

# 1 **Synchronised brood transport by ants occurs without** 2 **communication**

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13

## 14 **Abstract**

15 **Collective behaviours in societies such as those formed by ants are thought to be**  
16 **the result of distributed mechanisms of information processing and direct**  
17 **decision-making by well-informed individuals, but their relative importance**  
18 **remains unclear. Here we tracked all ants and brood movements to investigate**  
19 **the decision strategy underlying brood transport in nests of the ant *Camponotus***  
20 ***fellah*. Changes in environmental conditions induced workers to quickly**  
21 **transport the brood to a preferred location. Only a minority of the workers,**  
22 **mainly nurses, participated in this task. Using a large number of statistical tests**  
23 **we could further show that these transporters omitted to recruit help, and relied**  
24 **only on private information rather than information obtained from other**  
25 **workers. This reveals that synchronised group behaviour, often suggestive of**  
26 **coordinated actions among workers, can also occur in the complete absence of**  
27 **communication.**

28

## 29 **Introduction**

30 The success of group actions frequently relies on communication between  
31 individuals. Communication is manifest in animal groups as different as jellyfish  
32 that use bioluminescence to locate each other and team up<sup>1</sup>, prairie dogs that call

33 to warn their family of predators<sup>2</sup> and honeybees that use waggle dance to signal  
34 a food source to nest mates<sup>3,4</sup>. In all these cases communication serves to  
35 enhance the efficiency and safety of the group. However, communication is  
36 complex. It requires that the sender recognizes the appropriate circumstances  
37 and produces a correct signal, and that the receivers are able to understand the  
38 signal and react appropriately. These inherent difficulties constrain when and  
39 under what conditions groups of animals might communicate.

40

41 In ant societies communication is widespread and individuals make use of an array of  
42 olfactory, vibrational and tactile communication strategies. Therefore, communication  
43 is often assumed to be underlying all group behaviours<sup>5,6,7,8,9,10</sup>. Ants optimize foraging  
44 by creating pheromone trails<sup>11,12</sup>, and by recruiting help to retrieve food through  
45 tandem runs, a method whereby a knowledgeable ant induces a naive ant through  
46 tactile and chemical signals to follow it<sup>13</sup>. In emergencies, ants release highly volatile  
47 alarm pheromones<sup>11</sup>. If a nest is destroyed knowledgeable ants first lead tandem runs  
48 to new nest sites before switching to brood transport<sup>14</sup>. In all these instances  
49 communication is manifest and beneficial to the society. Pheromone trails and tandem  
50 recruitment reduce the risks of random food searches and ensure that a sufficient  
51 number of workers locate and retrieve food before it disappears, thereby enhancing  
52 the colony's chances of survival and reproduction. Similarly in emergencies the  
53 survival of the colony is at stake. Alarm pheromones ensure that workers are alerted  
54 and leave the nest<sup>15</sup> for fight or flight. Tandem runs ensure that a sufficient number of  
55 workers know the location of a safe alternative nest before evacuating brood<sup>9</sup>.  
56 However, there is a range of other group behaviours such as nest construction or  
57 brood relocation where the advantages of communication are less apparent. For  
58 example, many ant species regularly move brood within a nest and between nests to  
59 raise offspring under optimal temperature and humidity<sup>16,17,18,19,20</sup>. Such controlled  
60 responses to environmental variables are a central part of colony organisation in social  
61 insects because they have direct impacts on colony growth, metabolic expenditure,  
62 survival and reproduction<sup>19,20,21</sup>.

63

64 In this study we conduct a detailed analysis of brood transport in the ant *Camponotus*  
65 *fellah* to investigate to what extent workers communicate to displace the brood after

66 changes in environmental conditions. We took advantage of the fortuitous observation  
67 that workers moved the brood in response to environmental changes in three colonies  
68 (colony size=197, 192, and 206 workers, brood items=150, 60 and 35) to investigate  
69 whether workers communicate about observed changes in local conditions. In *C.*  
70 *fellah*, as in most other ants, workers quickly respond to environmental changes to  
71 move the brood to the nest regions with the best conditions<sup>22, 23, 24, 25</sup>.

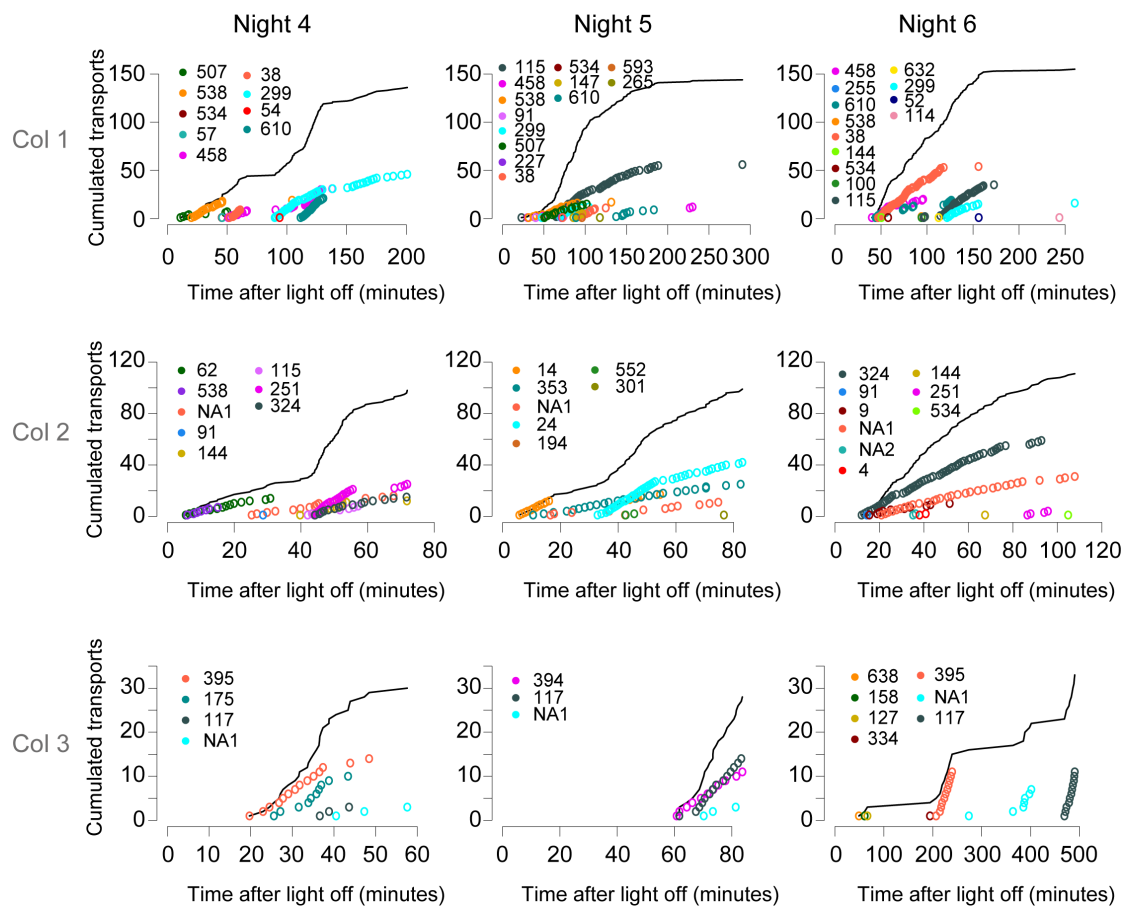
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## 73 Results

### 74 Colonies transport brood in synchrony

75 In each of the three colonies, and each of the nights, workers responded to the  
76 environmental change, initiating brood transport  $22.4 \pm 6.2$  minutes (mean $\pm$ SEM) after  
77 the light was turned off in the tunnel (Fig. 1). There were neither consistent  
78 differences across colonies, nor a change in the response delay over the three days  
79 (ANCOVA, colony:  $F=0.9$ ,  $p=0.37$ ; day:  $F=0.77$ ,  $p=0.41$ ; interaction colony\*day:  
80  $F=0.41$ ,  $p=0.69$ ). On average workers took  $160.0 \pm 48.0$  minutes to move all the brood  
81 from the nest to the tunnel once transport was initiated. Workers also performed this  
82 task in synchrony with multiple workers transporting in parallel during  $66.1 \pm 28.0\%$  of  
83 the time. The average time taken by a worker to transport one brood item was  
84  $36.7 \pm 4.0$  seconds (see Supplementary Video 1). Workers that transported more brood  
85 items were faster to transport brood than those transporting fewer brood items  
86 (Spearman rank correlation:  $\rho=-0.51$ ,  $p<0.0001$ ; Supplementary Fig. 2). There were  
87 again neither significant differences across colonies, nor over days, in the time  
88 required to transport all the brood (ANCOVA on log-transformed duration: colony:  
89  $F=1.5$ ,  $p=0.31$ ; day:  $F=1.3$ ,  $p=0.24$ ; colony\*day:  $F=1.2$ ,  $p=0.40$ ).

