

Influence of colony associated factors on nest selection in an Indian queenless ant

RAJBIR KAUR and SUMANA ANNAGIRI Behaviour & Ecology Lab, Department of Biological Sciences, Indian Institute of Science Education and Research (IISER) Kolkata, Mohanpur, India

Abstract. 1. Organisms face the difficult task of selecting an optimal new nest from the available options during relocation. Studies on honeybees and ants in their natural habitat indicate that scouts encounter multiple options that vary in their physical and biotic characteristics.

2. Architectural features, location, odour, and the presence of nest mates impact their choice of nest site selection. In order to examine the influence of diverse parameters on final nest site selection we conducted choice experiments on ants in the context of relocation.

3. After controlling for any influence by physical characteristics, we found that the presence of brood, adults, and colony odour acted as attractants with more colonies relocating into these new nests than expected by chance alone. In contrast, the presence of a reproductive female, or familiarity of location had no influence on the choice. New nests containing dead ants evoked cleaning responses from scouts, which may interfere with relocation into these nests.

4. Even although colonies consist of hundreds of adults and brood, colony integrity was maintained in 98.7% of colonies. Furthermore, we found that none of the eight studied colonies relocated when faced with minor flooding in their natural habitat, indicating that the cost of relocation is non-trivial and that this species is capable of minor damage repairs.

5. These observations highlight the complexity of relocation in general, allow the characterisation of desirable nest attributes in this species, and highlight the need for similar exploration in other social insects.

Key words. *Diacamma indicum*, gamergate, relocation, tandem running.

Introduction

Many animals, including social insects, dwell in nests. Nests are a physical space where inhabitants live, reproduce, rear offspring, and gain protection from harsh environments and predators (Hansell, 1993). Many ground-dwelling ants are known to use pre-existing holes for nesting and they have the capability to remodel their dwelling to suit their changing requirements (Hölldobler & Wilson, 1990; Andrade *et al.*, 2007; Kaur *et al.*, 2012; Miranda *et al.*, 2012). Forces such as physical disturbance, changes in microclimatic conditions, increased predation, competition, and colony reproduction are known to cause

relocation in insect societies (Hölldobler & Wilson, 1990; McGlynn, 2012). During relocation, scouts find multiple options in the field (Visscher, 2007; Seeley, 2010; Gilbert *et al.*, 2011; Evison *et al.*, 2012; Kaur *et al.*, 2012; McGlynn, 2012) and choosing the optimal new nest among these options then becomes an important task. Variation among these options in their physical and biotic features makes the process of arriving at a decision complicated. A range of physical features, such as nest entrance, height, light penetration, cavity size, and other colony associated features like the presence of reproductives, workers or brood, species odour, or even being an old location (Dahbi *et al.*, 2008) may influence the choice of their new dwelling.

To date, few experiments have been conducted to examine the role played by these factors. These previous studies that have been conducted have explored the role of physical attributes associated with available options. In a serially monodomous ant species *Aphaenogaster araneoides* Emery, nest odour is known

Correspondence: Sumana Annagiri, Behaviour & Ecology Lab, Department of Biological Sciences, Indian Institute of Science Education and Research (IISER) Kolkata, Mohanpur 741246, West Bengal, India. E-mail: sumana@iiserkol.ac.in

to influence site selection (McGlynn, 2007, 2010), whereas in *Eciton burchellii* Westwood and *Formica neorufibarbis* Emery temperature and relative humidity play a major role (McCaffrey & Galen, 2011; Soare *et al.*, 2011). In honey bees, the preferred nest site selection involves the judgement of many nest parameters including volume, dryness, draftiness, and the presence of other combs within the chamber. In addition, the direction, the height from the ground, and position of the nest entrance are also known to influence nest selection (Seeley, 2010). Different physical attributes of the nest such as floor area, light penetrance, cavity thickness, and the size of the entrance have been found to influence selection of new nests in two species belonging to the genus *Temnothorax* (Pratt & Pierce, 2001; Franks, 2003). Based on these studies, the ideal nest architectural attributes for *Temnothorax* spp. have been deciphered under lab conditions. A dark, thick-walled cavity with a narrow entrance are the most preferred qualities in their nests (Franks, 2003; Pratt, 2005). On the basis of this information researchers were able to design nests of different quality and examine two important aspects of relocation. First, the influence of various factors such as distance, prior experience of individual scouts, and that of the colony (Dornhaus *et al.*, 2004; Franks *et al.*, 2008; Healey & Pratt, 2008; Robinson *et al.*, 2009), and second, the processes involved in collective decision making were explored. It has been shown that these ants were able to choose the best available option using a decentralised system involving recruitment latency and quorum sensing without having individual scouts directly compare alternative sites (Mallon *et al.*, 2001; Franks *et al.*, 2002; Pratt *et al.*, 2002).

