



Spatial fidelity and uniform exploration in the foraging behaviour of a giant predatory ant

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Social organisms benefit from division of labour and collective behaviours. However, if individuals overlap widely in their efforts, these benefits may not be proportional to the number of individuals that take part in an activity. We examined foraging behaviour and route fidelity in colonies of the ant *Dinoponera grandis* (formerly *Dinoponera australis*), a large species with relatively few active foragers that lack nestmate recruitment and chemical trailing behaviour. For 12 colonies, we marked individual foragers and mapped their foraging routes to test the hypothesis that each ant specializes in a particular area around the nest and that this route fidelity increases the overall area covered by the colony. For each individual, we recorded the mean direction and duration of each foraging trip, foraging success and maximal distance from the nest. For each colony, we measured the number of workers and the total foraging area. Additionally, we measured Shannon's entropy to describe foraging behaviour structure of the colonies. Overall, we mapped 272 foraging routes from 95 different foragers. The total area used by each colony averaged 66.2 m². Within colonies, over 68% of foragers exhibited a high degree of route fidelity, with most foragers following different foraging directions. Most colonies had a high Shannon's entropy, suggesting an even exploration of the foraging territory. Our results suggest that *D. grandis* exhibit route fidelity and high entropy. This strategy likely increases foraging efficiency and search area and may be particularly important for species with relatively few foragers.

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Finding and exploiting resources is essential for survival, reproduction and growth. Resource distribution can favour cooperative behaviours in some environments, and social organisms benefit from division of labour and group foraging through a variety of mechanisms (Clark & Mangel, 1986; Ribbands & Wigglesworth, 1952; Sutton et al., 2015). Division of labour can increase efficiency by having different tasks done in parallel and by assigning multiple individuals to the same task (Robinson, 1992). Group foraging can increase overall foraging area, encounter rates with prey and prey capture (Clark & Mangel, 1986). However, if group members do not use information from previous foraging trips or overlap widely in their search routes, then many of these benefits will not be proportional to the number of individuals taking part in foraging (Valone, 1989).

In eusocial insects like ants, food is acquired to meet current needs of the colony for growth (the production of new workers) and reproduction (the production of new queens and males). Obtaining resources for growth is particularly important for small colonies as larger colonies often have lower mortality rates from competitors or from environmental stochasticity and a higher reproduction rate (Adams & Tschinkel, 1995; Gordon, 2010; Gordon & Kulig, 1998; Jeanne, 1999; Ryti & Case, 1986; Thurber et al., 1993). Furthermore, small colonies may have different colony organization and task allocation strategies compared to larger colonies, for example, with workers spending less time foraging and exhibiting less task specialization (Thomas & Elgar, 2003).

Social insects exhibit a variety of solitary and group foraging behaviours (Dornhaus & Powell, 2010; Richter, 2000; Traniello, 1989). Principal factors in the structuring of the search pattern and foraging behaviour in ant species include food abundance and distribution, intra- and interspecific interactions (Bernstein, 1975; Guénard & McGlynn, 2013; Nonacs & Dill, 1988; Pol et al., 2011;

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Taylor, 1977; Traniello, 1989) and colony size (Thomas & Elgar, 2003). For example, solitary foraging seems to be correlated with food randomly distributed in space and time (Lanan, 2014; Pie, 2004). Additionally, abiotic conditions like temperature and humidity can affect foraging, creating diurnal and seasonal variation in behaviour (Gordon, 2013; Porter & Tschinkel, 1987; Raimundo et al., 2009). Nutritional state and requirements of the colony can also regulate decisions and diet preference of the foragers (Josens & Roces, 2000). Finally, individual variation, experience and age of the foragers can also influence an individual's decision making (Gordon, 2010; Mandal & Brahma, 2019).

Route fidelity, or spatial specialization while foraging, is common in many animals that forage on predictable resources (e.g. trap lining for flowers: Ohashi et al., 2008; Tello-Ramos et al., 2015). Foraging site fidelity may also be important for reducing intra-specific competition in colonial organisms (Bolton et al., 2019; Ramellini et al., 2022). Route fidelity has been observed in several social insects (Azevedo et al., 2014; Buchkremer & Reinhold, 2008; Fewell, 1990; Fourcassié et al., 1999; Fresneau, 1985; Ohashi et al., 2008; Pie, 2004; Traniello, 1989), and for species that do not use chemical trails for orientation, it may provide a mechanism to reduce the possibility of solitary foragers getting lost (Fourcassié et al., 1999). It may also enhance foraging success in environments with heterogeneous resource distributions (Buchkremer & Reinhold, 2008). In addition, if workers forage in different directions, route fidelity can increase colony exploration efficiency by reducing overlap in searched areas: unless resources are clumped or have a predictable location, a disproportionate number of workers exploring the same area would decrease the total area explored by the colony and reduce colony food intake (Pie, 2004). In contrast, route fidelity can reduce efficiency if foragers are less likely to switch to new or better foraging sites (Elizalde & Farji-Brener, 2012; Fewell, 1990).

In this study, we quantified the foraging behaviour of individual *Dinoponera grandis* (formerly *Dinoponera australis*) workers. Specifically, we were interested in how this species, which has small colonies (average \pm SD = 44.6 ± 21.4 adults per nest; Tillberg et al., 2014) and a small proportion of foragers (average 26% of the colony; Smith et al., 2011), can be among the most successful species (in terms of biomass and abundance) of the Atlantic Rainforest ant community where they reside (Hanisch et al., 2018; Tillberg et al., 2014). By examining foraging direction when workers were 1 m away from the colony entrance, Tillberg et al. (2014) suggested that route fidelity might be a mechanism to increase colony foraging efficiency in this species, and they proposed that an efficient foraging behaviour could be one of the factors explaining the high biomass of *D. grandis* in Iguazú (2.5 kg/ha; Tillberg et al., 2014). But observations of complete foraging trips are needed to confirm route fidelity and determine whether it increases the area explored by a colony.

