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Symmetry breaking and pivotal individuals during the reunification of ant colonies

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ABSTRACT

Maintenance of a social group requires the ability to reach consensus when faced with divisive choices. Thus, when migrating colonies of the ant *Temnothorax rugatulus* split among multiple sites, they can later reunify on the basis of queen location or differences in site quality. In this study, we found that colonies can reunify even without obvious cues to break the symmetry between sites. To learn how they do so, we observed both symmetric reunifications (between identical nests) and asymmetric reunifications (between nests of unequal quality) by colonies of individually marked ants. Both reunification types were accomplished by a tiny minority that carried nestmates from the 'losing' to the 'winning' site. Reunification effort was highly skewed in asymmetric splits, where the majority of the work was done by the first ant to transport, which nearly always came from the winning site. This contrasted with symmetric splits, where the initiator did not play an outsize role and was just as likely to come from the losing site. Symmetric reunifications were also characterized by high transporter attrition, which may help to prevent deadlocks. Tandem runs were abundant in both types and were typically led by transporters as they returned to the losing site to fetch another nestmate. Few tandem followers joined the transport effort, suggesting that tandem runs do not serve to recruit transporters but may have another, as yet unidentified role. Our results underscore the potentially large contribution of highly active individuals to group behaviour, even in decentralized societies such as ant colonies.

KEY WORDS: Tandem running, Emigration, Consensus decision making, Polydomy, *Temnothorax*

INTRODUCTION

Animal societies often face the need for consensus to avoid breakup when choosing among foraging grounds, nesting sites or other options (Conradt and Roper, 2005; Couzin et al., 2005; Franks et al., 2013; McCreery et al., 2016; Sumpter et al., 2008). Consensus is especially important during colony migration by eusocial insects. Although some species are well adapted to frequent fission–fusion cycles or to permanently occupying multiple nests (Buczkowski and Bennett, 2009; Ellis et al., 2014; Holway and Case, 2000; Traniello and Levings, 1986), others pay a fitness cost if part of the non-reproductive workforce is cut off from their queen and so cannot contribute to the colony's growth and reproduction. Studies of

colony migration by honeybees and ants have revealed elaborate decentralized mechanisms by which consensus emerges on the best of several sites, without the need for well-informed leaders to coordinate the move and ensure cohesion (Cronin, 2012; Karunakaran and Annagiri, 2017; Pratt, 2005b; Pratt et al., 2002; Robinson et al., 2014; Seeley, 2010; Visscher, 2007). These strategies rely on site quality-dependent recruitment amplified by non-linear quorum rules that reduce the likelihood of commitment to more than one site.

Despite their consensus-building stratagems, migrating colonies do not always avoid splitting among sites (Franks et al., 2013; Stroeymeyt et al., 2010). When this happens, they must reunify to avoid the fitness costs of permanent division. Even seasonally polydomous species, in which temporary colony division is part of the normal lifecycle, must have ways to reunite the colony at the appropriate time (Buczkowski and Bennett, 2008; Herbers, 1986; Roberts et al., 1999; Snyder and Herbers, 1991). Reunification may use different mechanisms from colony migration, but little research has been done on the topic, beyond showing that some species can successfully reunify after such divisions (Droual, 1984; Kaur et al., 2012; Stroeymeyt et al., 2010).

This study addressed the behavioural mechanisms of colony reunification by the ant *Temnothorax rugatulus*. Nest-site selection in this genus is a well-developed model system for collective decision making. Because these ants dwell in pre-formed cavities such as rock crevices, rather than constructing their own nests, colonies benefit from effective selection of the best available cavity. Extensive research has uncovered the elements of how they do so, largely by examining their behaviour when forced to move by destruction of their current nest (Mallon et al., 2001; Möglich, 1978; Pratt and Sumpter, 2006; Sasaki and Pratt, 2011). In short, a subset of active scouts combs the surrounding area for candidate new homes. Upon finding one, a scout assesses it and initiates recruitment of nestmates with a probability that depends on the site's quality. Recruitment is initially directed at fellow scouts using a slow method called tandem running, in which a single recruit is led from the old nest to the candidate site. Recruits may themselves start recruiting, thus creating positive feedback on the number of ants visiting the site. If multiple sites are found by different scouts, recruitment may start at more than one, but it will tend to be more effective at better sites because of the quality dependence of recruitment initiation. This difference is amplified by a quorum rule, under which recruiters switch from tandem runs to speedier social transports once their site's population has reached a threshold. Transports are mainly directed at the passive majority of the colony, including queens and brood, which have been waiting at the old nest. Ideally, all of these ants will be carried to the new site before any competing site has reached the quorum, ensuring consensus on a single site. However, this is not always the case, leading to transient colony divisions that are subsequently resolved by a second phase of movement (Franks et al., 2008).

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In a recent study on *T. rugatulus*, monogynous colonies that were equally divided between two artificial nests reunified at one of them, choosing it on the basis of both nest quality and queen location (Doering and Pratt, 2016). If the sites were physically identical, the ants chose the one that contained the queen. If one site had a dimmer interior (a strongly preferred nest trait for these ants), the ants reliably reunified there, even when the queen was in the brighter nest. Reunification for *Temnothorax* thus involves balancing risks to transporting the queen and considerations of nest structure. How well colonies make a decision if no such asymmetries exist is not yet known, nor have any observations been made on the individual behaviour underlying reunification.

The first goal of this study was to determine whether *T. rugatulus* colonies can reunify after symmetric divisions; that is, when they are evenly divided between identical nests, neither of which contains a queen. Such splits may occur in nature if *T. rugatulus*, like other *Temnothorax* species, fractionates between multiple nests in spring and recoalesces at one site in autumn (Alloway et al., 1982; Cao, 2013; Partridge et al., 1997; Roberts et al., 1999; Stroeymeyt et al., 2017). *Temnothorax* colonies in the wild may occupy three or more nests at one time (Alloway et al., 1982), and recoalescence therefore plausibly occurs in stages and involves unions between queenless groups inhabiting similar nests. To test the ants' ability to deal with such splits, we divided colonies across several treatments varying in the degree of asymmetry. We then observed whether the frequency of successful reunification was influenced by the amount and type of asymmetry present in the initial division.

