Title: Interactions, information and emergence: Exploring task allocation in ant colonies using network analysis

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ABSTRACT

In animal societies, individuals may take on different roles to fulfil their own needs and the needs of their groups. Ant colonies display high levels of organisational complexity, with ants fulfilling different roles at different timescales (what is known as *task allocation*). Factors affecting task allocation can be at the individual level (e.g., physiology), or at the group level (e.g., interaction histories). In this work, we focus on group level processes by exploring the impact of the history of interaction networks on task allocation and task switching using a previously published dataset (Mersch et al., 2013) tracking the behaviour of six *Camponotus fellah* colonies over 41 days. First, we investigated the architecture of interaction networks using node (individual) level network measures and their relation to the individual's task – foraging, cleaning or nursing – and whether or not the ant switched tasks. We then explored how noisy information propagation is among ants, as a function of the colony composition (how many ants are

carrying out which tasks), through the information-theoretic metric of effective information. Our results show that interaction history affected task allocation, with ants more likely to switch to a task if they had interacted with other ants carrying out that task. The degree to which interaction history affected task allocation, as well as the noise in their interactions, depended on which groups of ants are interacting. Overall, we showed that colony cohesion is stable even as ant-level network measures vary more for ants when they switched functional groups; thus ant colonies maintain a high level of information flow as determined by network analysis and ant functional groups play different roles in maintaining colony cohesion.

Keywords: Ant behaviour, effective information, emergent behaviour, insect social networks, task allocation, information flow

Highlights

- We analysed the interaction networks of six *Camponotus fellah* colonies
- We tested how centrality and information flow affected task switching
- Node-level network metrics and the information theoretic measure of effective information explain differences among functional groups
- Interaction histories predicted task switching, but the strength of the effect differed across functional groups

INTRODUCTION

In animal societies, individuals may carry out different tasks to fulfil their own needs and the needs of their group (Sumpter, 2006; Clutton-Brock, 2009; Jeanson & Weidenmuller, 2014). Larger and more complex societies can self-organise to fulfil tasks beyond basic sustenance and reproduction (Boomsma and Frank, 2006; Sumpter, 2010). Local exchange of information, between individuals of a group and between individuals and their environment, is key to self-organisation (Sumpter, 2006; Boomsma and Frank, 2006; Couzin, 2009; Cavagna et al., 2010; Swain and Fagan, 2019). Social insect colonies display high levels of organisational complexity (Lukas & Clutton-Brock, 2018), where individual tasks may include foraging, nest construction and caring for the young (Gordon, 2002). The assignment of tasks, also referred to as *task allocation*, is the result of patterns of factors that vary across different scales (Gordon, 2015). These tasks can be fixed throughout each individual's lifetime due to physiological reasons, for example when only a fertile subset of the population is responsible for reproduction, or when a subset is responsible for providing food (Sumpter, 2010; Clutton-Brock et al., 2001).

Task allocation can also result in individuals changing their main task over time. Factors affecting task changes can occur at the individual level or at the group level. Individual-level factors include age, corpulence or physiology (Anderson and Shea, 2001; Tripet and Nonacs, 2004; Robinson et al., 2009). Studying individual-level factors associated with task change is often simpler than studying group-level ones. For example, individual-level changes can be easier to track because their rate of change is slower and often follows a consistent and predictable pattern, as in the case of ageing. Individual-level factors can also be directly quantified, e.g., by measuring age, corpulence, or

physiological features, and traditional statistical approaches can be used to predict task changes.

Changes in task allocation affected by group-level factors are currently not well understood. Structural features or macro-level social properties of groups can affect micro-level individual actions if the social system is affected by feedbacks (Flack, 2017; Hobson et al., 2019). However, quantifying relevant macro-to-micro feedbacks can be challenging and can require large amounts of data. The development of automated tracking systems has made this level of data collection possible. While these systems have improved researchers' ability to track detailed social behaviour (Robinson et al., 2009; Smith and Pinter-Wollman, 2021), assigning quantitative metrics to group dynamics is still a non-trivial task. In the case of interaction patterns, tracking physical interactions among individuals does not necessarily map onto the amount of meaningful (predictive) information exchanged with each interaction (Valentini et al., 2020). Although tracking technologies can tell us how many times individuals in a social group interact with one another, they cannot explain to what extent these interactions drive task allocation.

Task allocation in ants has been the subject of much previous work (Anderson and Shea, 2001; Gordon, 2015). Across ant species, studies have shown that, depending on the tasks and on the colony, ants may display varying degrees of task flexibility, from small colonies of totipotent ants to larger ones with a structured division of labour (Anderson and Shea, 2001). Individual-level factors include physiology (Anderson and Shea, 2001), age (Tripet and Nonacs, 2004), corpulence (Robinson et al., 2009) and past experience (Ravary et al., 2007), whereas group-level factors involve colony size (Ravary et al., 2007) and short-term interactions (Gordon and Mehdiabadi, 1999). However, we

do not possess a good understanding of how the nature of past interactions and topology of the social interaction network structure affect an ant's propensity to switch to a new task.

