

Article

Network approach to understanding the organization of and the consequence of targeted leader removal on an end-oriented task

Sumana ANNAGIRI^{a,*}, Swetashree KOLAY^a, Bishwarup PAUL^a, and Chandan SONA^b

^aBehaviour & Ecology Lab, Department of Biological Sciences, Indian Institute of Science Education and Research, Kolkata, Mohanpur, West Bengal, 741246, India and ^bDepartment of Pharmacology, CSIR-CDRI, Jankipuram Vistar, Lucknow, Uttar Pradesh, 226021, India

*Address correspondence to Sumana Annagiri. E-mail: sumana@iiserkol.ac.in.

Received on 20 February 2016; accepted on 29 April 2016

Abstract

Relocation is an important event in the lives of several social insects whereby all colony members have to be transferred to a new nest when conditions in the old nest become unfavorable. In the current study, network tools were used to examine the organization of this goal-oriented task in the Indian queenless ant *Diacamma indicum* which relocate their colonies by means of tandem running. Individual ants were used as nodes and tandem runs as directed edges to construct unweighted networks. Network parameters were characterized in control relocations (CRs) and in relocations where the node with the highest outdegree, that is, the Maximum tandem leader (Max TL) was experimentally removed. These were then compared to 1) randomized networks, 2) simulated networks in which Max TL was removed, and 3) simulated networks with removal of a random leader. Not only was there complete recovery of the task, but the manner in which it was organized when Max TL was removed was comparable to CRs. The results obtained from our empirical study were significantly different from the results predicted by simulations of leader removal. At an individual level, the Max TL had a significantly higher outdegree than expected by chance alone and in her absence the substitute Max TL did comparable work. In addition, the position of the Max TL in the pathway of information flow was conserved in control and experimentally manipulated conditions. Understanding the organization of this critical event as more than the sum of individual interactions using network parameters allows us to appreciate the dynamic response of groups to perturbations.

Key words: *Diacamma indicum*, division of labor, networks, relocation, tandem running.

Division of labor is a central theme in the organization of social insect colonies and is thought to be one of the major reasons for their ecological success (Wilson 1985; Robinson 1992). Multiple tasks are performed simultaneously by different groups of individuals within the colony leading to increased efficiency and higher productivity. However, the contributions of individuals involved in the particular task is unequal as few individuals perform most of the task

while others contribute very little (Robinson 1992; Gordon 1996; Beshers and Fewell 2001). Hence, it is common to see certain individuals perform a particular task more frequently than others (Robinson and Page 1989). There may be certain members of the colony who influence efficient execution of specific tasks in a variety of ways. These key individuals either perform majority of the work required or impact the functioning of nestmates involved in a task

by increasing their work rate and/or maintaining cohesion amongst them (Robson and Traniello 1999). Colony members who play a significant role in the context of nest site selection and during colony relocations by transporting majority of the nestmates have been recorded in several species of ants such as *Formica sanguinea* and *Camponotus sericeus* (Moglich and Holldobler 1974), *Myrmica rubra* (Abraham and Pasteels 1980), *Tapinoma erraticum* (Meudec and Lenoir 1982), *Temnothorax albipennis* (Dornhaus et al. 2008; Stroeymeyt et al. 2011), and *Linepithema humile* (Hui and Pinter-Wollman 2014). Although the role of such individuals have been extensively studied in social insects in different contexts, presence of individuals who play disproportionately important roles in their groups have been observed in other animals like fish, birds, and mammals as well (Modlmeier et al. 2014). The duration for which key individuals remain within their groups can also affect group dynamics and task performance of the group members in a social spider (Pruitt and Pinter-Wollman 2015). The importance of key individuals in a particular task can be elucidated by causing perturbations in the form of removal of such individuals. In some cases, when certain individuals are removed the work rate is not affected significantly (Breed et al. 2002). In other instances, rate of task performances decreases for up to several days (Moglich and Holldobler 1974; Gardner et al. 2007; O'Donnell 1998) or leads to failure in accomplishing the task (Robson and Traniello 2002).

Social insect colonies are highly complex units that exhibit multiple levels of organization with local interactions giving rise to global attributes that cannot be understood simply by studying interactions between individuals (Fewell 2003). These interactions are critical to the ability of relatively simple individuals to display complex behaviors at the level of the colony. Traditionally, the focus has been on examining dyadic interactions between individuals of the social group. However, network theory provides a powerful tool to study the role of these individuals on the emergent organization and functioning of their group (Krause et al. 2009; Pinter-Wollman et al. 2013). Network studies have been used to identify individuals who occupy key positions in animal social groups. Most of these studies are based on non specific interactions, such as antennation or proximity between individuals of a group, which are relatively common and lack an explicit functional connotation. For example, a few individuals are known to hold structurally important positions in dolphin social networks and are essential for maintaining cohesion (Lusseau and Newman 2004). Similarly, positions of individuals within the network can have important implications for transmission of diseases in populations of meerkats (Drewe 2009) and Tasmanian devils (Hamede et al. 2009). Another application of network studies is to examine the effect of removal of key individuals, both experimental and simulated, on network properties. While some animal groups are not affected by such manipulations (Lusseau 2003), others are highly susceptible to the removal of key individuals (Flack et al. 2005; Flack et al. 2006; Williams and Lusseau 2006; Manno 2008; Chaverri 2010). However, the experimental removal of key individuals from a social group could yield very different results from the effects that are predicted by simulated removals of individuals (Flack et al. 2006). Hardly any study has used network tools previously to examine the role of key individuals in the context of goal-oriented tasks such as relocation and the effects of removal of such individuals on these networks.

Relocation is a frequent and necessary event in the lives of many social insects and can be brought about by various factors (Holldobler and Wilson 1990; Visscher 2007). We examined the role played by key individuals during colony relocation in the

queenless Indian ant *Diacamma indicum* using network analysis. This is a primitively eusocial species recorded from different parts of the Indian subcontinent (Viginier et al. 2004) and has colonies consisting of 20–300 monomorphic adults. Colonies are known to relocate by tandem running of adults while males and brood are carried (Kaur et al. 2012; Sumana and Sona 2013). Tandem running is a primitive form of recruitment where individuals known as leaders lead their nestmates one at a time from the old nest to the new one while maintaining physical contact (Franklin 2014). Tandem running is also the means of transfer of information regarding location of and path to the new nest to potential leaders (Franks and Richardson 2006, Kaur et al. 2012).

