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Tandem Recruitment and Foraging in the Ponerine Ant *Pachycondyla harpax* (Fabricius)

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Abstract

Tandem running is a common recruitment strategy in ant species with small colony sizes. During a tandem run, an informed leader guides a usually naïve nestmate to a food source or a nest site. Some species perform tandem runs only during house hunting, suggesting that tandem running does not always improve foraging success in species known to use tandem running as a recruitment strategy, but more natural history information on tandem running under natural conditions is needed to better understand the adaptive significance of tandem recruitment in foraging. Studying wild colonies in Brazil, we for the first time describe tandem running in the ponerine ant *Pachycondyla harpax* (Fabricius). We asked if foragers perform tandem runs to carbohydrate- (honey) and protein-rich (cheese) food items. Furthermore, we tested whether the speed and success rate of tandem runs depend on the foraging distance. Foragers performed tandem runs to both carbohydrate food sources and protein-rich food items that exceed a certain size. The probability to perform a tandem run and the travelling speed increase with increasing foraging distances, which could help colonies monopolize more distant food sources in a competitive environment. Guiding a recruit to a food source is costly for leaders as ants are ~66% faster when travelling alone. If tandem runs break up (~23% of all tandem runs), followers do not usually discover the food source on their own but return to the nest. Our results show that tandem running to food sources is common in *P. harpax*, but that foragers modify their behaviour according to the type of food and its distance from the nest. Competition with other ants was intense and we discuss how tandem running in *P. harpax* might help colonies to build-up a critical number of ants at large food items that can then defend the food source against competitors.

Introduction

Ants are well known for using pheromone trails to recruit large numbers of workers to profitable resources, nest sites or battle grounds (Czaczkes *et al* 2015, Detrain & Deneubourg 2008, Hölldobler & Wilson 1990, Lanan 2014). However, pheromone trails decay if they are not regularly reinforced, which makes them less suitable for colonies with only a few workers (Beckers *et al* 1989, Beekman *et al* 2001, Planqué *et al* 2010). As a result, many species with small colonies use a recruitment method called tandem running (Beckers *et al* 1989, Franklin 2014). In tandem running, an experienced ant leads a usually naïve nestmate to a location of interest, such as a food source or a nest site (Franklin 2014, Hölldobler *et al* 1974, Wilson 1959). Contact between the leader and the follower is maintained by frequent

physical interactions and short-range pheromones emitted by the leader (Basari *et al* 2014, Hölldobler & Engel 1978, Möglich *et al* 1974). If contact is lost, leaders often wait until contact is re-established (Franks & Richardson 2006, Richardson *et al* 2007).

Interestingly, in some species tandem running is only used during colony emigration (e.g. *Neoponera apicalis* (Latreille), *Neoponera obscuricornis* (Emery), *Paltothyreus tarsatus* (Fabricius)*,* Fresneau 1985, Hölldobler 1984, Traniello & Hölldobler 1984, *Diacamma indicum* (Santschi)*,* Rajbir Kaur, pers. communication), whereas other species use tandem running in both colony emigration and foraging (Table S1) (e.g. *Temnothorax rugatulus* (Emery), *Pachycondyla striata* (Smith) or *Polyrhachis proxima* (Roger), Franklin 2014, Liefke *et al* 2001, Medeiros & Oliveira 2009, Pratt 2008). In slave-making ants, tandem recruitment is used during raids of other nests (Buschinger & Winter 1977). It is likely that the spatiotemporal distribution of resources and competition with other species determine the adaptive significance of tandem recruitment during foraging, as has been suggested for other recruitment methods in ants and bees (Dornhaus *et al* 2006, Hubbell & Johnson 1978, I'Anson Price & Grüter 2015, Lanan 2014, Schürch & Grüter 2014, Sherman & Visscher 2002). Tandem running is phylogenetically widespread and has been found in more than 40 species belonging to four subfamilies (Myrmicinae, Formicinae, Ponerinae and Pseudo-Myrmicinae) (Table S1). These include both primitive and more derived species, suggesting that tandem running may have evolved repeatedly. It is also possible that tandem running represents an ancestral recruitment strategy from which group and mass recruitment have evolved (Hölldobler 1977, Wilson 1959). Tandem running has mainly been studied in house-hunting myrmecine ants in the laboratory where it plays a key role in collective decision-making and an efficient colony emigration (e.g. Dornhaus *et al* 2004, Franks *et al* 2003, Mallon & Franks 2000, Pratt *et al* 2002, Robinson *et al* 2014, Stroeymeyt *et al* 2017). Studies on tandem running in ponerine ants and under natural conditions are relatively rare (but see Fresneau 1985, Kaur *et al* 2012, Medeiros & Oliveira 2009, Schultheiss *et al* 2015).