In this paper, we leverage social network methods to gain new insight into task allocation changes in an existing dataset of ant interactions (published by Mersch et al. 2013). Mersch et al. studied task switching in *Camponotus fellah* by tracking and analyzing the movements and interactions of individually-identified ants. Worker ants were categorized into three *functional groups* (nurse, cleaner or forager). Analyses showed that the ants had more interactions with others in their same functional group. Communities defining the functional groups exhibited distinct behavioural signatures and were highly spatially divided. Nurses spent most of their time with the brood, while foragers spent time at the nest entrance and cleaners were located between the other two groups and the rubbish pile (Mersch et al. 2013). Mersch et al. also explored the questions of task switching cost, i.e., a time and energy investment associated with learning new tasks (Goldsby et al., 2012), and of age polytheism, i.e., the correlation between the age of an ant and which task they perform. The original study identified spatial fidelity as a key regulator of ant social organization and interaction frequency (Mersch et al. 2013). They also found that task switches were present but uncommon and that when a shift in functional group occurred, ants showed a preferred direction of task transition, from nurses to cleaners to foragers, mostly based on age (Mersch et al., 2013). Task changes were thus hypothezied to be driven by age polyethism, but the patterns were fairly noisy.

In this new analysis we focus specifically on this noisy process of task switching. A question not addressed in the previous study is whether the history of an ant's interactions with others and the resulting information flow within the colony could be one of the elements explaining task switching. In other species, information flow patterns have been shown to affect task allocation, interactions, and overall colony behavior, such as in the case of midden workers in red harvester ants (*Pogonomyrmex barbatus*; Gordon and Mehdiabadi, 1999, Pinter-Wollman et al., 2018), tandem running recruitment (Franklin and Franks, 2012) and consensus-forming in rock ants (*Temnothorax albipennis*; Sasaki & Pratt, 2018). To test whether the history of interactions or information flow could explain the noise seen in task switching dynamics that was not explained by age polyethism alone, we evaluate several potential macro-scale predictors of task switching not addressed in the original paper.

First, we described the architecture of the interaction networks by focusing on information flow (which in our case refers to the possible information exchange due to interactions among ants). We tested whether the role played by individual ants in regulating information flow in the colony and the functional group that they belong to were correlated. To do this, we quantified three network measures that are tied to the architecture of information flows at the local level for ant-ant interactions, strength, betweenness centrality, bridge betweenness centrality; and a new measure, *effective information* (EI) at the global level for the whole colony. While strength, betweenness centrality and bridge betweenness centrality are common node-level measures in network science and have been applied to animal social networks in the past (Holme et al., 2002; Lusseau and Newman, 2004; Krause et al., 2009; Farine and Whitehead, 2015), EI is

central to our analysis and is a novel information theoretic metric reflecting how noisy a mechanism connecting nodes (ants, in our case) is within a system. It is calculated by perturbing a system through its repertoire of possible states and evaluating the effects of the perturbation on the system's mechanisms (Hoel, Albantakis, & Tononi, 2013; Klein and Hoel 2020). In interaction networks, EI reflects the noisiness of the interactions among individuals (Hoel et al., 2020): a higher EI means that a system is more deterministic, with information spreading in a more effective way throughout the network.

Second, we tested whether these four measures of information flow in the interaction network were correlated with task switching to better understand the noise in task allocation not explained by age polyethism as determined by Mersch et al. (2013). We hypothesized that an ant's previous interactions with other ants affect switching behaviour and tested whether interacting with a certain functional group increased the probability of an ant then switching to that group. The relationship between the architecture of information flows and the different functional groups, as described by network measures, inform our understanding of the varying correlations between interaction history and switching behaviour during task allocation. Our use of network metrics, including the novel effective information metric, allowed us to determine the influence of interaction history on task allocation and information flow among functional groups in *Camponotus fellah* colonies.

METHODS

Data, network construction, and functional group assignment

The published Mersch et al. (2013) dataset contains summaries of interactions among a total of 985 individually-marked ants in six *Camponotus fellah* colonies. The authors collected interaction data for every pair of ants at a daily resolution over the 41-day monitoring period, and the published dataset contains data pooled at the number of interactions per dyad per day per colony. We matched this published dataset with the colony metadata to inform our analyses (Supplementary material 1).

Consistent with Mersch et al. (2013), we used the pairwise daily number of interactions to construct separate weighted, undirected, unipartite networks for each colony per day. Each ant in a colony was represented by an individual node. An edge between two nodes represents an interaction between those two ants on a given day. The edge weight is proportional to the number of pairwise interactions between them on that particular day. We used the available published dataset to recreate the 246 networks for the 6 colonies over 41 days used by Mersch et al. (2013) as well as the general pattern of task switching across the length of the experiments.

Mersch et al. (2013) assessed each ant's functional group every 10 days to categorize them as a nurse, cleaner, or forager, representing their main task in the colony. They assigned functional groups based on what community an ant spent at least 70% of their time in, using the 'infomap' community detection algorithm. They split the ants into the functional groups foragers (F), cleaners (C), nurses (N), queen (Q), and NA for ants who were counted as missing at a time point (e.g., if they were dead or had lost their tags). In our analyses, we used a similar method to assess functional groups and split the ants into the same five groups used in the original study via community detection. However, unlike the Mersch et al. approach, we assigned community membership using

182 a Louvain community detection algorithm (Csardi and Nepusz, 2006). This algorithm was
183 used as it performs better than the infomap algorithm on multiple metric tests (Emmons
184 et al., 2016). This approach resulted in very high agreement with previous task
185 assignments, as we will show in the Results.

