

RESEARCH ARTICLE

Response to a change in the target nest during ant relocation

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ABSTRACT

Decisions regarding spatial and temporal choices pertaining to a wide range of activities such as mating, feeding and resting are necessary for all organisms. Social species encounter another level of complexity, wherein inputs from multiple individuals have to be consolidated to yield a consensus. One platform on which decision making can be examined is the relocation of animal societies. Relocation is the process by which organisms move from their old dwelling to a new nest along with all the inhabitants. This exposes them to the elements and thus impacts their survival and reproduction. *Diacamma indicum*, the model system for our experiments is a ponerine ant that uses tandem running for colony relocation. In the present study an artificial manipulation was performed to cause a shift in the target nest. The flexibility of the relocation process and, more specifically, the response of tandem leaders to a changed target were studied. A majority of these leaders ($N=262$) not only re-evaluated and adapted to the change, but did so with negligible error (1.65%). This enabled colonies ($N=10$) to reunite at the target nest in every case. The only cost to this flexible decision making was paid in terms of additional time. Although considered to be a primitive method of recruitment, we reveal that tandem running allows *D. indicum* leaders to incorporate assessment of the available options at every step. This inherent flexibility in decision making would be a good strategy for organisms that need to function with incomplete information or inhabit environments that change frequently.

KEY WORDS: Decision making, Transport latency, Tandem running, *Diacamma indicum*

INTRODUCTION

Groups of individuals, be it humans, chimpanzees, birds, fishes, locusts or honeybees, perform activities together in a coordinated manner to achieve a common goal. There are many examples of these communal activities across different taxa: migration, roosting, predator avoidance and nesting to mention a few. Achieving this scale of coordinated activity is possible only if the members of these groups can communicate effectively to arrive at a consensus (Conradt and Roper, 2005; Sumpter, 2006). The manner in which individual group members, who each have limited information, compare this to arrive at a consensus has been an active area of exploration (Reebs, 2000; Stroeymeyt et al., 2011).

Nest relocation is one such activity wherein all the members living within a nest need to coordinate their activities and move in a collective manner into their new dwelling. This problem becomes even more interesting to consider in social insects because their nests often contain thousands of individuals and group cohesion is

essential. Members left behind or lost have a very small chance of survival. Honeybees represent one such species and their relocation has been well studied. These highly eusocial hymenopterans are known to scout the surroundings for alternative nests and report their findings by means of a waggle dance to their colony mates. Using elegant experiments and modelling it has been shown that the quality of different nests influences a scout's dance performance and attrition of dances to poor quality nests is faster. The persistence for good nests results in the building of a consensus. Subsequently, the colony relocates *en masse* into the new nest (Britton et al., 2002; Camazine et al., 1999; Seeley and Visscher, 2004).

Colony relocation in ants, another subfamily of Hymenoptera, is even more complicated for the following three reasons. They need to transfer their immature young and stored resources together with all the adults. Second, ants cannot communicate the bearings of potential new nests to their fellow members indirectly because they lack the dance language. In addition, their movement to the new nest will be more gradual as the entire colony marches on chemical trails from their old nest. The pheromones used along these trails are complex mixtures, giving information regarding direction and strength; the trail may also include short-lived repellants (Hölldobler and Wilson, 1990; Robinson et al., 2008). Aspects of relocation, including the manner of decision making has been studied in *Temnothorax* species. These ants use tandem running initially to recruit followers, and on reaching consensus, switch to carrying colony members to the new site (Franklin, 2014; Möglich et al., 1974; Pratt, 2005). Studies in *Temnothorax* species and *Monomorium pharaonis* have examined whether ants can make decisions regarding an optimal nest when presented with different choices at the beginning of the relocation process. They found that these social insects are indeed capable of picking the best option in most cases (Evison et al., 2012; Pratt et al., 2002). Furthermore, it is understood that once the quorum is reached at a potential new nest, scouts cease monitoring the nest's contents in any detail, as their visit duration reduces drastically (Pratt, 2005).