Most ponerine ants are generalist arthropod predators and scavengers (e.g. Nascimento *et al* 2012, Schmidt 2013), but some species also collect substantial amounts of liquid food, such as honey dew from aphids or coccids, fruit juice and water (Hölldobler 1985). Ponerines employ an external social bucket, i.e. they transport liquids in the form of a droplet in their mandibles (Hölldobler 1985, Paul & Roces 2003) and distribute it to other colony members (Hölldobler 1985). The majority of ponerines are thought to be solitary foragers without recruitment of nestmates, but numerous species use tandem running as a recruitment strategy (Table S1). Social foraging is most developed in the mass-raiding ponerine *Simopelta* (Schmidt

2013). This variation suggests that the Ponerinae are an interesting group to study the ecological factors favouring recruitment and communication in different contexts. Unfortunately, the natural history and foraging ecology of tandem running species are often not well understood, and as a result, it remains unknown why some species use tandem running in foraging, while others forage solitarily even though tandem running is part of the behavioural repertoire of workers. Here, we describe tandem running in the ponerine ant *Pachycondyla harpax* (Fabricius). Hölldobler & Engel (1978) mentioned that *P. harpax* performs tandem runs, but without specifying the context or providing descriptions of the behaviour. Therefore, we tested whether foragers perform tandem runs to carbohydrate food sources (honey) or protein-rich food sources (cheese, type "queijo minas") and explored how the likelihood and success rate of tandem runs depend on the type of food and the foraging distance. We also describe basic aspects of foraging, such as foraging distances and type of prey collected.

Methods

Study site and species

We conducted the study in March 2017 on the campus of the University of São Paulo in Ribeirão Preto, Brazil (21°9′55S, 47°51′30W). *Pachycondyla harpax* is a common New World species, ranging from the Southern USA to Northern Argentina (Mackay & Mackay 2010). It is among the most common ponerine ants on the campus and nests underground (García-Pérez *et al* 1997). Previous observations have found that colony sizes range from 15 to 100 individuals (Wheeler 1900). Our study colonies had inconspicuous nest entrances in grassy vegetation (1–5 entrances per colony, often a few centimeters from each other; 0.47 ± 0.14 cm diameter, mean ± StDev, $N = 13$ entrances), usually found in the vicinity to trees (0–5-m distance), possibly because trees provide shade. This is different from the Southern USA, where nests were mainly found under stones or logs (Wheeler 1900). We chose this species because we observed several tandem runs to natural food sources, such as beetle larvae (Fig 1a), and nest entrances on the University of São Paulo campus in Ribeirão Preto.

