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Division of labor promotes the spread of information in colony emigrations by the ant *Temnothorax rugatulus*

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Abstract. The fitness of group-living animals often depends on the efficiency with which members share information about resources, so that the group can collectively decide how best to allocate its efforts. Theoretical studies have shown that collective choices can emerge from homogeneous individuals following identical rules, but real animals show much evidence for heterogeneity in the degree and nature of their contribution to group decisions. In the social insects, for example, the transmission and processing of information is influenced by an often-neglected but well-organized division of labor of behaviorally heterogeneous workers. Studies that accurately quantify how this behavioral heterogeneity affects the spread of information among group members are still lacking. In this paper, we look at nest choices during colony emigrations of the ant *Temnothorax rugatulus* and measure the degree of behavioral heterogeneity of workers. Using both machine learning and network science methods, we identify and characterize behavioral categories of workers, and we analyze workers' contributions to the spread of information during each emigration.

Introduction

Group-living animals frequently need to make decisions as a coherent collective (Conradt and Roper 2005; D.J.T 2006). Choosing where to establish a new home (Visscher 2006; McGlynn 2011), deciding among

foraging patches (Detrain and Deneubourg 2008; Pablo et al. 2010), or suddenly changing the direction of group motion (Couzin et al. 2005; Conradt and Roper 2010) are just a few among many examples of collective decisions. Despite the diversity in behavioral mechanisms that have evolved to address these and similar problems, the underlying strategies for gathering, sharing, and processing the information necessary to address the problem at hand share many commonalities across species. Collectives pool information to mitigate the effect of uncertainty and increase decision accuracy (Conradt 2012), which requires efficient spread of information from informed individuals to uninformed ones (Ward et al. 2008; Franks et al. 2002; Couzin et al. 2005).

Insights about how information spreads among group members can be obtained by adopting tools from network science to study the behavior of group-living animals (J Krause, Croft, and James 2007; Jens Krause et al. 2015; Pinter-Wollman et al. 2013). Using this approach, a group of animals is reduced to a graph where a set of nodes, each representing a group member, are connected to each other through edges that represent pairwise interactions between individuals (Newman 2018). Given a particular experimental setup, a challenge of this approach is to correctly identify each interaction and possible information transfer event to encode it in the network structure. Sometimes interactions between a pair can be precisely observed, as in food transfer (Naug 2008; Sendova-Franks et al. 2010) and social dominance (McDonald and Shizuka 2012; Shizuka and McDonald 2012; Hiroyuki et al. 2014). When precise observation is not possible, physical proximity of a pair of animals is often used as a criterion of whether they are interacting (Pinter-Wollman et al. 2011; Blonder and Dornhaus 2011; Jeanson 2012; Waters and Fewell 2012; Richardson and Gorochowski 2015). However, proximity alone does not necessarily mean that an interaction occurred or, more importantly, that there was any transfer of information between the pair (Castles et al. 2014; Carter, Lee, and Marshall 2015; Farine 2015; J Krause, Croft, and James 2007).

An additional challenge to studying the spread of information in collectives is accounting for behavioral heterogeneity among group members. Many theoretical models of collective decision-making make the assumption that group members all behave similarly to each other (Couzin 2009; Gordon 1996; Bonabeau et al. 1997). This assumption has allowed valuable insights into how simple rules acted on by a mass of identical individuals can produce complex and functional group-level outcomes (Pratt et al. 2002; Britton et al. 2002; Marshall et al. 2009; Couzin et al. 2011; Camazine et al. 2001). However, a full understanding of collective behavior must account for well-known differences in the behavior of members of real groups. In recent years acknowledgement of these differences has driven research efforts in what has come to be called animal personality (Bergmüller and Taborsky 2010). In eusocial insects, a long research tradition has focused on division of labor and worker specialization (Hölldobler and Wilson 1990). Previous studies on division of labor have explored its basis in worker age, physiology, morphology, and experience; its degree of development in different species and contexts; its adaptive response to internal and external demands; and the ultimate forces contributing to its evolution (Tschinkel 1987; Seid and Traniello 2006; Tschinkel 2011; Kwapich and Tschinkel 2013, 2016; Tofts 1993; Franks and Tofts 1994).

However, the role of division of labor in collective decision-making is less well understood (Robson and Traniello 1999).

In this study, we analyze behavioral heterogeneity in the context of collective nest site choice by the rock ant *Temnothorax rugatulus*. Ants of this genus nest in pre-formed cavities, such as rock crevices, and their effectiveness at emigrating to the best of several candidate sites has made them a model system for understanding collective decision-making. Emigrations are organized by a minority of active ants who search for candidate sites, assess them, and then recruit nestmates to promising finds (Richardson et al. 2018; Pratt et al. 2005, 2002). The probability of recruitment initiation depends on site quality; hence visitor numbers grow more rapidly at a better site, favoring its eventual selection. Active ants generally recruit one another using a behavior called tandem running, in which a single nestmate is led from the current nest to the candidate new home. Once a quorum of ants has arrived at a site, they switch to the faster method of social transport, in which the passive majority of the colony is simply carried to the new site (Pratt et al. 2002; Pratt 2005). This quorum rule amplifies the effect of quality-dependent recruitment and ideally leads to all ants being carried to the best site before any competing site has reached the quorum.

Prior work on ants of the genus *Temnothorax* has emphasized a distinction between the active minority of ants that organizes the emigration and the colony majority that makes no obvious contribution to the decision (Sendova-Franks and Franks 1995; Pratt et al. 2002, 2005; Dornhaus et al. 2008; Richardson et al. 2018). In addition, there is evidence for differences in the degree and consistency of participation by active ants, such that an 'oligarchy' of very active ants may play an outsized role over successive emigrations (Richardson et al. 2018). This oligarchy of ants seems to be further organized in two subgroups, leaders of tandem runs and their followers, with levels of communication between these two groups higher than within each of them. However, these studies focus only on a minority of key individuals; they do not provide a complete characterization of the contribution to the final decision of each worker and of their role in the necessary spreading and processing of information.

