

1 **Title:** Interactions, information and emergence: Exploring task allocation in ant colonies

2 using network analysis

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10 **ABSTRACT**

11
12 In animal societies, individuals may take on different roles to fulfil their own needs
13 and the needs of their groups. Ant colonies display high levels of organisational
14 complexity, with ants fulfilling different roles at different timescales (what is known as *task*
15 *allocation*). Factors affecting task allocation can be at the individual level (e.g.,
16 physiology), or at the group level (e.g., interaction histories). In this work, we focus on
17 group level processes by exploring the impact of the history of interaction networks on
18 task allocation and task switching using a previously published dataset (Mersch et al.,
19 2013) tracking the behaviour of six *Camponotus fellah* colonies over 41 days. First, we
20 investigated the architecture of interaction networks using node (individual) level network
21 measures and their relation to the individual's task – foraging, cleaning or nursing – and
22 whether or not the ant switched tasks. We then explored how noisy information
23 propagation is among ants, as a function of the colony composition (how many ants are

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

33

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

36

37 **Highlights**

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

44

45

46 INTRODUCTION

47 In animal societies, individuals may carry out different tasks to fulfil their own needs
48 and the needs of their group (Sumpter, 2006; Clutton-Brock, 2009; Jeanson &
49 Weidenmuller, 2014). Larger and more complex societies can self-organise to fulfil tasks
50 beyond basic sustenance and reproduction (Boomsma and Frank, 2006; Sumpter, 2010).
51 Local exchange of information, between individuals of a group and between individuals
52 and their environment, is key to self-organisation (Sumpter, 2006; Boomsma and Frank,
53 2006; Couzin, 2009; Cavagna et al., 2010; Swain and Fagan, 2019). Social insect
54 colonies display high levels of organisational complexity (Lukas & Clutton-Brock, 2018),
55 where individual tasks may include foraging, nest construction and caring for the young
56 (Gordon, 2002). The assignment of tasks, also referred to as *task allocation*, is the result
57 of patterns of factors that vary across different scales (Gordon, 2015). These tasks can
58 be fixed throughout each individual's lifetime due to physiological reasons, for example
59 when only a fertile subset of the population is responsible for reproduction, or when a
60 subset is responsible for providing food (Sumpter, 2010; Clutton-Brock et al., 2001).

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

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

71 Changes in task allocation affected by group-level factors are currently not well
72 understood. Structural features or macro-level social properties of groups can affect
73 micro-level individual actions if the social system is affected by feedbacks (Flack, 2017;
74 Hobson et al., 2019). However, quantifying relevant macro-to-micro feedbacks can be
75 challenging and can require large amounts of data. The development of automated
76 tracking systems has made this level of data collection possible. While these systems
77 have improved researchers' ability to track detailed social behaviour (Robinson et al.,
78 2009; Smith and Pinter-Wollman, 2021), assigning quantitative metrics to group dynamics
79 is still a non-trivial task. In the case of interaction patterns, tracking physical interactions
80 among individuals does not necessarily map onto the amount of meaningful (predictive)
81 information exchanged with each interaction (Valentini et al., 2020). Although tracking
82 technologies can tell us how many times individuals in a social group interact with one
83 another, they cannot explain to what extent these interactions drive task allocation.

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

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

95 In this paper, we leverage social network methods to gain new insight into task
96 allocation changes in an existing dataset of ant interactions (published by Mersch et al.
97 2013). Mersch et al. studied task switching in *Camponotus fellah* by tracking and
98 analyzing the movements and interactions of individually-identified ants. Worker ants
99 were categorized into three *functional groups* (nurse, cleaner or forager). Analyses
100 showed that the ants had more interactions with others in their same functional group.
101 Communities defining the functional groups exhibited distinct behavioural signatures and
102 were highly spatially divided. Nurses spent most of their time with the brood, while
103 foragers spent time at the nest entrance and cleaners were located between the other
104 two groups and the rubbish pile (Mersch et al. 2013). Mersch et al. also explored the
105 questions of task switching cost, i.e., a time and energy investment associated with
106 learning new tasks (Goldsby et al., 2012), and of age polytheism, i.e., the correlation
107 between the age of an ant and which task they perform. The original study identified
108 spatial fidelity as a key regulator of ant social organization and interaction frequency
109 (Mersch et al. 2013). They also found that task switches were present but uncommon
110 and that when a shift in functional group occurred, ants showed a preferred direction of
111 task transition, from nurses to cleaners to foragers, mostly based on age (Mersch et al.,
112 2013). Task changes were thus hypothesized to be driven by age polyethism, but the
113 patterns were fairly noisy.

