Key relocation leaders in an Indian queenless ant

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ABSTRACT

Division of labor is a central feature in social insects, wherein, simple individuals come together in groups to perform tasks that could be quite complex. It is generally believed that individuals who perform a specific task are themselves simple, interchangeable units. However, the variances in the performances of these individual insects need to be explored in greater detail. In this study, individual specialization in the context of colony relocation was examined in the Indian ponerine ant *Diacamma indicum*. One ant termed the maximum tandem leader (Max TL) was found to have a key role. Max TL performed 24% of the adult relocation in the colony and recruited more tandem leaders than other leaders thereby contributing to the organization of the relocation. The Max TL's role in the relocation process was further examined by comparing control relocations with experiments in which the Max TL was removed during the relocation process. Even though all the colonies relocated successfully, the relocation dynamics was significantly altered in the absence of the Max TL. We find that a single individual, the Max TL, takes up roles of a performer, organizer and catalyst during the colony relocation process, which challenges the norm that all workers are equal.

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1. Introduction

A central theme in organized societies is the division of labor (Wilson, 1971). In social insect colonies division of labor is considered as the means by which work efficiency can be increased by allowing individuals to specialize on fewer tasks (Oster and Wilson, 1978). While morphological differences generally accompany specialization of reproductive and non-reproductive castes within the colony, morphological differences are not so common among the non-reproductive castes (Anderson and McShea, 2001). Division of labor among non-reproductive workers is brought about by age, context or genetic predisposition and is considered to be more flexible (Wilson, 1976; Lenoir, 1987; Robinson, 1992; Stuart, 1997). Even though individuals themselves are not very complex, they achieve very complex tasks by following simple principles of self organization (Fresneau and Dupuy, 1988; Jeanne, 1988). For example pattern formation in the context of foraging, construction of pillar and distribution of brood within social insect colonies like honeybees has been examined by means of experiments and simulations to understand the self organizing processes involved (Deneubourg and Goss, 1989; Deneubourg et al., 1990; Bonabeau et al., 1997; Camazine et al., 2001).

There is prior evidence indicating that individuals forming the worker caste are not necessarily simple interchangeable homogenous units (Gordon, 1996; Calabi and Traniello, 1989; Langridge et al., 2007; Dornhaus et al., 2008; Sumpter, 2006). Furthermore, there is a disparity in the proportion of individuals involved in the task and the proportion of work they contribute (Lindauer, 1952; Herhers, 1983; Schmid-Hempel, 1990). Individuals that showed exceptionally high levels of activity as compared to other members within the same age-size cohorts were defined as "elites" (Oster and Wilson, 1978). In an attempt to make this definition more functional and quantitative, Robson and Traniello (1999) defined behaviorally specialized individuals as those who perform a given behavior far more frequently than others of similar age or group engaged in the same activity. Some studies have found individual specialization in ant colonies. In the context of colony emigration, transport specialists have been recorded in *Temnothorax albipennis* (Dornhaus et al., 2008), *Tapinoma erraticum* (Meudec, 1977), *Formica sanguine*, *Formica fusca* and *Camponotus sericeus* (Moglich et al., 1974). In the context of foraging, the ponerine ant *Ectatomma ruidum* Roger has been recorded to have 31% foragers specialized in collecting honey and 15.4% specialized in collecting protein sources (Schatz et al., 1995). In the harvester ant *Pogonomyrmex rugosu*,

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individuals specialized on a single species of seed (Rissing, 1981). Differences in the rate of undertaking were observed in *Acromyrmex versicolor* with a small number of ants specializing on the task and performing this task with a higher efficacy (Julian and Cahan, 1999). In *Formica schaufussi* it was observed that the individual ant that located prey also played an important role in organizing the prey retrieval by colony members and the removal of this ant resulted in a failure to retrieve prey (Robson and Traniello, 2002).