90



91

92 **Fig 1. Brood transport dynamics on three consecutive days in three colonies.** The black  
 93 line indicates the cumulated number of brood transports to the tunnel of all workers. Each  
 94 coloured circle represents a single brood transport event by one worker, and data are shown as  
 95 cumulative transports. Different colours represent different workers.

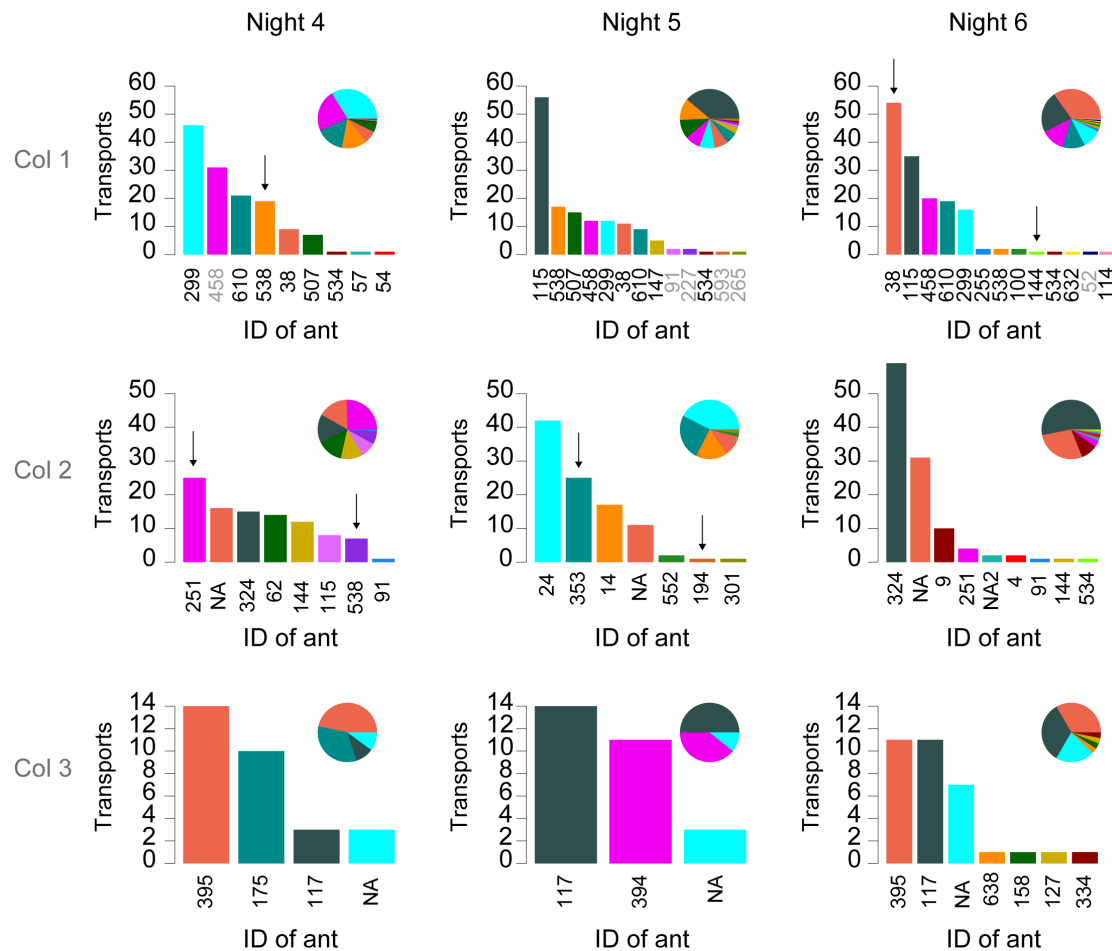
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### 97 *A small minority of a colony's workforce transports brood*

98 The number of workers involved in brood transport was consistently low, with only  
 99  $8.1 \pm 1.1$  workers ( $4.1\% \pm 0.6\%$  of the workforce) participating in brood transport on  
 100 any given day in any given colony (Fig. 2). Colonies did not differ in the distribution  
 101 of the workload among workers, and there was no significant change over days in the  
 102 way the workload was distributed among transporters (ANCOVA: colony:  $F=0.40$   
 103  $p=0.67$ ; day:  $F=0.15$   $p=0.86$ ; colony\*day:  $F=0.14$ ,  $p=0.97$ ). However, there was  
 104 variation among transporters in their relative contribution with the notable effect that  
 105 more than 80% of all brood transports were performed by less than 1.8% of all  
 106 workers. In addition, there was also a high worker turnover with  $66.9 \pm 5.2\%$  of the  
 107 transporters working on a single night, while only  $18.8 \pm 11.9\%$  of the transporters  
 108 worked on all three nights. Importantly, however, the persistent transporters were  
 109 responsible for  $44.3 \pm 25.3\%$  of all transports while those that worked a single night

110 contributed together to  $24.8 \pm 18.7\%$  of the transports.

111



112 Color ranking based on total transports : most  fewest

112

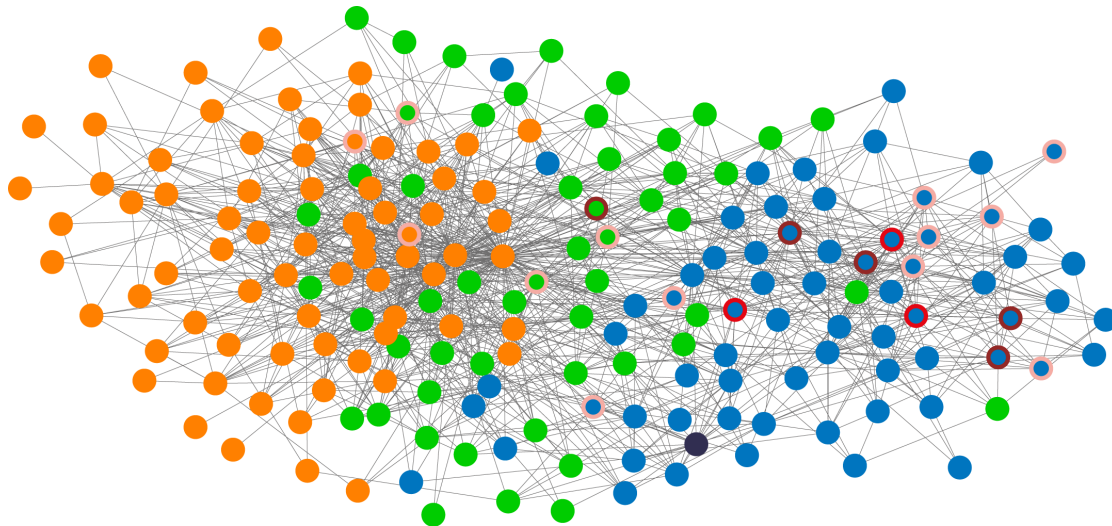
113 **Fig 2. The workload is distributed unevenly among the transporters.** Absolute numbers  
 114 are given in the histogram, and proportions are indicated in the pie chart. Arrows indicate  
 115 workers that transport without being privately informed (i.e. they had not visited the tunnel  
 116 before starting to transport). Transporters with ID labels in black are nurses, while those with  
 117 labels in grey belong to the cleaner or forager groups.

