foraged on the ground that appeared to be less directed and travelled smaller distances (Fig. 2c, 3.7 ± 2.9 m). Out of 31 ants tracked at nest B, 17 ants headed in specific directions to trees and travelled distances greater than 8 m (Fig. 2b, 9.4 ± 0.5 m, mean ± SD) compared to ants that foraged on the ground that appeared to be less directed and travelled smaller distances (Fig. 2b, 6.0 ± 3.0 m). At nest A, sectors to the North-West (with vegetation patch) and South-West (with trees) had high forager traffic. At nest B, sectors to the North East, East and West (all with trees) had high forager traffic.

This trend of travelling longer distances to specific trees and travelling shorter distances in random directions when hunting for prey on the ground was also obvious at the individual level where we obtained three tracks per ant (Fig. 3: Nest A: 8; Fig. 4: Nest B: 13). At nest A, ants travelled mostly in sectors with trees T_1 and T_2 (Figs. 3a and 3b) and individuals travelled longer distances to these trees (Fig. 5, 9.7 ± 2.0 m, n = 7 tracks) compared to those that foraged on the ground (Fig. 5, 2.2 ± 1.2 m, n = 17 tracks). At nest B, ants travelled mostly in sectors with trees T_1, T_2 and T_3 (Fig. 4) and individuals travelled longer distances to these trees (Fig. 5, 9.4 ± 0.8 m, n = 18 tracks)
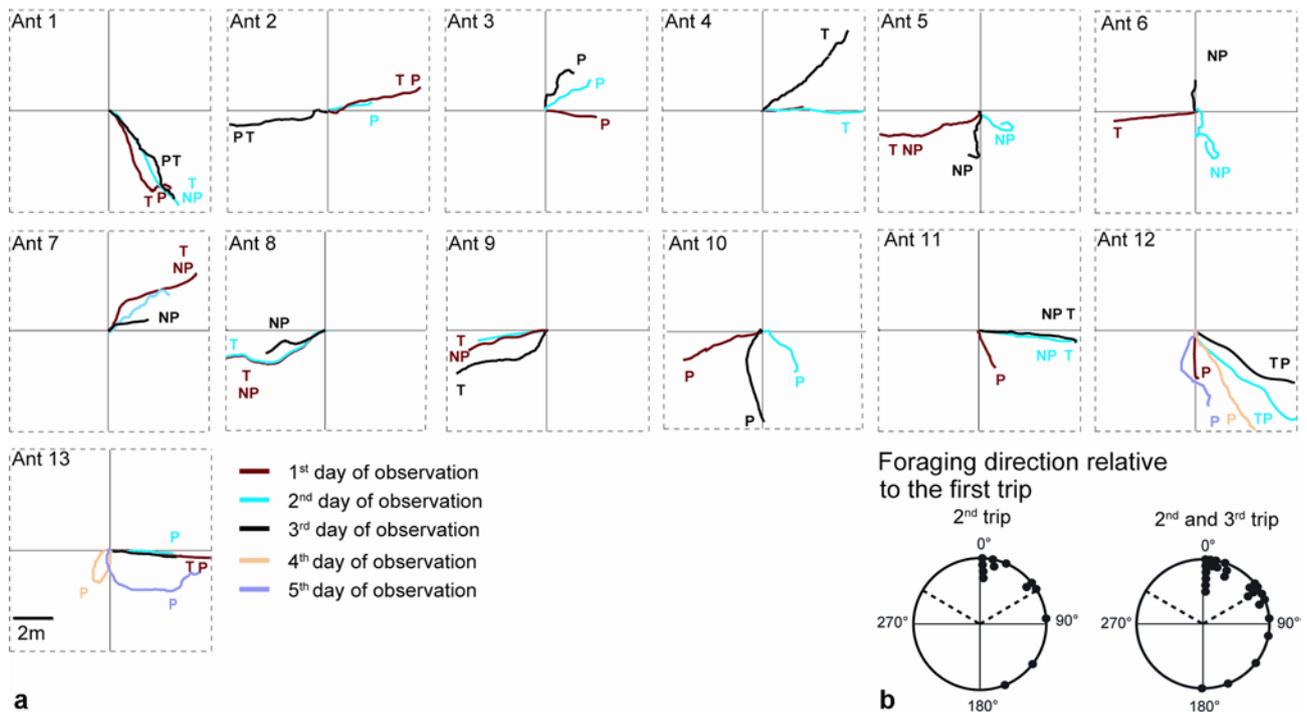
Fig. 4: Sector fidelity at the individual level in *Myrmecia croslandi* at Nest B. (a) Three to five outbound paths of individual ants are shown. (b) Circular histograms indicate bearings of the 2nd trip relative to the 1st (ø = 37.98°, r = 0.70, n = 13) and bearings of the 2nd and 3rd trip relative to the 1st (ø = 38.99°, r = 0.71, n = 26). First trip = 0°. Conventions as in Figure 3.

