Insectes Sociaux

CrossMark

Individual and colony level choice during relocation to unequal target nests in an Indian queenless ant *Diacamma indicum*

Anoop Karunakaran[1] · Sumana Annagiri[1]

Abstract

Most organisms need to make temporal and spatial choices pertaining to a wide range of activities like mating, feeding and resting. Arriving at a consensus on facing a choice could be even more challenging in social insects as inputs from multiple individuals need to be consolidated. Colony relocation is one such event that showcases the interplay between individual inputs and colony level choices. *Diacamma indicum* is a ponerine ant that uses tandem running for colony relocation. A small subset of the colony become transporters by either transporting brood or males in their mandibles or by becoming tandem leaders and leading all adult females via tandem running to the new nest. Previous studies show the importance of these individuals in the relocation process and document the presence of leader following leader events, which may be a means for information exchange among leaders. The present set of experiments evaluate colony relocation dynamics in the context of two unequal, but equidistant target nests by following 1135 uniquely marked ants. When faced with a light and dark nest, indecision was minimal and all ten colonies relocated to the dark nest. Knowledge of both targets was not crucial for choice of the better option as less than 10% of transporters had visited both targets before initiating transports. A transporter's latency to start transportation was not influenced by the number of individuals present at the target nest or by the mode of discovery; independent exploration or through leader following leader event. Further the contribution of dependent transporters was found to be significantly lower than independent transporters. Examining decision making by individual transporter and how they influence colony level choice across this simple scenario will enable in understanding the versatility of tandem running recruitment.

Keywords Tandem running · Decision making · Nest choice · Transport-latency · Colony cohesion

Introduction

Nests are central for rearing their young as well as storing colony resources in eusocial insects like ants and bees (Wilson 1971; Andersson 1984). Hence, relocation from one nest to another would be an important process in these species. Ant colonies move from their old nest to a new one for various reasons that impact survival and reproduction directly or indirectly (Visscher 2007; McGlynn 2012). In bee and wasp colonies the immature young (eggs, larvae, and pupae) are not transported from the old nest to the new nest while in ant colonies they are carried to the new nest. This is an important part of the colony's investment and their transportation would complicate the relocation process (Hölldobler and Wilson 1990; Visscher 2007). Further as ants lack the dance language that enables honeybees to share information with their nest-mates regarding various nesting sites in their environment (Seeley 2010), maintaining colony cohesion and choosing an optimal nest is expected to be more complicated. Ant colonies generally rely upon pheromone trails to recruit individuals to a target (Wilson 1971). Studies of ant colony recruitment to food sources suggest that varying levels of these chemical signals are used based on the quality of the target (Beckers et al. 1993; Jackson and Châline 2007), however, such trails could be subject to runaway positive feedback (Sumpter and Beekman 2003) and the amplification of initial choices could lead to selection of sub-optimal

✉ Sumana Annagiri
  sumana@iiserkol.ac.in

[1] Behaviour and Ecology Lab, Department of Biological Sciences, Indian Institute of Science Education and Research, Kolkata, Mohanpur 741246, India

outcomes in terms of energy intake (Beckers et al. 1990; Nicolis and Deneubourg 1999). It may be argued that the costs of selection of a sub-optimal target are higher in the context of colony relocation and multiple studies conducted on ant species with low colony sizes (with less than 500 ants per colony) examine the choice of targets in the context of house-hunting (Franks et al. 2003; Franks et al. 2007; Stroeymeyt et al. 2011; Kaur et al. 2012; Cronin 2012; Cronin 2013; Robinson et al. 2014; Anoop and Sumana 2015). Interestingly, these studies deal with ant species that rely upon different modes of adult transport. *Myrmecina nipponica* colonies range from about 10 to 70 individuals and rely solely upon chemical trails for adult transport (Cronin 2012). *Temnothorax albipennis* colonies on the other hand range from about 50–400 individuals and are known to tandem run as well as carry adults from one location to another during colony relocation (Pratt et al. 2002). Tandem running is a process of recruitment by which an ant leads a nest-mate from one location to another by means of frequent physical contact (Adlerz 1896; Franklin 2014). In the few species of ants which rely upon tandem running, the entire process of relocation is dependent on tandem leaders (Möglich et al. 1974; Möglich 1978; Hölldobler and Wilson 2009; Sumana and Sona 2012; Kolay and Annagiri 2015a).