We predicted that *D. grandis* workers would repeatedly forage in a particular area around the nest (i.e. exhibit route fidelity) and that different workers would forage in different parts of a colony's territory, resulting in even exploration of the whole territory. To test these predictions, we mapped multiple foraging routes for 95 workers from 12 colonies. We also generated heat maps of the foraging area explored for each colony and calculated Shannon's entropy (Lourenço et al., 2020; Shannon, 1948). Colonies with small entropy generally explore less area and cover their territory unevenly (for example by having set foraging paths). In contrast, if a colony evenly explores its territory and follows a foraging strategy that aims to cover as much area as possible, then it will have larger entropy (homogeneous or equitable probability distribution).

METHODS

Study Area

The study was performed during summer of 2017 and 2020 in Iguazú National Park (INP), a 67000 ha protected area in north-western Misiones, Argentina (25°40'49'S, 54°27'15'W). The climate is humid subtropical with no defined dry season. Average annual temperature is 20–21 °C, with a maximum temperature of 40 °C (December–February) and a minimum temperature of –3 °C (June–August). Average annual rainfall is 2000 mm (Schiaffino et al., 2003). Data were collected in an area of secondary forest with little understory.

Study Organism

The genus *Dinoponera* is restricted to South America and currently comprises eight species, with body sizes ranging from 3 to 4 cm (Dias & Lattke, 2021), making them among the largest ants in the world. Dietary studies of *Dinoponera* reveal they are largely predatory but will also scavenge for dead insects, seeds and fruit (Araújo & Rodrigues, 2006; Fourcassié & Oliveira, 2002; Hanisch et al., 2020; Tillberg et al., 2014). They lack morphologically specialized queens and reproduction is carried out by a single mated worker known as gamergate (Paiva & Brandão, 1995). In northern Argentina, there is a single representative of this genus, *D. grandis*, which was recently synonymized with its historical name *D. australis* (Dias & Lattke, 2021).

In *D. grandis*, nutritional state is correlated with division of labour; the probability of foraging and foraging effort are associated with decreased fat storage (Smith et al., 2011). In *D. grandis* and *Dinoponera gigantea*, foragers leave the nest in a preferred initial direction and forage solitarily in the search of food (Fourcassié & Oliveira, 2002; Tillberg et al., 2014). If an encounter with a non-nestmate occurs, the ants will engage in ritualized antagonistic behaviour, fight or avoid confrontation (Fourcassié & Oliveira, 2002; Tillberg et al., 2014). If food is found, foragers do not recruit nestmates to help with food transportation (Fourcassié & Oliveira, 2002; Fowler, 1985) and foraging routes do not seem to be based on any chemical substance laid down during previous trips (Fourcassié et al., 1999).

Foraging Behaviour

To investigate the spatial pattern of foraging routes, we observed 12 *D. grandis* colonies during March of 2017 and 2020. First, we made maps of the terrain surrounding each colony with the help of an x – y coordinate system with the origin located at the colony entrance, measuring tape and a compass (Appendix, Fig. A1). All reference points in the terrain, like trees and logs, were added to the map. At each colony, foragers were individually marked with colour/number tags or nontoxic enamel paint (Testers Co., Rockford, IL, U.S.A.).

Once all the foraging ants were individually marked, tagged ants were observed and followed and their foraging route was drawn on the map. We took note of the departure/exit time and whether the forager returned to the colony with food (successful trip). If successful, we marked the location where food was collected. To help maintain an accurate position of where the ants were foraging, we placed small coloured flags into the soil to mark the location where an ant had been when necessary, for later measurement (Appendix, Fig. A1). *Dinoponera grandis* workers rarely climbed high onto vegetation, but when they did, we noted the climbing event. Each

colony was observed the necessary time needed to obtain at least three complete foraging trips for most of the marked ants. The required observation time varied among the colonies and depended on weather conditions, ant activity levels and number of foraging ants. On average, all observations were made within a 3–4-day window for each colony. To estimate the error associated with drawing the position of an ant on the maps, all observers were asked to mark the positions of 109 flags (~3–4 flags per observer per colony). The mean (\pm SD) difference of the measured positions of the flags in the terrain in comparison with the positions of the flags on the maps was 0.23 ± 0.13 m. After data collection was complete, we recorded colony size for 9 of the 12 colonies (3 colonies in 2017 and all the 6 colonies in 2020) by colony excavation or colony flooding.

Individual Ant Analysis

Foraging routes were digitized by scanning the maps. For each trip, we calculated the duration, maximum distance from the nest entrance, the total foraging area and the mean foraging direction. The mean foraging direction is defined as the angle at the centre of the angular range, defined by the two angles that enclose the foraging path for each foraging trip (see [Appendix, Fig. A2](#)). Directions were measured using north (0°) as a reference. A few routes (3 foraging trips by 2 ants in colony D5_2017 and 2 foraging trips by 2 ants in colony DA6_2017) did not have a clear foraging direction (i.e. ants toured a circular area around the nest), so a mean direction was not calculated for these cases. We calculated area (defined as the area enclosed by the foraging path; [Appendix, Fig. A2](#)) with the software 'Octave' ([Eaton, 2012](#)) and a function generated for this purpose. Distances were calculated using Fiji software ([Schindelin et al., 2012](#)). To investigate nonrandom distribution patterns of foraging trip directions, we performed a Rayleigh test of the mean foraging direction for each forager with at least three complete trips. The Rayleigh test uses as input a sample of angles and it is based on analysing the normalized length of the vector that results in summing all the directions defined by the input angles (the resultant vector length R). The idea behind this analysis is that, if the angles are randomly distributed, then the norm of the resulting vector will be small, but if they are biased towards a particular direction, then the resulting norm will be significant ([Berens, 2009](#)). Note that we were only interested in testing a unimodal departure from uniformity, where the Rayleigh test is the recommended test ([Landler et al., 2018](#)). This analysis was performed with 'CircStats' package ([Lund & Agostinelli, 2018](#)) in R version 4.0.5 ([R Core Team, 2021](#)).

Colony Analyses

We calculated the total foraging area for each colony as the enclosed area by all overlapping foraging routes. As in the previous analysis examining mean foraging direction at the individual level, we also investigated whether the mean direction of foraging trips for the whole colony were biased towards a particular direction with a Rayleigh test. Similarly, we also examined the resource direction distribution using the direction where food was found by the ants. We used a generalized least square regression (GLS) to test the relationship between foraging area (response variable) and the number of foragers (explanatory variable). The 'varPower' function was incorporated to correct for heteroscedasticity. The model was fitted with the 'gls' function in the 'nlme' package ([Pinheiro et al.,](#)

2007). Model validation was performed graphically following the protocol of [Zuur et al. \(2010\)](#). To study the foraging patterns of the colonies and the exploration evenness of the territory, we calculated the explored probability distribution of the colony. For this, we divided the black and white foraging map of each colony into 1089 equally sized cells (33×33) and calculated the proportion of black pixels (explored areas) for each square in Python with the help of Pandas library ([Pandas Development Team, 2023](#)). We used the resulting probability matrix to build a heat map of the foraging area explored by each colony.