Very few previous studies have investigated the role of factors other than physical attributes of the nest. Franks *et al.* (2005) found that the presence of dead ants at a potential new nest had a repelling effect. In one other study on a paper wasp, the presence of brood, queen, and adult members were explored in the context of site selection. Given that in paper wasps brood is lodged inside cells, it was not possible to tease apart the influence of physical, chemical, and biological components in their selection (Kumano & Kasuya, 2001). As there are very few field relocation studies, the importance of colony associated factors in natural relocation and its role in nest-site selection have barely been explored (McGlynn, 2007). The only field relocation data of which we are aware, that of a ponerine ant *Diacamma indicum* suggests that during relocation a colony splits and occupies as many as 2–6 different locations but these sub-colonies then merge into a single final nest (Kaur *et al.*, 2012). However, this study had no quantitative or qualitative information on the temporary or final nest. Nevertheless, two important observations were the differential distribution of colony components, i.e. adult and brood among different nest sites during the relocation process, and that the final nest site occupied by the colony was always a pre-existing ground hole. The latter leads to the hypothesis that *D. indicum* reuses nests of its own, conspecific or other ground-dwelling organisms. Thus scouts have to contrast the cost incurred in searching for the ideal nest, and then compare the temporary sites in terms of colony associated and physical characteristics, before arriving at a decision on the final nest site. Given that these ground-dwelling ants presumably have the potential to modify the architecture

component somewhat more than cavity dwelling rock ants or honeybees the scouts would be facing a very complex scenario indeed.

Diacamma indicum, a primitively eusocial ant, lacks a morphologically distinct queen, but one mated worker functions as a reproductive female and is called the gamergate (Peeters & Higashi, 1989; Peeters & Billen, 1991). Nest relocation begins with a few individuals looking for a suitable nest site. As part of relocation scouts need to transport the gamergate, female workers, and males (adults of the colony); egg, larvae, and pupae (brood of the colony), and any stored food to the new nest. During colony relocation, *D. indicum* employs tandem running (Hölldobler & Wilson, 1990), a mechanism by which one ant leads another colony member who in turn maintains tactile contact with the tandem leader by means of her antennae and move from one place to other (Hölldobler & Wilson, 1990; Kaur *et al.*, 2012; Sumana & Sona, 2012, 2013).

The costs associated with relocation, including the associated vulnerability of colony integrity and brood, are expected to play an important part on the decision to relocate. If relocation costs are relatively low, or if these ants are incapable of minor damage repair, we would expect colonies to relocate on being subjected to small disturbances. In the present study we first explored if *D. indicum* colonies move whenever there is a slight disturbance to their colony in its natural habitat. By mimicking the effects of rainfall using an artificial method we examined the impacts of partial flooding and observed nest occupancy for the next 24 h. In the second set of experiments we went on to examine the influence of different colony associated factors on nesting decisions. Adults and brood and the reproductive individual together with colony odour were examined using choice relocation experiments.

Materials and methods

In this study we used 66 colonies of *D. indicum* from Mohanpur (Nadia district, West Bengal, India, 22°56'N, 88°31'E) from May 2011 to May 2013. These colonies were subjected to one of the following eight series of experiments as described below.

Partial dislodging experiment

Eight colonies experienced partial dislodging from their original nest in their natural habitat. This was carried out by pouring water inside the nest entrance. This caused many adults from the colony to emerge and some of them were carrying brood in their mandibles. After a minimum of 10 adults carrying brood had emerged we stopped pouring water inside the nest and followed the actions of the adults that had emerged. In addition we checked the nest for the next 24 h and confirmed nest occupancy.

