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

2   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., the network of interactions). We focus on group

17   level processes by exploring the relationship between interaction networks, task

18   allocation and task switching using a previously published dataset (Mersch et al., 2013)

19   tracking the behaviour of six *Camponotus fellah* colonies over 41 days. In our new

20   analyses, our goal was to better explain the noisy process of task switching beyond simple

21   age polyethism. First, we investigated the architecture of interaction networks using node

22   (individual) level network measures and their relation to the individual's task – foraging,

23   cleaning or nursing – and whether or not the ant switched tasks. We then explored how

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24 noisy information propagation was among ants, as a function of the colony composition

25 (how many ants carried out which tasks), through the information-theoretic metric of

26 *Effective Information*. Our results show that interaction history was tied to task allocation:

27 ants who switched to a task are more likely to have interacted with other ants carrying out

28 that task. The degree to which interactions related to task allocation, as well as the noise

29 in those interactions, depended on which groups of ants were interacting. Overall, we

30 showed that colony cohesion was stable even as ant-level network measures varied more

31 for ants when they switched functional groups; thus, ant colonies maintained a high level

32 of information flow as determined by network analysis, and ant functional groups played

33 different roles in maintaining colony cohesion through varied information flows.

34

35 **Keywords:** Ant behaviour, Effective Information, emergent behaviour, insect social

36 networks, task allocation, information flow

37

38 ***Highlights***

39 ● We analysed the interaction networks of six *Camponotus fellah* colonies

40 ● We tested how centrality and information flow were tied to task switching

41 ● Node-level network metrics and the information theoretic measure of *Effective*

42   *Information* explained differences among functional groups

43 ● Interactions were correlated with task switching, but the strength of the

44   correlation differed across functional groups

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   Task allocation in ants has been the subject of much previous work (Anderson and Shea,

63   2001; Gordon, 2015). Across ant species, studies have shown that, depending on the

64   tasks and on the colony, ants may display varying degrees of task flexibility, from small

65   colonies of totipotent ants to larger ones with a structured division of labour (Anderson

66   and Shea, 2001). Factors affecting task changes can occur at the individual level or at

67   the group level. Individual-level factors include physiology (Anderson and Shea, 2001),

68   age (Tripet and Nonacs, 2004), corpulence (Robinson et al., 2009) and past experience

69   (Ravary et al., 2007), whereas group-level factors involve colony size (Ravary et al., 2007)

70   and interaction rates at the colony level (Gordon and Mehdiabadi, 1999). Studying

71   individual-level factors associated with task change is often simpler than studying group-

72   level ones. For example, individual-level changes can be easier to track because their

73   rate of change often follows a consistent and predictable pattern, as in the case of ageing.

74   Individual-level factors can also be directly quantified, e.g., by measuring age,

75   corpulence, or physiological features, and traditional statistical approaches can be used

76   to predict task changes.

77   An ant's propensity to switch to a new task could also be linked to nature of its

78   interactions and the topology of the group's social interaction network structure. However,

79   changes in task allocation affected by group-level factors are currently not well

80   understood. Structural features or macro-level social properties of groups can affect

81   micro-level individual actions if the social system is affected by feedbacks (Flack, 2017;

82   Hobson et al., 2019). However, quantifying relevant macro-to-micro feedbacks can be

83   challenging and can require large amounts of data. The development of automated

84   tracking systems has made this level of data collection possible. While these systems

85   have improved researchers' ability to track detailed social behaviour (Robinson et al.,

86   2009; Smith and Pinter-Wollman, 2021), assigning quantitative metrics to group dynamics

87   is still a non-trivial task. In the case of interaction patterns, tracking physical interactions

88   among individuals does not necessarily map onto the amount of meaningful (predictive)

89   information exchanged with each interaction (Valentini et al., 2020). Although tracking

90   technologies can tell us how many times individuals in a social group interact with one

91   another, they cannot explain to what extent these interactions are tied to task allocation

92   without considering the structure of these interactions and without including behavioural

93   observations. Network methods and metrics allow us to explore the interaction structure.

94   In this paper, we leverage social network methods to gain new insight into task

95   allocation changes in an existing dataset of ant interactions (published by Mersch et al.

96   2013). Mersch et al. studied task switching in *Camponotus fellah* by tracking and

97   analysing the movements and interactions of individually-identified ants. Worker ants

98   were categorised into three *functional groups* (nurse, cleaner or forager). Analyses

99   showed that ants had more interactions with others in their same functional group.

100   Communities defining the functional groups exhibited distinct behavioural signatures and

101   were highly spatially divided. Nurses spent most of their time with the brood, while

102   foragers spent time at the nest entrance and cleaners were located between the other

103   two groups and the rubbish pile (Mersch et al. 2013). Mersch et al. also explored the

104   questions of task switching cost, i.e., a time and energy investment associated with

105   learning new tasks (Goldsby et al., 2012), and of age polytheism, i.e., the correlation

106   between the age of an ant and which task they perform. The original study identified

107   spatial fidelity as a key regulator of ant social organisation and interaction frequency

108   (Mersch et al. 2013). They also found that task switches were present but uncommon and

109   that when a shift in functional group occurred, ants showed a preferred direction of task

110   transition, from nurses to cleaners to foragers, mostly based on age (Mersch et al., 2013).

111   Task changes were thus hypothesised to be driven by age polyethism, but the patterns

112   were fairly noisy.

113   In this new analysis we focus specifically on this noisy process of task switching

114   and its predictability. A question not addressed in the previous study is whether the history

115   of an ant's interactions with others could be one of the elements explaining task switching.

116   In other species, information flow patterns have been shown to affect task allocation and

117   overall colony behaviour, such as in the case of midden workers in red harvester ants

118   (*Pogonomyrmex barbatus*; Gordon and Mehdiabadi, 1999, Pinter-Wollman et al., 2018),

119   tandem running recruitment (Franklin and Franks, 2012) and consensus-forming in rock

120   ants (*Temnothorax albipennis*; Sasaki & Pratt, 2018). To test whether the history of

121   interactions or information flow could explain the noise seen in task switching dynamics

122   that was not explained by age polyethism alone, we evaluated several potential macro-

123   scale predictors of task switching not addressed in the original paper.