186 Mersch et al. (2013) reported that their ants mostly did not change their task affiliation
187 within the 10-day observation period between task assessment points. We used the same
188 10-day snapshot window in our analyses which resulted in three time points at which a
189 switch in task to a new category could be detected. We assess whether ants switched
190 tasks by comparing the functional group assignments for each ant in one time period to
191 its assigntment in the next time period. For our analyses, we categorized each ant as
192 "switched" or "consistent", depending on whether they remained within the same
193 functional group, or were categorized as part of a different functional group.

194

195 ***Quantifying individual network metrics for each ant***

196 Node metrics and centralities define various types of influence that individual nodes
197 exert on network connectivity and dynamics. For each network, we used R (v 3.6.2) and
198 the packages *igraph* (Csardi and Nepusz, 2006) and *networktools* (Jones, 2020) to
199 calculate three node-level, local metrics: strength, betweenness centrality, and bridge
200 betweenness. These local measures were calculated for every ant on each day of the
201 experiment for all six colonies.

202 Node strength was calculated as the sum of the weights of a node's edges. Thus, in
203 our context, it is a measure of not only how many interactions (edges) an ant (node) had
204 to other ants, but also of how frequently those interactions occurred during a day. While

degree is an index of potential communication activity (Freeman, 1979), strength improves upon this index by weighting degrees according to frequency of communication to better inform total interaction and information flow potential.

Node betweenness, also known as betweenness centrality, is a measure of importance in a network based on shortest paths between pairs of nodes. For a given pair of nodes in a weighted network, there exists at least one path between them such that the sum of the link weights is minimized, thus forming a shortest path. The betweenness of a node is therefore defined as the number of shortest paths that pass through it. Freeman (1979) identified high betweenness centrality as a key indicator of whether a node occupies a central location in the network for information transmission. An ant with a high betweenness is an ant that is centrally located in the network, serving as a key connection for seemingly disparate ants. Individuals with high betweenness are responsible for maintenance of communication, group coordination, and network stability (Lusseau and Newman, 2004; Farine and Whitehead, 2015).

Bridge betweenness extends the betweenness centrality metric to the level of communities and is defined as the number of times a node lies on the shortest path between two nodes from different communities. In network science, a community is defined as a group of nodes that have a higher likelihood of connecting to each other than to nodes from other communities. Ants with a high bridge betweenness serve as key connectors for different groups in the network. This means that they are more integral to network cohesion and information flow across groups, thus they may play an important role in driving switching dynamics. We calculated bridge betweenness for ants using the

community structure determined when assigning functional groups via the Louvain community detection algorithm.

We generated randomized networks to serve as null models for the daily interaction networks of the six colonies. In order to preserve the underlying structure of the networks, a degree-based randomization was used (through the R package *VertexSort*; Abd-Rabbo, 2017) to randomize the ant-to-ant interactions. We created 500 seeded null networks for each colony's daily interaction network, for a total of 123,000 null networks. All metrics calculated for the empirical ant-to-ant interaction networks were then calculated for this new ensemble of null networks. Daily node-level metrics were compared to the distribution of values determined by the null networks. Values were then Z transformed to be compared across groups and measures.

Quantifying global network measures for each colony

We used Effective Information (EI) and its normalized measure of effectiveness to measure colony-level noisiness in the system, with respect to its underlying mechanisms (Hoel et al., 2020). Since we are considering the mechanism of communication and information flow among ants, EI measures the level of noisiness in ant-to-ant interactions. To calculate effectiveness, we first characterized the weight of the edges connected to a node. We defined this weight as a vector W_i of the same length as the total number of nodes, and referred to each element as ω_{ij}, signifying the normalized value of edge weight between nodes *i* and *j*, such that for any index *i*, $\sum_j \omega_{ij} = 1$. Here, each term ω_{ij} can be seen as the probability of moving from *i* to *j*, if a random walker is on the node *i*. Next, we characterized the uncertainty associated with each node *i*, calculated using

Shannon's entropy measure $H(W_i)$. The average of this value across all the nodes in the network is $< H(W_i) >$. This means that, if $< H(W_i) >$ is equal to 0, the network is deterministic. We then assessed the certainty of the network by calculating the term $H(< W_i >)$, which is Shannon's entropy of the average out-weights from nodes. If this expression is equal to 0, the network is degenerate, with all edges leading to the same node. Finally, we calculated EI using the following equation:

$$EI = H(< W_i >) - < H(W_i) > \quad (1)$$

As the value of EI can depend on the size of the network (Klein and Hoel, 2020), we calculated effectiveness, the normalized EI with respect to network size, where *N* is the number of nodes in the network:

$$Effectiveness = \frac{EI}{log_2 N} \quad (2)$$

Effectiveness was calculated for each constructed network (i.e., for each day, for every colony), using the R package *einet* (Byrum et al., 2020). Linear models were fit to the effectiveness for each constructed network as a function of the proportion of each functional group in the network to determine significant relationships between effectiveness and a colony's functional group composition.