compared to those that foraged on the ground (Fig. 5, 5.2 ± 1.2 m, n = 21 tracks). At both nests, there was a significant difference (Fig. 5) between the distance travelled by individuals that visited trees compared to those who foraged elsewhere (Nest A: t-test, t = -11.38, d.f = 22, *P* < 0.001; Nest B: t-test, t = -12.26, d.f = 37, *P* < 0.001).

A smaller proportion of ants from Nest A exhibited sector fidelity compared to nest B (Fig. 3a). This was determined by the variation in heading direction of the second and third foraging trip relative to the first foraging trip. At nest A, three foraging trips occurred within 60° of the first foraging trip direction on the subsequent recorded trip (Fig. 3b, 2nd trip only) and four foraging trips occurred within 60° of the initial foraging direction on the subsequent two recorded trips (Fig. 3b, 2nd and 3rd trips only). At nest B, ten foraging trips occurred within 60° of the first foraging direction on the subsequent trip (Fig. 4b, 2nd trip only) and 18 trips occurred within 60° of the first foraging direction on the subsequent two recorded trips (Fig. 4b, 2nd and 3rd trips only). At both nests sector fidelity between the 1st and 2nd (Nest A and Nest B: trip 1 vs. trip 2, GLM, Wald statistic = 0.07, d.f = 17, *P* = 0.02) and the 1st, 2nd and 3rd trips (Nest A and Nest B: trip 1 vs. trip 3, GLM, Wald statistic = 0.03, d.f = 17, *P* = 0.03) was significantly different.

Most individuals developed idiosyncratic routes to different foraging locations at both nests and most ants that visited trees used similar, but not identical routes on the next trips (Fig. 4a, e.g., Ant 8, 9 and 13).

At both nests, the success of catching prey on the first trip did not increase fidelity to that sector in the following two trips (Figs. 3a and 4a, trip 1 vs. trip 2: GLM, Wald statistic = 0.06, d.f = 17, *P* = 0.79; trip 1 vs. trip 3, Wald statistic = 0.11, d.f = 17, *P* = 0.86). Distance travelled by
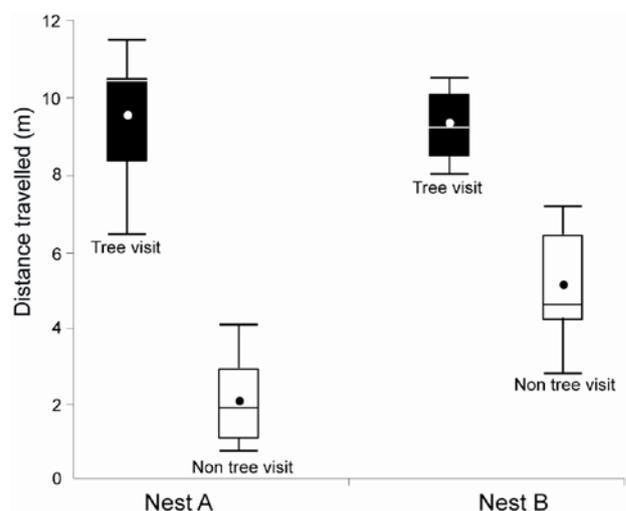

Fig. 5: Distance travelled by ants heading towards trees or elsewhere. Data are presented as box plots with mean (circle), median (white line), 25th, 75th percentile and the minimum and maximum values. Nest A: n = 8; Nest B: n = 13.

individuals did not significantly increase after the 1st recorded trip, over the next two trips (Nest A: one way ANOVA, $F_{2,22}$ = 0.20, *P* = 0.80; Nest B: one way ANOVA, $F_{2,37}$ = 1.00, *P* = 0.40).