The second goal of this study was to describe how consensus emerges from the behaviour of individual ants in both symmetric and asymmetric contexts. Colony emigrations are typically carried out by a subset of active workers, with the bulk of the colony waiting at the old nest to be carried to their new home (Dornhaus et al., 2008; Franks et al., 2006). The active workers themselves vary in how much they contribute to the move, with some, occasionally referred to as 'elites', showing consistently higher activity or influence than others (Dornhaus et al., 2008; Pinter-Wollman et al., 2012; Richardson et al., 2018; Stroeymeyt et al., 2011). We were therefore interested in whether a similar division of labour is present during reunification and, if so, whether the workload is evenly distributed or concentrated in a few highly active ants.

In addition to the distribution of work, we also focused on recruitment communication, to determine its role in reunification and how it resembles or differs from recruitment during emigration. Of particular interest are 'reverse' tandem runs, so called because they run from the new nest back to the old, opposite to the direction of transport. During emigrations, they are seen after a quorum has been reached and are typically led by transporters as they return to the old nest to find another nestmate to carry to the new site. Their role is unclear, but it has been hypothesized that they serve to recruit additional transport effort during the final stage of emigration (Franks et al., 2009; Planqué et al., 2007). Evidence for this role is equivocal, and observations of reverse tandem followers show that most have already started to transport before following (Pratt et al., 2002). It may be that the function of this behaviour is more apparent when a colony is divided among multiple sites. In this situation, reverse tandem runs could serve to reallocate recruitment from one source of transportees to another, thus facilitating coalescence at a single site. Such a role would be obscured in simple laboratory emigrations where all transports originate in the old nest, of which all transporters are already informed. To test this hypothesis, and to provide a detailed description of individual behaviour during reunification, we video recorded reunifications by colonies in which

every ant was paint-marked with a unique label. We then reviewed the recordings to extract the sequence of each recruiter's key behaviours, particularly tandem runs and transports.

MATERIALS AND METHODS
Nest designs
Nests consisted of a 2.4 mm thick balsa wood slat with a 38 mm diameter nesting cavity drilled through the centre. Glass microscope slides (50×75 mm) above and below the slat provided a floor and ceiling. Ants accessed the cavity via a 2 mm wide slit cut through one side of the slat. To dim the cavity interior, neutral density filters (Rosco Cinegel) were sandwiched between two microscope slides and placed on top of the nest. Because the ants prefer darker homes, we adjusted nest quality by varying the filter's opacity. 'Good' nests had three 3-stop filters, 'mediocre' nests had one 1-stop filter and 'poor' nests had no filter. Balsa slats were discarded after each experiment, but slides were re-used after cleaning in a commercial dishwasher. See Sasaki et al. (2015) for further details on nest construction.

Subjects
We used twenty-two colonies of *Temnothorax rugatulus* (Emery 1895) collected in the Pinal Mountains of Arizona (33.317N 110.876W). Sixteen colonies collected in February 2017 were used in experiment 1; three colonies collected in October 2015 and May 2016 were used in experiment 2; and three colonies collected in February 2017 were used in experiment 3. All colonies were monogynous and had 50–200 workers and 10–90 brood items. Colonies were housed in nests of the poor design described above. Each nest was kept in a covered plastic box (11×11×3 cm) and was provided with water in a cotton-stopped plastic tube. Colonies were fed weekly with an agar-based diet (Bhatkar and Whitcomb, 1970). Voucher specimens were deposited at the Arizona State University Natural History Collections in Tempe, Arizona.

Experiment 1: effect of symmetry level on likelihood of reunification
In this experiment, colonies were evenly divided between two nests and given the opportunity to reunify. The degree of asymmetry (i.e. the differential in attractiveness to the ants) between the nests was varied across four treatments by manipulating two parameters, namely nest quality and the location of the colony's queen. Treatment 1 had the highest asymmetry, with the queen and half the colony's workers and brood placed in a good nest, and the other half of the workers and brood placed in a poor nest. Because both queen location and nest quality are known to influence reunification location (Doering and Pratt, 2016), this choice was expected to have a clear favourite. Treatment 2 offered a less clear choice, as both nests were mediocre, and the queen was randomly assigned to one nest via a virtual coin flip. Treatments 3 and 4 both offered perfectly symmetrical choices, as the nests were identical, and the queen was removed from the colony and kept in a separate container throughout the reunification process. Treatments 3 and 4 differed only in the quality of the nests, which were mediocre in treatment 3 and poor in treatment 4. The experiment ran for 16 days; on each day four colonies were tested, one in each treatment. By the end of the experiment, each of the 16 colonies had received each treatment exactly once.

The procedure for splitting the colonies between nests largely followed the methods of Doering and Pratt (2016). In brief, each colony, still in its original nest, was placed in a circular plastic arena and the roof of its nest was removed. After 1–3 min, colony

members were moved one by one into two separate arenas containing the target nests. Workers were moved with soft forceps and brood were moved with a moist pinhead to which they lightly adhered. To ensure that the two nests received equal numbers of the active scout ants that carry out colony emigration, we evenly divided the workers that had left the destroyed original nest and were thus likely to be scouts. We also equally divided the ants that remained in the destroyed nest, and the colony's brood. Colonies were then given 1–3 h to move into the target nests, after which both nests were placed in a single new arena with their entrances facing one another at a distance of approximately 40 mm. This level of separation between nests is similar to that seen in other studies of nest relocation in *Temnothorax*, which typically use distances between 20 and 600 mm (Doering and Pratt, 2016; Dornhaus et al., 2004, 2008; O'Shea-Wheller et al., 2016a; Pratt, 2005b; Pratt et al., 2002; Sendova-Franks and Franks, 1995; Stuart, 1985). After 12–15 h, we noted whether the colony had reunified and, if so, which nest it had chosen. A colony was considered to have reunified if approximately 80% or more of its workers and all of its brood were found in a single nest.

Colonies were always split in the late morning or early afternoon. To mitigate possible order effects, we systematically varied the sequence in which colonies received the four treatments. Colonies were grouped into four-colony cohorts, each of which received a different treatment order. For cohort A the order was 1, 2, 3, 4; for cohort B it was 2, 1, 4, 3; for cohort C it was 3, 4, 1, 2; and for cohort D it was 4, 3, 2, 1.