As a parameter of foraging structure, for each colony, we measured Shannon's entropy ([Shannon, 1948](#)), a measure of the disorder or information of a system, using the following equation:

$$H = - \sum p_{ij} \ln p_{ij}$$

where $i = 1, 2, \dots, 33$, $j = 1, 2, \dots, 33$ and p_{ij} is the probability of finding an ant in a particular (i, j) cell. This probability was calculated by counting the number of black pixels (space occupied by an ant) in the black and white maps divided into 33×33 cells. For example, if the number of black pixels in one colony was 1000 and the number of black pixels in cell ij was 100, then $p_{ij} = 100/1000 = 0.1$. We normalized entropy scores by the maximum entropy calculated using the entire area (including unexplored areas) (H_1) and by the maximum entropy calculated using only the area occupied by the colony (H_2). The first measure allows comparison of colonies in terms of the explored area and the exploration evenness. The second measure allows a comparison of entropy regardless of the foraging territory of each colony. The normalized Shannon entropy values range from 0 to 1 (where 0 = a totally ordered system and 1 = a totally disordered system).

Ethical Note

This study complies with all Argentinean laws, as well as national, institutional and ASAB/ABS guidelines for the care and use of animals in research. Ants were handled under a scientific license granted by the Administración de Parques Nacionales (Permit number NEA353 Rnv3). During the study, ants may have experienced temporary stress but not any physical harm. The marks used to individualize the ants were temporary.

RESULTS

We observed 272 foraging trips by 95 individual workers, resulting in more than 229 h of direct worker observation. Only 13 trips had incomplete information (i.e. return time). The median (\pm SD) time spent outside the nest for all foragers was 50.6 ± 46.6 min. The median (\pm SD) maximal distance travelled per each ant was 4.8 ± 2.7 m. Each foraging trip covered an average (\pm SD) area of 6.4 ± 5.9 m² but varied greatly among individuals (range 0.06–35.1 m²). On average, workers returned with food in 31% of the foraging bouts ([Table 1](#)). For each forager, 90% of the data was collected within a 3-day observation window. During that time, no temporal pattern was detected in relation to the foraging direction ([Fig. 1](#)). Finally, in support of our predictions, 46 of the 67 foragers (68%) foraged in a preferred foraging direction ([Figs 2, 3, Appendix, Table A1](#)). Another five foragers (7%) had a high, but nonsignificant, R vector (>0.90) ([Appendix, Table A1](#)). Additionally, the angle of the resultant R vector from the Rayleigh test revealed most foragers explored in a different direction than their nestmates ([Fig. 3](#)).

Table 1
Summary data for all the colonies

| Colony code | Foragers (foragers with at least 3 completed trips) | Colony size | Observed trips (completed observed trips) | Successful trips (%) | Observed time (min) | Total nest foraging area (m ²) | Average foraging area per ant (m ²) | Average foraging time (min) | Average maximum distance per ant (m) |
|-------------|---|-------------|---|----------------------|---------------------|--|---|-----------------------------|--------------------------------------|
| DA1_2017 | 8 (6) | 52 | 20 (19) | 53 | 967 | 71 | 5 | 51 | 4 |
| DA2_2017 | 4 (4) | 52 | 12 (12) | 42 | 347 | 43 | 5 | 29 | 5 |
| DA3_2017 | 9 (4) | 84 | 21 (20) | 45 | 1538 | 86 | 7 | 61 | 5 |
| DA4_2017 | 7 (6) | — | 20 (20) | 15 | 1058 | 35 | 4 | 52 | 4 |
| DA5_2017 | 14 (8) | — | 37 (37) | 22 | 1309 | 46 | 4 | 37 | 3 |
| DA6_2017 | 5 (4) | — | 17 (17) | 0 | 516 | 36 | 5 | 29 | 3 |
| DA1_2020 | 15 (7) | 101 | 37 (34) | 46 | 2244 | 82 | 6 | 64 | 5 |
| DA2_2020 | 3 (3) | 52 | 12 (12) | 17 | 821 | 42 | 8 | 73 | 5 |
| DA3_2020 | 8 (6) | 68 | 22 (22) | 18 | 1286 | 97 | 9 | 59 | 8 |
| DA4_2020 | 6 (4) | 41 | 18 (15) | 50 | 918 | 46 | 3 | 46 | 4 |
| DA5_2020 | 10 (10) | 88 | 36 (34) | 44 | 1461 | 126 | 9 | 44 | 6 |
| DA6_2020 | 6 (5) | 79 | 20 (17) | 25 | 1307 | 85 | 9 | 63 | 6 |
| Total | 95 (67) | — | 272 (259) | — | 13772 | — | — | — | — |
| Average | 8 (6) | 69 | 23 (22) | 31 | 1148 | 66 | 6 | 51 | 5 |

Foraging patterns exhibited some variation among the 12 colonies, but they showed similar overall structure (Figs 2–4), with most areas having a similar probability of being explored by foragers (Fig. 4). Shannon entropy (H_1) values varied among colonies from 0.66 to 0.83. When controlling for area, Shannon entropy (H_2) was high, ranging from 0.92 to 0.97 (Fig. 4). Furthermore, foraging directions were not biased among colonies except for colony DA5_2020 (Table 2), and the direction where food was found was also not biased except for two colonies (DA1_2017 and DA4_2020). We determined the size of 9 of the 12 colonies, which had 41–101 individuals, revealing that foraging workers accounted for an average of 11% of the total number of ants in the colony (range 5–15%). The total area covered by the 12 colonies averaged (\pm SD) 66.2 ± 29.3 m² (Table 1). Finally, we fitted a GLS to predict foraging area with the number of foragers. We found a positive effect of the number of foragers on foraging territory (beta = 5.95, 95% CI [1.43; 10.48], $t = 2.57$, $P = 0.02$; Appendix, Fig. A3). Some of the studied colonies were neighbours, but there was no foraging territory overlap except between one pair of ants from separate colonies (DA3_2017 and DA5_2017). This pair had a small overlap in the area where workers foraged (around 2 m²; P. E. Hanisch, personal observation), and foragers from these two colonies were seen fighting in this area (Appendix, Fig. A4).