How organisms respond to a midway change has hardly been explored (but see Franks et al., 2007). In the present study, we analyse the flexibility of the relocation process. We ask whether ants that have initiated relocation to one destination change their decision when the quality of this destination suddenly changes. In other words, whether evaluation of the destination is a continuous process or a discrete one? We used *Diacamma indicum* as the model system for our experiments. This is a queenless ponerine ant found in the south and east of India and in Sri Lanka. One fertile female who is not morphologically different from other females of the colony, except for the retention of an appendage called the gemma, is termed as the gamergate. She is responsible for the production of all female offspring in the colony (Cuvillier-Hot et al., 2002; Wheeler and Chapman, 1922). Colony relocation in this species has been documented under natural and laboratory conditions. These studies highlight the importance of tandem running and the contribution of tandem leaders while detailing the dynamics of colony relocation (Kaur et al., 2012; Sumana and Sona, 2012, 2013). Tandem running

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Received 10 October 2014; Accepted 12 January 2015

is a method of recruitment involving an informed individual (leader) leading colony members from the old to the target nest one at a time, maintaining frequent physical contact along the journey (Adlerz, 1896). Although all adults in this species are transported through tandem running, brood is carried to the new nest. Brood transport is initiated later than adult transport but remains coupled to adult movement. More than 98% of the brood are carried in the mandibles of the follower ants while following a tandem leader (Kaur and Sumana, 2014). Multiple leaders can be simultaneously involved in a relocation process and even followers of tandem runs could become leaders of subsequent tandem runs as is the case in *Temnothorax albipennis* and *Temnothorax rugatulus* (Hölldobler and Wilson, 2009; Möglichen, 1978).

In the present study, artificial manipulation of the nest quality was performed during colony relocation, so as to cause a shift in the target nest. The manipulation was performed halfway through the relocation process, which ensured that the workload was conserved in spite of the manipulation. The flexibility of the entire relocation process, the collective movement of the colony and the response of individuals to this disturbance was analysed in light of the dynamics of unmanipulated relocations. This enabled us to investigate whether ants evaluate their environment in a continuous manner in order to recalibrate their decision to the optimal in a changing environment.

RESULTS

Ten colonies of *Diacamma indicum* consisting of 65.0 ± 13.15 (mean \pm s.d.) adult females, 17.1 ± 20.08 pupae, 12.2 ± 10.44 larvae, 36.1 ± 21.52 eggs and 0.4 ± 0.97 males were used for the experiments. Each of these colonies was subjected to two types of relocation experiments in a random order. The start of all experiments involved placement of a new shelter and the removal of the shelter from the old nest in the experimental arena (Fig. 1). Whereas the manipulated relocation (henceforth flexibility experiment) involved a change in the target nest mid-relocation, the unmanipulated relocation (henceforth control experiment) simulated the physical disturbance without changing the target nest mid-relocation. Every ant was uniquely marked and every transport was documented manually and cross-checked using videos recorded throughout the 20 relocation experiments. 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 was initiated or terminated.

All 10 colonies relocated to the target nest in the control experiment. In the flexibility experiment, where manipulation reversed the nest qualities and made the old nest more favourable mid-relocation, all colonies relocated to the new target nest showing 100% flexibility. Not a single case of colony splitting into subgroups was observed and thus colony cohesion was maintained. In order to understand how this flexibility was achieved and its implication for relocation dynamics, we conducted analysis at two levels: colony and individual.

Initially, few ants explored the arena for probable nesting alternatives. Upon finding a suitable option, they initiated the transportation of colony members. While adults were transported by tandem running, brood and males were carried to the target nest by tandem leaders or followers of tandem runs. The total number of transports in the flexibility experiment (72.00 ± 20.20) was not significantly different from that in the control experiment (63.90 ± 24.89 ; Wilcoxon paired-sample test: $T=12$, $N=10$, $P=0.13$, Fig. 2). Also, the percentage of transporters in the flexibility experiment (21.25 ± 3.67) was not significantly different from that in the control experiment (19.07 ± 5.14 ; Wilcoxon paired-sample test: $T=15$, $N=10$, $P=0.30$, Fig. 2). The manipulation was performed halfway through the relocation; hence number of transports required for relocating the entire colony into any one of the two options was equivalent. This experimental design conserved the total workload across the control and flexibility experiments, provided ants performed transports only to the target nest. The comparable number of transports in the control and flexibility experiments indicates a negligible increase of erroneous transports in the flexibility experiment. In order to confirm this directly we compared the percentage of walks terminating anywhere in the arena outside the target nest (error index). The error index for the flexibility experiment ($1.65 \pm 2.04\%$) was not significantly different from the control experiment ($0.23 \pm 0.48\%$; Wilcoxon paired-sample test: $T=4$, $N=10$, $P=0.09$). Additionally, we compared the identities of followers in tandem runs before and after manipulation and found that $70.53 \pm 14.53\%$ of them were identical. Thus, individuals that were tandem run to the new nest were tandem run back to the target nest in the flexibility