Leaders play a central role in colony relocation as they have knowledge of the location of the new nest and transfer nestmates one at a time to the new shelter. However, it has been observed that removal of these leaders does not negatively impact relocation dynamics as other colony members replace the removed individuals and perform tandem runs to relocate the colony (Kolay and Annagiri 2015). In both field and laboratory-based relocations, it has been observed that division of work among these leaders is not uniform with few leaders performing most of the tandem runs (Kaur et al. 2012; Sumana and Sona 2012). One individual, designated as Max TL, has a disproportionately high influence on the dynamics of colony relocation. This individual is a performer, organizer, and catalyst as she performs significantly more tandem runs than other leaders, recruits other leaders, and enhances the efficiency of colony relocation. Removing the Max TL impacts relocation dynamics as well as performance of other leaders (Sumana and Sona 2013).

In the current study, we used network tools to examine work organization in *D. indicum* colonies during relocation which is an end-oriented task. Networks were constructed based on tandem runs conducted by leader–follower pairs as they walk from the old nest to the new nest. Thus, tandem running is a directed interaction initiated by the leader toward the follower and it has a clear functional connotation. In these networks, ants were represented as nodes and tandem runs as edges that were directed from leaders toward specific followers. Network structures of control or unmanipulated relocations and manipulated relocations where Max TL was physically removed were compared to: 1) random networks (RNDs); 2) simulated networks where Max TL was removed; and 3) simulated networks where a random leader was removed. This allows us to look at organization of work within the colony during relocation under two different circumstances and assess how this organization differs from random distribution of tandem runs between individuals. The influence of colony size on network properties was studied as there is evidence to suggest that there are differences in the patterns of task organization in colonies of different sizes (Jeanne 1999). Lastly, the position of the Max TL who is known to play an important part in colony relocation was also explored in detail.

Materials and Methods

In the course of this study, colony relocations performed in the lab were compared with simulations. Along with a description of the experimental protocols, details of different simulations and an outline of the network parameters have been presented in this section.

Experimental protocols

Eleven colonies of *D. indicum* consisting of adults and brood were collected from their natural habitat in Mohanpur, Nadia district, West Bengal, India (22°56'N, 88°31'E). They were maintained in

the laboratory under standardized conditions (Sumana and Sona 2013). All the adults in the colony (91.8 ± 26.1) were uniquely marked for individual identification with a combination of colors of the non toxic enamel paints (Testors, Rockford, IL, USA). *D. indicum* uses tandem running to recruit colony members during relocation. This mode of recruitment involves a leader who leads followers one at a time from the old nest to the new nest while maintaining physical contact along the journey. Two relocations, one control and the other manipulated, were conducted with each colony in random order. In control relocations (CR), colonies were given the stress of light and removal of the nest cover which caused them to initiate relocation into a new nest placed 152 cm away. The individual performing the highest number of tandem runs was designated as Max TL. We conducted a set of manipulated relocations termed as Maximum tandem leader removal relocation (MLR) where a single ant, the Max TL, was removed. This would allow us to examine the role played by the Max TL and the consequence of her removal on the process of relocation. In *D. indicum*, there is no clear method of predicting the identity of the individual that will become the Max TL in a given relocation *a priori* and this can only be determined after tandem running has been initiated. Thus, after initiation of relocation the number of tandem runs performed by each leader was tabulated at 10 min intervals. When a single leader had performed two tandem runs more than any other leader she was designated as the Max TL and subsequently removed on her return trip to the old nest. This process of removing did not cause any noticeable disturbance to the colony. For each tandem run, the identities of the leader and follower were noted. Only tandem runs that terminated at the new nest were considered for this analysis. A total of 1496 tandem runs initiated by 304 tandem leaders across 11 colonies were used for the subsequent analysis.

For the purposes of analysis, all the tandem runs observed during CR and MLR were divided into pre manipulative and post manipulative phases. All tandem runs performed before removal of Max TL were considered in the pre manipulative phase while those performed after Max TL removal were considered in the post manipulative phase in MLR. The number of tandem runs in the pre manipulative phase of MLR for a given colony was calculated and the same number of tandem runs from CR was considered as the pre manipulative phase for comparison. The remaining tandem runs of CR were included in the post manipulative phase. Even though the Max TL was not removed in CR, tandem runs were divided into the two phases so that comparisons would be robust to any differences in the temporal dynamics of relocation. Depending on the analysis undertaken the whole relocation or the post manipulative phase of control and Max TL removal relocations was compared.

Network analysis

Networks were constructed using colony adults as nodes and tandem runs as edges for control and Max TL removal relocations separately for each of the 11 colonies. Tandem runs are directed ties with leaders taking the followers to the new nest one at a time; hence, directed networks were considered. Since there were very few instances of multiple tandem runs between the same pairs of leaders and followers (CR— $2.8\% \pm 2.4\%$, MLR— $3.7\% \pm 4.8\%$), we constructed only unweighted networks. Colony members who participated in at least one tandem run either as leader or follower were considered for the network analysis. Several network-level parameters were calculated for each relocation network; these parameters and their relevance to relocation are explained below. Density gives an estimate of how many ties were actually present as a proportion

