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RESEARCH ARTICLE

Deterioration in nest quality triggers relocation without affecting its dynamics in an ant

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Abstract Nests play an important role in the lives of organisms that occupy them and a suitable nesting site has to be selected carefully. Sometimes, a nest of better quality may be available near the current shelter and it may become advantageous to relocate into it rather than occupying a sub-optimal nest. Thus, organisms have to move for the sole purpose of improving their nest. We asked whether colonies of the Indian queenless ant, *Diacamma indicum*, would relocate if a better quality nest was available. We examined the response of the colonies and individual ants when relocating to improve their nests as compared to relocations from completely deteriorated nests when the deterioration was brought about rapidly. Colonies relocated to improve their nest quality as in all cases, low quality nests were abandoned in favour of nests of better quality. The condition of the old nest did not affect the temporal dynamics of relocation. In addition, the degree of deterioration of the old nest affected neither the decision-making process nor the organization of work in the colony during relocation contrary to what has been documented in other species of ants. Thus, the manner in which the colonies move to improve their nests is comparable to the dynamics of relocation when the old nest is totally destroyed. Although relocation is a costly event in terms of energy expenditure and the risks involved, colonies relocate to improve their nest as the costs of occupying a sub-optimal nest presumably outweigh the costs associated with relocation.

Keywords Nest quality · Relocation · Tandem running · *Diacamma indicum*

Introduction

Nests play an important role in the lives of organisms that occupy them. Not only do organisms reproduce and rear their young within the nests, but the nests also provide them with shelter from environmental adversities (Hansell 1993). In the case of social insects, such as ants, wasps, and honeybees, nests also provide colonies a communal platform for coordinating tasks and exchanging information (Wilson 1971). Social insects are known to build complex nests which provide an appropriate environment for sheltering the colonies and rearing their brood. Both time and energy are spent in constructing and maintaining these elaborate nests. However, sometimes, nests have to be abandoned and colonies have to move into a new shelter for a multitude of reasons, such as nest deterioration, competition, predation, availability of resources, and colony growth (McGlynn 2012).

Nest quality is a combination of various physical, chemical, and biological factors, and it is difficult to understand how social insects assess nest quality during relocation (McGlynn 2012). In honeybees, at least six factors, including the height of the nest entrance from the ground, entrance size, cavity volume, and presence of combs inside the chamber, are assessed while selecting a nesting site (Seeley 2010). In *Temnothorax albipennis* and *Temnothorax curvispinosus*, light ingress into the nest, volume, and size of the nest cavity and size of the nest entrance influence nest site selection (Pratt and Pierce 2001; Franks et al. 2003, 2006). Temperature and relative humidity in *Eciton burchellii* and *Formica neorufibarbis* (Mccaffrey and

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Gallen 2011; Soare et al. 2011) and nest odour in *Aphaenogaster araneoides* (McGlynn 2007) are decisive factors in nest site selection. In *Diacamma indicum*, colonies prefer to relocate into nests which contain the odour of conspecifics, i.e., nests that had previously been occupied by other colonies (Kaur and Sumana 2015).

Relocating from one nest to another is a costly process in terms of time and energy and involves risks, such as predation, loss of resources, and colony fragmentation (Breed et al. 2012; Tschinkel 2014). However, a nest of better quality may be available in the vicinity and it may become advantageous to relocate into it rather than occupying a sub-optimal nest. Thus, colonies move for the sole purpose of improving their nest in the absence of any actual damage or disturbance to the current shelter. Colonies of *Proformica longiseta* that nest under rocks relocate if larger rocks are available (Tinaut et al. 1999). In *Polyrhachis ammon*, smaller nests are abandoned more readily than larger nests (Gibb and Hochuli 2003). The condition of the old nest not only causes relocation but may also affect the dynamics of colony movement itself. Spending extended periods searching for the optimal nest may not be a favourable strategy when the old nest is completely destroyed leaving the colony unsheltered; however, this may be ideal when there is minimal damage to the old nest. Laboratory experiments with *Temnothorax albipennis* suggest that colonies relocate to improve their nests whenever a superior quality nest becomes available. In addition, the difference in the quality of the old and new nests determines the speed at which the new nest is selected with colonies strongly favouring selection of the best alternate nest over speed when relocating from intact nests (Dornhaus et al. 2004).