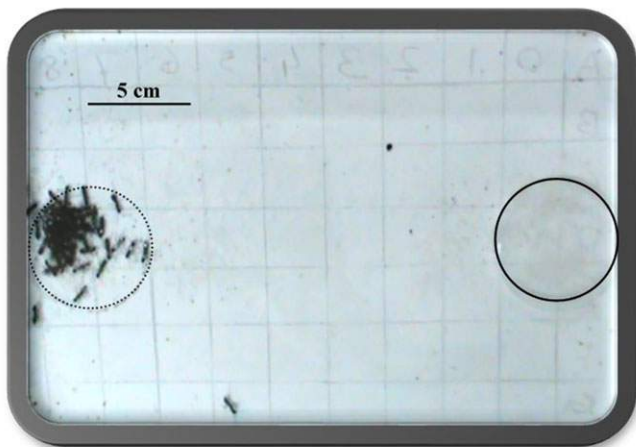


Fig. 1. Experimental arena. Plastic box ($30 \times 20 \times 7$ cm) that was used for all the colony relocation experiments. The dotted circle represents the position of the old nest prior to its removal at the start of the experiment. The solid circle shows the new nest at the start of the experiment. In this picture, the ant colony DI-216 with 50 adult females is positioned at the old nest site.

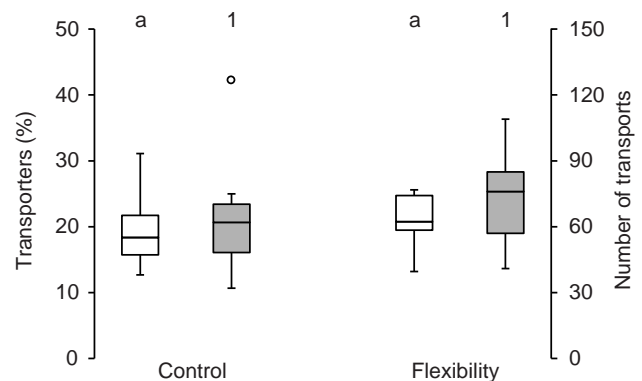


Fig. 2. Percentage of transporters and number of transports. The percentage of ants in the colony who became transporters (white boxes) is plotted on the primary y-axis and the number of transports (grey boxes) is plotted on the secondary y-axis across 10 replicates each for the control and the flexibility experiments. Line within the box represents the median and the box indicates the 25th and 75th percentiles. Whiskers extend to data points that are less than 1.5 times the interquartile range and outliers are represented by open circles. Boxes with same letter or number are not significantly different, Wilcoxon paired-sample test ($P > 0.05$).

experiment. Together, these observations not only stress the importance of transporters involved in the relocation process but also show that they make little error in responding to a change in nest quality.

However, the decision to change their target nest caused on average a 50% increase in relocation time. Total relocation time for the flexibility experiment (30.60 ± 16.28 min) was significantly greater than that for the control experiment (21.00 ± 6.28 min; Wilcoxon paired-sample test: $T=8$, $N=10$, $P=0.05$, Fig. 3A). This increase in time was partly because of an overall reduction in the rate of transports in the post-manipulation phase of the flexibility experiment. The rate of relocation for the control experiment in the post-manipulation phase (4.84 ± 2.27 transports per min) was comparable to its rate in the pre-manipulation phase (6.16 ± 2.17 transports per min; Wilcoxon paired-sample test: $T=11$, $N=10$, $P=0.09$, Fig. 3B). However, the rate of relocation for the flexibility experiment in the post-manipulation phase (3.88 ± 2.27 transports per min) was significantly lower than its rate in the pre-manipulation phase (5.79 ± 2.01 transports per min; Wilcoxon paired-sample test: $T=8$, $N=10$, $P=0.05$, Fig. 3B).

