Title:

Flexibility of tandem leaders resolves traffic jams during colony relocation in an ant

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SA conceptualized the study; MP and SA designed the experiment. MP and SA conducted the data collection. MP conducted the statistical analysis with inputs from SA. MP drafted the initial manuscript, which was critically revised by SA. SA provided supervision and guidance.

Abstract

Ants, renowned for their intricate social behaviors, exhibit remarkable collective movement patterns that enable them to forage and tunnel efficiently. Despite significant research into their navigation skills and traffic avoidance mechanisms mostly in the context of central-place foraging, the dynamics of bi-directional movement during colony relocation remains an underexplored domain. This study delves into the behavior of *Diacamma indicum*, an ant species, that recruits by tandem running during the relocation of their nest. Our findings reveal that constricted pathway linking the old and new nests lead to frequent interruptions and traffic jams, and this significantly extended transportation durations when compared to control. Through analysis of 56 traffic jam instances, we unveil the adaptability of tandem leaders. Their decisions on recruiting followers midway and adjusting heading directions amalgamates into emergent mass orientation towards the new nest acting as critical factors in untangling the traffic jam. This study not only illuminates the intricacies of collective ant movement during nest relocation but also unveils insights into the mechanisms that underscore their exceptional traffic jam mitigation abilities. By addressing this uncharted aspect of ant behavior, we contribute to a broader comprehension of the remarkable strategies these superorganisms employ to navigate complex environments.

Introduction:

In the realm of natural phenomena, the prevalent occurrence of collective motion stands as a captivating manifestation wherein an individual's conduct becomes entwined with that of its proximate companions, thereby enabling a harmonized movement (Vicsek 2001). Several instances of collective motion has been meticulously documented across disparate domains of life, unveiling a tapestry of group dynamics that span bacterial colonies (Czirók et al., 2001; Sokolov et al., 2007), amoebic aggregations (Kessler & Levine 1993; Nagano 1998; Rappel et al. 1999), congregations of fish in shimmering shoals (Parrish et al. 2002; Hemelrijk & Kunz 2005; Becco et al. 2006; Ward et al. 2008), avian assemblies orchestrating graceful aerial ballets (Ballerini et al. 2008a; Bajec & Heppner 2009; Hayakawa 2010), the synchronized peregrinations of migratory mammalian herds (Fischhoff et al. 2007; King et al. 2008; Sueur & Petit 2008), and even the enigmatic coordination among clusters of human pedestrians traversing urban landscapes (Helbing et al., 2000; Faria et al. 2010; Moussaïd et al. 2011). This multifaceted tapestry of examples underscores the pervasiveness of collective motion and beckons an exploration into the underlying mechanisms driving this remarkable phenomenon (Bonabeau et. al, 1999).

Insects have long captivated researchers due to their remarkable collective behaviors, none more captivating than the iconic locust swarms that have garnered attention for centuries (Couzin & Franks, 2003; Buhl et al., 2006). Social insects, engage in intricate group dynamics within shared nests, diligent care of their young, and expeditions to diverse foraging grounds to procure food for their nestmates (Gordon, 2014; Czaczkes et al., 2015; Poissonnier et al., 2019). However, navigating confined passages presents a distinct challenge, often culminating in head-on collisions between individuals, as observed in various studies (Dussutour et al. 2004; Fourcassié et al. 2010a). In the realm of chemical trail-following, the flux of ants can

surge to several hundred per minute, a phenomenon that has been exhaustively explored. Astonishingly, despite the elevated ant densities, these social insects exhibit a prowess in traffic management surpassing that of humans (Burd et al. 2002; Dussutour et al. 2004; Fourcassié et al. 2010; Hönicke et al. 2015). Numerous investigations have illuminated the remarkable absence of traffic congestions in ant pathways, an intriguing subject of scientific inquiry (Burd et al. 2002; John et al. 2009; Hönicke et al. 2015; Poissonnier et al. 2019). Of particular interest is the manifestation of "clog avoidance behavior" witnessed in fire ants (*Solenopsis invicta*) during tunnel excavation, where incoming ants conscientiously yield passage to their outbound counterparts, thereby mitigating the potential for blockages in narrow confines (Aguilar, 2018).

Social insects performing colony level tasks exemplifies cooperation and efficiency. Beyond the well-studied domains of foraging and tunnelling, nest relocation emerges as a critical endeavor demanding the coordination of a multitude of individuals within the colony. This intricate process involves intra-nidal workers, largely inexperienced in the extranidal environment, as well as reproductively active individuals and the colony's brood. The endeavor becomes even more formidable due to exposure to a range of environmental factors, including fluctuating temperatures, humidity, and precipitation. Simultaneously, relocation makes the colony even more vulnerable due to biotic pressures such as predators, brood-stealing neighbors, and parasitic organisms, each posing considerable threats to its viability (McGlynn, 2012).

Intriguingly, the strategies employed for recruitment during colony relocation exhibit remarkable diversity across ant species. Pheromone trails, carrying, and the fascinating phenomenon of tandem running are among the mechanisms driving this process. Tandem running, a mode of nestmate recruitment, entails an informed ant leading an uninformed nestmate to the new nesting site. Impressively, some followers may themselves evolve into tandem leaders for subsequent journeys (Wilson, 1959). This process, while efficient, also

gives rise to a scenario where several informed individuals conduct multiple trips between old and new nests, resulting in bi-directional movement. Consequently, such kind of interactions can lead to increased head-on encounters and, subsequently, congestion along narrow pathways (Dussutour et al., 2005).

It is imperative to recognize that nest relocation is a goal-oriented task (Annagiri, 2021), demanding rapid execution due to the direct exposure of colony members, both adults and brood, to adversities of both biotic and abiotic origins. The ramifications of congestion and traffic jams during this critical process could exert a profound impact on the overall fitness of relocating colonies. Our study focusing on the primitively eusocial tandem-running Ponerinae ant, *Diacamma indicum*, that relies solely on tandem running for relocation as a model organism (Sumana & Sona 2012). This species inhabits regions across India, Sri Lanka, and certain parts of Japan. Workers and reproductively active females are morphologically similar, these ants are approximately 1 cm in length, predominantly black, and maintain a single reproductively active female per colony. Each colony comprises primarily of adult females (85.35 ± 38.79; mean ± SD), alongside a limited number of winged males and brood (Annagiri & Halder, 2023).