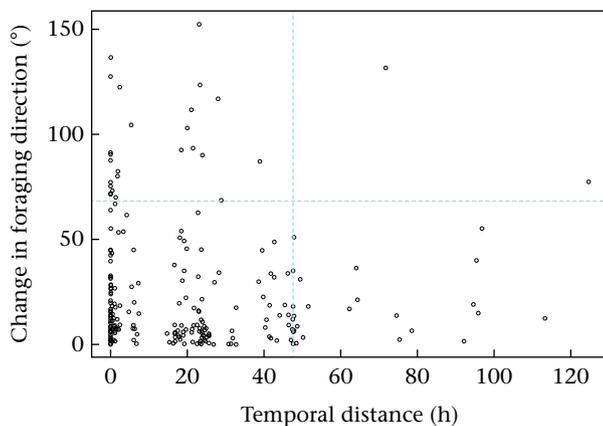


Figure 1. Change in foraging direction (the difference between the foraging direction from one trip and the mean foraging direction) through time (in relation to the first foraging trip that was recorded) for the same individual. Dashed lines represent 90th percentiles for foraging direction and time (68.175°, 47.5 h).

Ants returned to the nest with a range of food items, including small frogs, earthworms, coleopterans, lepidopterans, hemipterans, caterpillars, ‘Pindo’ seeds, ‘Yacaratiá’ fruits and other ants (mostly *Camponotus sericeiventris* and *Atta* sp.). They scavenged for dead animals but also actively hunted prey and sometimes robbed food from other foraging ant species. We also observed them extracting nectar from fallen flowers of *Luehea divaricata*, a flower known to have two large nectar-rich nectaries (Lattar et al., 2018). Ants from two nests (L from colony DA4_2017 and F from colony DA3_2017) were observed climbing trees, occasionally returning with caterpillars.

DISCUSSION

We observed the foraging behaviour of 95 *D. grandis* workers from 12 colonies at Iguazú National Park. By mapping and observing 259 complete foraging routes, we found that most of the foragers exhibited route fidelity by having a preferred foraging area (Fig. 2) and that different foragers from the same colony explored different locations around the colony (Fig. 3). However, 32% of ants did not show a significant preference for a particular foraging site. These foragers may still use route fidelity, but higher variation in the area they covered made it difficult to detect, with only three recorded foraging trips per individual. Alternatively, these foragers may not exhibit route fidelity, possibly due to age (Mandal & Brahma, 2019) or experience (Klein et al., 2019; Ohashi et al., 2008). Variation in foraging strategy has been seen in many social insects (Jeanne, 1988; Lemanski et al., 2019). Individual heterogeneity in foraging behaviour might help increase the foraging efficiency of the colony or decrease variation in resource acquisition in changing food distribution scenarios (Burns & Dyer, 2008). Finally, in most colonies, the territory was explored evenly (Fig. 4). Taken together, our results suggest that route specialization by individual workers increases overall foraging exploration of the colony.

The duration of the foraging trips we observed (mean \pm SD = 50.6 ± 46.6 min) were similar to other species of *Dinoponera* (*Dinoponera quadriceps*: 36 min, range 10–175 min: Araújo & Rodrigues, 2006; Azevedo et al., 2014; *D. gigantea*: 30–60 min: Fourcassié & Oliveira, 2002). In contrast, foraging success (31%) and maximum distance travelled (4.8 ± 2.7 m) was lower than for *D. quadriceps* (foraging success: 76%, distance range 1.52–172.56 m: Azevedo et al., 2014). Fowler (1985) observed foragers of *D. grandis* travelling more than 40 m from the nest, a distance three times higher than our maximum observed distance. This difference might be related to the higher density of colonies in INP, leading to more intensive intraspecific

territoriality interactions (Tillberg et al., 2014) and a division of foraging territories among colonies. Nest distributions of *D. grandis* at Iguazú are overdispersed (Tillberg et al., 2014), suggesting strong territorial competition among colonies as in other ants (Ryti & Case, 1986; Thurber et al., 1993). Furthermore, Tillberg et al. (2014) counted 83 colonies in an area of 4600 m² in INP. Assuming the foraging territories of these colonies were equally divided, each colony would have a foraging area of 55.4 m². Notably, this number is close to the mean (\pm SD) foraging territory of 66 ± 29.3 m² calculated in this study. Colonies varied in foraging territory size (range 35–126 m²), with a positive relationship between foraging area and the total number of foragers (Appendix, Fig. A3). Moreover, the number of foragers was correlated with the size of the colony (0.79), with bigger colonies (>80 individuals) usually having more than nine foragers (Table 1).

Although all the studied colonies were in the same area and many of the colonies were neighbours, foraging territory overlap

was uncommon. An exception was colony DA3_2017 and colony DA5_2017, for which the foragers from these two colonies were seen interacting with each other in the overlapping area, sometimes ending in the death of one of these ants. These fights were not the ‘ritualized’ interactions between non-nestmates described in other studies of *D. grandis* (Fourcassié & Oliveira, 2002; Tillberg et al., 2014), although this was observed in laboratory-maintained colonies when two ants from different colonies were placed together (P. E. Hanisch, personal observation). As found by Tillberg et al. (2014), colonies in INP were bigger (41–101 individuals) than previously reported for populations in Brazil (12–25 individuals; Fowler, 1985; Monnin et al., 2003). The percentage of the colony that took part in foraging in our study (11%) was lower than that observed by Smith et al. (2011) in slightly smaller colonies (26% of workers in colonies consisting of 36–86 individuals). Taken together, the large colony sizes and high densities suggest that antagonistic interactions among colonies are likely common. In fact, at INP *Dinoponera* workers are often seen with missing legs