Temporal fidelity: At both nests, individuals exhibited different schedules for time of exit (Figs. 6 and S1, the latter as digital supplementary material to this article, at the journal's web pages). At the colony level, time of forager exit could be categorised into three distinct time slots: (a)
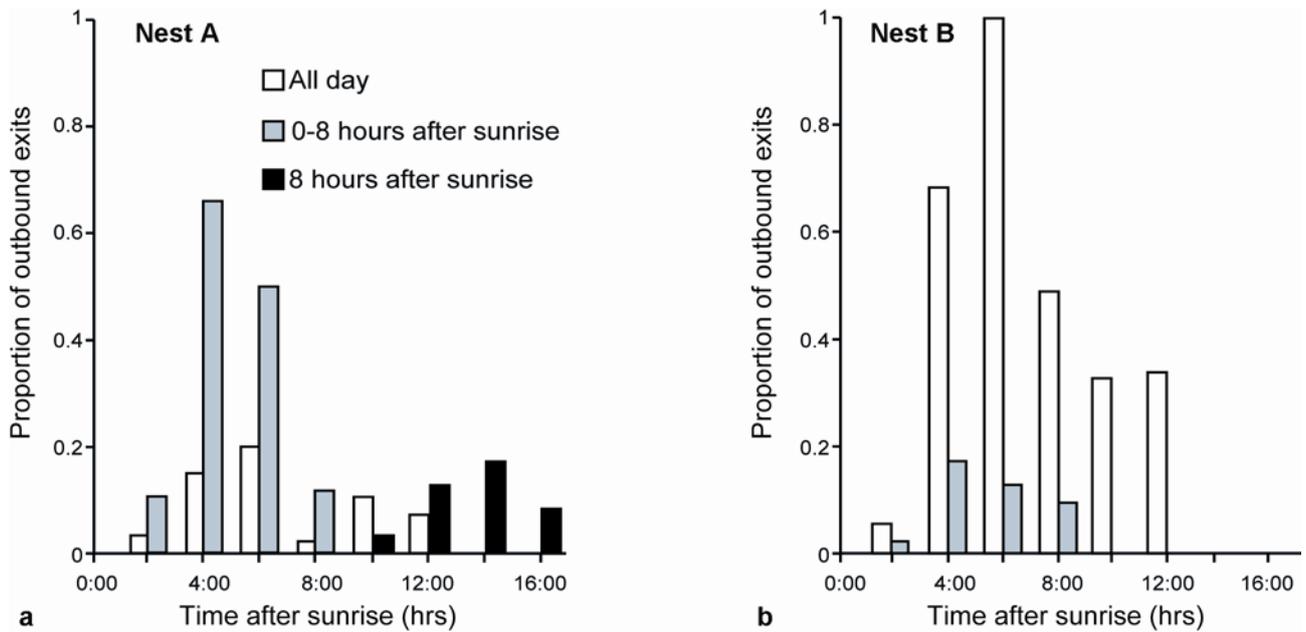
Fig. 6: Temporal fidelity in *Myrmecia croslandi* ants. Distribution of the number of ants that exit the nest relative to sunrise time at (a) Nest A and (b) Nest B. Sunrise time = 0:00 hrs. Departure times were grouped as: active all day; active within eight hours after sunrise and active after eight hours after sunrise. See Figure S1 for departure times of individual ants.
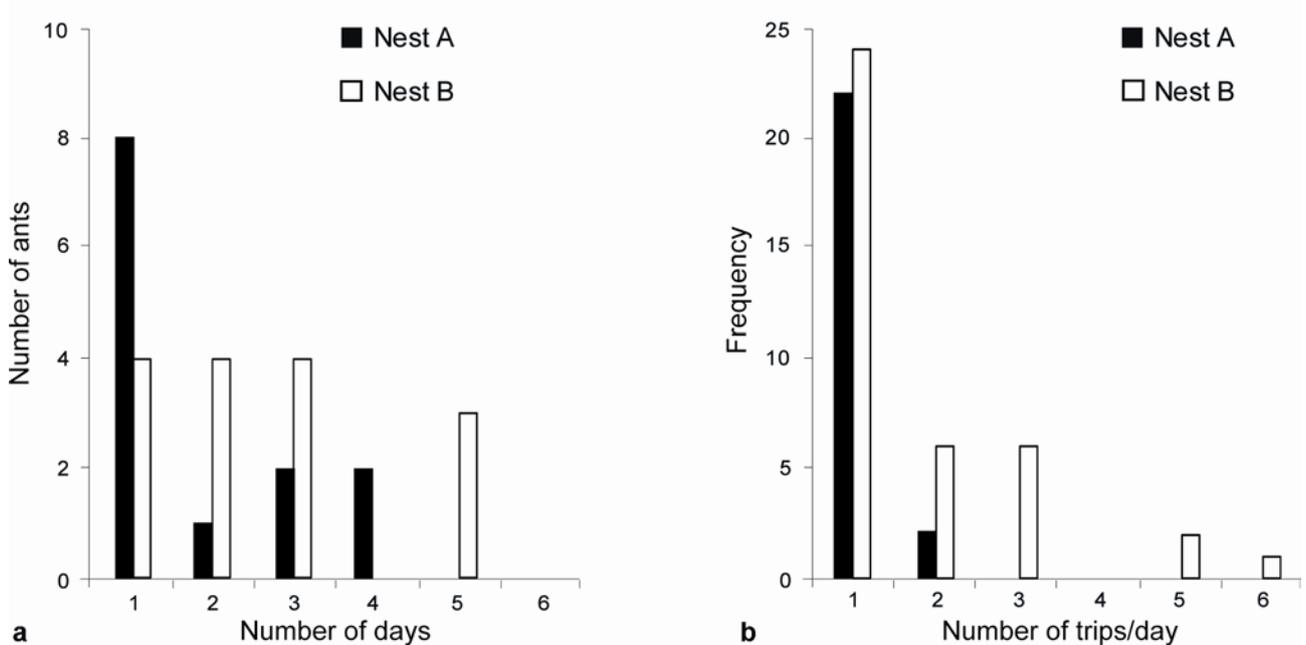

