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Adjustments in the Time, Distance and Direction of Foraging in *Dinoponera quadriceps* Workers

Dina L. O. Azevedo · Jeniffer C. Medeiros · Arrilton Araújo

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Abstract We measured individual decisions regarding the adjustments of time, distance and direction of foraging in *Dinoponera quadriceps*. We observed two colonies in an area of secondary Atlantic Forest, FLONA-ICMBio, in Northeastern Brazil. The workers were individually marked. We recorded the displacement of workers, their returns to the nest with and without food, the time spent searching for food, maximum and total distance, inter-trip latency and direction of trips. The time spent searching for food, maximum distance and transport velocity did not vary with food size. The previous trip success reduced the latency between foraging trips and increased the percentage of success on the next trip. However, this previous success did not demonstrate a significant variation relative to the time spent searching on the next trip or direction of search. The workers maintained an individual directional fidelity during foraging. The adjustments of these foraging variables under individual control contributed to the efficiency at the colony level. *D. quadriceps* is compatible with the central place theory and risk sensitivity model of behavior.

Keywords Ants · time · distance · directional fidelity · decision making · foraging strategy

Introduction

According to the optimization theory, each selected foraging strategy represents the best executable balance between costs and benefits that maximizes the net energetic profit for the colony (Detrain and Deneubourg 1997). An appropriate foraging strategy consist of decisions that specify which options the forager analyzes, the currency that informs the evaluation of available choices, which can maximize the net gain rate, efficiency, or survival, or minimize the risk of starvation, and constraints, which limit the feasible

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D. L. O. Azevedo · J. C. Medeiros · A. Araújo (✉)
Department of Physiology, Universidade Federal do Rio Grande do Norte, Post-box 1511,
59078-970 Natal, RN, Brazil
e-mail: arrilton@gmail.com

choices and currency that can be obtained, such as travel time, energetic costs, and daily energy budget (Stephens and Krebs 1986; Ydenberg et al. 2007). The decisions of foragers may be related to the time spent in exploration, a cost that can induce error if there is no relationship between the search time and amount of food acquired (Charnov 1976). Because foraging generally involves trade-offs between the acquisition of food and risk, options that increase the gain rate in foraging also increase the probability of predation (Bednekoff 2007). In relation to behavioral responses to the risk of predation, the animal may be risk-reckless and ignore the danger, risk-avoiding and minimize the danger, risk-adjusting and change its behavior proportionally in response to the level of danger, or risk-balancing and tolerate higher or lower levels of danger depending on the potential gain (Nonacs and Dill 1990).

The trade-off between costs and benefits depends on some factors that do not depend on the individual, extrinsic factors, or that are under the control of the individual, intrinsic factors. Extrinsic factors are ambient properties such as abundance and the distribution of resources and predators (Whelan and Schmidt 2007). The higher the productivity of the habitat, the higher the estimated number of ant colonies; the access to resources is decreased by poor conditions and competition among ant populations and others organisms (Kaspari 2000). The conflict in foraging areas depends on how the resources are distributed in time and space (Gordon 1993). The ephemeral availability of such resources makes for the costly and difficult maintenance of an absolute territory (Fourcassié et al. 2012). The ants can differentiate in size and density of a resource to varied degrees (Kaspari 2000). The decision regarding prey size implies a trade-off because a low level of selectivity indicates that the forager could spend more time in transit with small prey items, whereas high selectivity indicates that the forager could spend much more time at the capture site searching for the appropriate items (Ydenberg 2007). Another important characteristic within the strategy is spatial orientation, which is defined as self-controlled maintenance or changes of body position to the environmental space and is composed of both directional and distance orientations (Jander 1975). An increased number of workers that leave the nest without directional orientation related to the food site could result in a disproportionate number of workers in some sections of the foraging area (Carroll and Janzen 1973). An ant that returns with a superior food item may provoke an increased number of foraging forays from the nest (Carroll and Janzen 1973).

In colonies of social insects, individuals change or adjust their behavior in response to the accumulation of information. In large colonies, the individual workers appear to consider the disseminated and sampled information. In some cases, the workers invest time and effort in sampling information before deciding on an action. In smaller colonies, the tendency is for the workers to make independent decisions (Franks 1999). Because the aspect of the food search pattern has consequences for the entire colony, foragers at the individual level may develop estimates of prey size and rules of thumb (Detrain and Deneubourg 1997). Multiple solitary foragers explore a greater proportion of available patches than a group of identical foragers because several patches can be explored concomitantly by independent foragers (Beauchamp 2005). Economic interdependence indicates that the reward gained from a foraging strategy simultaneously depends on the behavior of all competitors (Giraldeau and Caraco 2000). There are theoretical models used to verify foraging optimization: the central place model (Orians and Pearson 1979; Schoener 1979), marginal value theorem (Charnov 1976), and risk sensitivity theory (Stephens 1981; Nonacs and Dill 1990).