To further understand the underlying dynamics, we examined the characteristics of the transporters involved and their contribution in the control and flexibility experiments. The percentage of transporters that retired following manipulation (retirees) in the flexibility experiment ($25.56 \pm 10.17\%$) was not significantly different from that in the control experiment ($16.53 \pm 9.32\%$;

Wilcoxon paired-sample test: $T=12$, $N=10$, $P=0.13$). Active transporters in this phase comprised two classes: substitutes, who initiated transportation in the post-manipulation phase and persisters, who transported during the pre-manipulation and post-manipulation phase. The percentage of persisters in the post-manipulation phase of the flexibility experiment ($55.68 \pm 19.56\%$) and control experiment ($64.11 \pm 23.61\%$) was not significantly different (Wilcoxon paired-sample test: $T=17$, $N=10$, $P=0.35$, Fig. 4). The percentage of transportation carried out by persisters in the post-manipulation phase of the flexibility experiment ($64.62 \pm 18.03\%$) and control experiment ($66.09 \pm 24.44\%$) was also not significantly different (Wilcoxon paired-sample test: $T=21$, $N=10$, $P=0.59$). Hence, persisters not only performed the majority of the transports following a small disturbance but also contributed an equivalent amount, even when the disturbance was accompanied by a change in the quality of the nests.

We examined the manner in which persisters modified their transport behaviour in terms of their individual latency to transport on encountering a disturbance. The delay between any two random transports by the same persister was called the random latency. Similarly, the delay for the very first transport following an initial visit by a persister to the new nest was termed the initial latency. In addition, the latency for the very first transport by a persister after manipulation was termed its manipulation latency. The initial latency of a persister in the flexibility experiment (10.94 ± 7.00 min) was not significantly different from that of a persister in the control experiment (11.72 ± 14.30 ; Mann–Whitney U -test: $U=510.50$, $N_1=34$, $N_2=36$, $P=0.23$, Fig. 5) as expected. Similarly, the random latency for a persister in the flexibility experiment (1.33 ± 1.77 min) was not significantly different from that in the control experiment (1.53 ± 2.25 min; Mann–Whitney U -test: $U=1463.50$, $N_1=49$, $N_2=64$, $P=0.52$, Fig. 5). However, the manipulation latency for a persister in the flexibility experiment (8.57 ± 5.20 min) was significantly greater than that for a persister in the control experiment (3.98 ± 3.99 min; Mann–Whitney U -test: $U=558.00$, $N_1=49$, $N_2=64$, $P<0.01$, Fig. 5).

The manipulation latency for a persister in the control experiment was significantly higher than its random latency (Mann–Whitney U -test: $U=991.00$, $N_1=64$, $N_2=64$, $P<0.01$, Fig. 5) and significantly lower than the initial latency (Mann–Whitney U -test: $U=723.00$, $N_1=64$, $N_2=36$, $P<0.01$, Fig. 5) showing that mere physical

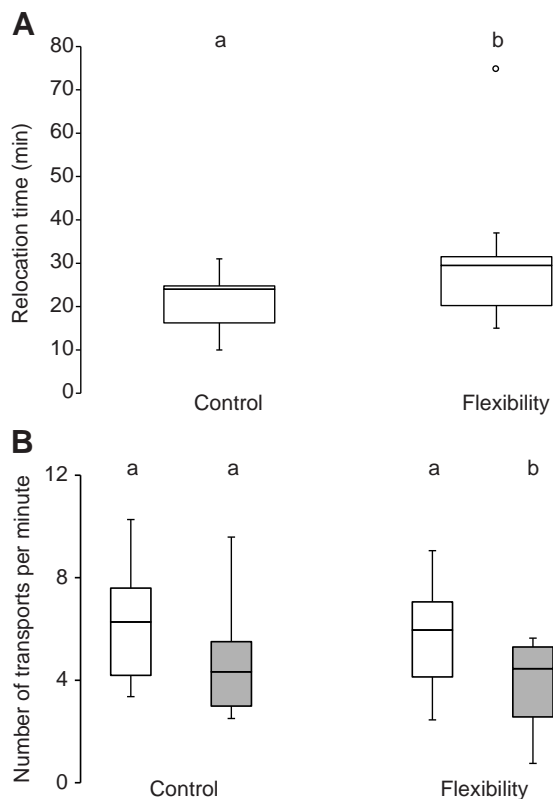


Fig. 3. Relocation time and rate of transportation. (A) Total relocation time across 10 replicates each for the control and the flexibility experiments is plotted in this box and whisker plot. (B) Rate of transportation – the number of transports per minute in the pre-manipulation phase (white boxes) and the post-manipulation phase (hatched boxes) – plotted across 10 replicates each for the control and the flexibility experiments. Box plot description as in Fig. 2. Boxes with same letter are not significantly different, Wilcoxon paired-sample test ($P>0.05$).