Task interaction matrix and task switching

To investigate patterns of ants switching between functional groups and taking on new colony tasks, we first tested whether we could replicate Mersch et al.'s (2013) results of age polyethism using our task assignment method, i.e., the Louvain community detection algorithm. We determined the probability that an ant would switch tasks once, twice, or three times, against the age of the ant (Supplementary material 2, Figure S1A).

275 We further explored the possibility of a switching cost by determining the likelihood that
276 an ant would stay in the same task throughout the experimental time versus performing
277 two or three tasks (Supplementary material 2, Figure S1B).

278 If functional group identity of ants affected how individuals contributed to information
279 flow within a colony, then the number of times an ant switched to a new functional group
280 also affected the flow of information. Here we asked a question not addressed in the
281 original paper: if the number of interactions per ant were kept constant, and the
282 interactions were redistributed among everyone, did the proportion of interactions with
283 different functional groups significantly affect an ant's final functional group, as opposed
284 to what we saw in the original network? To test this, we quantified the average proportion
285 of an ant's interactions with each functional group before switching from its original
286 functional group to another in both the observed dataset and in the ensemble of random
287 networks described above. We compared the distribution of values computed from the
288 actual networks against those given by the null network distribution using a chi-square
289 distribution for all possible types of transition (including non-transitions), and calculated
290 differences significant at the alpha level of 0.05.

291

292 **RESULTS**

293 ***Functional group assignment comparison***

294 Comparisons of our functional group assignments (via the Louvain community
295 detection algorithm) with groups assigned by Mersh et al. (2013; via infomap) showed
296 high levels of overall agreement. Community membership assignments from infomap and
297 Louvain, compared at an individual node level for a given network, resulted in an average

298 90.13 ± 7.25% similarity between the two methods across all the networks in the dataset.
299 Figure 1 shows a summary of the tasks of ants within all six colonies and how those tasks
300 changed over time (Figure 1; for details, see Supplementary material 2, Table S1).

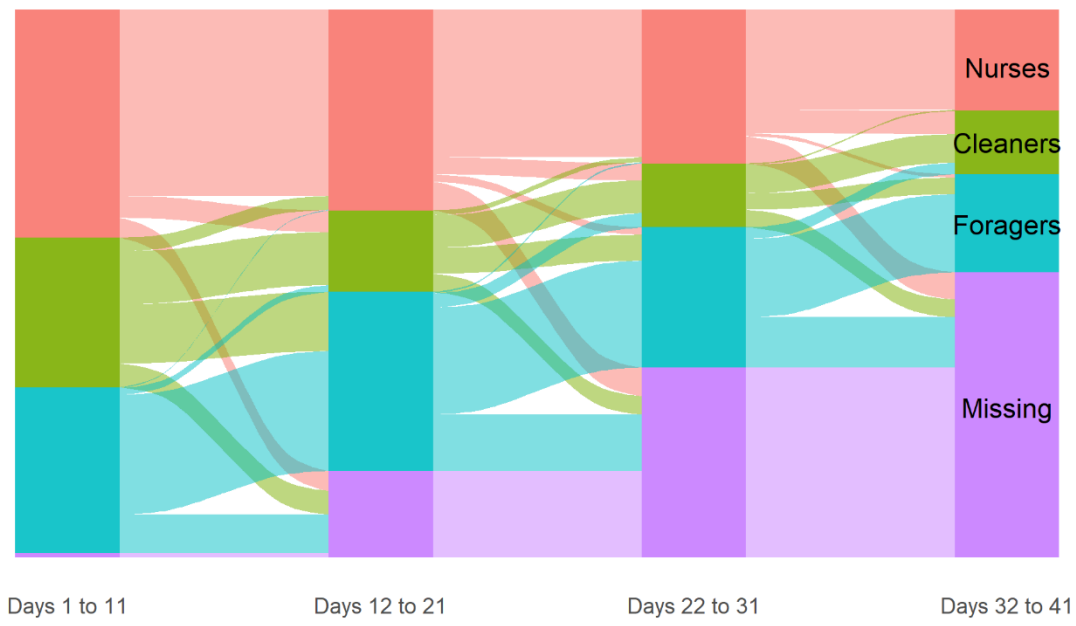

Figure 1: Dynamics of task allocation across the experimental time for all ants in all six colonies, with functional group assigned via Louvain community detection algorithm (~90% assignments consistent with Mersch et al. 2013). The alluvial diagram shows the number of ants per functional group and number of ants staying in the same group or transitioning to a new functional group between time periods as proportional to box and flow sizes, respectively.

301

302 ***Individual network centrality measures and task switching***

303 We compared network measures (and the variance in the measures) across each of
304 the functional groups for three categories: overall across all ants, for just switching ants,
305 and for just ants that remained consistent in their tasks during the assessment periods
306 (summarized in Figure 2; all values listed in Supplementary material 2 Table S2).