One must understand the individual strategies to test the models and understand the optimization strategy used at the colony level. The foraging modes of the Ponerinae ant subfamily range from solitary to group hunters and from specialist to generalist predators (Fourcassié and Oliveira 2002). The mass foraging of classic army ants was already described in *Leptogenys distingueda* (Witte and Maschwitz 2000) and *L. nitida* (Duncan and Crewe 1994). Species of the Neotropical genus *Dinoponera* are among the largest known ants, and their distribution is restricted to South America. The species *Dinoponera quadriceps* (Santschi) is endemic to the area of Brazil known as the "polygon of dryness" (Kempf 1971). *D. quadriceps* nests at the base of trees and has more than 50 workers on average (Paiva and Brandão 1995). *D. quadriceps* workers forage solitarily and never recruit nest mates. When the workers leave the colony, they move at a slow speed and begin foraging immediately (Araújo and Rodrigues 2006). The pattern of foraging in semi-arid regions is associated with changes in temperature and the availability of food resources throughout the year (Medeiros et al. 2012). There is little information regarding individual behavior of this species during foraging. In this study, we measured the actual decision performed by individual *D. quadriceps* foragers in their natural environment, considering the individual decision variables, such as travel time, distance traveled and direction of displacement while foraging. We noted how individual *D. quadriceps* workers make adjustments to these variables and how their adjustments can benefit the colony. Therefore, we analyzed the individual level and discussed how it should shed light on the underlying foraging strategy mechanism in terms of the colony.

Materials and Methods

Study Site

The study was conducted in the Floresta Nacional de Nísia Floresta (FLONA) of the Instituto Chico Mendes de Conservação da Biodiversidade (6°5'S, 35°12'W) located in Nísia Floresta, state of Rio Grande do Norte, Brazil. The region has a 12 h:12 h ±15 min light:dark photoperiod. The research station encompasses an area of 180 ha, of which 80 ha are secondary Atlantic Forest and 40 ha are plantations of exotic species. Although the northeastern region of Brazil is primarily dry, the coastal region (60 m altitude) has distinct seasonality: the rainy season (March–July) and dry season (August–February). The temperatures are highest during the dry season, reaching 33 °C, and drop as low as 20 °C during the rainy season (Santee and Arruda 1994).

Ants

Two colonies of *D. quadriceps* (Hymenoptera, Formicidae, Ponerinae) were randomly chosen within an area of secondary forest. Only two colonies were observed because this study forms part of a long-term observational research (19 months, non-successive). One of the colonies had more than one entrance; in this case, we chose the entrance that was discovered initially as a reference point for the observations. The colonies were located 13.1 m from one another.

The workers were marked throughout the study. When an unmarked individual ant left the nest, it was captured, and a numbered plastic tag was affixed to the thoracic region using an ester-based cyanoacrylate glue (Corbara et al. 1986). Workers from different colonies were identified using different colored tags. There was a break of at least 24 h between marking and observation.

Behavioral Records

The observations occurred intermittently over 19 months between February 2006 and June 2008 and occurred at least once a week for 10 h per day, in light phase based on the natural foraging times. We observed one worker at a time, from its nest exit to its return from foraging. For such observations, we adopted the focal time sampling method with 15-min sample intervals and recordings every minute (Martin and Bateson 1994).

The following behavioral categories were recorded during observations of ant activity:

- Searching for food: the worker moved slowly, touching the substrate with its antennae and searched the area following a winding route;
- Capture and transport of food: the worker captured a food resource (plant or animal; alive or dead) with its mandibles.

Among the ants observed, we considered only those that traveled for at least 10 min because in a pilot experiment, we observed workers leave the nest, remain near the nest entrance and return quickly after less than 10 min. During this time, the ants did not search for food and either performed nest maintenance activities or remained in the entrance of the nest moving their head from side to side. To analyze the inter-trip latency inside the nest, we considered ants that were recorded on at least two trips and recorded the duration of each trip, the return with or without a food item and the time spent between the return to the nest and next trip. One worker may have been observed more than once on different days. Except for marking, there was no handling of the workers during their trajectory or extra-nest activities.

Recording of Worker Displacements

We adapted the technique described by Turchin et al. (1991) to map ant positions and placed small numbered flags every 5 min during the observations. After a pilot experiment to test the methodology, we verified that placing small flags every 1 min versus every 5 min did not make a difference in the estimated routes. Therefore, we placed a flag every 5 min. After the worker returned to the nest, the distances and angles between the flags were measured using a fiberglass measuring tape and compass, respectively. From these data, we built an estimated trajectory of each worker during its activities and calculated its total distance traveled, the maximum distance ventured from the nest, distance from the capture site to the nest and direction of the foraging activities. We calculated the mean velocity of prey transport during each successful trip, considering the time spent returning to the nest after capturing a food item and the distance between the nest and capture site.