Experiment 2: individual behaviours in asymmetric reunification

In this experiment, we obtained detailed individual-level descriptions of worker behaviour during reunification. In each of three colonies, every worker was marked with a unique combination of paint dots on the head, thorax and abdomen using Pactra R/C Car Lacquer paint. Each colony was then split between two nests of unequal quality, as described above, and each ant's nest assignment was recorded. Reunification was video-recorded in HD or 4K resolution, and the recordings were reviewed to obtain the timing and direction of every tandem run and transport, as well as the identities of every leader, follower and transporter. Each of the three colonies was recorded three separate times, for a total of nine reunifications. Two of the colonies were always split between a good nest and a mediocre nest; for the third colony, we replaced the mediocre nest with a poor nest, because its transparent roof allowed us to better see activity inside the nest. This made subsequent video analyses less laborious than for the first two colonies tested. In all cases, the queen was placed in the lower quality nest. If a colony did not reunify within 24 h, no data were collected and the colony was induced to move into a third nest by destroying the other two nests. The colony was then returned to its nest box for at least 1 day before the experiment was attempted again.

Experiment 3: individual behaviours in symmetric reunification

This experiment repeated the individual-level observations of experiment 2, but for symmetrical splits between identical nests. All colonies in this experiment were evenly split between two poor nests, and the colony's queen was removed and kept in a separate container throughout the reunification process. Thus, neither queen presence nor nest quality was available as a cue to direct the colony's choice. Methods generally followed those of experiment 2, except that the two nests were closer together (about 30 mm) to

ensure that both nest interiors were visible in the video recordings. This allowed us to track each nest's population throughout reunification, which was not possible in experiment 2 because of the darkened interiors of the higher quality nests. It also obviated the need to record each ant's nest assignment at the time of splitting, as this information could readily be determined from the video recordings (except for three transporters in a single reunification). Three colonies (different from those used in experiment 2) were each observed three times, for a total of nine reunifications. In addition, we recorded a partially successful reunification (i.e. one of the nests ended up with a higher population than the other, but less than 80% of the total). In one colony, some active ants had lost their paint marks. We were nonetheless able to distinguish them from one another via differences in physical traits such as body size and by continuously monitoring each one through a given reunification. However, across reunifications of this colony, the identity of paint-free ants could not be tracked.

Statistical analysis

Summary data are presented as means±s.d., unless otherwise noted. We used linear mixed effects (LME) models to test for differences between asymmetric and symmetric reunifications in recruitment participation and timing; colony ID was included as a random factor, and timing data were log-transformed to achieve normality and equal variance of the model residuals. All statistical analyses were performed in R version 3.4 (https://www.r-project.org). Venn diagrams were produced using a tool available at http://bioinformatics.psb.ugent.be/webtools/Venn, and ethograms were produced using MATLAB version 9.4, 2018a (MathWorks). A χ^2 test of independence was used to evaluate differences in reunification probability across treatments in experiment 1.

RESULTS
Experiment 1: effect of symmetry level on likelihood of reunification

Colonies could successfully reunify at a single nest even with no differences in nest quality, queen location or ant number to break the symmetry between sites. Of the 32 symmetric splits, 18 reunified within 15 h, the same number as for the 32 asymmetric splits (Fig. 1). Overall, there was wide and statistically significant variation across treatments in the proportion of colonies that reunified ($\chi^2_3=14.7$, $P=0.002$). However, this difference was more associated with nest quality than with degree of symmetry. Reunification was rarest for symmetrical splits between mediocre nests (4 of 16 splits) and most common for symmetrical splits between poor nests (14 of 16 splits), a statistically significant difference ($\chi^2_1=12.7$, $P<0.001$). In the two asymmetric cases, there were somewhat more reunifications for the higher degree of asymmetry, but this difference was not significant ($\chi^2_1=2.0$, $P=0.154$). In the asymmetric reunifications, colonies chose as expected based on prior observations (Doering and Pratt, 2016): they always chose the good queenright nest over the mediocre queenless nest (treatment 1), and they chose the mediocre queenright nest over the mediocre queenless nest 6 out of 7 times (treatment 2).

Experiment 2: individual behaviours in asymmetric reunification

All colonies followed a similar behavioural sequence during reunification. A single ant from the better nest started the process by transporting nestmates from the worse to the better nest. This 'initiator' typically followed each transport by leading a 'reverse'
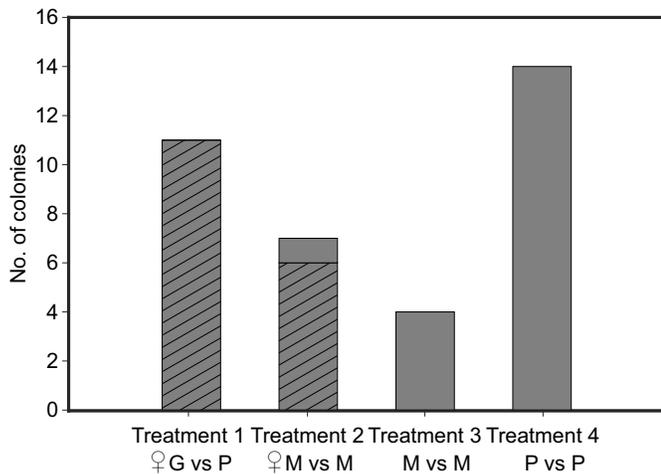
Fig. 1. Effects of asymmetry and nest quality on reunification probability (experiment 1). Bar heights show the number of colonies (out of 16) that reunited (χ_3^2=14.7, P=0.002). In each treatment, colonies were evenly divided between two nests as follows: treatment 1: good nest (G) with queen (♀) versus poor nest (P) without queen; treatment 2: mediocre nest (M) with queen versus mediocre nest without queen; treatment 3: mediocre nest versus mediocre nest (no queen present); treatment 4: poor nest versus poor nest (no queen present). Hatching on the bars in the asymmetric treatments represents the number of colonies that reunified at the nest containing the queen.

tandem run from the better nest to the worse one. This produced an interdigitated pattern of alternating transports and tandem runs in opposite directions. Additional ants subsequently joined the initiator in transporting to the better nest, but the total number of transporters per reunification was consistently low (3.4±1.4). Within this small group, the initiator played an outsize role, performing the majority of all transports in eight of the nine reunifications (64.0±20.0% overall) and always leading the majority of tandem runs (86.0 ±15.0%). The large role of the initiators is clearly visible in the ethograms of each reunification (Fig. 2).