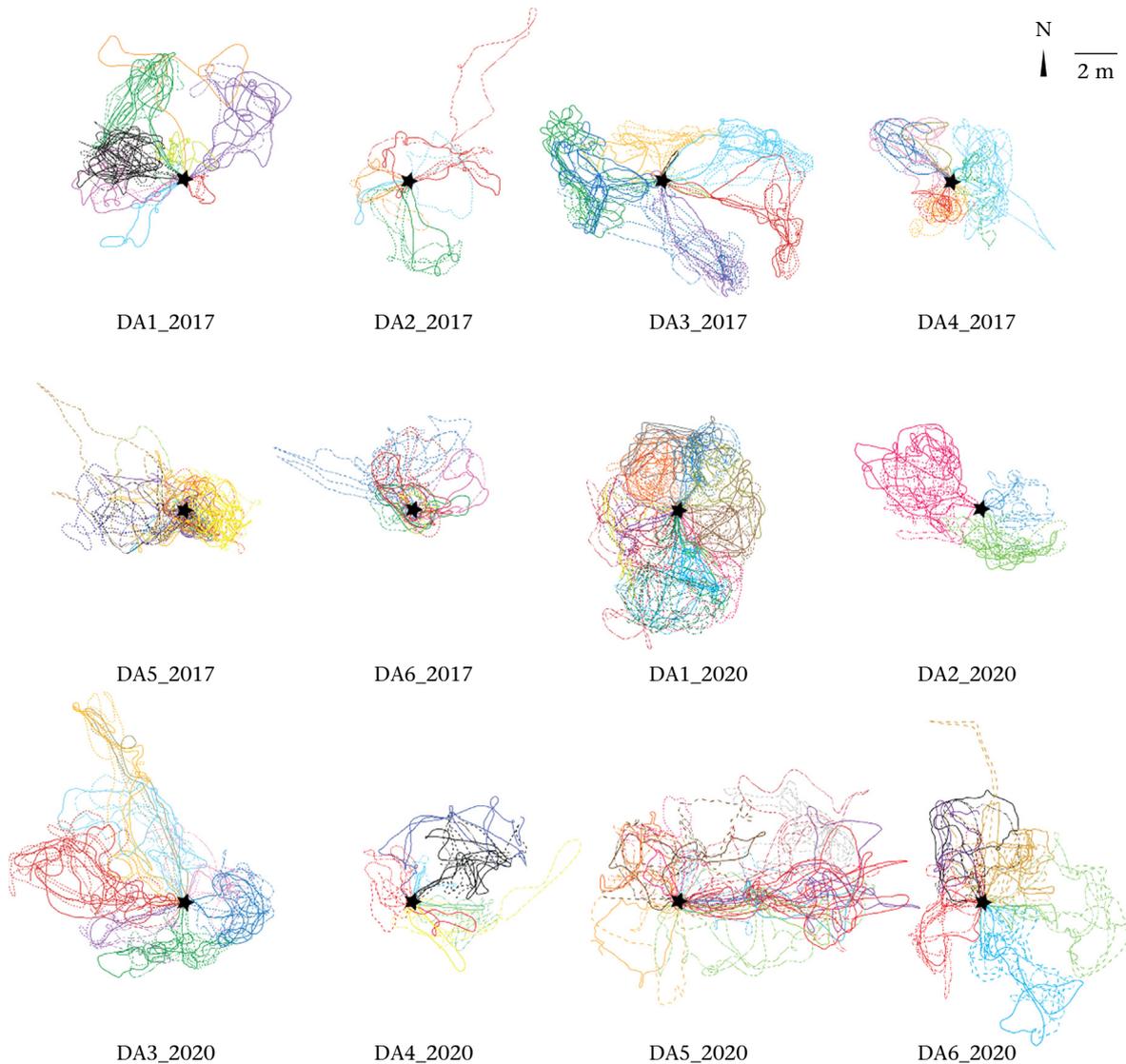


Figure 2. Foraging routes for workers from all studied colonies. Different foragers are marked with different colours. Each line type represents a different foraging trip. The colony entrance is marked with a black star. All colonies are oriented according to the north direction.