Estimation of Prey Size

When a worker captured and transported a food item, its approximate size was recorded. This approximate prey size was based on a scale constructed regarding the size of *D.*

quadriceps. We decided to construct the scale based on the length of the workers (see below) because we did not want to interfere with their activities:

- Proportion 0–the worker returned with no food item;
- Proportion 1–the food item size was equivalent to the distance from the mandible to the end of the head: 8.37±0.27 mm ($\bar{x} \pm sd$);
- Proportion 2–the food size was equivalent to the distance from the mandible to the end of the petiole: 16.93±1.44 mm ($\bar{x} \pm sd$);
- Proportion 3–the food size was equivalent to the distance from the mandible to the end of the abdomen: 25.83±1.49 mm ($\bar{x} \pm sd$);
- Proportion 4–the length of the food item was longer than the worker: longer than 28 mm.

In addition, we collected food items that workers from four other colonies brought to their nests. The lengths and weights of these food items were measured, and a correlation test was applied (N=120, Rs=0.70, p<0.05) to justify the use of a food size index such as the measurement of the food items collected.

Statistical Analysis

We used Spearman's correlation test (R_S) to verify the occurrence of a relationship between the time spent outside the nest and distance traveled. We then applied a Kruskal-Wallis (H) test to the time spent searching for food, maximum distance ventured and transport velocity variables and a Mann–Whitney (U) test to the inter-trip latency inside the nest, time spent searching on the next trip and difference in the angles between the trips to analyze the success of the trips in relation to returns with or without a food item. We then conducted a Chi-square (χ^2) test to compare the percentage of success.

To investigate whether there was a directional preference to a specific area around the colonies among the workers, we initially obtained the mean vector of each trip with the positions data. We then measured the average absolute angle between the different trips, which were separated into successful and unsuccessful trips; except for when there was only one trip recorded, and applied the Rayleigh (Z) test (Batschelet 1981). Therefore, the result provided us with both the directional fidelity of each worker and distribution of the workers across the foraging area of each colony in regard to the success in searching. We considered a two-tailed significance level of 5 % in analyses. Statistica 7.1, PASW Statistics 18 and Oriana 2.01 software programs were used to perform the tests.

Results

In this study, we observed 265 trips by 109 different workers: 62 workers from colony I and 47 workers from colony II. The two colonies together accounted for 235 h of direct observations. The frequency of searching for food behavior represented 94.6 % of the observations, whereas food capture and transport events comprised 5.4 % of the observation time.

The more time that workers spent outside the nest, the more they moved within their home range because the time spent outside the nest and total distance traveled in the observed foraging trips exhibited a positive correlation (R_S=0.88, p<0.05, N=265;

Fig. 1a). The median time spent outside the nest was 36 min (quartiles: 21.0–63 min, range: 10–401 min). The median distance traveled was 24.67 m (quartiles: 15.1–38.42 m, range: 1.52–172.56 m). The number of trips observed by the workers varied (2.4±1.6) with a greater number of individuals in more than one trip (Fig. 1b). The variation of velocity in the trips (0.012±0.008 m/s) showed a similar pattern among individuals (Fig. 1c) but was an individual characteristic, which varied among the trips.

The workers returned with food in 57 % of the 265 observed trips (food size index: 0, N=106; 1, N=105; 2, N=39; 3, N=12; 4, N=3). Because of the small number of food items categorized as proportion 4, these data were not included in the statistical analyses but included in Fig. 2. The time spent searching for food and maximum distance ventured from the nest did not show a significant difference in relation to prey capture success. Despite this result, the individuals had a prolonged search trip time to capture larger food items (H=4.49, df=3, p>0.05, N=262; Fig. 2a) and venture greater distances (H=6.68, df=3, p>0.05, N=262; Fig. 2b). During the observations, we occasionally recorded workers ingesting a captured food item when it was small (~3 mm), after which it pursued its search for food. Food size did not affect the velocity of food transport (H=2.92, df=2, p=0.23, N=156; Fig. 2c) despite the variable speeds. We emphasize that behavior varied among the workers, e.g., some left rapidly on a new search even when the prior trip was unsuccessful; however, this did not cause changes in the overall behaviors.