of all possible ties between individuals of the colony (Wasserman and Faust 1994). High density indicates presence of more ties between individuals. During relocation by tandem running most followers are led to the new nest only once by a single leader. Thus, density is expected to be low in case of relocation to a single new nest. Average path length gives an estimate of the mean number of edges between pairs of individuals in the network (Wasserman and Faust 1994). Higher path length shows that some individuals are connected to others only indirectly. Diameter indicates the longest path in the network (Wasserman and Faust 1994). Small diameter would allow for faster transfer of information to all individuals in the network, whereas large diameter indicates that information passes through many intermediates before reaching all individuals. Closeness gives a measure of the manner in which each individual is connected to every other member within the network (Wasserman and Faust 1994). High closeness values indicate that individuals share direct ties with each other, whereas low values indicate that individuals are connected to each other indirectly through ties they share with others. As tandem runs are directed ties, the outcloseness for each node was calculated based on the number of tandem runs initiated and the average closeness values for all nodes in a network have been presented. Degree centralization is a measure of the number of direct ties an individual has with others and indicates the prominence of one or a few nodes in the network (Wasserman and Faust 1994). Since tandem runs are directed interactions, outdegree centralization was calculated for all networks. High outdegree centralization would indicate that the network is dependent on a few individuals who initiate most tandem runs. Low centralization values signify that ties are more evenly spread among individuals. The number of ties initiated by the Max TL herself would be of particular interest to understand work organization within the colony. Thus, the outdegree value of the Max TL was obtained for each network and analyzed further. After obtaining the network parameters for CR and MLR of each colony, these were compared using nonparametric two-tailed tests with statistiXL (Version 1.8). Network parameters were calculated using R software (version 3.1.0).

Simulation protocols

To better understand task organization within the colony in the context of relocation, experimental networks were compared with simulated ones. Three different categories of simulations were performed.

Random networks (RNDs): using the colony sizes and tandem runs observed in the CRs for a given colony as the input parameters, RNDs were created. These networks were constructed by keeping the number of nodes and edges constant but redistributing the edges among the nodes in a completely random manner.

Major leader reallocation (MLRA): in these simulations, the node with the highest number of edges was removed from the CR networks along with all its edges. Since the followers are tandem run to the new nest by other leaders and not simply abandoned in the actual experiments, we redistributed the removed edges among the remaining nodes in a random manner.

Random leader reallocation (RLRA): in this category, a randomly selected node from CR networks was removed and its edges were reallocated randomly among the remaining nodes.

In each category of simulations, that is, RND, MLRA, and RLRA, 1,000 iterations were carried out for each colony. After each iteration, the unconnected nodes were removed and the same network parameters as CR and MLR—density, average path length,

diameter, outcloseness, outdegree centralization along with outdegree of Max TL were calculated. The average value across these 1,000 iterations were obtained and used as the representative value for the colony for the given simulation and used for further analysis. The network of the complete CR has been compared to the RND networks while for comparisons with MLR, MLRA and RLRA networks only the networks of the post manipulative phase of CR has been used. All simulations and subsequent calculations of network parameters were done using R software (version 3.1.0). In the ensuing analysis all descriptive statistics are average and standard deviation unless mentioned otherwise. Nonparametric statistical tests were used for comparisons and statistiXL (Version 1.8) was used for conducting them.

Results

Comparison between CR and RND

The percentage of colony members who were not involved in tandem runs either as leader or follower was significantly higher in CR (28.2 ± 9.4) than in RND simulations (20.9 ± 6.5) (Wilcoxon Paired Sample test, $t = 4.0$, $n = 11$, $P = 0.007$). The pattern of organization of CRs was considerably different from random. The percentage of leaders observed in CR (14.4 ± 4) was significantly lower than the percentage obtained in the RND networks (54.6 ± 6.7) (Wilcoxon Paired Sample test, $t = 0.0$, $n = 11$, $P = 0.001$, Figure 1A). The average number of times each follower followed a leader was also significantly lower in CR (CR— 1.2 ± 0.1 , RND— 1.5 ± 0.1 , Wilcoxon Paired Sample test, $t = 0.0$, $n = 11$, $P = 0.001$, Figure 1A). Task distribution among leaders was uneven in both cases with most leaders performing only a few tandem runs, but the skew was less in RND (Kolmogorov–Smirnov test, $t = 71.1$, $df = 9,145$, $P = 0.001$, Figure 1B).

Network structure of CRs was not similar to RND networks. A representative graph of CR and RND for one colony has been shown in Figure 2. Although density was lower in RND networks, diameter of the network and average path length between individuals was significantly higher in RND networks than in CR (Table 1). Outdegree centralization was higher in CR indicating that task organization during relocations was different from random (Table 1). Outcloseness was higher in CR networks than in RND networks (Table 1). Average path length between colony members is not correlated to colony size in either CR (Spearman Rank Correlation test, $r_s = 0.23$, $df = 11$, $P = 0.5$) or RND (Spearman Rank Correlation test, $r_s = 0.08$, $df = 11$, $P = 0.8$). In both CR and RND networks density (Spearman Rank Correlation test, CR — $r_s = -0.8$, $df = 11$, $P = 0.004$, RND — $r_s = -0.96$, $df = 11$, $P = 0.001$), outdegree centralization (Spearman Rank Correlation test, CR — $r_s = -0.66$, $df = 11$, $P = 0.03$, RND — $r_s = -0.98$, $df = 11$, $P = 0.001$) as well as outcloseness (Spearman Rank Correlation test, CR — $r_s = -0.87$, $df = 11$, $P = 0.001$, RND — $r_s = -0.97$, $df = 11$, $P = 0.001$) were negatively correlated to colony size.

CR and MLR comparisons

To study the effects of removal of Max TL on relocation dynamics, the post manipulative phase of CRs was compared to that of the MLR. Comparison of the tandem runs performed by each leader revealed that work distribution in MLR was more right skewed than in CR (Kolmogorov–Smirnov test, $t = 15.6$, $df = 11,159$, $P = 0.001$, Figure 3). However, removal of only the major leader did not bring about any discernible changes in the network structure as all the network measures were comparable between control and MLR (Table