The present study deals with the ponerine ant *Diacamma indicum*, which have colonies ranging from about 30–300 individuals and rely solely upon tandem running for adult transport (Sumana and Sona 2012; Kolay and Annagiri 2015a). *D. indicum* is a primitively eusocial queenless ant species reported from parts of India and Sri Lanka (Viginier et al. 2004). Colonies of *D. indicum* reside in holes or cavities present in the ground or tree trunks (Kolay and Annagiri 2015b). There is one reproductive in each colony known as the gamergate and a subset of the colony members become tandem leaders during colony relocation (Sumana and Sona 2013). While males and the immobile brood (and food) are carried by individual ants in their mandibles, all adult females in the old nest are transported to the target nest by means of tandem running (Sumana and Sona 2012; Kaur et al. 2012). Any individual who has transported a brood item or led an adult via tandem running has been termed as a transporter. Previous experiments show that transporters in *D. indicum* colonies are able to incorporate assessment of their target at every transport event and hence retain flexibility in the selection of a target nest throughout the relocation process (Anoop and Sumana 2015). In the current study we examine the individual level responses to discovery of these target nests through a set of relocation experiments involving unequal, but equidistant target nests. Further, we look into the role of tandem runs as a means of information exchange regarding the location of potential targets between transporters. Our goal is to understand how decisions made by individual ants to recruit are influenced by two factors;

the quality of the new nest and how information regarding the new nest was acquired.

Materials and methods

Ten colonies of *D. indicum* were collected from Mohanpur (Nadia district, West Bengal, India, 22°56′N, 88°31′E) across February 2014 to July 2015. Colonies consisted of 113.5 ± 27.52 adult females (mean $\pm$ SD, range 81–156), 17.1 ± 14.13 pupae, 12.2 ± 9.72 larvae and 35.5 ± 16.39 eggs. Every ant was uniquely marked with enamel paint (Testors, Rockford, IL, USA) for individual identification. In all colonies only a single reproductive female (gamergate) was present and she was identified by the presence of gemma (Wheeler and Chapman 1922; Cuvillier-Hot et al. 2002). Colonies were maintained in the lab for 14 ± 13.29 days (range 2–44) prior to each experiment inside a nest consisting of a closed Petri dish (circular nest 9.0 cm in diameter and 1.3 cm in height with about 0.7 cm thick base made of Plaster of Paris). The lid of the Petri dish was covered with an opaque paper to keep the nest dark and it had a hole of 1 cm diameter that formed the nest entrance. The entrance diameter was decided based on previous observations from natural nests in this species and similarly the nest cover was kept opaque to simulate the interior of an underground nest where light percolates only through the nest entrance. The colonies were provided ad libitum water and ant cake (Bhatkar and Whitcomb 1970; Hölldobler and Wilson 1990). Each colony was subject to a single relocation experiment in a rectangular sand arena with dimension 180 cm × 150 cm. This arena was lined with aluminium sheet and the walls were coated with petroleum jelly (Vaseline™, Hindustan Unilever Ltd, India) to prevent ants from escaping the setup.

The old nest (along with the colony) was placed at the centre of the experimental arena (schematic representation, supplementary Fig. 1). Two target nests were provided at adjacent corners of a randomly chosen side before the start of each experiment. It hence follows that these two nests were equidistant from the old nest. While one of the targets had a transparent cover, the other had an opaque cover. While the two nests were always placed on adjacent corners, the position of these was decided randomly. This was achieved by picking one of four covered chits, to select one of the four sides. Then, we tossed a coin to decide which of the two nests would be placed at the left or right corner adjoining the chosen side. Apart from having an opaque cover or a transparent one, the two nests were identical in all other aspects like entrance size, nest size, height and nest base material. In this manner, every experiment had two unequal target nests throughout the relocation. Each experiment was initiated by the removal of the roof (top of Petri dish) from the old nest. This rendered the old nest
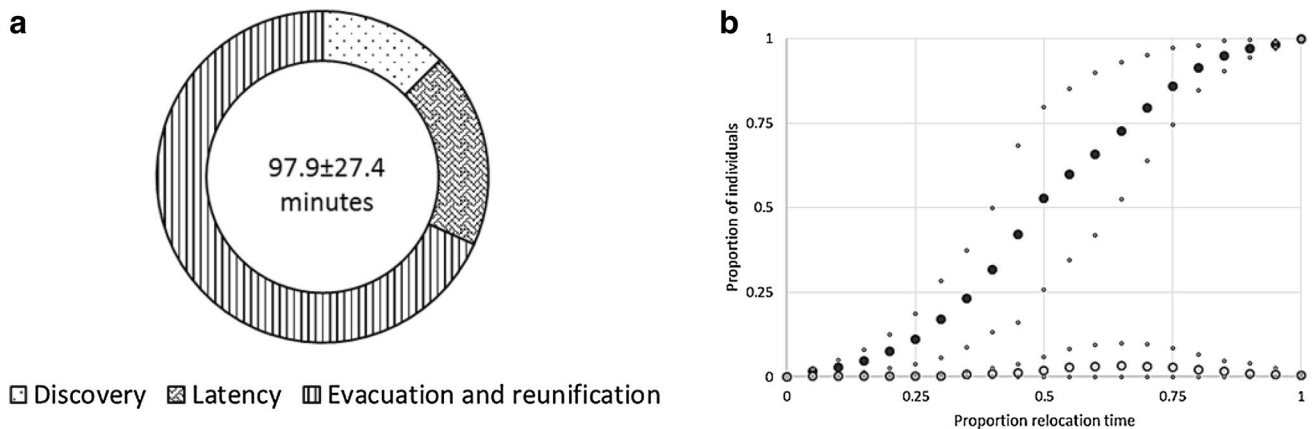
a