118

### 119 *Transporters are nurses*

120 To determine whether brood transport was preferentially conducted by a specific  
 121 group of workers, we used the Infomap algorithm<sup>26</sup> to determine the daily interaction  
 122 networks of workers and assign each of them to a specific social group<sup>27</sup>. Colonies  
 123 had on average  $55.9\% \pm 11.3\%$  nurses,  $16.5\% \pm 4.9\%$  cleaners and  $25.1\% \pm 7.4\%$   
 124 foragers (Fig. 3). Nurses were 3.8 times more likely to transport than cleaners, and 7.3  
 125 more likely to transport than foragers (ANOVA,  $F=51.38$ ,  $p<0.0002$ ). There was also  
 126 an effect of age, with transporters being on average younger (83.5 days) than non-

127 transporters (119.5 days; Kruskal-Wallis:  $\chi^2=12.1$ ,  $p<0.001$ ). This effect was due to  
128 age differences between the three groups of workers (average age nurses 93.8 days,  
129 cleaners 124.2 days, foragers, 159.4 days; Kruskal-Wallis:  $\chi^2=138.6$ ,  $p<0.00001$ ).  
130 When only nurses were considered, there was no significant age difference between  
131 transporters and non-transporters (Kruskal-Wallis:  $\chi^2=0.81$ ,  $p=0.37$ ; insufficient data  
132 was available to conduct similar tests for nest cleaners and foragers).  
133



134  
135 **Fig 3. Transporters are mainly nurses.** The network shown is that of colony 10 on day 4.  
136 Each node represents a worker, and links between nodes are shown for workers who had more  
137 than 10 interactions on that day. The network layout is a spring embedded layout. Group  
138 membership is indicated by the node colour: nurse (blue), cleaner (green), forager (orange).  
139 Red-shaded circles around nodes highlight transporters, with light red indicating transports on  
140 one day, medium red indicating transports on two days, and dark red indicating transports on  
141 three days.  
142

### 143 *Transporters gather information themselves*

144 To determine whether workers make use of information available to others to decide  
145 when to initiate brood transport, we tracked the information available to each worker  
146 after the light was turned off. Because the nest entrance was constructed with two 90°  
147 bends and painted in matt black on the inside thereby preventing light from entering  
148 the nest, the only means for workers to know whether there was light in the tunnel  
149 was to access it. Workers were therefore considered as having private information  
150 once they had left the nest for at least three seconds, which is the minimum amount of  
151 time an ant needs to reach the tunnel and return to the nest. Ants were considered as  
152 socially informed once they interacted with a privately informed worker.

153

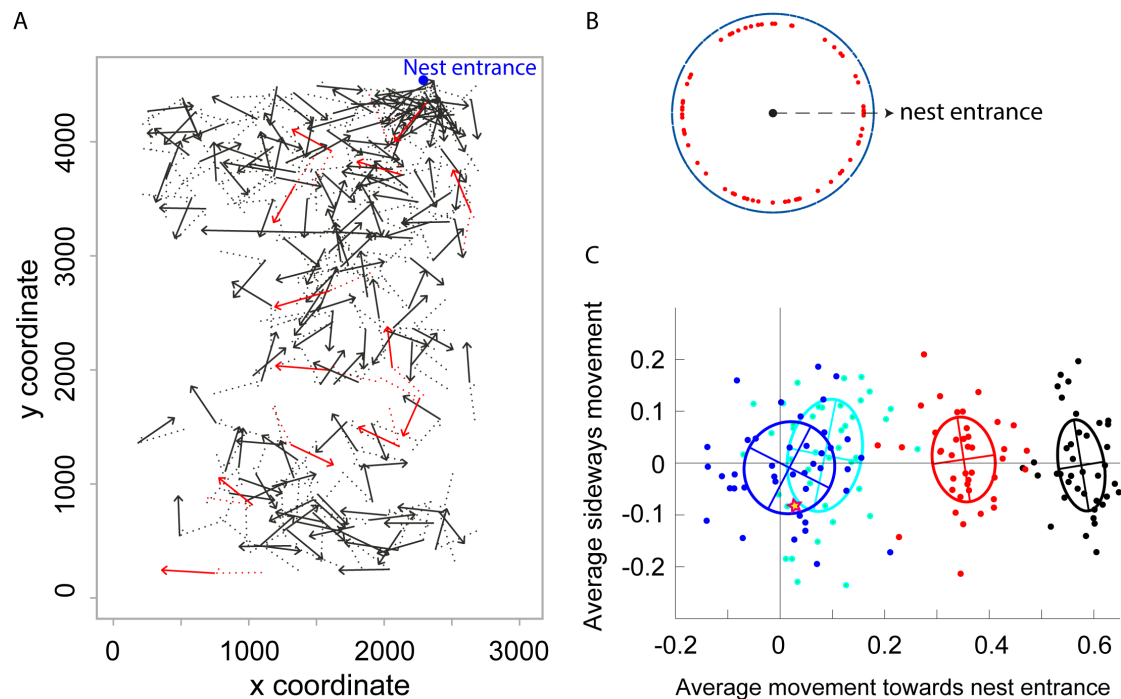
154 At the start of brood transport, only  $31.6\% \pm 2.9\%$  of all workers and  $37.8\% \pm 8.7\%$  of  
155 the nurses had private information. However, almost all transports (99.8%) were  
156 performed by privately informed ants. Of the seven workers, which had not visited the  
157 tunnel before initiating brood transport, four had transported brood on previous days  
158 (Fig. 2). The three remaining workers had visited the tunnel the nights before when it  
159 contained brood. Thus, these transporters may have used this information together  
160 with circadian timing to initiate transport<sup>24,25</sup>. Therefore, these observations suggest  
161 that private information is the primary or only source of information workers use to  
162 decide when and where to transport the brood.

163

#### 164 *Transporters neither communicate nor recruit help*

165 Five lines of evidence further support the view that workers do not use information  
166 obtained from other workers to initiate brood transport. First, transporters did not  
167 increase their interaction frequency with other workers once it was dark in the tunnel.  
168 The rate of interactions in the hour preceding light-off was not significantly different  
169 from the rate during the interval between light-off and the first brood transport  
170 (Kruskal-Wallis:  $\chi^2=0.05$ ,  $p=0.82$ ; Supplementary Fig. 3). Second, transporters did not  
171 change their activity after interacting with a privately informed ant. Their increase in  
172 speed — a signature of information transfer in ants<sup>28</sup> — was similar after interacting  
173 with a privately informed or an uninformed ant (Kruskal-Wallis:  $\chi^2=2.8$ ,  $p=0.09$ , see  
174 Supplementary Table 1). Third, brood accumulating in the tunnel did not speed up the  
175 recruitment of additional transporters. The average time elapsed before one additional  
176 worker contributed to brood transport was  $16.6 \pm 3.4$  min. The number of workers  
177 already participating in brood transport did not alter the time needed to rally an  
178 additional worker (Spearman rank correlation:  $\rho=0.06$ ,  $p=0.60$ ; Supplementary Fig.  
179 4). Fourth, the first interaction with a privately informed ant did not trigger a change  
180 in behaviour. After interacting with a privately informed ant, transporters and non-  
181 transporters were neither more likely to approach the nest entrance (Wilcoxon signed  
182 rank test: transporters:  $V=1232$ ,  $p=0.79$ ; non-transporters:  $V=495789$ ,  $p=0.97$ ) nor to  
183 orient towards it (Rao's spacing test for uniformity: transporters: Test  
184 Statistic=139.98,  $p>0.05$  with a critical value=148.34; for non-transporters: Test  
185 Statistic=134.13,  $p>0.05$  with a critical value=136.94; Fig. 4A, 4B). Simulations were  
186 conducted to determine the expected effect if 90%, 50%, 10% or 0% of the

187 transporters were able to understand a message that they should go to the tunnel after  
188 interacting with a privately informed ant (Fig 4C). These simulations revealed that the  
189 observed pattern was consistent with a complete lack of communication between  
190 privately informed ants and non-informed transporters. Finally, and most importantly  
191 we did not observe any successful recruitment through tandem running although these  
192 ants are capable of tandem running (see Supplementary Videos 2, 3).  
193