The ecological setting of the natural habitat further amplifies the complexity of relocation endeavors. Heterogeneous terrains, particularly during the monsoon seasons, pose formidable challenges. Notably, the need for colonies to navigate waterlogged landscapes via available substrates creates bottlenecks and restrictions in their travel paths (Karunakaran et. al, 2021; Kolay & Annagiri, 2015). This context underscores the urgency of comprehending the dynamics of traffic flow during nest relocation, given its direct implications on the overall fitness and survival of colonies facing such adversities.

This study attempts to unraveling the intricate interplay of bi-directional movement during nest relocation across constricted pathways, with a primary focus on the potential emergence of traffic congestion and its subsequent resolution. By comparing relocation scenarios along both restricted and wider paths, we have formulated the following key inquiries: Does travel on constrained pathways result in heightened disruptions to tandem runs, subsequently giving rise to traffic congestions? Moreover, what implications do such traffic jams bear on the dynamics of nest relocation? Delving deeper, we seek to illuminate methods employed by these ants in resolving the traffic congestion, which will likely allow further understanding of the complexities of collective behaviour within confined spaces.

Methods:

Colony collection and maintenance:

Eighteen colonies of *Diacamma indicum* were collected from their natural habitat in Nadia district, West Bengal, India (22° 57’ 47” N, 88° 31’ 38” E) between April and August 2018 using the water flooding method (Kaur et al. 2012). The colonies comprised a gamergate, brood, and adult female workers (87.0 ± 32.23; mean ± SD, range 57-160). Each ant was individually marked with different colours of enamel paint (Testors, Rockford, IL, USA) to uniquely identify all colony members. The colony adults were examined under a stereomicroscope (Leica MZ6, Leica Microsystems, Wetzlar, Germany) to identify the individual with gemma, the only reproductive female in the colony, termed the gamergate. The colonies were housed in an artificial nest made of a Petri dish (9 cm diameter) with a lid covered with red cellophane paper and a nest entrance of 1.5 cm diameter. This artificial nest was placed in a plastic box (28.5 x 21.5 x 12 cm) with plaster of Paris base and provided *ad libitum* water and ant cake (Bhatkar & Whitcomb 1970). The colonies were allowed to acclimatise to lab conditions for 24 hours before being used for experimentation.

Experimental set-up

All experiments were performed in a water-filled rectangular plexiglass arena. The new and old nest boxes were placed 77 cm apart and connected by a floating plexiglass path (77 x 2.5 cm). This distance was chosen because it is similar to the distance across which colonies relocate in their natural habitat (Kaur et al. 2012). In this set-up, ants could only walk on the connecting plexiglass bridge and in the nest as the surrounding area was immersed in water that was 2.5 cm deep, preventing ants from stepping away or escaping the set-up. The new nest was identical to the old nest except for the roof covered with red cellophane film, which provided a sheltered dark chamber (Fig. 1A). The position of the new nest within the arena was randomised. The experimental set-up for manipulation was identical to the control set-up except for one point: the plexiglass path connecting the two nests was different. The only difference from the control set-up was the presence of a narrow region (15 x 0.5 cm) at the centre of the connecting plexiglass in the manipulation set-up (Fig. 1B). The 2.5 cm wide path in the control allowed five ants to walk side by side at the same time.

In contrast, the 0.5 cm path allowed the movement of only one ant at a time. Thus, we called the 2.5 cm path the control or multi-lane set-up and the 0.5 cm path the one-lane or manipulation set-up. Relocation on the one-lane path will cause resistance to the smooth flow of the ant's bi-directional traffic during relocation. This set-up mimics a situation in the natural habitat during monsoons when heavy rains inundate colonies and force them to relocate, and they have been observed to traverse water-logged regions and cross these regions using bridges formed by branches or leaf blades (personal observations).

Relocation:

Twelve colonies that were used for this experiment underwent two relocations each. Each colony underwent a one-lane (manipulation) and a multi-lane (control) relocation in random

order. They were given a 24-hour rest in between experiments. Before the start of each relocation, the experimental set-up was thoroughly cleaned, and the water was replaced. An experiment was initiated by placing a colony of *D. indicum* with its old artificial nest in one of the nest boxes within the experimental arena.

The nest box across the bridge contained an intact new nest identical to the old one in all aspects. After giving 5 min for the ants to settle down, we removed the roof of the old nest and put a 9Watt white LED bulb as a light source at the height of 20 cm. This light stress on the exposed old nest stimulated a few colony members to explore the set-up and discover the new nest. After discovering the new nest, they started relocating into the new nest by tandem running. We recorded (a) Discovery time: defined as the period from when the roof of the old nest was removed to the discovery of a new nest by any worker of the colony. (b) Latency is when ants start a tandem run after the new nest has been discovered. (c) Transport time is defined as the duration from the first tandem run to the time of the last run into the new nest. (d) Total relocation time is the time duration from the discovery of the new nest to the entry of the last tandem pair into the new nest.

We used a video camera (Sony Handycam model HDR-CX200) to delineate the traffic flow and recorded the proceedings in a 30 cm long focal area on the bridge (Fig. 1A and B). These recordings were observed multiple times to decode the data into observation sheets.

Behavioural observation.

