

Tandem carrying, a new foraging strategy in ants: description, function, and adaptive significance relative to other described foraging strategies

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Abstract An important aspect of social insect biology lies in the expression of collective foraging strategies developed to exploit food. In ants, four main types of foraging strategies are typically recognized based on the intensity of recruitment and the importance of chemical communication. Here, we describe a new type of foraging strategy, “tandem carrying”, which is also one of the most simple recruitment strategies, observed in the Ponerinae species *Pachycondyla chinensis*. Within this strategy, workers are directly carried individually and then released on the food resource by a successful scout. We demonstrate that this recruitment is context dependent and based on the type of food discovered and can be quickly adjusted as food quality changes. We did not detect trail marking by tandem-carrying workers. We conclude by discussing the importance of tandem carrying in an evolutionary context relative to other modes of recruitment in foraging and nest emigration.

Keywords Ants · Foraging behavior · *Pachycondyla chinensis* · Recruitment · Tandem carrying

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Introduction

Foraging success is critical for survival. In order to exploit their environment efficiently, organisms have developed a wide variety of foraging strategies (Danchin et al. 2008). Within social insects, elaborate foraging strategies have been demonstrated which often include specific forms of resource-dependent recruitment of nest mates to food (Jackson and Ratnieks 2006). Ant recruitment foraging strategies have received considerable attention with four main types generally recognized, based largely on the number of individuals recruited and the complexity of the communication (Carroll and Janzen 1973; Peeters and Crewe 1987; Beckers et al. 1989; Traniello 1989; Hölldobler and Wilson 1990; Passera and Aron 2006). Solitary foraging is the simplest strategy, requiring no recruitment. More complex foraging strategies (tandem running, group foraging, and mass foraging) are usually distinguished according to the importance of the solicitation by an exploring worker (scout) and the role of chemical communication during recruitment (Passera and Aron 2006). Here, we re-describe a foraging recruitment strategy observed in the Ponerine ant, *Pachycondyla (Brachyponera) chinensis* Emery: *tandem carrying*. This behavior was previously described in Japanese by Takimoto (1988), however to our knowledge, none of the reviews or studies on foraging recruitment published later considered this study (Beckers et al. 1989; Traniello 1989; Hölldobler and Wilson 1990; Baroni Urbani 1993; Passera and Aron 2006).

One attribute shared by the foraging strategies documented to date in ants is that recruitment intensity following the discovery of food by scouts depends on the quality (Cammaerts and Cammaerts 1980; Breed et al. 1987;

Beckers et al. 1990; de Biseau and Pasteels 1994; Portha et al. 2002; Cassill 2003) quantity (Hölldobler et al. 1978; Cammaerts and Cammaerts 1980; Traniello 1983; Breed et al. 1987; de Biseau and Pasteels 1994; Schatz et al. 1997; Mercier and Lenoir 1999; Mailleux et al. 2000) and/or density (Bernstein 1975; Johnson et al. 2003) of the food resource discovered. Food quantity and especially mobility of the resource are important in recruitment decisions (Traniello 1983; Breed et al. 1987; Schatz et al. 1997). For instance, prey items that cannot be moved by a single individual tend to lead to decisions by foraging ants to recruit more workers in colonies of both *Lasius neoniger* (Traniello 1983) and *Paraponera clavata* (Breed et al. 1987). For these reasons, we hypothesize that in tandem carrying, large and immobile prey should induce more intense recruitment than small but abundant prey that can be individually transported.