124   First, we described the architecture of the interaction networks by focusing on

125   information flow (which in our case refers to the possible information exchange due to

126   interactions among ants). We tested whether the role played by individual ants in

127   regulating information flow in the colony and the functional group that they belong to were

128   correlated. To do this, we quantified three network measures that are tied to the

129   architecture of information flows at the local level for ant-to-ant interactions: strength

130   mode, betweenness centrality, and bridge betweenness centrality. We also quantified a

131   network level measure, *Effective Information* (EI), for the whole colony. At the scale of

132   ant-to-ant interactions, strength measures the quantity and frequency of interactions of

133   an ant, and strength mode finds the value in the distribution of strengths most commonly

134   observed across all the ants in the group. Betweenness centrality measures the number

135   of shortest paths between pairs of ants that pass through it. Bridge betweenness centrality

136   extends betweenness to measure the number of shortest paths that pass through a node

137   and connect separate highly connected groups of nodes, or communities. While strength,

138 betweenness centrality, and bridge betweenness centrality are common node-level

139 measures in network science and have been applied to animal social networks in the past

140 (Holme et al., 2002; Lusseau and Newman, 2004; Krause et al., 2009; Farine and

141 Whitehead, 2015), Effective Information is a new information theoretic metric reflecting

142 how noisy a mechanism connecting nodes (ants, in our case) is within a system. It is

143 calculated as the difference between degeneracy and determinism of the network (Hoel,

144 Albantakis, & Tononi, 2013; Klein and Hoel 2020). In interaction networks, Effective

145 Information reflects the noisiness and predictability of the interactions among individuals

146 (Hoel et al., 2020): a higher Effective Information means that a system is more

147 deterministic, with information spreading in a more effective way throughout the network.

148 Second, we tested whether these four measures of information flow in the

149 interaction network were related to task switching, to better understand the noise in task

150 allocation not explained by age polyethism as determined by Mersch et al. (2013). We

151 hypothesised that an ant's previous interactions with other ants affect switching behaviour

152 and tested whether interacting with a certain functional group increased the probability of

153 an ant switching to that group. We found that the relationship between the structure of the

154 interaction network and the different functional groups, as described by network

155 measures at the node and the global level, could explain the varying correlations between

156 interaction history and switching behaviour during task allocation. Our use of network

157 metrics, including the Effective Information metric, allowed us to determine the

158 relationship between interaction history, task allocation and information flow among

159 functional groups in *Camponotus fellah* colonies.

160

161 **METHODS**

162 ***Data, network construction, and ant categorisation***

163   The published Mersch et al. (2013) dataset contains summaries of interactions

164 among a total of 985 individually-marked ants in six *Camponotus fellah* colonies. The

165 authors collected interaction data for every pair of ants at a daily resolution over the 41-

166 day monitoring period, and the published dataset contains data pooled at the number of

167 interactions per dyad per day per colony. We matched this published dataset with the

168 colony metadata to inform our analyses (Supplementary material 1).

169   Consistent with Mersch et al. (2013), we used the pairwise daily number of

170 interactions to construct separate weighted, undirected, unipartite networks for each

171 colony per day. Each ant in a colony was represented by an individual node. An edge

172 between two nodes represents the interactions between those two ants on a given day.

173 The edge weight is proportional to the number of pairwise interactions between them on

174 that particular day. We used the available published dataset to recreate the 246 observed

175 networks for the 6 colonies over 41 days used by Mersch et al. (2013) as well as the

176 general pattern of task switching across the length of the experiments.

177   Mersch et al. (2013) assessed each ant's functional group every 10 days to

178 categorise them as a nurse, cleaner, or forager, representing their main task in the colony.

179 They assigned functional groups based on what community an ant spent at least 70% of

180 their time in, using the 'infomap' community detection algorithm paired with behavioural

181 observations. They split the ants into the functional groups foragers (F), cleaners (C),

182 nurses (N), queen (Q), and NA for ants who were counted as missing at a time point (e.g.,

183 if they were dead or had lost their tags).

184   Mersch et al. (2013) reported that their ants mostly did not change their task affiliation

185 within the 10-day observation period between task assessment points. We used the same

186 10-day snapshot window in our analyses which resulted in three time points at which a

187 switch in task to a new category could be detected. Based on Mersch et al's (2013)

188 observational data, when an ant switches functional groups, it switches tasks to that of

189 the new group. For our analyses, we categorised each ant as "switched" or "consistent",

190 depending on whether they were categorised as part of a different functional group, or

191 remained within the same functional group after each task assessment point in the

192 original behavioural data. These labels were assigned for each 10-day observation

193 period, meaning that an ant could be labelled as "consistent" in one time period because

194 it did not change tasks from the previous period, and "switched" in the next if it then

195 changed tasks, and thus functional groups during that next period. We utilised these

196 labels and the functional groups set by Mersch et al. (2013), throughout our work.

197   Before performing new analyses, we first investigated whether we could replicate

198 Mersch et al.'s (2013) results of age polyethism. We also tested whether we could

199 recapitulate Mersch et al.'s results about task switching by determining the likelihood that

200 an ant would stay in the same task throughout the experimental time versus performing

201 two or three tasks.

202

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

204 Our new analyses focused first at the individual scale within the networks. Node

205 metrics and centralities define various types of influence that individual nodes exert on

206 network connectivity and dynamics. For each network, we used R (v 3.6.2) and the

207   packages *igraph* (Csardi and Nepusz, 2006) and *networktools* (Jones, 2020) to calculate

208   three node-level, local metrics: (1) strength, (2) betweenness centrality, and (3) bridge

209   betweenness. Since networks were constructed for each daily set of interaction

210   observations for each colony, these metrics were calculated for each ant in every colony,

211   every day. Differences in these metrics were then analysed as a function of functional

212   groups at the colony level, and for just ants that switched or ants that remained consistent.

213   First, we calculated each ant's node strength as the sum of the weights of its edges.

214   Thus, in our context, it is a measure of not only how many interactions (edges) an ant

215   (node) had with other ants, but also of how frequently those interactions occurred during

216   a day. While degree is an index of potential communication activity (Freeman, 1979),

217   strength improves upon this index by weighting degrees according to communication

218   frequency, to better inform total interaction and information flow potential. To measure the

219   structure of the distribution of this node level metric at the network level, we calculated

220   the maxima of the density distribution of strength of all ants (or all within a functional group

221   subset) in a given colony on a given day to find the *strength mode*. The mode was used

222   instead of the mean because the strength distributions were skewed. The strength mode

223   provides a summary of how these strengths are generally distributed across each

224   network.