□ Discovery ⊠ Latency ⊞ Evacuation and reunification

b

Fig. 1 **a** Doughnut representing the temporal distribution of different phases of colony relocation. The value at the centre denotes the duration (mean ± standard deviation) for the entire relocation across the ten relocations. **b** Net proportion of individuals present at the dark nest (filled circles) and light nest (open circles) as calculated by the cumulative number of tandem runs. The horizontal axis denotes proportion relocation time and readings at every 5% increment of total relocation time have been plotted to provide an overview of the relocation dynamics

inhospitable and triggered colony relocation. Subsequently about 5–15% of ants from the colony started exploring the arena for potential nesting site(s). We documented individual visits made by these scouts to each of the target nests manually in observation sheets and also performed video recording of these target nests, to verify these observations afterwards. The time taken for a scout to enter a target nest after the start of the experiment is termed as the discovery time for the respective target. Having discovered the target, some of these scouts initiated transport of colony members and were hence classified as transporters. Following the discovery of a target, the time taken to start the first transport by a transporter was termed as its initial transport-latency. While adults were transported by tandem runs, brood were carried by individual transporters or by followers of tandem runs to the new nest. For every transport we recorded the identity of the transporter, the initiation and termination sites, identity of the follower and brood, if any, and the time at which the transport initiated or terminated. Through this we could identify if a transporter had visited a target nest by independent exploration or by following another transporter (during a tandem run). Subsequently, transporters who initiated transports before being tandem run even once to the respective target were termed as independent transporters and those transporters who participated as a follower in a tandem run to the respective target before initiating transports were termed as dependent transporters. After the start of a relocation, the absence of any transport for more than 1 h formed the working definition for the end of a relocation. This allowed us to capture the relocation of the entire colony from the old nest to one or more target nests. In this manner we documented a total of 1263 transports involving 1135 uniquely marked ants across 10 experiments involving as many number of colonies, spanning over 979 min of video recorded colony relocation. Unless otherwise stated, the mean and standard deviation of the different parameters are presented. StatistiXL version 1.8 (http://www.statistixl.com) was used to conduct the Wilcoxon paired-sample test and the Mann–Whitney U test. Two tailed p values less than or equal to 0.05 were considered significant.

Results

All of the ten *D. indicum* colonies showed a clear preference for the dark nest over the light nest. In response to the disturbance rendering the old nests inhospitable, all ten colonies finally relocated to the dark nest. While eight of the colonies performed transports only to the dark nest throughout the relocation process, the remaining two colonies evacuated to both dark and light nests and reunited at the dark nest. These observations suggest that *D. indicum* colonies show a strong preference for nests with a dark interior as compared to nests in which light can enter (Z test of proportions, $Z = 3.16$, $N = 10$, $p < 0.01$).

Colonies devoted majority of time for evacuation and reunification of colony members (Fig. 1a). Initially 5–15% of ants from the colony exit the disturbed old nest and explored the arena. We termed this as the discovery phase and the average discovery time for a potential target nest was found to be 12.3 ± 8.6 min (mean ± SD) across the ten relocations. After discovering one or more targets, some of these scouts initiated transportation of adult colony members by tandem running from the old nest to the respective targets. The delay to start evacuation following the discovery of any of the targets was termed as the transport-latency for the colony. The

transport-latency for colonies was 18.7 ± 16.2 min following the discovery of a target. Subsequently the colonies took 66.9 ± 24.6 min to complete transportation of colony members from the old nest to the final target (Fig. 1a). Hence, it was observed that colonies took 97.9 ± 27.4 min for a complete relocation and colony size did not have an effect on the relocation time (Spearman rank correlation, $\rho = 0.41$, $N = 10$, $p = 0.23$). Across the 10 relocations we witnessed 1263 transports performed by 147 unique transporters. Thus, it follows that evacuation and reunification took majority of the time, while discovery and transport-latency took only $31.0 \pm 18.0\%$ of the relocation duration on average.

Individual transporters showed an innate preference for the dark nest irrespective of knowledge about alternative nests available in their vicinity. We performed individual analysis of all the transporters across each of the relocation experiment and observed that the percentage of ants in the colony performing at least one transport to the light nest (0.6 ± 1.2) was significantly lower than the percentage of ants performing at least one transport to the dark nest

(12.9 ± 3.1; Wilcoxon paired sample test, $N = 10$, $p < 0.01$, Fig. 2a). Additionally, the percentage of total transports to the light nest (2.8 ± 5.7) was significantly lower than the percentage of total transports to the dark nest (97.2 ± 5.7; Wilcoxon paired sample test, $N = 10$, $p < 0.01$, Fig. 2a). It may be reiterated that the two target nests were placed at random adjacent corners of the arena and were equidistant from the old nest, to avoid any bias in the discovery of these targets. Nevertheless, we checked for any differences in the discovery time of these target nests and found that the time taken for discovery of the light nest (29.7 ± 21.2 min) was not significantly different from the time taken for the discovery of the dark nest (16.6 ± 14.8 min; Wilcoxon paired sample test, $N = 10$, $p = 0.10$). Hence, the colony level preference for the dark nest was not due to temporal differences in site discovery, but possibly due to differential responses elicited following the discovery of these targets. Subsequently, we examined the behaviour of all the ants who discovered either or both of the target nests before the start of tandem running. If such an individual became a transporter, we documented