In this paper, we analyze colony emigrations of the rock ant *Temnothorax rugatulus* when subject to a binary choice between two nests of different quality. We record the behavior of individually paint-marked ants over the course of the entire emigration, characterize the level of behavioral heterogeneity observed among workers, and use machine learning methods (Valletta et al. 2017) to group them into separate behavioral castes. In the experimental setup of colony emigrations of *T. rugatulus*, information transfer events correspond to conspicuous tandem runs and transport of adult workers. We leverage this property to reconstruct the network of pairwise interactions both between ants participating in specific emigrations as well as over the course of all emigrations of the same colony. By means of tools from network science (Newman 2018) and from the theory of information (Gorelick et al. 2004; Gorelick and Bertram 2007), we look at how information spreads across the members of the colony and how this process correlates with the division of labor among individual workers as well as across different behavioral castes. By doing so, we are able to provide an accurate characterization of the magnitude of each behavioral caste

within a colony of *T. rugatulus* as well as a deeper understanding of the role played by each caste in the collective decision-making process leading a colony to choose a new home.

Material and methods

Experimental subjects. We used 3 colonies of *T. rugatulus* ants (ID numbers 6, 208, 3004), each with one queen and, respectively, 78, 81, and 33 workers. Colonies were collected in the Pinal Mountains near Globe, Arizona (N 33° 19.000', W 110° 52.561'), during 2009. They were housed in nests composed of a balsa wood slat (50 mm × 75 mm) sandwiched between two glass slides. In the center of the slat was a rectangular cavity (25 mm × 33 mm) to house the colony while the top slide had a 2 mm hole that served as an entrance. The nest was kept in a plastic box (110 mm × 110 mm) that was provided with a water tube and an agar-based diet replaced on a weekly basis (Bhatkar and Whitcomb 1970). Each ant received a unique pattern of four paint marks (one on the head, one on the thorax, and two on the abdomen), to allow individual identification during data collection.

Experimental procedure. Colony emigrations were observed in a rectangular arena (37 cm × 65 cm) whose walls were coated with Fluon to prevent ants from leaving. We positioned two candidate new nests at one side of the arena and the old nest housing a colony at the opposite side with a distance of 50 cm between new and old nests. The candidate nests differed in their quality: the good nest was as described above; the mediocre nest was identical except that it had a larger entrance (5.5 mm diameter). *Temnothorax* ants are known to strongly prefer smaller nest entrances [(Mallon, Pratt, and Franks 2001; Franks, Mallon, et al. 2003)]. The ants were induced to emigrate by removing the top slide of their nest. Each colony emigrated 5 times, with a rest interval of 2 to 5 days between emigrations.

Data collection. Experiments were video recorded using 3 cameras with 1K resolution. One camera gave a bird's-eye view of the whole arena; the other two were positioned above each candidate nest and captured the nest interior at sufficiently high resolution to make the ants' paint marks identifiable. We manually reviewed these recordings to compile a complete record of each ant's arrivals, departures, and recruitment acts (see Table 1 for a complete list of recorded actions). For each action, we noted the time of occurrence, the identity of the ant and the nest at which the action occurred. We also recorded the origin and destination of every tandem run and transport, as determined from the recording of the whole arena.

Table 1 List of individual behaviors observed in video-recorded emigrations. Each row shows the symbol and definition of a particular action, along with the set of identifiers used to specify where it occurred.

Symbol	*Definition*	*Location*
E	Enter a candidate nest	$\{good, mediocre\}$
L	Leave a candidate nest	$\{good, mediocre\}$

LB	Begin leading a tandem run	$\{old \to good, old \to mediocre, mediocre \to good\}$
FB	Begin following a tandem run	$\{old \to good, old \to mediocre, mediocre \to good\}$
TB	Transport a brood item (*i.e.*, egg, larva, pupa) into a candidate nest	$\{good, mediocre\}$
TU	Transport an unknown object (*i.e.,* detritus for use as building material) into a candidate nest	$\{good, mediocre\}$
TA	Transport an adult ant into a candidate nest	$\{good, mediocre\}$
BC	Be carried into a candidate nest	$\{good, mediocre\}$
TBO	Transport a brood item out of a candidate nest	$\{good, mediocre\}$
TAO	Transport an adult ant out of a candidate nest	$\{good, mediocre\}$
BCO	Be carried out of a candidate nest	$\{good, mediocre\}$

Behavioral features of individual ants. To characterize the role played by each ant during an emigration, we measured a number of different behavioral features summarizing their activity pattern over all trials. We measured features concerning visits to candidate nests, participation in tandem runs, and participation in transports (Table 2). As ants can perish or lose their paint-marks between trials, each ant's features were averaged over the number of trials in which she participated. When measuring the time of the first visit to a nest or of the first transport event, we normalized times in the unit interval $[0; 1]$ where 0 represents the beginning of the trial and 1 represents the completion of the emigration. Features that are conditioned on the occurrence of a transport event (e.g., time of first transport) are defined only for those ants transporting items in a trial and averaged only over trials satisfying the condition.

Table 2 List of measured features, their definitions, domain and whether they are defined for all ants or only for those ants involved in transport activity.

Feature	*Definition*	*Domain*	*Always defined*
Visits	Average number of visits to any potential new nest (*i.e.*, good or mediocre nest)	$0 \leq x < \infty$	✓
Visit duration	Average duration of visits to any potential new nest	$0 \leq x < \infty$	✓
Visits both	Proportion of emigrations in which the ant visits both the good and the mediocre nest before transporting an item or be carried	$0 \leq x \leq 1$	✓
Total visits duration	Cumulative duration of visits to any potential new nest before transporting an item	$0 \leq x < \infty$	×
Time of 1st visit	Average proportion of the emigration at which the ant visits a potential new nest for the first time	$0 \leq x \leq 1$	✓
Tandem runs led	Average number of tandem runs led including runs from the old nest to either of the two potential nests and from the mediocre nest to the good nests	$0 \leq x < \infty$	✓

Tandem runs followed	Average number of tandem runs followed including only runs from the old nest to either of the two potential nests and from the mediocre nest to the good nests	$0 \leq x < \infty$	✓
Items transported	Average number of items (*i.e.*, adult ant, brood, dirt or unknown object) transported towards any nest	$0 \leq x < \infty$	✓
Transport duration	Average duration of a round-trip transport of any item	$0 \leq x < \infty$	×
Time of 1st transport	Average proportion of the emigration at which the ant transports her first item	$0 \leq x \leq 1$	×
Be carried	Averaged number of times an ant is carried towards any nest	$0 \leq x < \infty$	✓

Measures of heterogeneity. To quantify the degree of inequality in the distribution of a behavioral feature, we used both Lorenz curves and Gini coefficients. A Lorenz curve plots the cumulative portion of the total amount of a certain feature (*e.g.*, total number of tandem runs) against the cumulative portion of the population of ants, with ants ordered by increasing values of the feature. When a feature is equally distributed across the population, the corresponding Lorenz curve is a line with slope 1 (line of equality); the higher the degree of inequality of the distribution, the larger the area between the line of equality and the Lorenz curve. The Gini coefficient summarizes the results showed in the Lorenz curve in a single index. It is the ratio of the area between the line of equality and the Lorenz curve over the total area under the line of equality. A value of 1 for the Gini coefficient represents a case of maximal inequality while a value of 0 correspond to a case of perfect equality in the distribution of a feature across the population.