Tandem running to carbohydrate food sources

We used 12 colonies located at different sites on the campus to study tandem recruitment (Fig 1b) to carbohydrate food sources. We placed a droplet of honey on a small piece of wood or leaf and offered it to scouts that we discovered as they searched for food. Subsequently, we observed scouts as
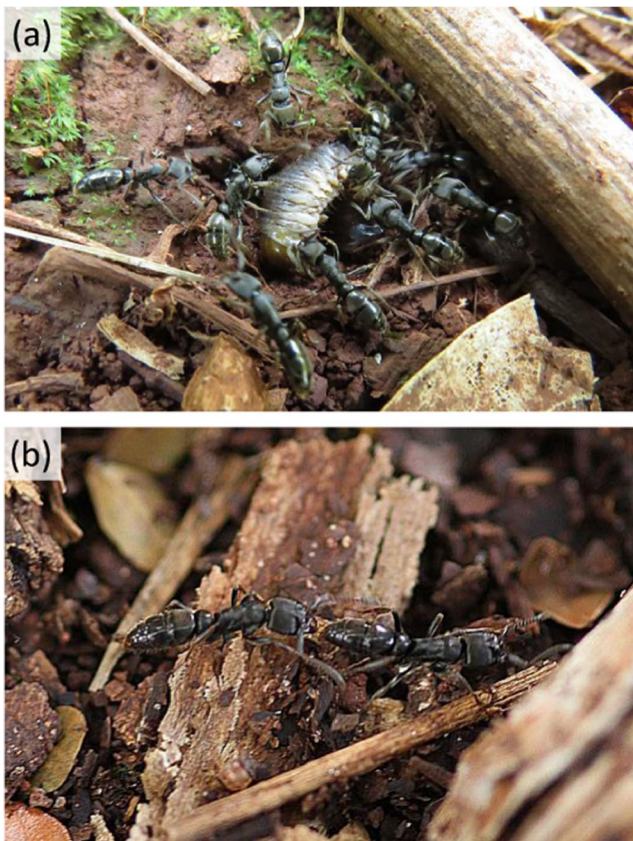
Fig 1 (a) *Pachycondyla harpax* foragers at a prey item (beetle larvae) (photo by Miriam Wüst), which we discovered after following a tandem run (b) (photo by Fanny Vogelweith).

they returned to their nest to locate the entrance. As a consequence of this procedure, foraging distances varied between colonies and ranged from 6 to 142 cm (45.0 ± 35.6 cm). After the first ant returned to the nest, we filmed the food source and nest entrance with a HD camera for 30 min. We filmed each colony only once. Other ants (e.g. *Monomorium*, *Neoponera*, *Odontomachus* or *Pheidole*) competed with *P. harpax* and occasionally displaced focal foragers before the latter started to recruit. In this case, we excluded the colony and tested a different one. We recorded the time it took scouts and, later, returning foragers to travel from the food source to the nest. Furthermore, we recorded the time it took leaders of a tandem run to travel from the nest to the food source. We did not mark the ants to avoid disturbing colonies, which prevented us from identifying individual ants during the course of our observations. If tandem runs were unsuccessful, we recorded the approximate location of the breakup: we divided the foraging trajectory into three similarly sized sections, a near-nest section, a middle section and a near-food section. We also recorded the reason for the breakup and whether the leader and follower returned to the nest or continued their journey to the food source. If tandem runs broke up under vegetation, it was not possible to determine which of the two ants was the leader

or the follower. We considered tandem runs to be successful if the pair came within a 3-cm distance of the food source or, if they broke up outside this radius, the follower discovered the food source in less than 30 s after the breakup. We recorded the time that passed between a returning forager entering the nest and a tandem run leaving the nest to estimate the time that foragers spend inside the nest.

Tandem running to protein food sources

"Methods" mostly followed the methods described for carbohydrate food source. We used 12 different colonies and offered small cubes of cheese (0.3–0.6 g) instead of a droplet of honey. Cheese has previously been used as a protein-rich food source to study the foraging behaviour of neotropical ants (e.g. Czaczkes *et al* 2011). This size made sure that ants were not able to carry the cheese to the nest by themselves. We also tested smaller cubes of cheese (< 0.1 g, *N* = 35), but found that these were all carried to the nest by the ant that discovered the cheese.