225   Second, we calculated each ant's node betweenness. Also known as betweenness

226   centrality, this measure is another way to assess the influence of a node for the

227   connectivity of the network. For a given pair of nodes in a weighted network, there exists

228   at least one path between them such that the sum of the link weights is minimized, thus

229   forming a shortest path. The betweenness of a node is therefore defined as the number

10

230   of shortest paths that pass through it. Freeman (1979) identified high betweenness

231   centrality as a key indicator of whether a node occupies a central location in the network

232   for information transmission. Individuals with high betweenness are often responsible for

233   maintenance of communication, group coordination, and network stability (Lusseau and

234   Newman, 2004; Farine and Whitehead, 2015). An ant with a high betweenness is an ant

235   that is centrally located in the network, serving as a key connection for seemingly

236   disparate ants.

237   Third, we measured the bridge betweenness for each ant in the network. Bridge

238   betweenness extends the betweenness centrality metric to the level of communities and

239   is defined as the number of times a node lies on the shortest path between two nodes

240   from different communities. In network science, a community is defined as a group of

241   nodes that have a higher likelihood of connecting to each other than to nodes from other

242   communities. Ants with a high bridge betweenness serve as key connectors for different

243   communities in the network, where communities mostly overlap with functional groups.

244   This means that ants with high bridge betweenness would be more integral to network

245   cohesion and information flow across groups, thus they may play an important role in

246   driving switching dynamics.

247   To quantify each ant's bridge betweenness, we needed to assign ants to network

248   communities in both the observed networks but also in our 123,000 reference networks

249   (see below). Assigning ants to network communities using the original network community

250   detection algorithm Infomap (used in Mersch et al. 2013) was computationally prohibitive

251   when applied to our many reference networks. Because of the computational demands

252   of the bridge betweenness analysis, we used a Louvain community detection algorithm

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253   (Csardi and Nepusz, 2006) which saved computational time and memory (Emmons et al.,

254   2016) compared to the Infomap algorithm. These new network community assignments

255   were solely used for computing bridge betweenness and did not change the functional

256   group assignments of the ants made by Mersch et al. (2013), which we use in all other

257   cases in our analyses. To check that the Louvain algorithm assigned ants to network

258   communities in ways consistent with the original community assignments from Infomap,

259   we compared our community assignments to those found by Mersch et al. (2013): as we

260   show below, our new assignments were similar enough to the original assignments that

261   we could use our new method to assess bridge betweenness and the likelihood ants

262   would be connected to others within different functional groups (see results, below). All

263   other analyses involving functional group assignments of ants use the functional groups

264   assigned in Mersch et al. (2013).

265

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

267
268   We used *Effective Information* and its normalised measure, *Effectiveness*, to measure

269   colony-level noisiness in the system, with respect to its underlying mechanisms (Hoel et

270   al., 2020; Klein et al., 2022). Since we are considering the mechanism of communication

271   and information flow among ants, Effective Information measures the level of

272   predictability, or degeneracy, in ant-to-ant interactions. To calculate Effectiveness, we first

273   found the sum of weights of all edges connected to each node in the interaction network,

274   where edge weights correspond to the number of interactions between a pair of ants. An

275   ant who had no interactions in a given network would have a weight of 0. We defined this

276   weight as a vector W_i of the same length as the total number of nodes and referred to

277   each element as ω_{ij}, signifying the normalised value of edge weight between nodes *i* and

278   *j*, such that for any index *i*, $\sum_j \omega_{ij} = 1$. Here, each term ω_{ij} can be seen as the probability

279   of moving from *i* to *j*, if a random walker is on the node *i*. Next, we characterised the

280   uncertainty associated with each node *i*, calculated using Shannon's entropy measure

281    $H(W_i)$. As node *i* has more connections, and as the weights $\omega_{ij}s$ of those connections to

282   other nodes (*j*) become more equal, Shannon's entropy (i.e., the uncertainty about where

283   a random walker would go) increases. The average of this value across all the nodes in

284   the network is $< H(W_i) >$. When $< H(W_i) >$ is equal to 0, the network is deterministic

285   (e.g., in the case of a line network or a ring lattice, both in directed and undirected cases,

286   where information can only flow in one dimension). We then assessed the certainty of the

287   network by calculating the term $H(< W_i >)$, which is Shannon's entropy of the average

288   out-weights from all nodes. When this expression is equal to 0, the network is degenerate,

289   with all edges leading to the same node. Finally, we calculated Effective Information using

290   the following equation:

291    $$EI = H(< W_i >) - < H(W_i) > \tag{1}$$

292   Here, the first term of the equation is determinism, and the second is degeneracy. Thus,

293   the Effective Information for a line graph or a ring lattice, which are maximally

294   deterministic and minimally degenerate, is the maximum. For the cases of a star

295   network, which is both maximally deterministic and degenerate, and that of a complete

296   graph, which is both minimally deterministic and degenerate, the value of Effective

297   Information is zero. As the value of Effective Information can depend on the size of the

298   network (Klein and Hoel, 2020), we calculated Effectiveness, the normalised Effective

299   Information with respect to network size. Effective Information is normalized by *log₂N*,

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300   which is the maximal possible value of the entropy, where N is the number of nodes in

301   the network. For comparison, this is akin to the normalisation of Shannon diversity to

302   Shannon equitability in ecological studies.

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

304   Effectiveness was calculated for each observed network (i.e., for each day, for every

305   colony), using the R package *einet* (Byrum et al., 2020; Klein et al., 2022).

306   If node level properties were affected by which functional group an ant was in, then

307   system level measures could be affected by the proportion of ants in each functional

308   group, so we tested how group composition affected Effective Information. We used the

309   functional group assignment from Mersch et al. (2013), then fit linear models to the

310   Effectiveness for each observed network as a function of the proportion of each functional

311   group in the network to determine significant relationships between Effectiveness and a

312   colony's functional group composition.

313

Building reference models to test interaction patterns and task switching

315   To test how interaction patterns resulted in different network metrics and/or task

316   switching patterns than expected, we constructed randomised networks that served as

317   null models, or reference networks, for the daily interaction networks of the six colonies.

318   Using randomised networks as reference networks is a common method for testing the

319   effect of interaction structure and significance on various network properties and

320   dynamics (Hobson et al. 2021; Farine 2017). Constructing a reference model allowed us

321   to randomise some aspects of the interaction patterns while preserving other relevant

322   structural features of the networks (Hobson et al. 2021). We used a degree-based

323   randomisation (through the R package *VertexSort*; Abd-Rabbo, 2017) to generate our

324   reference networks. This approach preserved the total number of interaction partners per

325   any one ant on a given day but changed (1) who they interacted with and (2) how many

326   times they interacted. This process distributed the total number of original interactions

327   among the newly constructed edges of the randomised network.