Clustering analysis. We performed a two-level clustering analysis to identify the role played by each ant during an emigration, using the `stats` package in R version 3.4.3. At the higher level, we considered only behavioral features that are defined for all workers (i.e., excluding features conditioned on transport events). At the lower level, we redefined the selection of behavioral features on the basis of the results at the higher level using either all features or only those associated with visits and be carried events (some features have zero variance and cannot be used in the clustering analysis). Data from each colony were analyzed separately from each other to prevent differences in feature distribution from affecting the results of the clustering. For each clustering level, we computed the Pearson correlation coefficients between all pair of variables (package `stats`, function `cor`) to explore the possibility of feature reduction. We then centered and scaled our estimates of the behavioral features for each ant by subtracting the mean value of a feature and dividing the result by its standard deviation. We then proceeded to perform a clustering analysis of the normalized data using the k-means algorithm (package `stats`, function `kmeans`, $k = 2$) and visualized the results using principal component analysis (package `stats`, function `prcomp`). No rotations were necessary and all features with non-zero variance were retained due to their limited number (between 4 and 11

features) and good spread between their corresponding vectors. Finally, we analyzed the distribution of features across clusters to characterize the role played by ants in each category during an emigration.

Construction of recruitment networks. We represented the recruitment events for each colony emigration as a directed network whose properties we then studied using tools from network science. Recruitment in these ants lends itself to this approach because it consists of pairwise events in which one ant either leads (tandem running) or carries (transport) another ant to a candidate nest. A recruitment network was constructed for each trial following a simple procedure. Each ant participating in an experimental trial is represented as a separate node in the network. For each tandem run and transport event, we add a directed link that connects the node representing the recruiter ant (*i.e.*, the leader of a tandem run or the carrier of a transportee) to the node representing her recruitee (*i.e.*, the follower of a tandem run or the transportee in a transport event). We also labelled each link of the network depending on the type of the particular recruitment event, distinguishing between three different types: transport of an adult ant, forward tandem run, and reverse tandem run. The latter two are distinguished by their direction: forward tandem runs start at the original nest and end at either of the candidate new nests; they are usually seen early in the emigration before the start of transport. Reverse tandem runs start at a candidate site and end at the original nest; they generally occur after transport has begun.

In addition to the recruitment networks built for each colony emigration, we also constructed and analyzed an aggregate recruitment network for each colony. The aggregate recruitment network was built similarly to those for individual trials, but it included links for every recruitment event in all trials of a single colony. Aggregate networks are not representative of single colony emigrations, as they are generally much denser. However, their topology provides us with a visualization of the long-term interaction pattern between pairs of ants that is less susceptible to the limited chance that ants have to encounter and possibly interact with each other during a single emigration.

Core of aggregate recruitment networks. For each colony, we analyzed the corresponding aggregate recruitment network and separated ants into two sets: 1) ants represented by nodes that belong to the core of the network and 2) ants represented by nodes that instead belong to its periphery (*i.e.*, leaves). The presence of a core in a network has implications about the robustness of its controllability (Liu, Slotine, and Barabási 2011; Jia and Barabási 2013). We determined the core of each aggregate network by removing all nodes without out-going links (*i.e.*, ants with no active recruitment events) and all links directed at any of the removed nodes (i.e., events where the removed ants were recruited by others). As this pruning may result in new nodes without out-going links, this procedure is repeated until no more nodes can be removed (*i.e.*, either the network is empty or all remaining nodes have at least one out-going link). The resulting core is a type of k-core (Liu, Slotine, and Barabási 2011; Liu et al. 2012) for directed networks in which nodes have at least one out-going link to another node in the core.

Measures of division of labor. For each colony, we analyzed the degree of division of labor among its workers. We used an information-theoretic framework that measures both the degree of specialization of each *ant* and the degree at which *tasks* are performed by the same individuals (Gorelick et al. 2004; Gorelick and Bertram 2007). Specialization of individual workers, i.e., the tendency of individual ants to perform specific tasks over others, can be quantified by the index

$$DOL_{indiv} = \frac{I(ant, task)}{H(task)},$$

while the degree at which tasks are performed by the same individuals is defined as

$$DOL_{task} = \frac{I(ant, task)}{H(ant)}.$$

In the above equations, function I is the mutual information between two variables (*i.e.*, the amount of uncertainty shared by the two processes) and function H is the Shannon entropy of one variable (i.e., the amount of uncertainty of one process). DOL_{indiv} measures the proportion of uncertainty about how often a task will be performed explained by knowledge of the individual ant performing it. DOL_{task} measures instead the proportion of uncertainty about which individual ant will perform a certain task explained by knowledge of the task to be performed. Both indexes can be summarized by the aggregate measure

$$DOL = \sqrt{DOL_{indiv}\, DOL_{task}}.$$

Values close to 1 correspond to high degree of division of labor while values close to 0 represent instead the absence of any predictive relationship between a task to be performed and the ants that perform it. To compute these measures for each colony, we considered 6 tasks: leading a forward tandem run, following a forward tandem run, leading a reverse tandem run, following a reverse tandem run, transporting an item to a nest, and being carried to a nest. We then counted how many times each ant performed each task over the course of all emigrations. Using this data, we computed DOL measures both across all individuals of the colony (i.e., variable *ant* represents the unique id of each ant) and across behavioral roles (i.e., variable *ant* represents the role assigned to each ant during the clustering analysis). Mutual information and Shannon entropy were computed in R version 3.4.3 using the `rinform` package (Moore et al. 2018).

Results

We observed a total of 15 emigrations in which a colony faced a choice between a *good* and a *mediocre* nest (5 emigrations each by 3 colonies). The first trial by colony 208 was not analyzed, because a lighting disruption interfered with the quality difference between sites. In all but one emigration (colony 3004, trial 3), the colony made the expected choice and moved to the good nest. In two emigrations (colony 208, trials 2 and 3), the colony initiated parallel emigrations to both the good and the mediocre nest, but later reunified at the good nest. From these 14 trials, we collected time-stamped behavioral data for each individual ant and analyzed the contribution to the decision-making process of different members of the colony.