In our study, we documented the identity of the first ant to discover the new nest and recorded the time of discovery. Additionally, we noted the time of the first transport to the new nest and the identity of the leader of the first tandem run. We also recorded the time of the last tandem run and waited 30 minutes to ensure the relocation was complete and no further transports

occurred. Video recordings were extracted for three different types of information. Firstly, we analysed the heading direction of ants in the focal area to determine if traffic moved synchronously. In order to do so, we randomly selected 30 frames from the video records for each colony and analysed them to see if ants moved in both directions or in a particular direction as a cohort until they reached the new nest. Out of the 360 frames considered, only 328 contained ants in the focal area, and these frames were used for further analysis. We used a random time frame generator to select frames during the transportation time, and in each of these frames, we recorded the heading direction of all the ants present. We tabulated the proportion of ants heading towards the new nest in each frame to determine if traffic was moving in a particular direction at any given time. Secondly, we recorded any policing behaviour at the entry and exit points of the one-lane path, such as aggression or immobilisation and the ants' identity. Lastly, we noted all tandem runs and transports, including the time they occurred and the identities of all leaders, followers, and brood transporters in the focal area. We calculated the percentage of colony members who became tandem leaders and the number of tandem runs they performed. We defined a successful tandem run as one that reached the new nest without losing the initial leader-follower pairing. Sometimes the leader and follower pair can lose the contact between each other and this is termed as interrupted tandem run. Based on what occurs subsequently, if they resume within a couple of seconds they were termed as resumed tandem run (RTR). If a new leader tandem run with the focal follower, we termed it midway tandem run (MTR). This can be of two kinds, in first, a returning leader (RL) moving toward old nest to recruit another nestmate, starts inviting the follower of another ongoing pair and make new tandem pair by switching over (SO) the leader to relocate to new nest, we called it as- midway recruitment by switching over (MR-SO). Secondly, a returning leader were seen to invite a lost follower on the path and recruit it for tandem run, we called it as midway recruitment of a lost follower (MR-LF).

Sometimes, interruptions can become prolonged, leading to traffic jams. When ants cannot move even one body length (about one centimetre) for at least 4 seconds and another pair/brood transporter gets stuck, we term it a traffic jam. By tracking the movement of ants on the path just before the traffic jam initiates, we note down the individuals responsible for the interruption that led to a traffic jam. Reviewing the video recordings, we record the number of interruptions that ants encounter and the number of jam events in the focal area and note which ant(s) caused them. We use 4 seconds as the threshold to define jams because *D. indicum* is known to tandem run at an average speed of 4.2 cm/sec (Kaur et al. 2017). Thus, it would take an average leader 4 seconds to cross the entire focal area (15cm), but they do not move even a single body length (approximately 1 cm) during a jam. We observe a unique behaviour when several ants that are stuck in a jam. Most of these ants (at least 80%) orient themselves towards one direction and start moving in that direction, causing the jam to resolve. We call this behaviour mass orientation. We note when this behaviour is observed and also the direction towards which these ants move.

Statistical analysis:

The data were decoded from datasheets and videos and entered into an MS Excel spreadsheet for analysis. The StatistiXL Version 2.0, an add-in for MS Excel, was used to conduct two-tailed non-parametric tests such as the Wilcoxon paired-sample test, Pearson correlation, Z-test of proportion, and chi-square test for goodness of fit. A generalised linear mix-model (GLMM) was performed using the 'lem4' package (Bates et al. 2014) in R Studio with the software R (version 4.0.3) to analyse the effect of various parameters on the relocation. The colony identity was treated as a random effect in these models. A p-value < 0.05 was taken as the cut-off for significance across all the statistical tests.

Results:

Impact of path constraints:

We examined colony relocation across one-lane and compared it with multi-lanes. Firstly, we investigated the occurrence of tandem run interruptions and followed this with investigations of traffic jams. One-lane relocations showed a significantly higher number of interruptions (23.66 ± 10.12; mean ± standard deviation) as compared to multi-lane (8.25 ± 4.71) relocations (Wilcoxon paired-sample test, T=0, n=12, $p<0.01$; Fig. 2A). The number of jams in one-lane (4.66 ± 2.99) relocation was significantly higher than multi-lane (0.25 ± 0.62) relocations (Wilcoxon paired-sample test, T=0, n=12, $p<0.01$; Fig. 2B). The one-lane path had a significant impact on the jam events (GLMM, z= 3.058, Intercept= -1.42, Estimate= 1.96 $p<0.002$, electronic supplementary material; Table S1). Furthermore, there was a significant positive correlation between colony size and the number of jams (Spearman correlation coefficient, r2=0.73, n=12, $p<0.01$).

To examine if the ants synchronised their traffic flow at congested path, we quantified the number of ants heading towards the new nest as a proportion of the total ants in a given frame. We found that on average (0.54 ± 0.29) ants were heading towards the new nest, while the remaining ants were walking towards the old nest, and some were not facing either of these two directions. We collected information regarding the presence of ants at the entry and exit points of the one-lane path to examine if there were any traffic regulators. Across the 12 relocations, we did not see any single case of a unique ant positioned at either of these positions for more than 4 seconds. We did not observe a single act of immobilisation of an ant or a tandem pair during the relocation, and no active interference of tandem running was observed at these points.

Relocation dynamics:

In order to quantify the impact of one-lane on the overall relocation dynamics, we divided the processes into three sections. The time to discover the new nest or the discovery phase, the

time to initiate tandem running or latency, and the time to complete transportation to the new nest or the transport phase. Given that only a small percentage of the colony gets involved at the start of the process, as expected, the discovery phase and latency were comparable, involving a small fraction of ants. The time taken to discover the new nest was (2.96 ± 2.90 min) in the case of one-lane relocation, while it was (4.68 ± 3.13 min) in multi-lane relocation, which was statistically comparable (Wilcoxon paired-sample test, T=20.5, n=12, p=0.16; Fig. 3A). Latency in one-lane relocation (6.59 ± 6.04 min) was comparable to multi-lane relocation (5.17 ± 2.78 min) (Wilcoxon paired-sample test, T=36.0, n=12, p=0.85; Fig. 3B). However, the time taken to complete relocation, i.e., the transport phase, was not comparable across the experiment, as ants in one-lane took (19.25 ± 6.36 min) more time to relocate than in multi-lane (14.58 ± 4.54 min) relocation (Wilcoxon paired-sample test, T=9, n=12, p=0.02; Fig. 3C).