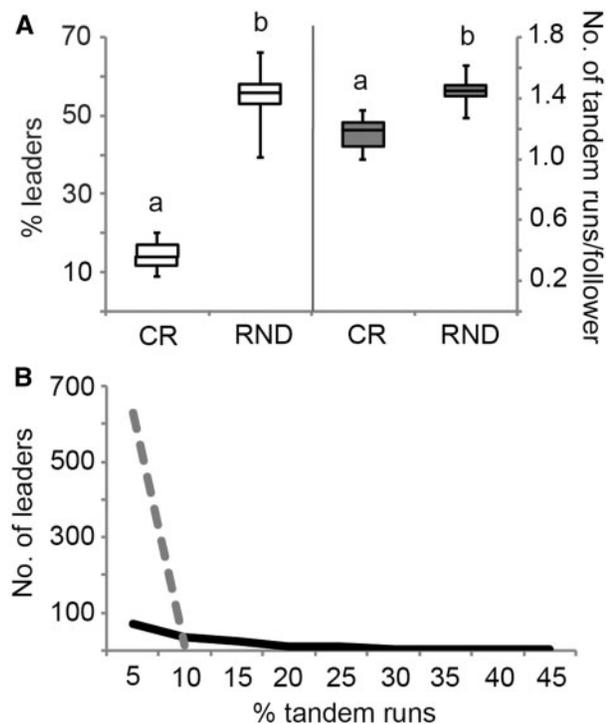


Figure 1. (A) Box and whisker plot depicting the percentage of leaders (white boxes) and average number of times the followers were tandem run to the new nest (gray boxes) has been presented for the CRs and RND simulations for 11 colonies. Each box represents the interquartile range, the line inside the box represents the median, and the whiskers represent the range of the values. Comparisons of parameters were carried out using Wilcoxon paired sample test and boxes carrying different letters are significantly different. (B) Frequency distributions of tandem runs performed by leaders in the CRs (black solid line) and RND simulations (gray dashed line) are shown. Percentage of tandem runs is plotted against number of leaders who performed them. Data has been pooled across 11 colonies for CR and across 1,000 iterations for each colony in RND simulations.

2). Networks for the post manipulative phase of CR and MLR have been depicted in Figure 4A and B.

Comparisons between MLR and simulations MLRA and RLRA

Effects of experimental removal of the Max TL were compared to simulated removal of a single leader, either Max TL or a random leader, during relocation. Networks for a single iteration of MLRA and RLRA for one colony have been illustrated in Figure 4C and D. Removal of a random leader other than the Max TL caused the density and average outcloseness values to be higher in RLRA simulations as compared to MLR (Table 2). Density was significantly higher in case of MLRA simulations while diameter, average path length, and outdegree centralization did not show significant differences between MLR and MLRA. Outcloseness was higher in MLRA as compared to MLR networks (Table 2).

Role of Max TL

The outdegree of the Max TL in CRs (16.1 ± 5.1) was significantly higher than the individual with the highest outdegree in random simulations (3.6 ± 0.3) (Wilcoxon Paired Sample test, $t = 0.001$, $n = 11$, $P = 0.001$; Figure 5A). Max TL in CR performed four times as many tandem runs as expected by chance alone. The outcloseness of the

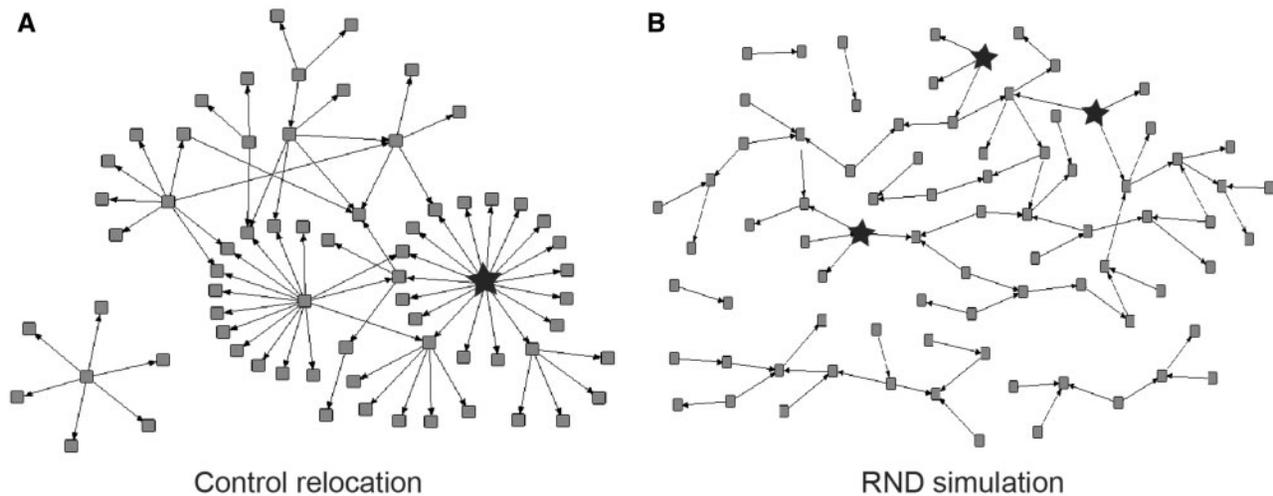


Figure 2. Directed unweighted interaction networks with individual ants as nodes and tandem runs as directed edges connecting the leader to the follower are presented for the entire CR of a single colony DI-57 (A) and for a single iteration of RND simulations of the same colony (B). The star-shaped node(s) represent individuals with the highest outdegree in each network.

Table 1. Average and standard deviation of the various network parameters for the entire CR and RND across 11 colonies are presented in the first two rows. Critical values and P values obtained by comparing the values of the network parameters between the two categories using Wilcoxon Paired Sample test are indicated in the third row. Comparisons that were significantly different ($P < 0.05$) have been indicated in bold.