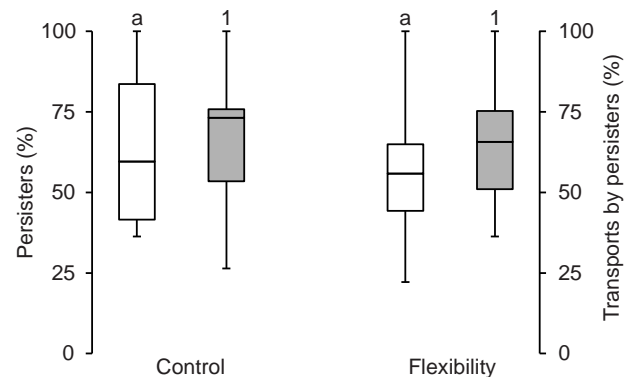


Fig. 4. Post-manipulation phase: percentage of persisters and their contribution. The percentage of persisters (white boxes) is plotted on the primary y-axis and the percentage of transports that they performed (hatched boxes) is plotted on the secondary y-axis across 10 replicates each for the post-manipulation phase of the control and the flexibility experiments. Box plot description as in Fig. 2. Boxes with same letter or number are not significantly different, Wilcoxon paired-sample test ($P>0.05$).

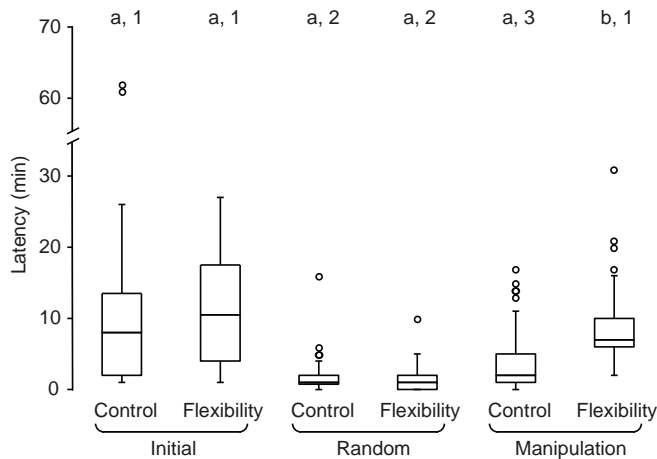


Fig. 5. Transport latency of the persisters. The initial latency ($N_1=34$, $N_2=36$), random latency ($N_1=49$, $N_2=64$) and manipulation latency ($N_1=49$, $N_2=64$) of persisters who performed transports in the control and flexibility experiments. Box plot description is the same as in Fig. 2. Within each of the three categories comparisons across control and flexibility experiments are represented using letters; boxes labelled with the same letters are not significantly different, Mann–Whitney U -test ($P>0.05$). Comparisons carried out across the three categories within control and flexibility experiments are represented using numbers; boxes labelled with the same number are not significantly different, Mann–Whitney U -test ($P>0.05$).

disturbance made the transporters pause briefly before resuming transport. Interestingly, the manipulation latency for a persister in the flexibility experiment was not only significantly higher than its random latency (Mann–Whitney U -test: $U=74.00$, $N_1=49$, $N_2=49$, $P<0.01$, Fig. 5) but also comparable to the initial latency (Mann–Whitney U -test: $U=695.50$, $N_1=49$, $N_2=34$, $P=0.20$, Fig. 5). This shows that physical disturbance accompanied by a change in target nest made transporters pause their transport and re-evaluate the situation afresh before initiating transport to the target nest.