Reunifications were generally complete within a few hours. The first transport occurred 169±201 min after the split colonies were placed together in the single arena, and the last one occurred after another 114±52 min. In calculating the latter times, we excluded outlier transports in two reunifications (colony 1, reunification 1; and colony 1, reunification 3), where the final or penultimate transport occurred more than 100 min after the transport preceding it.

Ants showed a tendency to transport to their 'home' nest. That is, 74% of transporters, including all but one of the initiators, began transporting to the nest to which they had been assigned during the initial split. In other words, ants from the better nest that found the inferior nest were more likely to start transporting than ants from the inferior nest that found the better nest. In one case (colony 2, reunification 2), an ant from the superior nest initiated the reunification by carrying ants in the 'wrong' direction (i.e. from the better to the worse site). Three other ants (from the inferior nest) joined her, but one of them suddenly switched direction about 90 min into the reunification (Fig. 2). The others stopped transporting altogether, and the colony was eventually moved to the better nest by the ant that switched and two others that subsequently joined her.

Over the nine reunifications, ants led a total of 159 tandem runs, or 18±11 tandem runs per reunification (Table 1). Of these, 152 (95.6%) were reverse tandem runs, meaning that they were led in the opposite direction from transports. Of the seven forward tandem runs, five were seen in a single reunification, and none showed the typical pattern previously reported for emigrations, in which tandem runs are led from the original nest to the new nest before any transport has begun. Instead, all reunifications began with transport, before any tandem run was led. The absolute number of distinct ants that followed tandem runs (9.9±5.4 per reunification) was lower than the total number of tandem runs, reflecting the fact that several ants followed multiple tandem runs in each reunification. While the majority of followers participated in either one or two tandem runs across all three of their colony's reunifications, some ants followed as many as nine (Fig. 3A). Reunifications varied in the number of
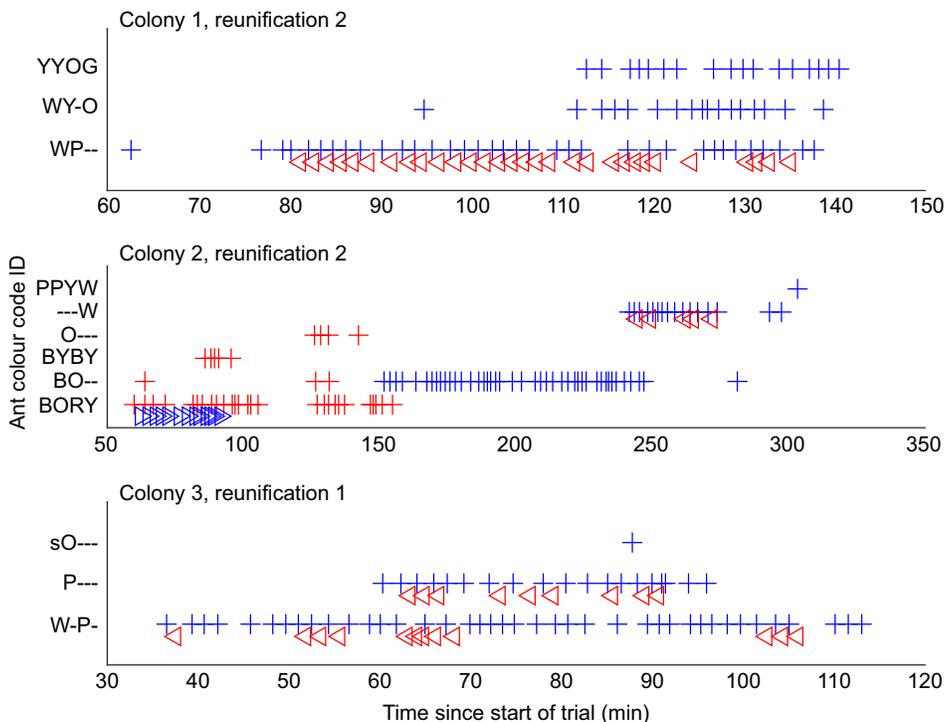

Fig. 2. Recruitment by participating ants during reunifications after division between a good and a poor/mediocre nest (experiment 2). Three representative trials are shown. Each line of icons corresponds to a different ant, indicated by the codes on the vertical axis. Crosses and triangles indicate transports and tandem runs, respectively. Blue symbols indicate transport or recruitment to the better nest, and red symbols to the worse nest. The horizontal axis indicates time since the two nests were placed together in the same arena. For a given ant, tandem symbols are offset from transport symbols to improve clarity. Note the different time scales for each trial.

Table 1. Colony size and counts of recruiters and recruitment events during reunifications by colonies split between asymmetric nests (experiment 2)

	Reverse tandem runs	Forward tandem runs	Followers	Leaders	Transporters	Followed before	Followed after
Colony 1 (75 workers)							
Trial 1	25	0	17	2	5	4	0
Trial 2	30	0	12	1	3	0	2
Trial 3	22	2	14	1	3	0	1
Colony 2 (64 workers)							
Trial 1	9	0	8	2	3	1	0
Trial 2	19	0	12	2	6	1	0
Trial 3	0	0	0	0	1	0	0
Colony 3 (61 workers)							
Trial 1	22	0	11	2	3	1	0
Trial 2	21	5	11	2	3	0	1
Trial 3	4	0	3	1	4	0	0
Total	152	7	89	13	31	7	4
Mean	16.9	0.8	9.9	1.4	3.4	0.8	0.4
s.d.	10.2	1.7	5.4	0.7	1.4	1.3	0.7

Colonies 1 and 2 were split between a mediocre nest with queen versus a good nest; colony 3 was split between a poor nest with queen versus a good nest. The columns labelled 'Followed before' and 'Followed after' indicate, respectively, the number of reverse tandem run followers who started transporting after following and the number that started transporting before following.

tandem runs; in one case (colony 2, reunification 3), there were none at all, and a single ant performed all transports (Fig. S1).

The timing of reverse tandem runs led us to hypothesize that initiators use them to recruit more transporters to help with reunification. This hypothesis predicts that we should see tandem followers go on to become transporters, but this prediction was not fulfilled. Only 11 of 89 followers (12.4%) ever transported (Table 1), and four of these had already started transporting before following a tandem run. Of the remaining seven, four were confined to a single reunification. Furthermore, tandem following was clearly not necessary for the initiation of transport, as 50% of secondary transporters (i.e. excluding the first transporter in each reunification) never followed a tandem run. Nor were transporters especially prolific followers. Although a few ants followed five or more runs over three emigrations (Fig. 3A), transporters followed, on average, only 1.4±0.9 runs. Despite not contributing much to transport, followers were common participants in reunification. Of the 82 distinct ants that participated in at least one reunification, 56 were exclusively followers, never transporting or leading a tandem run (Fig. 4A). Twenty-six ants transported other ants in at least one emigration, and only 13 ants led at least one tandem run. However, every tandem leader was also a transporter at some point, and six of these ants also followed at least one tandem run (Fig. 4).