Robson and Traniello (1999) proposed the key leader concept in an attempt to characterize the different roles played by individual members involved in a task. They classified individuals into three categories: performers, catalysts and organizers. Very active individuals who performed a large proportion of the task were termed as performers and example of this category has been documented among transport specialists in the context of nest relocation mentioned earlier. Individuals who influence the cohesion of the group performing a task were termed as organizers and examples of this category has been documented in the context of successful retrieval of prey in *F. schaufussi* (Traniello and Beshers, 1991; Robson and Traniello, 1998). Individuals whose activities increased the rate at which the task is executed were termed as catalysts and examples of this category has been documented in the context of shaking behavior in honeybees (Biesmeijer, 2003) and during excavation in *Camponotus japonicas* (Chen, 1937).

Ant colonies move from their old nest into new nest for various reasons and this relocation is more common than has been underscored in the literature (McGlynn, 2012). Relocation is an important component of the natural history of ants and is essential for its survival and reproduction (Visscher, 2007). This clearly defined event can be initiated in the laboratory and its dynamics are amicable for a comprehensive study, unlike some other tasks like foraging or brood care. How colonies assess the quality of different nests available in the environment and the influence of the quality of the old nest on their choice has been studied in addition to how they converge on plausibly the best option both in honey bees and *Temnothorax* sp. (Seeley and Buhrman, 2001; Sumpter and Pratt, 2009; Stroeymeyt et al., 2011). Thus, the relocation process provides a useful platform to explore the involvement and influence of individual members in an important aspect of colony dynamics.

In the current study, colony relocation has been examined in *Diacamma indicum*, a ponerine ant that has been found in Sri Lanka, South India and East India. In this queenless ant the role of reproduction is taken up by a single mated female called gamergate. It is noteworthy that all females in this species are born with a pair of thoraxic appendages termed gemma. On eclosion these appendages are mutilated by the gamergate of the colony thus designating her to the role of a worker – as she will not be able to mate or lay diploid eggs (Peeters and Higashi, 1989; Peeters and Billen, 1991; Karpagakunjaram et al., 2003). In *D. indicum*, a majority of the females including the gamergate are tandem run from their old to their new nest while the brood and other males are carried in both laboratory and field based relocations (Kaur et al., 2012; Sumana and Sona, 2012). Tandem running was first described by Adlerz (1896) and is known to be used for recruitment in the context of defense, slave raids and prey retrieval (Hölldobler and Wilson, 1990). This stereotypical behavior is used by leaders to lead members of their colony from one place to another, one follower at a time. In this study we focused on the manner in which individuals that are informed of the new site – i.e. tandem leaders – allocate the work load. We compared the activities of individual tandem leader during relocation by conducting control and manipulative relocations in which one individual – Max TL was removed during the relocation. By contrasting the dynamics of the relocation in these contexts we examined the contribution of this individual to the relocation process.

2. Materials and methods

Twelve colonies of *D. indicum* were collected between June and November 2010 in Mohanpur (Nadia district, West Bengal, India, 22°56′N, 88°31′E). All individuals were marked with unique combinations of enamel paints (Testors, Rockford, IL, USA) to allow individual identification. The gamergate was identified in all of the 12 colonies by the presence of gemmae on her thorax. Colonies were composed of adults (ranging from 59 to 149 with an average of 89.1 and standard deviation of 26.6), pupae (15.8 ± 9.1), larvae (8.8 ± 5.6) and eggs (24.1 ± 16.2).