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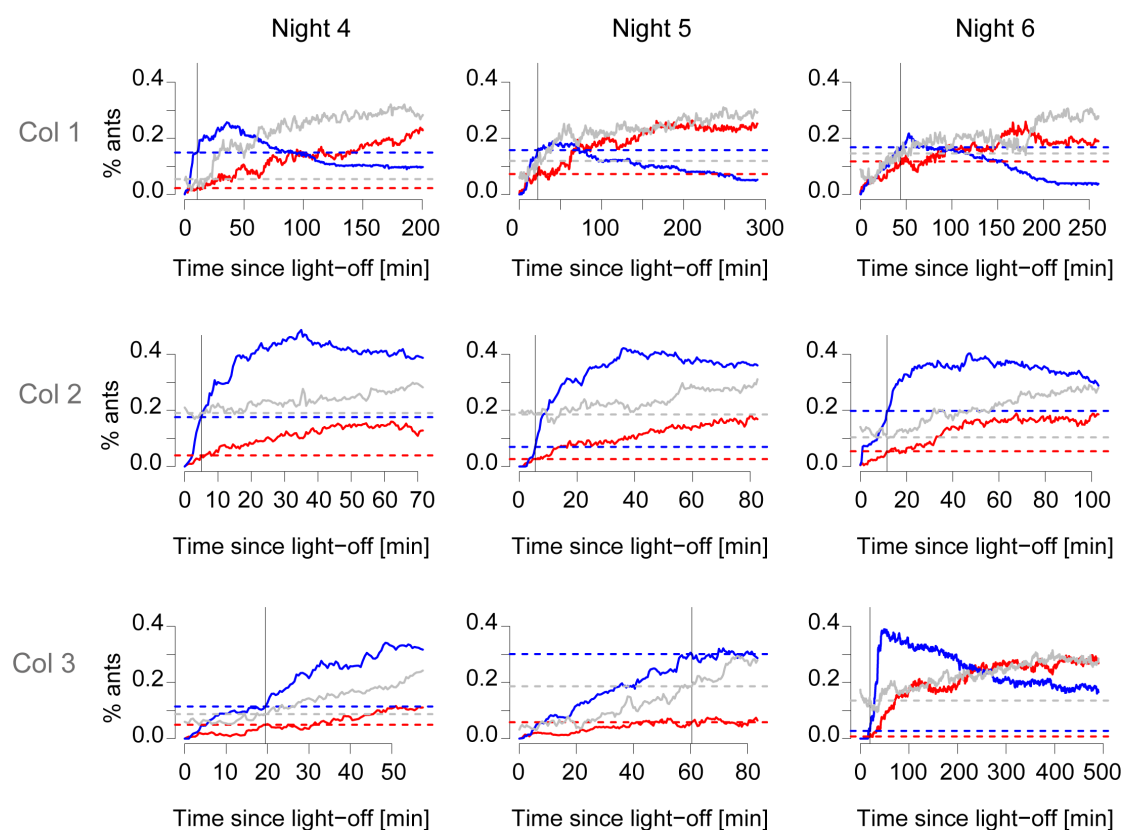
195 **Fig 4. No evidence for communication between workers.** (A) Changes of trajectory  
196 following the first interaction with a privately informed ant. Arrows indicate the trajectories  
197 after the first interaction with a privately informed ant and the dotted lines the trajectories just  
198 before this interaction. Transporter trajectories are in red and those of other ants in black. The  
199 blue circle indicates the nest entrance. Data shown are those of colony 1 on day 5.  
200 (B) Distribution of directions after the first interaction with a privately informed ant. Each dot  
201 represents the direction relative to the nest entrance of a single worker on a given day. Red  
202 dots indicate transporters and blue dots (forming a ring) indicate other ants. The arrow  
203 indicates the direction of the nest entrance. (C) Expected change in direction from simulated  
204 data in which 0% (blue), 10% (cyan), 50% (red) or 90% (black) of the ants understood a  
205 message. Each dot is the average movement towards the nest entrance of 66 simulated  
206 transporters. The cross and ellipse show the average and the standard deviation across 40  
207 simulations with the same set of parameters. The star shows the average of the observed data.  
208

### 209 *Colonies do not use quorum sensing to initiate brood transport*

210 At the colony level there was also no indication of a system of quorum sensing  
211 leading to the onset of brood transport. At the time of first transport, the percentage of  
212 privately and socially informed workers and the percentage of workers in the tunnel



213 varied greatly (privately informed: 0.6% to 12.0%; socially informed: 1.9% to 47.5%,  
214 ants in tunnel: 6.0% to 19.4%; Fig. 5). Furthermore, the use of a quorum would imply  
215 that colonies deferred the onset of brood transport on some days for almost one hour  
216 after reaching the quorum, while starting to transport just minutes after reaching the  
217 quorum on other days (delays for privately informed: 4.3–59.8 minutes; socially  
218 informed: 2.8–58.8 minutes; ants in tunnel: 5.4–59.1 minutes). Given that the  
219 variability was large for both the quorum threshold and the delay until transport onset,  
220 it seems unlikely that a minimum colony level information threshold or a minimum  
221 ant proportion in the tunnel needs to be reached for brood transport to be initiated.  
222



223  
224 **Fig 5. No evidence for a quorum threshold triggering brood transport.** Each line shows  
225 the percentage of ants: privately informed ants in red, socially informed ants in blue, ants in  
226 the tunnel in grey. The vertical line indicates when the first transport occurred, and the dashed  
227 lines highlight the percentages of ants at the time of first transport.  
228

229 Finally, our analyses also revealed high consistency in the direction of brood transport  
230 (Supplementary Fig. 5). Overall, there were only 20 return-transports (2.3%) among  
231 the 859 transports recorded. Interestingly, the majority of the workers (69.2%)  
232 performing return transports did not transport brood to the tunnel while the vast  
233 majority (91.7%) of the workers transporting brood to the tunnel did not perform

234 return-transporters.

235

## 236 Discussion

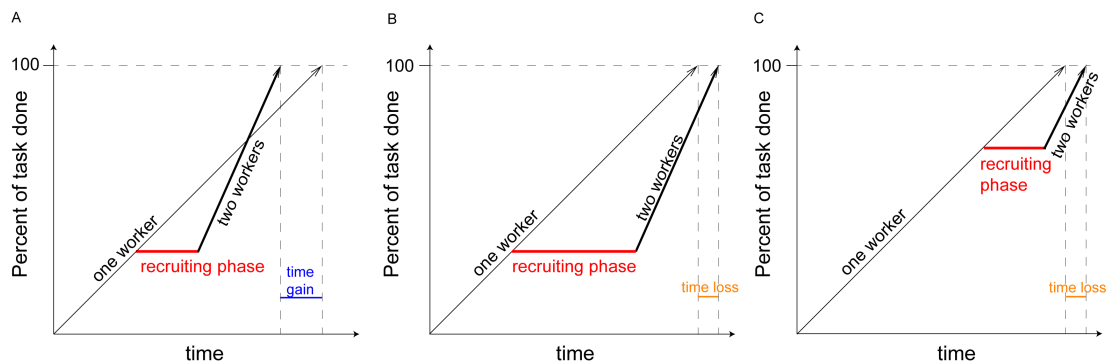
237 The use of an automated system allowed us to obtain detailed and individual-level  
238 information on the processes regulating brood transport in response to environmental  
239 changes, a process central to the organization of social insect colonies. Overall,  
240 workers quickly transported the brood to the preferable location after the light was  
241 turned off, and workers almost never transported brood in the wrong direction.  
242 However, this seemingly coordinated transport occurred without any detectable sign  
243 of communication among workers. While workers frequently interacted, these  
244 interactions resulted in no visible change in the behaviour of the transporters, even if  
245 the interaction partner had knowledge about the tunnel being dark. Instead,  
246 transporters appeared to rely exclusively on self-gathered information, because they  
247 initiated brood transport only after having noticed the change of state of the tunnel  
248 themselves. Together, these data indicate that synchronised behaviour at the colony  
249 level can occur without communication.

250

251 Visual inspections of our videos also revealed no evidence that workers relied on  
252 chemical signals to initiate and communicate brood transport. Transporters never  
253 dragged their gaster over the ground, as ants typically do when depositing trails. There  
254 were also no instances of worker tandem running, thereby excluding targeted  
255 recruitment that could have been mediated by secretions from a gland<sup>13</sup>. The only  
256 targeted recruitment that we observed was that of the queen and in one instance that of  
257 non-transporting workers (see Supplementary Videos 2, 3). In these cases a worker  
258 approached the head of the queen or worker and pulled on her mandibles, with the  
259 effect that the pulled ant became active and followed the worker in a tandem-run to  
260 the tunnel.

261 The observed lack of communication is likely due to the inherent difficulty of reliably  
262 communicating a message in a noisy environment. Communication requires that an  
263 informed individual intentionally encodes a message, transmits it successfully, and  
264 that an uninformed individual is able to receive it, decode it, and act upon it<sup>29</sup>. Ants  
265 have a limited ability to convey a message through tactile communication alone<sup>28,30,31</sup>.

266 In addition, the density of workers is extremely high in the nest, resulting in numerous  
267 interactions not only with informed individuals but also with uninformed ones. Such a  
268 situation leads to a very noisy system where conflicting feedbacks may readily  
269 compromise any attempts of communication. Moreover, investing time in recruiting a  
270 helper would only be beneficial if the time needed for successful recruitment is short,  
271 and if recruitment occurs early on (see Figure 6).



272

273 **Figure 6. Cost and benefit of successful recruitment.** The time invested in recruiting help is  
274 indicated in red. The time gained from recruiting a helper is shown in blue, and the time lost  
275 due to recruiting help in orange. (A) Recruiting a helper early on after the task is initiated and  
276 with little time investment enables faster completion of the brood transport than without a  
277 helper. (B) Recruiting a helper early on but with high time investment delays the completion  
278 of the brood transport compared to a situation without a helper. (C) Recruiting a helper later  
279 while the task is performed also delays the completion of the brood transport compared to a  
280 situation without a helper.

