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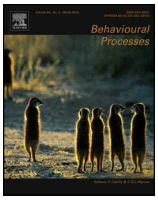

Key relocation leaders in an Indian queenless ant

Annagiri Sumana[a,*], Chandan Sona[b]

[a] Behaviour & Ecology Lab, Department of Biological Sciences, Indian Institute of Science Education and Research, Mohanpur, Kolkata 741252, West Bengal, India
[b] National Institute of Science Education and Research, Institute of Physics Campus, Bhubaneswar 751005, Orissa, India

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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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* Corresponding author. Tel.: +91 33 25873118–25873121x206; fax: +91 33 25873122.
E-mail addresses: sumana@iiserkol.ac.in, annagiri.sumana@gmail.com (A. Sumana).

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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 × 34 cm × 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.

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