In addition to flexibility, a second attribute common to many but not all ant recruitment systems is a dependence on chemical cues. Pheromones, in particular, play a crucial role in foraging behavior, especially in recruitment, and increasingly with complexity in group and mass-foraging species (Hölldobler and Wilson 1990; Beckers et al. 1989; Passera and Aron 2006). Nonetheless, for some species, particularly those employing a less complex foraging strategy, e.g., tandem running, the role of chemical communication may be limited (e.g., Traniello and Hölldobler 1984). Instead, these ants use landmarks or celestial cues to orient between their nest and a food source (Wehner et al. 1996; Collett et al. 2001, 2003; Collett and Collett 2002; Harris et al. 2007; Graham and Cheng 2009). It is unclear whether tandem carrying might be expected to involve pheromonal communication, but we hypothesize that pheromone trails could be one mechanism involved in the recruitment process of tandem carrying.

Herein, we detail the sequence of behaviors observed in the formation and separation of tandem carrying. Then, we test empirically whether prey characteristic (i.e., ease of prey removal) influences the expression of this behavior and its flexibility in time and space. Furthermore, we determine if pheromone trails are used in tandem carrying. Lastly, we discuss the relationship of tandem carrying with other recruitment behaviors and its importance in the evolution of foraging recruitment strategies in ants.

Methods

Studied species

P. chinensis is a ground-dwelling Asian ant species found primarily in forested habitat of Japan, China, and Korea and preying on a diverse range of invertebrates as well as vertebrate carrion (B.G., unpublished data). Recently, this

species has been described as a successful invader within forested ecosystems of the Eastern USA (Guénard and Dunn 2010).

Context-specific tandem carrying

We explored whether food retrieval strategies were flexible or fixed and if they were flexible whether tandem carrying was employed more often when food was too large to be retrieved by a single-worker *P. chinensis*. We conducted our experiments in a mixed hardwood–pine forest near Raleigh, NC, USA (Yates Mill Pond Nature reserve, 35.719 N, –78.692 W) in the summers of 2009 and 2010. We selected downed timber with *P. chinensis* for our experiments. *P. chinensis* are polydomous (each colony includes multiple nest sites) within its introduced range (B.G., unpublished data), with a colony within a large fallen tree containing several nests.

Each of three downed logs contained numerous surface entrances leading to the *P. chinensis* nest(s) within. We identified a nest entrance of *P. chinensis* in each log. We then created two adjacent foraging cells (8×5 cm) with a 2-cm wide entrance 30–60 cm from a nest entrance. These cells were bordered by an impenetrable barrier of foam shaving cream (Gillette, Cincinnati, Ohio), which provided a corridor to a food source and, thereby, facilitated an accurate count of the number of individuals entering and leaving each cell. The shaving cream acted only as a physical barrier: we did not observe any behaviors by *P. chinensis* that would suggest that the shaving cream was repellent. We placed a freshly killed adult female cockroach, *Blattella germanica* L. (mean weight, 71 mg), held in place with a dissecting pin (fixed prey) in one cell and a dozen to 20 freshly killed first instar nymphs (individual mean weight, 2.3 mg; movable prey) in the adjacent cell. A single *P. chinensis* worker could collect each individual nymph; however, a *P. chinensis* worker alone could not remove the pinned adult cockroach. Small nymphs were continuously replenished to maintain recruitment throughout the experiment. We randomly introduced either fixed or movable prey in either right or left chambers for each replicate.

The beginning of a replicate occurred when we gently seized a *P. chinensis* worker near our cell with forceps and placed it on the food item in either chamber. The ant explored the food and then either returned to the nest with a movable prey item or without food (stationary prey). We then recorded the number of tandem-carrying events at the entrance of each cell for each of nine continuous 5-min periods (total duration, 45 min). We then switched the prey type between cells: any workers attached to prey were gently dislodged and left within the cell to avoid contact with the new prey item with workers already used to it. Thus, the cell with the adult pinned cockroach during the

first 45 min contained young cockroach nymphs and was monitored for a second period of 40 min and vice versa. Five replicates for each prey type were performed. The numbers of carrying events were analyzed between treatments using paired Wilcoxon's signed-rank tests. This was done separately for each (5 min) time interval. Tests were realized in the statistical software JMP (SAS Institute 2009).