The success of prey capture on a trip influenced the time spent by the workers inside the nest before initiating a new search. The inter-trip latency was shorter when the previous trip of the worker had been successful (U=1009, z=6.30, p<0.05, N=153; Fig. 3a). Some workers observed in this research always returned to the nest without food, whereas others always came back with food, and there were workers that returned without food on some trips and with food on others. The percentage of success on the next trip increased after a successful previous trip (χ^2=12.82, p<0.05; Fig. 3b). Nevertheless, the effect of the previous trip did not show significant differences on the time spent searching for food on the subsequent trip (U=1058, z=1.12, p>0.05; Fig. 3c) or direction of searching (U=1173, z=0.33, p>0.05; Fig. 3d).

The workers' home range to search for food comprised a 35 m radius of action around the nest. The individual workers began their search for food and left the nest, without displacement, for a foraging patch to initiate searching for food. After locating a food item, the workers returned to the nest in a nearly straight line (Fig. 4). The workers that returned without food continued to exhibit a zigzag movement pattern until entering the nest. We did not observe workers help one another in the transport of food or collectively transport prey.

Each worker maintained an individual directional preference during all of the trips based on individual tests (see Materials and Methods). However, more than one worker searched within the identical area around the nest (Fig. 5). When we regard the data at the colony level in relation to the success of search trips, we observe that colony I showed uniform worker distributions within the area surrounding the nest in two situations, successful (N=42, Z=0.01, p=0.99; Fig. 5a) or unsuccessful trips (N=40, Z=0.06, p=0.94; Fig. 5b). However, colony II demonstrated a slight directional pattern of successful (N=36, Z=1.86, p=0.03; Fig. 5c) and unsuccessful trips (N=26, Z=7.62, p=0.01; Fig. 5d). The individual workers continued showing a directional preference although their trip had been unsuccessful, and the workers from colony II appear to have avoided searching in the overlapping areas of the colonies.

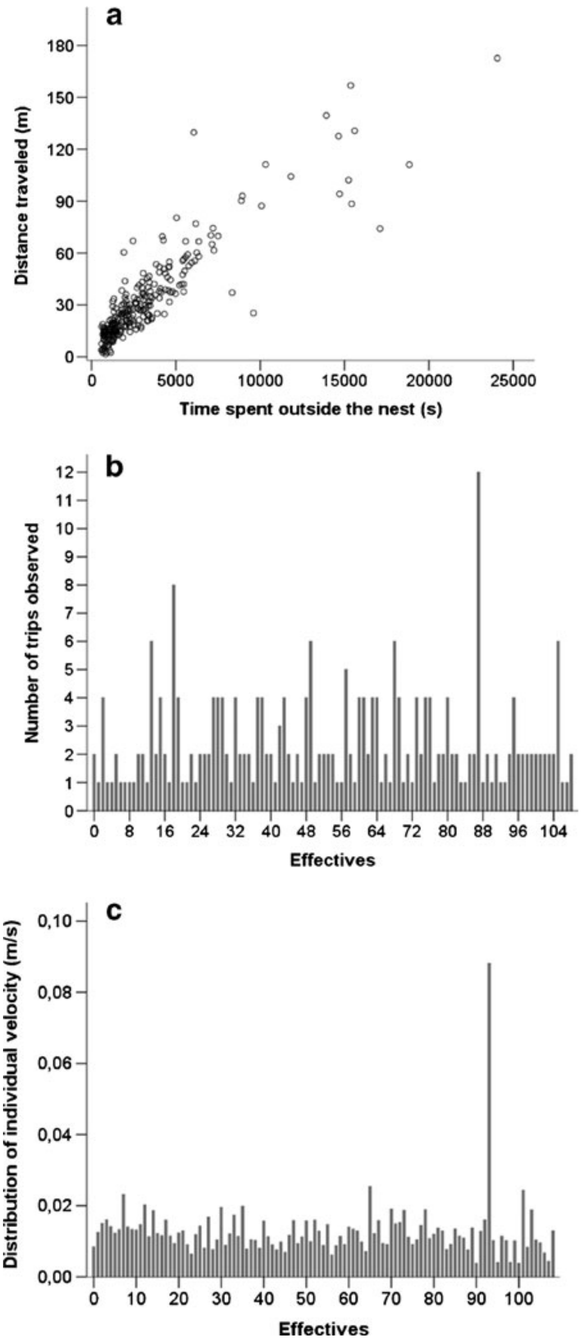
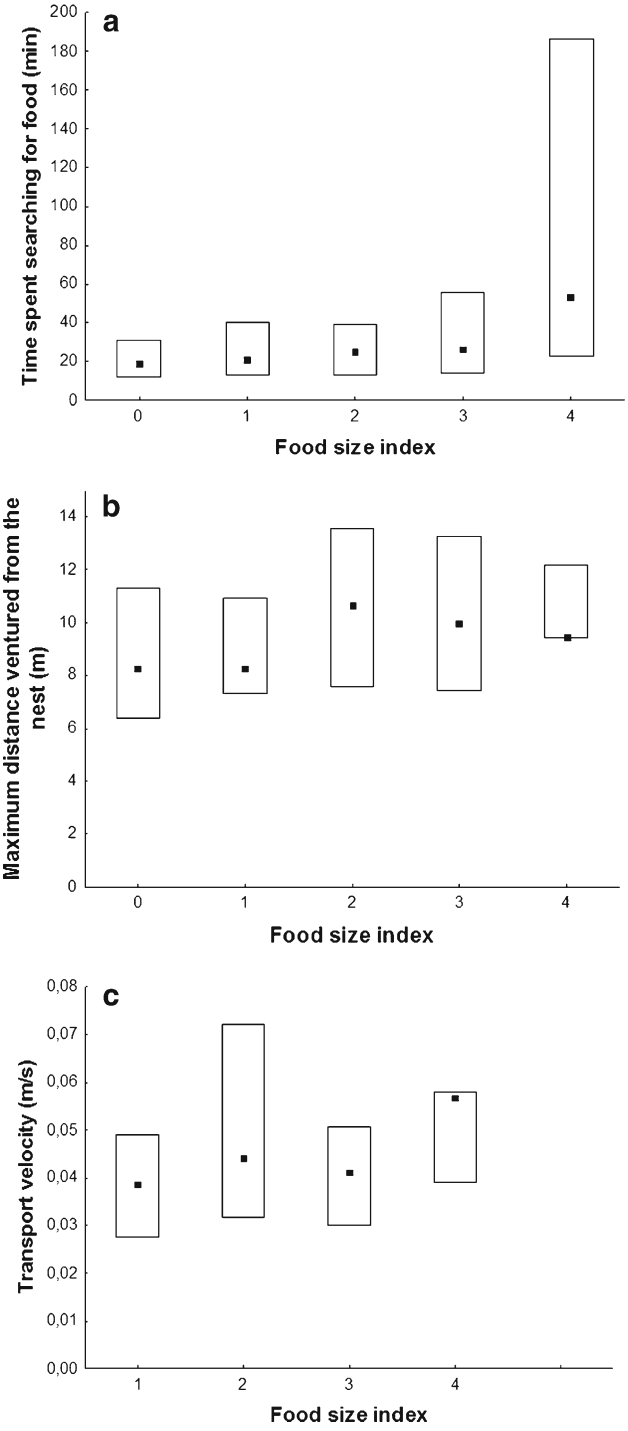


