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Tandem running by foraging *Pachycondyla striata* workers in field conditions vary in response to food type, food distance, and environmental conditions

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Abstract

Ants show collective and individual behavioral flexibility in their response to immediate context, choosing for example between different foraging strategies. In *Pachycondyla striata*, workers can forage solitarily or recruit and guide nestmates to larger food sources through tandem running. Although considered more ancestral and less efficient than pheromone trail-laying, this strategy is common especially in species with small colony size. What is not known is how the decision to recruit or follow varies according to the immediate context. That is, how fine adjustments in information transfer affect immediate foraging decisions at the colony level. Here, we studied individually marked workers and evaluated their foraging decisions when food items varied in nature (protein versus carbohydrate), size, and distance from the nest at different temperatures and humidity levels. Our results show that tandem run leaders and potential followers adjust their behavior according to a combination of external factors. While 84.2% of trips were solitary, most ants (81%) performed at least 1 tandem run. However, tandem runs were more frequent for nearby resources and at higher relative humidity. Interestingly, when food items were located far away, tandem runs were more successful when heading to protein sources (75%) compared with carbohydrate sources (42%). Our results suggest that the social information transfer between leaders and followers conveys more information than previously thought, and also relies on their experience and motivation.

Key words: collective behavior, decision-making, emotional states, flexibility, Ponerinae, social learning.

Optimal foraging theory predicts that decision-making, based on the costs and benefits of the different available strategies in a specific context, allows animals to adapt to their immediate environment and thus maximize resource acquisition (Krebs and Davies 1997). In social insects, collective foraging is based on sharing and/or learning information about food sources. This allows recruiting individual foragers, most often through pheromone deposition (Hölldobler 1976; Goss et al. 1989), optimizing resource exploitation. The spatial distribution of resources and their predictability across time/space influences foraging strategies from an evolutionary and context-dependent perspective. It also determines the costs of foraging in terms of time and energy expenditure, exposure to harsh environmental conditions or predators, as well as competition with other colonies, influencing foraging decisions (Anderson 2001). Additionally, collective foraging becomes costly when it reinforces the exploitation of suboptimal choices. For example, mass-recruitment via trail pheromones can cause ants to ignore profitable sources or stay trapped on a depleted source longer than necessary (Beckers et al. 1989; Grüter et al. 2011).

The ecological success of ants is in part attributed to their ability to adapt to different environmental conditions (Detrain and Deneubourg 2008; Blight et al. 2016; Gordon 2019), and different species vary in respect to their foraging strategies (reviewed by Traniello 1989). Solitary foraging is characterized by an absence of cooperation in searching, capturing, transporting, and manipulation of the food between workers outside the nest. Efficient when food items can be transported to the nest by a single individual, it is normally observed in species living in small colonies or showing fidelity to fixed foraging areas (Fresneau 1985; Beckers et al. 1989; Fourcassié and Oliveira 2002), and among ants that prey on other arthropods (Lach et al. 2009). However, even in such species, individuals sometimes engage in cooperative foraging. One example is recruitment of nest mates by tandem running (Pratt 2008; Franklin 2014; Glaser and Grüter 2018; Grüter et al. 2018), in which an ant knowing the location of a food source (the leader) recruits and guides to it a naive ant (the follower). During the trip, the follower keeps antennal contact with the gaster of the leader, which in turn allows the follower to learn the path and guide other individuals to the source. This maximizes the workforce involved and the energy intake at the source (Wilson 1959; Franklin 2014).

To decide whether to recruit nest mates to a food source, foragers must acquire and evaluate information about the type, quantity, and quality of the food, its distance from the nest (Hölldobler 1976; Fewell et al. 1992), and likely social information (e.g., the foraging force available at a given time). The ability to do this adaptively maximizes the energetic gains for the colony (Fewell et al. 1992). In the ant *Gnamptogenys moelleri*, solitary foraging is prevalent when food items are small (e.g., flies), whereas cooperative foraging is used for large prey items (e.g., crickets). This implies that information about availability and location of food sources is shared among nest mates (Cogni and Oliveira 2004). Very few studies have looked at the factors potentially influencing foraging choices in species using tandem running (but see Glaser and Grüter 2018; Grüter et al. 2018), for example, when individuals decide whether information should be socially shared or not. In the ant *Pachycondyla harpax*, Grüter et al. (2018) found an increase in the probability of performing tandem runs when food items were larger and located far away from the nest. This could help colonies to monopolize more distant food sources in a competitive environment (Grüter et al. 2018). Besides, recruitment via tandem running in *P. harpax* also increases the access to food sources, reducing the probability for competing species to take these over (Glaser et al. 2021).