The workforce involved in the process was compared by examining the percentage of tandem leaders involved in the relocation. Tandem leaders in one-lane relocations were 20.54 ± 6.69% of the colony size, while 18.07 ± 5.47% became leaders in multi-lane relocations, which was statistically comparable (Wilcoxon paired-sample test, T=16, n=12, p=0.07). However, successful tandem runs declined by about 21% in one-lane relocations. The percentage of successful tandem runs in one-lane (65.14 ± 12.59%) was significantly lower than in multi-lane (82.69 ± 9.54%) relocations (Wilcoxon paired-sample test, T=2, n=12, p<0.01).

Traffic jams:

We recorded 56 traffic jam events during one-lane relocations and found that the width of the path significantly affected the jams (GLMM, p<0.05, electronic supplementary material; Table S1). Most of these jams were caused by returning leaders (RLs), with 59% of jams events being caused by RLs, 27% by brood transporters, and 14% by lost followers. This proportion

significantly differed from the equal contribution of these three categories of individuals who could initiate jams (Goodness of Fit test, Chi-Square value = 17.821, df= 2, $p < 0.01$; Fig. 2C).

We also found that the total relocation time was significantly affected by discovery time, latency, transport time, and the number of jams (GLMM, $p<0.05$, electronic supplementary material; Table S2). Of the 56 jams, 52 or 92.85% were resolved when most of the ants involved showed orientation toward the new nest (see supplementary material S01 for video of mass orientation). This aligning of multiple individuals toward the new nest was mainly brought about by returning leaders performing either a switchover or starting a new tandem run with a lost follower. In 65.8% of cases of mass orientation, one of these events occurred (Z-test of proportion, Z=2.219, n=52, p=0.01; Fig. 5A and B for a schematic representation of midway recruitment).

We observed that MR-SO (midway recruitment by switching over) increased 75% in one-lane relocations. The MR-SO in one-lane relocations was 7.31% ± 5.60%, while it was 4.23% ± 4.07% in multi-lane relocations, and this difference was found to be significant (Wilcoxon paired-sample test, T=9, n=12, p=0.02; Fig. 5A). MR-LF (midway recruitment by lost follower) also increased by 115.38% in one-lane relocations. The MR-LF in one-lane relocations was 27.53% ± 10.72%, while it was 13.07% ± 7.89% in multi-lane relocations, and this difference was also significant (Wilcoxon paired-sample test, T=2, n=12, $p < 0.01$; Fig. 5B). Combining these two components, we found that midway recruitment by returning leader was significantly higher in one-lane relocations (61.19% ± 14.70%) as compared to multi-lane relocations (40.38% ± 13.47%) during jams (Wilcoxon paired-sample test, T=2, n=12, $p<0.01$).

Discussion:

Navigating traffic congestion in bi-directional collective movements within constrained environments necessitates precise strategies. Ants have been extensively studied for their optimization behaviour, mainly in the context of foraging and tunnelling (Reid et al., 2011; Mukhopadhyay et al., 2019; Buhl et. al, 2004). Examples of their efficient traffic flow management include lane formation in army ants and density-flow relationship adjustment in Argentine ants during foraging (Poissonnier et al., 2019). Intriguingly, the existing literature lacks evidence of traffic jams or impeded ant movement. Instead, ants have been noted for employing diverse techniques to avoid congestion, highlighting their adaptability (John et al., 2009; Fourcassié et al., 2010a; Gravish et al., 2015; Aguilar et al., 2018; Poissonnier et al., 2019). In parallel with their adeptness in foraging and tunnelling, few ant species are known for frequently performing nest relocations—a goal-oriented task that significantly influences colony fitness (Annagiri, 2021; McGlynn, 2012). This task involves the entire colony, comprising members with varying degrees of habitat familiarity, in contrast to foraging, that often involve experienced individuals. Such complexity further amplifies the challenge of maintaining colony cohesion during relocation, particularly for species employing tandem running for nestmate recruitment. Tandem running ants, *D. indicum*, with their tactile communication and average speed of approximately 4.2 cm per second, introduce an inherent time cost due to their capacity to recruit only one follower at a time (Kaur et al., 2017).

During relocation by tandem running, tandem leaders, play a pivotal role as they have knowledge about the new nest's location. We found that the bi-directional nature of movement and the requirement for uninterrupted tactile feedback could cause clogging and impede traffic flow along constrained paths. Our finding unveil the threefold surge in interruptions and an unprecedented eighteenfold escalation in traffic jams along one-lane paths, which sharply contrasts with earlier investigations of smooth traffic flow performed on the trail laying ant species during foraging. Subsequent analysis of focal area video-recordings delineated three

categories of ants responsible for causing the jam phase—returning leaders (59%), brood transporters (27%), and lost followers (14%).

As ants were capable in resolving the jams; the potential strategies for mitigating traffic jams were explored. While a logical approach would be to engage fewer tandem leaders to curtail transportation rates and, consequently, jams, our observations did not confirm this expectation. The involvement of tandem leaders in one-lane (20.54%) and multiple-lane (18.07%) relocations remained statistically comparable, even under path constraint. The possible idea of enforcing traffic regulations through ants stationed at constrained path entry and exit points. We did not find any particular ant taking the role of traffic regulators. We did not find any particular ant taking the role of traffic regulators. No unique ants positioned themselves at the entry or exit points and no one showed any direct interference with the traffic or any aggression. Ruling out the existence of such regulatory behaviors. The synchronized traffic flow could also act as a potential solution, yet empirical analysis of heading directions across numerous relocation frames did not furnish evidence of such coordination. Instead, the mean proportion of ants moving toward the new nest was modest (0.54).