We looked at the effect of the quality of the old nest on relocation dynamics in the Indian queenless ant, *Diacamma indicum*. This is a primitively eusocial ponerine species found extensively in the Indian subcontinent (Viginier et al. 2004) and colony sizes range from 20 to 300 individuals. All adults of the colony are morphologically identical, and reproductive functions are carried out by a single mated worker known as gamergate who can be identified by the presence of a pair of thoracic appendages known as gemmae (Peeters and Billen 1991). Colonies generally occupy subterranean nests consisting of a single chamber which houses all adults and brood (pupae, larvae, and eggs) and is connected to the exterior by a tunnel. However, during the monsoon season, the colonies tend to occupy opportunistic nesting sites at higher elevation (Kolay and Annagiri 2015a). During relocation, the majority of the colony members (followers) are led via tandem runs from the old nest to the new one by nestmates (leaders) who have knowledge of the new nest (Kaur et al. 2012; Sumana and Sona 2012). Most of the brood items are carried by followers, while some are carried by leaders and no specialist brood transporters are present (Kaur and Sumana 2014). Given the proximity of *D. indicum* colonies to human habitation, sudden degradation of the nests due to anthropogenic as well as natural causes is a common occurrence (personal observations). Using laboratory based experiments, we asked whether colonies of *D. indicum* would relocate if a better quality nest—as compared to their current shelter—was provided and if the quality of the old nest influenced relocation dynamics. We examined the response to differential deterioration of the old nest at the level of the colony as well as individuals in terms of speed of relocation and organization of work.

Methods

Ten colonies of *Diacamma indicum* were collected from Mohanpur, Nadia, India (22º56′N, 88º31′E) between May and July 2015. The colonies contained 143.6 ± 35.7 adult females along with gamergate and different stages of brood (pupae, larvae, and eggs). Each colony member was marked with a unique colour combination using non-toxic enamel paints (Testors, Rockford, IL, USA) to provide individual identification. The colonies were maintained in the laboratory in artificial nests which consisted of the bottom half of a petriplate of 9 cm diameter lined with plaster of paris. This was covered with the top half of the petriplate which had a hole of 1 cm diameter that served as the nest entrance. Red cellophane was placed on the cover to create a darkened chamber inside. Depending on the type of nest cover, three sets of nests—poor, mediocre, and good—were used for relocation experiments. The good nests were similar to the nests in which the colonies were maintained in the laboratory. These nests would mimic the conditions inside the natural nests of the ants in terms of a closed dark chamber and a single entrance (Kolay and Annagiri 2015a). The mediocre nests were covered with the top half of the petriplate that had a semicircular hole of 4.5 cm diameter leaving the nest partially sheltered. In addition, light could penetrate inside the nest chamber as the red cellophane was not placed on the cover. The poor nests were not provided with any cover leaving the nests completely unsheltered. All colonies were kept in the good nests within nest boxes for 2–3 days prior to relocation.

Relocation experiments were performed in the laboratory in a 1.52 m × 1.83 m arena which had a base of sand. The sides of the arena were coated with petroleum jelly (Vaseline™, Hindustan Unilever Ltd, India) to prevent the ants from escaping. Each colony was subjected to two relocations—unsheltered relocation (UR) and partially sheltered relocation (PSR)—which were performed in random order on consecutive days. At the beginning of each experiment, the nest containing the colony was placed in a randomly selected corner of the arena and an empty good nest was placed in the diagonally opposite corner. The distance between the old and the new nests was 1.95 m which was similar to the average distance travelled by this species while relocating in their natural habitat (Kaur et al. 2012). The quality of the new nest and the distance between the old and the new nests was similar in the two relocations. In UR, the cover of the old nest containing the colony was completely removed and light was placed above the unsheltered nest; thereby, the old nest was reduced to a poor nest. In PSR, the old nest was converted into a mediocre nest by removing the old nest cover and replacing it with a partial cover while a light was placed above the nest at the same time. Thus, the colonies had to relocate from a poor nest to a good one in UR and from a mediocre nest to a good one in PSR. Data were collected with the help of video cameras placed above each nest.