A series of seven other relocation experiments were conducted using 58 colonies housed in the laboratory in a plastic box (28.5 × 21.5 × 12 cm³) with a plaster of Paris base, which contained a Petri plate (diameter 9 cm) also covered in plaster of Paris which acted as its nest. This nest was covered with a watch glass and red cellophane paper in order to make the inside dark

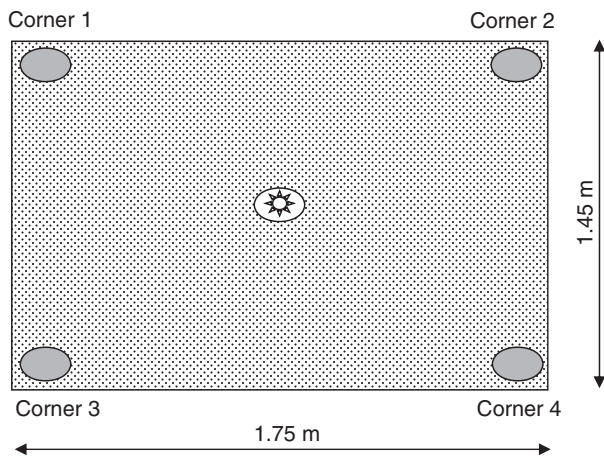


Fig. 1. Experimental arena: top view of the experimental set-up in the arena (not to scale) with a new nest at each of the four corners (grey) and the old nest with the focal colony at the centre (white). All new nests had a glass cover on top, while the same was taken off from the old nest at the beginning of the experiment. On top of the centre nest, at a distance of 10 inches, light source was provided, depicted by ☀.

(Kaur *et al.*, 2012). Colonies received water, ant food (Hölldobler & Wilson, 1994) daily and were occasionally supplied with termites. In order to examine the influence of different colony associated factors on nest selection, relocation experiments were conducted in the arena ($1.4 \times 1.7 \text{ m}^2$) inside the laboratory. The test colony was placed at the centre of the arena and four alternate blank nests, with identical physical features such as plaster of Paris base, nest cover, and entrance, were placed at the corners (see schematic representation in Fig. 1). Colony relocation was initiated by removing the nest cover exposing the nest to light and air current. The test colony was allowed to choose their new nest from these four options. Under the null hypothesis each of the four options would have equal probability of occupation by the colony. Depending on the experiment we introduced a colony associated factor into one or more of these blank nests. Once all the brood items were transferred to a single nest along with the majority of the colony (excluding scouts who kept exploring arena) that destination was recorded as the final choice and the experiment was ended. The time at which each nest option was discovered and the colony's final nest choice were recorded in every experiment. Among the four locations (four corners of the arena), the number of times each location was occupied by any of the colony associated factors did not differ significantly ($\chi^2 = 0.9$, d.f. = 3, $P = 0.81$). Binomial analysis was performed for contrasting a factor with blank options and/or two factors. Based on the number of sites with factors the expected probabilities were calculated and used for the analysis (Table 1). All statistical analysis was carried out using statistiXL1.10.

Brood influence. All brood items (eggs, larvae, and pupae) were separated from the test colony and placed in a blank nest at a randomly chosen corner of the arena. Twelve colonies were tested under this regime and thus under the null hypothesis we

expect three colonies to relocate to the brood containing nest by chance alone.

Adult influence. Two sets of experiments were conducted to delineate the influence of the gamergate and workers. In the first set of relocations ($n = 12$), 10% of the adults were placed in one blank nest whereas another blank nest received 10% of the adults together with the gamergate of the colony. The colony with 80% of the adults and all the brood in their old nest was placed at the centre of the arena and allowed to select their new dwelling. As two nests would be with nest mates whereas other two would be blank, the number of colonies that are expected to relocate to a new nest containing their colony mates would be 6/12. However, if the gamergate has any influence on the colony's choice of new nest we would expect a difference between adult and adults with gamergate, the latter to be chosen more often than expected by chance between these two options.

In the second set of experiments, the gamergate of the colony was secured by tethering her with a thread to a blank nest whereas a second blank nest contained 10% of the colony members. Both of these nests were placed at randomly selected corners of the arena. This experiment was replicated using 10 colonies (Table 1). In this experiment, the number of colonies that would move to the new nest with the tethered gamergate by chance alone would be 2.5/10.

