



## Leaders follow leaders to reunite the colony: relocation dynamics of an Indian queenless ant in its natural habitat

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Several factors cause animals to relocate. In this context, ant species are unique in that they not only have to relocate adults, but they must also move their brood while maintaining colony cohesion. We explored the colony relocation dynamics of the ponerine ant *Diacamma indicum* in its natural habitat. Irrespective of whether ants relocated from their original nest in their natural habitat or from a nestbox in an unfamiliar but natural habitat, colonies experienced fission and multiple fragmentations. However, this fission was transient, and the colonies eventually unified at a single site. The movement of the ants did not exhibit any directional preference, and the gamergate did not enjoy any special attention during the relocation process. Tandem running, a behaviour in which one ant leads a follower ant from one site to another, was used to relocate about 96% of the colony members, and 28% of the colony became tandem leaders on average. The evacuation phase was significantly shorter than the reunification phase, and this may be an adaptive response to a disturbance in the ant's dwelling. Unlike other ants, the leaders were sighted at most of the temporary sites and thus, in principle, had the opportunity to compare the conditions of alternative sites directly. Most leaders discovered the final site by following other leaders; leaders following leaders occurred throughout the relocation process and constituted 30% of the total tandem runs. In the context of these experiments, the colony relocation and reunification dynamics of ants in their natural habitat are discussed.

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Whether they are simple or complex in their design, nests are important to the organisms that occupy them. For many organisms that use nests to rear their immature young, nests provide protection from predators and shelter from adverse changes in the environment. Although organisms expend significant resources in nest construction, sometimes nests need to be evacuated. Environmental disturbance, increased predation and dwindling resources are some of the factors that cause animals to change their nesting site. Social insects such as ants, bees and wasps are examples of species in which nests play a central role, both for rearing their immature young and for storing resources. For these species, nest relocation would be a complex endeavour, as a large number of nestmates and stored resources would need to be transported from one site to another. Ants also need to transport their immature young (egg, larva and pupa) which are particularly vulnerable and represent a significant ratio of the colony's resource investment (Hölldobler & Wilson 1990; Visscher 2007). Despite the costs involved, relocation is necessary for colony reproduction to

occur in some species of social insects. Honeybees, swarm-founding wasps and some species of ants reproduce by colony fission. In this process, the reproductive class and a subset of workers split from the parental colony and disperse to initiate the formation of another colony (Wilson 1971; Banschbach & Herbers 1999; Peeters & Ito 2001; Cheron et al. 2011).

The process of nest relocation has been studied in few species of social insects. Previous research has addressed different aspects of relocation, including the assessment of the quality of new nesting sites, convergence-related decision making for available sites and the flight mechanics of relocating honeybees (Camazine & Visscher 1999; Seeley & Buhrman 1999; Seeley & Buhrman 2001; Seeley 2003; Schaerf et al. 2011). In contrast to honeybees, ants need to transport their brood during the relocation process, making the relocation of ant colonies a more complex process. Ants also lack the dance language that enables honeybees to share information with their nestmates regarding various nesting sites in their environment (Seeley 2010).

Instead of mass movement to a new site, as occurs in honeybees (Visscher 2007), most ants use chemical trails to demarcate the path to a new nest (Hölldobler & Wilson 1990) while others use either carrying and/or tandem running (Hölldobler & Wilson 1990). During tandem running, an ant leads a nestmate to a new location while

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maintaining physical contact (Adlerz 1896). In species of ants that use tandem running, the entire process of relocation is dependent on tandem leaders. Often, tandem leaders recruit other leaders at the beginning of the relocation process to accelerate the rate of nestmate transfer, as has been observed in *Temnothorax rugatulus* (Möglich et al. 1974; Möglich 1978; Hölldobler & Wilson 2009).

The process of nest site relocation has been studied in only a few species of ants. The nest site selection process of *Temnothorax albipennis* shows several similarities to that found in the honeybee *Apis mellifera*; however, there are also significant differences between the two (Franks et al. 2002; Visscher 2007). A study of the relocation process in the ant species *Aphaenogaster senilis* found that colony members reach the new colony site by walking there, rather than being carried or through tandem running. The accumulation of colony members at the new location follows a sigmoid curve (Avargues-Weber & Monin 2009).

Most studies of nest relocation in ant species have been performed in the laboratory under controlled conditions. As a result, there is a lack of information on the behaviour of individual ants when relocating under more natural conditions. Relocation is difficult to observe in a natural setting owing to the unpredictability of natural relocation occurrences and the difficulty of marking and tracking individual ants. Some field studies have focused on nest site characteristics (Thomas 2002) and relocation frequency, which can range from a few days to a decade (Smallwood 1982; Fowler 1986; Tsuji 1988; Briano 1995; Brown 1999; Cerdá et al. 2002; McGlynn et al. 2004). In other field studies, relocation was caused primarily by environmental disturbances (Wheeler 1910; Hölldobler & Wilson 1990; Briano 1995), while nomadic lifestyle, increased competition (Gordon 1992; Brown 1999) and severe predatory pressure was also found to cause relocation (Wheeler 1936; Wilson 1958; Hays et al. 1982; McGlynn et al. 2004; McGlynn 2006; Dahbi et al. 2008; Boulay et al. 2010).