Initially, the ants scout the arena searching for an alternate nesting site and upon discovering such a site some return to the old nest to initiate tandem running. We recorded the identities of the ants that entered the new nest until tandem running to the new nest started. These individuals were designated as scouts. Identities of the scouts, the number of times they visited the new nest, and the time they spent within it were decoded from the video recordings. After the initiation of tandem running, the identities of the leader and the follower for each tandem run, any brood item that was transported as well as the time at which each tandem run terminated inside the new nest were recorded. Only the tandem runs that terminated at the new nest were considered for analysis. The total time for relocation from placement of the new nest in the arena to the last tandem run was divided into three components—search time, decision time, and relocation time. Search time was defined as the time from the placement of the new nest in the arena to the time when the first ant entered it. The time taken for colonies to initiate tandem running to the new nest from the time the first ant entered it was defined as the decision time. The duration between the first tandem run to the new nest to the last one was designated as the relocation time. The duration of brood transport was calculated as the time between the transport of the first brood item to the new nest to the last such transport.

To assess whether tandem runs were performed at a constant rate across relocation time, the instantaneous rate of tandem running was compared between UR and PSR with generalized least squares (GLS) model using the nlme package of R (Pinheiro et al. 2016). For each relocation, the duration between the first tandem run and last tandem run was divided into bins of 5% relocation time and the instantaneous rate of relocation was obtained by calculating the percentage of tandem runs performed in each time bin. This was used as the response variable with relocation type and relocation time as the predictor variables. A correlation factor for an auto-regressive model of order 1 (AR-1) was incorporated. The work done by the leaders in terms of tandem runs performed in UR and PSR was analyzed using generalized linear mixed-effect models (GLMM) with the lme4 package of R (Bates et al. 2015). Since the work distribution was right skewed with most leaders, performing few tandem runs gamma distribution was used for the analysis. The percentage of tandem runs performed by each leader was used as the dependent variable, while relocation type was used as the predictor variable. Colony identity was used as the random factor, and identity of individual leaders was used as the nested random factor. Statistical analysis was carried out with statistiXL (version 1.8) and R 3.1.0 (R Development Core Team 2008). Average and standard deviation of all parameters have been presented unless otherwise mentioned.

Results

All ten colonies moved from the mediocre nest to the good one in partially sheltered relocations (PSR) and from the poor nest to the good one in unsheltered relocations (UR) without splitting of the colony. The condition of the old nest did not affect the overall dynamics of relocation. The search time was comparable in UR and PSR (UR 10.8 ± 11.3 min, PSR 17.2 ± 16.1 min, Wilcoxon paired sample test, $T = 13.0$, $n = 10$, $p = 0.2$, Fig. 1). The decision time was comparable in UR and PSR (UR 19.1 ± 17.6 min, PSR 19 ± 12.8 min, Wilcoxon paired sample test, $T = 26.0$, $n = 10$, $p = 0.9$, Fig. 1). The relocation times in UR (61.2 ± 24.2 min) and in PSR (124.2 ± 105.1 min) were also comparable (Wilcoxon paired sample test, $T = 13.0$, $n = 10$, $p = 0.2$, Fig. 1). The brood items were carried either by leaders (69 out of 423 transport events) or by followers, while they were being led to the new nest (354 out of 423 transport events). Brood transport lasted for 49.3 ± 21.3% of the relocation time in UR and 38.4 ± 16.2% of the relocation time in PSR (Wilcoxon paired sample test, $T = 18.0$, $n = 10$, $p = 0.4$, Fig. 1). The movement of the gamergate was not affected by the condition of the old nest, and she was led via tandem running to the new nest towards the middle of colony relocation in both cases (UR: 49 ± 20.1% of relocation time, PSR: 60 ± 21.1% of relocation time, and Wilcoxon paired sample test, $T = 16.0$, $n = 10$, $p = 0.3$, Fig. 1).