To elucidate traffic flow dynamics, we devised a schematic detailing events during relocation, traffic jams, and their resolution under path constraint (Fig. 6). This schematic portrays two possible outcomes for tandem pairs and brood transporters originating from the old nest. In the absence of obstructions, smooth tandem runs—where the leader and follower remain uninterrupted—prevail, as observed in most relocations over open fields and in control experiments. However, constrained path scenarios introduce a new dynamic—interruptions due to returning ants. While some pairs successfully resume tandem running after interruption, lost followers venture off in random directions, causing disruptions to ongoing tandem pairs and brood transporters and traffic jams with additional members queued behind. Returning

tandem leader-enhanced their tendency to perform midway recruitment of lost followers (MR-LF) and switchovers from returning leaders (MR-SO), ultimately resolving the congestion. Jam culminates when the emergent phenomenon of mass orientation towards the new nest occurs. Further exploration of the mechanisms that bring about synchronised mass-orientation in a particular direction needs to be conducted.

Overall, current study offers a novel perspective on the intricacies of traffic dynamics within goal-oriented task of nest relocations over a narrow path. Contrary to previous assumptions, our findings unveil instances where ants encounter traffic congestion. However, what sets ants apart is their remarkable behavioural flexibility in resolving such congestion. This revelation not only deepens our comprehension of abilities these superorganisms (Hölldobler & Wilson, 1990; Wilson & Hölldobler, 2009) have but also presents strategies that hold the potential to enhance traffic flow regulation within our society.

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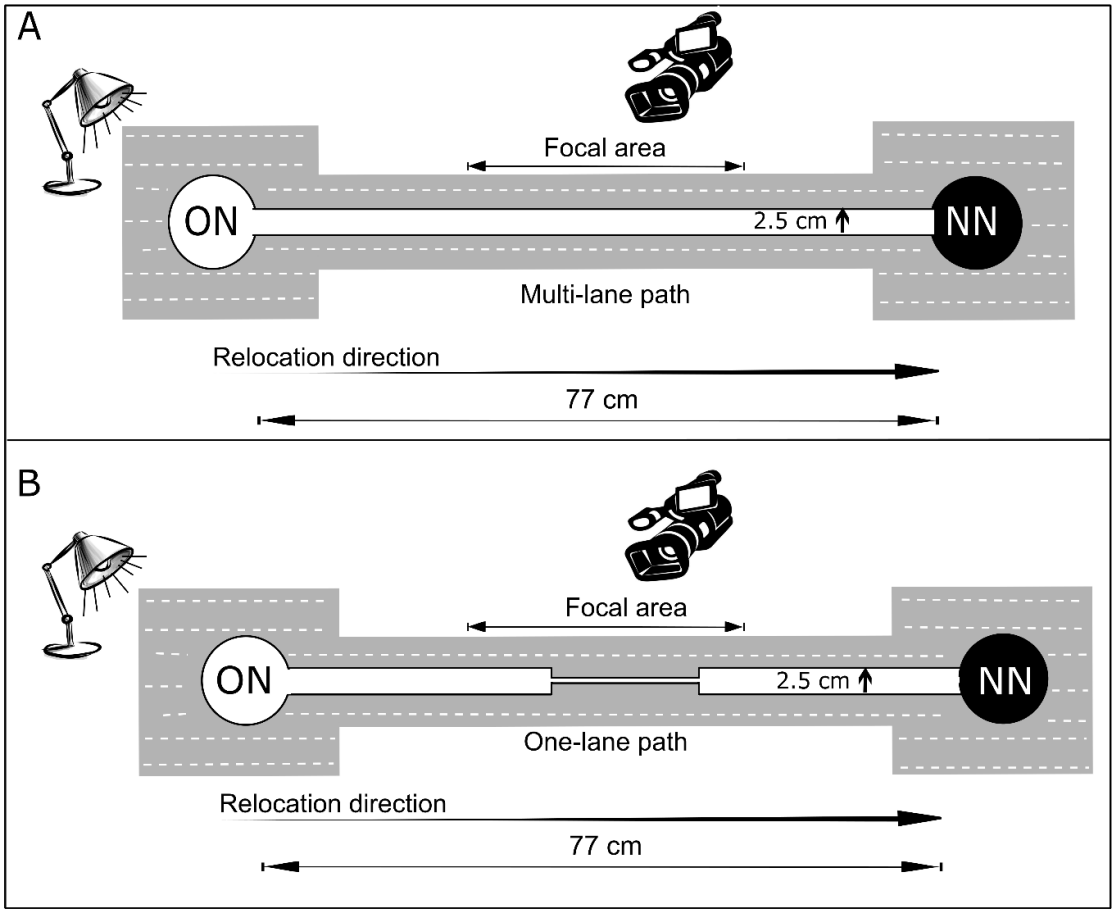

Figure 1: Experimental Setup: (A) The top panel illustrates a schematic diagram of the control condition involving multiple-lane relocation. (B) The bottom panel depicts a schematic diagram of the manipulation condition involving single-lane relocation. The multi-lane path maintained a consistent width of 2.5 cm, whereas the single-lane path encompassed a 15 cm area, of which 0.5 cm represented the path width, and the remaining 2.5 cm constituted the rest of the area. These pathways facilitated the connection between the old uninhabitable nest (ON), subjected to light stress from a table lamp, and the new optimal nest (NN). Notably, events occurring within the focal area (30 cm along these paths) were meticulously recorded via video for subsequent analysis. The experimental setup was immersed in water (depicted by the gray area with white dots), exclusively exposing the top surface of the arrangement to water. This design constraint restricted ant movement exclusively to the specified paths and thwarted any possibility of their escape from the experimental configuration.