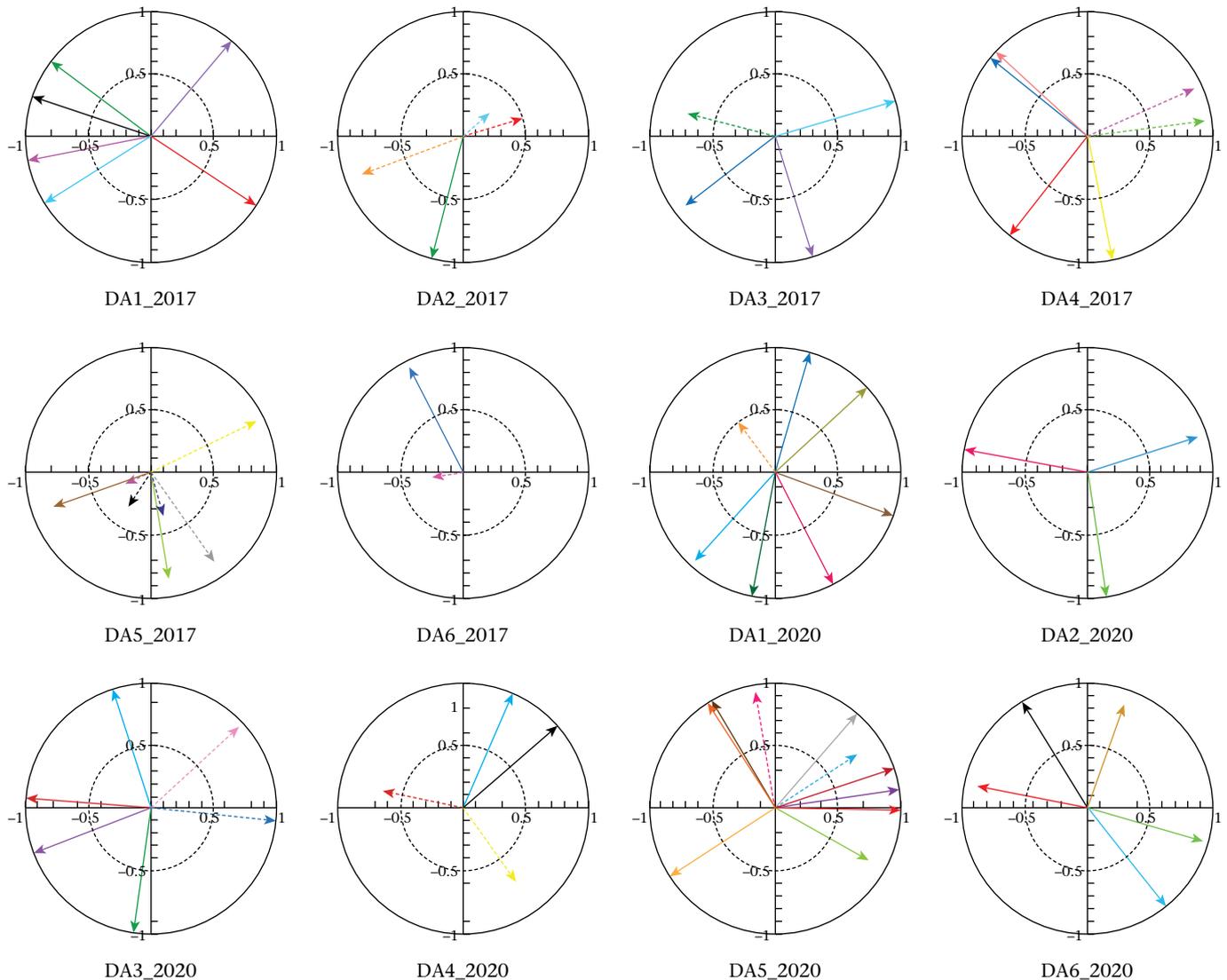


Figure 3. For all the studied colonies, R vectors obtained with the Rayleigh test for all foragers with three or more trips. Different foragers are marked with different colours (as in Fig. 2). Solid lines denote foragers with a significant result from Rayleigh test.

and antenna, perhaps as a result of territorial disputes (P. E. Hanisch & A. Suarez, personal observations).

Shannon's entropy is a useful measure to quantify the overall efficiency of foragers, with lower scores indicating more overlap in visited areas and higher scores suggesting more even coverage of the territory. We found that *D. grandis* exhibited moderate to high entropy in their foraging; colonies with bigger foraging areas had higher entropy (Fig. 4, Table 1). However, when controlling for foraging area (H_2), entropy values were consistently high, suggesting that all areas had a similar probability of being explored within a colony's territory. Our foraging data corresponded to three foraging trips for most foragers; therefore, even with relatively few foragers (3–15) and three foraging trips each, colonies were capable of evenly exploring their territory. This was also achieved in less than 3 days (Fig. 1), but this is likely an overestimate since different ants foraged simultaneously. Remarkably, the colony with the lowest entropy (DA6_2017) also had the lowest food intake (0% of the foraging trips were

successful; Table 1) and the lowest route fidelity (Fig. 3, Appendix, Table A1). Moreover, two of the five foragers from this colony foraged around the nest entrance without any preferred direction (Fig. 2). This might suggest that food availability and forager experience may influence foraging decisions.

An even foraging probability distribution of the foraging territory coupled with randomly distributed food likely increases resource encounter rate. Using entropy of foraging trails in ants was recently explored by Lourenço et al. (2020), who developed a computer model corresponding to a gradient of pheromone concentration along a foraging trail with recruitment of other nestmates to a food source. According to this model, entropy values decrease during trail formation. This is expected for ants using trail pheromones because, once a resource is found, they establish a stable foraging trail to recruit other nestmates and subsequently decrease the probability of exploring new areas. In this system, we speculate that entropy increases over time as areas are first explored and later revisited regularly over time.