The total number of tandem runs performed was unaffected by the condition of the old nest (UR 139 ± 32.6, PSR 143.3 ± 33.7, Wilcoxon paired sample test, $T = 20.0$, $n = 10$, $p = 0.5$). The overall rate at which tandem runs were performed was also comparable in the two relocations (UR: 2.5 ± 0.7 tandem runs per min, PSR: 2.1 ± 1.6 tandem runs

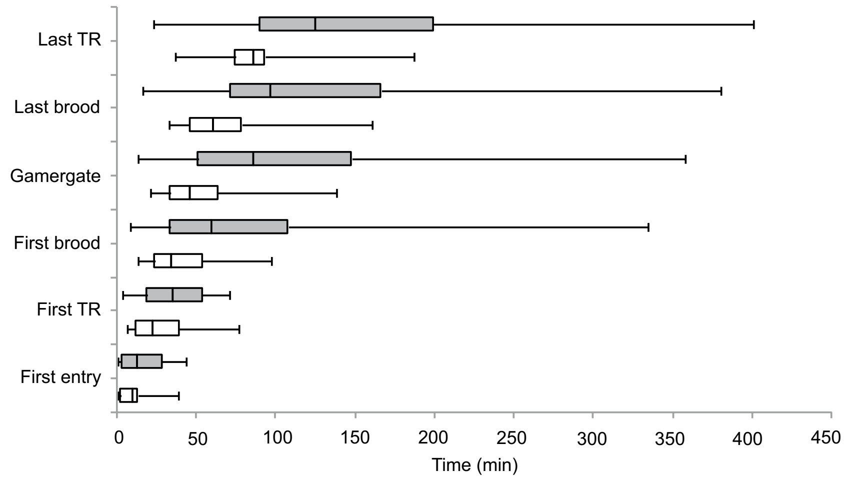

Fig. 1 Time when the first ant entered the new nest, the first and last tandem runs (TR) terminated at the new nest, the first and last brood transports and the gamergate was taken to the new nest is presented for UR (*white bars*) and PSR (*grey bars*) for ten colonies. The *boxes* represent the interquartile range of the data, the *lines inside the boxes* represent the median, and the *whiskers* represent the range of the data

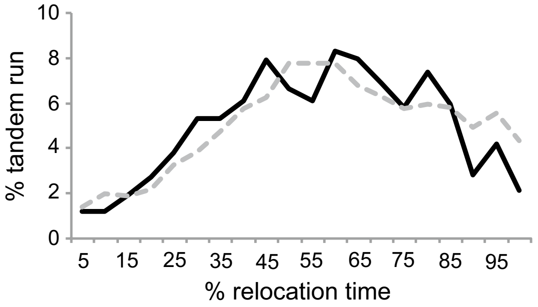

Fig. 2 Average of the instantaneous rate of relocation, i.e., the percentage of tandem runs that were performed in each time bin for ten colonies in UR (*black solid line*) and PSR (*grey dashed line*) is presented. Generalized least square measure was used to compare the instantaneous rate of relocation across relocation time in UR and PSR