*Diacamma indicum*, our model system for the current study, is a queenless ponerine ant found in the south and east of India and in Sri Lanka. They form colonies in which the eggs are laid by a mated worker called the gamergate (Wheeler & Chapman 1922). Very little is known about this ant species except that it has a constant species-specific chromosome number and that its genetic variability is lower than that of other sympatric species (Viginier et al. 2004; Karnik et al. 2010). Colony relocation in a closely related species, *Diacamma rugosum*, has been studied under laboratory conditions by Fukumoto & Abe (1983). They found that tandem running was the only means used for relocation and that 5–25% of the colony became tandem leaders.

In this study, we examined the relocation mechanism used by *D. indicum* in its natural habitat. We performed two sets of relocation experiments in which we artificially stimulated the colony to vacate their old nest. In the first experiment, colonies (unmarked ants) relocated from native nests in their original habitat. In the second experiment, colonies (of individually marked ants) relocated from artificial nests placed in an unfamiliar, but natural habitat. This allowed us to assess qualitatively the overall process of relocation in the ants' undisturbed natural terrain and subsequently observe the mechanism of relocation at the scale of individual colony members.

## METHODS

Eighteen colonies of *D. indicum* were identified in Mohanpur (Nadia district, West Bengal, India, 22°56'N, 88°31'E) between March 2010 and December 2011. We conducted two experiments with these colonies in their natural habitat. In the first experiment, referred to as the dislodging experiment, colonies were made to relocate from their original nests. In the second experiment,

referred to as the displacement experiment, colonies were made to relocate from nestboxes placed in a location different from their collection site. In the dislodging experiment, eight colonies were allowed to relocate in their natural habitat by application of water stress. Qualitative observations were made of the relocation process, and focal observations were made of incidences of tandem running. Water was initially sprayed and later poured into the nest to initiate the relocation. This caused the ants to evacuate the nest with or without brood in their mandibles. While some of these individuals waited at the nest entrance, others dispersed. Soon after finding a suitable shelter, scouts started tandem running colony members into multiple shelters (temporary sites), thus causing colony fission. The number of temporary sites occupied and the different parameters of the temporary sites, such as the nature of the site and the minimum distance and compass direction from the original nest entrance, were noted. Later, ants from these temporary sites merged into one shelter (final site). The final site was defined as the location to which the majority of the colony members converged, and it required ants from temporary sites to relocate to it, although some temporary sites became the final site. The sites from which tandem runs initiated and terminated were recorded. Once the temporary sites were vacated and there were no tandem runs for 30 min, we considered the relocation process to be complete. In cases where the colony did not merge but dispersed to different shelters, we followed ant activities for 6 h and all colonies reunified within this time period. Subsequently, the colonies were observed sporadically over the next 24 h to confirm that no further relocations took place.

In the displacement experiment, 10 colonies were collected and all of the ants were marked with unique combinations of enamel paint colours (Testors, Rockford, IL, U.S.A.) to allow individual identification. In all colonies, the gamergate was identified by the presence of gemma. Colonies consisted of  $81.5 \pm 34.2$  adult females (mean  $\pm$  SD, range 36–133) and  $64.7 \pm 38.4$  (range 19–133) different stages of brood. Each marked colony was placed in a plastic box (28.5  $\times$  21.5 cm and 12 cm high) with a plaster of Paris base and a circular nest chamber (10 cm in diameter) and provided with ad libitum water, honey, ant cake (Hölldobler & Wilson 1994) and termites. One wall of the plastic box had a circular exit (2 cm diameter), which was closed with a cotton plug until the start of the experiment. Colonies were housed in the laboratory for a period of  $17 \pm 15$  (range 1–45) days before the start of the relocation experiment. An area measuring 30.2  $\times$  19.5 m was identified before the start of the experiment as the release area. The release area was selected based on the following three criteria: relatively sparse undergrowth, low human activity and the presence of *D. indicum* colonies in the surrounding area. On the day of the relocation experiment, the colony was placed on a sand bed in the release area without the glass cover on the nest chamber. Similar to other laboratory-based studies, the standard treatment of removing the top glass cover was applied to stimulate colony relocation (Sendova-Franks & Franks 1995).

The process of colony fission and fusion was tracked by conducting focal observations on tandem running of individually marked ants. The movement of ants from the release site to the temporary sites was classified as evacuation. The evacuation phase starts with the first tandem run out of the release site and ends when the release site is vacated by the ants. The movement of ants from the temporary sites into one final site was categorized as re-establishment. The re-establishment phase starts when tandem running is initiated from the temporary sites to the final site and ends when no tandem running is observed at the final site for at least 30 min. To determine the length of the evacuation phase, it was essential to ensure that the release site was vacated by all of the ants. This was not possible in the dislodging experiment, and we

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