	Density	Diameter	Average path length	Outdegree centralization	Average outcloseness
CR	0.018 ± 0.005	3.27 ± 0.91	1.44 ± 0.19	$25.85\% \pm 12.51\%$	1.81 ± 0.65
RND	0.015 ± 0.004	7.88 ± 1.66	2.76 ± 0.55	$3.96\% \pm 0.91\%$	1.59 ± 0.45
	$t = 3.0$ $P = 0.005$	$t = 0.001$ $P = 0.001$	$t = 0.001$ $P = 0.001$	$t = 0.001$ $P = 0.001$	$t = 7.0$ $P = 0.02$

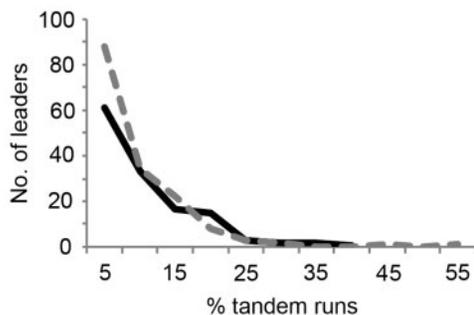


Figure 3. Frequency distributions of tandem runs performed by leaders in the post manipulative phases of CRs (black solid line) and MLRs (gray dashed line) are shown. Percentage of tandem runs is plotted against number of leaders who performed them for data pooled across 11 colonies for each type of relocation.

Max TL in CRs (8.6 ± 18.8) was significantly higher than that of the equivalent individual in RND simulations (1.7 ± 0.5) (Wilcoxon Paired Sample test, $t = 0.0$, $n = 11$, $P = 0.001$; Figure 5A).

The outdegree of Max TL in CR (10.8 ± 5.4) on considering only the tandem runs in the post manipulative phase is comparable to that of the individual who performs the highest number of tandem runs after removal of the original Max TL in MLR (14 ± 7) (Wilcoxon Paired Sample test, $t = 14.0$, $n = 11$, $P = 0.1$; Figure 5B). The outdegree of the individual who emerged as the Max TL in MLR after

removal was comparable to that of the corresponding individual in RLRA (10.5 ± 5 ; Wilcoxon Paired Sample test, $t = 13.0$, $n = 11$, $P = 0.08$; Figure 5B) but significantly higher than the individual with the highest outdegree in MLRA simulations (7.5 ± 2.7 ; Wilcoxon Paired Sample test, $t = 0.0$, $n = 11$, $P = 0.001$, Figure 5B). The outcloseness of Max TL was comparable in CR (3.9 ± 2.5) and MLR (8.9 ± 20.8) on considering only the post removal phase in both cases (Wilcoxon Paired Sample test, $t = 28.0$, $n = 11$, $P = 0.7$; Figure 5C). The Max TLs in MLR had similar outcloseness values as the corresponding individuals in both RLRA (4.6 ± 3 ; Wilcoxon Paired Sample test, $t = 19.0$, $n = 11$, $P = 0.2$; Figure 5C) and MLRA (4.3 ± 2.2 ; Wilcoxon Paired Sample test, $t = 17.0$, $n = 11$, $P = 0.2$; Figure 5C).

Discussion

In the current study, we looked at the task organization and information flow in *D. indicum* colonies during the goal-oriented task of relocation with the help of network tools. Leaders are responsible for relocating their colonies as they tandem run nestmates one at a time to the new shelter. In particular, a single leader designated as the Max TL plays a pivotal role in the organization and execution of colony relocation (Sumana and Sona 2013). We examined the position occupied by the Max TL in relocation networks. We also studied the effects of experimental removal of such a leader on the network structure and how it differed from the effects of the simulated removal of a single leader.

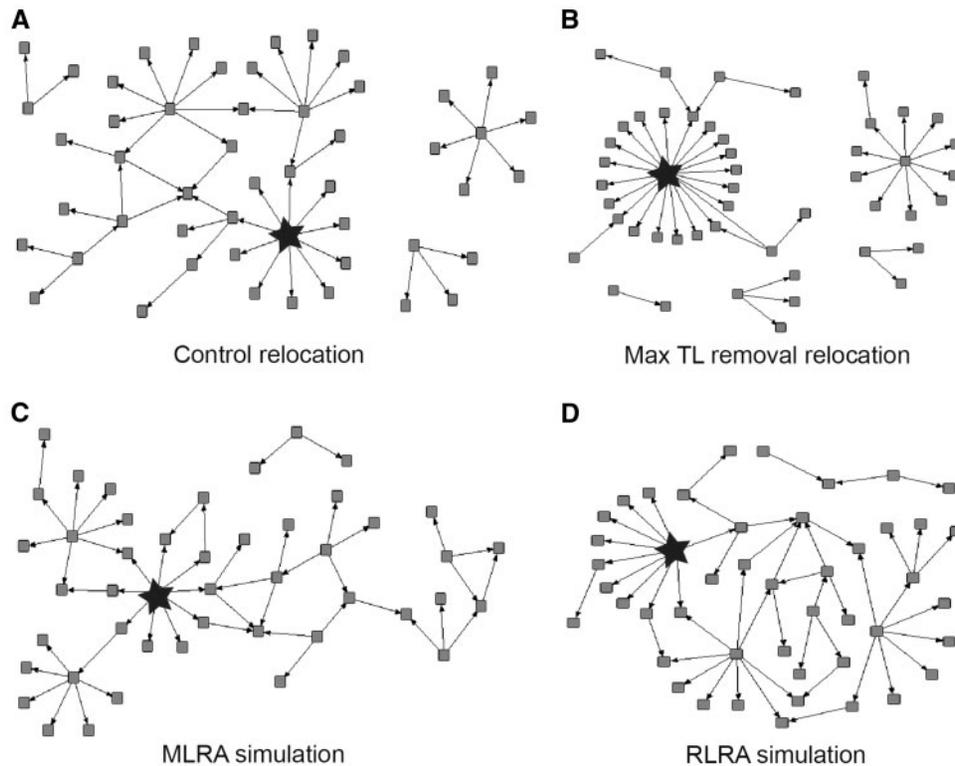


Figure 4. Directed unweighted interaction networks have been created using only the tandem runs observed in the post manipulation phases of CRs and MLRs for a single colony DI-57 (A and B). Network graphs for a single iteration of each of MLRA and RLRA simulations for the same colony have also been constructed (C and D). The individual(s) with the highest outdegree in each network has been represented by star-shaped nodes.

Table 2. Average and standard deviation of the various network parameters for the post manipulative phase of CR and MLR as well as MLRA and RLRA simulations across 11 colonies have been presented. Critical values and *P* values obtained by comparing the values of the network parameters between the different categories using Wilcoxon Paired Sample test are also given and comparisons that were significantly different ($P < 0.05$) are indicated in bold.