328   This reference model approach allowed us to test how specific ant interaction

329   patterns affected the node and network level properties, while preserving the distribution

330   of connections in relation to functional groups of the ants (functional group assignment

331   and the degree of individual ants remained unchanged). As an example, a nurse that had

332   20 interaction partners (degree = 20) would still have a degree of 20 in the reference

333   network but would be interacting with 20 different ants with different frequencies, as the

334   edge weights were also randomly assigned from the initial distribution for each reference

335   network. This hypothetical reference model ant would then have a different total

336   frequency of interactions while maintaining their original number of partners. For

337   reproducibility, we created 500 seeded reference networks for each colony's daily

338   interaction network, for a total of 123,000 reference networks.

339   To test how observed network measures differed from those expected with the

340   identity of interaction partners and the number of interactions randomised, we compared

341   the observed node-level network measures to the distribution of those measures in our

342   reference networks. We found the strength mode, mean betweenness, and mean bridge

343   betweenness for every observed ant network (each colony, for each day) and for each of

344   the reference networks. We also estimated the variance for each metric for every ant in

345   a given colony on each day for the observed network and all the reference networks

346 associated with the observed one (please note that in the case of strength, the variance

347 is the standard variance in the strength distribution). The metrics were investigated

348 separately for each functional group within the following subsets: overall (all ants),

349 switching and consistent ants. Variance measured the individual variation of metrics

350 among ants of one group in a colony. The distribution of variances, in conjunction with

351 those of the central tendencies, helps us to explore the variation of these metrics across

352 colonies and through time. Central tendencies (mode for strength, and mean for

353 betweenness and bridge betweenness) and variance values were Z-transformed,

354 separately for each metric and individual observed network with its respective reference

355 networks, to facilitate comparison across observed networks which can vary in size

356 (number of ants), allowing us to find each metric's value for a given group, colony and

357 day relative to its own reference models. The Z-transformation allowed us to combine

358 values across colonies and days, and to visualize the means of those metrics across all

359 samples (groups, days and colonies). We then calculated the 95% confidence intervals

360 of the Z-transformed values for each functional group and ant subset (switching,

361 consistent and overall ants) to determine differences in the network measures in relation

362 to ant role and task switching. Since the distribution of variances indicates the variation

363 of a network metric both across colonies and through time, the size of the 95% confidence

364 intervals of the variances provides a proxy metric for stability of the network metrics, when

365 interpreted in conjunction with the distribution of the central tendencies of those metrics.

366 To test if the frequency of interactions with different functional groups significantly

367 affected an ant's functional group membership and whether these interactions could

368 explain how ants switched tasks, we compared the observed patterns of interactions in

369   relation to switching behaviour to that of the reference models. If the functional group

370   identity of ants affected how individuals contributed to information flow within a colony,

371   then the number of times an ant switched to a new functional group should affect the flow

372   of information. We tested how observed patterns differed from reference networks that

373   preserved the number of interactions per ant but redistributed the interactions among

374   every ant. We also tested whether the frequency of interactions with different functional

375   groups significantly affected an ant's final functional group. At each task assessment

376   point, we quantified the frequency of interactions with each functional group before

377   switching from its original functional group to the final one in both the observed dataset

378   and in the ensemble of randomised reference networks. We compared the distribution of

379   values computed from the observed networks against those given by the reference

380   network distribution using a suite of chi-square (independence/homogeneity)

381   comparisons separately for each possible type of task transition (including non-

382   transitions) and each observed network, wherever the specific transition/non-transition

383   occurred. To use the chi-square test, we assume that each interaction is independent as

384   it involves transfer of new information between two individuals, even if it might be biased

385   by more contact with certain individuals by choice. In addition, individual recognition is

386   not particularly well established for ants, although they can recognize brood mates and

387   their colony queen (see Esponda and Gordon, 2015; Sprenger and Menzel, 2020),

388   lending more credibility to our assumption.

389   The significance results from each type of transition across all observed networks

390   were then combined using Stouffer's method (see Heard and Rubin-Delanchy, 2017) and

391   significant differences at the alpha level of 0.05 were noted after accounting for multiple
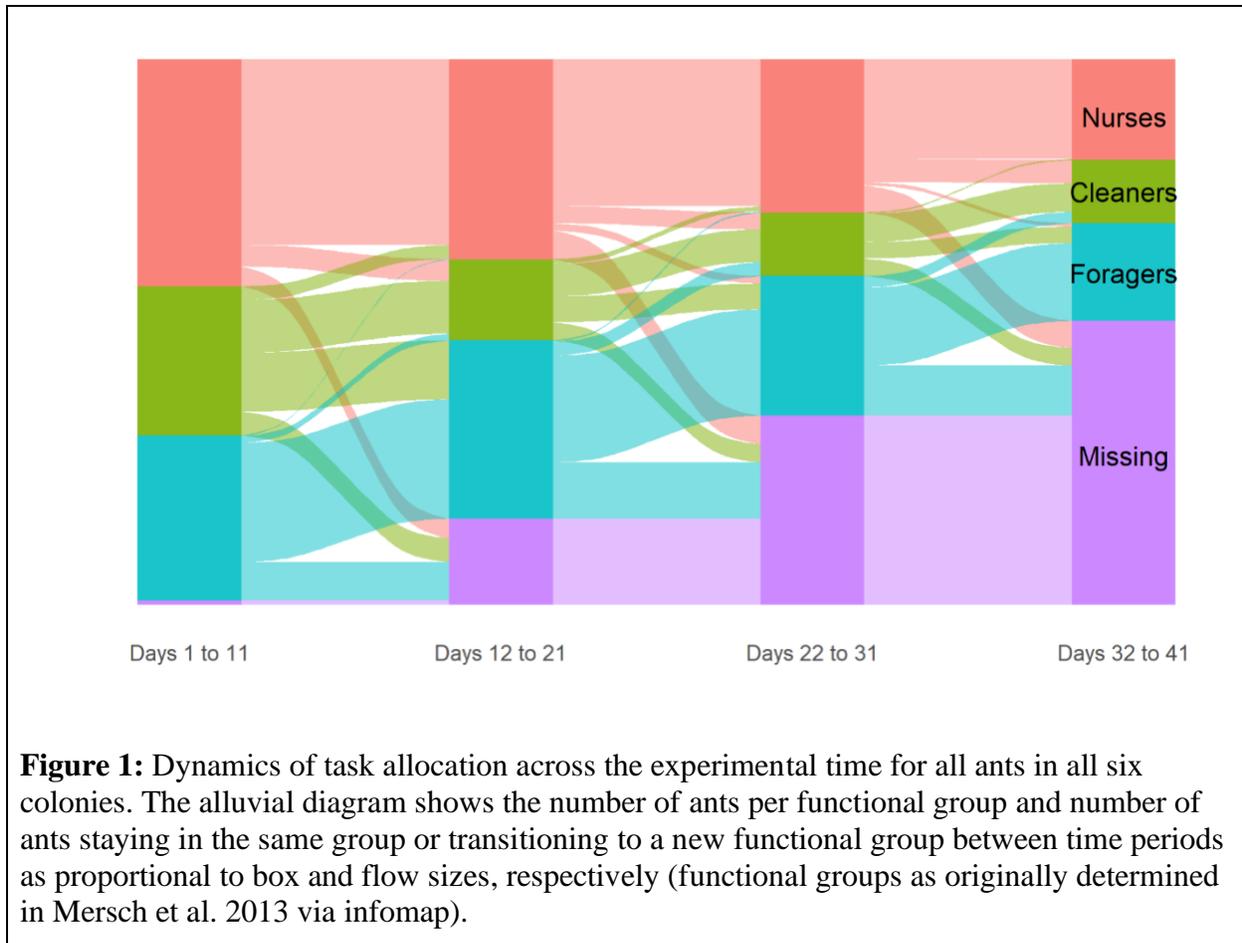
392 comparisons (across transitions) through the Benjamini-Hochberg (BH) correction. We