281

282 Our observation that transporters check the state of the tunnel themselves, before  
283 starting to transport brood, suggests that individual workers gather cues from the  
284 environment before deciding to transport brood. The most likely cues used by the  
285 transporters in our experiments are the confinement, absence of light and presence of  
286 workers in the tunnel<sup>32,33</sup>. The use of cues for decision-making also occurs in other  
287 ants, and for processes unrelated to brood transport. For instance, in harvester ants,  
288 potential foragers decide whether or not to initiate a foraging trip based on the  
289 frequency with which they meet returning foragers<sup>34,35</sup>. Workers of the black garden  
290 ant *Lasius niger* use the chemical profile of the nest wall and their own body size  
291 compared to the height of nest pillars as cues to decide whether to switch from wall  
292 building to building a roof<sup>36</sup>. These data, together with our results, suggest that the use  
293 of cues as a mean to obtain private information might be more widespread and easier  
294 to implement in ant colonies than information exchange through tactile

295 communication.

296 The use of cues combined with the lack of communication and the absence of a  
297 quorum means that transporters most likely decide independently of each other  
298 whether, when and where to transport the brood. Such individual-led decisions are  
299 further supported by rare instances in which a worker mistakenly returned brood from  
300 the tunnel to the nest, while transporters were already moving brood to the tunnel.  
301 Interestingly, the vast majority of transporters arrived at the same decision and  
302 transported brood from the nest to the tunnel. This strong uniformity in behaviour  
303 suggests that there is high homogeneity in preferences among group members.

304 Our results indicate that colonies can display synchronized behaviour without  
305 communicating thus emphasizing that not all group-level behaviours in social insects  
306 are driven by communication. We suspect that communication is context-dependant  
307 and only used when cue-based options are insufficient. For instance, the  
308 communication that precedes brood transport in house-hunting ants occurs in the  
309 context of an emergency after their nest has been destroyed<sup>9,14</sup>. In contrast,  
310 synchronization without communication is optimal when reliable communication is  
311 expensive, hard to achieve, or when perfect synchrony is not needed<sup>29,37</sup>. It can be  
312 achieved if workers share similar preferences and react to the same cues, which are  
313 limited in time. In our experiments light in the tunnel acted as this strong time-limited  
314 cue. Synchronized group behaviour exists also in solitary bees, who congregate at  
315 nesting sites for reproduction<sup>38</sup>, bats and starlings that converge at seasonal feeding  
316 and sleeping spots<sup>39,40</sup> and Mormon crickets, who migrate in masses in search for salt  
317 and proteins<sup>41</sup>. In ants simulations further suggest that food choice during foraging  
318 could be achieved without communication through individual learning and  
319 preference<sup>42</sup>.

320

321 Our results also revealed that only a tiny fraction of the individuals, 1.5%–6.6% of the  
322 colonies' workforce —as few as three workers in some cases— contributed to brood  
323 transport. Moreover, within colonies there was strong variation in the relative  
324 contribution of workers with more than 80% of all transports being carried out by less  
325 than 1.8% of the workers. Similar fractions of transporters and workload disparities  
326 were observed in colony emigrations of *Formica sanguinea* and *Camponotus*

327 *sericeus*<sup>43</sup>. The large variability in behaviour is puzzling and we offer two possible  
328 explanations. There could be specialist nurses that focus on brood transport. Indeed  
329 nine out of 48 transporters moved brood every single night and did slightly less than  
330 half of the work, thus acting as key individuals<sup>44</sup> during the brood displacement.  
331 Similar specialization has been reported for foraging, brood care, stone  
332 collection<sup>45,46,47</sup> and could result from inherent and consistent differences between  
333 workers, for example in motivation, physiology, or sensory threshold<sup>48,49</sup>. Another  
334 explanation is that transporters represent a varying subset of the nurses, whose  
335 likelihood to transport depends on the individual's state in the early night. This idea is  
336 supported by the observation that two thirds of the transporters only worked a single  
337 night.

338 Importantly, a small minority of transporters imposed their transport decision on the  
339 colony. Such an outcome was only possible because the other workers did not oppose  
340 the brood transports or if they did so initially, never persisted in their opposition.  
341 Minority-driven behaviour occurs also in *Paratrechina longicornis* ants, where a  
342 single worker can temporarily decide the pull direction during collective transport<sup>50</sup>.  
343 Our results therefore highlight that a small minority of the workforce can determine  
344 the colony fate through persistent activity in a largely indifferent society. Similar  
345 observations exist for fish schools and human crowds where few knowledgeable  
346 individuals can lead large groups of uninformed individuals to a new location<sup>51,52</sup>.  
347 Ultimately, the social unresponsiveness of the majority might be the optimal strategy  
348 because social unresponsiveness can ensure that the colonies react to environmental  
349 change while also being robust to noise and avoiding losses in information accuracy  
350 resulting from an over-reliance on social information<sup>53</sup>.

351

352 **Acknowledgements.** We thank M. Chapuisat, O. Feinerman, N. Stroeymeyt, T.  
353 Richardson, T. Kay and S. McGregor for comments on an earlier version, and B.  
354 Sutcliffe for proofreading. DPM was supported by a grant from HFSP, JPE was  
355 supported by an advanced ERC grant, LK was supported by grants from the Swiss  
356 NSF and an advanced ERC grant.

357

358 **Contribution.** DPM and LK planned the experiment. DPM and AC designed the  
359 experimental system and performed the experiment. DPM and JPE analysed and  
360 interpreted the data. DPM wrote the paper with input from JPE and LK. All authors  
361 revised the paper.

## 362 **Material and Methods**

363 The three colonies were each established from a single queen collected after a mating  
364 flight in Tel Aviv on March 23<sup>rd</sup> 2007. The experiment started when queens were 3  
365 years old, out of a maximum life span of 26 years<sup>54</sup>. At the start of the experiment,  
366 colonies each comprised a queen, brood and 197, 192 and 206 workers, for colonies 1,  
367 2 and 3 respectively. The colony sizes were those naturally reached by queens of that  
368 age, and reflect normal growth rates in the laboratory; no data are available for field  
369 colonies. All workers were the offspring of a single queen, which in *Camponotus*  
370 *fellah* is usually singly-mated<sup>55</sup>.

371 To determine workers' age, new-born workers were paint-marked on a weekly basis  
372 during the 12 months preceding the experiment. Because 38 out of the 45 transporters  
373 were nurses, we limited the analysis on the effect of age to nurses only.

374

375 During experiments colonies were kept in a dark nest chamber connected by a 60 cm  
376 long and 1cm wide tunnel to a foraging chamber. The tunnel and the foraging box had  
377 12h light-12h dark cycles, and the ants had access to food (gelatinous sugary water)  
378 and water in the foraging box. The temperature (30 °C), humidity (60%), light  
379 (~500 Lux), and food supply were computer-controlled, and both chambers were  
380 filmed from above with high-resolution monochrome cameras operating under  
381 infrared light, as previously described<sup>27</sup> (Supplementary Fig. 1). All colony members  
382 were video-tracked using fiducial identification labels over 14 consecutive days. We  
383 recorded the position and orientation of all individuals twice per second.

384

385 During the night, workers transported the brood to the tunnel and brought it back to  
386 the nest at dawn, presumably because they prefer to keep the brood in a confined  
387 environment rather than an open environment when both are dark. We tracked the  
388 transport of brood items manually during three consecutive nights. A brood transport

389 was defined as the time interval from when an ant collected one (or several) brood  
390 items from the nest box, to when the ant disappeared with it into the tunnel. We also  
391 recorded cases where brood was transported from the tunnel to the nest. In these  
392 return-transport, the transport was defined as the time interval from when the ant  
393 entered the nest with brood until the ant dropped the brood. For each transporter and  
394 each night we defined its workload as the number of transports during that night and  
395 its work time as the time from the start of its first transport until the end of its last  
396 transport. Using the work times of all workers, we estimated synchrony as the  
397 percentage of time during which at least two workers worked in parallel. We also  
398 visually inspected the videos for instances of tandem running, that is events where one  
399 ant guides another ant to the tunnel. A tandem-run results in successful recruitment if  
400 the follower ant subsequently starts transporting brood. We did not track brood  
401 transports in the mornings when the lights turned on in the tunnel, because in these  
402 conditions all ants in the tunnel were immediately informed of the environmental  
403 change, thus making the question of communication inane.