Fig. 1 The relationship between time spent outside the nest and distance traveled by *Dinoponera quadriceps* workers during foraging behavior (**a**), the distribution of the number of trips (**b**) and individual velocity (**c**). The equation of the *straight line*: Distance traveled = 922,8818+43,0311*Time spent outside the nest

Discussion

In this study, all measures that we analysed they were considering the activities of individual *D. quadriceps* workers to verify their effect on the efforts at the colony

Fig. 2 The assessment of the foraging efficiency of *Dinoponera quadriceps* workers in relation to the time spent searching for food (**a**), maximum distance traveled from the nest (**b**) and transport velocity (**c**). There was no significant difference. The *small quadrate* represents the median, whereas the *long rectangle* shows the quartiles



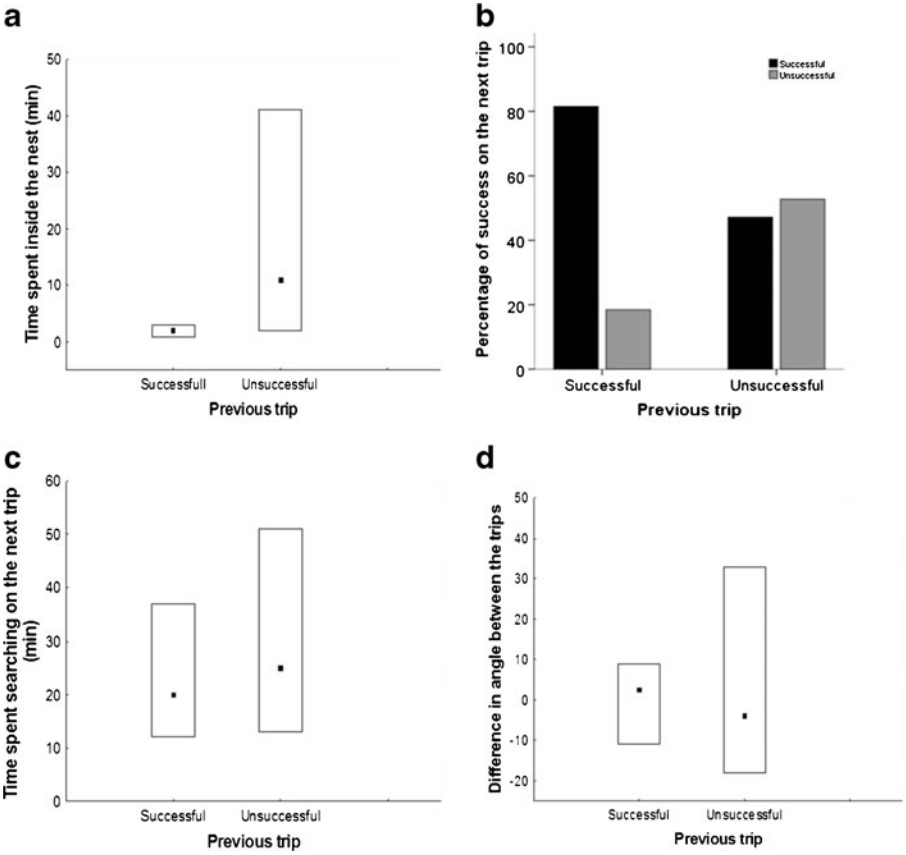


Fig. 3 The effect of the foraging success of a previous trip on the latency of the next trip (**a**), success on the next trip (**b**), time spent searching for food (**c**), and difference in the angle of trips (**d**). The *small quadrate* represents the median, whereas the *long rectangle* shows the quartiles

level. The *D. quadriceps* workers did not move far from the nest before initiating their search. The workers began their search when leaving the nest and invested the majority of their time in searching for food. Food items were likely to be initially depleted near the nest. This may have forced the workers to travel increasingly longer distances to locate food, even when success was not guaranteed. Sites that are further from the nest must be explored for a longer time than those located closer to the nest (Bonser et al. 1998).

All food items collected by *D. quadriceps* were solid and preferentially of animal origin, confirming the results of Araújo and Rodrigues (2006). Solid food requires greater foraging distances compared to liquid food (Fourcassié and Oliveira 2002). Single prey loaders, such as *D. quadriceps*, bring only one food item at a time to the nest. Individual foraging is generally favored with an increased distance to the food source (Carroll and Janzen 1973); however, food availability influences search duration. The availability low will stimulate the workers to a prolonged search (Schafer et al. 2006). The selection of minimum prey size, according to the type of resource, varies between species. For *Pheidole pallidula*, the main selection factor is the resistance of the prey to traction, which may promote a change from individual to collective foraging (Detrain

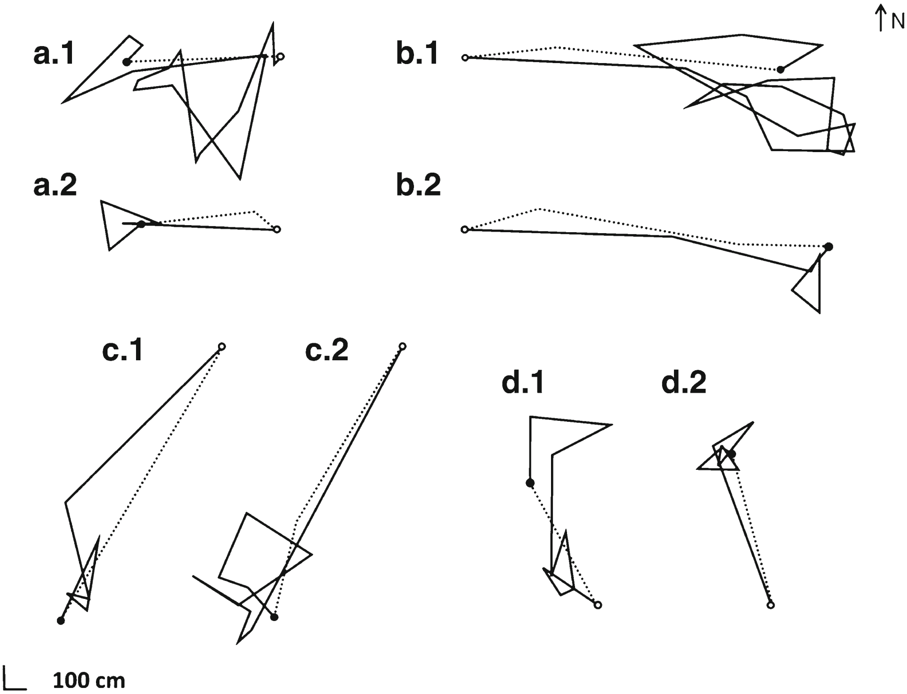


Fig. 4 A representation of some individual paths. Each different letter represents an individual worker in two separate trips. The workers '**a**' and '**b**' belong to colony II, '**c**' and '**d**' belong to colony I. The *full line* shows the path to search for food and *dotted line* shows the homing path. The *open point* marks the entrance of the nest and *closed point* marks the site of the capture of food

and Deneubourg 1997). Prey size and weight are factors that determine the response for capture in *Cataglyphis iberica* (Cerdá 1988) and *Dorymyrmex goetschi* (Torres-Contreras and Vásquez 2004), respectively.