Brood versus adult. All the brood were separated from the test colony ($n = 12$) and kept in a blank nest whereas a second blank nest received 10% of the colony and both of these nests were placed randomly in the arena. This allowed us to examine the relative influence of these two colony associated factors (Table 1). In this comparative experiment, the number of colonies that would move to the either of colony associated factors by chance alone would be 3/12.

Influence of dead ants. In order to check the influence of dead conspecifics within a nest site we placed 15 conspecific dead ants in a blank nest at a randomly selected corner ($n = 8$). The number of colonies expected to move to the nest with dead ants by chance alone would be 2/8 (Table 1).

Influence of nest location and nest odours. The test colony was placed in the arena for 24 h to allow the ants to familiarise themselves with the arena, after which the colony, together with its original nest (minimum 7 day old) was moved into a plastic box. Within this plastic box the colony was driven to relocate into a new nest. The used old nest was placed at one of the randomly chosen corners. Subsequently the test colony was allowed to choose between the four options, one represents the old location, the other self-odour and two blank nests. For the old location the expected probability was 2.5/10. Similarly, for the self-odour choice test only one among the four available nest option hold the colony cue and hence the expected probability for selecting the already used nest by chance alone was taken as 2.5/10.

Table 1. The influence of colony associated factors on nest site selection.

Colony component	<i>N</i>	Nest options	Exp	Obs	χ^2	<i>P</i> -value
Brood	12	1-brood; 3-blank	3/12	8/12	11.11	0.001
Adult	12	1-10% adult & 1-10% adult with gamergate; 2-blank	6/12	11/12	8.3	0.004
	11	1-10% adult; 1-10% adult with gamergate	5.5/11	7/11	0.82	0.37
	10	1-10% adult; 1-tethered gamergate; 2-blank	2.5/10*	3/10	0.13	0.72
	12	1-10% adult & 1-brood; 2-blank	5.5/11 [†]	4/11	0.82	0.37
	8	1-dead ants; 3-blank	2/8	2/8	0.0	1.0
Old location and nest odour-self	10	1-old location 3-new location	2.5/10	2/10	0.13	0.72
	10	1-old nest; 3-blank	2.5/10	6/10	6.53	0.01
Nest odour-conspecific	12	1-conspecific nest odour; 3-blank	3/12	8/12	11.11	0.001

*Analysed w.r.t. gamergate, five colonies relocated to nest with 10% adult and two to blank.

[†]Number of colonies relocated to either adult or brood nest. Out of 12, 7 relocated to brood nest and 1 to blank.

Various choice experiments that were conducted are listed. *N* = sample size, Obs = observed number of colonies relocating into a given option. Exp = number of colonies expected to relocate by chance alone based on the experimental set up (indicated in bold). χ^2 values and *P*-value from the Binomial analysis is given in the last two columns for each comparison.

Influence of conspecific odour. Six colonies each were collected from two different locations which were separated from each other by approximately 2183 m. These colonies were maintained in the laboratory for 7 days. On the eighth day, a colony from one location was driven to move into a new nest inside the plastic box and its 7-day-old nest was placed at a randomly selected corner. The test colony collected from the alternate location was placed at the centre of the arena and allowed to choose its new nest. After relocation the 7-day-old nest of the test colony was used as a conspecific odour choice for the former colony. In this manner six replicates were conducted (12 relocations). Only one out of the four available options held the cue for the used nest and hence the expected probability for the nest with conspecific odour to be chosen as a final site by chance alone was taken as 3/12.

Results

Nest fidelity

All eight colonies that experienced partial dislodging remained in their original nest site after 24 h. Adults that emerged from three of these colonies initiated tandem running towards other locations but later showed tandem running back to their original nest.

Influence of colony associated factors

In the 76 relocations conducted there were 304 options and scouts explored 288 of them. Of the 16 undiscovered nests,

14 were blank nests i.e. did not contain any colony associated factors. The nests with colony associated factors were discovered earlier than blank nests. The average discovery time of nests with colony associated factors was 12.3 ± 11.1 min which was significantly shorter than blank new nests (20.1 ± 17.9 min; Wilcoxon's paired sample test: $T = 3.9$, $N = 73$, $P = 0.0001$). There was no difference between the time taken to discover nests that contained adult and brood as compared with colony odour and dead ants (Mann-Whitney *U*-test: $U = 735.5$, d.f._{1,2} = 46, 29, $P = 0.46$).