	Density	Diameter	Average path length	Outdegree centralization	Average outcloseness
CR	0.022 ± 0.009	2.73 ± 0.91	1.3 ± 0.23	21.97% ± 10.89%	2.55 ± 1.4
MLR	0.02 ± 0.005	3.55 ± 1.44	1.55 ± 0.38	23.87% ± 15.85%	2.07 ± 0.83
MLRA	0.03 ± 0.014	4.62 ± 1.37	1.87 ± 0.47	16.4% ± 4.85%	3.17 ± 1.85
RLRA	0.026 ± 0.013	3.38 ± 0.71	1.47 ± 0.2	22.73% ± 10.45%	2.88 ± 1.74
Network comparisons					
CR vs MLR	$t = 25.0$ $P = 0.5$	$t = 15.0$ $P = 0.2$	$t = 12.0$ $P = 0.07$	$t = 33.0$ $P = 1.0$	$t = 15.0$ $P = 0.1$
MLR vs MLRA	$t = 1.0$ $P = 0.002$	$t = 13.0$ $P = 0.08$	$t = 15.0$ $P = 0.1$	$t = 22.0$ $P = 0.4$	$t = 7.0$ $P = 0.02$
MLR vs RLRA	$t = 10.0$ $P = 0.04$	$t = 30.0$ $P = 0.8$	$t = 23.0$ $P = 0.4$	$t = 31.0$ $P = 0.9$	$t = 9.0$ $P = 0.03$

The organization of the process of relocation was considerably different from random work distribution within the colony illustrating that results obtained from simulation studies should be interpreted with caution (Christley et al. 2005; Pinter-Wollman et al. 2013). Fewer leaders were active in CRs than predicted by chance alone. Work distribution among these leaders was significantly more right skewed in CRs than in the RND networks where the interactions were distributed randomly with very few leaders initiating more than 5% interactions. Although most leaders in CRs led few tandem runs, there were a few who performed up to 45% of the total tandem runs. There are several underlying mechanisms operating within animal societies that make their structure and functioning

significantly different from random organization (Hamede et al. 2009; Naug 2009). Further studies will have to be conducted to understand the mechanisms that determine which individuals will become leaders during a given relocation and the amount of work they perform in *D. indicum* colonies. Lower average path length and diameter in CR indicate optimization of the paths of information flow within the colonies ensuring faster transfer of information among colony members. The higher outdegree centralization of CR networks as compared to RND networks indicate that task execution, relocation in this case, is dependent on only a small subset of colony members. Several short paths are maintained between all individuals of the colony during relocation as is signified by the higher

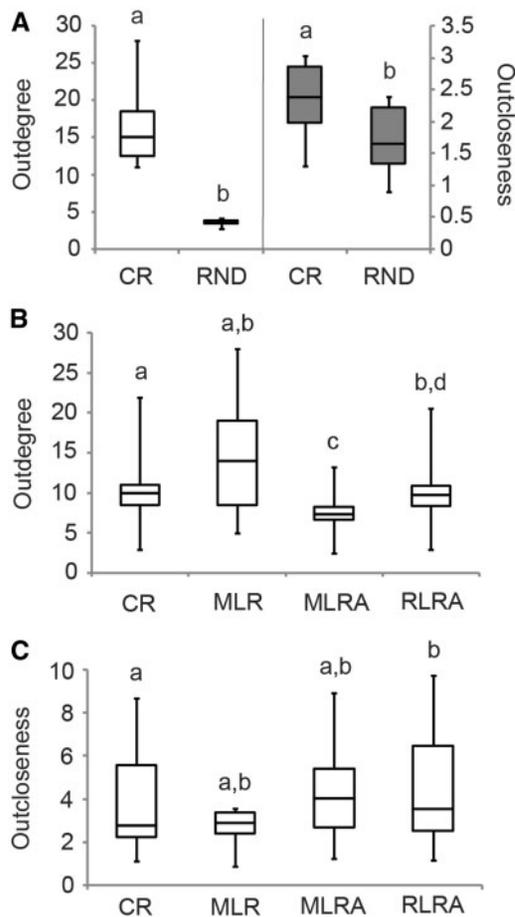


Figure 5. (A) Box and whisker plots depicting the outdegree (white bars) and outcloseness (gray bars) has been presented for the CRs and RND simulations for 11 colonies. (B) Outdegree of the post manipulative phases of CR and MLR as well as MLRA and RLRA simulations for 11 colonies have been presented using box and whisker plots. (C) Box and whisker plots representing the outcloseness of the post manipulative phases of CR and MLR as well as MLRA and RLRA simulations for 11 colonies have been presented. Each box represents the interquartile range, the line inside the box represents the median, and the whiskers represent the range of the values. Comparisons of parameters were carried out using Wilcoxon paired sample test and boxes carrying different letters are significantly different.

outcloseness values of CR networks. These together ensure fast, efficient, and accurate transfer of information within all colony members which in turn will maintain colony cohesion during relocation.

It has been speculated that colony size could affect task organization and the consequent pattern of information flow within social insect colonies. In general, individuals in smaller groups are more homogeneously connected to each other and heterogeneity in connectivity tends to increase as group size increases (Fewell 2003; Naug 2008; Naug 2009). Spatial constraints prevent all individuals of large groups from interacting with each other at random giving rise to non random patterns of interaction within larger insect societies. These studies are based on non specific interactions such as proximity between individuals while we have used tandem running, a behavior that has specific functional significance. We observe the same connectivity patterns as has been reported earlier with most of the network parameters being negatively correlated to colony size in both control and randomized networks. Density decreases with increasing colony size indicating that relatively fewer tandem runs

are required to relocate larger colonies. This could be due to the fact that followers are usually led only once to the new nest; hence, the increase in the actual number of ties is low compared to the number of potential ties as colony size increases. Decreasing centralization signifies that more leaders become involved in performing tandem runs as colony size increases. Diameter decreases in larger colonies while average path length is not correlated to colony size which indicates that individuals in larger colonies are equally well connected to each other as individuals in smaller colonies. Relocation becomes more complex as group size increases since more individuals have to be relocated to the new nest while at the same time chances of fragmentation of the colony also increases. In addition, there may be an upper limit to the number of tandem runs that can be performed by each leader. These constraints may result differences in patterns in work organization in colonies of different sizes (Jeanne 1999; Naug 2009).