Examining the role of trail pheromones in *P. chinensis* recruitment

We determined whether *P. chinensis* carriers carrying other workers used a chemical trail by recording the path followed by carriers. The experiment was conducted in the field within a composition board arena (33×33×1.5 cm). This board was installed at ground level ca. 50 cm from a known colony of *P. chinensis* within a large fallen tree. To do this, we drew two concentric areas centered on the board. The outer circle had a radius of 12 cm. We marked on its external periphery every 5° (the space between two 5° marks was 9 mm). The inner circle had a 2 cm radius, marked every 22.5° (the space between two 22.5° marks was 9 mm). We used a pin to secure a freshly killed adult cockroach to the center of the inner circle. The outer circle area was initially covered by a layer of plastic film (12-cm radius) to create a barrier impermeable to pheromones and overlaid with paper to facilitate the ants' walking.

Once foraging and recruitment started, we randomly selected individual tandem carriers walking past the edge of the board and recorded their position on the outer circle (0–359°). We followed the pair and recorded whether the carried worker was released on the prey (success) or until the pair left the outer circle without finding the prey (failure). If the carried worker was deposited within the outer circle, the event was recorded as a failure. In successful instances, we recorded the point where the pair entered the inner circle to obtain an estimate of the path used by the tandem carriers. We also recorded the time (seconds) that the pair remained within the outer circle until either the prey was located (inner circle entered) or the pair vacated the outer circle.

We changed both the plastic and paper substrates 30 min after the initial tandem pair was identified. The path and duration of subsequent tandem pairs entering the outer circle was again recorded. We predicted the following outcomes if *P. chinensis* used accumulated trail pheromones for orientation to food during tandem carrying:

- A decrease in the time required for successive tandem pairs to reach the food
- A decrease in the failure rate with time (although this is not exclusive of visual orientation)

- An increase in the foraging time and a decrease in the success rate from the last 20 min of the first period (before the change of substrate) to the first 20 min of the second period.
- Repeated occurrences of specific entrance and exit positions on the outer circle.

We used linear regression in JMP (SAS Institute 2009) to compare the time tandem carriers remained in the foraging area between the first (1–17 events) and second (1–26 events) main periods (the main periods are those periods before and after substrate change). We only analyzed successful tandem-carrying events.

We created three subperiods of 10 min for each of these main periods and used chi-square to compare the proportion of successes/failures observed within each of the subperiods.

We used chi-square to compare the proportion of successful recruitments between the first period and the second period after the change of substrate and a *t* test was used to compare the time tandem-carrying ants crossed the foraging area between periods. Data were log transformed prior to parametric analysis to fulfill the condition of normality.

We created a contingency table, followed by a chi-square test to determine if the distribution of the number of entrances observed for each 5° range in the outer circle was different from one that could be expected by chance.

Results

Description of tandem carrying, a recruitment foraging strategy close to carrying behavior

Tandem carrying was first observed in June 2007 in Cary, NC, USA (35.724 N, –78.786 W). We later tested for the occurrence of this behavior near other *P. chinensis* colonies in four separate locations in Cary and Raleigh, NC by providing cockroaches, adult *B. germanica* L, to elicit recruitment. In all cases, tandem carrying was observed in response to food placement. This same behavior was also later observed in the native range of *P. chinensis* in Okayama, Japan (34.688 N, 133.919 E).

