Coupled adult-brood transport augments relocation in the Indian queenless ant *Diacamma indicum*

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Abstract Colony relocation is an important aspect in the lives of social insects. In ants, the process of relocation is further complicated as brood, in addition to adults, have to be transported to the new nest. Here, we have investigated brood transport in the Indian ponerine ant *Diacamma indicum*, which uses tandem running—a primitive mode of recruitment—for the entire colony to relocate. We have found that there were no brood transport specialists and most of the brood was transported in the mandibles of followers that were being tandem run. Therefore, in a single tandem run, one adult and one brood item was effectively transported by tandem leaders augmenting the relocation process.

Keywords Transport specialist · Tandem running · Colony relocation

Social insects deal with the something of relocating their nests as an essential part of their survival and reproduction (Hölldobler and Wilson, 1990). Unlike honeybees and social wasps which lodge their brood (egg, larva and pupa) in cells, ants maintain their brood in a common pile, and thus this large investment is amenable for transport during relocation. In ants that use chemical trails, workers carry the brood from the old to new nest (Meudec and Lenoir, 1982; Bouchet and Peeters, 2013). *Temnothorax albipennis* lacks brood transport specialists (Dornhaus et al., 2008), uses tandem running in the beginning of the relocation but later

switches to carrying both adults and brood. In species that use only tandem running for relocation like many ponerine ants (Fukumoto and Abe, 1983), a leader who has the knowledge of the new nest invites a single follower ant to tandem run while maintaining physical contact throughout the journey (Franklin, 2014). This time consuming process that is dependent on a few leaders is considered a primitive form of recruitment (Wilson, 1959). In this study, we use an ant species that uses only tandem running and investigate how the brood was transported.

Twelve colonies of D. indicum were collected from Mohanpur (Nadia district, West Bengal, India, 22°56'N, 88°31'E) during February 2011 to October 2011. Colonies contained 23-147 adults (median 90.5 adults, quartile 52-118.2 adults), a gamergate and brood in various development stages (median 23.5 brood, quartile 12-52 brood). All members of a colony were uniquely marked and housed inside the laboratory (Kaur et al., 2012). The old and new nest were placed at two random corners of a rectangular arena (1.45 m \times 1.75 m) that was filled with a mixture of sand and soil. Relocations were initiated by removing the glass cover from the old nest. Ants explored the arena, discovered the new nest and initiated transport. Focal observations were conducted on all transport events and the identities of the transporter, follower and brood (if any) were recorded. Observations were terminated when all brood items were transported and there were no tandem runs for 30 min. Three different types of transporters were identified. Adult transporter: tandem leaders that only tandem lead other adults who did not carry anything in their mandibles. Brood transporters: ants that only carried brood items (egg, larvae and pupae). Adult + brood transporters: tandem leaders that transported both adults and brood. The brood transport by adult + brood transporters were divided into two categories based on the manner it was transported. Directly, if

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tandem leaders carried brood in their mandible (ABT) and indirectly, if tandem leaders led a follower who was carrying brood (ABT*). Tandem leaders that led a follower that was carrying brood were termed indirect brood transporters. Statistics was performed using statistiXL1.10. In the course of this study we examined 1,205 transport events by 141 transporters from 12 colonies which contained 1,019 individual ants.

Brood transportation (median 73.5 min, quartiles 45.5-216.0 min) was initiated significantly later than quartiles adult transportation (median 69.0 min. 32.0-186.2 min, Wilcoxon paired sample test: T = 0.001, N = 12, p = 0.001). The overall duration of the brood transport (median 33.5 min, quartiles 25.2-38.7 min) was significantly shorter than the duration of adult transport (median 61.5 min, quartiles 54.7–82.5 min, Wilcoxon paired sample test: T = 0.001, N = 12, p = 0.001). Only a median of 14.7 % workers (quartile 9.6–21.4 % workers) of the colony became transporters and relocated either an adult or a brood or both. The gamergate was never observed carrying any brood item. Among the transporters, those that transported both adults and brood (i.e. adult + brood transporters) were significantly higher (even after applying the Bonferroni correction for multiple comparisons) than brood transporters (Wilcoxon paired sample test: T = 0.001, N = 12, p = 0.001) or adult transporters (Wilcoxon paired sample test: T = 1.0, N = 12, p = 0.001, Fig. 1a). Brood transporters transferred only a median of 0.0 % brood (quartiles 0-1.7 % brood) which was significantly less than a median of 100.0 % brood (quartiles 98.3-100.0 % brood) transported by adult + brood transporters (Wilcoxon paired sample test: T = 0.001, N = 12, p = 0.0001). Indirect brood transport was significantly more (Wilcoxon paired sample test: T = 0.001, N = 12, p = 0.0001) than direct brood transport (Fig. 1b).

Thus, in *D. indicum* tandem running allows tandem leaders to transport two components—an adult and a brood item—in a single trip. In sharp contrast, in *Temnothorax albipennis*, brood and adults are transported separately (Dornhaus et al., 2008). In *Aphaenogaster senilis*, adults are known to walk along a chemical trail with brood in their mandibles (Avargues-Weber and Monnin, 2009)—which is somewhat analogous to *D. indicum*. Like other ants studied so far, brood transport specialists were absent in *D. indicum* also. Even though brood transport started later than adult transport in all the 12 colonies studied, there was a large overlap between adult and brood transport due to the coupling of the two.

Ants' ability to move a large part of the colonies' investment enables them to be more vagile as compared

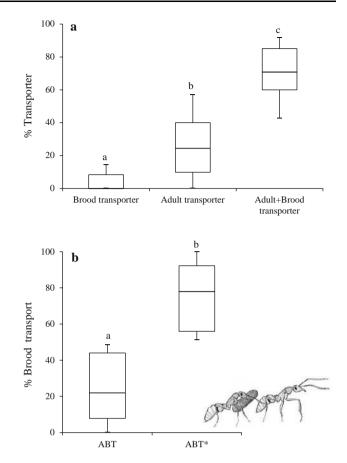


Fig. 1 Types of transporters and mode of brood transport: *Box* and *whisker* plot representing (a) the percentage of transporters that participated as brood transporters, adult transporters and adult + brood transporters and (b) the percentage of brood that was transported directly (ABT) or indirectly (ABT*). *Box* represents the lower and upper quartile, *whisker* represents the range and the *line* inside the *box* represents the median. *Bars* carrying *different alphabets* are significantly different from each other. A *line* drawing depicting the most common method of brood transportation is presented as an *inset*

to some other social insects like honeybees and social wasps. Further, coupling brood movement to that of adults minimizes the cost of transport and allows ants to better utilize ephemeral resources and respond to micro or macro changes in their environment. We conjecture that this ability to relocate without sacrificing their investments may have endowed ants with an adaptive advantage. This conjecture requires detailed exploration based on comparative sociobiological studies across honeybees, social wasps and ants.

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