Although the underlying dynamics and the economy of tandem running are well studied, what is not known is how choosing between solitary or tandem foraging is affected by attributes of the immediate context. These include differences in food types (protein versus carbohydrate), distances between food sources and the nest, and differences in environmental conditions (air temperature and air relative humidity [RH]). We hypothesize the latter to be very important since exposure to dry and hot conditions is risky, and foraging strategies determine the time the workers are exposed.

Ants in the Ponerinae subfamily show prevalence for solitary foraging (Peeters 1997; Peeters and Ito 2001). *Pachycondyla striata* (Smith, 1858) is endemic to the Neotropics and ranges from Panama to Northern Argentina (Kempf 1961), normally foraging during the daytime, with season-dependent variations (Medeiros and Oliveira 2009). Mainly predators foraging in the leaf litter (Medeiros and Oliveira 2009), these ants paralyze their prey by delivering a toxic substance via their stinger (Ortiz and Mathias 2006; Silva-Melo and Giannotti 2012). As *P. striata* workers forage solitarily or in tandem runs, they can be used to experimentally investigate the factors determining the choice of one or the other foraging strategies.

Most studies on tandem runs are conducted in the laboratory using ants of the genus *Temnothorax* (Mallon and Franks 2000; Pratt et al. 2002; Franks et al. 2003; Dornhaus and Chittka 2004; Robinson et al. 2014; Stroeymeyt et al. 2017; Glaser and Grüter 2018; Richardson et al. 2021; Wagner et al. 2021). Experiments conducted in natural conditions are rare and focus mostly on the effects of food item size and its distance from the nest in the dynamics of tandem running (Medeiros and Oliveira 2009; Grüter et al. 2018), as well as on the influence of tandem runs in competitive interactions (Glaser et al. 2021). In these studies, workers are not individually identified and foragers are observed opportunistically without knowing the location of their nests. Conversely, a study on the arboreal foraging *Camponotus consobrinus* illustrates detailed tandem run characteristics in individual ants and the fact that leaders can also behave as followers when local conditions and information reliability vary (Schultheiss et al. 2015). However, the study does not manipulate food sources and other foraging-relevant variables to investigate the mechanisms underlying tandem running.

To control for interindividual differences and evaluate both environmental and context-specific factors (i.e., food type and distance), a combination of controlled variables must be tested in a natural environment, and individually identified workers from several previously known colonies must be followed throughout the experiment. In this study, we monitored individually marked workers across 12 wild colonies of *P. striata*. We manipulated factors that may affect decision-making during foraging, such as (i) food type, (ii) its quantity, (iii) its distance from the nest and carefully monitored other environmental variables such as (iv) temperature and humidity, and (v) the presence of competing species. Our data include duration and number of both solitary trips and tandem runs, as well as the percentage of ants performing tandem running and their rate of success. We aimed at understanding which factors are involved in the decision to recruit. Our experiments allow formulating hypotheses about which information is important and potentially communicated to potential tandem followers, as well as how motivation and internal state shape collective responses during the recruitment process.

Materials and Methods

Study sites and colonies

Our research was carried out in the campus of the Universidade de São Paulo, São Paulo, Brazil, between December 2015 and April 2016. This period corresponds to the southern hemisphere summer and beginning of autumn, where temperatures are stable and high and rain frequent and abundant. This is also the period when reproductive individuals are produced, and therefore, brood rearing requires large quantities of protein. The study area originally included patches of Brazilian Atlantic Forest intercalated with farms, pastures, plantations and urban areas (Kraus et al. 2005), and is now mostly urbanized with some forest fragments and green areas. The vegetation includes native and exotic decorative trees, low bushes, and grasses (Kraus et al. 2005). Colonies of *P. striata* were found by actively looking for nest entrances at the base of trees in urban gardens, or by placing baits (tuna and honey) on foraging areas and following foragers back to the nest. To ensure that colonies had enough individuals for the experiments, we first placed baits near the entrance of marked nests during daytime. Then, we marked all ants collecting baits or more generally performing activities outside the nest, painting ink dots (uni-paint Mitsubishi® PaintMarker PX-20) of different colors for different colonies on the ants' mesosoma, petiole, and/or gaster. Among 45 nests identified, we used 12 in the study. These were separated from each other by at least 4 m, had at least 24 foragers (an indication of a large colony with active foragers), and had entrances distributed inside a circle of 1 m diameter. They contained an average of 58.6 ± 27.1 ($N = 703$ marked ants) foragers (range [24–99]). We observed ants for 192 h (48 h for colony selection and forager counting and 144 for experimental procedures).