A successful tandem carry by *P. chinensis* comprises several steps. A scout returns to the nest following the discovery of food too large to be moved by a single individual. Upon return to the nest, the scout solicits a nestmate worker by drumming it with its antennae. The antennated worker assumes a pharate (pupal)-like posture with legs appressed to the thorax. The scout, now referred to as the carrier, then picks it up. The carrier holds the recruited worker within its mandibles between the worker's first and second pairs of legs of the mesometasternum. The carried worker's head is positioned upwards (Fig. 1) while

Fig. 1 Tandem carrying between two workers of *P. chinensis*. Note that the carried worker is held between the first and second pair of legs of the mesometasternum



being transported to the food, after which it is released directly adjacent to or nearly within a 2-cm radius of the food. Interestingly, the path taken by the tandem pair to the food is not linear but instead typically convoluted. Out of 28 observations, the carrier worker returned to the nest in 26 cases (93%) after the release of the carried worker but remained at the food in two cases. In most cases, carrier workers were observed turning around and inspecting the food prior to returning to the nest but without carrying any food themselves. We observed the dissection of large prey into smaller pieces, which were then transported to the nest by individual workers.

Context-specific tandem carrying

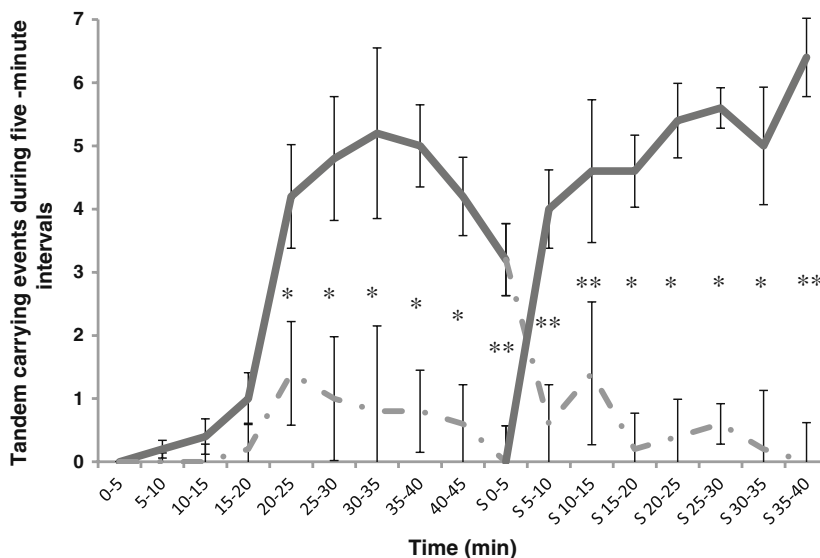
We predicted that recruitment by tandem carrying would be more likely with large, nonmovable prey than with smaller more easily retrieved prey. The first tandem-carrying event was observed 5 and 15 min after placement of the small movable and large nonmovable prey, respectively. We recorded no difference (paired Wilcoxon's test; $P > 0.1$) in the number of tandem-carrying events between the moveable and nonmoveable prey chambers in the first 20 min of

observation (Supplement 1 in the Electronic supplementary material (ESM)). However, tandem carrying recorded within the nonmovable prey cell was roughly fivefold higher (4.7 ± 0.5) than that in the movable prey cell (0.9 ± 0.3) during observations taken between 20 and 45 min (paired Wilcoxon's test; $P < 0.05$) (Fig. 2; Supplement 1 in the ESM). After the large and small prey were switched, *P. chinensis* adjusted their behavior in less than 5 min. Tandem carrying occurred more often within the cell formerly holding small moveable prey but subsequently contained large nonmoveable prey (paired Wilcoxon's test; $P < 0.05$) (Fig. 2; Supplement 1 in the ESM).

Examining a role for trail pheromones in *P. chinensis* recruitment

If a *P. chinensis* pheromone trail was present, we expected that the time to cross the arena would decrease as the pheromone trail was reinforced. However, there was no correlation between the time to cross the arena and the arrival sequence of the tandem-carrying pair in either the first ($R^2 = 0.003$; $P = 0.84$) or second ($R^2 = 0.04$; $P = 0.35$) period (Fig. 3).