393 combined all the cases where specific transitions were present, across all colonies and

394 days. Importantly, we were comparing the total number of interactions in these tests

395 pooled across all ants for a given subset, and not the number of ants that switched or

396 remained consistent in their tasks. In all cases, the frequency of interactions with each

397 type of functional group exceeded the minimum number required for using chi-square

398 tests, even though in certain cases the number of ants who were interacting were less

399 than five – their frequency of interactions exceed that number by a several orders of

400 magnitude. This process allowed us to assess whether interactions within the previous

401 observation period predicted functional group in the next observation period.

402

403 **RESULTS**

404 ***Replication of original results and visualisation of task switching***

405   Figure 1 shows a new visualisation that summarizes the tasks of ants within all six

406 colonies and how those tasks changed over time (Figure 1; for details, see

407 Supplementary material 2, Table S1). To ground our analyses, we first replicated the main

408 results from the original Mersch et al. (2013) paper. We were able to replicate the original

409 results of age polyethism and recapitulated the distribution of the age of an ant that would

410 switch tasks once, twice, or three times (results from Mersch et al., novel visualisation in

411 Supplementary material 2, Figure S1A). We were also able to replicate Mersch et al.'s

412 results about task switching by determining the likelihood that an ant would stay in the

413 same task throughout the experimental time versus performing two or three tasks

414 (Supplementary material 2, Figure S1B).

18

Figure 1: Dynamics of task allocation across the experimental time for all ants in all six colonies. 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 (functional groups as originally determined in Mersch et al. 2013 via infomap).

415

416   We also compared our interaction community assignments used in calculating bridge

417   betweenness (via the Louvain community detection algorithm) with those obtained

418   through the Infomap algorithm originally used by Mersch et al. (2013; for the task of

419   functional group allocation). Community membership assignments, compared at an

420   individual node level for a given network, resulted in an average 90.13 ± 7.25% similarity

421   between the two methods across all the networks in the dataset. While the functional

422   group assignments used in our analyses were taken directly from Mersch et al.'s analysis

423   (which were validated by behavioural observations), this similarity of community

424   assignment is important as we wanted to certify that the structure of communities

425   detected by both algorithms was not divergent. The bridge betweenness metric used the

426   communities from the Louvain algorithm as it provided a substantial reduction in

427   computational time, and was indicative of the potential for an ant to connect ants from

428   different functional groups because of the high similarity with the community assignments

429   used to determine functional groups (i.e. by infomap and Mersch et al., 2013).

430

431   ***Individual network centrality measures and task switching***
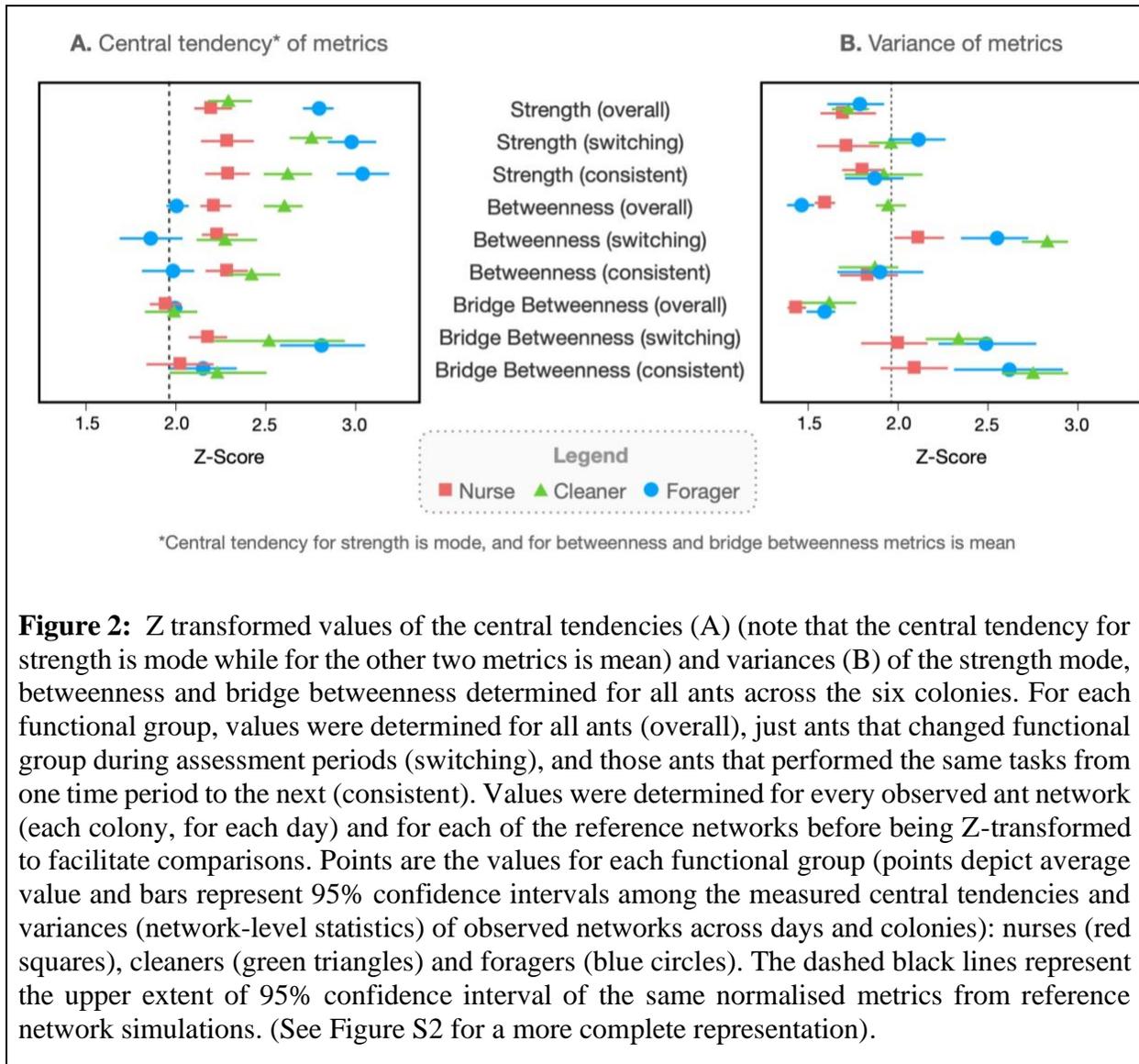
432   We compared network measures and their variances across each of the functional