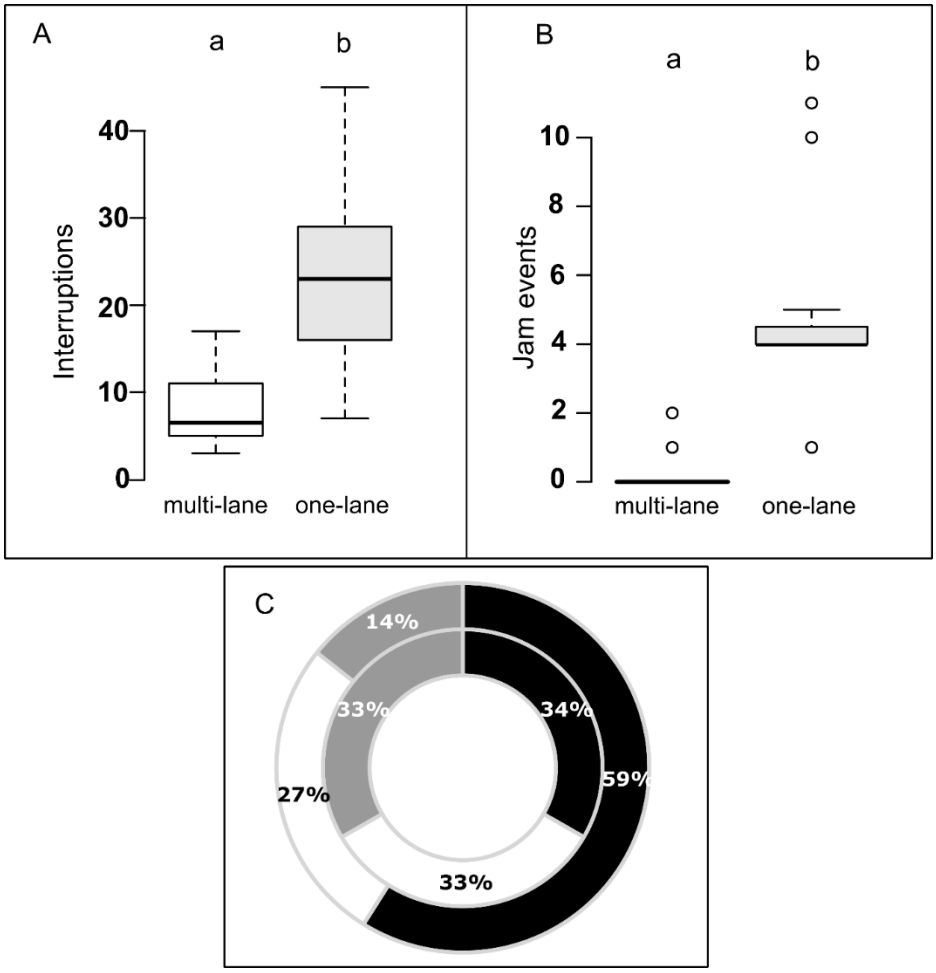

Figure 2: Transport Dynamics: (A) Comparative analysis of interruption frequency between multi-lane and one-lane relocations is depicted using box and whisker plots. The median is indicated by the line within the box, encompassing the interquartile range (25th and 75th percentiles). The whiskers illustrate the range from the minimum to maximum values. Alphabetic symbols atop the whiskers denote significant inter-category disparities (Wilcoxon paired-sample test, n=12, $p<0.05$). (B) Box and whisker plots presenting the occurrence of jam events in multi-lane and one-lane relocations (Wilcoxon paired-sample test, T=0, n=12, $p<0.01$). (C) Pie chart representation illustrating the anticipated proportion of jams in the inner ring, juxtaposed with the observed distribution of jam causes in the outer ring. Categories include returning leaders (black area), brood transporters (white area), and lost followers (grey area).

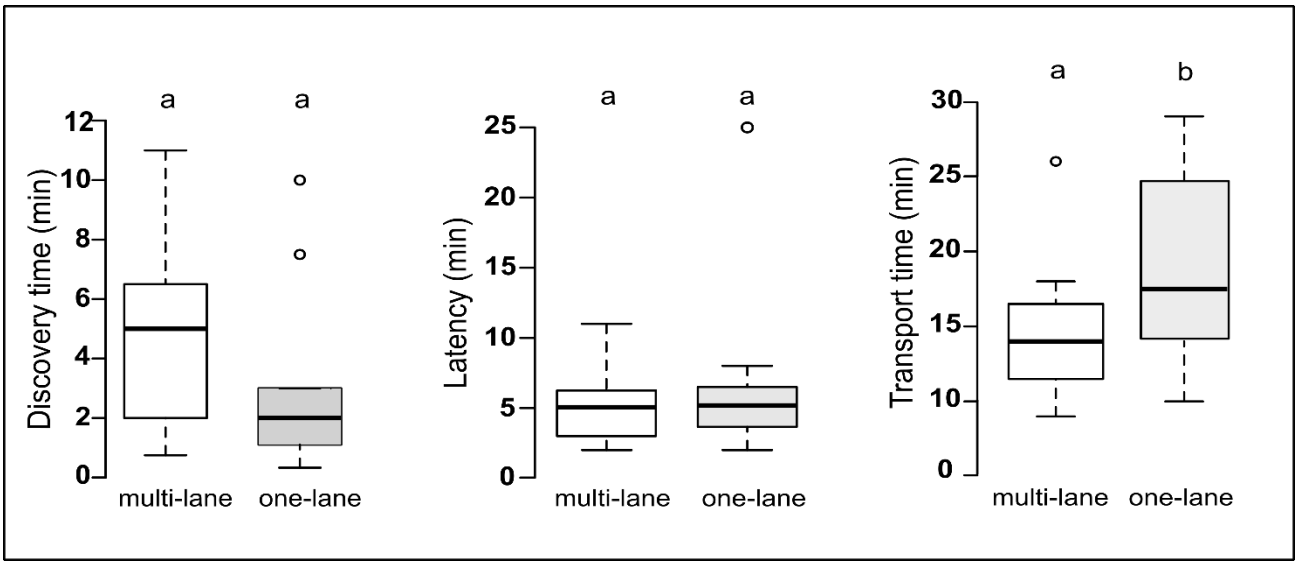

Figure 3: Relocation Dynamics: Box and whisker plots comparing the discovery time (A), latency (B), and transport time (C) are depicted. The median is illustrated by the line within the box, while the box itself represents the 25th and 75th percentiles of the data. The whiskers extend to display the minimum and maximum values of the data points. Different letters atop the whiskers signify a statistically significant difference between categories (Wilcoxon paired-sample test, $n=12$, $p<0.05$).