Fig. 2 Mean \pm SE tandem carrying events in response to prey type for the first period (0 to 45 min) and the second period (S 0 to S 40 min). The line structure (full or dashed) represents the type of prey present during a given period: large prey, continuous black line; small prey, dashed line. Each line denotes a separate chamber. * $P < 0.05$; ** $P < 0.01$ (paired Wilcoxon's test, $n = 5$)



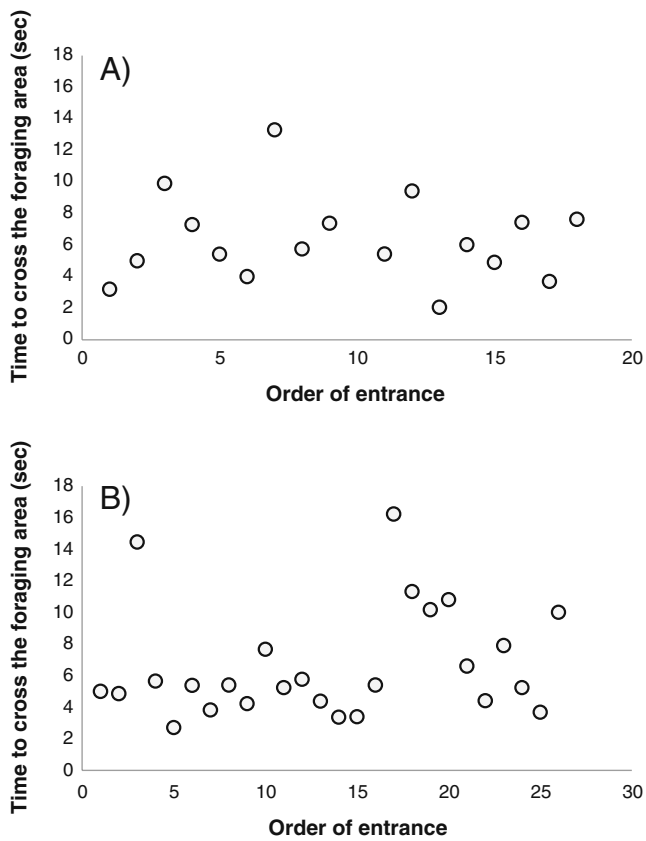


Fig. 3 Time required by each tandem-carry pair to reach prey relative to the order of entry to the experimental arena for **a** the first period and **b** the second period

We observed 18 successful tandem-carrying events out of 33 (54.5%) in the first 30 min following the initial pair entering the arena and 26 successful tandem carrying events out of 51 (51%) in the remaining 30 min ($\chi^2=0.1$; $P=0.75$). The number of instances a pair failed to locate the prey was unchanged throughout the first ($\chi^2=0.15$; $P=0.92$) and second (original substrate covered) periods ($\chi^2=4.93$; $P=0.09$) (Table 1). No differences were recorded in time for successful pairs to cross the foraging arena between the first and the second period of the experiment ($df=35$; $t_{ratio}=-0.2$; $P=0.84$). The time

Table 1 Number of successful/failed tandem carrying events during each 10-min period

Time period (in minutes)	Number of tandem carryings	Number of successes	Number of failures
0–10	10	5	5
10–20	11	6	5
20–30	12	7	5
Change of substrate			
30–40	16	8	8
40–50	19	13	6
50–60	16	5	11

required for successful pairs to cross the arena in the last 20 min of the first period vs. the first 20 min of the second period was the same ($df=23$; $t_{ratio}=-0.18$; $P=0.86$). The distribution of the observed entrances was not different from random distribution ($\chi^2=60.6$; $P=0.81$) (Fig. 4). The higher number of entrances observed for some ranges (15° to 65°) and (280° to 350°) corresponded to the presence of nesting sites located in a large fallen trunk located on that side of the board. From the 84 tandem-carrying events observed, all, but two used a different entrance for the outer and inner circles. A high rate of failure was observed in this experiment, which was not seen previously (B. Guénard, personal observation).