404

405 To determine group membership of each worker, *i.e.* nurse, cleaner or forager, we  
406 used the same approach as in Mersch *et al.* (2013)<sup>27</sup>. In brief, we inferred all social  
407 interactions between workers based on their distance and orientation, and analysed the  
408 social networks with the Infomap algorithm<sup>26</sup> to assign each worker to a group.  
409 Because the majority of workers were in the tunnel at night and thus undetectable  
410 with our tracking setup, we built daily interaction networks using only data collected  
411 between 8am and 7pm, when the majority of workers were detectable.

412

413 To measure the speed change following interactions, we calculated the speed during  
414 the 10 seconds prior to the interaction and during the 10 seconds after the interaction.  
415 We included only those interactions for which we had data on the speed before the  
416 interaction for both partners and on the speed after the interaction for the focal ant. As  
417 a consequence, 50 interactions (10.2%) were excluded from the analysis. Excluding  
418 these interactions had neither an impact on the average duration of an interaction  
419 ( $10.5 \pm 29.9$  s *vs.*  $10.3 \pm 30.5$  s) nor on the proportion of interactions with privately  
420 informed partners (7.72% *vs.* 7.69%). To further ensure that our results are not  
421 influenced by the chosen interval (10 s), we repeated the same analyses for shorter

422 (5 s) and longer (20 s) time intervals. Because the results were the same for all time  
423 intervals (see Supplementary Table 1), we only report data for the 10-second interval.

424

425 To investigate whether a privately informed ant can communicate information about  
426 the change of state in the tunnel to its interaction partner we estimated the change in  
427 trajectory of each worker following its first interaction with a privately informed ant.  
428 We calculated the heading of the ant's trajectory after it had moved away from the  
429 interaction point, transforming data of all colonies so that an orientation of  $0^\circ$   
430 corresponds to an orientation towards the nest entrance. We also calculated the  
431 distance to the entrance at the time of the interaction and after the ant had moved at  
432 least 2 cm ( $\approx$  queen body length) away from the interaction point. Workers who did  
433 not interact with a privately informed ant before the end of the brood transport were  
434 not included in the analysis (351 out of 1785 ant-days excluded).

435

436 To estimate how communication about the change of state in the tunnel could modify  
437 the trajectory of workers, we generated simulated datasets in which 0%, 10%, 50% or  
438 90% of the transporters moved toward the nest entrance after interacting with a  
439 privately informed ant. Understanding the message meant that one bit —that is, one  
440 unit of information— was transferred from the privately informed ant to the  
441 transporter. Such one-bit information could convey two options —towards and away  
442 from nest entrance— and signal to the transporter to move towards the nest entrance.  
443 Each dataset was the average of 66 simulated direction vectors  $v_j$  defined as

444  $v_j = (\cos(\alpha_j), \sin(\alpha_j))$

445 with  $\alpha_j$  being the angle of the direction relative to the line connecting the interaction  
446 point with the nest entrance. For each informed transporter, we randomly chose a  
447 direction from a uniform distribution limited to angles between  $-\pi/2$  and  $\pi/2$ , for all  
448 other transporters we randomly chose an angle from a uniform distribution between  $-\pi$   
449 and  $\pi$ . We repeated this process 40 times for each information level. We also  
450 calculated the average direction of the 66 transporters from the observed data.

451

452 To test whether a quorum triggered the observed brood transport, we determined the  
453 number of ants, the number of informed ants, and the number of ants in the tunnel at



454 the time of the first brood transport. To estimate whether the quorum induced brood  
455 transport, we also calculated the duration between the time the quorum was reached  
456 for the first time and the first brood transport. Because the estimated quorum varied  
457 between colonies and days, we calculated the delays for all colonies and days using  
458 the smallest estimated quorum threshold.

459 We performed all statistical analysis in R (Version 3.4.0)<sup>56</sup>. When the test assumptions  
460 were met, we used two-tailed parametric tests and included the colony ID as a random  
461 factor in our analysis; otherwise we used non-parametric tests. For statistical tests on  
462 colonies, each colony was one replicate. For statistical tests on individual workers,  
463 each transporter on each day was a replicate. The data analysis code will be available  
464 as a zip file.

465 The data used to prepare all figures and perform statistical tests will be available on  
466 Dryad DOI after publication in a journal.

467

## 468 **References**

469

- 470 1. Kaartvedt S, Ugland KI, Klevjer TA, Røstad A, Titelman J, Solberg I (2015)  
471 Social behaviour in mesopelagic jellyfish. *Scientific Reports* 5:11310. DOI:  
472 10.1038/srep11310
- 473 2. Kiriazis J, Slobodchikoff CN (2006) Perceptual specificity in the alarm calls  
474 of Gunnison's prairie dogs. *Behavioral Processes*. 73:29–35. DOI:  
475 10.1016/j.beproc2006.01.015
- 476 3. Rohrseitz K, Tautz J (1999) Honey bee dance communication: Waggle run  
477 direction coded in antennal contacts? *J Comp Physiol A* 184:463–470.
- 478 4. von Frisch K. *Tanzsprache und Orientierung der Bienen*. (Springer Verlag,  
479 Heidelberg 1965) 566
- 480 5. Conrad L, List C (2009) Group decisions in humans and animals: a survey.  
481 *Philosophical Transactions of the Royal Society of London B: Biological*  
482 *Sciences* 364:719–742. DOI: 10.1098/rstb.2008.0276
- 483 6. Pratt SC (2005) Quorum sensing by encounter rates in the ant *Temnothorax*  
484 *albipennis*. *Behav Ecol* 16:488–496. DOI: 10.1093/beheco/ari020

- 485 7. Conrad L, Roper TJ (2005) Group decision-making in animals. *Nature*  
486 421:155-8. DOI: 10.1038/nature01294
- 487 8. Seeley TD (2003) Consensus building during nest-site selection in honey bee  
488 swarms: the expiration of dissent. *Behav Ecol Sociobiol* 53:417. DOI:  
489 10.1007/s00265-003-0598-z
- 490 9. Franks NR, Pratt SC, Mallon EB, Britton NF, Sumpter DJT (2002)  
491 Information flow, opinion polling and collective intelligence in house-hunting  
492 social insects. *Philosophical Transactions of the Royal Society B: Biological*  
493 *Sciences* 357:1567–1583.
- 494 10. Britton NF, Franks NR, Pratt SC, Seeley TD (2002) Deciding on a new home:  
495 how do honeybees agree? *Proceedings of the Royal Society of London B:*  
496 *Biological Sciences* 269:1383–1388. DOI: 10.1098/rspb.2002.2001
- 497 11. Hölldobler B, Wilson EO, *The Ants* (Springer, Berlin, 1990).
- 498 12. Attygalle AB, Morgan ED, Berridge MJ, Treherne JE, Wigglesworth VB. Ant  
499 Trail Pheromones, in *Advances in Insect Physiology* (Academic Press 1985)
- 500 13. Möglich M, Maschwitz U, Hölldobler B (1974) Tandem calling: A new kind  
501 of signal in ant communication. *Science* 186:1046–1047. DOI:  
502 10.1126/science.186.4168.1046
- 503 14. Stroeymeyt N, Franks NR, Giurfa M (2011) Knowledgeable individuals lead  
504 collective decisions in ants. *J Exp Biol* 214:3046–3054. DOI:  
505 10.1242/jeb.059188
- 506 15. Amoore JE, Palmieri G, Wanke E, Blum MS (1969) Ant alarm pheromone  
507 activity: Correlation with molecular shape by scanning computer. *Science* 165:  
508 1266–1269. DOI: 10.1126/science.165.3899.1266
- 509 16. Kadochová S, Frouz J (2013) Thermoregulation strategies in ants in  
510 comparison to other social insects, with a focus on *Formica rufa*.  
511 *F1000Research* 2:280. DOI: 10.12688/f1000research.2-280.v2
- 512 17. Abril S, Oliveras J, Gómez C (2010) Effect of Temperature on the  
513 Development and Survival of the Argentine Ant, *Linepithema humile*. *J Insect*  
514 *Science* 10:97. DOI: 10.1673/031.010.9701
- 515 18. Fielde AM (1905) Temperature as a factor in the development of ants. With  
516 further observations on ants deprived of food. *Biological Bulletin* 9:361–367.  
517 DOI: 10.2307/1535632