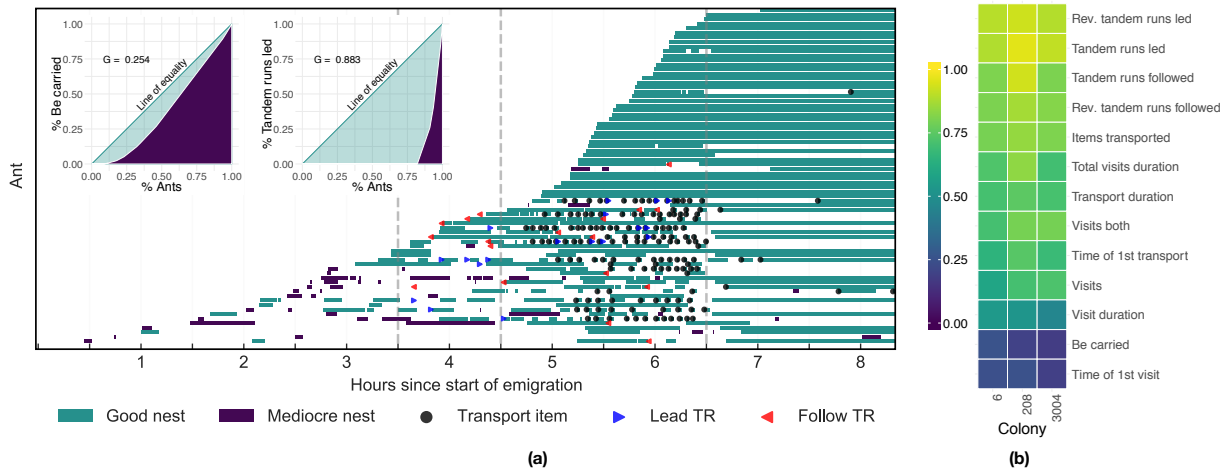


Figure 1. Panel (a) shows the ethogram detailing the individual behavior of each ant in colony 6 during the first treatment and (insets) the Lorentz curves of the distribution of behaviors transport and leading tandem run across the members of colony 6 in all treatments. Horizontal bars denote time spent inside a candidate nest; symbols denote the occurrence of transport and tandem running behaviors. Panel (b) provides a heatmap representation of the Gini coefficients computed for a number of different behavioral features for each considered colony (higher values correspond to more unequal distributions).

Behavioral diversity of workers. As described previously for the related species *Temnothorax albipennis* (Mallon, Pratt, and Franks 2001), individual workers participate in an emigration to a fairly different extent. The majority of colony members experience the decision-making process only passively, when carried from one nest to another by a nestmate (Figure 1a, upper portion of the ethogram). A smaller portion of the workforce instead contributes actively to finding a new home and moving there (Figure 1a, lower portion of the ethogram). Initially, a few ants discover and perform short visits to the candidate nests (0-3.5 hours). Some of these ants later recruit other colony members through a number of tandem runs (3.5-4.5 hours). Finally, the bulk of the colony is carried to the chosen nest by this hard-working minority (4.5-6.5 hours).

For each colony, we measured the distribution of several behavioral features across colony members. Over different emigrations, colony members perform few of these behaviors at a relatively equal frequency with respect to each other. This is the case, for example, for being carried to a nest, which happens to most ants one time (Figure 1a, inset). Other behaviors, such as leading a tandem run, are characterized by a much more unequal distribution among colony members with only few workers performing them (Figure 1a, inset). Figure 1b provides a compact representation of the diversity in the distribution of behavioral features among the members of each colony. Leading and following tandem runs and transporting an item are the most unequally distributed behavioral features while the first visit time and the number of times an ant is carried to a nest are the most equally distributed ones. The remaining behavioral features, mostly concerned with visits to candidate nests, lie in between these two extremes and are characterized by an intermediate level of diversity.

Workers roles during the emigration. Although all ants in a colony behave differently from each other, even if only slightly, but with no pair of ants performing the same, it is conceptually advantageous to

separate them into a few distinct classes depending on their role in the collective decision. To do so, we performed a 2-level hierarchical clustering of the workers of each colony based on their behavioral features. As certain features are conditionally defined (*e.g.*, features related to the timing of transport events are defined only for ants that engage in transport), we considered different subsets of behavioral features at the two levels of the clustering hierarchy (see Methods).

At the higher level, where we look at all ants in a colony, features related to tandem running and being carried generally have a low level of correlation with each other and with all other behavioral features (see Figure 2a for colony 6, Figure S1 for all colonies). In contrast, features related to the number and timing of visits and to the number of transported items are more correlated with each other. The number of visits and the number of transported items are positively correlated with the likelihood of visiting both nests while the time of first visit is positively correlated with the average visit duration. The remaining correlations among this subset of features are all negative: ants that perform many visits, visit both nests, and/or transport many items make shorter visits and discover candidate nests earlier in the emigration process.

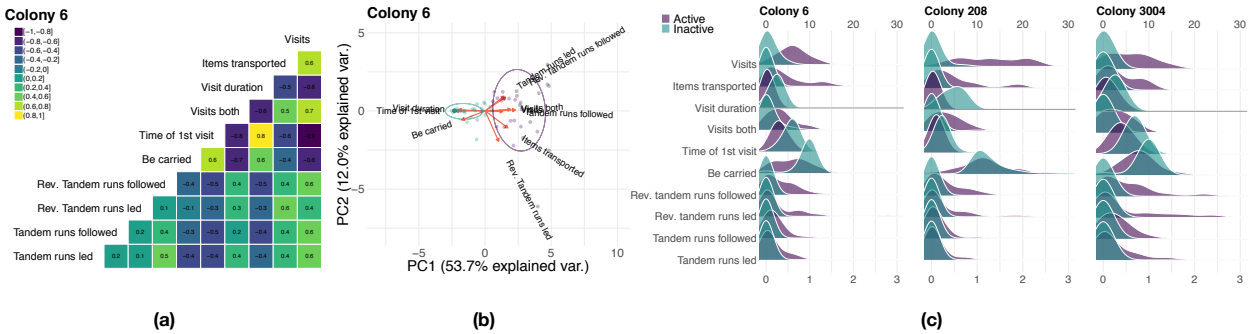


Figure 2 Illustration of the higher level of the clustering analysis. Panel (a) shows the matrix of Pearson correlation coefficients between behavioral features for colony 6. Panel (b) shows a PCA representation over the first two components of the PCA loadings and of clustered workers for colony 6 (purple symbols represent active ants, green symbols represent inactive ants). Panel (c) shows the distribution of behavioral features divided in active and inactive workers for all colonies (the average visit duration is reported in hours).