Discussion

Carrying behavior, also known as adult transport or social carrying behavior has been described in many species in the context of nest emigration (Duelli 1973; Hölldobler 1974; Möglich and Hölldobler 1974; Traniello and Hölldobler 1984; Peeters and Crewe 1987), where usually more experienced workers carry younger ones to a new nest site (Abraham and Pasteels 1980). Since carrying behavior pertains to nest emigration, we propose the term tandem carrying in reference to the transport of one individual by another in the context of foraging recruitment. Etymologically, the term tandem carrying is similar to the recruitment behavior called “tandem running” (Wilson 1971; Hölldobler 1977; Baroni Urbani 1989, 1993). Several elements tend to differentiate tandem carrying from other forms of adult

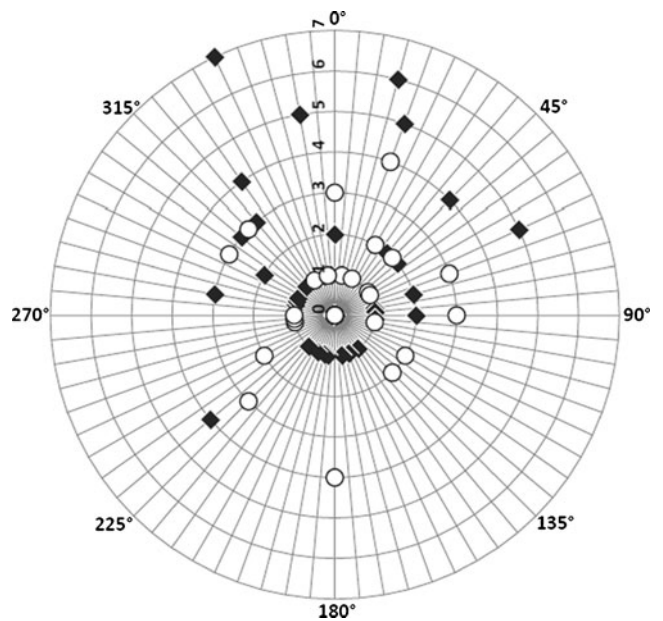


Fig. 4 Location and number of tandem-carrying pairs entering the outer circle (black diamonds) and the inner circle (white circles)

transport. First, as presented, tandem carrying is specific to foraging for food. Secondly, the posture adopted by the carried worker in *P. chinensis* differs from the described postures of adult transport in *Pachycondyla obscuricornis* (Traniello and Hölldobler 1984), *Cataglyphis bicolor* (Duelli 1973), *Camponotus sericeus* (Hölldobler 1974), or *C. castaneus* (personal observation, see Supplement 2 in the ESM), *Formica rufa* (Möglich and Hölldobler 1974) where transported workers are grasped by the mandibles or those of *Temnothorax nylanderi*, *Temnothorax rugatulus*, *Pogonomyrmex maricopa*, and *Aphaenogaster cockerelli* where transported individuals are grasped by the neck or mandibles in an upside-down posture (Möglich and Hölldobler 1974; Möglich 1978). None of the different behaviors described in the review of carrying behavior during nest emigration by Möglich and Hölldobler (1974) is similar to the posture observed in tandem carrying. The carried worker's position is somewhat closer to the posture of *Pachycondyla berthoudi* or *Odontomachus* sp. where the worker is seized by the thorax but on its side (Möglich and Hölldobler 1974; Peeters and Crewe 1987) and not ventrally as observed in *P. chinensis*. Finally, transported workers during tandem carrying return to the nest individually while to our knowledge, observations on adult transport reveal that carried workers do not return to the original nest following transport (Möglich 1978).