307 When we compared strength across ants in each of the tasks, we found that foragers
308 had the highest mean strength of any of the groups across all three of the categories,

309 showing that they had the most frequent interactions over a day regardless of whether
310 they remained foragers or switched task at some point. When considering the overall
311 mean strength, foragers had the strongest interaction potential (2.96). The strength of
312 cleaners (2.35) and nurses (2.25) were not significantly different from each other but were
313 still significantly greater than the null networks' strength (Figure 2A1). Overall strength
314 variance did not significantly differ across functional groups or from the null networks
315 (Figure 2A2), indicating that strength values remained fairly stable through time at the
316 colony level. When we looked at strength just for switching ants, we found that the mean
317 strength differed significantly across functional groups and was significantly greater than
318 for the null networks (Figure 2A3). Out of these, foragers that switched had the highest
319 strength (3.17), while cleaners that switched had a higher strength (2.92) than nurses that
320 switched (2.35). Strength variance of switching ants did not vary significantly among
321 functional groups or from the null networks (Figure 2A4). When we looked at strength just
322 for ants that were consistent, we found that the mean strength and strength variance
323 followed the same pattern seen for ants that switch (Figure 2A5 and 2A6).

324 When we compared betweeness across ants in each of the tasks, we found that
325 cleaners (2.73) had significantly higher betweenness than nurses (2.25) who also had
326 significantly higher betweenness than foragers (2.01, no different from null) and the null
327 networks (Figure 2B1). Overall, variance of betweenness did not differ among functional
328 groups or from the null networks (Figure 2B2). At the colony level, the betweenness metric
329 was stable and the cleaners played the most important role in connecting individual ants
330 for flow of information. When we looked at betweenness just for ants that switched, we
331 found that mean betweenness centrality measures were significantly greater than those

332 for the null networks (Figure 2B3). Cleaners (2.33) and nurses (2.29) that switched had
333 higher betweenness than foragers that switched (1.83). Variance of betweenness was
334 greater for foragers (2.67) and cleaners (3.01), however the variance of nurses was still
335 greater than that of the null networks (2.14, Figure 2B4). Betweenness of foragers and
336 cleaners was more unstable before these ants switched tasks. When we looked at
337 betweenness just for ants that were consistent, we found that they had the same patterns
338 of mean betweenness centrality (Figure 2B5). However, the variance of betweenness
339 was no longer significantly different than the null networks, thus consistent ants
340 maintained a stable betweenness position through time (Figure 2B6).

341 Since the communities we detected mapped primarily onto the previously determined
342 functional groups, a high bridge betweenness indicated a high potential for connecting
343 functional groups in a colony. When we compared bridge betweenness across each of
344 the tasks at the colony level, we found that the overall mean bridge betweenness values
345 did not vary among the functional groups or from the null networks (Figure 2C1).
346 Additionally, the overall variance remained similar across the functional groups and did
347 not vary significantly from the null networks (Figure 2C2). When we looked at bridge
348 betweenness for ants that switched compared to those that were consistent, we found
349 that mean bridge betweenness was higher for the switching ants for all functional groups,
350 though only significantly higher for foragers (Figure 2C 1,3,5). All ants that switched had
351 significantly higher mean bridge betweenness than the overall colony values per
352 functional group, suggesting that ants that switched played an important role in
353 connecting communities for information flow in the colony. Within the ants that switched,
354 foragers had the highest mean bridge betweenness (2.97), though they were not

355 significantly different from cleaners (2.63). Both foragers and cleaners had higher mean
356 bridge betweenness than nurses (2.22). All mean bridge betweenness values of ants that
357 switched were higher than the null networks. The variances of foragers (2.59) and
358 cleaners (2.41) that switched were greater than nurses (1.99) that switched (Figure 2C4).
359 Only the variance of foragers was significantly greater than that of nurses, which did not
360 differ from the null networks. The mean bridge betweenness of consistent ants did not
361 vary significantly among the functional groups or from the null network distribution (Figure
362 2C5). The variances of consistent cleaners (2.91) and foragers (2.75) were significantly
363 higher than nurses (2.11) and the null networks (Figure 2C6). Although the variance of
364 cleaners and foragers for both ants that switched and consistent ants did vary, the overall
365 colony values remained stable; these results may indicate that these stuctures could be
366 important for colony cohesion at the community level.
367