Experiment 3: individual behaviours in symmetric reunification

As in the asymmetric trials, reunifications were carried out by a small number of transporters, some of which led reverse tandem runs between transports (Figs 5 and 6). Transport effort was also skewed, with the most active ant responsible for 51.2±18.3% of transports and leading 92.3±11.5% of tandem runs. However, unlike the asymmetric case, the first ant to transport was typically not the most active transporter, taking that role in only three of the nine reunifications. The initiators did not play an outsize role in reunification, performing only 36.4±26.8% of transports and leading no tandem runs. Symmetric reunifications also differed in lacking any tendency for ants to transport to their 'home' nest: 45.7% of transporters began by bringing ants to the nest they had been assigned during the split, significantly less than the corresponding value of 74% observed in the symmetric case (χ_1^2=6.2, P=0.013). Additionally, although there were more transporters overall in symmetric reunifications than in

Table 2. Colony size and counts of recruiters and recruitment events during reunifications by colonies split between symmetric nests (experiment 3)

	Reverse tandem runs	Forward tandem runs	Followers	Leaders	Transporters	Followed before	Followed after
Colony 10 (72 workers)							
Trial 1	0	0	0	0	3	0	0
Trial 2	0	0	0	0	2	0	0
Trial 3	4	0	3	1	6	0	0
Colony 11 (87 workers)							
Trial 1	14	0	11	2	6	1	0
Trial 2	3	0	3	2	8	0	0
Trial 3	1	0	1	1	15	0	1
Colony 12 (118 workers)							
Trial 1	40	0	21	3	8	3	1
Trial 2	17	0	12	1	4	1	1
Trial 3	6	0	6	1	2	0	0
Total	85	0	57	11	54	6	3
Mean	9.4	0	6.3	1.2	6	0.7	0.3
s.d.	13.0	0	7.1	1.0	4.1	1.3	0.5

Colonies were symmetrically split between two poor nests (no queen). The columns labelled 'Followed before' and 'Followed after' indicate, respectively, the number of reverse tandem run followers who started transporting after following and the number that started transporting before following.
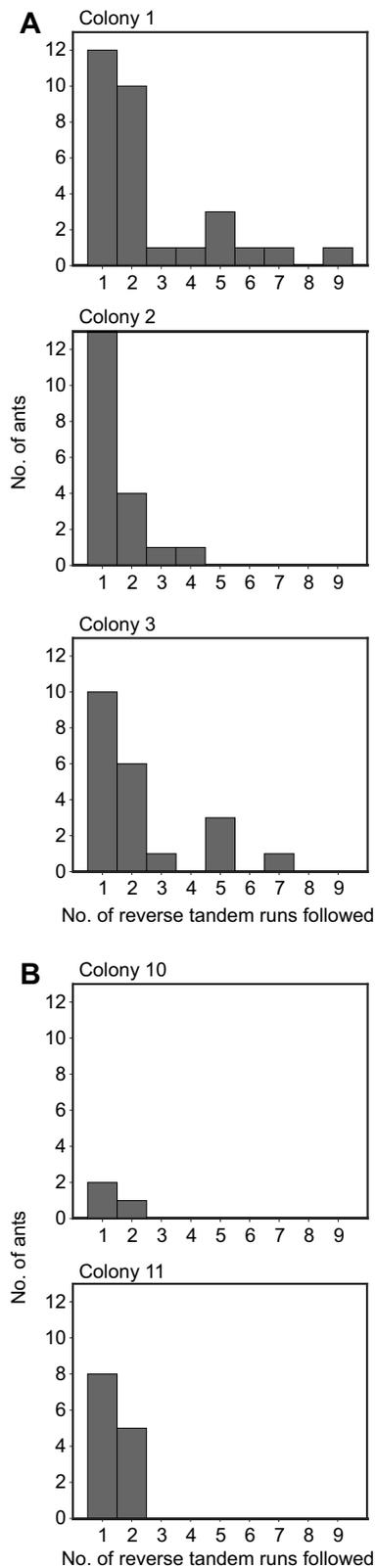
Fig. 3. Histograms of the number of reverse tandem runs followed by individual ants. Results are shown for reunification after (A) asymmetric (colonies 1–3) and (B) symmetric (colonies 10 and 11) splits. For each ant that followed at least one reverse tandem run, we summed the total number that she followed across all three of her colony's trials. Colony 12 from experiment 3 was omitted because it contained unmarked tandem followers that could not be tracked across trials.

asymmetric ones, the proportion of ants participating in transport was not higher in colonies with symmetric reunifications (LME model: t_4=0.69, P=0.53).

In two of the nine symmetric reunifications, transport to the two sites occurred simultaneously (Fig. S2). Left unchecked, this disagreement would make reunification impossible, as conflicting transporters would repeatedly move the same items back and forth between nests. We hypothesized that colonies avoid this fate via transporter attrition, with ants ceasing transport even when items remained to be carried. To quantify attrition, we counted the number of transport 'interruptions' and 'cessations' in each reunification. We defined an interruption as a gap of at least 40 min between transports, and a cessation as a gap of at least 40 min between an ant's last transport and the final transport of the reunification. We counted these events only for transporters that carried at least 10 nestmates during a reunification. The proportion of transporters that exhibited either interruptions or cessations was significantly greater in symmetric reunifications, with 14 out of 22 transporters compared with 5 out of 17 transporters in asymmetric reunifications (χ^2_1=4.496, P=0.034). The instance where the ants did not meet our criterion for reunification further illustrates the potential value of attrition for resisting deadlock. In this trial, competing transports to the two nests prevented full convergence to just one site (Fig. 6). However, the colony was partially successful in merging its two halves. The spontaneous extinction of individuals' transport efforts enabled the last remaining ants that carried nestmates to exert a strong influence, thereby shifting the colony's population so that 70% of all workers resided at the left-side nest.