A principal components analysis (PCA) of the distribution of behavioral features (see Figure 2b for colony 6, Figure S2 for all colonies) shows that, at the higher level, workers can be divided into two separate groups: ants that are carried to a candidate nest and ants that instead engage in transport and tandem running behaviors. When projected over the first two components of the PCA, which explain between 62% and 75% of the observed variance in each of the 3 studied colonies, the loadings form two sets approximately orthogonal to each other. On this basis, we performed a clustering analysis of each colony (k-means algorithm, data scaled and centered) and looked for 2 clusters (see Figure 2c). As previously found for the case of task allocation in the same species (Charbonneau and Dornhaus 2015), the higher level of the clustering analysis separates *active* workers (*i.e.*, those that actively contribute to the emigration) from *inactive* ones (i.e., those that passively experience the emigration). Approximately a third of the workers of each colony (38%, 25%, and 27%, respectively, for colonies 6, 208, 3004) are classified as active ants while the remaining two thirds are classified as inactive ants (62%, 75%, and 73%, respectively, for colonies 6, 208, and 3004).

The statistical classification described above is prone to noisy results due to the limited number of trials. Inspection of the behavioral profiles of typical members of each category suggests more robust heuristic rules for classification. Active workers (see Figure 2c) are those that lead and follow most tandem runs, transport more items and therefore visit candidate nests more often; their visits are shorter, more likely to discover both nests, and happen earlier in the emigration process. Inactive workers are carried to a candidate nest approximately one time for each emigration, do not participate in tandem runs and do not transport items. They perform far fewer visits, generally visiting only one candidate nest (*i.e.*, the one where they have been carried to), and remain in that nest for longer than active workers. Based on these distributions of behavioral features, we defined as active workers any ant in the colony that 1) participates in at least one (forward or reverse) tandem run (as a leader or as a follower) or 2) transports at least one item. All workers that did not satisfy this definition were classified as inactive. After relabeling workers according to these criteria, the proportions of active versus inactive workers in each colony are split approximately equally with 50% active versus 50% inactive for colony 6, 40% versus 60% for colony 208, and 52% versus 48% for colony 3004.

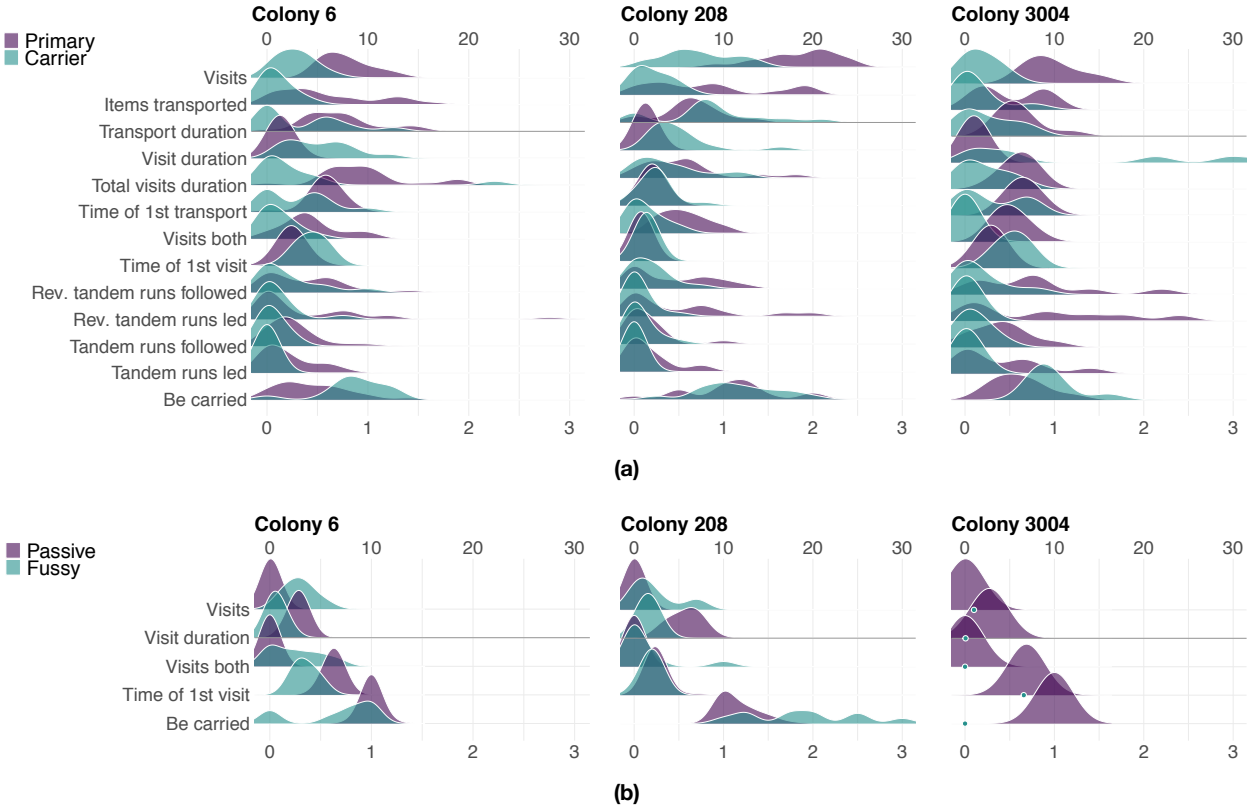


Figure 3 Distribution of behavioral features at the lower level of the hierarchy for all colonies. Panel (a) shows the results for active workers clustered in the groups primary and carrier ants. Panel (b) shows the results for the inactive workers clustered in the groups passive and fussy ants. The average visit duration and the total visit duration before transport are reported in hours; the average transport duration is reported in minutes.