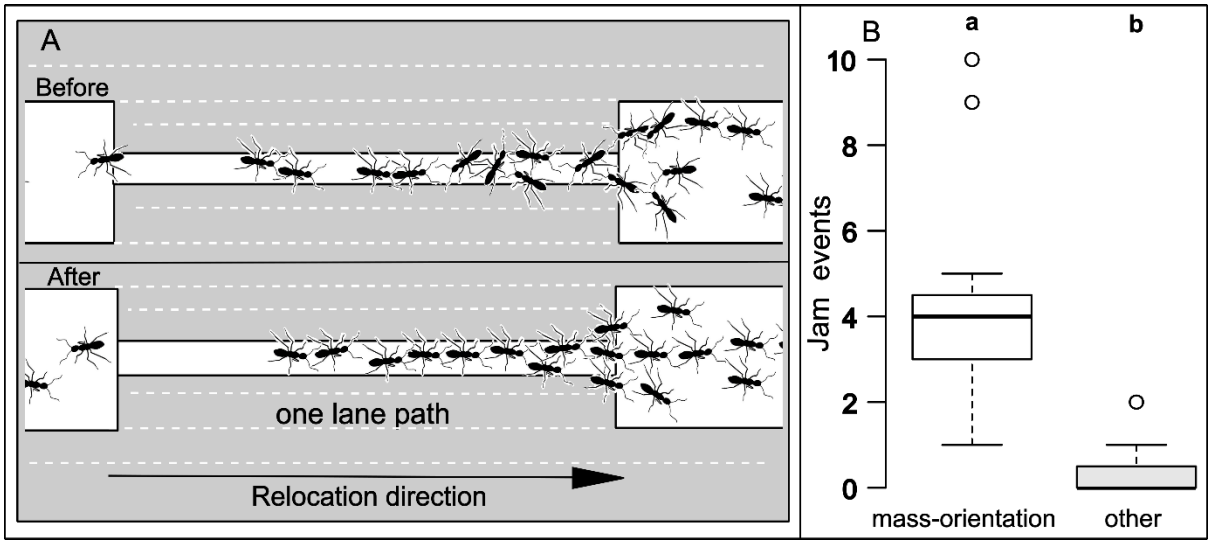

Figure 4: Mass-Orientation of ants. (A) This figure illustrates the mass-orientation process in panel, where the upper panel portrays a jam event with several ants unable to proceed to the new nest, while the lower panel depicts ants during the mass orientation towards the new nest. (B) The comparison of jam events between mass orientation (white bar) and other methods (grey bar) is presented as a box-whisker plot. The box encompasses the 25th and 75th percentiles, with the median indicated by the line within the box. Whiskers display the minimum and maximum data points. Alphabets above the whiskers indicate statistically significant differences between categories (Wilcoxon paired-sample test, $n=12$, $p<0.05$).