Fig. 7: Foraging frequency of *Myrmecia croslandi* ants over seven consecutive days. (a) The number of ants that were active for different days over seven consecutive days at Nest A (n = 13) and Nest B (n = 15). (b) The number of daily trips by individuals over a total of seven days at Nest A and Nest B. See Figure S2 for foraging frequency of individual ants.

active all day, (b) only within eight hours after sunrise and (c) only after eight hours after sunrise. At nest A, individuals were active in all three distinct time slots (Figs. 6a, S1a). At nest B, individuals were active only in two time slots (Figs. 6b and S1b). Of the ants that left the nest throughout the day at nest A, most ants avoided leaving the nest between six to eight hours after sunrise (Fig. S1a, n = 6). These results support previous findings of bimodal activity in this species (JAYATILAKA & al. 2011) where workers avoid leaving the nest to forage during the hottest parts

of the day (Fig. 1b). However, this bimodal activity pattern was not obvious at nest B (Fig. S1b).

Foraging frequency: Not a single worker foraged for seven consecutive days at both of the nests (Fig. S2a). The number of days individuals were active over seven consecutive days varied from one to four days at nest A (Fig. 7a, 1.2 ± 1.6 days, n = 13) and from one to five days at nest B (Fig. 7a, 0.9 ± 1.0 days, n = 15). The number of daily trips by individuals over a total of seven days varied at both nests (Figs. 7b and S2b, Nest A: one trip / day = 22, two

trips / day = 2; Nest B: one trip / day = 24, six trips / day = 1). There were on average, 3.7 trips per day at nest A (range 3 - 5) and 10.7 trips per day at nest B (range 0 - 29).

At nest A, an individual on average foraged for 69.7 ± 75.7 min (n = 8 ants, range 13 - 325, n = 24 tracks) whereas at nest B an individual foraged for 72.7 ± 53.2 min (n = 13 ants, range 17 - 261, n = 39 tracks). When visiting trees, individuals from nest A, spent a shorter time foraging (32.1 ± 13.3min, range 22 - 52, n = 7 tracks) compared to individuals that did not visit trees (84.6 ± 85.5 min, range 13 - 325, n = 17 tracks). We found a significant difference for foraging duration between the two types of foragers at this nest (t-test, t = 2.40, d.f = 22, P = 0.03) but not at nest B (Nest B_{trees}: 81.9 ± 78.3 min, range 17 - 261, n = 18; Nest $B_{notrees}$: 65.3 ± 15.7 min, range 42 - 94, n = 21; t-test, t = 0.62, d.f = 37, P = 0.54).

Discussion

We documented differences in the individual foraging patterns of the solitary foraging Australian jack jumper ant *Myrmecia croslandi*. These ants did not forage in all directions around the nest. Individual ants typically walked long distances to head to nest-specific eucalyptus trees, on which they foraged for prey and liquid food. Some ants travelled short distances in different directions around the nest to exclusively forage for prey on the ground. In the small sample of ants, for which we recorded at least three paths for individual ants, it appears that the change from foraging on the tree to elsewhere and vice versa did not depend on their foraging success. Foraging frequency of ants was variable both with regard to the number of trips carried out on a single day and the regularity of foraging.

