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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.

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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