Experimental procedure

The behavioral measures took place during the day between 10 AM and 2 PM, the period of colonies' highest extranidal activity. To measure foraging behaviors, we used the focal sampling method on single foragers and the all-event sampling method during foraging trips (Altmann 1974). Durations (measured in seconds) were recorded for each behavior, except for competition (see below). Each trial consisted of following a focal ant leaving the nest and walking a pre-defined linear distance, classified as either near (0.5 m) or far (4 m) from the nest entrance. Distances were linear measures from nests, not total distance traveled by the forager. If the focal ant had not been previously marked, this was done at the moment of behavioral observations. This constituted the majority of cases, because among all the ants marked in the first observations ($N = 703$), only 12 (1.7%) foraged at the moment of the experiments, and we marked the other 84 on the spot. When the marking influenced the worker's behavior (freezing and escape), workers were excluded from our data. After traveling the predefined distance, we carefully deposited a bait placed on a piece of filter paper on the ant's path. This consisted either of protein (crumbled canned tuna in water) or carbohydrate (mix of honey and ≅2 × 2 mm pieces of apple) and weighed either 3 (large) or 7 g (very large). Once the focal ant interacted (antennation) with the food source, we followed it while going back and forth between the nest and the food source (e.g., solitary trip or tandem running used by the ant) for 90 min or until the depletion of the food source. We chose this duration for practical reasons, to standardize observation time between trials and because previous observation suggested that this was adequate to monitor individual foraging behavior. We did not record the behavior of additional ants arriving at the food source.

The combination of food type (protein and carbohydrate), food quantity (3 and 7 g), and food distance (near and far) resulted in 8 different treatments. For each treatment, we tested 1 worker per colony ($N = 12$ colonies, 8 treatments, 96 trials). The order of the colonies and trials was randomized using Random.org. We excluded trials in which paint marking affected the behavior of ants (e.g., fleeing), or trials where focal ants did not pick the food items. The following parameters were analyzed in each trial: number of foraging trips, duration of trips (seconds), air temperature, and RH (at the beginning of each trial at 10 cm from the ground). Interaction with competing species was also noted and considered as a binary variable.

Statistical analyses

Statistical analyses were performed in R 4.0.2 (R Core Team 2020) using R Studio (version 1.2.5033). Since the number and duration of foraging trips varied greatly between foraging strategies (solitary and tandem running) and food distances (near and far), tests were conducted separately for all 4 treatments resulting from these 2 predictors: tandem running—near, tandem running—far, solitary—near and solitary—far. The Shapiro–Wilk's test was used for checking the normality of the data distribution of dependent variables measured as count data (number and duration of foraging trips). Only the number of solitary trips, for both near and far distances, followed a normal distribution, thus we analyzed it using linear regression. The number of tandem runs as well as the duration of foraging trips were analyzed using generalized linear models (GLM). We opted for GLMs, and not for GLM models (GLMMs) including the colony as a random factor, because we analyzed each of our 8 treatments in a separate test, and each of these treatments included a single individual per colony. To select the best error distribution for GLMs, we first built models using 3 different error distributions (Poisson, quasi-Poisson, and negative binomial). The following predictors were included: food distance, food quantity, food type, competition, temperature, and humidity. In the analyses of the duration of foraging, the order of sequential consecutive trips was also included as a predictor to identify differences in duration of trips, in cases where focal ants returned to the source multiple times. This way, we were able to include repeated measures for each individual without explicitly implementing random factors. We estimated the overdispersion of the models by obtaining the ratio between the residual deviance and degrees of freedom, as well as by using the overdispersion test from the *AER* R package (Cameron and Trivedi 1990). Since models using Poisson and quasi-Poisson distributions were overdispersed, the analyses were conducted using a negative binomial distribution using the *MASS* R package (Venables and Ripley 2002). The frequency of tandem running was analyzed using a binomial GLM with logit link function, where the frequency of recruitment of each forager was set to 0 (when the ant failed to recruit) or 1 (when the ant successfully recruited another ant). The number of predictors and the inclusion of interactions, for each treatment, were defined based on the Akaike's information criterion (AIC), using the *AICcmodavg* R package (Mazerolle 2020). We tested for significant differences in tandem run failure rate with a Chi-square test on the contingency table of the number of failures and successes.