Spatial foraging patterns: Spatial foraging patterns have been best described in desert ants that are primarily scavengers relying on insects that succumbed to the desert heat (WEHNER & al. 1983, WEHNER & al. 2004). In these ants, individuals randomly select a sector to forage in, which enables the colony to exploit their unpredictable food resource in all compass directions around the nest (see fig. 9 in WEHNER & al. 1983, HÖLLDOBLER & WILSON 1990). With their short foraging lifespan of six days, individual ants continue to forage in a particular sector all their life, increasing their foraging distance with age and experience. They switch foraging to a different sector only when the number of unsuccessful trips outweighs the successful ones (SCHMID-HEMPEL 1984). Given their short foraging lifespan it would be futile to persist foraging in unsuccessful sectors.

In contrast, in the visually complex environments of *Myrmecia croslandi*, ants appear to rely on a two-pronged approach to foraging. One, where individuals visit spatially predictable but distant food sources located on nest-specific trees, which as a consequence leads to sector and route fidelity (Figs. 3 and 4). Two, where individuals hunt for scattered food resources on the ground in close proximity to the nest (Figs. 3 and 4). While ants foraging on the ground were exclusively hunters, those that foraged on trees captured prey and also collected carbohydrates from sap-sucking insects and from sap produced by trees. Ants were not restricted to foraging at a particular location and regularly switched between foraging on the tree to foraging on the ground independent of their foraging success. Individuals that foraged on nest-specific trees travelled a distance

of nearly three times greater than ants that foraged on the ground. It is unclear why the hunting ants foraged only for short distances (~ 4 m) around the nest. As shown in the earlier work on desert ants (SCHMID-HEMPEL 1984, WEHNER & al. 1983, WEHNER & al. 2004) both experience and age play a significant role in the understanding of spatial foraging patterns. Given the long lifespan of *M. croslandi*, we were unable to determine the age or the experience of individual ants in this study. Nevertheless, it is clear that the spatial foraging strategies used by these ants are remarkably different compared to the desert ants.

Temporal and individual foraging patterns: Our study indicates that individual foragers of *Myrmecia croslandi* exhibit temporal fidelity to some extent. How animals choose their foraging times and what information they use to maintain temporal fidelity is however unknown. For this, animals could use information about the rate of change of surface temperature (e.g., JAYATILAKA & al. 2011), the presence of competitors (CARROLL & JANZEN 1973), ambient light intensity (NARENDRA & al. 2010), or their internal circadian rhythms (ROSENGREN 1977b, ROSENGREN & FORTELIUS 1986b, SAUNDERS 2009).

Both trip duration and foraging regularity vary greatly in *Myrmecia croslandi*. Only very few foragers carry out more than one trip a day. The individuals that carry out multiple trips could be those that are more efficient or have more experience. Such variation in the number of daily foraging trips has been documented in seed harvester ants, *Pogonomyrmex barbatus*, where most foragers typically make a few but long trips and only a small number of ants make many but short trips (BEVERLY & al. 2009). The foraging duration in these ants has been shown to be strongly related to the extent of searching by an individual and not to the distance from the nest. Our observations indicate that ants heading to trees are well directed and do not search, whereas ants that hunt for prey on the ground engage in extensive search behaviour. Furthermore, at one nest, we found that foraging durations when visiting trees are shorter compared to when foraging on the ground, which supports the argument that the extent of searching may influence the foraging duration. Over a week's observation we found that not a single ant foraged for seven consecutive days in comparison to the desert ants *Cataglyphis fortis* and *Melophorus bagoti* where individuals foraged regularly on a daily basis for six to ten days (A. Narendra, unpubl.). This intermittent activity in *M. croslandi* could be the direct result of the longevity of each worker compared to the short lifespan of the desert ants.

The differences in activity times between the two neighbouring nests could be explained by competition, colony size or different micro-climates. Nest A was located within 2 m of an active meat ant nest, *Iridomyrmex purpureus*. Foragers of *Myrmecia croslandi* from nest A had to cross a trunk trail of meat ants to reach their foraging trees. At nest B, there were no meat ant trails in the ants' typical foraging route and this could have allowed foragers of this nest to be active throughout the day. Meat ants are one of the most behaviourally dominant ants in Australia and interfere with foraging of other ant species (GREENSLADE 1976, ANDERSEN 1997, GIBB & HOCHULI 2004). We have often observed meat ants stealing prey from foragers of *M. croslandi* or even killing the foragers. Forager force at nest B was significantly lower compared to Nest A, which

also could have affected the activity times of the colony. Such differences in foraging behaviour between nests located close to each other highlight the need to study multiple nests to understand the foraging dynamics of ant colonies.

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