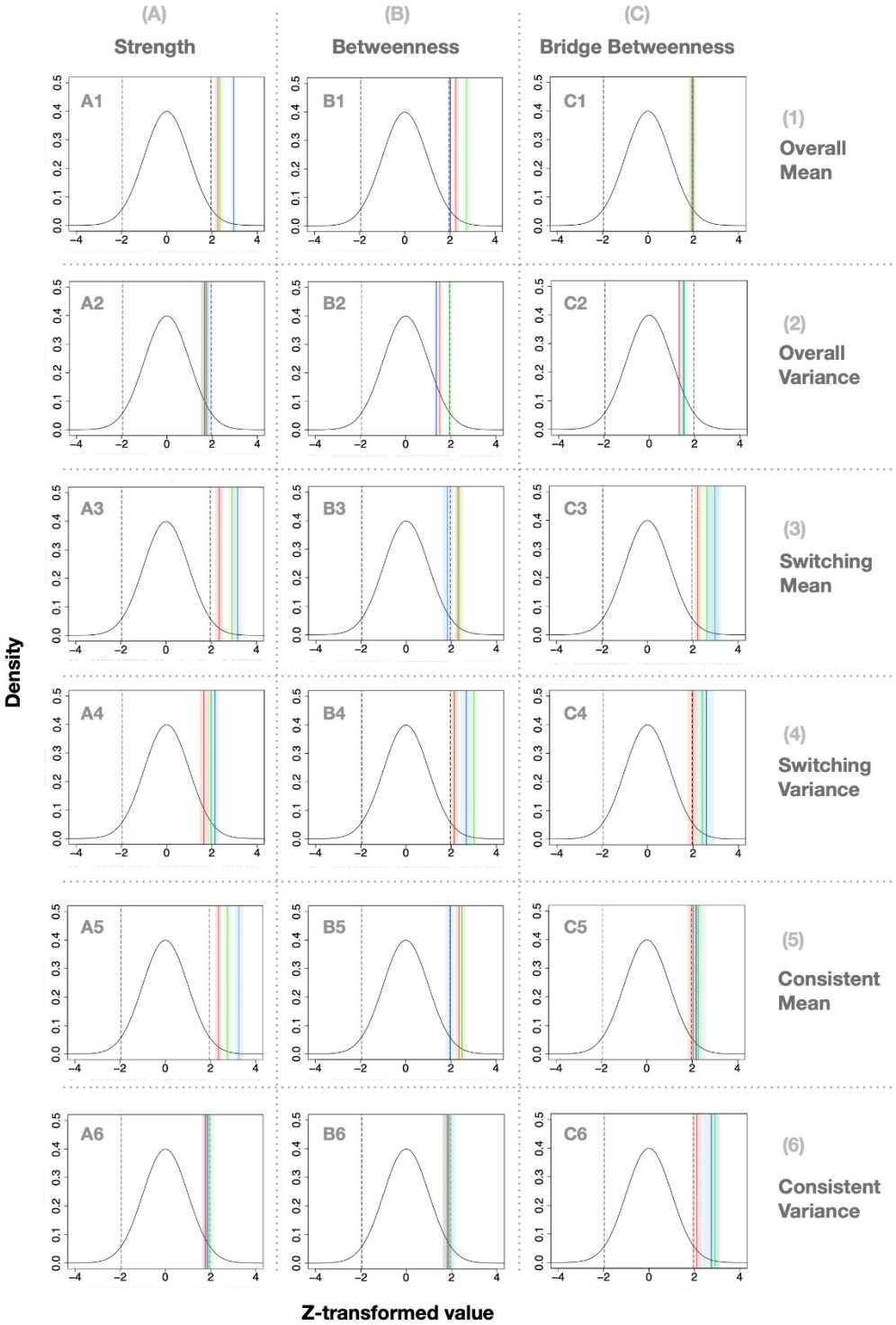

Figure 2: Z transformed values of the mean and variances of the strength, betweenness and bridge betweenness (columns A, B and C respectively) determined for all ants across the six colonies. The first two rows (rows 1 and 2; A1-C2) are values for all the ants in the experiment (overall colony values). The next two rows (rows 3 and 4; A3-C4) show values

for ants that switched during the experiment, and the last two rows (rows 5 and 6; A5-C6) show values for for consistent ants (no switching) during the experiment. Line colors correspond to ant functional group type: nurses (red), cleaners (blue), and foragers (green). Shaded areas are the 95% confidence intervals based on seeded random networks. The null distribution created from the null network simulations is shown in black with a marked confidence interval (dashed lines).

Global information flow and task switching

We measured effectiveness as a function of the proportion of nurses, cleaners or foragers in each colony for each day (resulting in 246 effectiveness measures, Figure 3). We found that the colony networks with high proportions of nurses and cleaners had lower effectiveness, but that the dependencies based on the linear model were weak and non-significant (adj. R^2=0.12, P = 0.063, Figure 3A for nurses; and adj. R^2=0.11, P = 0.052, Figure 3B for cleaners). Effectiveness significantly decreased with increasing proportions of foragers in a colony (adj. R^2=0.22, P = 0.037, Figure 3C). This negative relationship between increased numbers of foragers and decreased colony-level effectiveness shows that the interactions mediated by foragers were noisier than those of nurses or cleaners.