Table 1. Number of solitary trips and tandem running per treatment (CF, carbohydrate far; CN, carbohydrate near; PF, protein far; and PN, protein near), including total number of trips per category

	Treatment				
	CF	CN	PF	PN	Total
Solitary	188	478	192	731	1589
Successful tandem	21	81	44	78	224
Failed tandem	28	19	14	13	74
Total	237	578	250	822	1887
% Successful tandems	0.42	0.81	0.75	0.85	0.75
% Solitary trips	0.79	0.83	0.77	0.89	0.84

The design is balanced between treatments, each having the same number of tested workers ($N = 12$ per treatment, summing 96 workers). Solitary, solitary trip; successful tandem, successful tandem runs; failed tandem, incomplete or interrupted (failed) tandem runs; % successful tandems, percentage of successful tandem runs.

Results

The 96 workers we observed (8 individuals from each of our 12 colonies) performed a total of 1,886 foraging trips between the nest and the food source, of which 1,587 (84.2%) were solitary and 298 (15.8%) were tandem runs. Although solitary foraging was the most frequent strategy, 81.3% of focal ants ($N = 78$) performed tandem running, indicating that most individuals rely on both strategies. Three ants that were selected as focal (leader) in 1 trial were observed following the focal leader in a subsequent trial. A total of 224 tandem runs (75.17%) were successful in leading the follower to the food source (Table 1). Interestingly, although the proportion of tandem runs for both food treatments was similar, a significant difference in failure rate was found in tandems heading to far carbohydrate food sources (<50% success, $\chi^2_{3,299} = 34.67$, $P < 0.001$; Table 1). On average, more trips (including tandem runs and solitary foraging) were taken to near distance and protein sources than to far distance and carbohydrate (Table 1). Regarding the duration of foraging bouts, solitary trips were shorter (mean ± SD: 63 ± 85 s) than recruiting by tandem running (mean ± SD: 93 ± 89 s). As expected, food items located near the nest were attained quicker by foragers than those located further away (mean ± SD, near versus far: 33 ± 48 s; 172 ± 95 s).

Solitary foraging

Only 18.8% ($N = 18$) of focal ants relied exclusively on solitary foraging during the experiments. Near the nest, we found that focal ants engaged in a significantly larger number of trips when food items consisted of protein (mean ± SD: 30 ± 12) and fewer when they consisted of carbohydrate (mean ± SD: 19 ± 10, $F_{4,42} = 2.537$, $P = 0.004$, Figure 1 and Supplementary Table S1). When the food was far from the nest, the number of trips did not differ based on the 2 food types (protein versus carbohydrate, mean ± SD: 7 ± 2 versus 7 ± 3, Figure 1 and Supplementary Table S1). The quantity of food, air temperature, air RH, and the presence of competing species did not affect the number of solitary trips (Supplementary Table S1). We found that RH significantly affected the duration of trips at both analyzed distances (near distance, incidence rate ratio [IRR] = 0.98, $z = 9.087$, $P < 0.001$; far distance, IRR = 0.99, $z = -3.184$, $P = 0.001$, Supplementary Table S2). Ants traveled faster when RH was higher (near distance, RH >65%, mean ± SD: 29 ± 24 s; RH <65%, mean ± SD: 35 ± 82 s), especially for trips to far food items (far distance, RH >65%, mean ± SD: 158 ± 101 s; RH <65%, mean ± SD: 179 ± 73 s). Near the nest, we found that the duration of trips significantly decreased at lower temperatures (temperature <26°C, mean ± SD: 34 ± 36 s; >26°C, mean ± SD: 28 ± 55 s; Temperature, IRR = 0.88, $z = -7.528$, $P < 0.001$, Supplementary Table S2). Interestingly, for both examined distances, the duration of consecutive solitary trips progressively decreased as ants kept returning to the food source multiple times, that is, the ants were faster at going to the source with more experience (near distance, IRR = 0.99, $z = -6.073$, $P < 0.001$; far distance, IRR = 0.96, $z = -6.073$, $P < 0.001$, Figure 3 and Supplementary Table S5).

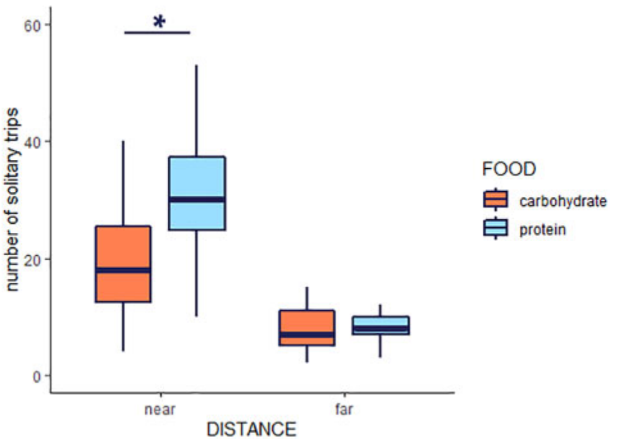

Figure 1. Boxplot showing the overall number of solitary foraging trips between the nest and the food source, separated by food distance and food type. The number of trips in near distance was higher toward protein sources. In far treatment, the number of trips remained similar between the 2 food types (see Supplementary Table S1 for details of the statistics). *Linear regression, $F_{4,42} = 2.537$, $P = 0.004$.