DISCUSSION

When colonies of *Diacamma indicum* were faced with a change in the target nest after about half of the colony had been transported, they adapted by relocating to the new target in 100% of the cases and not a single case of colony splitting was observed. In a different study on *Temnothorax albipennis*, involving multiple target options which increased the degree of complexity for the ants, colony splitting was observed. When the preferred nest was degraded after relocation had been initiated, only 15% of the colonies were able to switch their choice and occupy the new target nest and 22% of the colonies split between the available options (Franks et al., 2007). In a study on *T. albipennis* dealing with quorum sensing, it was found that these ants do not switch back from carrying to tandem running (Pratt, 2005). This indicates that *T. albipennis* transporters, having assessed the quorum and made the switch to carrying, possibly stop evaluating the site, at least until all the carrying is complete. *Apis mellifera* swarms have only occasionally been observed to display uncertainty after take-off (Lindauer, 1957), because in the majority of cases they arrive at a consensus before movement *en masse* (Camazine et al., 1999; Visscher, 2007). In the current study, not only did the colonies show remarkable flexibility, they also adapted to this change in the target nest without a significant increase in the number of transports. This was achieved by transporters who reassessed the situation and switched their initiation and termination sites. Additional studies that verify these findings in the presence of multiple target options as well as in the natural habitat of these ants

will allow us to examine the degree of flexibility in their decisions and whether the need to be flexible is universal.

Studies at the individual level (Chittka and Dyer, 2003), as well as at the group level (Chittka et al., 2009; Franks et al., 2009), on decision-making in animals have documented the trade-off between accuracy and speed. Accuracy can be considered in terms of erroneous transports and colony cohesion whereas speed can be interpreted in terms of transportation time, in the context of colony relocation. Fast decisions lead to lower degrees of cohesion while slow decisions allow higher degrees of cohesion in *Temnothorax* species (Franks et al., 2013). In experiments with multiple options when colonies encountered a shift in the target nest, 6–25% of the colonies were unable to decide upon one option and reunite there, even after extended periods of time (Franks et al., 2006, 2007; Pratt, 2005). In the current experiments with a single option when *D. indicum* colonies encountered a shift in the target nest, 100% of the colonies reunited in the target nest with negligible erroneous transports. However, this high degree of accuracy was achieved at the cost of additional relocation time. Colonies took 50% more time to complete their relocation when the target nest was changed. This extra time can prove to be an important component because the colony would be exposed to the elements in this period. The balance between accuracy and speed of decision making should be examined in greater detail in *D. indicum* by varying both the nest options and the degree of stress applied to the colonies in future studies.

Analysis of transport latency revealed that even a slight disturbance to the new nest caused transporters to pause briefly. When this disturbance was accompanied by a change in the target nest they reinitiated transportation after the same latency as at the beginning of the relocation. This was because the transporters made additional exploration trips of the arena and presumably looked for available options. Interestingly, the post-manipulation latency of these transporters were comparable to their initial latency, despite the fact that in the former case 50% of the colony members were present in the target nest. This indicated that having a quorum at a site perhaps does not influence the transporter's latency. There is already proof that quorum threshold values vary depending on the stress faced by the colony. When colonies relocated from intact nests, the threshold values were as high as 17.5 ants whereas emergency relocations had threshold values as low as 8 ants (Dornhaus et al., 2004). We can envisage several situations in which fulfilling the quorum threshold alone does not make a new nest acceptable: for example, cases where colonies move to improve the quality of their nest or into temporary shelters before moving into a final nest site. This has been highlighted through studies of colony relocation in the lab (Dornhaus et al., 2004; Franks et al., 2008) as well as in nature (Kaur et al., 2012). Nevertheless, studies across a broader range of social insects are required to clarify this point.

It should be reiterated that *D. indicum* uses tandem running to transport all the adult members of the colony, carrying only males and brood into the new nest. Even though tandem running itself is considered a primitive method of recruitment (Hölldobler and Wilson, 1990; Möglich et al., 1974), we saw that tandem leaders do not stop assessing their destination, but continue to evaluate the site throughout the transportation process. Thus, they are able to incorporate assessment of their target at every step (each transport) enabling the colony to be flexible in their selection of a new nest. In an environment that is prone to change or where complete information is not guaranteed, such flexibility in decision making would enable organisms to readapt with minimal cost.