Araújo and Rodrigues (2006) reported that when a *D. quadriceps* worker captures prey, it returns to the nest at varying velocities in a nearly straight line. In this study, we observed that velocity varied over the return trajectory to the nest not as a function of prey size, perhaps because of load weight. The unpredictability of food resources within the colony environment requires a foraging strategy regulated by a behavioral change of the workers to increase efficiency (Traniello 1989). Ants move within their environment in different manners, but after locating prey, they return to their nests in a straight line (Herbers and Choiniere 1996). The return to the nest along a near-straight trajectory in a natural environment was observed in *Myrmica punctiventris* (Herbers and Choiniere 1996) and *Gigantiops destructor* (Beugnon et al. 2001). The species *Ectatomma ruidum* returns to the nest at a higher velocity along its preferred route (Franz and Wcislo 2003).

The environment in which we observed *D. quadriceps* workers contains an unpredictable prey distribution. Some workers spent more than 7 h outside of the nest, which is a risky endeavor given their exposure to predation and large energetic expenditure. There was an overlap in the foraging areas of the two colonies, but no direct conflict occurred if the worker did not locate non-nest mates around its nest, agonistic interactions could occur or they ran away when they met. To travel long distances and

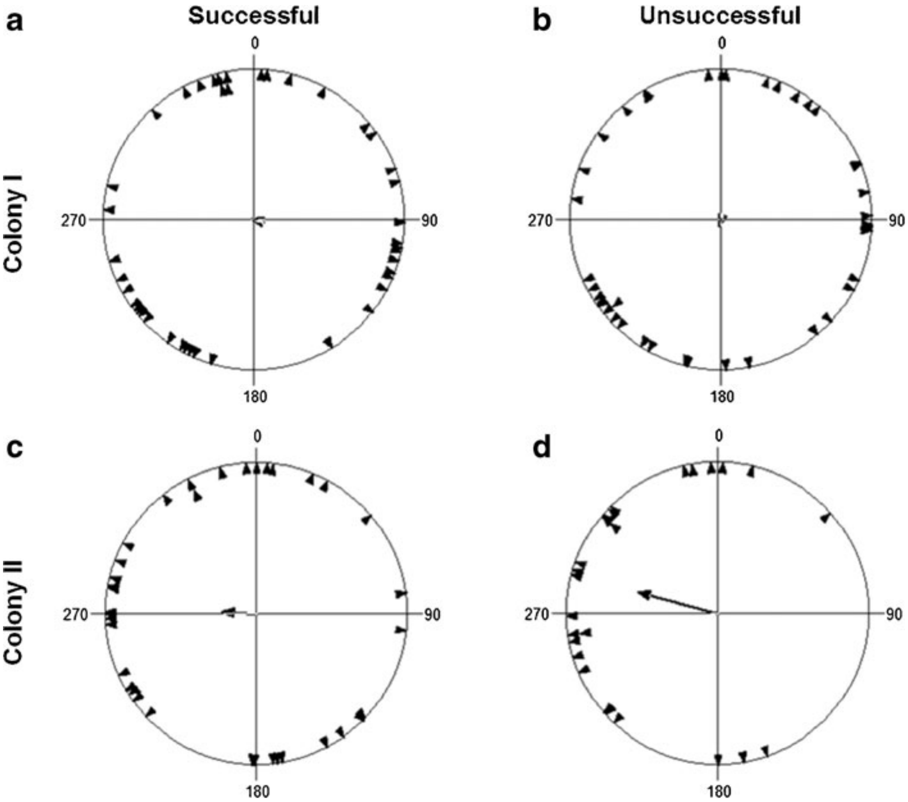


Fig. 5 The spatial distribution of the workers observed in the home range of each colony during foraging activity. Each *triangle* represents the average absolute angle of the mean trip vectors of ants in two situations: a successful or unsuccessful trip. The *center arrow* is the mean vector (μ) with its length (r) (Colony I: a. μ=284,342°, r=0,016; b. μ=198,402°, r=0,039. Colony II: c. μ=274,81°, r=0,227; d. μ=285,358°, r=0,542)

remain for long periods outside of the nest, the workers must orient themselves appropriately to increase the likelihood of a successful trip. Heterogeneous habitats lead to the organisms to experiment acquisitions, transfers and information processing events that may improve the performance of different behavioral tasks (Torres-Contreras and Vásquez 2007). A simple spatial reinforcement process may lead to high spatial fidelity at the individual level, and a division of the foraging area among the workers at the colony level (Harkness and Maroudas 1985).