Fig. 2 **a** The primary *y*-axis denotes percentage of ants from the colony who became transporters to the light nest and dark nest across the ten relocation experiments. The secondary *y*-axis denotes percentage of transports that occurred to the light nest and dark nest across the ten relocation experiments. **b** The delay for start of transportation by scouts who had visited the light nest and dark nest. **c** The proportion of scouts to the light nest and dark nest who became transporters to the respective target. **a–c** Line within the box represents the median and the box indicates the 25th and the 75th percentiles. Whiskers extend 1.5 times the inter quartile range from the 25th and 75th percentiles and outliers are represented by open circles. Asterisk represents statistically significant difference
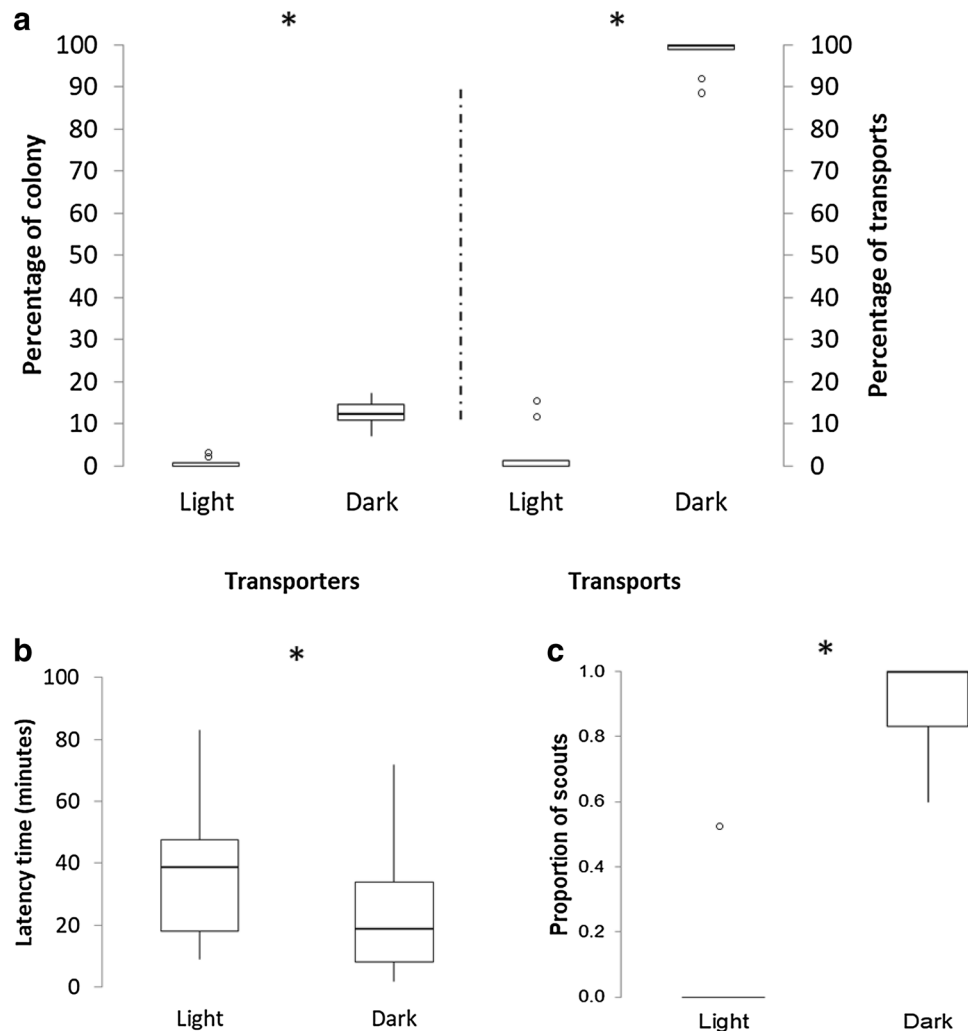
the delay for start of transportation by this transporter following its first visit to any of the targets to obtain its transport-latency. Interestingly, the transport-latency for a scout who had visited the light nest (38.3 ± 23.8 min) was significantly higher than the transport-latency for a scout who had visited the dark nest (22.7 ± 19.3 min; Mann–Whitney test, $N_1 = 12$, $N_2 = 29$, $p = 0.03$, Fig. 2b). Hence, individual ants showed a differential latency to initiate transportation with respect to the quality of the target that was discovered. In addition, we observed that while only $10 \pm 22.4\%$ of the scouts who visited the light nest became transporters to this target, $89.8 \pm 15.3\%$ of the scouts who visited the dark nest became transporters to this target (Mann–Whitney test, $N_1 = 5$, $N_2 = 10$, $p < 0.01$, Fig. 2c). It may be noted that 133 of the 147 transporters had not discovered the alternate nest site before initiation of transports and hence were unaware of the relative quality of the target to which they initiated transports. The few individuals (14 out of 147 transporters) who had explored both the targets before initiating their first transport, performed transports only to the dark nest throughout the relocation.