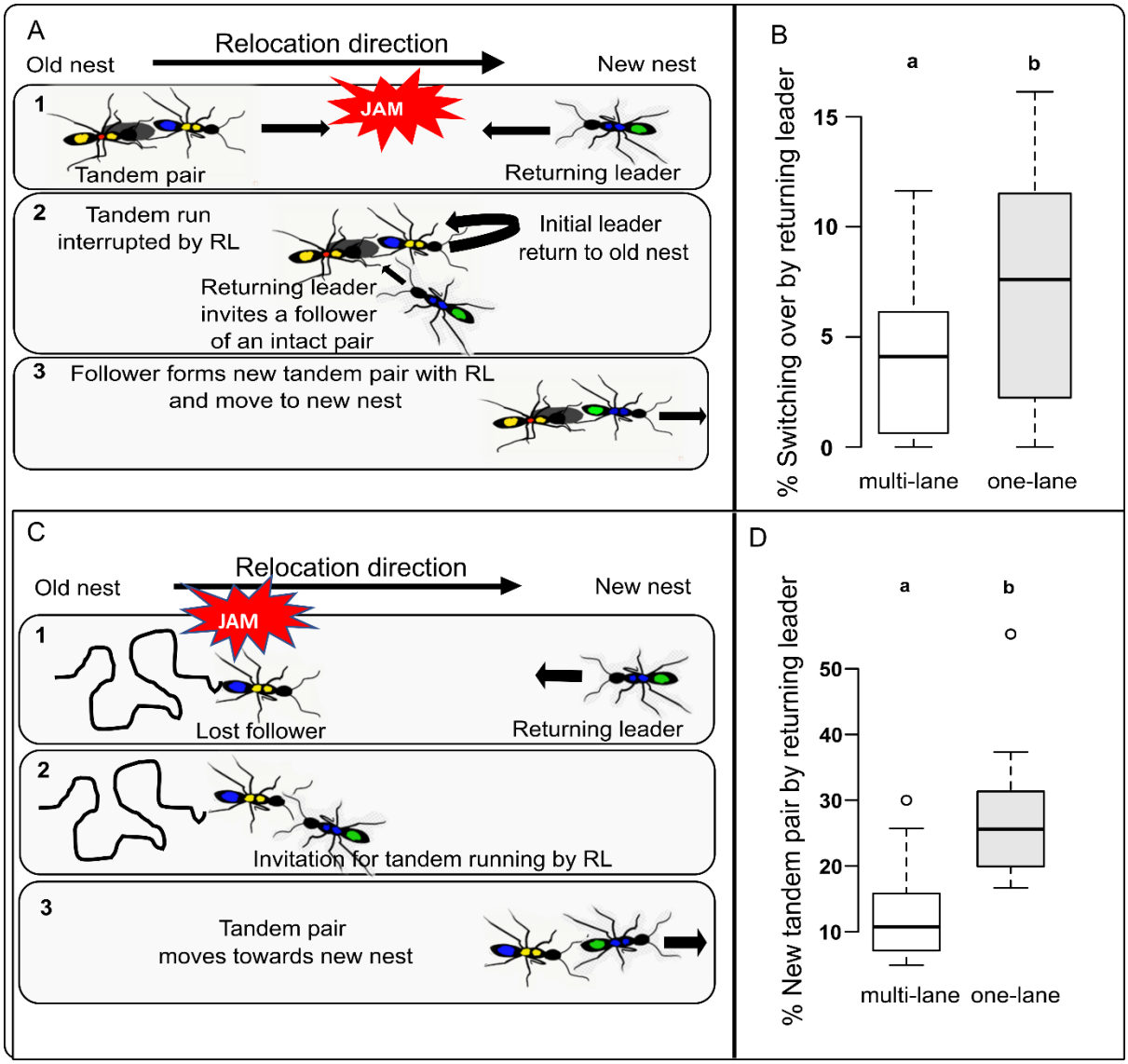

Figure 5: Dynamics of Midway Recruitment. (A) Panel presents a stepwise schematic diagram illustrating the process of switching over. (B) The percentage of switchover events initiated by returning leaders in multi-lane and one-lane relocations is depicted as a box and whisker plot in panel (Wilcoxon paired-sample test, n=12, p=0.02). (C) Panel provides a stepwise schematic diagram elucidating the process of midway tandem pair formation. (D) The extended whiskers denote the minimum and maximum values of data points. Distinct letters above the whiskers signify significant differences between categories (Wilcoxon paired-sample test, n=12, p<0.01).

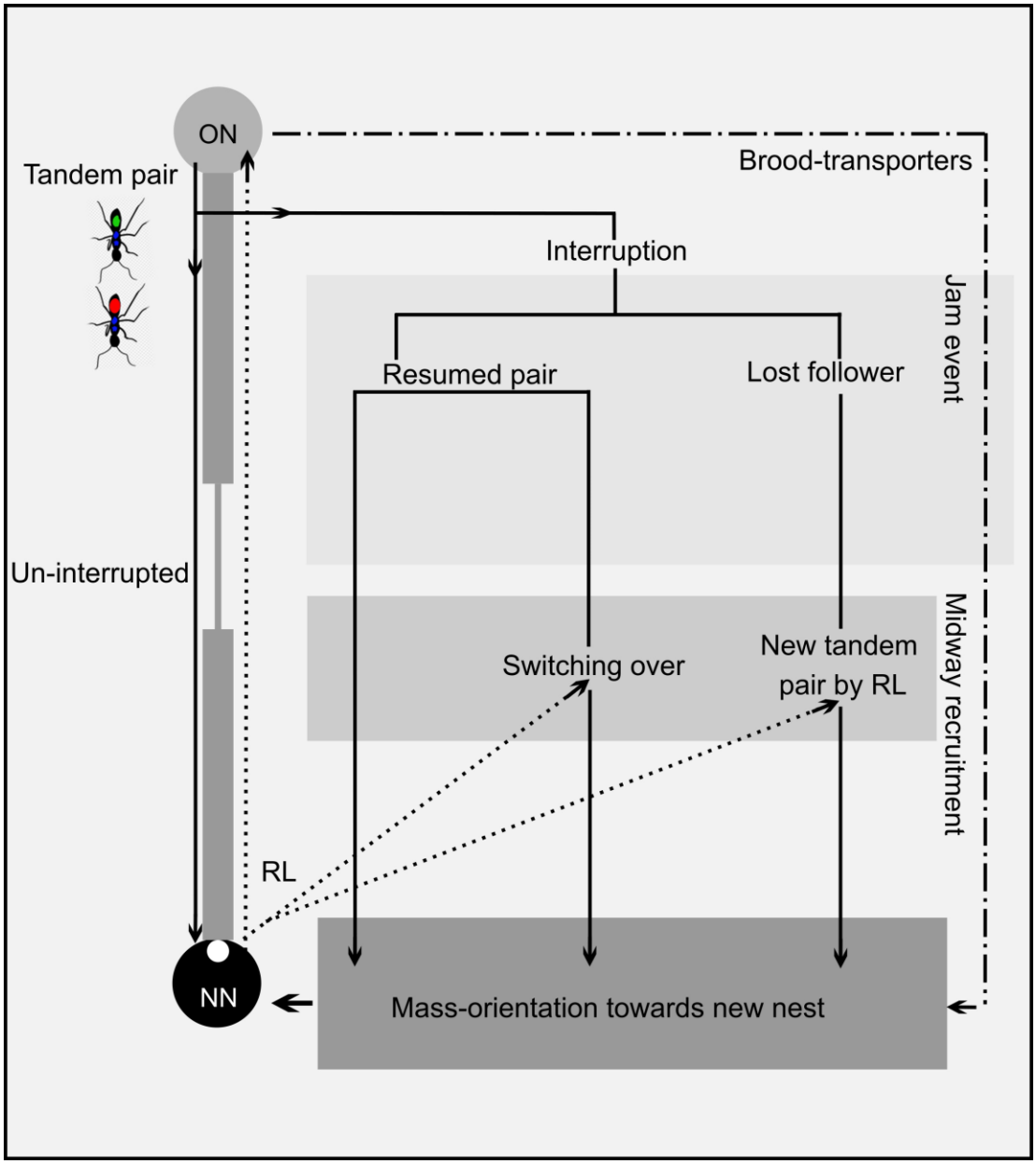

Figure 6: Schematic of Jam Resolution: This figure illustrates the sequence of events during the relocation of ants from their uninhabitable old nest (ON) to their new nest (NN) within the experimental setup. Solid lines denote tandem runs, while dashed lines depict tandem leaders making their way from the new nest back to the old nest (Returning leaders); arrowheads indicate the direction of movement. The schematic outlines the potential outcomes for tandem pairs (comprising one leader and one follower) departing from the old nest and the subsequent developments when encountering a traffic jam (depicted in light grey) and the mechanisms employed for resolution (depicted in dark grey).