Tandem running recruitment

Out of the 298 tandem runs, 74 were unsuccessful and ended prematurely as the 2 ants lost contact (Table 1). Success rate was high and did not improve with the number of trips (Table 1). None of the predictors influenced the number of tandem runs at both analyzed distances (Figure 2 and Supplementary Table S3). However, when the food was far from the nest, the percentage of ants performing tandem running was lower toward carbohydrate compared with protein sources (odds ratio [OR] = 16.46, $z = -2.624$, $P = 0.019$, Figure 4 and Supplementary Table S4). Far from the nest, the percentage of ants performing tandem running was significantly higher in 2 cases: when the food source was very large (very large versus large = 87.5% versus 66.6% of ants, OR = 11.06, $z = 2.148$, $P = 0.032$) as well as when RH was high (% of recruitment: 93% when RH > 65% versus 64% when RH < 65%, OR = 1.24, $z = 2.131$, $P = 0.033$) (Supplementary Table S4). Regarding the duration, we found that the duration of tandem running near the nest significantly decreased at higher temperatures (<26°C, mean ± SD: 52 ± 25 s; temperature >26°C, mean ± SD: 44 ± 21 s; temperature, IRR = 0.92, $z = -2.624$, $P = 0.009$, Supplementary Table S5). Far from the nest, we also found a significant reduction in duration of consecutive tandem runs, as ants returned to the food source multiple times (IRR = 0.94, $z = -6.073$, $P < 0.001$, Figure 3 and Supplementary Table S5).

Discussion

In this study, we tested hypotheses about the factors influencing recruitment decisions in tandem running. This behavior has previously been studied only in very restrained laboratory conditions (Richardson et al. 2007; Franklin 2014; Glaser and Grüter 2018; Richardson et al. 2021; but see Kaur et al. 2017), and in most instances in a nest emigration rather than in a foraging context (Healey and Pratt 2008; Franklin 2014; O'Shea-Wheller et al. 2016; but see Kaur et al. 2017). Our results provide novel insights about the mechanisms associated with information transfer and decision-making of foragers, both leaders and potential followers (Grüter and Czaczkes 2019). Most ants in our sample used tandem running (Table 1), which shows that, although less frequent than solitary return trips, this strategy is regularly used for foraging in *P. striata*. The structure of the foraging bouts varied according to food type and quantity, as well as distance from the nest and external factors such as RH and temperature.

For solitary foraging, we observed a larger number of trips to the protein food source near the nest (see Figure 1). Besides, more ants performed tandem runs in far distances toward protein food of very large size. Workers therefore seem to tune their behavior as a function of the encountered food type and size, similar to collective-foraging trail-laying species for which this allows regulating the colony-level nutrient intake (Feldhaar 2014; Csata and Dussutour 2019). Similarly, another ant from the same genus, *P. harpax*, also seems to perform faster trips when foraging for protein, despite also consuming both protein and carbohydrate (Grüter et al. 2018). In tandem runs at far distances, workers were probably able to identify

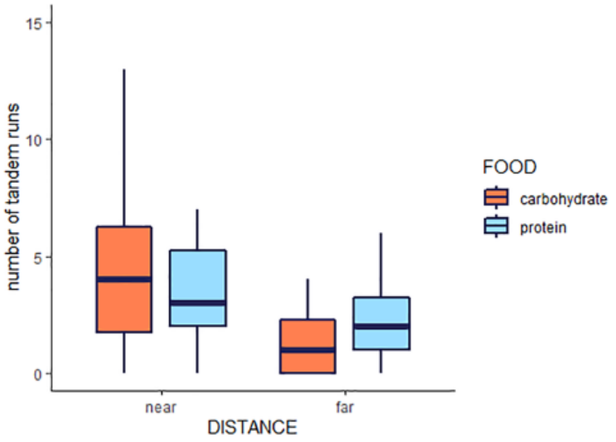

Figure 2. Boxplot showing the overall number of tandem runs between the nest and the food source, separated by food distance and food type. The number of trips remained similar between the treatments.