Foraging ecology

García-Pérez *et al* (1997) found that *P. harpax* colonies studied in Mexico were nocturnal and collected exclusively termites. Others have reported that workers also collect seeds and, thereby, might aid in seed dispersal (Horvitz & Schemske 1986a,b). We collected preliminary data on the diet of *P. harpax* at our field site. When we discovered foragers carrying food items during our observations, we captured the ant and removed the food item. Since we collected the ants carrying food items in different locations it is likely that each forager came from a different colony.

To estimate colony foraging distances (i.e. the distance from the nest where foragers were observed searching for food), we selected several sites on the campus, started at one arbitrarily chosen end of the site and systematically walked in straight lines in a zig-zag fashion, stopped every 3 m and searched for *P. harpax* foragers in a circle of 1-m radius for 1 min. If we discovered a forager, we offered a small piece of cheese to motivate her to return to her nest. We followed her until she entered a nest and measured the distance between the location where the forager was discovered and the nest entrance.

Statistical analysis

We performed all tests using R 3.3 (R Development Core Team 2016). Since we did not mark the ants, we could often not be certain whether we recorded the same ant repeatedly or different ants. Therefore, we average all observations of the same colony when comparing the walking speed of ants travelling alone or in a tandem pair. We used standard

analysis of variance (ANOVA) to compare speed when foraging for cheese vs. honey. We used Shapiro-Wilk tests to check whether errors were normally distributed and square-root-transformed the response variable if necessary to achieve normal distribution. To test if the success rate and speed of individual tandem runs depended on the foraging distance and the food type, we performed general and generalized mixed-effect models (LMEs and GLMMs) and included colony as a random effect to account for the non-independence of observations from the same colony (Zuur *et al* 2009). To test for the significance of interactions, we used likelihood ratio tests (LRT) and compared the model containing the interaction with the model without the interaction. We removed non-significant interactions from the model. To test the significance of the main effects, we used Wald tests (Zuur *et al* 2009).

Results

Tandem running

Overall, we observed 138 tandem runs, 81 to honey and 57 to cheese. Five of the 138 tandem runs (3.6%) were in reverse direction, i.e. from the food source to the nest. We observed 189 instances when a forager returned from the food source to the nest and in 94 instances (49.7%) a tandem run to the food source left the nest within 90 s. In 93 instances (49.2%), a forager was seen returning to the food source alone. In the remaining two instances, a tandem left the nest more than 90 s after a forager entered the nest.

Of all tandem runs, 106 (76.8%) were successful. Of the 32 unsuccessful tandem runs, 15 broke up near the nest (46.9%), 12 in the middle section (37.5%) and 5 near the food source (15.6%). In the majority of cases, it was not clear what caused the tandem run to fail, but in 6 cases, vegetation, e.g. leaves, appeared to cause the breakup. In 3 cases, another ant caused the breakup and in another 3 cases the leader appeared to walk too fast without paying attention to the follower. In 55.6% of all breakups (10 of 18 observed instances), leaders continued alone to the food source. In the remaining 44.4% they returned to the nest. Followers returned to the nest in 90.9% of all cases (20 of 22 observed instances) after short searches of usually less than 30 s. Only two followers (9.1%) discovered the food source alone after a breakup. In both cases the breakup occurred relatively close to the food source (~ 5–15 cm). The probability of success did not depend on either the distance of the food source or the type of food (binomial GLMM, distance: z value = −1.14, p = 0.25; food type: z value = −1.24, p = 0.22; interaction: LRT = 2.08, df = 1, p = 0.15).

The probability that a tandem run left the nest to a food source was significantly higher after foragers returned from honey and if they returned from more distant food sources (Fig 2) (binomial GLMM; food type: z-value = 2.53, p = 0.011; distance: z-value = 2.31, p = 0.02; interaction: LRT = 0.05, df = 1, p = 0.83). We then tested whether the speed (food source distance/duration of tandem run) of the tandem pair depended on the distance of the food source and the type of food. We found that ant pairs walked faster to more distant food sources and when walking to protein-rich food (Fig 3) (LME, distance: t value = 2.27, p = 0.026; Food type: t value = −2.53, p = 0.013, interaction: LRT = 0.1, p = 0.76).