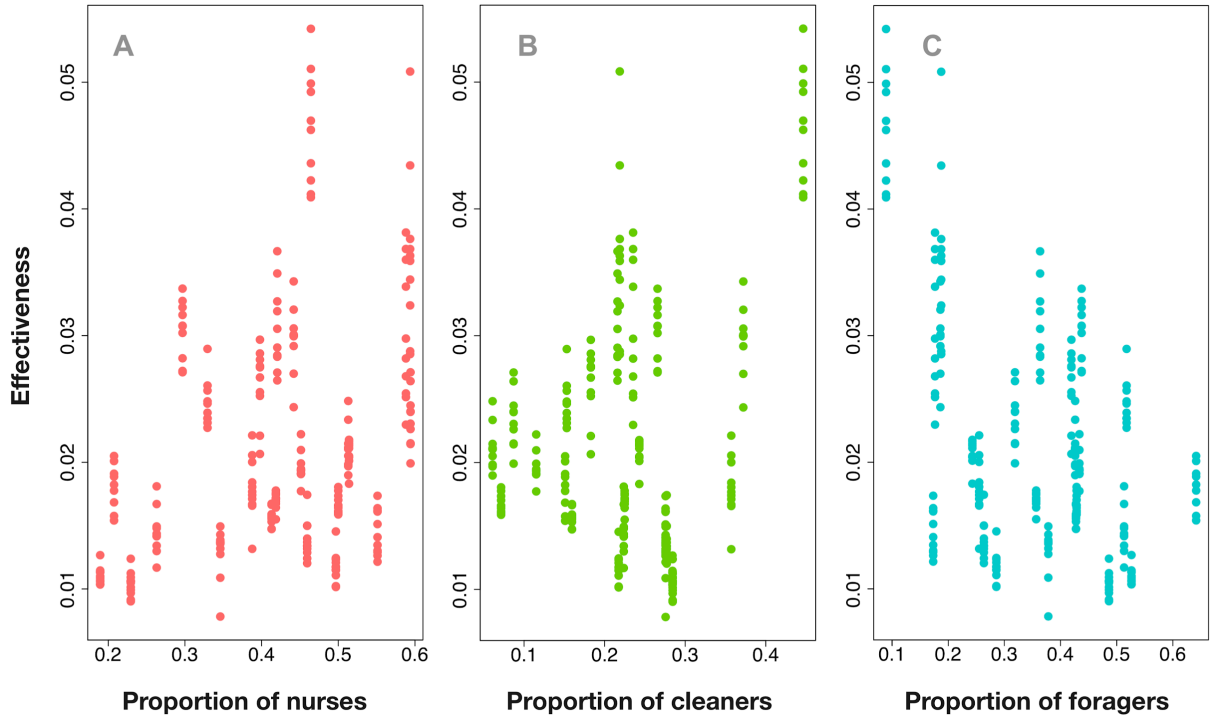

Figure 3: Effectiveness (normalized EI) of the interaction networks constructed for each colony and every day of the experiment as a function of the proportion of different functional groups in the networks. Data are stacked because the available granularity for task allocation was at a 10-day interval. Linear models fit to effectiveness as a function of the proportions of nurses (A) and cleaners (B) separately return a nominally positive dependence (adj. R^2=0.12, P = 0.063 for nurses; and adj. R^2=0.11, P = 0.052 for cleaners). Effectiveness as a function of the proportion of foragers (C) returns a strong negative dependence (R^2 =0.22, p-value = 0.037).

Task interaction matrix and task switching

We tested whether previous interaction patterns affected switching behaviour using a task interaction matrix. We found that ants that remained consistent in their tasks usually interacted most with other ants occupying their same task (Table 1, Consistent ants). For example, consistent nurses were significantly more likely to only have interacted with other nurses (90% of nurse interactions, P=0.0326). Although cleaners and foragers who stayed within their functional group also more commonly interacted with other cleaners or

409 foragers, this difference in interaction proportions was not significantly higher than

410 expected by chance.

	Original task	Final task	Proportion interactions with other ants by role			p-value (Original task vs final task)
			Nurse	Cleaner	Forager	
Consistent ants	Nurse	Nurse	**0.9**	0.09	0.01	**0.0326***
	Cleaner	Cleaner	0.23	0.4	0.37	0.2105
	Forager	Forager	0.2	0.4	0.4	0.6744
Switching ants	Nurse	Cleaner	0.22	**0.71**	0.07	**0.0489***
	Cleaner	Forager	0.04	0.41	**0.55**	**0.0310***
	Forager	Nurse	0.05	**0.65**	0.3	**0.0446***
	Nurse	Forager	0.27	0.35	0.38	0.3671
	Cleaner	Nurse	**0.71**	0.24	0.05	**0.0229***
	Forager	Cleaner	0.02	**0.64**	0.34	**0.0019****

Table 1: The task interaction matrix, showing the proportion of an ants' interactions with a specified functional group before switching from its original to final group. P-values were calculated using a chi-square test contrasting the observed interaction proportions with the null model results for each type of task transition; values significantly differing from random expectations are indicated with asterisks. Bold type indicates the task and proportion of interactions with ants of that task that were significantly higher than expected.

411

412 However, most ants that switched to a new task interacted with ants currently

413 occupying a different task prior to switching (Table 1, Switching ants). For example,

414 nurses who switched to cleaning had interacted more frequently with cleaners (71% of

415 nurse interactions) and this was significantly more likely to occur based on interaction

history than by random chance (P = 0.0489). The result that an ant would transition to a group that it previously interacted with the most was significant for the following other transitions: cleaner to nurse, cleaner to forager, and forager to cleaner. Interestingly, foragers who switched to nursing were significantly more likely to have interacted more with ants of a different functional group, the cleaners (65% of forager interactions).

DISCUSSION

We explored task allocation in ant colonies to determine whether we could explain how ants switched tasks based on information flow among functional groups and the interaction history of the individuals. Mersch et al. (2013) attributed the pattern of ants switching tasks to in this dataset to age polyethism based on the spatial division of workers mediating the structure of the interaction network. The original authors determined that task switching was a noisy process with a lot of individual variation, but that at least some of the task switching could be explained by age polyethism based on the spatial division of workers mediating the structure of the interaction network. Through our reanalysis, we focused specifically on this noisy process of task switching. Our approach allowed us to determine that previous interaction history can explain much more of the noise behind task switching in *Camponotus fellah* colonies.