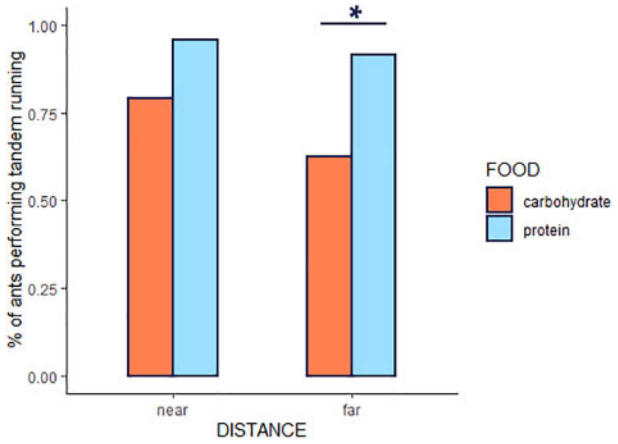

Figure 4. Percentage of successful tandem recruitments separated by food type and distance. Success percentage was significantly lower for carbohydrates located far away (see Table 1). *GLM, $z = -6.073$, $P < 0.001$.

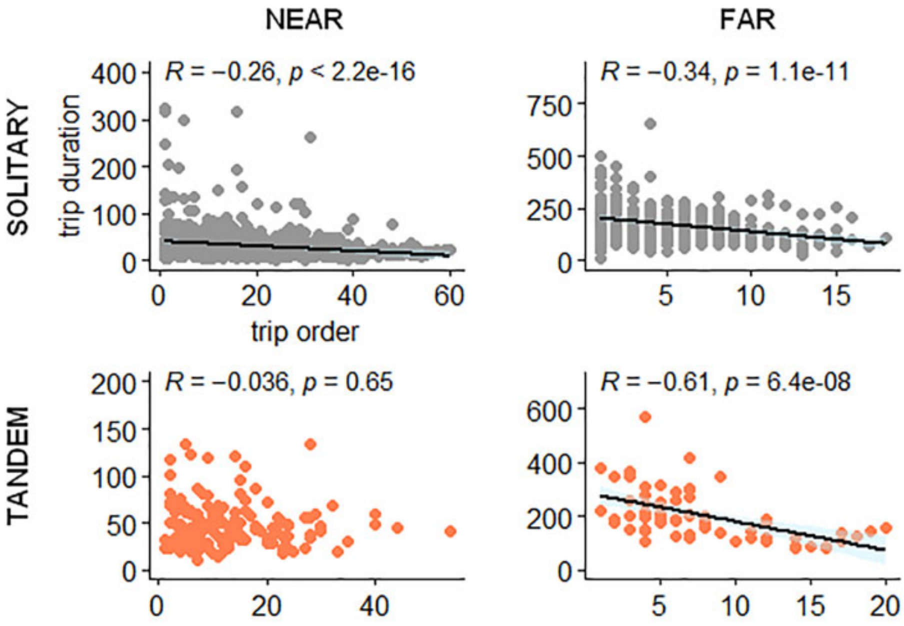

Figure 3. Evolution of foraging duration (seconds) according to the succession of consecutive foraging trips (separated by food distance and foraging strategy), showing a decrease in duration as ants returned to the source multiple times (except for tandem runs at near source) (see Supplementary Tables S2 and S5 for details of the statistics).

not only the food type but also its size. This unexpected result suggests that ants can evaluate quantitatively the size of food items without direct comparison (d'Ettorre et al. 2021) and increase the motivation to recruit fellow workers in specific conditions. This can be related to the possible intense competition at these resources over time (Glaser et al. 2021). In the case of *P. striata*, a generalist species with a preference for insect prey, brood demand probably explains this higher motivation to exploit protein (and possibly lipid, from the tuna bait) sources. This difference is not present for solitary foraging at a far distance (Figure 1). This suggests that travel distance may not be the important factor for the continued exploitation of a particular food source (near and far), but rather a differential satiation effect according to the food type (Grüter and Czaczkes 2019) and also of a proportionally shorter time window for exploration since trips at far distances are longer.

Optimal foraging and cognitive theory predict that more tandem runs should be observed if far sources were more at risk of being exploited by other species, and a fast exploration would allow limiting competition (Glaser and Grüter 2018; Grüter et al. 2018). In our experiment, more tandem runs were observed near the nest (Table 1). In this population, competition is more frequent at the food sources near the nest, which is often in a shaded and more protected area (Silva et al. 2017). Grüter et al. (2018) suggested that more distant food resources are more at risk to be exploited by competing species. In our study site, the nests of *P. striata* coexist with nests of different species, *Gnamptogenys striatula* being the most common and most frequent competitor (Lanhoso and Châline 2017; Silva et al. 2017). Our results suggest that competition may be intense even in the proximity of the nest. It must be noted, however, that as hypothesized by Glaser et al. (2021) for *P. harpax*, *P. striata* is often successful in excluding supposedly more dominant or aggressive species (Lanhoso and Châline 2017) and shows a diversity of responses such as guarding the resource, robbing from other species, or tandem runs to exploit a source efficiently despite the presence of aggressive species such as *Wasmannia auropunctata* or *Solenopsis saevissima* (Silva et al. 2017).