In order to study emigration all the adults and brood of the colony were placed in a plastic box ($20\,cm \times 34\,cm \times 12\,cm$) which had a plaster of Paris base. In one corner of this box a circular chamber (with a diameter of $9\,cm$) was created in the plaster of Paris and covered with a glass petri plate to act as the nest chamber. Colonies were supplied with *ad libitum* termites, honey water and ant cake (Hölldobler & Wilson, 1994). In order to initiate relocation in both the control and manipulated experiments the nest chamber was disturbed by removing the Petri plate cover and placing a table lamp over the nest chamber. This lack of shelter and increased light in the nest chamber trigged relocation in every case studied and was thus used as a standard method in all colony relocation experiments (Sumana & Sona, 2012). Colonies were provided with another identical plastic box and a covered nest chamber at the end of a wooden bridge that was 152 cm long. The process by which ants moved into the new nest was recorded by both direct observations and a video camera. Focal observations were made on tandem running behavior. Ants that initiated tandem running were defined as tandem leaders and ants that accepted the leaders' invitation for tandem running and followed were defined as followers. Thus, for every tandem run there was a leader and a follower. We recorded the identity of leaders and followers, the destinations and the time at which each tandem run was initiated. Tandem runs which were unsuccessful in reaching the new nest were not considered for further analysis.

Each of the 12 colonies used in this study were subjected to two relocation (control or manipulated) in a random order. One in which the colonies were allowed to move into the new nest without any disturbance – these experiments were termed as control relocations. In a set of manipulated experiments, termed as Max TL removal relocations, colonies were at first allowed to explore and start tandem running. The number of tandem runs performed by different tandem leaders was tabulated every 10 min and when one individual showed a higher number of tandem runs compared to others (a minimum of 2 tandem runs higher than other leaders), she was designated as maximum tandem leader (Max TL). The identified Max TL was then removed while on a return trip from the new to the old nest – when she did not have any followers – ensuring minimal disturbance to the relocation.

The Max TL removal time was recorded as T_m for each colony. Across 12 colonies T_m ranged from 10 to 33 min and the average and standard deviation was 20.2 ± 6.8 min. Therefore in the Max TL removal experiment, for each colony, the relocation data were divided into two categories; pre-removal with no interference and post-removal with the Max TL absent. In order to compare the relocation dynamics with and without the Max TL, the data collected from the control relocation were *post facto* divided into pre-removal and post-removal periods using the T_m for the colony. Thus we were able to compare the pre-removal and post-removal periods separately in the Max TL leader removal experiment with that of the control experiment, both of which was carried out on the same colony. Designing the analysis in this way allows our findings to be generic, and independent of any inherent temporal dynamics in the relocation process.

For the purpose of the analysis, tandem leaders were divided into three categories; maximum, average and recruited tandem leaders. The maximum tandem leader (Max TL) is the ant that shows the highest number of tandem runs in the colony in control relocation or in the pre-removal period in the manipulated relocation. All other tandem leaders were categorized as average tandem leaders (Avg TL). This category was characterized by the average value of tandem runs. Followers that became tandem leaders were termed as recruited tandem leaders and the leader that tandem ran them to the new nest for the first time was recorded as the recruiter. Since the total number of tandem runs varied across colonies, we used the percentage of tandem runs to make comparisons across colonies.

How the new nest was discovered, when it was discovered and when tandem running was initiated was deduced for individual ants using the following method. We tracked the identity of all ants entering the new nest until the initiation of tandem running. With this background information, once tandem running started, we were able to find out the identity of all the ants that found the new nest by explorations and those that found the new nest by following other leaders. With this same information we were also able to identify the first ant to locate the new nest and so forth which enabled us to assign discovery ranks to individuals in the relocation process. The ant that discovered the new nest first was given rank one and so on. Having discovered the new nest some individuals started tandem running soon after and we were able to assign tandem running ranks based on when they started tandem running. The leader, who started tandem running first, was assigned the first rank and so forth. Focal observations/recordings were carried out on tandem running until the majority of adults and all the brood had been transported to the new nesting site. A total of 1959 tandem runs, performed by 368 tandem leaders across 12 colonies were observed and analyzed in the course of this study.

In the ensuing analysis, all descriptive statistics are average and standard deviation unless mentioned otherwise. Non-parametric statistical tests were used for comparisons and StatistiXL (version 1.8) was used for conducting them.