Our results suggest that ants in different functional groups had varying levels of importance for information flow between individuals and groups in a colony. Additionaly, ants that switched tasks often occupied positions in the interaction network that had high potential for supporting information flow. Network analyses, combined with the task

interaction matrix, allowed us to describe how the architecture of interactions influences the distribution of and switching among tasks in an ant colony.

At the scale of ant-to-ant interactions, we found that ants classified into the three main tasks (forager, cleaner, nurse) differed in how they interacted with each other. This affected their role in information flow for the colony as described by network measures. Foragers had the highest interaction strength – they interacted longer and more frequently than cleaners and nurses. Cleaners, however, had higher betweenness and thus were key connections between ants interacting in the colony.

Ants that switched tasks functioned as key connectors for information flow in the colony, supporting colony cohesion. In general, betweenness was higher for ants that switched than for ants that remained consistent in their task. This suggests that ants who switched tasks throughout the course of the experiment, and particularly cleaners, played an important role in connecting other ants through information flows. Their high betweenness means that they occupied a key network position for receiving and transmitting information before they switched. If learning is required when ants switch tasks, this increased access to information may have allowed them to be able to learn new behaviours more quickly, helping them transition to a new task. Bridge betweenness indicates how ants connected different communities within the colony. Ants who switched tasks had higher bridge betweenness than those who remained consistent in their task. In particular, foragers and cleaners had higher bridge betweenness than nurses, showing that they were key connectors among the different functional groups. Cleaners especially were less likely to interact within their functional group (consistent with Mersch et al.'s 2013 results). The low group cohesion of cleaners may strengthen colony-wide cohesion.

The instability of the centrality metrics may be related to cleaners' and foragers' ability to transition tasks. Cleaners and foragers who switched functional groups had significantly higher variances of betweenness and bridge betweenness, showing that these individual measures of social network connectivity changed more over time. However, when all ants in a colony were grouped for calculating the node-level network metrics, pooled variances were not higher than those for the null networks. So while these metrics varied significantly among functional groups and when ants switched tasks, overall information flow in a colony remained fairly stable and colony cohesion was maintained.

At the group level, the operationalization of effective information as a measure of the noisiness of network mechanisms is relatively new and under-explored. Our effectiveness results for the six *Camponotus fellah* colonies show a correlation between variations in effectiveness and the functional group composition of each colony. We found that a higher proportion of foragers lead to noisier communication among ants. Paired with the results on interaction strength, this means that foragers interacted more than ants in other tasks and that their interactions were noisier than interaction patterns of ants performing different tasks. Results on centrality measures and effectiveness can be linked with task allocation through our task interaction matrix. The matrix shows how previous interactions with ants in a given task lead to a higher probability of the ant switching to that task. These results are consistent with previous work in another species: Gordon and Mehdiabadi (1999) found that, in red harvester ants, ants switching from other tasks to midden work were more likely to have interacted with midden workers, and that switching was more likely to occur the more frequent those interactions. In our results, interactions with

foragers appeared to drive switches to foraging: both cleaners and nurses who switched to foraging had a higher probability of having interacted with foragers. Switches from foragers to other tasks, however, showed different dynamics. Both foragers who switched to nursing and foragers who switched to cleaning had a higher probability of having interacted with cleaners, although the experimental data only showed two cases of the former switch. This is in line with betweenness results, showing that cleaners are central in driving switching patterns. These patterns suggest that, while previous interaction patterns do affect switching behaviour, they do so to varying degrees depending on the role played by the interacting ants and on the overall information flow of the system.

In future research, it would be interesting to further explore task switching in systems with a higher granularity of data collection across both behaviours and interactions. One limitation to the Mersch et al. (2013) dataset and to the original and current analyses is that the task each ant was assigned to is assessed based on the interaction patterns, not the types of actions or tasks the ant completes in the colony. Assessing not just who an ant interacts with, but what actions that ant is actually completing, would provide useful additional insight into the timing of behavioral and social change. This kind of data would allow researchers to determine whether an ant alters its behaviors first (for example, decreasing cleaning behaviors and increasing nursing behaviors) which then results in a change in the social interaction patterns or whether an ant first begins to change its social interaction patterns (for example, interacting less with other cleaners and more with nurses) and then altering its behavior from cleaning actions to nursing actions. Another open question is how the content of information flows, paired with the architecture of interaction netowrks, affects individual and group behaviour (e.g., under conditions of

emergency). Future targeted data collection, involving both social and behavioral observations, paired with statistically robust network methods, could be used to further explore the relationships between patterns of interactions, individual-level behaviour, and group-level behaviour.

ACKNOWLEDGEMENTS

We sincerely thank the organizers of 2019 Complex Networks Winter Workshop (CNWW) for bringing us together and Brennan Klein for helpful discussions. A.S.'s contribution to this research was supported in part through training by NSF award DGE-1632976. S.W.'s contribution was supported in part by a NSF-GRF.

*Author contributions***:** All the authors conceived the idea and the methodology together; AS and SW did the analysis, and all the authors wrote the manuscript.

Competing interests: The authors declare no competing interests.

Data availability: All scripts and data used in this project are available at https://github.com/anshuman21111/ant-colony-networks. A reformatted version of the Mersch et al. (2013) dataset can be found as Supplementary material 1.

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