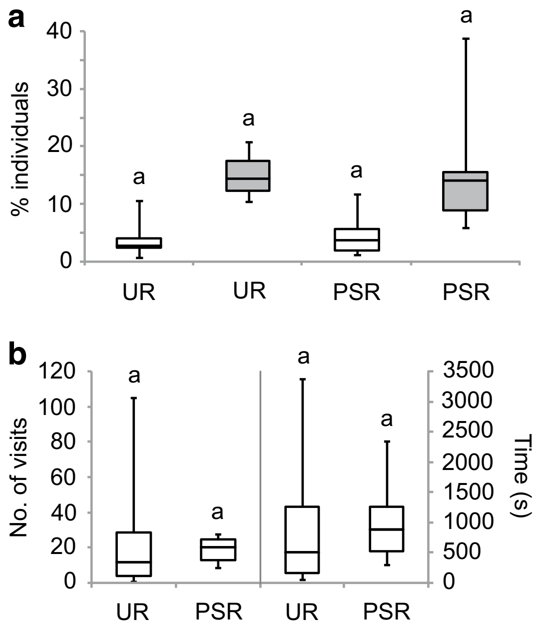

Fig. 3 Percentage of colony members that were scouts (*white boxes*) and leaders (*grey boxes*) **a** along with the number of times the scouts visited the new nest (on primary *Y*-axis) and the total time spent by the scouts inside the new nest (on secondary *Y*-axis) before initiation of tandem running **b** in UR and PSR for ten colonies have been presented. *Each box* represents the interquartile range, the *line within the box* represents the median, and the *whiskers* represent the range of the data. Comparisons were carried out using Wilcoxon paired sample test, and *boxes* carrying *different letters* are significantly different

per min, AND Wilcoxon paired sample test, 17.0, $n=10$, $p=0.3$). The instantaneous rate of relocation varied across relocation time (GLS, value = 0.02, standard error = 0.01, t value = 2.9, $p<0.01$, Fig. 2) with few tandem runs being performed in the initial stages of relocation and the rate of tandem running increasing as relocation progressed. This pattern was consistent in both UR and PSR as there was no effect of the type of relocation on the instantaneous rate of relocation (GLS, value = −0.8, standard error = 0.7, t value=−1.1, $p=0.3$, Fig. 2). Very few reverse tandem runs from the new nest were observed and this was also comparable between the two sets of relocations (UR 4.8 ± 13.8, PSR 3.2 ± 6.8, Wilcoxon paired sample test, $T=17.0$, $n=10$, $p=0.9$).

During the decision time several colony members who were designated as scouts discovered the new nest independently. In UR, 4.2 ± 3.5% of the colony members became scouts, while 4.4 ± 3.2% of the colony became scouts in PSR (Wilcoxon paired sample test, $T=24.0$, $n=10$, $p=1.0$, Fig. 3a). These individuals together visited the new nest 25.6 ± 33.6 times in UR and 19.2 ± 6.9 times in PSR (Wilcoxon paired sample test, $T=27.0$, $n=10$, $p=1.0$, Fig. 3b) and spent 1038.1 ± 1211.7 s inside the new nest in UR and 999.5 ± 636.1 s in PSR (Wilcoxon paired sample test, $T=26.0$, $n=10$, $p=0.9$, Fig. 3b).

In UR, 14.8 ± 3.6% of the colony, and in PSR, 15 ± 9.4% of the colony became leaders and led at least one follower to the new nest (Wilcoxon paired sample test, $T=19.0$, $n=10$, $p=0.5$, Fig. 3a). The work distribution among leaders was not affected by the condition of the old nest (GLMM, value < 0.001, standard error < 0.001, t value $= 0.0$, $p = 1.0$, Table 1). The leader who performed the first tandem run was designated as the first leader. Before initiation of tandem running, this individual visited the new nest 3.4 ± 2.1 times in UR and 4 ± 1.9 times in PSR (Wilcoxon paired sample test, $T = 19.5$, $n = 10$, $p = 0.5$) and spent 117.5 ± 71.7 s and 123.4 ± 61.8 s inside the new nest in UR and PSR, respectively (Wilcoxon paired sample test, $T = 24.0$, $n = 10$, $p = 0.8$). On the last visit to the new nest prior to the first tandem run, she interacted with 1 ± 1.2% nestmates inside the new nest in UR and 0.7 ± 0.6% nestmates in PSR (Wilcoxon paired sample test, $T = 21.0$, $n = 10$, $p = 0.8$).