Work distribution among leaders was right-skewed with the majority of the leaders performing few tandem runs while there were a few leaders who performed many tandem runs in the post removal period of MLR as well as in the corresponding period of CRs. This confirms previous observations in *D. indicum* (Kaur et al. 2012; Sumana and Sona 2012) and is consistent with patterns of task distribution observed in other social insects (Robinson 1992; Gordon 1996; Beshers and Fewell 2001). However, frequency distribution of tandem runs among leaders was more right-skewed in MLR than in CR signifying that work distribution became more unequal upon removal of only the Max TL. This is contrary to the response shown when a large number of leaders are removed as substitute leaders distribute the task more evenly among themselves (Kolay and Annagiri 2015). However, removal of Max TL does not have any impact on the structure of relocation networks as all network parameters are comparable between CR and MLR indicating that work organization within the colony remains unaffected. In contrast, density and closeness was observed to increase when many leaders were removed during relocation (Kolay and Annagiri 2015). Thus, the colony seems to respond to different degrees of stress in different ways to accomplish the same task. We further compared these results with the effects of simulated removal of a single leader, either the Max TL or a random leader and find that simulated networks were different from networks based on experimental data. Density and outcloseness are higher in both MLRA and RLRA simulations than MLR while network diameter, average path length, and outdegree centralization were comparable. This indicates that removal of any node with a nonzero outdegree value (leaders) produces a similar effect as removing a node with the highest outdegree value in the simulations. This interesting disparity with experimental removal required further investigation. This also illustrates that the empirical effects of removing an important individual from a social group could be different from that predicted by simulated removals (Flack et al. 2006; Hamede et al. 2009). This could be due to the fact that biological systems have intrinsic mechanisms to cope with the loss of individuals and respond in an appropriate manner which are not clearly understood and, therefore, not accounted for while performing simulations.

Most studies on task organization in social insect colonies focus on the behavior of groups of individuals performing the task but there is evidence to suggest that there is behavioral variability among individuals within this group rather than equal participation by all (Kaur et al. 2012; Pinter-Wollman et al. 2012). Although nearly 20% of colony members become leaders during a single relocation event in *D. indicum*, all of them do not perform equally

with few leaders carrying out most of the workload. This is further exemplified by the disproportionate role played by the Max TL. Not only does she perform significantly more tandem runs than other leaders, she also plays a crucial role in the process of information transfer among nestmates during relocation. This is indicated by the significantly higher outdegree and outcloseness values of Max TL in CRs than predicted by the RND simulations.

The role of the Max TL during relocation is conserved as indicated by the comparable outdegree and outcloseness of Max TL in both CR and MLR. However, the identity of the individual who assumes this position varies from one relocation to the next and persistence of an individual in the position of Max TL is for the duration of one relocation event in most cases. In fact, it is so flexible that even when the prospective Max TL is removed during the course of relocation, another leader can seamlessly take up this role without any discernible perturbations to task organization. This is evident from the fact that the outdegree and outcloseness of the individual who emerges as the Max TL in the post manipulative phase of MLR is comparable to that of the Max TL in the equivalent phase of CR. In fact, the performance of the emergent Max TL in MLR is better than that of the leader who performs highest number of tandem runs after simulated removal of the initial Max TL in MLRA and is comparable with performance of the Max TL after a random leader is removed in RLRA. However, there is a slight reduction in efficiency of relocation with an overall decrease in the rate at which tandem runs are performed and the time taken to complete relocation (Sumana and Sona 2013). Thus, it seems that there are several individuals in the colony who are capable of becoming the Max TL during colony relocation. Further studies need to be carried out to elucidate the factors which determine the identity of the Max TL during a given relocation.

The use of simulations and social network analysis in this study allows us to compare the consequences of targeted leader removal during relocations with observed results and contrast our findings with changes occurring by chance alone. The leaders organize the movement of the colony from the old nest to the new one in a manner that is very different from random and they also maintain this organizational structure in the absence of the most hardworking leader (Max TL). This study allows us to get a glimpse of task organization as more than the sum of individual events and its robustness to perturbations within social insect colonies.

Acknowledgments

We would like to thank Noa Pinter-Wollman for inviting us to write for a special issue that led us to consider these lines of thought. C.S. performed the experiments, simulations were performed by B.P., S.K. performed the statistical analysis and wrote the manuscript, S.A. performed the experiments, wrote the manuscript, and supervised the work.

Funding

This study was funded by Science & Engineering Research Board (SR/FT/LS-179/2009) of the Department of Science & Technology, India. S.K. was funded by the Council of Scientific and Industrial Research, India. B.P. was funded by Indian Institute of Science Education & Research, Kolkata. C.S. was funded by the IISER Kolkata summer research program.

References

Abraham M, Pasteels JM, 1980. Social behavior during nest-moving in the ant *Myrmica rubra* L. (Hym. Form.). *Insect Soc* 27:127–147.