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

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

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

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

156

157 **METHODS**

158 ***Data, network construction, and functional group assignment***

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

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

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

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

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

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

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

229 We generated randomized networks to serve as null models for the daily interaction
230 networks of the six colonies. In order to preserve the underlying structure of the networks,
231 a degree-based randomization was used (through the R package *VertexSort*; Abd-Rabbo,
232 2017) to randomize the ant-to-ant interactions. We created 500 seeded null networks for
233 each colony's daily interaction network, for a total of 123,000 null networks. All metrics
234 calculated for the empirical ant-to-ant interaction networks were then calculated for this
235 new ensemble of null networks. Daily node-level metrics were compared to the
236 distribution of values determined by the null networks. Values were then Z transformed
237 to be compared across groups and measures.

238

239 ***Quantifying global network measures for each colony***

240

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

251 Shannon's entropy measure $H(W_i)$. The average of this value across all the nodes in the
252 network is $\langle H(W_i) \rangle$. This means that, if $\langle H(W_i) \rangle$ is equal to 0, the network is
253 deterministic. We then assessed the certainty of the network by calculating the term
254 $H(\langle W_i \rangle)$, which is Shannon's entropy of the average out-weights from nodes. If this
255 expression is equal to 0, the network is degenerate, with all edges leading to the same
256 node. Finally, we calculated EI using the following equation:

$$257 \quad EI = H(\langle W_i \rangle) - \langle H(W_i) \rangle \quad (1)$$

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

$$261 \quad Effectiveness = \frac{EI}{\log_2 N} \quad (2)$$

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

267

268 ***Task interaction matrix and task switching***

269

270 To investigate patterns of ants switching between functional groups and taking on
271 new colony tasks, we first tested whether we could replicate Mersch et al.'s (2013) results
272 of age polyethism using our task assignment method, i.e., the Louvain community
273 detection algorithm. We determined the probability that an ant would switch tasks once,
274 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).