We repeated the same clustering analysis at a lower level of the hierarchy for both active and inactive workers. In the case of active workers, we considered all behavioral features included at the higher level of the hierarchy plus 3 additional features related to transport: the average duration of a transport event, the time of first transport, and the cumulative visit duration before transporting an item. Behavioral features generally had a low level of correlation with the exception of 2 sets of features with high intra-set correlation (Pearson correlation coefficients in Figure S3). One set included features related to transport events and the other included features related to the timing of visits. As the PCA analysis (see Figure S4) still showed two separate groups of workers, we further divided active workers in two groups: *primary* workers and *carrier* workers (see Figure 3a).

Primary workers make up about a quarter of the colony (33%, 20%, and 27%, respectively, for colonies 6, 208, and 3004). These workers visit candidate nests more often; their visits are generally faster than those of carrier workers but, cumulatively, they spend more time within these nests before beginning to transport items. Consequently, they begin transporting later, at about three-fourths of the emigration process. Despite this, they tend to transport a marginally higher number of items. Primary workers are those that participate more frequently in tandem runs and that are carried less frequently to a candidate nest. The remaining active workers that are not classified as primary are instead carrier ants (17%, 20%, and 24% of the colony, respectively, for colonies 6, 208, and 3004). These workers are generally transported to a candidate nest but, soon after, begin frequent journeys to the old nest to transport items back to the new home. Unlike primary workers, they do not visit both candidate nests and they begin transporting items earlier in the emigration process.

In the case of inactive workers, we can considered only a few behavioral features: the number of times they have been carried to a nest, the number of visits, their average duration, time of the first visit, and whether they visited both nests (this feature was not considered for colony 3004 as inactive workers never visited both nests). The number of visits to a candidate nest is positively correlated to the likelihood of visiting both nests whereas the mean visit duration is positively correlated with the number of times a worker is carried to a nest (Figure S5). From the PCA analysis (Figure S6), we can observe that loadings are still divided in two separate sets pointing in opposite directions. We therefore cluster inactive workers in two groups: *passive* workers and *fussy* workers.

Passive workers (40%, 48%, and 46% of the colony, respectively, for colonies 6, 208, and 3004) are true inactive ants (Figure 3b): they are carried to a nest only once (slightly more for colony 208 due to 2 colony reunifications) during the entire emigration and spend the rest of their time there without visiting other nests. Fussy workers (10%, 12%, and 3% of the colony, respectively, for colonies 6, 208, and 3004) are instead ants that are inactive with respect to the decision-making process underlying the emigration but still show remarkable levels of activity in terms of their number of visits to candidate nests. They make frequent and brief visits but never contribute to the emigration by engaging in recruitment behaviors (*i.e.*, tandem running and transport). A possibility is that fussy workers consists of a minority of foragers, possibly ignoring the ongoing emigration, that spend their time exploring the environment in search for food or water.

Recruitment networks. Primary, carrier, passive, and fussy ants differ from each other in their contribution to the colony's final choice. These differences can be conveniently visualized by constructing a network of recruitment events (*i.e.*, tandem runs and transport of an adult) for each colony emigration (see Methods). In a recruitment network, ants are represented by nodes; a recruitment event is represented by a directed link from the node of the recruiter to that of the recruit. Following this procedure, we extracted the recruitment network for each of the 14 experimental emigrations (Figures S7–S9).

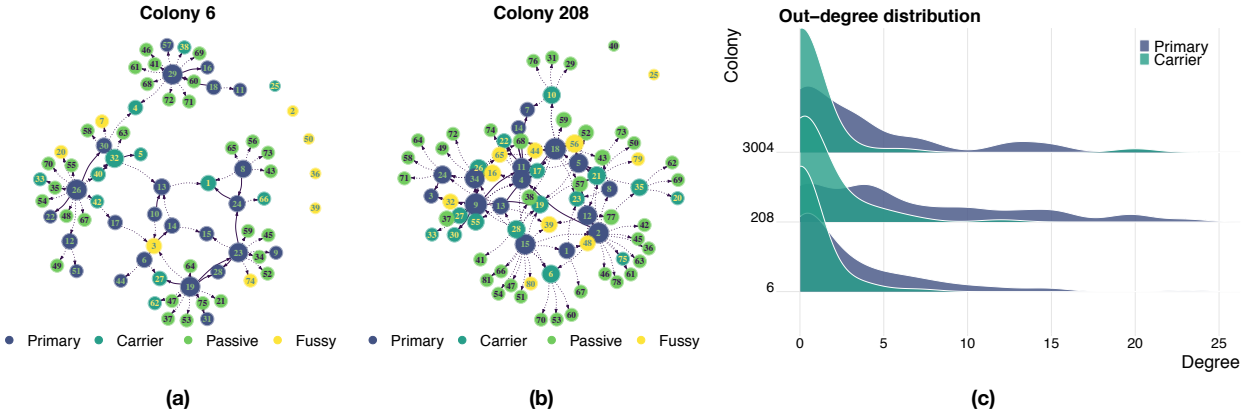


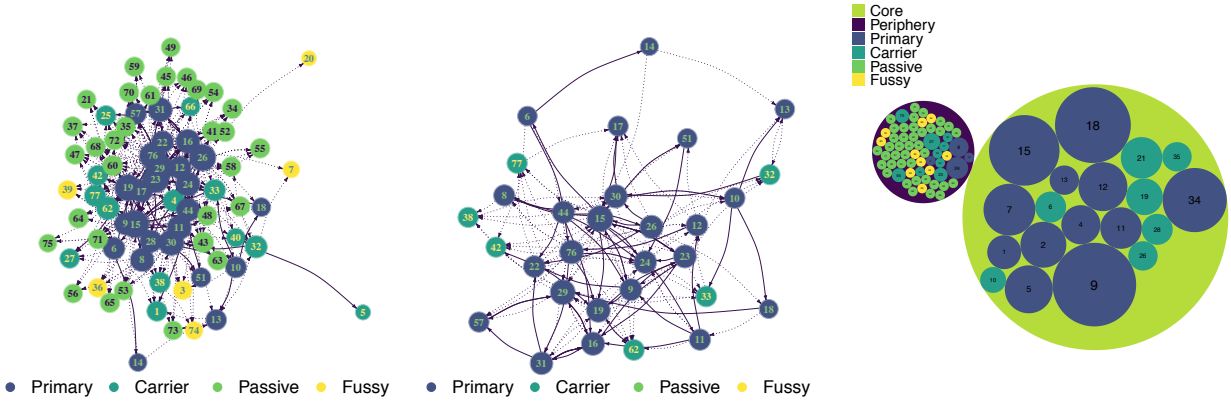
Figure 4 Illustration of recruitment networks and their out-degree distribution. Panel (a) shows the recruitment network for colony 6, treatment 1. Panel (b) shows the recruitment network for colony 208, treatment 2. Solid arrows represent tandem runs (both direct and reverse), dotted arrows represent transport events. Panel (c) shows the out-degree distribution for primary and carriers ants for all colonies.