3. Results

Maximum tandem leaders were found to play a critical role in the relocation dynamics. Max TL discovered the new nest by independent exploration in 23 of the 24 relocations. In one relocation, the Max TL was led to the new nest by another tandem leader. Max TL was the first to discover the new nest in 7 of the 24 emigrations. Max TLs' discovery rank was 2.92 ± 1.61. Max TL was the first to start tandem running in 15 of the 24 colonies and Max TL's tandem running rank was 1.4 (± 0.6). In the control colonies, Max TL performed $24.2\% \pm 10.5\%$ of the tandem runs during the relocation and it ranged from 10.6% to 43.2%. Max TL performed significantly more tandem runs (Wilcoxon paired samples test, $T = 0$, $n = 12$ and $p = 0.0001$) as compared to Avg TL ($6.7\% \pm 2.5\%$) and the second ranking tandem leader (Wilcoxon paired samples test, $T = 0$, $n = 12$ and $p = 0.0001$) who performed $16.4 \pm 4.7\%$ of the tandem runs.

There was no significant relationship between colony size and percentage of tandem running performed by the Max TL (Spearman rank correlation, $r_s = -0.42$, $df = 12$ and $p = 0.2$). In two of the twelve colony relocations examined in this study the same individual became the Max TL in both control and experimental relocation. Thus in the majority of the colonies the same ant did not become the Max TL in two successive relocations indicating that the Max TL is not predetermined but plausibly emerges spontaneously when the colony is faced with relocations.

The reliability of the method used to identify the Max TL in the Max TL removal experiments was checked using the dataset
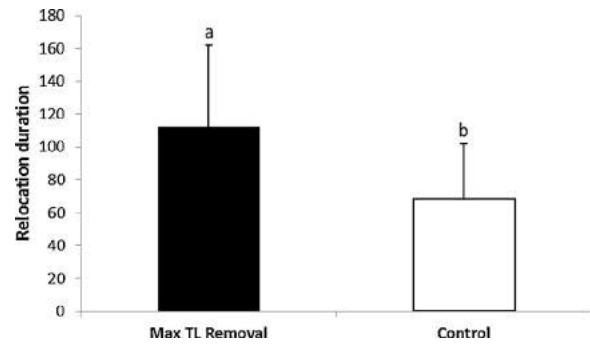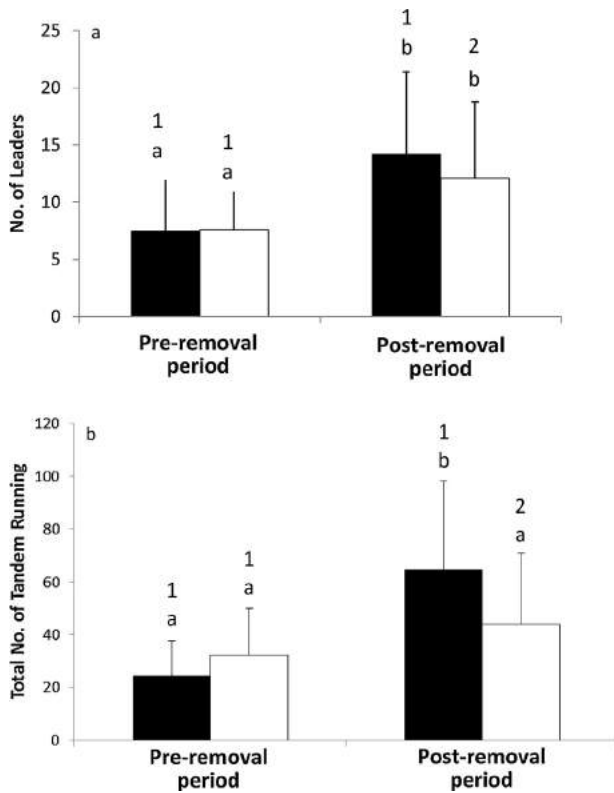