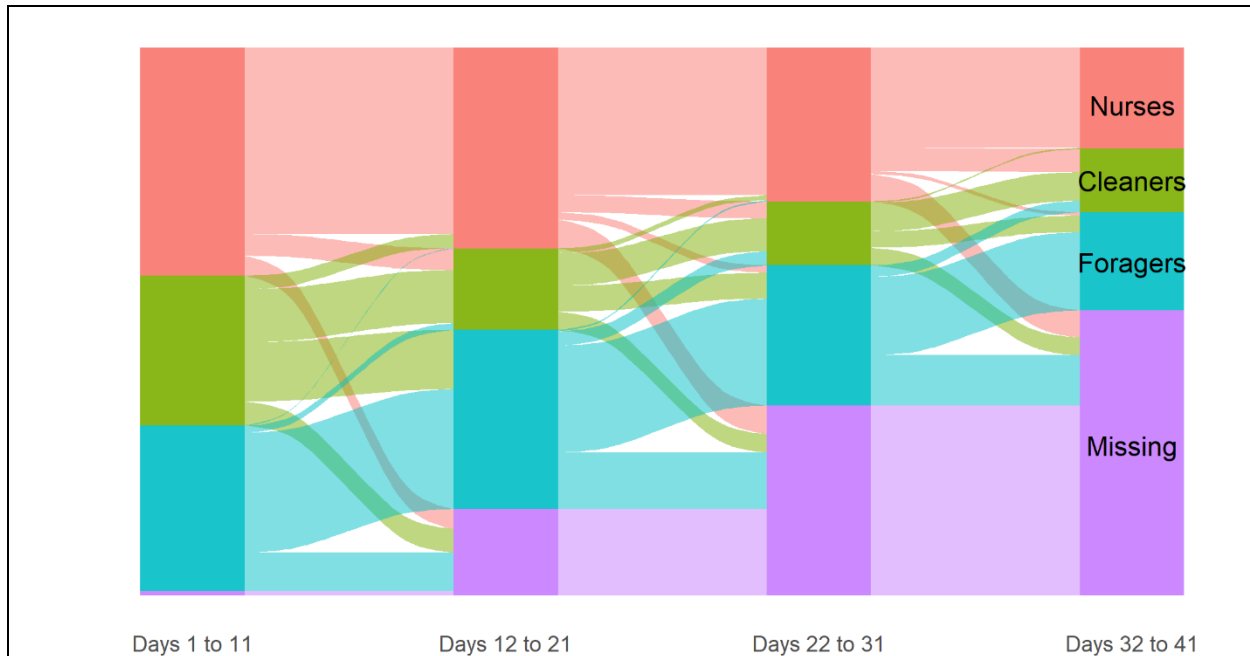


Figure 1: Dynamics of task allocation across the experimental time for all ants in all six colonies, with functional group assigned via Louvain community detection algorithm (~90% assignments consistent with Mersch et al. 2013). The alluvial diagram shows the number of ants per functional group and number 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,

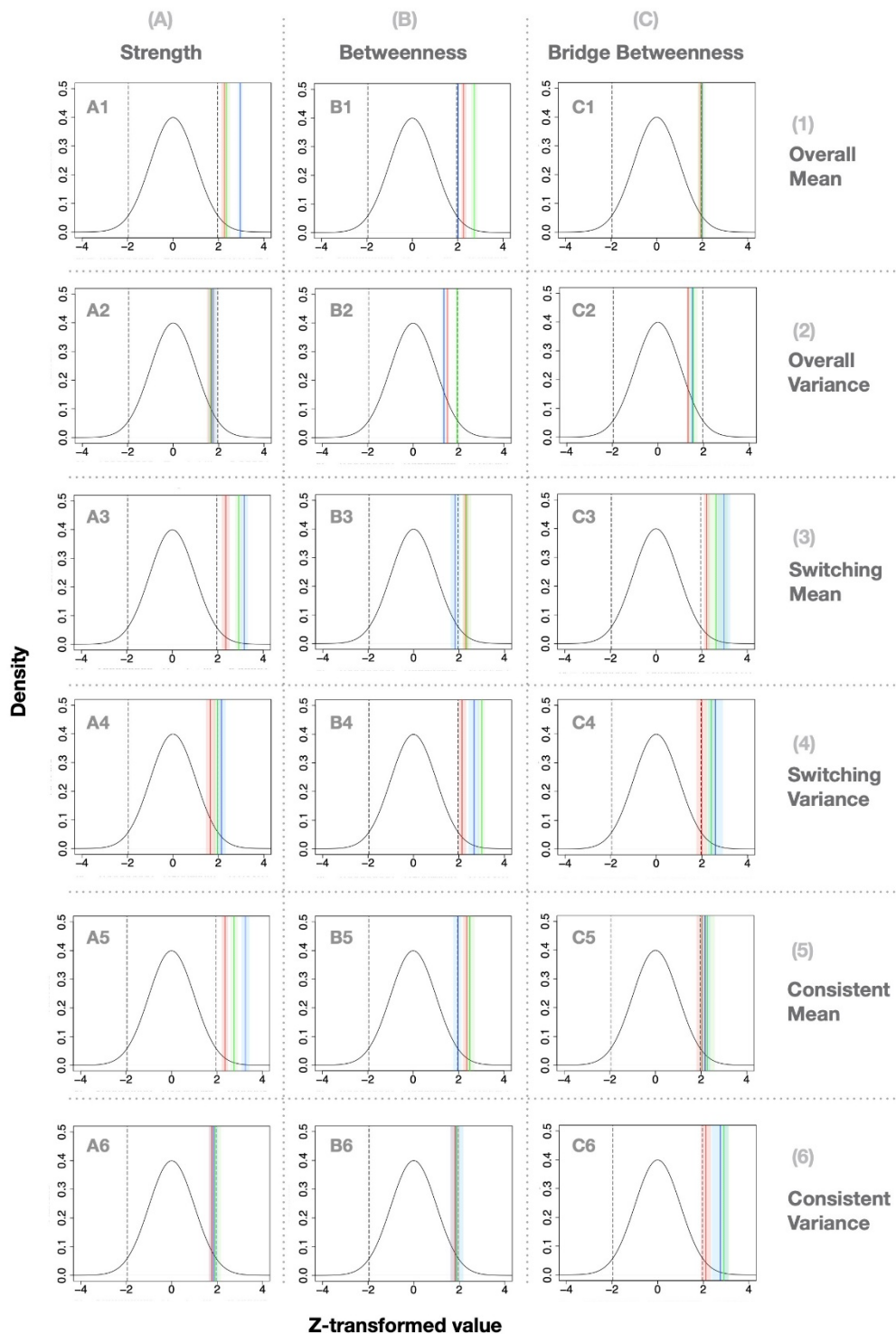
309 showing that they had the most frequent interactions over a day regardless of whether
310 they remained foragers or switched task at some point. When considering the overall
311 mean strength, foragers had the strongest interaction potential (2.96). The strength of
312 cleaners (2.35) and nurses (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 betweenness 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 structures could be
366 important for colony cohesion at the community level.
367