MATERIALS AND METHODS

Experimental setup

All our experiments complied with the regulations for animal care in India. Ten colonies of *Diacamma indicum* Santschi 1920 were collected from Mohanpur (Nadia district, West Bengal, India, 22°56'N, 88°31'E) over a period of 3 months starting in September 2012. Colonies consisted of 65.0±13.15 adult females (mean±s.d., range 47–89), 17.1±20.08 pupae (range 0–59), 12.2±10.44 larvae (range 0–33), 36.1±21.52 eggs (range 17–84) and 0.4±0.97 males (range 0–3). Every ant was uniquely marked with enamel paint (Testors, Rockford, IL, USA) for individual identification and every transport was documented and video recorded throughout the relocation experiments. In all colonies, the gamergate was identified by the presence of gemma. Each colony was maintained in an inverted perforated Petri dish (termed the 'shelter', 5.8 cm in diameter and 1 cm in height). The shelter was placed at the centre of one of the shorter sides of the experimental arena, which comprised a plastic box with dimensions 30×20×7 cm and a plaster of Paris base (Fig. 1). The colonies were housed in the lab and were provided *ad libitum* water and ant cake (Hölldobler and Wilson, 1994). Each colony was subject to two different types of relocation experiments in a random order, thus totalling 20 experiments. 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 was initiated or terminated. Colonies were allowed to settle in for a minimum of 20 h between relocations.

Relocation experiments

The start of all experiments involved removal of the shelter from the old nest and the placement of a new shelter at the opposite side of the arena. Initially, few ants explored the arena for a probable nesting site before initiating transport of colony members. While adults were transported by tandem runs, brood and males were carried by followers of tandem runs or by individual leaders to the new nest. When ~45–55% of the adults in a colony had been transported to the new nest, either one of the following two manipulations was conducted. In the first set – the control experiment – the petri plate that acted as a shelter in the new nest was momentarily lifted and replaced to cause a physical disturbance. This procedure simulated the slight disturbance that would occur during manipulation in the flexibility experiment. Note that this did not cause a change in the location or the quality of the target nest. In the second set – the flexibility experiment – the shelter from the new nest was permanently removed and the shelter for the old nest was replaced to simulate a manipulation that caused a reversal in the nest quality. Hence the new nest became inhospitable whereas the old nest became hospitable and thus the target nest. The target nest was defined as the nest that had a clear entrance and a roof. In this manner, every relocation at any given time had a single target nest. Each experiment had two phases: a pre-manipulation phase and a post-manipulation phase. By definition, the first transportation of a colony member from the old nest to the new nest initiated the pre-manipulation phase of the experiment and this phase lasted until the manipulation was performed. The manipulation itself spanned about 10 s. The post-manipulation phase started right after placing the target nest and lasted until the end of the relocation. Total relocation time was defined as the sum of the duration of pre-manipulation and post-manipulation phases. After transportation of all colony members and brood from the old nest, the absence of subsequent transports for a period of at least 1 h formed the working definition for the end of a relocation. Video recording from the start of the experiment till the end of a relocation, also enabled us to record all the visits by leaders before and after the relocation. This allowed us to cross-check entries made during real-time observations.

In the pre-manipulation phase, transports towards the new nest were considered to be in the right direction whereas in the post-manipulation phase transports towards the target nest were considered to be in the right direction. Transports that terminated outside the target nest were labelled erroneous. An error index was calculated for every relocation separately. This was computed by dividing the number of erroneous transports by the total number of transports in a given relocation. The experimental design adopted, allowed us to examine the flexibility of the relocation process.

More specifically, we were able to investigate whether ants can evaluate their environment in a continuous manner and alter their decisions to best suit the conditions or whether they adhere to a decision once taken. If in fact transporters change their decision, how long do they take to do so?

A total of 1359 transports by 262 transporters were observed and documented in 20 experiments, spanning over 944 min of video recorded colony relocation. Unless otherwise stated, the mean and s.d. of the different parameters are presented. SPSS version 16.0 (SPSS, Inc., Chicago, IL) was used to conduct non-parametric statistical tests such as 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.

Acknowledgements

We thank Guha Dharmarajan for comments on K.A.'s Master's thesis, which helped during the writing of this manuscript.

Competing interests

The authors declare no competing or financial interests.

Author contributions

K.A. carried out the behavioural observations. A.S. and K.A. designed the experiments, carried out data analyses and wrote the manuscript.

Funding

K.A. conducted this research project as part of his Master's thesis and was funded by the Innovation in Science Pursuit for Inspired Research (INSPIRE) programme. K.A. is currently funded by the University Grants Commission, Government of India. Experiments were conducted through the research grant received by A.S. from Department of Science and Technology grant (SR/FT/LS-179/2009), Government of India.

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