433   groups for three categories: overall across all ants, for just switching ants, and for just

434   ants that remained consistent in their tasks during the assessment periods (summarised

435   in Figure 2; all values listed in Supplementary material 2 Table S2 and additional

436   visualisation in Figure S2), relative to their respective reference networks. Variance was

437   assessed due to apparent substantial fluctuations in the metrics for ants that switched

438   within the 10-day period leading to a task assessment point (Figure S3). These

439   fluctuations are represented by the 95% confidence intervals of the variances which

440   indicate how stable the relative network measures were across colonies and over time

441   (i.e., a larger confidence interval represents more fluctuations and less stability).

442   When we compared the distribution of the strength metric using the mode across

443   each of the tasks, we found that foragers had the highest strength mode of any of the

444   groups across all three of the categories, showing that they had the most frequent

445   interactions over a day regardless of whether they remained foragers or switched task at

446   some point. Values of variance (relative to their respective reference networks) of the

447   overall strength did not significantly differ across functional groups or from the reference

448   networks (see the 95% confidence intervals in Figure 2B) and the mode of strength

20

449   remained fairly consistent across functional groups (see the 95% confidence intervals in

450   Figure 2A). When we looked at strength just for switching ants, we found that the mode

451   differed significantly across functional groups and was significantly greater than for the

452   reference networks. Out of these, foragers that switched had the highest strength mode.

453   Strength mode variance of switching ants did not vary significantly among functional

454   groups. However, variance of the strength mode of switching foragers was higher and

455   more variable (i.e. larger confidence interval) than the reference networks, indicating less

456   stability of this metric among these individuals and over time. When we looked at strength

457   just for ants that were consistent, we found that the mode and variance followed the same

458   pattern seen for ants that switched, i.e., consistent foragers had higher strengths and the

459   values for all groups were of the same magnitude as those for the ants that switched.

460   At the colony level, the betweenness metric was stable (i.e., confidence intervals were

461   small for the both mean and the variance relative to the reference networks) and cleaners

462   played the most important role in connecting individual ants for flow of information, as

463   they had significantly higher betweenness than nurses and foragers (Figure 2). When we

464   assessed betweenness just for ants that switched, we found that mean betweenness

465   centrality measures were significantly greater than those for the reference networks,

466   except for foragers. Betweenness of switching ants was more variable than for consistent

467   ants. Consistent ants had the same relative patterns and magnitude of mean

468   betweenness centrality as ants that switched: consistent cleaners and nurses had higher

469   mean betweenness than consistent foragers. However, the variance of betweenness was

470   no longer significantly different than the reference networks, thus consistent ants

471   maintained a less variable betweenness distribution among networks and through time

21

472   (i.e., the mean and variance remain within small confidence intervals, and that the

473   variance is not significantly different from reference networks) than switching ants (where

474   even if the mean has similar values, the variance is much higher than reference

475   networks).