Fig. 1. Mean (±standard deviation) time taken (in minutes) for nest relocation in control relocations (white bar) and in relocations in which Max TL was removed (black bar). Bars carrying different letters are significantly different, Wilcoxon paired test, $T = 11$, $p = 0.027$, $n = 12$.

obtained from the control colonies. In 6 out of 12 colonies the ant identified as the major leader in t_m was ranked 1 in her contribution to the total tandem running performed in her colony. In the remaining 6 colonies the ant identified as Max TL in t_m was ranked either 2nd or 3rd in terms of her overall contribution to tandem running. The average rank of the tandem leaders in the control experiment (that would have been removed had this been the Max TL removal experiment) was 1.60 ± 0.81.

Let us now discuss the impact of Maximum leader removal. In the absence of the Max TL all the 12 colonies relocated successfully. However the relocation dynamics was different as compared to control colonies. The time taken for relocation to be completed was significantly longer in Max TL removal relocations as compared to control relocations (Fig. 1). Max TL removal relocations on average took $21 \pm 34\%$ longer than control relocations to complete. Both the number of leaders and the number of tandem runs were impacted by the absence of the Max TL. The number of leaders participating in the relocation was significantly higher in the Max TL removal relocations in the post-removal period in both the control and Max TL removal relocations (Fig. 2a). In addition, in the absence of the Max TL significantly more tandem leaders participated in the process as compared to controls (Fig. 2a). The number of tandem runs also showed a similar pattern. In the absence of Max TL, the number of tandem runs increased significantly and this was also significantly higher than the control experiments (Fig. 2b).

The number of tandem runs performed by average leaders increased significantly in the post-removal period in the absence of the Max TL. In relocations from which the Max TL was removed the Avg TL performed 5.4 ± 3.2 tandem runs in the post-removal period, while they performed 2.9 ± 1.6 tandem runs in the pre-removal period (Wilcoxon paired sample test, $T = 10.5$, $n = 12$, $p = 0.02$). In control relocations there was no difference in the tandem runs performed by average leaders during the pre-removal (3.5 ± 1.7) and post-removal period (5.1 ± 4.5) (Wilcoxon paired sample test, $T = 29$, $n = 12$, $p = 0.5$). Gamergate movement was not impacted in the absence of the Max TL. In control relocations she was taken to the new nest at $27.9 \pm 17.5\%$ of the duration it took for the whole colony to relocate, while in relocation experiments with Max TL removed the gamergate was relocated at $52.1 \pm 15.8\%$ (Wilcoxon paired sample test, $T = 20$, $n = 12$, $p = 0.15$).

The presence of the Maximum tandem leader was also found to be a positive influence through other factors. The rate of nestmate transfer (number of nestmates transferred per leader per minute) from the old to the new nest decreased significantly in the absence of the Max TL (Fig. 3), while in control relocations there was no significant difference. Some members of the colony strayed out from the new nest and had to be tandem run to the new site more than once. The fraction of these repeat tandem runs (0.2 ± 0.01)
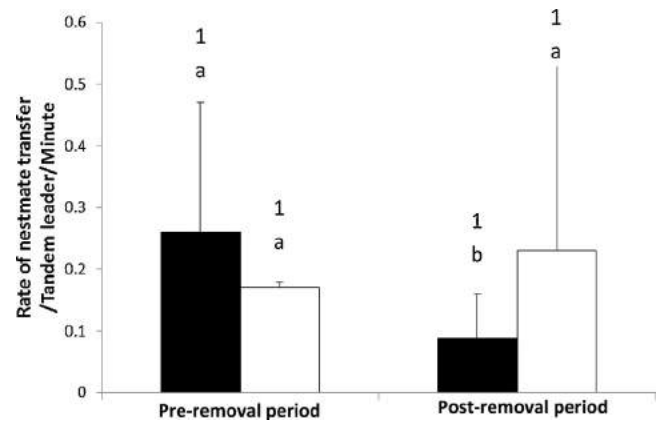
Fig. 3. Mean (±standard deviation) rate of nestmate transfer per tandem leader per minute during the pre- and post-removal period in control relocations (white bars) and Max TL removal relocations (black bars). Comparisons were carried out within the pre- and post-removal categories in the Max TL removal ($T = 5$, $p = 0.005$, $n = 12$) and control relocations ($T = 39$, $p = 1$, $n = 12$) by Wilcoxon paired test. Bars carrying different letters are significantly different. Comparisons across the control and Max TL removal relocations were carried out by Wilcoxon paired test separately for pre-removal period ($T = 25$, $p = 0.32$, $n = 12$) and post-removal period ($T = 19$, $p = 0.13$, $n = 12$) and bars carrying different numbers are significantly different.