Tandem runs played an important role in information exchange of target nests amongst transporters. Majority of the transporters (68.7%) participated as a follower in a tandem run at least once during the relocation process. We examined whether these transporters relied upon such a tandem run (leader follow leader event) to gather information before initiating their maiden transport to the respective target. The number of transporters who initiated transportation only after they participated as a follower in a tandem run at least once to the respective target (termed as dependent transporters, 7.6 ± 3.0) was comparable to the number of transporters who initiated transportation before participating as a follower in a tandem run to the respective target (termed as independent transporters, 7.1 ± 2.9; Wilcoxon paired sample test, $T = 22.5$, $N = 10$, $p = 0.67$, Fig. 3a). Hence, tandem runs enabled passage of information regarding location of a target nest to about half of the transporters. Dependent transporters depended on independent transporters to get information regarding the new nest and it follows that dependent transporters initiated transports significantly later than independent transporters (49.1 ± 18.7 vs. $32.8 \pm 25.5\%$ of the relocation time respectively; Mann–Whitney test, $U = 3743.5$, $N_1 = 76$, $N_2 = 71$, $p < 0.01$, Fig. 3c).

Even though the transport-latency was comparable, the overall contribution towards colony relocation by a dependent transporter was lower than an independent transporter. The transport-latency for a dependent transporter (11.5 ± 8.3 min) was not significantly different from the transport-latency for an independent transporter (19.5 ± 18.7 min; Mann–Whitney test, $N_1 = 68$, $N_2 = 34$, $p = 0.13$, Fig. 3b). However, the number of transports performed by an average dependent transporter

(6.1 ± 6.0) was significantly lower than the number of transports performed by an average independent transporter (11.6 ± 9.6; Mann–Whitney test, $U = 3163.0$, $N_1 = 73$, $N_2 = 65$, $p < 0.01$, Fig. 3a).

Discussion

Colonies of *D. indicum* reside in holes or cavities present in the ground, trunks or similar debris found in nature. Generally being covered with opaque material on all sides except the entrance, most of the nests would not receive any sunlight and thus remain dark (Kolay and Annagiri 2015b). This lab based study shows that these ants not only relocate to a cavity present in their environment, but also show an active preference for nests that are dark. Similar studies on other house-hunting ant species like *T. albipennis* and *M. nipponica*, which have comparable colony sizes also show a strong preference for dark nests (Franks et al. 2003; Franks et al. 2007; Cronin 2013). In *M. nipponica* colony relocations where ants rely upon chemical trails, 83.3% of colonies moved into the darker nest and colony splitting was absent (Cronin 2013). In *T. albipennis* colony relocations where ants use tandem running as well as carrying, 90% of colonies moved into the darker nest and the remaining colonies split across the two options and could not achieve cohesion even at the end of the relocation experiment (Franks et al. 2007). Our results reveal that, in *D. indicum* colony relocations where ants rely solely upon tandem runs, 100% of colonies moved into the dark nest. However, it is interesting to note that 20% of these colonies performed transports to both target nests leading to colony splitting, before reuniting to the dark nest. These experiments suggest that the preference for dark nests is common among such subterranean ant species in the context of house-hunting; however, the dynamics of the relocation process that leads to this choice could be different.