The presence of brood had a positive influence on nest selection. Nests containing brood were chosen significantly more than expected by chance alone (Table 1). Colony members who discovered a nest with brood items were seen handling the brood and collecting them into a single pile. In the cases where the colony did not move to the nest that contained the brood (4/12) they shifted the brood items into the nest of their choice. The presence of adult colony members at one of the nests also had a significant positive influence on nest selection. Colony members that were present at the start of the relocation in the 10% adults or adults with gamergate nest sites were not seen initiating tandem running to their site but were seen walking around in close vicinity to the nest in general. Of the 12 replicates, 11 moved in with their colony mates (Table 1). The presence of the gamergate did not impact nest site selection. In the first set of relocations where the gamergate was free to move, there was no significant difference between the numbers of the colonies that moved to the nest that contained the gamergate (7/11) than expected by

chance alone (Table 1). Experiments with the tethered gamergate also confirmed these results. Only 3 of 10 colonies moved to the nest that contained the tethered gamergate, which was not significantly different than expected (Table 1). Tandem leaders were seen inviting the gamergate and other colony members to tandem run to the final nest and were successful in transferring other colony members. In the third set of relocation experiments where colonies faced the choice between adults and brood as two different new nest options, we found no significant difference (Table 1). Combined, however, there was a clear preference for brood or adult nests. Eleven colonies chose either the nest with adults (7) or with brood (4) as their final nest and one chose the blank nests (Binomial test: $\chi^2 = 8.3$, $P = 0.004$). In one out of the eight cases the site with dead ants was not discovered. In six out of seven cases scouts were seen clearing the nest and in four out of seven cases scouts initiated tandem runs to this site whereas only in two cases the test colony relocated to the site (Table 1). Of the two colonies that relocated to a dead ant nest, one showed a 50-50 split between this nest and a blank nest, and tandem running continued in both directions for an extended period of time.

The odour of their own colony acted as an attractant as significantly more colonies relocated into their old nest. In contrast, the old location did not influence nest choice, only 2 of the 10 colonies tested moved into the nest that was located at the same position as their old nest (Table 1). Odour from conspecific nests also acted as an attractant and significantly more colonies, 8 of the 12 tested, relocated into a nest that was already used by a conspecific (Table 1).

To summarise, we found that in the 76 relocations conducted, 75 colonies were relocated to a single new nest and in one case tandem running continued between two sites occupied by the colony until the end of the observation period. In the experiment series where the gamergate was tied and unable to move, all other members relocated to a single new nest. Among the colony factors studied presence of brood, colony members, and chemical cues of already used nests (self or conspecific) had a positive influence on nest-site selection.

Discussion

Previous nest-site selection studies have focused on nest architecture or have tried to understand the collective decision-making process in social insect colonies (Hölldobler & Wilson, 1990; Visscher, 2007; McGlynn, 2012). Neither of these contexts were the focus of this study. In the present study we investigated the role of colony associated factors in nest-site selection while keeping physical features of nests constant. Colony associated factors such as brood, colony members, and chemical cues that indicate its recent usage by either self or a conspecific colony were examined. Given that all the physical features in terms of nest structure and environment were held constant, the dynamics involved in selection were solely as a result of colony associated factors. It is noteworthy that the presence of brood and dead ants induced the scouts to reconsider their task. They stopped exploring the arena and did not initiate tandem running but started collecting the brood into a single pile in the first case and they cleared the nest of dead ants in the latter case. Unlike *T. albipennis* that avoided nests

containing dead conspecific, *D. indicum* showed a different reaction (Franks *et al.*, 2005). Scouts seemed to accept nests with dead ants but the time taken in preparing this nest (i.e. clearing dead ants) impacted its selection as the final site. The temporal dynamics of the relocation process was such that scouts showing tandem running to other sites had successfully transferred most of the colony members by the time the nest with dead ants was ready to receive nest mates.