To test whether food type affected walking speed also in other circumstances we analyzed walking speed in two different situations: (a) during tandem runs and for (b) scouts returning to the nest for the first time after discovering the food source. Again, tandem runs to cheese were significantly faster than tandem runs to honey (Fig 4) (ANOVA: $F_{1,20}$ = 8.33, p = 0.009), confirming the findings of the more complex model. Furthermore, the speed of scouts returning to the nest was higher when foraging for cheese than for honey (Fig 4b) (ANOVA, square-root-transformed response: $F_{1,17}$ = 5.09, p = 0.038). We used a paired t test to explore if walking speed differed depending on whether ants were walking alone or in a tandem pair (average scout speed vs. average tandem-speed of the same colony) (Fig 4a vs. Fig 4b). We found that tandem pairs were significantly slower (0.84 ± 0.31 cm/s) than ants walking alone (1.41 ± 0.69 cm/s) (paired t test: t = −3.13, df = 16, p = 0.006).

Foraging ecology

We recorded 19 natural food items collected by foragers: 4 myriapods (21%), 3 annelid worms (15.8%), 2 beetle larvae (10.5%), 2 ant corpses (10.5%), 2 termite workers (10.5%), 2 plant seeds (10.5%), 1 moth larvae (5.3%), 1 caterpillar (5.3%), 1 butterfly wing (5.3%) and 1 isopod (5.3%). Approximately half of the preyed upon animals were still alive.

Scouts were found at a distance of 54 ± 45.6 cm from the nest entrance (median = 48, range: 4 and 225 cm) (Fig 5) and 90% were found less than a meter from the nest entrance. The distribution of foraging distances is heavily left-skewed.

Discussion

Pachycondyla harpax foragers perform tandem runs to both carbohydrate food sources and protein-rich food items that are too large to be carried by an individual ant. After foragers returned from either honey or cheese, tandem runs to the respective food source left the nest in almost 50% of all observations. We also observed several tandem runs to nest entrances of wild nests and an artificial nest box in the laboratory (C.G. & M.W., personal observations), suggesting that tandems are used also in colony emigrations.
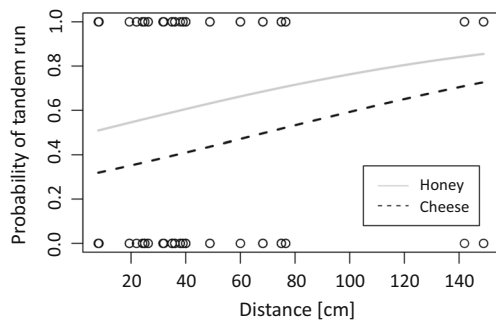
Fig 2 The probability that a tandem run left the nest after a forager returned from the food source, depending on the distance and the type of the food. The lines are based on the parameter estimates provided by the binomial GLMM with both food type and food distance as predictors. Each colony is represented by two dots, indicating that in some cases tandem runs left the colony after the return of a forager from our food sources, whereas in other instances foragers returned to the food alone.

Furthermore, we observed a small number of tandem runs in reversed direction, i.e. from the food source to the nest (5 of 138 tandem runs). Reverse tandem runs are often observed during colony emigrations in *Temnothorax* (Franklin 2014, Franks *et al* 2009), but to our knowledge, this phenomenon has not yet been reported in a foraging context. The main function of reverse tandem runs in *Temnothorax* seems to be to increase the number of active recruiters and, thereby, accelerate colony emigration (Franks *et al* 2009, Planqué *et al* 2007). However, it is not currently known if reverse tandem runs in *P. harpax* serve a function or if they are mistakes by followers that are stuck in "follower-mode", i.e. fail to end following other ants at food sources.