We found that RH and temperature influenced probability and duration of solitary foraging bouts and tandem runs. Higher RH increased the likelihood of tandem runs in the far food source condition. Solitary trips were faster with higher RH and at near distance also when temperature was low; tandem runs were faster near the nest and at higher air temperature. We do not know how workers perceive external humidity and temperature. However, if potential recruits stay in chambers close to the nest exit, as other studies have shown (Pinter-Wollman et al. 2013), workers could experience the conditions they will face if going out to forage. Since ants are ectotherms, temperature and humidity can directly interfere with their foraging (Traniello 1989; Gordon 2013). Thus, foragers prevent excessive dehydration which would occur during the long trips when following or recruiting when the humidity is high (Levings and Windsor 1984). In another ponerine ant, *Dinoponera quadriceps*, also from the Atlantic forest, humidity is positively correlated with foraging activity (Medeiros et al. 2014). It is expected that ants are faster at higher temperatures, which occurred in near tandem runs but not other situations. The fact that solitary trips are faster with higher RH and low temperature is puzzling, but we can hypothesize that ants in these conditions stop less to assess potential risks associated with desiccation. Indeed, *P. striata* workers are slow foragers which often stop for long periods en route to the food source under leaves in the typical cluttered environment and die within minutes if exposed to high and dry temperature (N. Châline, personal observation).

We observed that there was a decrease in duration in both solitary foraging and tandem runs on consecutive trips for the 2 distances (Figure 3). This suggests that the route learning process allows ants to become familiar with their environment, making increasingly linear paths and foraging more efficiently (Wystrach et al. 2011). Route learning allows to decrease exposure time as well as the probability for ants to be lost during foraging (Azevedo et al. 2014). Since *P. striata* does not use chemical trails, its orientation and route learning probably rely on visual cues or path integration (reviewed by Wehner and Srinivasan 2003). Accordingly, in a study where the eyes of *Temnothorax albipennis* workers were experimentally covered with paint, the use of visual landmarks seemed important to assume the role of leader, while followers mostly rely on olfaction and path integration (Franklin et al. 2011). Importantly, we conducted this study in natural conditions, where leaf litter and lower vegetation hamper foragers' movement. Learning processes also improve trip efficiency in conditions more complex than those created in the laboratory and in ants living in desert environments (Wystrach et al. 2011).

Although consecutive tandem runs were faster, we did not find any improvement in tandem run success with time. That is, experience did not make workers better at leading followers. Despite the cluttered environment, tandem running success was high (80% excluding the far carbohydrate treatment) and stable over time and across treatments. Contrary to what is found in *Temnothorax* spp., where 3 quarters of tandem runs are unsuccessful (Pratt 2005; Pratt et al. 2005), high success rates in ponerine ants such as *P. harpax* and *Diacamma indicum* (Kaur et al. 2017; Grüter et al. 2018) suggest that, in natural environments, communication about food location and the subsequent route learning are very efficient. It also indicates that the motivation of leader/follower pairs is high, or that leaders and/or followers both have previous knowledge of the environment, which may help route learning and limit delays during the tandem (Schultheiss et al. 2015; Stroeymeyt et al. 2017). In the far carbohydrate treatment, success was lower than 50% (Table 1) and a lower number of tandem runs were registered (Figure 4). This also suggests that followers can receive information about the nature of the food source (the only modified variable), and/or that the probability of tandem running recruitment and giving up probability en route to the food source in cases of break-ups by leaders and/or followers depends on this complex interacting information (Schultheiss et al. 2015). We cannot exclude the hypothesis that part of our data can be explained by the existence of experienced leaders preferring certain food types and having higher success (Richardson et al. 2021). However, a complementary hypothesis that needs to be tested would be that followers prefer following experienced leaders.