Discussion

Colonies of *Diacamma indicum* faced a sudden deterioration in the quality of their nests having lived in nests of good quality each of which had a darkened chamber with intact roof and a single entrance. These nests were degraded to mediocre nests which were partially sheltered and poor nests which were completely unsheltered due to the absence of a roof. The response of colonies to this sudden deterioration in nest quality was examined. The total lack of a roof is assumed to be a greater deterioration of nest as compared to a partial loss of the nest cover. Similar parameters of nest quality have been used in studies of *Temnothorax albipennis* (Dornhaus et al. 2004; Franks et al. 2006). Colonies of T. albipennis were initially maintained in nests of varying qualities before being provided with a superior alternative (Dornhaus et al. 2004), whereas colonies faced a sudden deterioration in their nest quality in the present study. *D. indicum* colonies relocated from both the mediocre and the poor nests into a nest of improved quality indicating that colonies not only move away from completely damaged nests but also try to relocate from partially damaged ones. This could have important consequences on colony survival, since inhabiting an inferior nest with its sub-optimal living conditions has several associated costs. Relocation involves several costs, such as energy expenditure and risks of predation, loss of adults and brood as well as colony fragmentation (Breed et al. 2012; Tschinkel 2014). However, the benefits of moving into a better quality nest seem to outweigh these costs.

The temporal dynamics of relocation are not affected by the quality of the nest from which the colonies are relocating. The time taken to search for and locate a new nest is not affected by the degree of deterioration of the old nest as is indicated by the comparable search times in UR and PSR. The time to select a new nest and start recruiting nestmates to it, i.e., the decision time is also not affected by the quality of the old nest. This is contrary to relocations in *T. albipennis*, where the time taken to decide upon the new nest is affected by the quality of the old nest, with more time taken to reach a consensus decision when colonies are under some shelter and, thus, at less risk (Dornhaus et al. 2004). Once tandem running started, the time taken to transfer all colony members including all brood items to the new nest was nearly 2 h in both UR and PSR. It is possible that *D. indicum* colonies perceived the sudden deterioration—both partial and complete—in nest quality in a similar manner and, thus, responded with the same level of urgency in both situations, while *T. albipennis* colonies which had been maintained in different quality nests for a prolonged period responded differentially while moving to a superior nest.

Upon exploring the behaviour of individual ants during colony movement, it was observed that the new nest was

Table 1 Results of the generalized linear mixed-effects model for the effect of type of relocation (Rel) on the percentage of tandem runs (TR) performed by tandem leaders

Model: model <- glmer (TR ~ Rel + (1|Col/Ind), family = Gamma)

	Value	SE	*t* value	*p* value
Fixed effects				
(Intercept)	2.639e−01	2.770e−02	9.527	<2e−16
Rel	8.506e−07	2.711e−02	0.000	1
Number of observations- 546; Ind:Col- 273; Col- 10				

		Variance	SD
Random effects			
Ind:Col	(Intercept)	0.00000	0.00000
Col	(Intercept)	0.00551	0.07423
Residual		1.35497	1.16403

Colony identity (Col) was used as the random effect and identity of individual leaders (Ind) was used as nested random effect discovered independently by 4% of colony members before initiation of tandem running after an initial search of the arena and the number of scouts was similar in UR and PSR. The number of times that these individuals visited the nest and the total time they spent exploring it was also comparable in the two relocations. The quality of the old nest, and hence, the urgency of the colony to relocate does not affect decision making at the level of the colony in *D. indicum*, at least in the current set of manipulations. The response of colonies to other methods of nest disruption, such as flooding and changed microclimate, needs to be explored further. In addition, the variation in the relocation dynamics after acclimatizing the colonies to nests of different qualities will have to be studied.

The first leader initiated the first successful tandem run to the new nest after discovering it independently and assessing its quality. This individual probably plays a crucial role in initiation of recruitment of nestmates to the new nest as her decision could influence other potential leaders and the overall dynamics of relocation. Thus, we examined her behaviour prior to the initiation of tandem running. This leader visited the new nest four times on an average and spent nearly 2 min inside it before the initiation of tandem runs. The time taken to decide on the new nest by the first leader is not affected by the degree of deterioration of the old nest. On her last visit to the new nest before leading a follower to it, she interacted with a single nest mate within the new nest on an average. This indicates that direct interaction with multiple nestmates inside the new nest is not essential for the leaders to reach a decision regarding the choice of new nest; rather, the leaders decide independently after individually assessing the quality of the new nest. This is contrary to observations in *Apis mellifera* and *Temnothorax albipennis*, where scouts are known to interact with multiple nestmates leading to a consensus decision regarding the new nest before initiating colony movement (Seeley and Visscher 2004; Pratt 2005).