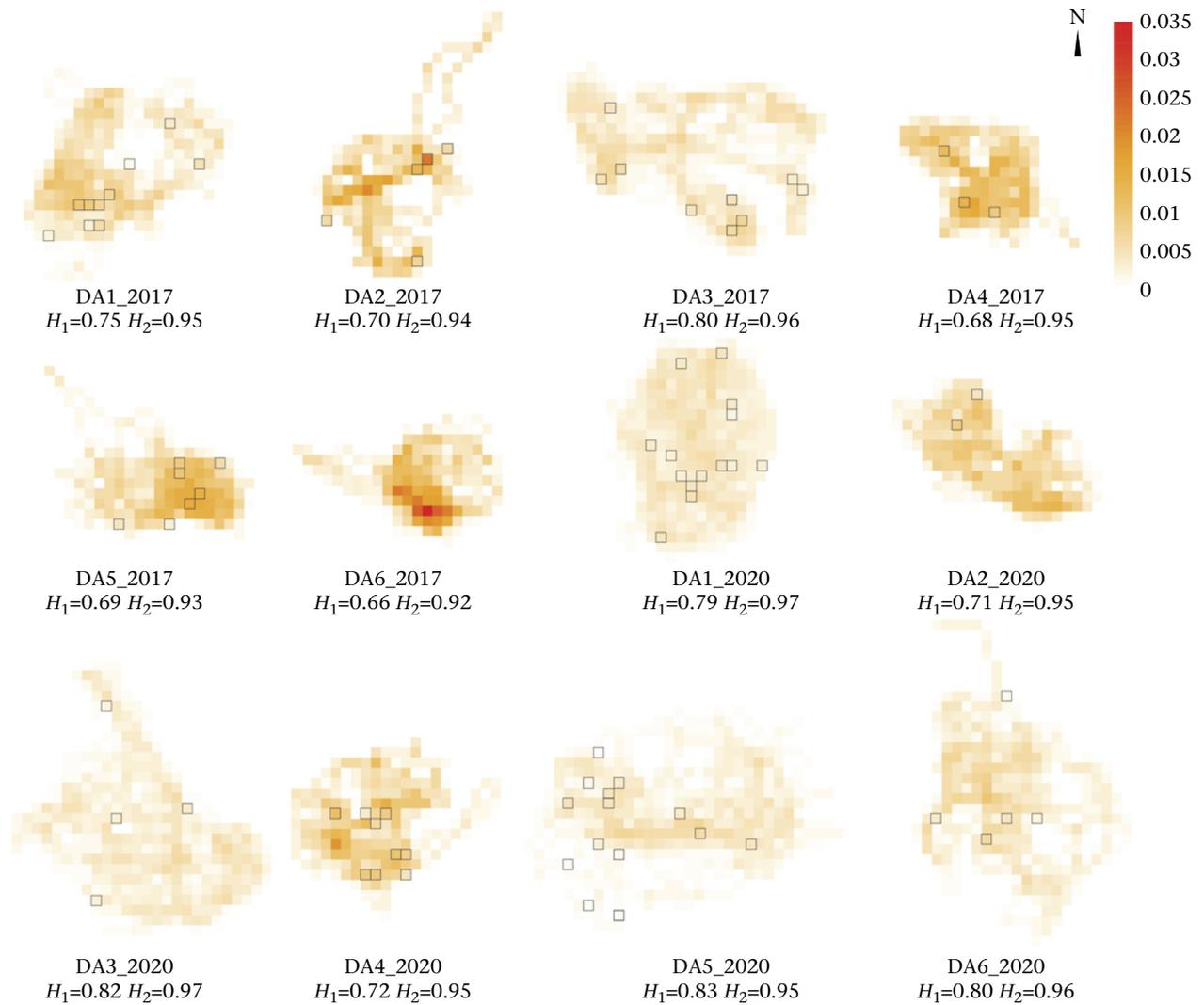


Figure 4. Heat map of the foraging route for each colony. Hot colours represent a higher probability of finding an ant in a particular cell. Shannon entropies (H_1 and H_2) are shown for each colony. Cells enclosed by a black line indicate areas where food was collected.

Table 2
Summary of Rayleigh test results for foraging direction and food direction for all the colonies

| Colony | Foraging direction | | Food direction | |
|----------|--------------------|-------------|----------------|-------------|
| | R | P | R | P |
| DA1_2017 | 0.34 | 0.11 | 0.60 | 0.02 |
| DA1_2020 | 0.21 | 0.23 | 0.43 | 0.06 |
| DA2_2017 | 0.25 | 0.49 | 0.50 | 0.30 |
| DA2_2020 | 0.10 | 0.89 | 0.97 | 0.16 |
| DA3_2017 | 0.05 | 0.94 | 0.52 | 0.08 |
| DA3_2020 | 0.25 | 0.26 | 0.74 | 0.11 |
| DA4_2017 | 0.07 | 0.90 | 0.41 | 0.64 |
| DA4_2020 | 0.38 | 0.12 | 0.75 | 0.00 |
| DA5_2017 | 0.28 | 0.09 | 0.13 | 0.88 |
| DA5_2020 | 0.40 | 0.00 | 0.22 | 0.50 |
| DA6_2017 | 0.25 | 0.43 | – | – |
| DA6_2020 | 0.25 | 0.35 | 0.52 | 0.36 |

Significant P values are shown in bold.

The use of probability distributions and information measures to describe the paths and foraging strategies of social insects could be particularly useful for quantifying and comparing behavioural patterns of different species. It allows the comparison of the probabilistic behaviour of individual workers, colonies or species with regard to different scenarios and distributions of food sources. Nevertheless, our methodology has the disadvantage that it does not distinguish between spaces (pixels) occupied once or many times. So, our probability distribution is an approximation. Hence, for a better interpretation of entropy in this context, models might be needed for this type of foraging pattern (including few foragers, no nestmate recruitment and an absence of chemical trails) and supplemented with a different experimental design.

In conclusion, our research supports the hypothesis that workers of *D. grandis* exhibit route fidelity when foraging. This preference of the ants for foraging in a particular area, coupled with foraging in different directions and an even exploration of the foraging territory, may

increase foraging success and search area. However, not all foragers exhibited route fidelity, suggesting that individual decisions regarding where to forage may depend on factors other than efficient space exploration. Variation in the degree to which individual foragers and whole colonies exhibit this behaviour suggests that environmental factors (such as food distribution and landscape) and experience may be important in determining foraging behaviour. Experiments that manipulate food abundance and distribution are needed to determine how these factors influence individual and colony level foraging decisions in this species.

Author Contributions

P.E.H.: Conceptualization, Investigation, Methodology, Data curation, Formal Analysis, Visualization, Writing – original draft, Writing – review & editing. **E.R.H.:** Methodology, Programming, Writing – review. **V.B.:** Methodology, Writing – review. **P.L.T.:** Funding acquisition, Project administration, Resources, Supervision, Writing – review and editing. **A.V.S.:** Funding acquisition, Resources, Supervision, Writing – review and editing.

Data Availability

The raw data for this study are available upon request.

Declaration of Interest

None.

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Appendix

Table A1

Summary of Rayleigh test results for all foragers that completed three or more trips