Despite the similar and even slightly larger colony sizes, tandem runs were less common in symmetric than in asymmetric reunifications, with 85 in all, or 9.4±13.0 tandem runs per reunification (Table 2). All of them were reverse tandem runs. The percentage of ants in a colony that followed tandem runs in symmetric reunifications (6.1±5.8%) was also lower than that in asymmetric reunifications (14.4±7.0%), but this difference was not statistically significant (LME model: t_4=−2.22, P=0.09). The proportion of ants in a colony that led tandem runs was not significantly different between asymmetric and symmetric reunifications (LME model: t_4=−1.83, P=0.14). No ants followed more than three tandem runs over the course of their colony's three reunifications (Fig. 3B), in contrast to asymmetric reunifications, where some ants followed as many as nine (Fig. 3A). Similar to the asymmetric case, colonies varied greatly in the number of tandem runs per reunification (Table 2).

As in asymmetric reunifications, there was only a weak relationship between transporting and tandem following. Of 57 followers only 9 (15.8%) also transported, and three of these had already started transporting before following (Table 2). Of the 45 non-initiating transporters, 36 (80.0%) never followed a tandem run. Overall, the average numbers of transporters (6.0±4.0) and tandem followers (6.3±7.1) was similar. Compared with the asymmetric reunifications, ants that exclusively followed tandem runs, without ever transporting or leading, were less common, at 13 of the total of 46 participants that could be tracked across multiple trials (Fig. 4B). Thirty-three ants transported and only five ants led at least one tandem run. All tandem leaders also transported, but none of them ever followed a tandem run. The timing of symmetric reunifications was statistically similar to that of the asymmetric ones, with the first transport occurring 160±151 min after the ants were placed together in the single arena (LME model: t_4=0.16, P=0.88), and the last transport seen after another 204±139 min (LME model:
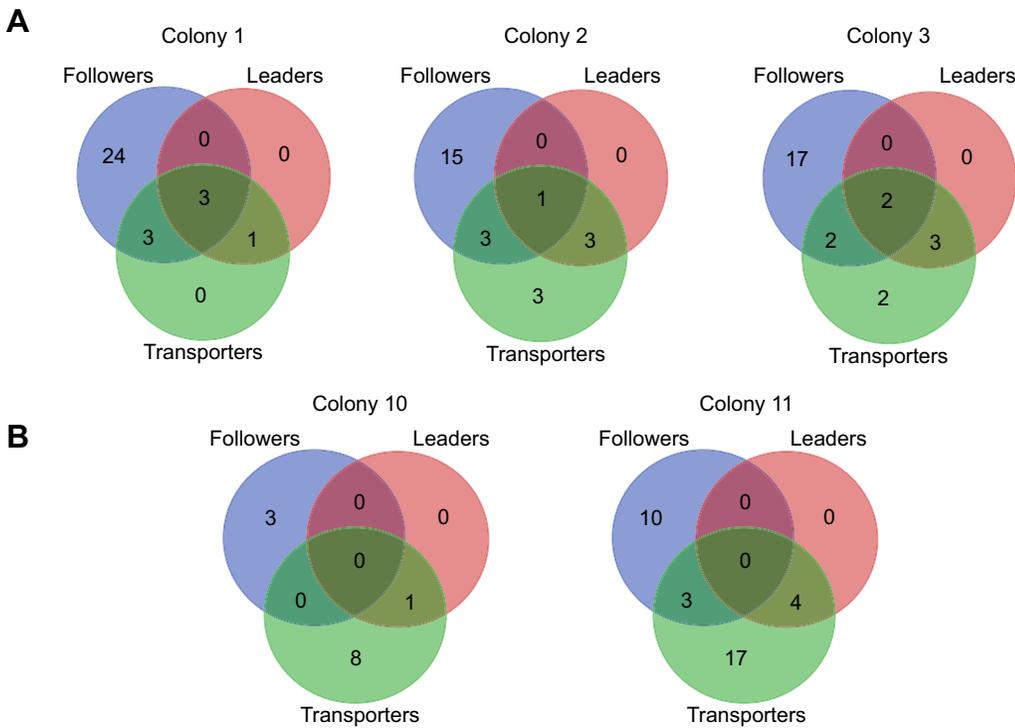
A

Fig. 4. Venn diagrams classifying ants by their participation as transporters, reverse tandem run leaders and reverse tandem run followers. Data are shown for (A) three colonies from experiment 2 and (B) two colonies from experiment 3. Colony 12 from experiment 3 was omitted because it contained unmarked tandem followers that could not be tracked across trials.

B

t_4=1.37, P=0.24). Across all symmetric reunifications, the ants showed no bias towards either the right or left nest (of the 9 reunifications, 5 chose the right nest and 4 the left nest; 2-tailed binomial test: P=1).

DISCUSSION

Our results demonstrate that *T. rugatulus* colonies can successfully reunify after symmetric divisions between two nests. Indeed, colonies were just as likely to reunify with symmetric as for asymmetric splits. This ability is potentially useful if, like some other *Temnothorax* species, *T. rugatulus* is seasonally polydomous, periodically recoalescing from multiple nests (Alloway et al., 1982; Cao, 2013; Partridge et al., 1997; Roberts et al., 1999; Stroeymeyt et al., 2017). Symmetry breaking could also be useful during emigration if colonies transiently split among many similar locations, eventually reuniting at a single one. Among symmetric divisions, there was a notable effect of nest quality, with reunification much more likely for colonies divided between poor
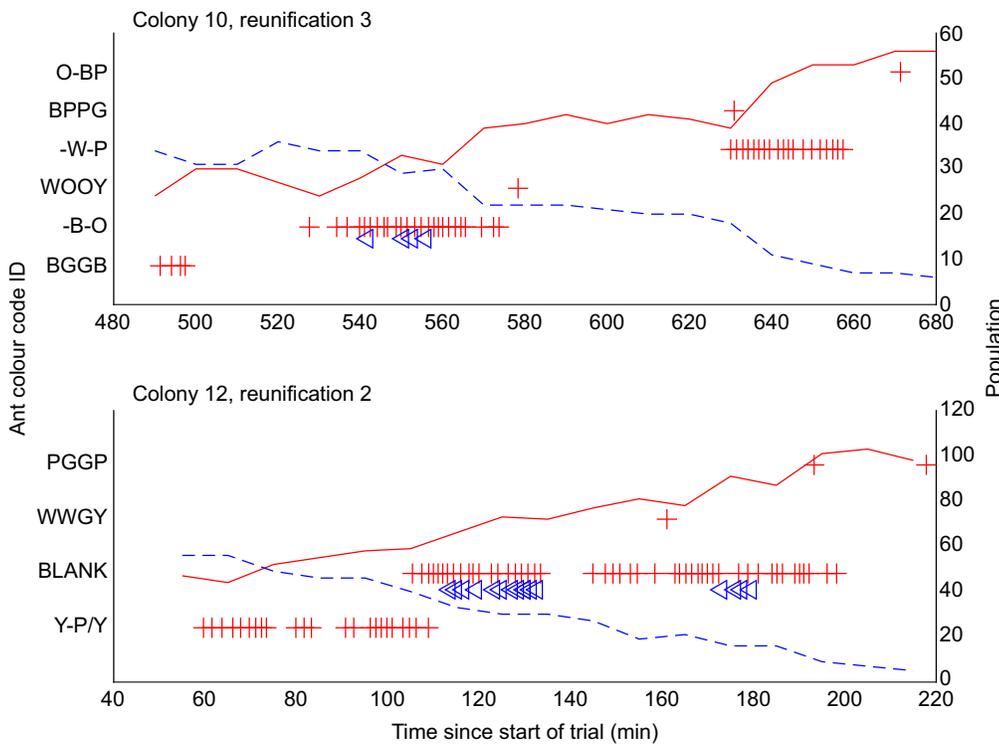