The number of leaders who performed tandem runs during each relocation was not affected by the quality of the old nest. The workload of these leaders in terms of the total number of tandem runs that were performed was also comparable in both cases. In *D. indicum*, the number of tandem runs performed depends on the number of followers that have to be recruited and the number of times each follower is led via tandem runs to the new nest. Individual ants are usually led only once to the new nest when a single alternate site is available. In a few cases, some individuals may have to be recruited multiple times to the new nest by different leaders leading to an increase in the total work. However, whether the colonies are relocating from a partially damaged nest or a completely damaged nest does not affect the number of tandem runs performed indicating that neither the number of followers who have to be recruited to the new nest nor the number of repeat tandem runs changes with the quality of the old nest. Work distribution among leaders was right skewed irrespective of the condition of the old nest with the majority of the leaders performing few tandem runs, while a few leaders performed most of the task. This manner of uneven task distribution has been observed among leaders during relocation in *D. indicum*, both in the natural habitat and in the laboratory (Kaur et al. 2012; Sumana and Sona 2012; Kolay and Annagiri 2015b), and in other social insects in the context of different tasks (Sendova-Franks et al. 2010; Pinter-Wollman et al. 2012).

Along with tandem runs from the old nest to the new nest, a few reverse tandem runs from the new nest were observed and this was not affected by the quality of the old nest. The precise role of these reverse tandem runs is not clear. In addition to being a mode of recruitment of nestmates, tandem runs enable leaders to transfer information about the new nest to other potential leaders (Franks and Richardson 2006). It has been speculated that reverse tandem runs serve to increase the number of active recruiters who have knowledge of the new nest and carry nestmates to it (Pratt et al. 2002). However, in *D. indicum*, where all adult members are led via tandem running to the new nest, every follower has the opportunity to learn the path to the new nest while being led to it. Thus, they should not have to be led back to the old nest to become active leaders themselves. At the beginning of relocation, it is likely that there may be some scouts who are undecided upon the new nest after discovering and exploring it. On finding colony members at this site, they lead these individuals back to the old nest to prevent these individuals from separating from the rest of the colony. Leading nestmates away from a new nest site may also be a means of communicating their rejection of the particular nest to other scouts. However, since very few reverse tandem runs (4 ± 10.6) are observed during the relocations, it is difficult to illustrate their function. Further experiments will have to be conducted to understand their role.

One-sixth of total brood items, pupae in all cases, were carried by leaders who walked with the brood item in their mandibles from the old nest to the new nest, while the rest were carried by followers as they followed other leaders to the new nest. This coupled adult-brood transport in a single tandem run is an intrinsic feature of relocation in *D. indicum* and augments the relocation process in this species (Kaur and Sumana 2014). The gamergate was not given any special treatment and she was led to the new nest just as any other follower towards the middle of relocation. The rate of relocation was not affected by the old nest condition as is indicated by the comparable number of tandem runs performed per min when colonies were relocating from completely unsheltered and partially sheltered nests. In both cases, the rate of tandem running was initially low and gradually increased towards the latter half of the relocations.

In conclusion, *D. indicum* colonies relocate whenever a better quality nest—as compared to their current shelter—is available in the vicinity and the degree of deterioration of the old nest affects neither the decision-making process, the relocation dynamics nor the organization of work. Relocation is a costly event in terms of the energy and time diverted from other tasks and also involves many risks. In spite of this, colonies relocate to improve the quality of their nests as the costs of occupying a sub-optimal nest appear to outweigh the costs associated with relocation.

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