Relocation in *D. indicum* colonies is largely dependent on less than one-fifth of the colony members who take up the job of transportation (Sumana and Sona 2013; Kaur et al. 2017). Hence, a preferential commitment by a small fraction of the colony (transporters) is sufficient to facilitate colony relocation to the respective target. In the current experiment about 13% of a colony on average became transporters to the dark nest and undertook more than 97% of transports, while less than 1% of colony members transported to the light nest yielding less than 3% of total transports within each colony relocation. Lab based studies on the trail making species *M. nipponica* report that about 45–50% of the colony became transporters during relocation experiments where one or two target nests were provided (Cronin 2012). As a result the transportation phase of *M. nipponica* colonies was much shorter than the discovery and assessment phases and
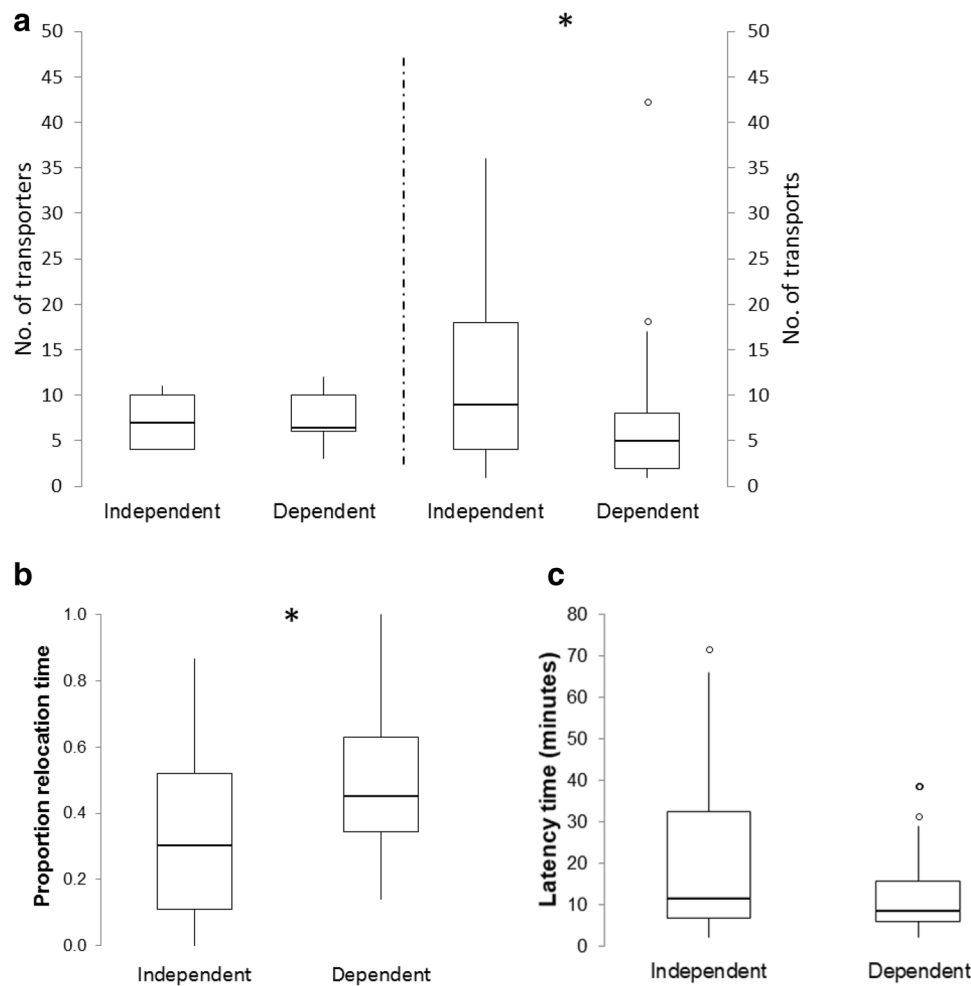
Fig. 3 a The primary *y*-axis denotes the number of transporters. Transporters who initiated transportation solely by means of independent exploration is compared with those who initiated transportation after following a tandem run to the respective target across the ten relocation experiments. The secondary *y*-axis denotes number of transports performed by independent exploration led transporters and tandem run led transporters across the ten relocation experiments. **b** The proportion relocation time that had elapsed at which the independent transporters and dependent transporters started transportation to the respective target nest. **c** The delay for start of transporta-

tion by independent transporters and dependent transporters. Note: ants who initiated transports before being tandem run to the respective target are independent transporters and ants who participated as a follower in a tandem run before initiating transports to the respective target are dependent transporters. **a**–**c** Line within the box represents the median and the box indicates the 25th and the 75th percentiles. Whiskers extend 1.5 times the inter quartile range from the 25th and 75th percentiles and outliers are represented by open circles. Asterisk represents statistically significant difference

no instance of colony splitting was observed. This denotes that these trail making ants commit themselves to one of the available target nests before initiating transportation of colony resources. However, in various tandem running species like *T. albipennis* and *T. crassispinus* the transportation phases are longer than the discovery and assessment phases and instances of colony splitting in lab-based experiments have been reported (Dornhaus and Franks 2006; Mitrus 2016) and could lead to a change in the target nest even after initiation of the transport phase (Franks et al. 2007). This suggests an inherent difference in the relocation dynamics with respect to the mode of recruitment employed by these

small ant colonies; from a definitive choice of the target nest in chemical trail making species to a more flexible choice of the target nest(s) in tandem running species. Relocation of *D. indicum* colonies in their natural habitat reveal that colonies could split up and occupy 8 different temporary shelters before reunifying to one nest (Kaur et al. 2012), showcasing the degree to which transporter initial choice varies.

The decision as well as the latency to initiate transportation to a particular target nest was an innate response to the quality of a target and not on information about alternative nests available in the environment. The experimental design ensured that both targets were equidistant and as expected

the discovery time for the light nest was comparable to the dark nest. Majority of the ants (133 out of 147 transporters across all colonies) initiated transportation to a target nest before visiting the alternative target nest and hence were unaware of the same. Nevertheless, individuals who discovered the light nest showed a higher latency for initiation of transports as compared to those who discovered the dark nest. Further analysis of all scouts revealed that while only 10% of the scouts who visited the light nest became transporters to the light nest, about 90% of the scouts who visited the dark nest became transporters to the dark nest. It was interesting to note that all of the remaining 14 ants who initiated transportation only after visiting both the target nests, invariably performed transports only to the dark nest throughout the relocation.