Context-specific tandem carrying

While tandem carrying appears ubiquitous within *P. chinensis*, expression of this behavior is context dependent. This is evidenced by the fact that tandem carrying occurred three to ten times more often with large nonmovable vs. small removable prey during peak foraging. Our results are consistent with those reported for other ant species using other forms of recruitment to process food that could not be transported by a single individual (Hölldobler et al. 1978; Markl and Hölldobler 1978; Traniello 1983; Breed et al. 1987; de Biseau and Pasteels 1994; Schatz et al. 1997; Daly-Schweitzer et al. 2007; Dejean and Lachaud 2010; Witte et al. 2010). Instead, large prey were dissected and, subsequently, transported to the nest by individual workers, similar to the observation of Yamamoto et al. (2009). We were surprised by the rapid (<10 min) response to the spatial change in food packaging. For comparison, *Lasius niger* and *Tetramorium caespitum*, two ant species with mass recruitment, show somewhat limited switching to new and better quality foods, especially *L. niger* (Beckers et al. 1990). Resource-dependent spatial and temporal recruitment modulation can improve colony performance in competitive interactions (Traniello 1989). Though seemingly inferior to mass-recruiting ant species that dominate food quickly, tandem carrying in *P. chinensis* might benefit from this flexible recruitment strategy.

Evidence for pheromones

We found no evidence for pheromone involvement in *P. chinensis* tandem-carrying recruitment. Trail fidelity is a universal feature of mass-recruiting species that employ pheromones, but we found no evidence of trail fidelity in this manipulated system. The success rate and the time to locate food did not improve through time and were similar before and after the original substrate was replaced, contrary to what is expected with chemical reinforcement by pheromones. Therefore, we exclude pheromones as a primary recruitment mechanism in *P. chinensis*. However, since we did not place identifying marks on individual workers, we cannot rule out the use of individual-specific trails (e.g., a worker follows its own trail) as documented for *Pachycondyla tesserinoda*, *Paraponera clavata*, *Temnothorax affinis*, and *Temnothorax unifasciatus* (Jessen and Maschwitz 1985; Maschwitz et al. 1986; Breed and Harrison 1987; Aron et al. 1988).

The mechanism by which the scout is able to return to the food and the mechanism by which the carried worker finds the nest are unresolved, although visual orientation cues may be employed (e.g., Jaffe et al. 1990; Collett and Collett 2002). The absence of or limited use of chemical communication and the predominant use of visual cues for orientation have been suggested for solitary foragers in *Dinoponera gigantea* (Fourcassié and Oliveira 2002), *Dinoponera quadriceps* (Araujo and Rodrigues 2006), *Pachycondyla tarsata* (Hölldobler 1980; Dejean et al. 1993a, b) *Pachycondyla apicalis* (Fresneau 1985), *P. hottentota* (Dean 1989), *Pachycondyla senaarensis* (Lachaud and Dejean 1994), or even for tandem running in *P. tesserinoda* (Jessen and Maschwitz 1986), *T. unifasciatus* (Aron et al. 1988), or *Temnothorax albipennis* (McLeman et al. 2002) or for adult transport in *P. berthoudi* (Peeters and Crewe 1987) or *Cataglyphis iberica* during nest emigration (Fourcassié et al. 2000). Similarly, during nest raiding by the slave-making *Rossomyrmex minuchae*, where adult transport is used to recruit workers during the attack of *Proformica* nests, no evidence of pheromone use was detected (Tinaut and Ruano 1998; Ruano and Tinaut 2004). The high rate of failures observed in the changing substrate experiment but not in previous experiments where the environment was more natural could be explained by the lack of complexity of our flat arena. Several studies have shown that ants use landmarks to orientate themselves spatially (Collett et al. 2001; McLeman et al. 2002) and a flat board might not possess enough asperity to provide useful landmarks for orientation. We suspect that visual cues are used by both *P. chinensis* carrier and carried workers; however, this hypothesis remains untested. Furthermore, the specific position of the carried worker in *P. chinensis* could be an adaptation for facilitating the memorization of landmarks allowing the return to the nest.