Both the foraging distance and the type of food affected tandem recruitment. Ants were more likely to perform tandem runs and they travelled faster to more distant food sources. Food sources discovered at greater distances might be more likely to be lost to other ant colonies, either because the food source is in the foraging territory of other colonies or because foragers spend more time travelling and, therefore, are less able to defend the food source against

Fig 4 Travelling speed when foraging at cheese or honey, either as part of a tandem pair (a) or when returning to the nest for the first time after discovering the food source (b). Colony averages were used for the boxplots and the statistical tests (see text for details). *$p < 0.05$, **$p < 0.01$. Boxplots show the median, 25th and 75th quartile and the 5th and 95th percentile.

competitors. Thus, increasing the number of tandem runs and the travelling speed could help colonies monopolize food sources that are more distant from the nest. An alternative explanation was proposed by O'Shea-Wheller *et al* (2016). They found that in *Temnothorax albipennis* (Curtis) tandem runs were more likely to more distant nest sites and argued that this could decrease the exposure to risks experienced by colonies. In our case, travelling as a pair could reduce predation risk compared to travelling individually. There are also alternative explanations for the effect of foraging distance on speed. First, navigation might be easier at larger distances, e.g. because walking trajectories are easier to compute if landmark positions change more during a trip. Second, slower workers might prefer to forage closer to the nest. The last explanation seems less likely, but detailed laboratory experiments would be needed to separate the different explanations.

Even though ants were more likely to recruit to honey, they travelled at slower speeds. This effect was found in both
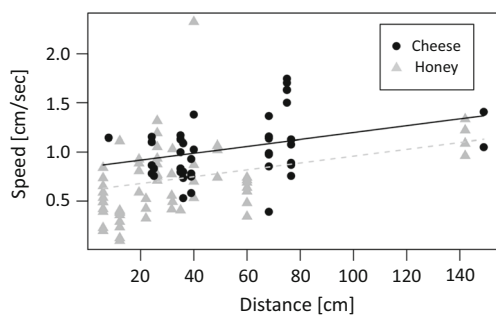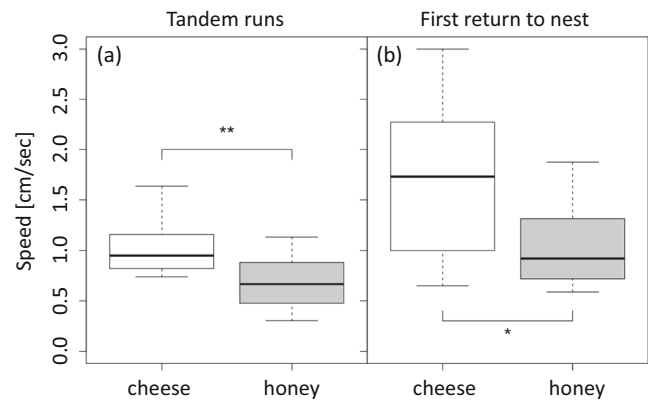

Fig 3 The effect of food type and food distance on the travelling speed of tandem pairs. To calculate the travelling speed, the food source distance was divided by the duration of the tandem run. The lines are based on parameter estimates provided by the LME with food type and food distance as predictor variables.
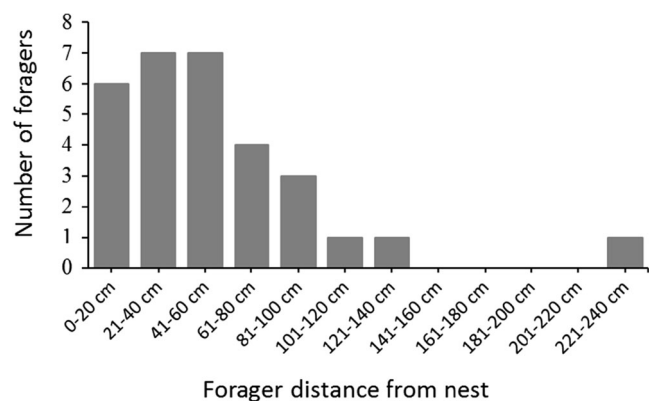