Colony relocation by *D. indicum* in the field documented the importance of tandem running in this species not only for transportation of adults and brood but also for passage of information regarding the location of target nests to potential transporters (Kaur et al. 2012). Potential transporter following other tandem leaders could be an effective way to impart knowledge of available target options. While the quality of the target options could not be controlled in the field relocation studies, the present study provides scope for examining the role of these 'leader following leader' events in the passage of novel information in the context of two unequal target options. We found that about 69% of transporters were tandem run at least once through the course of a relocation experiment. However, some of these transporters already possessed information regarding the target option to which they were tandem run and hence all 'leader following leader' events did not necessarily lead to the passage of novel information. However, 52% of transporters in each colony initiated transports only after they had followed a tandem run to the respective target and this supports our claim that tandem runs facilitate the discovery of potential targets to potential transporters.

Analysis of the transport latencies suggest that the decision to start transporting to a target nest was not affected by how the transporter discovered the target nest or how many individuals were present in the nests. It is worthwhile to ponder that the visit of a dependent transporter occurred later on in the relocation process as compared to an independent transporter and they would encounter different proportion of colony members at the old and new nest, respectively, when they initiate transportation (Figs. 1b, 3b). This, however, did not seem to affect the delay for start of transportation by these individuals as the transport-latency for a dependent transporter was not significantly different from that of an independent transporter. This suggests that while tandem run aids the discovery of potential target nests by transporters in the colony, it may not influence the assessment of a target nest by individual transporters. In other species of ants like

T. albipennis and *T. curvispinosus*, where quorum threshold at the new nest is used for switching from tandem running to carrying recruitment the scenario is different. Individuals reaching the new nest as followers are known to behave differently based on the number of nest-mates already present at the new nest (Pratt 2005a, b). If a threshold number is present they become transporters and recruit by means of carrying. But in *D. indicum* where only tandem running is used throughout the relocation for recruitment, such switching cannot be tested and only the latency to start tandem running can be checked. In the current experiment we see that there is no difference in the latency between independent and dependent transporters, despite the latter encountering more colony members inside the new nest.

This individual assessment by transporters before starting recruitment in *D. indicum* is likely to prevent any stochastic initial choices from developing a runaway positive feedback to a sub-optimal target nest. Further, the workload undertaken by dependent transporters was significantly lower than independent transporters. Analysis of the contribution of each transporter revealed that, transporters who had visited the target by means of following a tandem run performed only half as many transports as independent exploration led transporters. Hence it follows that, for the current experimental setup where two unequal target options are available, *D. indicum* colonies may depend largely upon choices made by individual transporters. Understanding different recruitment strategies under diverse natural conditions is essential to completely understand relocation dynamics and to appreciate the robustness of these societies.

Compliance with ethical standards

Ethics All our experiments complied with the regulations for animal care in India.

Conflict of interest The authors declare no competing or financial interests.

References

Adlerz G (1896) *Tomognathus sublaevis* Mayr. Bih Till Kongliga Sven Vetenskaps-Akademiens Handl 21:1–76

Andersson M (1984) The evolution of eusociality. Annu Rev Ecol Syst 15:165–189

Anoop K, Sumana A (2015) Response to a change in the target nest during ant relocation. J Exp Biol 218:887–892. https://doi.org/10.1242/jeb.115246

Beckers R, Deneubourg JL, Goss S (1993) Modulation of trail laying in the ant *Lasius niger* (Hymenoptera: Formicidae) and its role in the collective selection of a food source. J Insect Behav 6:751–759. https://doi.org/10.1007/BF01201674

Beckers R, Deneubourg JL, Goss S, Pasteels JM (1990) Collective decision making through food recruitment. Insectes Soc 37:258–267. https://doi.org/10.1007/BF02224053

Bhatkar A, Whitcomb WH (1970) Artificial diet for rearing various species of ants. Fla Entomol 53:229. https://doi.org/10.2307/3493193

Cronin AL (2012) Consensus decision making in the ant *Myrmecina nipponica*: house-hunters combine pheromone trails with quorum responses. Anim Behav 84:1243–1251. https://doi.org/10.1016/j.anbehav.2012.08.036

Cronin AL (2013) Conditional use of social and private information guides house-hunting ants. PLoS One 8:1–7. https://doi.org/10.1371/journal.pone.0064668

Cuvillier-Hot V, Gadagkar R, Peeters C, Cobb M (2002) Regulation of reproduction in a queenless ant: aggression, pheromones and reduction in conflict. Proc R Soc B Biol Sci 269:1295–1300. https://doi.org/10.1098/rspb.2002.1991