Fig. 5. Recruitment by participating ants during reunifications by colonies split between identical nests (experiment 3). Two representative trials are shown. Each line of icons corresponds to a different ant, indicated by the codes on the vertical axis. Crosses and triangles indicate transports and tandem runs, respectively. Blue symbols indicate transport or recruitment to the nest on the left side of the arena, and red symbols to the nest on the right side. Also plotted are the worker populations of the nests on the left (dashed blue line) and right (solid red line) over time. The horizontal axis indicates time since the two nests were placed together in the same arena. For a given ant, tandem symbols are offset from transport symbols to improve clarity. Note the different time scales for each trial.
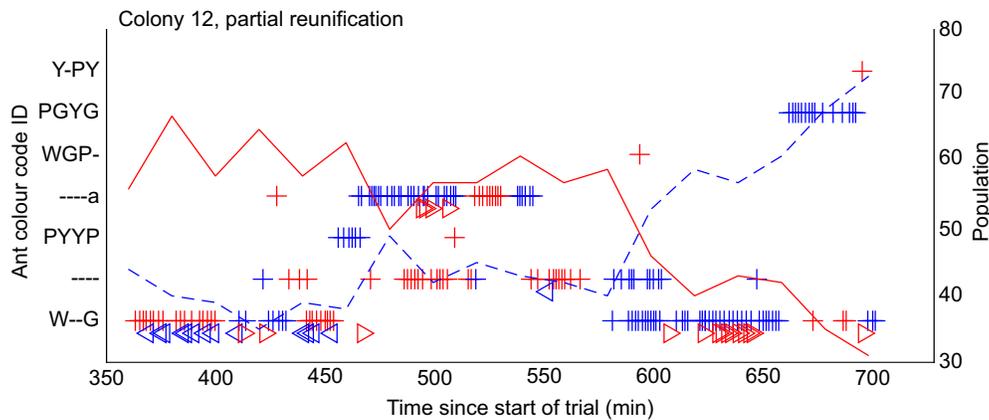
Fig. 6. Recruitment by participating ants during a partial reunification after division between identical nests (experiment 3). Each line of icons corresponds to a different ant, indicated by the codes on the vertical axis. Crosses and triangles indicate transports and tandem runs, respectively. Blue symbols indicate transport or recruitment to the nest on the left side of the arena, and red symbols to the nest on the right side. Also plotted are the worker populations of the nests on the left (dashed blue line) and right (solid red line) over time. The horizontal axis indicates time since the two nests were placed together in the same arena. For a given ant, tandem symbols are offset from transport symbols to improve clarity.

nests. The reason for this difference is unclear, but we can speculate that ants adjust their degree of polydomy according to the benefits and costs of occupying available nests (Debout et al., 2007; Robinson, 2014). For example, colonies might be more likely to unify when nests have weak walls or large entrances, making them hard to defend by a small number of ants.

The process of reunification was very similar for symmetric and asymmetric splits, but there were a few important differences. In both contexts, a small number of ants carried nestmates from the losing to the winning nest, and a subset of these ants also interspersed their transports with tandem runs in the opposite direction. In asymmetric splits, transporters almost always came from the winning nest, hence their behaviour can be seen as retrieval of lost nestmates to their home nest. In symmetric splits, about half of the transporters came from the losing nest, and thus changed their nest allegiance in the course of reunification. Their behaviour is similar to that of scouts in simple emigrations, which recruit nestmates from their old nest to a new home (Pratt, 2005b; Pratt et al., 2002). It is not obvious why changes of allegiance should be less common in asymmetric splits, but it may simply be that retrieval behaviour is more readily instigated when an ant finds nestmates away from her nest in a clearly inferior site. These retrievers then complete the reunification before many ants from the worse site have had the opportunity to switch allegiance.

Symmetric splits were also more likely to have transport in both directions, an unsurprising result given the lack of features favouring one site over the other. These competing efforts could result in prolonged and wasteful transport of the same ants back and forth between sites. Colonies clearly avoided this outcome, and one reason may be transporter attrition, whereby ants stopped transporting even when there were still nestmates available to be carried. Attrition of nest site scouts contributes to consensus building in honeybees (Seeley, 2003, 2010). If it plays a similar role here, there is evidence that it is context specific. That is, attrition was less marked in asymmetric splits than in symmetric ones, and attrition has not been reported in previous studies of simple emigrations, where transporters commit themselves to the task until there is nothing left to carry (Mallon et al., 2001). We can reject one simple explanation of this difference, namely that attrition occurs at a similar rate in all conditions but is revealed only in emigrations or reunifications that take an unusually long time. This explanation is

inadequate given the similar durations of symmetric and asymmetric reunifications. A possible alternative explanation is that transporters perceive some cue indicating a transport stalemate, such as encounters with competing transporters moving in the opposite direction or attempts by these competitors to solicit them for transport. Sensing encounter rates with nestmates can indeed modify ant behaviour in other contexts, including task allocation (Gordon and Mehdiabadi, 1999; Greene and Gordon, 2007), reorienting the direction of foraging individuals (Moffett, 1987) and detecting the achievement of a nestmate quorum (Pratt, 2005a). The probability of a worker continuing or ceasing her transport activity is conceivably tied to the rate at which ants are encountered in the target or home nest; if the population in the target nest perceived by a transporter is not changing fast enough, this might act as a cue for her to cease transport activity. However, further experimental probing of the function and mechanisms of transporter attrition is warranted.

