

Studies on colony relocation in the Indian queenless ant *Diacamma indicum*

Animals that live in nests often face challenges like harsh environmental conditions, increased competition and severe predatory pressure¹. In response to these stresses they relocate into new nests². This movement is particularly complex in the case of ants as hundreds of colony members, immature young and stored resources need to be transferred. The dynamics of ant emigration remains to be thoroughly explored. However, it is understood that the route to the new site is indicated by pheromone trails in several species, whereas a few species use carrying or tandem running to transfer their nestmates to the new nest. Tandem running was first described by Adlerz³, and is the behaviour in which one ant follows another while maintaining physical contact. This behaviour is used in the context of relocation and recruitment of colony members for nest defence, raiding and foraging².

Diacamma indicum is a queenless ponerine ant that has been recorded from East India, South India and Sri Lanka. They form colonies in which egg laying is performed by a worker called gamergate. The only information known about these ants is that their genetic variability is lower than some other sympatric species, and that they have a species-specific chromosome number^{4,5}. In the present study, we examine the mechanism by which relocation is conducted by *D. indicum* colonies in two different contexts.

Two types of relocation experiments were carried out – short distance relocation (SDR) and long distance relocation

(LDR), in which ants relocated over 30 and 183 cm respectively. Twelve colonies relocated over short distance with all their adults and brood (pupae 18.9 ± 12.2 [mean \pm standard deviation], larvae 12.3 ± 8.9 and eggs 20.6 ± 11.1) into a shelter. While in LDR another 12 colonies relocated with their adults and brood (pupae 15.8 ± 9.1 , larvae 8.8 ± 5.6 and eggs 24.1 ± 16.2) into an identical nest placed at the end of a wooden bridge. The number of adults in SDR (77.2 ± 40) and LDR (89.1 ± 26.6) was not significantly different from each other (Mann Whitney *U* test, $U = 85.5$, $df1 = 12$, $df2 = 12$, $P = 0.48$).

All the 24 colonies of *D. indicum* used in the relocation experiment were collected between July 2009 and November 2010 in Mohanpur, Nadia District, West Bengal, India ($22^{\circ}56'N$, $88^{\circ}31'E$) and housed in laboratory with *ad libitum* honey, water and termites. All individuals were marked with unique combinations of enamel paint colours (Testors, Rockford, IL, USA) to allow individual identification. The process by which ants moved into the new nest was recorded by both direct observations and using a video camera. Focal observations were carried out on tandem running and the identity of the tandem leader, follower, the time and location of initiation and termination were recorded for every tandem run. A total of 1504 tandem runs across 24 colonies were observed and analysed. StatistiXL (version 1.8) was used for conducting statistical tests.

The behaviour of tandem running can be described in *D. indicum* as follows. A tandem leader on encountering a potential follower repeatedly antennated and then turned around by 180° to present her abdomen to the follower. If the nestmate receiving this invitation was ready to follow the leader, she signals it by antennating the leader's abdomen. This leader and follower pair then moved towards the new nest with nearly continuous physical contact between them. All tandem runs had only one leader and one follower, and none of the adults in the colony were carried. Only the brood and males, if any, were carried to the new site.

Relocation duration, as measured by total time taken, for SDR and LDR was not significantly different (Figure 1a). Adult ants reached the new site by one of the three means – by becoming tandem leaders, by becoming followers of a tandem leader or by independent exploration. In SDR the percentage of nestmates that became followers ($42.7\% \pm 11.3\%$) was not significantly different from independent explorers (Wilcoxon paired sample test, $T = 17$, $n = 12$, $P = 0.09$). In LDR the percentage of nestmates that became followers ($63.3\% \pm 17.3\%$) was significantly higher than independent explorers (Wilcoxon paired sample test, $T = 10$, $n = 12$, $P = 0.02$). Thus we found that the percentage of nestmates that followed a leader to the new site was significantly higher in LDR as compared to SDR (Mann Whitney *U* test, $U = 122$, $df1 = 12$, $df2 = 12$, $P = 0.003$). In addition, the total number of tandem runs