As we already saw with the number of trips for solitary foraging in the near condition and the percentage of ant leading successful tandem runs in the far condition, workers seem less motivated to forage for carbohydrate sources. This probably happens because foraging costs become higher as ants move away from their nests, due to energy expenditure and exposure to predators and adverse environmental conditions (Fewell 1988). Therefore, our results support the novel hypothesis that communication during tandem run initiation is more complex than previously envisaged. All through the tandem running, from recruitment to completion, information about the food source affects the motivation of both actors. These complex interactions can finely modulate colony-level foraging efforts, since potential tandem run followers are probably weighing out decisions according to repeated interaction with potential scouts or leaders. One clear missing element in our study, and in foraging behavior studies in general, is how the recruitment process occurs through interactions between the informed leader and the available potential follower. In nest emigration, such interactions may not be so important since choices of a new nest are limited so both leaders and followers maintain high motivation. Studies on ants relying on chemical trails, such as *Pogonomyrmex*, suggest that nest entrances are the theatre of complex interaction regulating colony foraging, mostly mediated by specific hydrocarbons present on the cuticle of forager scouts (Gordon 2013; Pinter-Wollman et al. 2013). In ponerine ants, tactile interactions are common between nest mates (Denis et al. 2008; Yagound et al. 2014; Kaur et al. 2017). Although we did not elucidate the mechanisms, our results suggest that differences in the decision, success, and duration of tandem runs are not stochastic events, but are probably influenced by how the follower perceives the recruiting motivation of the leader, as occurs in dancing honey bees (Núñez and Giurfa 1996; Hrncir et al. 2011; George et al. 2020).

In 3 occasions, we observed leaders being led in subsequent trials. This is an indication that followers are not necessarily always naive (Schultheiss et al. 2015) but evaluate from public and private information treatment whether to exploit a discovered food source (Grüter and Leadbeater 2014). Thus, tandem running can be influenced not only by spatial learning cognitive abilities, but also by the internal and motivational states of both leader and follower, depending on the evaluation of distance, food type, RH, and temperature. Perhaps in our study the motivation was changed by offering preferred and non-preferred food types. An example of follower's decision-making was previously observed in *D. indicum* where the leader performs a stereotyped invitation call and the start of tandem run depends on follower's acceptance (Kaur et al. 2017). In a situation of lesser immediate risk than emergency nest emigration poses, followers could play an important role in the recruiting process, based on their prior experience and immediate evaluation of the present context. This is suggested by the fact that tactile and/or olfactory signals are indeed exchanged in early phases of recruitment, as both our results and research in other species suggest (Crawford and Rissing 1983; Greene and Gordon 2003; Pinter-Wollman et al. 2013). Future studies can elucidate the influence of these stimuli in tandem running and other foraging strategies. Ponerine ants constitute a great monophyletic group to study such diversity, since they also occur in ample sympatry (Schmidt and Shattuck 2014).

An important inference in this study is that the use of tandem runs is not an all-or-nothing process. This is because we did not observe a unique ideal situation where recruitment or solitary foraging was prioritized. A possible explanation is that ants may recruit as long as there are available foragers or until a certain number are recruited. When foragers become rarer, the increased time windows required to find new recruits, as well as the crowding at food sources, would prevent a linear increase in the benefits associated with more foragers (Grüter and Czaczkes 2019). Contrarily, the tandem runs in our study were not concentrated in the first trips after food discovery. This means that neither forager disponibility nor the number of foragers already recruited explain the combined use of solitary trips and tandem runs. Rather, we propose that decision-making is the result of how both leaders and the potential followers evaluate the current parameters according to their own experience (as foragers and of their social environment) together with more simple mechanisms (e.g., colony nutritional need) and environmental factors. We are left with the question of how *P. striata* and other individual characteristics of Ponerinae lead to interindividual differences in foraging behavior, and how the interaction between leaders and followers with different experience lead to the initiation and completion of the tandem run (Jeanson and Weidenmüller 2014; Lihoreau et al. 2021; Richardson et al. 2021).

In conclusion, our results suggest that foraging decision-making is also complex in species that do not use foraging trails and are considered ancestral regarding their social organization and division of labor (Châline et al. 2015). Communication between leaders and followers seems to be modulated in many species by both internal, external, and social factors, as well as immediate and prior experience and knowledge. This flexibility begins to be described in species with larger colonies that rely on pheromone trails (Czaczkes et al. 2019; Oberhauser et al. 2019). To determine the dynamics underlying this diversity and flexibility, it is crucial to produce comparative datasets using species with diverse social organization and foraging strategies, and occurring in different environments. Further research should explore possible complex information transfers between leaders and followers, and how these may be integrated with the followers' physiology and experience to determine decisions in constant feedback loops (Lihoreau et al. 2021).

Author Contributions

J.P.d.S. and N.C. conceived the project and designed the experiment. J.P.d.S. performed the experiment. L.V. and S.T. analyzed the data. N.C., J.P.d.S., L.V., S.T., and M.E.d.L.V. interpreted the results and wrote the manuscript.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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