Reverse tandem runs were abundant in colony reunifications, but forward tandem runs were rare. This differs from simple emigrations, where the discoverers of a site first lead forward tandem runs to it, only later switching to transport accompanied by reverse tandem runs. The lack of forward tandem runs in reunifications is consistent with a quorum rule governing the start of transport. Such a rule operates in simple emigrations, where forward tandem runs end once the population of the candidate site has surpassed a threshold (Pratt, 2005a; Pratt et al., 2002). In reunifications, both sites start with high populations; hence, ants may perceive them as already above quorum, even at the start of recruitment. In addition, a recruiter that brings ants to her home nest (i.e. the one to which she was assigned at division), is quite different from a scout in an emigration. Rather than assessing a novel site as a potential home, she is simply transporting stranded nestmates to her current home. In such a situation, there is no obvious role for forward tandem runs (i.e. tandem runs to the winning nest).

While reverse tandem runs were common, their function here remains a puzzle, as it does for simple emigrations. Mathematical models (Planqué et al., 2007) and some experimental data (Franks et al., 2009) suggest that reverse tandem runs can speed up emigration by activating more transporters, especially when initial transporter numbers are low. However, while followers of reverse tandem runs participate heavily in transport during emigrations

(Franks et al., 2009; Pratt et al., 2002), they usually begin to do so before following, casting doubt on an activating role. The apparent redundancy of reverse tandem runs might be an artefact of simplified emigration conditions in the laboratory, where transport is needed only from a single old nest of which all workers are aware. We predicted that the contributions of reverse runs might be more prominent in reunifications, where each half of the colony begins the process ignorant of the location of the other half. Thus, the first ant that discovers the other site and starts transporting from it to her own nest could usefully share information about the site's location with her uninformed nestmates, thus instigating them to start transporting. Indeed, transport initiators led many reverse tandem runs, and their followers were rarely already participating in transport. However, very few of these followers ever went on to transport, again contradicting the hypothesis that reverse tandem runs recruit additional transport effort.

An alternative role for reverse tandem runs is suggested by the fact that more of them occurred in asymmetric splits. It may be that these tandem runs serve as an error-correcting tactic to prevent transporters from moving nestmates from a better to a worse site. This might happen if the initial transporter misjudges the relative qualities of the two sites. By leading tandem runs to the one she has judged to be worse (i.e. the site from which she is transporting), she summons additional assessment of the site. If the recruited ants agree with her assessment, they do nothing; if they disagree (i.e. they judge the source site to be better than the target site), then they launch transport in the opposite direction. Under this view, ants that follow tandem runs would comprise a contingency plan rather than being conscripted labour that lends assistance in moving the colony. A tactic like this would be more useful when sites differ in quality, such that the colony would pay a cost by moving to the wrong site. This could account for the low overlap between transporters and tandem run followers observed in the experiments as the hypothesis predicts that most followers will not become transporters if transports are occurring from the worse site to the better site. These ideas are purely speculative but deserve further investigation.

Compared with emigrations, reunifications were carried out by a surprisingly small number of ants. On average, only three to four workers did all of the recruitment in each reunification. In contrast, as many as 25 ants (about 30% of the colony) transport nestmates during emigrations by colonies of similar size (Dornhaus et al., 2008; Pratt, 2005a,b; Pratt et al., 2005; Richardson et al., 2018). This difference may partially reflect a greater urgency in laboratory emigrations, which are typically induced by sudden destruction of the colony's nest, unlike our experiments, in which all ants occupied intact nests throughout reunification. Some previous studies have observed colonies emigrating from intact nests, and they report lower recruitment participation than when the nest is destroyed (Franks et al., 2003, 2009, 2013). However, even those cases had many more participants than we saw here.

With so few active ants, the outcome of reunifications may be strongly influenced by a few 'elite' or 'keystone' individuals (Modlmeier et al., 2014; Pinter-Wollman et al., 2012). Collective actions by insect societies are typically viewed as highly decentralized processes. Thus, earlier reports of symmetry breaking trace it to multiple non-linear interactions among many individuals, none of them playing an outsize role (Altshuler et al., 2005; Beckers et al., 1990; Detrain and Deneubourg, 2006; Sumpter and Beekman, 2003). In some situations, however, group behaviour is strongly influenced by a small number of leaders (Collignon and Detrain, 2010; Couzin et al., 2005; Feinerman and Korman, 2017; O'Shea-Wheller et al., 2016b; Petit and Bon, 2010; Robson and

Traniello, 1999). In *Temnothorax* emigrations, the number of active tandem run leaders is known to be mediated by distance, with longer distances between the old and the new nests encouraging more individuals to recruit (O'Shea-Wheller et al., 2016a,b). Thus, the few tandem run leaders that we observed may partly reflect the short distance between sites. However, previous research has failed to find any relationship between nest separation distance and the proportion of ants that engage in nestmate transport or the per capita number of reverse tandem runs (O'Shea-Wheller et al., 2016a). Even in more typical emigrations, there is evidence of outsize influence by an 'oligarchy' that consistently occupy central locations in the colony's information-sharing network (Richardson et al., 2018). Thus, decision making and collective movement in these small-colony ants may owe more to individual control than is generally recognized.

The combined results of our experiments hint at a suite of rules that allow efficient reunification in different contexts. Ants can resolve symmetric splits, and the absolute and differential quality of the nests that a scout ant encounters influences the likelihood of her carrying nestmates, the direction of her transports, and the probability that she will retire from an active role before all the ants and brood are moved. Furthermore, the division of labour in reunification diverges in key ways from emigration, notably with fewer ants playing an active role. Our results also show that our understanding of reverse tandem runs is incomplete, as their abundance and functional relevance to reunification remain unclear. Future studies that examine, in greater detail, the interactions between workers and the dynamics of activity within each nest during reunification are likely to shed light on these topics.

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