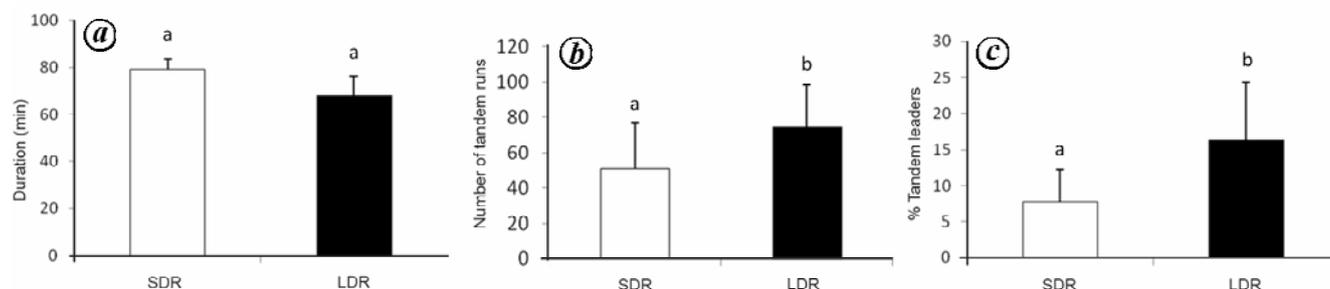


Figure 1. *a*, Mean (error bars represent standard deviation) duration for short distance relocation (SDR, white bar) was not significantly different from the duration for long distance relocation (LDR, black bar). Mann Whitney *U* test, $U = 73.5$, $df1 = 11$, $df2 = 12$, $P = 0.14$. *b*, Mean (error bars represent standard deviation) number of tandem runs in LDR (black bar) was significantly higher than SDR (white bar), Mann Whitney *U* test, $U = 108$, $df1 = 12$, $df2 = 12$, $P = 0.05$. *c*, Mean (error bars represent standard deviation) percentage of tandem leaders in LDR (black bar) was significantly higher than SDR (white bar), Mann Whitney *U* test, $U = 130$, $df1 = 12$, $df2 = 12$, $P = 0.0001$. Bars represented by different alphabets are significantly different from each other.

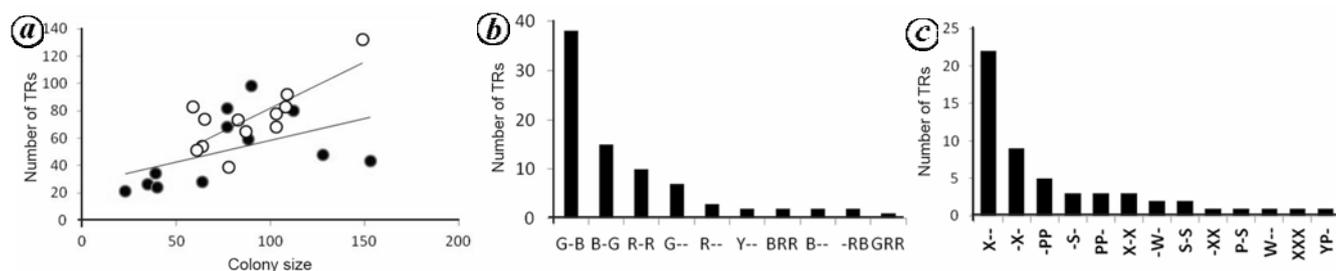


Figure 2. *a*, Relationship between the number of tandem runs observed and colony size. There was significant positive correlation in SDR (filled circles; Spearman rank correlation, $r_s = 0.7$, $df = 12$, $P = 0.02$) and in LDR (open circles; Spearman rank correlation, $r_s = 0.6$, $df = 12$, $P = 0.05$). *b*, Distribution of tandem runs performed by all the leaders during SDR in the colony DI 07. *c*, Distribution of tandem runs performed by all the leaders during LDR in the colony DI 54.

observed during LDR was significantly higher than that observed during SDR (Figure 1*b*).

In all 24 colony relocations studied, the gamergate was tandem run to the new site like other ‘ordinary’ workers and was not surrounded by a retinue. In two SDRs she was observed to be an independent explorer. The gamergate relocated when $40.7 \pm 25.5\%$ and $31.2 \pm 20.8\%$ of the colony had been tandem run to the new nesting site, for the SDR and LDR cases respectively.

The percentage of the colony that became leaders was significantly higher in LDR compared to SDR (Figure 1*c*). There was significant positive correlation between the number of tandem runs and colony size both in SDR and LDR (Figure 2*a*). All the leaders participating in the relocation, however, did not perform equal number of tandem running (Figure 2*b* and *c*). In SDR, a minimum of 1 and a maximum of 11 ants led at least one tandem run, whereas in LDR a minimum of 7 and a maximum of 26 ants participated.

In this, the first behavioural study of the primitively eusocial ponerine ant *D. indicum*, we examined the mechanism of relocation and surprisingly found that ants took almost the same time to relocate over short distances compared to a distance that was six times longer. This was brought about by the recruitment of additional leaders in LDR. The methodology employed by the colony to reach the new nest site was diverse and ranged from tandem running to independent

exploration depending on the distance that needed to be covered.

Studies on other species such as *Diacamma rugosum*, *Camponotus sericeus* and *Temnothorax albipennis* showed that a small group of workers participated in the relocation process^{6,7}. *D. indicum* colonies that relocated in their natural habitat also used tandem running and the characteristics of the relocation was similar, even though the colony experienced fission followed by reunification⁸.

We hypothesize that ants become tandem leaders through a need-based judgement involving the distance over which the relocation is conducted and the number of nestmates that need assistance to reach the new nest. Unlike other species of ants, in *D. indicum* the gamergate is relocated earlier than expected predominantly via the means of tandem running. Several aspects regarding relocation, e.g. the movement of the gamergate, the decision-making process and behavioural profiles of leaders need further exploration. Studying these Indian ants in their native habitat holds the potential to yield a variety of new and significant information regarding organization, cooperation and conflict in societies formed by these superorganisms.

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