Evolutionary considerations of tandem carrying

Of the recruiting methods documented prior to this paper, tandem running was generally considered the simplest or most primitive recruitment behavior (Wilson 1971; Lenoir and Jaisson 1982; Agbogba 1984; Passera and Aron 2006). Tandem carrying shares several attributes with tandem running. In both cases, for example, single workers are recruited one at a time. However, tandem running recruits (followers) are active and maintain contact with the scout (in cases where chemical communication is limited) while the recruiter is stimulated by the follower (Hölldobler et al. 1974; Agbogba 1984) such that tactile stimulation and information is shared by the two individuals. Tandem carrying, on the other hand, does not appear to involve active stimulation between individuals during the transport phase. The carried individual remains immobile during transport becoming active only when released on, or within the vicinity of, the food item. In some regards then, tandem carrying may be a simpler, or at least less elaborate, recruitment method than even tandem running.

However, simplicity is not always commensurate with ancestral and we believe it to be unlikely that tandem-carrying behavior is an ancestral form of recruitment for several reasons. First, studies examining a phylogenetic origin in the evolution of ant foraging strategies were inconclusive (Peeters and Crewe 1987; Traniello 1989; Baroni Urbani 1993), and foraging strategies appear to be more correlated with colony size (Wilson 1971; Beckers et al. 1989; Planqué et al. 2010) or ecological factors (Traniello 1989). Second, despite the similarity between tandem carrying and adult transport, the latter of which occurs in both advanced and derived clades of ants (Möglich and Hölldobler 1974), the two behaviors are not necessarily directly or evolutionarily linked. We noted earlier that workers carried during nest emigration are grasped in a manner distinct from tandem-carried *P. chinensis* (Duelli 1973; Hölldobler 1974; Möglich and Hölldobler 1974; Möglich 1978; Abraham and Pasteels 1980; Traniello and Hölldobler 1984; Peeters and Crewe 1987). Adults transported during nest emigration are generally gripped on the head, contrary to tandem carrying where workers are always grasped at the mesometasternum; the significance of which is unknown. It is at least plausible, that the specific posture of the carried worker observed in tandem carrying allows carried workers to collect information about the surrounding environment that can be used in orientation on the trip home. We expect that investigations of adult transport and foraging behavior in other *Pachycondyla* species, especially in the *Brachyponera* sub-genus, will provide important evolutionary insights. So far, studies of the related African *P. (Brachyponera) senaarensis* have not revealed extensive recruitment, except for occasional tandem running (Levieux and Diomande 1978; Lachaud and Dejean 1994).

Importance in the context of invasion biology

Although we conducted our experiments within the introduced range of *P. chinensis* in North Carolina, we have also observed tandem carrying in its native range in Japan (B. Guénard, personal observation). Thus, this behavior did not emerge following *P. chinensis* introduction to the USA. In southeastern USA, *P. chinensis* is a successful invader with pervasive negative impacts on native ant communities (Guénard and Dunn 2010). The contribution of the tandem carrying strategy to *P. chinensis* invasion success is not obvious. Mass recruitment is common and well elaborated in other invasive ants and proposed as one of several traits to explain invasion success (Holway et al. 2002). The example of *P. chinensis* makes clear that mass recruitment is not necessary for invasion.

In conclusion, we consider tandem carrying as documented here in *P. chinensis* to be an original recruitment foraging strategy, perhaps the simplest yet described. In *P. chinensis*, the expression of this behavior is characterized by a graded recruitment and by high spatial and temporal flexibility. First, the number of tandem carrying events is resource dependent, with more recruitment to large prey that cannot be carried by a single worker than smaller movable prey, even at high density. Second, the recruitment observed by tandem carrying can be adjusted quickly in space and within a time period of 5 to 10 min to maximize the exploitation of larger prey. The low recruitment efficiency of this behavior seems to be balanced by a strong flexibility and offers new opportunities to study how social organisms exploit their environments.

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