Fig. 2. (A) Mean (±standard deviation) number of tandem leaders participating during the pre- and post-removal period in control relocations (white bar) and relocations with Max TL removed (black bar). Comparisons were carried out between pre- and post-removal categories within the control relocations ($T = 12.5$, $p = 0.04$, $n = 12$) and Max TL removal relocations ($T = 0$, $p = 0.001$, $n = 12$) by Wilcoxon paired test and bars carrying different letters are significantly different from each other. Comparisons across the control and Max TL removal relocations were carried out by Wilcoxon paired test separately for pre-removal period ($T = 36$, $p = 0.9$, $n = 12$) and post-removal period ($T = 11.5$, $p = 0.03$, $n = 12$) and bars carrying different numbers are significantly different. (B) Mean (±standard deviation) number of tandem running during the pre- and post-removal period in control relocations (white bar) and Max TL removal relocations (black bar). Comparisons were carried out between pre- and post-removal categories within the control relocations ($T = 23$, $p = 0.23$, $n = 12$) and Max TL relocations ($T = 2$, $p = 0.002$, $n = 12$) by Wilcoxon paired test and bars carrying different letters are significantly different. Comparisons across the control and Max TL removal relocations were carried out by Wilcoxon paired test separately for pre-removal period ($T = 22.5$, $p = 0.21$, $n = 12$) and post-removal period ($T = 10$, $p = 0.02$, $n = 12$) and bars carrying different numbers are significantly different.

was significantly higher (Wilcoxon paired sample test, $T = 13$, $n = 12$, $p = 0.04$) in the post-removal period as compared to pre-removal period (0.11 ± 0.08) in the Max TL removal experiment. In the control relocations the fraction of repeat tandem runs in the post and pre-removal period were 0.12 ± 0.1 and 0.14 ± 0.08, not significantly different (Wilcoxon paired sample test, $T = 29$, $n = 12$, $p = 0.5$). The involvement of the Max TL in recruiting new tandem leaders was examined by quantifying the number of her followers that became tandem leaders in the control relocations. It was found that Max TLs recruited significantly higher number of leaders as compared to average TLs (Fig. 4).

4. Discussion

In the current study we demonstrate that in *D. indicium*, a single individual – the Maximum tandem leader - plays a very important role in the colony relocation dynamics. By removing a single individual (Max TL), who is typically amongst the top three contributors to the colony relocation, we were able to quantify her importance further. Max TL influenced the relocation process in three ways. Firstly, they were one of the first to discover the new

nest and start tandem running and they performed a large part of the tandem runs that occurred in their colony. Secondly, they enhanced the efficiency of colony relocation. In their absence, the colony's rate of relocation decreased, the number of repeat tandem running increased. Additional time, higher number of leaders and more work by other leaders was required to complete the relocation. Thirdly, Max TL influenced the relocation process by recruiting more of their followers to become leaders.