Most of these networks (12 out of 14) have a relatively simple hierarchical structure composed of one or, sporadically, a few connected components and some isolated nodes (see Figure 4a for colony 6, treatment 1). The corresponding colony emigrations proceeded smoothly with most recruiters committed to the (eventually) chosen nest (11 times the good nest, 1 time the mediocre nest) from early in the emigration; at most a few ants initially and only temporarily recruited to the alternative site. The prominent role of primary ants in the final choice of the colony is evidenced by their hub-like position in the corresponding recruitment networks. Likewise, carrier ants often appear as hubs but with fewer spokes than the hubs of primary ants. Passive ants largely correspond to the leaves of the network, generally subject of only one recruitment event, while fussy ants are either represented as isolated nodes or as nodes subject to a higher number of recruitment events.

Two emigrations (colony 208, treatment 2 and 3) differed from the rest in their markedly more complex recruitment networks, with only one large component and a higher link density (see Figure 4b for colony 208, treatment 2). In these emigrations the recruiters were initially split, with primary ants recruiting to both nests, but eventually choosing the same one (*i.e.*, the good nest). The higher density of links in the network is therefore a result of this initial indecision among recruiters and also of the additional recruitment effort necessary to later reunify the colony at a single site. As in the emigrations discussed above, primary ants appear as hubs with a high degree of recruitment. Carrier ants are more often involved in transport events and the corresponding hubs have a higher degree albeit still smaller than that of primary ants. Due

to the splitting and eventual reunification of the colony, a few passive ants were transported to both nests and therefore have two incoming edges. For most of them, as well as for the fussy ants, the situation is similar to that of more direct emigrations.

The probability distribution of outgoing links for a node in the network allows us to quantify the difference in recruitment effort contributed by primary and carrier ants (Figure 4c). In both cases, the out-degree distribution is right-skewed with similar shape across colonies. Primary ants are characterized by a distribution with a much longer tail (mean degree and standard deviation of 2.85 ± 4.03, 6.98 ± 7.05, 3.84 ± 5.03) that spans values of more than 20 recruitment events. Carrier ants instead nearly always score less than 5 recruitment events and often go as low as not recruiting at all (mean degree and standard deviation of 0.44 ± 1.28, 1.17 ± 2.15, 0.9 ± 3.33). While primary ants are often involved in recruitment behavior across treatments (probability of at least one recruitment of 0.61, 0.81, and 0.65), carrier ants participate more sporadically (probability of 0.14, 0.4, and 0.21).



(a) **(b)** **(c)**

Figure 5 Illustration of aggregate recruitment networks for colony 6. Panel (a) shows the aggregate recruitment network of all treatments for colony 6. Panel (b) shows the corresponding core of the aggregate recruitment network. Solid arrows represent tandem runs (both direct and reverse), dotted arrows represent transport events. Isolated nodes not shown. Panel (c) illustrate the relations between the role covered by each ant as defined from the clustering analysis and their location in the aggregate network (i.e., core or periphery).

Additional evidence of the central role played by primary ants is provided by analysis of the aggregate recruitment network for each colony. This network (Figure 5a and Figure S10) considers all recruitment events performed by a colony's members during all of its trials. The planar organization of the network, in which nodes are arranged as a function of the number of outgoing links with nodes at the center of the network having higher degree, confirms that primary ants provide the most important contribution to the final choice of the colony. Carrier, passive, and fussy ants follow in decreasing order of contribution and are arranged in increasingly distant circles from the center of the network.

We computed the core and the periphery of the network (Liu et al. 2012) to further verify the unique role of primary ants in the final choice of the colony (see Figure 5b and Figure S11). The core of a complex network, which is obtained by recursively removing all nodes without outgoing links (see Methods), has

been shown to have strong connections with the controllability of the underlying networked system (Liu, Slotine, and Barabási 2011; Jia and Barabási 2013). In our experiments, the core is composed of approximately a third of the colony (40%, 23.5%, and 34.4%) and largely consists of primary ants (80%, 63.2%, and 81.8%) and a remaining smaller portion of carrier ants (see Figure 5c and Figure S12). For all colonies, we found that the core is a strongly connected network (*i.e.*, it is possible to go from any node to any other node by walking along directed links). Every ant belonging to the core of the network is therefore recruited at least once across different treatments which highlights the egalitarian structure of the social network represented by the core.

Division of labor and spread of information. We investigated division of labor during colony emigrations using the framework proposed by (Gorelick et al. 2004; Gorelick and Bertram 2007). We considered 6 different tasks (leading and following a forward tandem run, leading and following a reverse tandem run, transporting an item and being carried) and analyzed both worker specialization (*i.e.*, whether workers focus on only a few tasks) and task segregation (i.e., whether certain tasks tend to be performed by the same workers). We performed the same analysis both by considering workers separately (i.e., identified by their unique color code) as well as by grouping them in the behavioral roles identified during the clustering analysis (see Section Methods and Table S1). When taking into account the identity of each individual worker, we found evidence of task specialization across colonies ($D\mathrm{OI}_{\mathrm{indiv}} = 0.42 \pm 0.07$) but low task segregation ($D\mathrm{OI}_{\mathrm{task}} = 0.13 \pm 0.02$) which results in a relatively low division of labor ($DOI = 0.23 \pm 0.01$). When grouping workers depending on their behavioral role instead, the level of worker specialization is lower ($D\mathrm{OI}_{\mathrm{indiv}} = 0.28 \pm 0.07$) but that of task segregation is higher ($D\mathrm{OI}_{\mathrm{task}} = 0.34 \pm 0.05$) resulting in an overall higher division of labor ($DOI = 0.3 \pm 0.04$). While the considered tasks are not uniquely performed by specific individuals, we found evidence that individual workers specialize on certain tasks more than others and that the problem of finding a new home for the colony is tackled by an organized structure of behavioral roles. This result is essential in understanding the spread of information that leads the colony to collectively chose a new home.