Fig 5 Frequency distribution of forager distances from the nest entrance.

tandem running ants and in ants travelling alone (Fig 4). This result seems puzzling because any preference for one food type should have positive effects on both the motivation to recruit and the walking speed. On the other hand, travelling speed might not reflect a preference for a food type, but may depend on the risk that the food item is lost to competitors. Thus, ants might travel faster to cheese because there is a risk that competitors, such as *Pheidole oxyops* (Forel), cooperatively transport the cheese item to their nest (e.g. Czaczkes *et al* 2011).

Tandem running appears to have costs, as foragers travelling alone were ~66% faster than tandem pairs. In comparison, *Camponotus consobrinus* (Erichson) foragers walking alone are about twice as fast (Schultheiss *et al* 2015) and *T. albipennis* ants are four times faster when travelling alone (Franks & Richardson 2006). *Diacamma indicum*, on the other hand, shows a moderate increase in walking speed of single ants compared to tandem running (~52%) (Kaur *et al* 2017). Due to the nature of our observations in natural vegetation we were not able to determine whether the increase in time needed by tandem pairs was due to slower walking speed, increased curviness or a combination of both.

The success rate of tandem runs was 76.8% and was not affected by the type of food or the distance to the food source. This differs from *Temnothorax curvispinosus* (Mayr) where tandem runs to more distant nest sites were less successful (Pratt 2008). The majority of breakups occurred either relatively close to the nest or in the middle section of the trajectory. An important reason for breakups (~19% of all breakups) were obstacles in the form of vegetation, e.g. pieces of leaves or small branches. Followers were usually not able to discover the food source on their own, but instead quickly returned to the nest (~91%). Leaders were about equally likely to continue their trip to the food source or return to the nest, often to initiate a new tandem run after a breakup.

Scouts searching for food were mainly found less than 1 m from the nest entrance, which suggests a short foraging range for a species of this size (~1-cm body length). Our results are similar to the findings of Horvitz & Schemske (1986a, b), who found that the seed dispersal distance of *P. harpax* was ~75 cm on average, but is in stark contrast to *Neoponera verenae* (Forel) or *N. apicalis*, two ponerine species with a similar diet, but with much greater foraging distances (Horvitz & Schemske 1986b, Francisca Segers, pers. communication). *Pachycondyla harpax* move relatively slowly compared to other species (see e.g. Kaur *et al* 2017, their table 1) and a diverse diet that includes live and dead myriapods, annelids, isopods, lepidopterans, coleopterans, termites, ants and seeds might enable colonies to collect enough food in a relatively small territory. In *P. striata*, foraging distances change with the season, but foragers often also collect food relatively close to their nest (Medeiros & Oliveira 2009).

It is intriguing that some ponerines (e.g. *Neoponera*) use tandem recruitment only during nest relocations, whereas others (e.g. *Pachycondyla*) use it also during foraging (Table S1). *Neoponera verenae* (Forel), for example, was often seen in the same locations as *P. harpax*, is of similar size and appears to have similar prey preferences but does not perform tandem running during foraging (Table S1). *Pachycondyla harpax* might be more combative than *N. verenae* and, therefore, workers are better able to defend food items against competitors. *Pachycondyla harpax* aggressively bites and chases after other ants that approached the food sources and were observed immobilizing *Pheidole* soldiers that attempted to take over the cheese with foam secreted from the tip of a worker's gaster (C.G., personal observation, see Maschwitz *et al* (1981) for a description of this defence mechanism in *Pachycondyla*). Single *P. harpax* foragers, however, were often displaced by other ants and a large *Odontomachus* worker was seen taking over a piece of cheese that was defended by several *P. harpax*. Based on our observations we suspect that groups of *P. harpax* workers are better able to defend large pieces of food and that, therefore, tandem recruitment helps colonies to secure more food items.

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