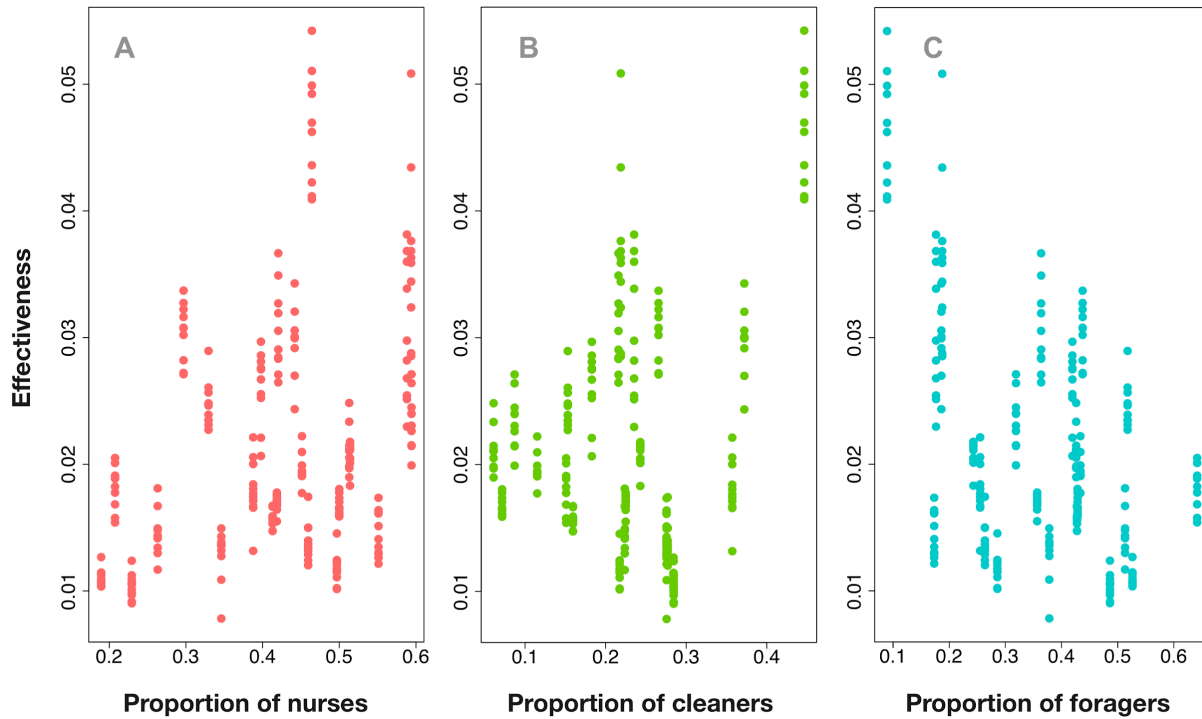
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369 **Figure 2:** Z transformed values of the mean and variances of the strength, betweenness
370 and bridge betweenness (columns A, B and C respectively) determined for all ants across
371 the six colonies. The first two rows (rows 1 and 2; A1-C2)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

373 for ants that switched during the experiment, and the last two rows (rows 5 and 6; A5-C6)
374 show values for for consistent ants (no switching) during the experiment. Line colors
375 correspond to ant functional group type: nurses (red), cleaners (blue), and foragers
376 (green). Shaded areas are the 95% confidence intervals based on seeded random
377 networks. The null distribution created from the null network simulations is shown in black
378 with a marked confidence interval (dashed lines).
379