| Colony | Ant | Foraging trips (N) | R | P |
|----------|----------------|--------------------|------|-------------|
| DA1_2017 | C | 3 | 0.98 | 0.04 |
| DA1_2017 | D | 3 | 0.99 | 0.04 |
| DA1_2017 | E | 3 | 1.00 | 0.03 |
| DA1_2017 | F | 3 | 1.00 | 0.03 |
| DA1_2017 | G | 3 | 0.99 | 0.04 |
| DA1_2017 | I | 3 | 1.00 | 0.03 |
| DA1_2020 | A | 3 | 0.95 | 0.05 |
| DA1_2020 | B | 3 | 1.00 | 0.03 |
| DA1_2020 | C | 4 | 0.52 | 0.36 |
| DA1_2020 | E | 4 | 0.99 | 0.01 |
| DA1_2020 | G | 3 | 1.00 | 0.03 |
| DA1_2020 | H | 4 | 0.98 | 0.01 |
| DA1_2020 | I | 3 | 0.99 | 0.04 |
| DA2_2017 | A | 3 | 0.51 | 0.49 |
| DA2_2017 | C | 3 | 0.85 | 0.11 |
| DA2_2017 | D | 3 | 0.27 | 0.83 |
| DA2_2017 | E | 3 | 0.98 | 0.04 |
| DA2_2020 | 47 | 3 | 0.99 | 0.04 |
| DA2_2020 | 72 | 5 | 0.91 | 0.01 |
| DA2_2020 | 96 | 4 | 0.99 | 0.01 |
| DA3_2017 | A | 3 | 0.71 | 0.23 |
| DA3_2017 | C | 3 | 0.90 | 0.08 |
| DA3_2017 | F | 3 | 1.00 | 0.03 |
| DA3_2017 | G | 3 | 1.00 | 0.03 |
| DA3_2020 | A | 3 | 0.99 | 0.04 |
| DA3_2020 | C | 3 | 0.98 | 0.04 |
| DA3_2020 | D | 3 | 1.00 | 0.03 |
| DA3_2020 | E | 3 | 1.00 | 0.03 |
| DA3_2020 | H | 3 | 0.94 | 0.06 |
| DA3_2020 | I | 3 | 0.97 | 0.04 |
| DA4_2017 | B | 3 | 0.95 | 0.06 |
| DA4_2017 | D | 4 | 0.97 | 0.01 |
| DA4_2017 | F | 3 | 0.97 | 0.05 |
| DA4_2017 | J | 3 | 1.00 | 0.03 |
| DA4_2017 | K | 3 | 0.93 | 0.06 |
| DA4_2017 | L | 3 | 0.97 | 0.04 |
| DA4_2020 | A | 4 | 0.72 | 0.12 |
| DA4_2020 | C | 3 | 0.65 | 0.19 |
| DA4_2020 | E | 3 | 0.97 | 0.04 |
| DA4_2020 | F | 3 | 1.00 | 0.03 |
| DA5_2017 | A | 4 | 0.99 | 0.04 |
| DA5_2017 | E | 4 | 0.22 | 0.89 |
| DA5_2017 | G | 3 | 0.33 | 0.75 |
| DA5_2017 | L | 3 | 0.94 | 0.06 |
| DA5_2017 | P | 3 | 0.86 | 0.10 |
| DA5_2017 | Q ¹ | 3 | – | – |
| DA5_2017 | R | 3 | 0.37 | 0.70 |
| DA5_2017 | S | 6 | 0.84 | 0.01 |
| DA5_2020 | A | 3 | 0.78 | 0.17 |
| DA5_2020 | C | 4 | 0.99 | 0.04 |
| DA5_2020 | D | 4 | 0.98 | 0.01 |
| DA5_2020 | E | 3 | 0.99 | 0.04 |
| DA5_2020 | H | 3 | 1.00 | 0.03 |
| DA5_2020 | I | 4 | 0.98 | 0.01 |
| DA5_2020 | J | 4 | 0.85 | 0.05 |
| DA5_2020 | K | 3 | 0.95 | 0.05 |
| DA5_2020 | M | 3 | 0.92 | 0.06 |
| DA5_2020 | N | 3 | 1.00 | 0.03 |
| DA6_2017 | A | 4 | 0.93 | 0.02 |
| DA6_2017 | C ¹ | 3 | – | – |
| DA6_2017 | F ¹ | 3 | – | – |
| DA6_2017 | G | 3 | 0.13 | 0.93 |
| DA6_2020 | B | 4 | 0.98 | 0.04 |
| DA6_2020 | D | 4 | 0.97 | 0.01 |
| DA6_2020 | E | 3 | 0.97 | 0.04 |
| DA6_2020 | F | 4 | 0.87 | 0.04 |
| DA6_2020 | G | 3 | 0.93 | 0.05 |

Significant *P* values are shown in bold.

¹ Foragers whose mean foraging direction during foraging trips could not be determined.



Figure A1. Greyscale photo, simplified for visual purposes, showing an observer at the study site of colony DA1_2020. The coordinate system is shown in red, the flags used to mark positions are shown in green, and the colony entrance is indicated with a blue arrow.

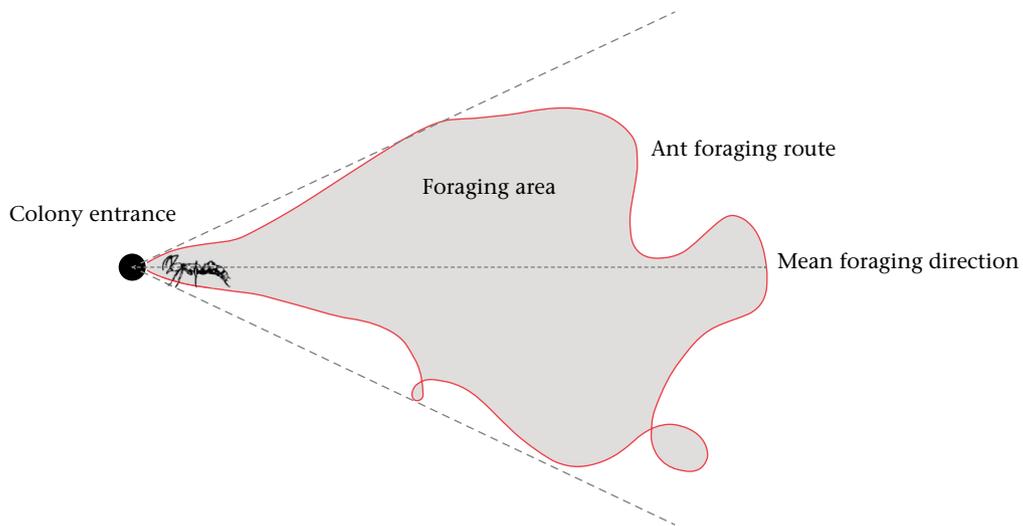


Figure A2. Diagram showing the foraging area (grey area) and how mean foraging direction was calculated.

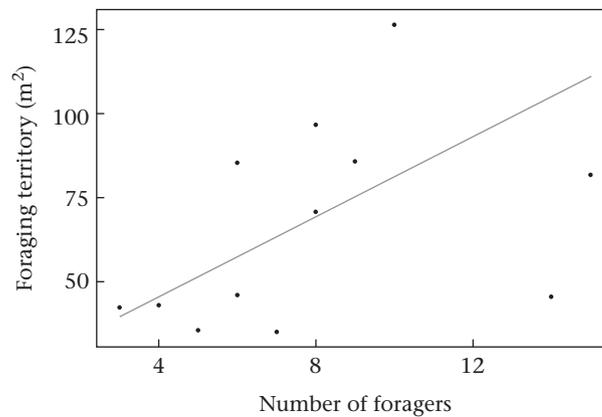


Figure A3. The relationship between the total number of foragers and the foraging area for each colony. The line represents the fitted generalized least square regression (beta = 5.95, 95% CI [1.43; 10.48], $t = 2.57$, $P = 0.02$).



Figure A4. One forager from colony DA3_2017 and another forager from colony DA5_2017 fighting in an area where the two colonies' territories overlapped.