- Beshers SN, Fewell JH, 2001. Models of division of labor in social insects. *Annu Rev Entomol* 46:413–440.
- Breed MD, Williams DB, Queral A, 2002. Demand for task performance and workforce replacement: undertakers in honeybee *Apis mellifera*, colonies. *J Insect Behav* 15:319–329.
- Chaverri G, 2010. Comparative social network analysis in a leaf-roosting bat. *Behav Ecol Sociobiol* 64:1619–1630.
- Christley RM, Pinchbeck GL, Bowers RG et al. 2005. Infection in social networks: using network analysis to identify high-risk individuals. *Am J Epidemiol* 162:1024–1031.
- Dornhaus A, Holley JA, Pook VG, Worswick G, Franks NR, 2008. Why do not all workers work? Colony size and workload during emigrations in the ant *Temnothorax albipennis*. *Behav Ecol Sociobiol* 63:43–51.
- Drewe JA, 2009. Who infects whom? Social networks and tuberculosis transmission in wild meerkats. *Proc R Soc B* 277:633–642.
- Fewell JH, 2003. Social insect networks. *Science* 301:1867–1870.
- Flack JC, Krakauer DC, de Waal FBM, 2005. Robustness mechanisms in primate societies: a perturbation study. *Proc R Soc B* 272:1091–1099.
- Flack JC, Girvan M, de Waal FBM, Krakauer DC, 2006. Policing stabilizes construction of social niches in primates. *Nature* 439:426–429.
- Franklin EL, 2014. The journey of tandem running: the twists, turns and what we have learned. *Insect Soc* 61:1–8.
- Franks NR, Richardson T, 2006. Teaching in tandem-running ants. *Nature* 439:153.
- Gardner KE, Foster RL, O'donnell S, 2007. Experimental analysis of worker division of labor in bumblebee nest thermoregulation (*Bombus huntii*, Hymenoptera: Apidae). *Behav Ecol Sociobiol* 61:783–792.
- Gordon DM, 1996. The organization of work in social insect colonies. *Nature* 380:121–124.
- Hamede RK, Bashford J, McCallum H, Jones M, 2009. Contact networks in a wild Tasmanian devil *Sarcophilus harrisi* population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecol Lett* 12: 1147–1157.
- Holldobler B, Wilson EO, 1990. *The Ants*. Cambridge (MA): Harvard University Press.
- Hui A, Pinter-Wollman N, 2014. Individual variation in exploratory behaviour improves speed and accuracy of collective nest selection by Argentine ants. *Anim Behav* 93:261–266.
- Jeanne RL, 1999. Group size, productivity, and information flow in social wasps. In: Detrain C, Deneubourg JL, Pasteels JM, editors. *Information Processing in Social Insects*. Basel, Switzerland: Birkhauser Verlag, 3–30.
- 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.
- Kolay S, Annagiri S, 2015. Tight knit under stress: colony resilience to the loss of tandem leaders during relocation in an Indian ant. *R Soc Open Sci* 2:150104.
- Krause J, Lusseau D, James R, 2009. Animal social networks: an introduction. *Behav Ecol Sociobiol* 63:967–973.
- Lusseau D, 2003. The emergent properties of a dolphin social network. *Proc R Soc Lond B* 270:S186–S188.
- Lusseau D, Newman MEJ, 2004. Identifying the role that animals play in their social networks. *Proc R Soc Lond B* 271:s477–s481.
- Manno TG, 2008. Social networking in the Columbian ground squirrel *Spermophilus columbianus*. *Anim Behav* 75:1221–1228.
- Meudec M, Lenoir A, 1982. Social responses to variation in food supply and nest suitability in ants *Tapinoma erraticum*. *Anim Behav* 30:284–292.
- Modlmeier AP, Keiser CN, Watters JV, Sih A, Pruitt JN, 2014. The keystone individual concept: an ecological and evolutionary overview. *Anim Behav* 89:53–62.
- Moglich M, Holldobler B, 1974. Social carrying behavior and division of labor during nest moving of ants. *Psyche* 81:219–236.
- Naug D, 2008. Structure of the social network and its influence on transmission dynamics in a honeybee colony. *Behav Ecol Sociobiol* 62:1719–1725.
- Naug D, 2009. Structure and resilience of the social network in an insect colony as a function of colony size. *Behav Ecol Sociobiol* 63:1023–1028.

- O'Donnell S, 1998. Effects of experimental forager removals on division of labour in the primitively eusocial wasp *Polistes instabilis* (Hymenoptera: Vespidae). *Behaviour* 135:173–193.
- Pinter-Wollman N, Hubler J, Holley JA, Franks NR, Dornhaus A, 2012. How is activity distributed among and within tasks in *Temnothorax* ants? *Behav Ecol Sociobiol* 66:1407–1420.
- Pinter-Wollman N, Hobson EA, Smith JE, Edelman EJ, Shizuka D et al., 2013. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav Ecol* 25:242–255.
- Pruitt JN, Pinter-Wollman N, 2015 The legacy effects of keystone individuals on collective behaviour scale to how long they remain within a group. *Proc R Soc B* 282:20151766.
- Robinson GE, 1992. Regulation of division of labor in insect societies. *Annu Rev Entomol* 37:637–665.
- Robinson GE, Page RE, 1989. Genetic basis for division of labor in an insect society. In: Breed MD, Page RE, editors. *The Genetics of Social Evolution*. Boulder, CO: Westview, 61–80.
- Robson SK, Traniello JFA, 1999. Key individuals and the organization of labor in ants. In: Detrain C, Deneubourg JL, Pasteels JM, editors. *Information Processing in Social Insects*. Basel, Switzerland: Birkhauser Verlag, 239–259.
- Robson SK, Traniello JFA, 2002. Transient division of labor and behavioral specialization in the ant *Formica schaufussi*. *Naturwissenschaften* 89:128–131.
- Stroeymeyt N, Franks NR, Giurfa M, 2011. Knowledgeable individuals lead collective decisions in ants. *J Exp Biol* 214: 3046–3054.
- Sumana A, Sona C, 2013. Key relocation leaders in an Indian queenless ant. *Behav Process* 97:84–89.
- Sumana A, Sona C, 2012. Studies on colony relocation in the Indian queenless ant *Diacamma indicum*. *Curr Sci* 102:1373–1374.
- 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.
- Visser PK, 2007. Group decision making in nest-site selection among social insects. *Annu Rev Entomol* 52:255–275.
- Wasserman S, Faust K, 1994. *Social Network Analysis: Methods and Applications*. New York (NY): Cambridge University Press.
- Williams R, Lusseau D, 2006. A killer whale social network is vulnerable to targeted removals. *Biol Lett* 2:497–500.
- Wilson EO, 1985. The sociogenesis of insect colonies. *Science* 228: 1489–1495.