After *D. quadriceps* workers returned to the nest, the time spent inside the nest was influenced by the previous trip. Foragers that returned without food they spent more time in the nest before their next searching trip, whereas successful ants spent less time. The percentage of success on the next trip increased when the previous trip was successful. A successful trip motivates a *D. quadriceps* worker to immediately depart from the nest and return to the capture site of previous prey. It is not obvious whether worker success inspires one or more foragers inside the nest to initiate their own foraging trips. In *D. quadriceps*, it appears that returning with food is a good indicator for leaving again to search for food, a pattern previously described for *Neoponera*

(=*Pachycondyla*) *apicalis* (Deneubourg et al. 1987) and *Pogonomyrmex barbatus* (Schafer et al. 2006).

In the course of the next trip, *D. quadriceps* workers expressed occasionally searching for food behavior, on arriving at the capture site they performed several circular movements around this site and increased the diameter of the circle with each movement. However, there was no difference between the directional angle of the former and latter trips. The ants come back to the identical area and develop a stereotypical route, if they have been previously rewarded (Collet et al. 1999; Wehner et al. 2002). In *D. gigantea* (Fourcassié and Oliveira 2002), *Cataglyphis bicolor* (Buchkremer and Reinhold 2008) and *N. apicalis* (Deneubourg et al. 1987) foragers leave their nest in a certain similar direction and search for food within a restricted area or sector fidelity. The area covered may be irregularly shaped and is often elongated away from the nest because of prey depletion (Gordon 1995). According to Fourcassié and Oliveira (2002), the cost of being lost when workers wander outside their familiar sector may restrict the spatial fidelity. None of the foraging directions is associated with any reward distribution but with the likelihood of locating a food item (Buchkremer and Reinhold 2008).

Therefore, *D. quadriceps* workers showed directional fidelity in a specific home range. The directional fidelity was previously registered in *N. apicalis* (Fresneau 1985). Individually foraging ants are known to learn individual stereotypic routes to increase their navigational efficiency (Kohler and Wehner 2005; Wystrach et al. 2011c; Mangan and Webb 2012). Even rainforest ants develop stereotypical routes for obtaining a food source (Macquart et al. 2006; Fresneau 1985) or home (Wystrach et al. 2011b). These routes are based mostly on panoramic views (Wystrach et al. 2011a) but also on other modalities (Buehlmann et al. 2012), as shown also in *D. gigantea* (Fourcassié et al. 1999). This study observed that the homing path in *D. quadriceps* is particularly straight because it is helped by path integration (Wehner 2003). At the individual level, the learning of a stereotypical route minimizes the time spent in displacement and the risk of becoming lost, and thus maximizes foraging efficiency. Additionally, route learning spontaneously leads to sector fidelity, which also increases efficiency at the colony level. The overall search pattern of the colony is a haphazard process that may be an efficient solution for foraging on prey whose distribution is unpredictable (Traniello 1989).

We can affirm that the maintained directional fidelity in foraging by each *D. quadriceps* worker uniformly distributed the foraging effort of the colonies around the nest. The slight directional pattern shown by colony II may have been influenced by the fission process that the colony was experiencing at that time. Another possibility would be related to competition among individuals from the identical or neighboring colony and to a non-homogenous distribution of food. Specialization through learning at the individual level in relation to time and space appears to be an appropriate solution for species that live in an environment that varies throughout the year (Deneubourg et al. 1987). Nevertheless, the simple fact that the forager has a memory and returns to the identical site does not ensure that it will capture prey because as the number of workers that discover a food source increases, the value of the food source decreases proportionately (Goss et al. 1989). Therefore, the consequences of individual action for the efficiency of the colony depend on the number of other individuals in the colony that perform similar tasks (Herbers and Choiniere 1996).

We conclude that the strategy adopted by *D. quadriceps* depends on the interactions among the decisions regarding the trip success and directions taken by the individual workers. At the individual level, *D. quadriceps* appears to follow a win-stay loose-shift strategy. This result was because the previous reward modified the individual behavior concerning the minimization of time spent searching and inside the nest before leaving it again. When several solitary ants are foraging and one fails, another may have a successful trip. Despite that the search for food is individual; foraging at the colony level is efficient because the total number of workers that visit the identical area varies. *D. quadriceps* adjustments of foraging variables make this species a good model for the study of foraging theory, in which the currency of individual foragers is the maximum efficiency of food collection.

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