Indeed, during a colony emigration, most workers of the colony received information about a potential nest site from other workers through a recruitment event. Only a few ants gathered this information first-hand (respectively, 8.6%, 5.6%, and 3.2% of the ants in colonies 6, 208, and 3004) and spontaneously initiated recruitment to a new nest. For colonies 6 and 3004, all spontaneous recruiters were primary ants. In colony 208, which temporarily split in 2 of its 4 trials, only 59.4% of spontaneous recruiters were primary ants while the remainder were carriers. Primary ants are therefore those workers in the colony that initiate the spread of information about a potential nest. Spreading information, however, is not sufficient by itself to generate an information cascade across all members of the colony. The quality of the nest site being advertised is the driving factor of information cascades. Indeed, with the exception of one emigration in which recruitment was exclusively focused on the mediocre nest (colony 3004, treatment 3), the information about the mediocre nest never cascaded across the members of the colony. In other words, no ant recruited

to the mediocre nest ever began recruiting herself to that nest. In contrast, all ants received information about the good nest within two hops of a spontaneous recruiter in the network.

The final nest choice of the colony seems therefore a prerogative of only primary workers with carrier workers instead involved in the implementation and spread of information about the final colony decision. Passive and fussy workers are only subjected to the choice made by the active ants. Indeed, while both tandem runs and transport of adult ants are recruitment mechanisms, tandem runs (mostly performed by primary workers) are more effective in recruiting recruiters than transport events (the primary task of carrier workers). This happens only a small fraction of the times ($10.62\% \pm 2.88$). Remarkably, we found nine occurrences in which an ant that was transporting to the mediocre nest switched her efforts to the good nest after being transported there by a nestmate.

Discussion

Division of labor is often credited for the ecological success of eusocial insects (Hölldobler and Wilson 1990) and generally studied in its natural context of allocations of tasks to different members of a society (Beshers and Fewell 2001). However, group-living animals not only need efficient ways to organize themselves during stable periods but often need to make sudden decisions of paramount importance for their survival (e.g., in face of the destruction of their nest). Previous studies of division of labor in the context of colony emigrations highlighted the disproportionate role of a minority of individuals in the final choice of the colony (Möglich and Hölldobler 1974; Pratt et al. 2002, 2005; Richardson et al. 2018; Sendova-Franks and Franks 1995; Dornhaus et al. 2008). In *Formica sanguinea* and *Camponotus sericeus*, these individuals usually have reduced ovaries with respect to other workers in the same colony (Möglich and Hölldobler 1974). In ants of the genus *Temnothorax* this minority of individuals, represented by about a third of the colony, consists of those workers that participate in tandem running (Richardson et al. 2018; Pratt et al. 2005, 2002). Moreover, this set of workers seems to be further divided into two subgroups: workers leading tandem runs and workers following them (Richardson et al. 2018).

Similarly to other *Temnothorax* species (Richardson et al. 2018; Pratt et al. 2005, 2002), we found that also in *T. rugatulus* about a fourth of the workers have a particularly relevant role in the final choice of the colony. These workers, which we called primary ants, are indeed those individuals that are more likely to lead and follow tandem runs. However, while previous studies only focused on workers participating in tandem running, we also found other behavioral castes among the remaining workers of the colony. About a fifth of the workforce of the colony consists of carrier ants that are generally transported to a candidate nest by a primary ant and, soon after, begin frequent journeys back to the old nest to carry other members of the colony, including brood, to the new nest. While carrier ants greatly contribute to the implementation of the final nest choice of the colony, they do not seem to contribute directly to the decision-making process that led to that choice. Their contribution, however, might be of indirect nature: by transporting other members of the colony, carrier ants might be favoring the establishment of a quorum by primary ants (Pratt

et al. 2002). Nearly all remaining workers (i.e., about half of the colony) consist instead of passive ants: workers that participate in the decision-making process underlying the colony emigration only passively when carried by a primary or carrier ant towards a candidate nest. Passive ants likely correspond to the lazy ants described in the genus *Temnothorax* in studies of task allocation (Charbonneau and Dornhaus 2015; Charbonneau et al. 2017). We also found a small proportion of workers, 3-12% of the colony, that do not fit any of the previous behavioral castes. While these fussy workers do not seem to participate in the decision-making process, they still perform an unusually high number of visits to candidate nests and may be foragers in search of food.

Primary, carrier, passive, and fussy ants provide different contributions to the collective decision-making process undergoing a colony emigration that can be regarded as dividing the labor of gathering, spreading, and processing the information necessary to achieve a collective decision. While the behavior of workers (and therefore their membership in a particular behavioral caste) is stable over the course of the 5 colony emigrations we performed, we know that individual workers change the tasks they perform over time as a function of their developmental age (Tschinkel 1987; Seid and Traniello 2006; Tschinkel 2011; Kwapich and Tschinkel 2013, 2016; Charbonneau et al. 2017). Although the proportion of workers engaging in tandem running (i.e., primary ants) seems relatively stable (Richardson et al. 2018; Pratt et al. 2005, 2002), it remains to be shown that this is still true for each behavioral caste we identified. Differences in these proportions might affect the information processing ability of the collective and result in different colony personalities manifested as different tradeoffs between speed and accuracy (Franks, Dornhaus, et al. 2003).

For the closely related *T. albipennis*, (Richardson et al. 2018) showed how workers participating in tandem running have a tendency to specialize into either of two available roles, leader or follower, which have different communication functions. Workers belonging to different behavioral castes fill different roles in the information processing leading to the final colony decision. Primary ants, with their reliable use of tandem runs, discover potential nest sites and then make sure that the newly gathered information spreads among other members of the colony. They also process this information by comparing different options both individually, when they visit both nests before start recruiting, and collectively, by modulating recruitment efforts as a function of quality. Among primary ants, only about 6% of the colony actually gather this information first-hand as a result of a random exploration of the environment. Recruitment of other primary ants through tandem running slowly processes the gathered information, resulting in the buildup of a quorum in one or (as happened in two of our emigration experiments) a few sites. Once quorum is reached, primary ants will start to recruit carrier ants. The role of carrier ants is to implement the collective decision of the minority: by transporting other carrier ants as well as passive ants, they allow the spread of information concerning the colony decision to the remaining members of the society. Passive ants might also contribute indirectly to the establishment of a quorum as, once transported to a candidate nest, these ants do not generally leave and might therefore affect encounter rates (Pratt et al. 2002; Pratt 2005). Only fussy ants seem not to contribute to the colony decision or, at least, their contribution still remains unclear.

Acknowledgments

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