Figure 2: Z transformed values of the central tendencies (A) (note that the central tendency for strength is mode while for the other two metrics is mean) and variances (B) of the strength mode, betweenness and bridge betweenness determined for all ants across the six colonies. For each functional group, values were determined for all ants (overall), just ants that changed functional group during assessment periods (switching), and those ants that performed the same tasks from one time period to the next (consistent). Values were determined for every observed ant network (each colony, for each day) and for each of the reference networks before being Z-transformed to facilitate comparisons. Points are the values for each functional group (points depict average value and bars represent 95% confidence intervals among the measured central tendencies and variances (network-level statistics) of observed networks across days and colonies): nurses (red squares), cleaners (green triangles) and foragers (blue circles). The dashed black lines represent the upper extent of 95% confidence interval of the same normalised metrics from reference network simulations. (See Figure S2 for a more complete representation).
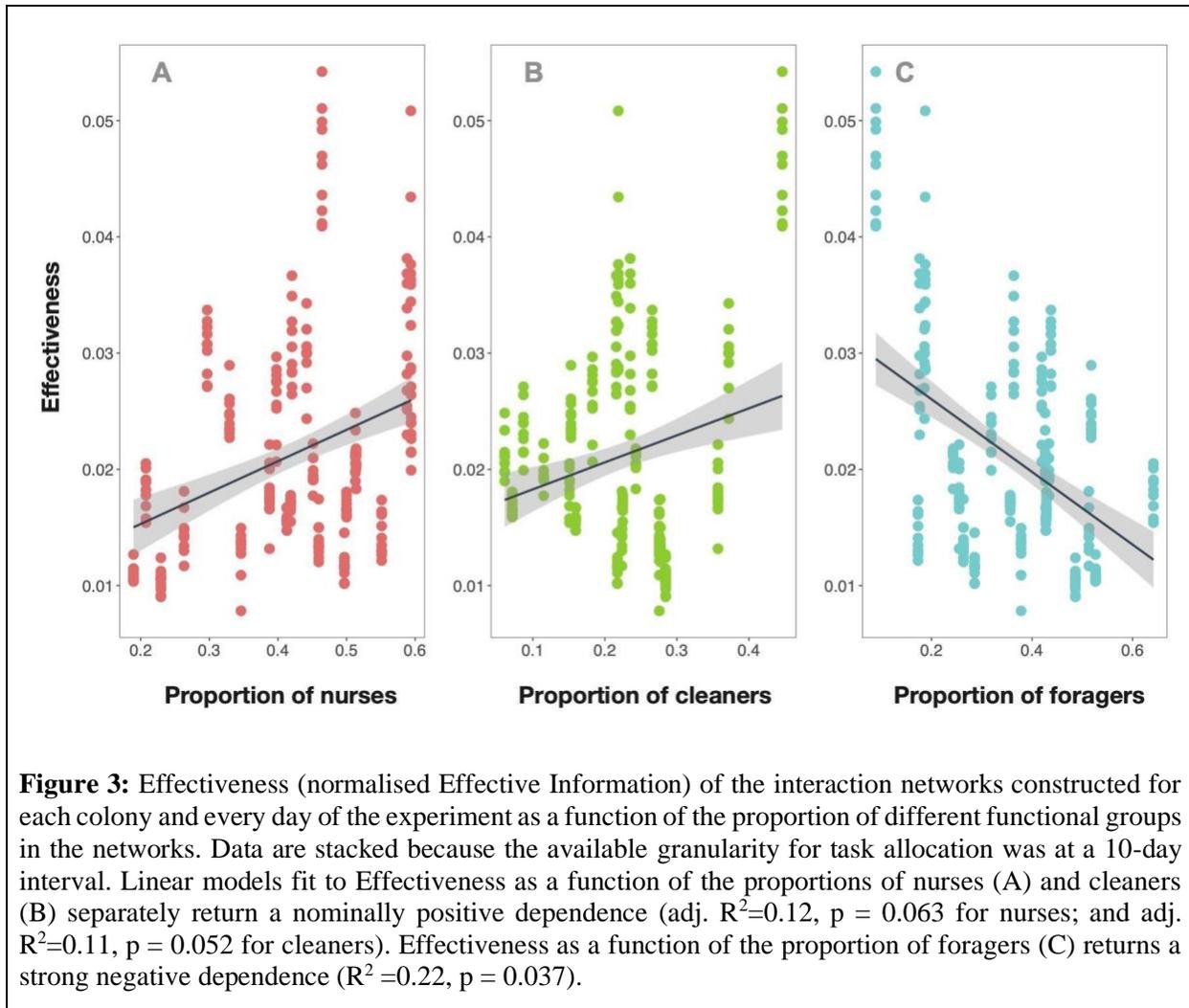
476

477   Since the communities we detected mapped primarily onto the previously determined

478   functional groups (see results above), a high bridge betweenness indicated a high

479   potential for connecting functional groups in a colony. When we compared bridge

480   betweenness across each of the functional groups at the colony level, we found that the

481   overall mean bridge betweenness values and their variance did not vary among the

482   functional groups or from the reference networks, indicating that connections among

483   network group communities stayed stable among networks and through time at the colony

484   level. Mean bridge betweenness was higher for the switching ants than for the consistent

485   ants for all functional groups, though only significantly higher for foragers. All ants that

486   switched had significantly higher mean bridge betweenness than the overall colony

487   values per functional group, suggesting that ants that switched played an important role

488   in connecting communities for information flow in the colony. The mean bridge

489   betweenness of consistent ants did not vary significantly among the functional groups or

490   from the reference network distribution. Although the variance of cleaners and foragers

491   for both ants that switched and those that were consistent was significantly higher and

492   more variable than the reference networks, the overall colony variance values remained

493   stable with small confidence intervals; these results may indicate that these interaction

494   structures could be important for colony cohesion at the community level.

495

496

497   ***Global information flow and task switching***

498   We measured Effectiveness, the normalised Effective Information (difference between

499   how deterministic and degenerate a network is), as a function of the proportion of nurses,

500   cleaners or foragers in each colony for each day (resulting in 246 Effectiveness

501   measures, Figure 3). We found that the colony networks with high proportions of nurses

502   and cleaners had higher Effectiveness, but that the dependencies based on the linear

503   model were weak and non-significant (adj. R^2=0.12, P = 0.063, Figure 3A for nurses; and

Figure 3: Effectiveness (normalised Effective Information) 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 = 0.037).

504 adj. R^2=0.11, P = 0.052, Figure 3B for cleaners). Effectiveness significantly decreased

505 with increasing proportions of foragers in a colony (adj. R^2=0.22, P = 0.037, Figure 3C).

506 This negative relationship between the proportion of foragers and colony-level

507 Effectiveness suggests that interactions involving foragers were noisier than those

508 involving only nurses or cleaners.

509

510 ***Task interaction matrix and task switching***

511 We tested whether previous interaction patterns affected switching behaviour using a

512 task interaction matrix. We found that ants that remained consistent in their tasks usually

513   interacted most with other ants occupying their same task (Table 1, Consistent ants). For

514   example, consistent nurses were significantly more likely to only have interacted with

515   other nurses (90% of nurse interactions, p=0.0326). Although cleaners and foragers who

516   stayed within their functional group also more commonly interacted with other cleaners or

517   foragers, this difference in interaction frequency was not significantly higher than

518   expected by chance. For simplicity and comparison throughout networks, we present the

519   average of proportion of interactions in each case in Table 1.

520   However, most ants that switched to a new task interacted with ants occupying a

521   different task prior to switching (Table 1, Switching ants). For example, nurses who

522   switched to cleaning had interacted more frequently with cleaners (71% of nurse

523   interactions) and this was significantly more likely to occur based on interaction history

524   than by random chance (p = 0.0489). The result that an ant would transition to a group

525   that it previously interacted with the most was significant for the following other transitions:

526   cleaner to nurse, cleaner to forager, and forager to cleaner. Interestingly, foragers who

527   switched to nursing were significantly more likely to have interacted more with ants of a

528   different functional group, the cleaners (65% of forager interactions who then switched to

529   nursing). However, it is important to note that this forager to nurse transition only occurred

530   in a few cases in the experimental data, so these results should be interpreted with

531   caution (due to the low number of observed ants), even though the interaction frequency

532   data was sufficient for the statistical comparison (see supplementary files for sample size

533   information).

534

	Original task	Final task	Proportion interactions with other ants by role			Corrected p-value (Original task to 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 ant's 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 reference model results for each type of task transition; values significantly different from those obtained from their reference networks (after multiple comparison corrections) are indicated with asterisks. Bold type indicates the task and proportion of interactions with ants of that task that were dominant in each category (and which were higher than expected by random chance).