The gamergate did not influence the choice of final nest. In cases where she was tethered and the colony selected an alternate nest, tandem leaders continued to put their efforts in releasing her. In *T. rugatulus* alarm pheromone released by the tethered individual repels the selection of that site (Sasaki *et al.*, 2014). We found that there was no significant difference between the number of times the site containing the tethered gamergate and free gamergate were chosen as the final nest. This indicates that the alarm pheromone is unlikely to play a role in this context. However, direct examination of alarm pheromone production especially among workers would be required to confirm this. In the scenario when the gamergate was present untethered she was relocated like any other worker to the selected nest site by tandem running. *Diacamma indicum* lacks morphologically differentiated queens but has functionally distinct gamergates like other ant species belonging to the genus *Diacamma* (Ramaswamy *et al.*, 2004) and the investment during development of a gamergate would be similar to any other worker in the colony. The reason why colonies did not necessarily choose nests that contained the gamergate even when she was tethered could be because of the fact that any newly enclosed worker can potentially become the gamergate. This further reinforces our previous finding that the gamergate has a very small role to play in colony relocation (Kaur *et al.*, 2012). We found that both adult and brood, the present and future workforce of the colony, along with chemical cues of the species positively influence nest-site selection. Interestingly adults and brood had a similar degree of influence.

Diacamma indicum colonies that experienced water stress in their natural habitat remained in their original nest in all of the cases. Even although three colonies initiated tandem running to other temporary sites, they were seen tandem running in the reverse direction bringing back colony members from temporary site(s) to the original nest after some time, presumably because the stress had reduced. This shows that *D. indicum* display fidelity to their nest and do not move as soon as there is a slight disturbance. It also shows the flexibility of tandem leaders who change their initiation and destination site based on several parameters, similar to what was observed in our previous study (Kaur *et al.*, 2012). In this particular case, presumably the cost of relocation outweighed the cost of remodelling their nest after the water-induced damage. Ground-dwelling ants possibly have a higher degree of flexibility as compared with cavity-dwelling honeybees or social wasps as soil would be more amicable to digging and restructuring.

The only other study that looked into the influence of colony members and brood has been carried out in a primitively eusocial wasp, *Polistes chinensis antennalis* (Fabricius). Here, the presence of the queen and workers played no role whereas the presence of the brood strongly influenced the decision of nest

maintenance. Further, when the brood was presented in two separate locations the colony experienced fission (Kumano & Kasuya, 2001). Given that brood items are lodged in cells and cannot be moved in the case of wasps it is not surprising that they choose to maintain nests that contained some brood even at the cost of colony division. However in *D. indicum* where both brood and adult are available for transport we found that they had a comparable positive influence on nest site selection, thus avoiding colony division.

Many species of ants show serial monodomy or are polydomous and maintains many nests (McGlynn, 2012). *Cataglyphis Iberica* (Emery) under attack migrate to previously used nests (Dahbi *et al.*, 2008), whereas *A. araneoides* emigrate once a week and maintain about 2–6 nests over a month. The latter species is known to avoid returning to a nest if it retained a colony odour (McGlynn *et al.*, 2004; McGlynn, 2010). Unoccupied nests were thought to retain the odour of previous users for an extended period of time and as nest architecture affects gas exchange, a gradient may exist even in relatively shallow nests (Tschinkel, 2004). Whether *D. indicum* indulges in serial monodomy has not been directly explored, although results of field study data Kaur *et al.* (2012) suggest that they do not maintain additional nests. As *D. indicum* occupies pre-existing ground holes it opens up the possibility of reuse of former nest or empty conspecific nests. In the present experiment, both self and conspecific chemical cues had a positive influence. This could be because of the ants' inability to distinguish self and conspecific chemical cues, which is unlikely, but would require further exploration to confirm.

Multiple nests open up an opportunity to compare and collect information about all options. The trade-off between collecting information, comparison, and leaving the colony exposed to different risks posed by predators and environment is balanced by scouts in the field every time a colony relocates. The manner in which individual scouts achieve this balance would be fascinating to explore. The present study is an essential pre-requisite for this exploration. In nature relocation dynamics are complex and many facets of this essential component in the life history of these superorganisms remain to be understood.

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