- 518 19. Porter SD (1988) Impact of temperature on colony growth and developmental  
519 rates of the ant, *Solenopsis invicta*. *J Insect Physiol* 34:1127–1133
- 520 20. Porter SD, Tschinkel WR (1993) Fire ant thermal preferences: behavioral  
521 control of growth and metabolism. *Behav Ecol Sociobiol* 32:321–329.
- 522 21. Penick CA, Diamond SE, Sanders NJ, Dunn RR (2016) Beyond thermal  
523 limits: comprehensive metrics of performance identify key axes of thermal  
524 adaptation in ants. *Functional Ecology* 31:1091–1100. DOI: 10.1111/1365-  
525 2435.12818
- 526 22. Steiner A (1929) Temperaturuntersuchungen in Ameisennestern mit  
527 Erdkuppeln, im Nest von *Formica exsecta* Nyl. und in Nestern unter Steinen.  
528 *Z vergl Physiol* 9:1–66.
- 529 23. Kay CAR (1978) Preferred temperatures of desert honey ants (Hymenoptera:  
530 Formicidae). *J Thermal Biol* 3:213–217
- 531 24. Roces F, Núñez JA (1989) Brood translocation and circadian variation of  
532 temperature preference in the ant *Camponotus mus*. *Oecologia* 81:33–37. DOI:  
533 10.1007/BF00377006
- 534 25. Roces F, Núñez JA (1995) Thermal sensitivity during brood care in workers of  
535 two *Camponotus* ant species: Circadian variation and its ecological correlates.  
536 *J Insect Physiol* 41:659–669. DOI: 10.1016/0022-1910(95)00019-Q
- 537 26. Rosvall M, Bergstrom CT (2008) Maps of random walks on complex  
538 networks reveal community structure. *Proc Natl Acad Sci USA* 105:1118–  
539 1123
- 540 27. Mersch DP, Crespi A, Keller L (2013) Tracking individuals shows spatial  
541 fidelity is a key regulator of ant social organization. *Science* 340:1090–1093.  
542 DOI: 10.1126/science.1234316s
- 543 28. Razin N, Eckmann JP, Feinerman O (2013) Desert ants achieve reliable  
544 recruitment across noisy interactions. *J R Soc Interface* 10:20130079. DOI:  
545 10.1098/rsif.2013.0079
- 546 29. Maynard-Smith J, Harper D. *Animal Signals*. 1st ed. Oxford: Oxford  
547 University Press; 2003.
- 548 30. Hölldobler B (1971) Recruitment Behavior in *Camponotus socius* (Hym.  
549 Formicidae). *Z vergl Physiol* 75:123–142.

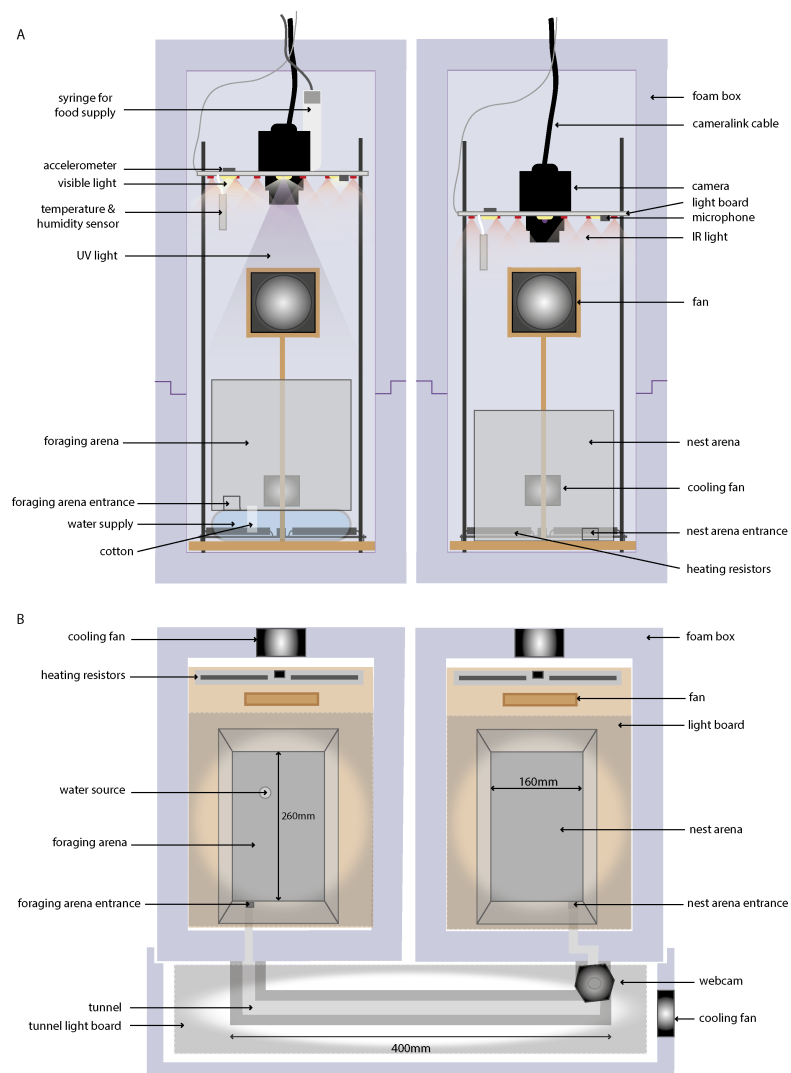
- 550 31. Traniello JFA (1977) Recruitment behavior, orientation, and the organization  
551 of foraging in the carpenter ant *Camponotus pennsylvanicus* degeer  
552 (Hymenoptera: Formicidae). Beh Ecol Soc 2:61–79. DOI:  
553 10.1007/BF00299289.
- 554 32. Franks NR, Mallon EB, Bray HE, Hamilton MJ, Mischler TC (2003)  
555 Strategies for choosing between alternatives with different attributes:  
556 exemplified by house-hunting ants. Anim Behav 65:215–223. DOI:  
557 10.1006/anbe.2002.2032.
- 558 33. Symonowicz B, Kieruzel M, Szczuka A, Korczyńska J, Wnuk A,  
559 Mazurkiewicz PJ, Chiliński M, Godzińska EJ (2005) Behavioral reversion and  
560 dark–light choice behavior in workers of the red wood ant *Formica polyctena*.  
561 J Insect Behav 28:245–256. DOI: 10.1007/s10905-015-9496-2.
- 562 34. Greene MJ, Gordon DM (2007) Interaction rate informs harvester ant task  
563 decisions. Behav Ecol 18:451–455. DOI: 10.1093/beheco/arl105.
- 564 35. Pinter-Wollman N, Bala A, Merrell A, Queirolo J, Stumpe MC, Stumpe,  
565 Holmes S, Gordon DM (2013) Harvester ants use interactions to regulate  
566 forager activation and availability. Anim Behav 86:197–207. DOI:  
567 10.1016/j.anbehav.2013.05.012.
- 568 36. Khuong A, Gautrais J, Perna A, Sbaï C, Combe M, Kuntz P, Jost C, Theraulaz  
569 G (2016) Stigmergic construction and topochemical information shape ant nest  
570 architecture. Proc Natl Acad Sci USA 113:1303–1308. DOI:  
571 10.1073/pnas.1509829113
- 572 37. Dostálková I, Špínka M (2007) Synchronization of behaviour in pairs: the role  
573 of communication and consequences in timing. Animal Behav 74:1735e1742.  
574 DOI:10.1016/j.anbehav.2007.04.014
- 575 38. Kierat J, Filipiak M, Szentgyörgyi H, Woyciechowski M (2017) Predation  
576 Cues in Solitary bee Nests. Journal of Insect Behavior 30:385–393. DOI:  
577 10.1007/s10905-017-9626-0
- 578 39. Lewis SE (1994) Night Roosting Ecology of Pallid Bats (*Antrozous pallidus*)  
579 in Oregon. The American Midland Naturalist 132: 219–226
- 580 40. Caccamise DF, Morrison DW (1986) Avian Communal Roosting:  
581 Implications of Diurnal Activity Centers. The American Naturalist 128:191–  
582 198. DOI: 10.1086/284553