Thus, in *D. indicium*, Max TL can be assigned the roles of a performer, a catalyst and organizer of relocation. Even though in other studies individual specialization has been seen in ant colonies in different contexts (reviewed in the introduction), to the best of our knowledge there is no report of an individual influencing an activity in the role of a performer, catalyst and an organizer.

Colony size usually influences task specialization and individual specialization (Gautrais et al., 2002; Bourke, 1999; Anderson and McShea, 2001; Thomas and Elgar, 2003; Jeanson et al., 2007; Dornhaus et al., 2008). In *T. albipennis*, a highly active individual played a relatively important role during relocation only in small colonies (Dornhaus et al., 2008). In *D. indicium*, Max TL's contribution to relocation as measured by her contribution was not correlated to colony size. Another factor that can influence the work distribution and individual specialization is the total amount of work that requires to be done. In experiments in which *D. indicium* colonies
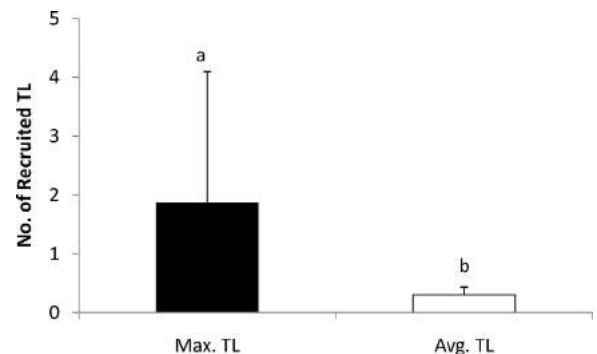
Fig. 4. Mean (±standard deviation) number of recruited tandem leaders by Max TL (black bar) and Avg TL (white bar). Bars carrying different letters are significantly different, Wilcoxon paired test ($T = 4$, $p = 0.003$, $n = 12$).

had to relocate over a short distance (30 cm) it was observed that fewer tandem leaders were involved and that in 1 of 12 relocations the Max TL performed 100% of the tandem running (Sumana and Sona, 2012).

What is intriguing is that a-priory identification of the Max TL was not possible in pilot experiments and as seen in the current study, only in 2 of the 12 colonies the same individual became the Max TL in two subsequent relocations. There seems to be some flexibility in individuals becoming tandem leaders in general, and particularly, in taking up the position of Max TL. Unlike in *F. schaufussi*, where cooperative prey retrieval comes to a stop on removing the individual who discovers and initiates the process (Robson and Traniello, 2002), in *D. indicum* we find that relocation is completed even in the absence of the individual who contributes to the process in multiple capacities. Thus, we postulate that Max TLs are not qualitatively different from other tandem leaders, but show quantitatively enhanced performance over the duration of one relocation. More studies characterizing the activity of tandem leaders in multiple relocations as well as before relocations is required in order to completely understand the role of the Max TL. Due to this unpredictability, a relatively complicated procedure was adapted to predict the Max TL in each of the relocations. However the robustness of our procedure was verified by examining the control experiment and it was found that in 6 of the 12 colonies we correctly identified the Max TL based on the early dynamics. The Max TL removal experiments clearly demonstrated that the loss of this one individual ant significantly impacted the relocation process.

In conclusion, our study questions the general validity of the dogma that all individuals performing a specific task in social insect colonies are interchangeable units and demonstrates that some individuals have much greater impact on colony functionality than others. However, our study also hints at the intriguing possibility that leaders are not born, but emerge dynamically when a society is faced with a challenging task or situation. Clearly, further studies paying closer attention to individual members of the colony and their relative contributions to different aspects of colony dynamics are necessary to conclusively establish the quality of leaders, how they come to be and what role they play in the societal dynamics. Procedural limitations and the challenges of individual level observations and book-keeping could prove to be hurdles toward such explorations, especially in highly eusocial societies. Nonetheless, such studies would be essential to examine individual specialization and the findings could potentially challenge basic principles of division of labor.

Acknowledgments

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