Franks D NR (2006) Colony size affects collective decision-making in the ant *Temnothorax albipennis*. Insectes Soc 53:420–427. https://doi.org/10.1007/s00040-006-0887-4

Franklin EL (2014) The journey of tandem running: the twists, turns and what we have learned. Insectes Soc 61:1–8. https://doi.org/10.1007/s00040-013-0325-3

Franks NR, Hooper JW, Gumn M et al (2007) Moving targets: collective decisions and flexible choices in house-hunting ants. Swarm Intell 1:81–94. https://doi.org/10.1007/s11721-007-0007-8

Franks NR, Mallon EB, Bray HE et al (2003) Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. Anim Behav 65:215–223. https://doi.org/10.1006/anbe.2002.2032

Hölldobler B, Wilson EO (1990) The ants. Springer, Berlin

Hölldobler B, Wilson EO (2009) The superorganism: the beauty, elegance, and strangeness of insect societies. Norton, New York

Jackson DE, Châline N (2007) Modulation of pheromone trail strength with food quality in Pharaoh's ant, *Monomorium pharaonis*. Anim Behav 74:463–470. https://doi.org/10.1016/j.anbehav.2006.11.027

Kaur R, Anoop K, Sumana A (2012) Leaders follow leaders to reunite the colony: relocation dynamics of an Indian queenless ant in its natural habitat. Anim Behav 83:1345–1353. https://doi.org/10.1016/j.anbehav.2012.02.022

Kaur R, Joseph J, Anoop K, Sumana A (2017) Characterization of recruitment through tandem running in an Indian queenless ant *Diacamma indicum*. R Soc Open Sci 4:160476. https://doi.org/10.1098/rsos.160476

Kolay S, Annagiri S (2015a) Tight knit under stress: colony resilience to the loss of tandem leaders during relocation in an Indian ant. R Soc Open Sci 2:150104. https://doi.org/10.1098/rsos.150104

Kolay S, Annagiri S (2015b) Dual response to nest flooding during monsoon in an Indian ant. Nat Publ Gr 5:13716. https://doi.org/10.1038/srep13716

McGlynn TP (2012) The ecology of nest movement in social insects. Annu Rev Entomol 57:291–308. https://doi.org/10.1146/annurev-ento-120710-100708

Mitrus S (2016) Emigration speed and the production of sexuals in colonies of the ant *Temnothorax crassispinus* under high and low levels of disturbance. Insectes Soc 63:127. https://doi.org/10.1007/s00040-015-0447-x

Möglich M (1978) Social organization of nest emigration in Leptothorax (Hym., Form.). Insectes Soc 25:205–225

Möglich M, Maschwitz U, Hölldobler B (1974) Tandem calling: a new kind of signal in ant communication. Science 186:1046–1047

Nicolis SC, Deneubourg JL (1999) Emerging patterns and food recruitment in ants: an analytical study. J Theor Biol 198:575–592

Pratt SC (2005a) Behavioral mechanisms of collective nest-site choice by the ant Temnothorax curvispinosus. Insectes Soc 52:383–392. https://doi.org/10.1007/s00040-005-0823-z

Pratt SC (2005b) Quorum sensing by encounter rates in the ant *Temnothorax albipennis*. Behav Ecol 16:488–496. https://doi.org/10.1093/beheco/ari020

Pratt SC, Mallon E, Sumpter D, Franks NR (2002) Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. Behav Ecol Sociobiol 52:117–127. https://doi.org/10.1007/s00265-002-0487-x

Robinson EJH, Feinerman O, Franks NR (2014) How collective comparisons emerge without individual comparisons of the options. Proc Biol Sci 281:20140737. https://doi.org/10.1098/rspb.2014.0737

Seeley TD (2010) Honeybee democracy. Princeton University Press, Princeton

Stroeymeyt N, Franks NR, Giurfa M (2011) Knowledgeable individuals lead collective decisions in ants. J Exp Biol 214:3046–3054. https://doi.org/10.1242/jeb.059188

Sumana A, Sona C (2012) Studies on colony relocation in the Indian queenless ant *Diacamma indicum*. Curr Sci 102:1373–1374

Sumana A, Sona C (2013) Key relocation leaders in an Indian queenless ant. Behav Process 97:84–89

Sumpter DJT, Beekman M (2003) From nonlinearity to optimality: pheromone trail foraging by ants. Anim Behav 66:273–280. https://doi.org/10.1006/anbe.2003.2224

Viginier B, Peeters C, Brazier L, Doums C (2004) Very low genetic variability in the Indian queenless ant *Diacamma indicum*. Mol Ecol 13:2095–2100. https://doi.org/10.1111/j.1365-294X.2004.02201.x

Visscher PK (2007) Group decision making in nest-site selection among social insects. Annu Rev Entomol 52:255–275. https://doi.org/10.1146/annurev.ento.51.110104.151025

Wheeler WM, Chapman JW (1922) The mating of Diacamma. Psyche A J Entomol 203–211

Wilson EO (1971) The insect societies. Belknap Press, Cambridge