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) 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. In our analyses, we focused specifically on this noisy process of task switching. Our approach allowed us to determine that

543   previous interaction history can help explain some of the noise behind task switching in

544   *Camponotus fellah* colonies and provides novel insight into task switching behaviour in

545   these ants.

546   Our results suggest that ants in different functional groups had varying levels of

547   importance for information flow between individuals and groups in a colony, based on

548   their individual roles in network connectivity as determined by the node-level metrics. Ants

549   that switched tasks often occupied positions in the interaction network that had high

550   potential for supporting information flow between groups. Network analyses, combined

551   with the task interaction matrix, allowed us to describe how the architecture of interactions

552   was related with the distribution of and switching among tasks in an ant colony.

553   At the scale of ant-to-ant interactions, we found that ants classified into the three main

554   tasks (forager, cleaner, nurse) differed in how they interacted with each other, which

555   affected their roles in information flow for the colony. Foragers had the highest interaction

556   strength mode – they interacted more frequently than cleaners and nurses. Cleaners,

557   however, had higher betweenness and thus were key connections between ants

558   interacting in the colony.

559   Ants that switched tasks functioned as key connectors for information flow in the

560   colony, supporting colony cohesion. In general, mean betweenness was higher for ants

561   that switched than for ants that remained consistent in their task, although confidence

562   intervals overlapped. Bridge betweenness (which indicated how ants connected different

563   communities within the colony) was significantly higher for ants that switched. This

564   suggests that ants who switched tasks throughout the course of the experiment, and

565   particularly foragers, played an important role in connecting functional groups through

27

566 information flows. Their high bridge betweenness means that they occupied a key

567 network position for receiving and transmitting information before they switched tasks. If

568 learning is required when ants switch tasks, this increased access to information may

569 have allowed them to learn new behaviours more quickly, helping them transition to a

570 new task. In general, cleaners were less likely to interact within their functional group

571 (which was consistent with Mersch et al.'s 2013 results). The low group cohesion of

572 cleaners may strengthen colony-wide cohesion.

573 The variability of the centrality metrics may be related to cleaners' and foragers'

574 ability to transition tasks. Cleaners and foragers who switched functional groups had

575 significantly higher variances of betweenness and bridge betweenness within networks.

576 Across networks and over time, these variances also had a larger range, showing that

577 these individual measures of social network connectivity changed more and were overall

578 less consistent among individuals. However, when all ants in a colony were grouped for

579 calculating the node-level network metrics, pooled variances were not higher than those

580 for the reference networks and had small confidence intervals. So, while these metrics

581 varied significantly among functional groups and when ants switched tasks, overall

582 information flow in a colony remained fairly stable and colony cohesion was maintained.

583 At the group level, the operationalisation of Effective Information as a measure of the

584 noisiness of network mechanisms is relatively new and under-explored. Our results for

585 the six *Camponotus fellah* colonies show a correlation between variations in Effectiveness

586 and the functional group composition of each colony. We found that a higher proportion

587 of foragers led to noisier potential communication among ants. Paired with the results on

588 interaction strength, this means that foragers interacted more frequently than ants

589 performing other tasks and that they had more diverse interactions with ants at different

590 positions in the interaction network. Results on centrality measures and Effectiveness

591 can be linked with task allocation through our task interaction matrix. The matrix shows

592 how previous interactions with ants in a given task are associated with a higher probability

593 of the ant switching to that task. These results are consistent with previous work in another

594 species: Gordon and Mehdiabadi (1999) found that, in red harvester ants, ants switching

595 from other tasks to midden work were more likely to have interacted with midden workers,

596 and that switching was more likely to occur the more frequent those interactions. In our

597 results, interactions with foragers were correlated with switches to foraging: both cleaners

598 and nurses who switched to foraging had a higher probability of interacting with foragers.

599 Switches from foragers to other tasks, however, showed different dynamics. Both

600 foragers who switched to nursing and foragers who switched to cleaning had a higher

601 probability of interacting with cleaners. These results should be interpreted with some

602 caution because ants switching from foragers to nursing was only observed three times

603 (the interaction frequency data, however, was sufficient for the chi-square comparison).

604 Consistent with betweenness results, these switching results show that cleaners were

605 central in driving switching patterns by occupying key positions for information flow in the

606 networks. These patterns suggest that, while previous interaction patterns were

607 correlated to switching behaviour, the degree of correlation varied depending on the role

608 played by the interacting ants and on the overall information flow of the system. It is

609 important to note that without more detailed data we cannot determine whether a change

610 in task or change in interactions happened first, but these insights provide valuable

611 information about system dynamics and suggestions for future experiments.

29

612   In future research, it would be interesting to further explore task switching in systems

613   with a higher granularity of data collection across both behaviours and interactions. One

614   limitation to the current analysis is that the task each ant was assigned to is assessed

615   based on the interaction patterns, not the types of actions or tasks the ant completes in

616   the colony. Even though interaction community membership was paired with behavioural

617   observations by Mersch et al. (2013), it may not have been at the level of detail needed

618   to assess fine-grain interaction patterns and task performance. It would be interesting to

619   use the combination of network methods and behavioural observations to further explore

620   existing results on the relationship between repetition (Langridge et al., 2004) and the

621   existence of experienced individuals (Langridge et al., 2007) on task performance.

622   Assessing not just who an ant interacts with, but what actions that ant is actually

623   completing, would provide useful additional insight into the timing of behavioural and

624   social change. This kind of data would allow researchers to determine whether an ant

625   alters its behaviours first (for example, decreasing cleaning behaviours and increasing

626   nursing behaviours) which then results in a change in the social interaction patterns, or

627   whether an ant first begins to change its social interaction patterns (for example,

628   interacting less with other cleaners and more with nurses) and then alters its behaviour

629   from cleaning actions to nursing actions. Future targeted data collection, involving both

630   social and behavioural observations, paired with statistically robust network methods,

631   could be used to further explore the relationships between patterns of interactions,

632   individual-level behaviour, and group-level behaviour.

633

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640

641   *Author contributions***:** All the authors conceived the idea and the methodology together;

642   AS and SW did the analysis, and all the authors wrote the manuscript.

643

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

645

646   *Data availability:* All scripts and data used in this project are available at

647   https://github.com/anshuman21111/ant-colony-networks. A reformatted version of the

648   Mersch et al. (2013) dataset can be found as Supplementary material 1.

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