380 ***Global information flow and task switching***

381 We measured effectiveness as a function of the proportion of nurses, cleaners or
382 foragers in each colony for each day (resulting in 246 effectiveness measures, Figure 3).
383 We found that the colony networks with high proportions of nurses and cleaners had lower
384 effectiveness, but that the dependencies based on the linear model were weak and non-
385 significant (adj. $R^2=0.12$, $P = 0.063$, Figure 3A for nurses; and adj. $R^2=0.11$, $P = 0.052$,
386 Figure 3B for cleaners). Effectiveness significantly decreased with increasing proportions
387 of foragers in a colony (adj. $R^2=0.22$, $P = 0.037$, Figure 3C). This negative relationship
388 between increased numbers of foragers and decreased colony-level effectiveness shows
389 that the interactions mediated by foragers were noisier than those of nurses or cleaners.
390
391



392

393 **Figure 3:** Effectiveness (normalized EI) of the interaction networks constructed for each
394 colony and every day of the experiment as a function of the proportion of different
395 functional groups in the networks. Data are stacked because the available granularity for
396 task allocation was at a 10-day interval. Linear models fit to effectiveness as a function of
397 the proportions of nurses (A) and cleaners (B) separately return a nominally positive
398 dependence (adj. $R^2=0.12$, $P = 0.063$ for nurses; and adj. $R^2=0.11$, $P = 0.052$ for
399 cleaners). Effectiveness as a function of the proportion of foragers (C) returns a strong
400 negative dependence ($R^2 = 0.22$, $p\text{-value} = 0.037$).
401

402 ***Task interaction matrix and task switching***

403 We tested whether previous interaction patterns affected switching behaviour using a
404 task interaction matrix. We found that ants that remained consistent in their tasks usually
405 interacted most with other ants occupying their same task (Table 1, Consistent ants). For
406 example, consistent nurses were significantly more likely to only have interacted with
407 other nurses (90% of nurse interactions, $P=0.0326$). Although cleaners and foragers who
408 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

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

421

422 **DISCUSSION**

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

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

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

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

446 Ants that switched tasks functioned as key connectors for information flow in the
447 colony, supporting colony cohesion. In general, betweenness was higher for ants that
448 switched than for ants that remained consistent in their task. This suggests that ants who
449 switched tasks throughout the course of the experiment, and particularly cleaners, played
450 an important role in connecting other ants through information flows. Their high
451 betweenness means that they occupied a key network position for receiving and
452 transmitting information before they switched. If learning is required when ants switch
453 tasks, this increased access to information may have allowed them to be able to learn
454 new behaviours more quickly, helping them transition to a new task. Bridge betweenness
455 indicates how ants connected different communities within the colony. Ants who switched
456 tasks had higher bridge betweenness than those who remained consistent in their task.
457 In particular, foragers and cleaners had higher bridge betweenness than nurses, showing
458 that they were key connectors among the different functional groups. Cleaners especially
459 were less likely to interact within their functional group (consistent with Mersch et al.'s
460 2013 results). The low group cohesion of cleaners may strengthen colony-wide cohesion.

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

470 At the group level, the operationalization of effective information as a measure of the
471 noisiness of network mechanisms is relatively new and under-explored. Our effectiveness
472 results for the six *Camponotus fellah* colonies show a correlation between variations in
473 effectiveness and the functional group composition of each colony. We found that a higher
474 proportion of foragers lead to noisier communication among ants. Paired with the results
475 on interaction strength, this means that foragers interacted more than ants in other tasks
476 and that their interactions were noisier than interaction patterns of ants performing
477 different tasks. Results on centrality measures and effectiveness can be linked with task
478 allocation through our task interaction matrix. The matrix shows how previous interactions
479 with ants in a given task lead to a higher probability of the ant switching to that task. These
480 results are consistent with previous work in another species: Gordon and Mehdiabadi
481 (1999) found that, in red harvester ants, ants switching from other tasks to midden work
482 were more likely to have interacted with midden workers, and that switching was more
483 likely to occur the more frequent those interactions. In our results, interactions with

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

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

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

511

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517

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520

521 *Competing interests:* The authors declare no competing interests.

522

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

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