- 583 41. Simpson SJ, Sword GA, Lorch PD, Couzin ID (2006) Cannibal crickets on a  
584 forced march for protein and salt. *Proc Natl Acad Sci USA* 103:4152–4156.  
585 DOI: 10.1073/pnas.0508915103
- 586 42. Oberhauser FB, Koch A, Czaczkes TJ (2018) Small differences in learning  
587 speed for different food qualities can drive efficient collective foraging in ant  
588 colonies. *bioRxiv preprint*. DOI: 10.1101/274209
- 589 43. Möglich M, Hölldobler B (1974) Social carrying behavior and division of  
590 labor during nest moving in ants. *Psyche* 81:219–236. DOI:  
591 10.1155/1974/25763
- 592 44. Robson S, Traniello J. Key individuals and the organisation of labor in ants, in  
593 *Information Processing in Social Insects* (Birkhäuser ed. 1999) pp. 239–259
- 594 45. Hammel B, Vollet-Neto A, Menezes C, Nascimento FS, Engels W, Grüter C  
595 (2016) Soldiers in a Stingless Bee. *The American Naturalist* 187:120–129.  
596 DOI: 10.1086/684192
- 597 46. Dornhaus A (2008) Specialization Does Not Predict Individual Efficiency in  
598 an Ant. *PLoS Biology* 6:e285. DOI: 10.1371/journal.pbio.0060285
- 599 47. Robson SKA, Traniello JFA (2002) Transient division of labor and behavioral  
600 specialization in the ant *Formica schaufussi*. *Naturwissenschaften* 89:128–131
- 601 48. Pruitt JN, Keiser CN (2014) The personality types of key catalytic individuals  
602 shape colonies' collective behaviour and success. *Animal Behav* 93:87–  
603 95. DOI: 10.1016/j.anbehav.2014.04.017
- 604 49. Robinson GE (1992) Regulation of Division of Labor in Insect Societies.  
605 *Annual Review of Entomology* 37:637–665. DOI:  
606 10.1146/annurev.en.37.010192.003225
- 607 50. Gelblum A, Pinkoviezky I, Fonio E, Ghosh A, Gov N, Feinerman O (2015)  
608 Ant groups optimally amplify the effect of transiently informed individuals.  
609 *Nature Communications* 6: 7729. DOI: 10.1038/ncomms8729
- 610 51. Reeb SG (2000) Can a minority of informed leaders determine the foraging  
611 movements of a fish shoal? *Anim. Behav* 59:403–409.  
612 DOI:10.1006/anbe.1999.1314.
- 613 52. Dyer JRG, Johansson A, Helbing D, Couzin ID, Krause J (2009) Leadership,  
614 consensus decision making and collective behaviour in humans. *Phil Trans R*  
615 *Soc B* 364:781–789. DOI: 10.1098/rstb.2008.0233.

- 616 53. Torney CJ, Lorenzi T, Couzin ID, Levin SA (2015) Social information use  
617 and the evolution of unresponsiveness in collective systems. *J R Soc Interface*  
618 12:20140893. DOI: 10.1098/rsif.2014.0893.
- 619 54. Vonshak M, Shlagman A (2009) A *Camponotus fellah* queen sets a record for  
620 Israeli ant longevity. *Isr J Entomology* 39: 165–168
- 621 55. Mersch DP, La Mendola C, Keller L (2017) *Camponotus fellah* queens are  
622 singly mated. *Insect Soc* 64:269–276. DOI: 10.1007/s00040-017-0543-1
- 623 56. R Core Team (2017) R: A language and environment for statistical computing.  
624 R Foundation for Statistical Computing, Vienna, Austria. URL [https://www.R-](https://www.R-project.org/)  
625 [project.org/](https://www.R-project.org/).
- 626

627 **Supplementary material**

628



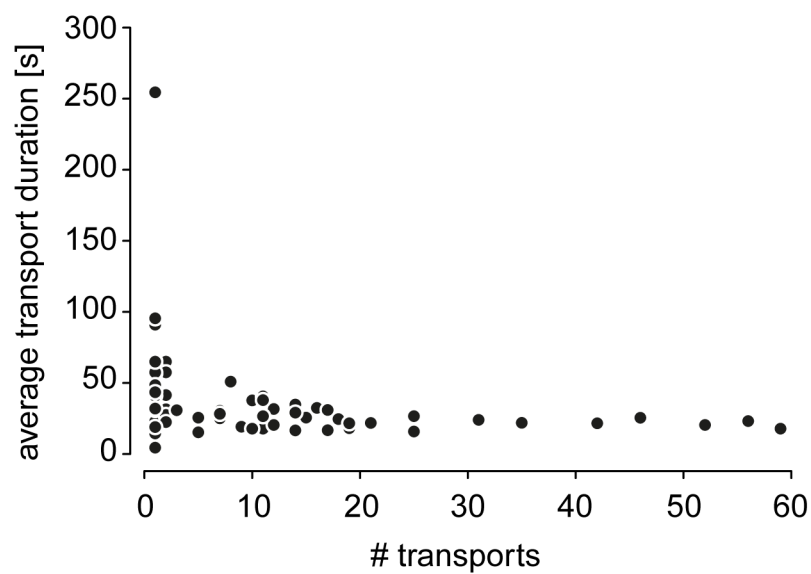
629

630

631 **Supplementary Figure 1:** Tracking setup (A) Lateral view (B) Top view; reproduced with

632 permission from Mersch *et al.* (2013)<sup>27</sup>

633



634

635

636 **Supplementary Figure 2. Individual workers transport brood rapidly.** Each black dot

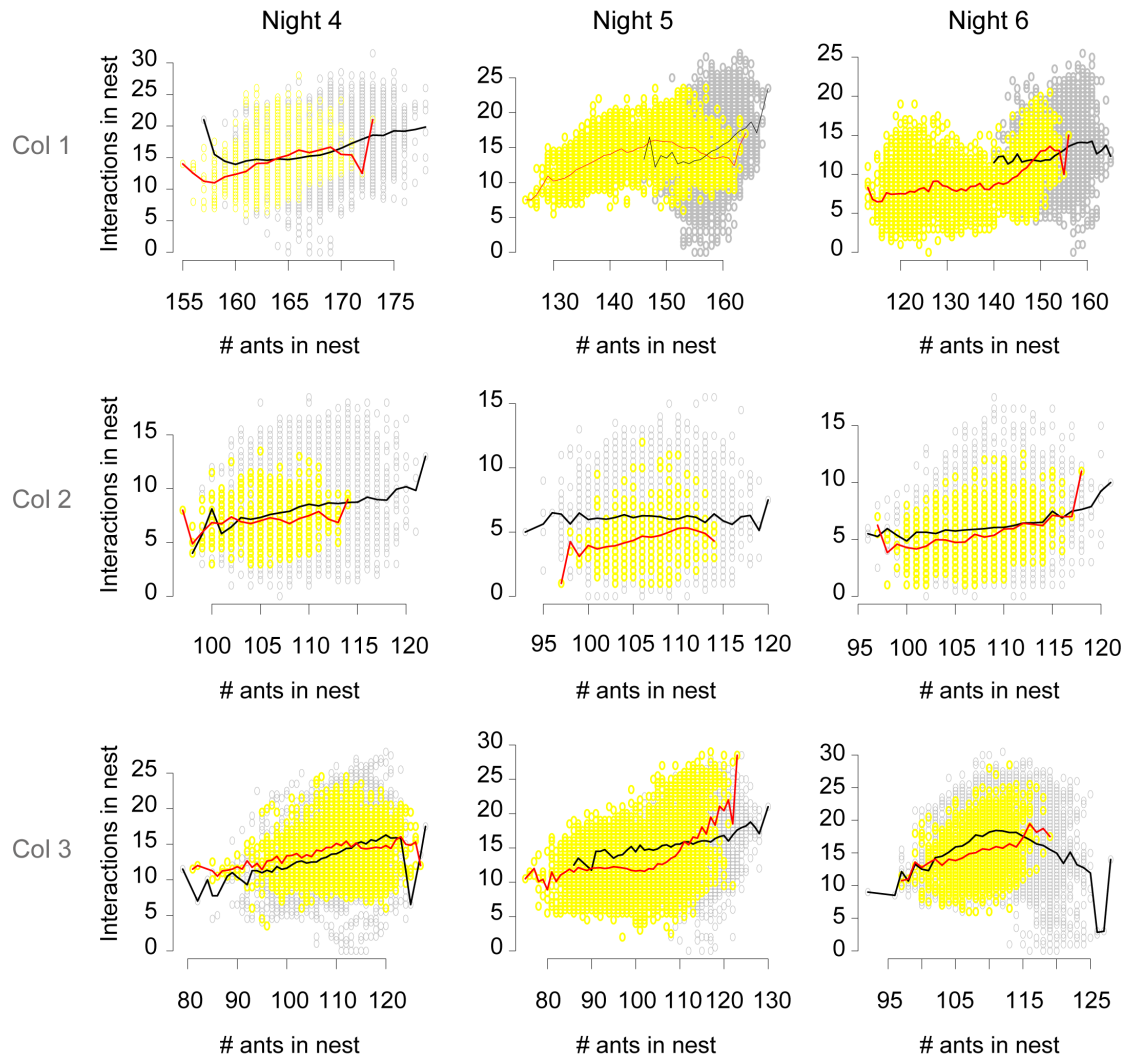
637 shows the average transport time needed by a single transporter.

638

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640





641

642

643 **Supplementary Figure 3. No change in interaction frequencies after light-off.** Grey

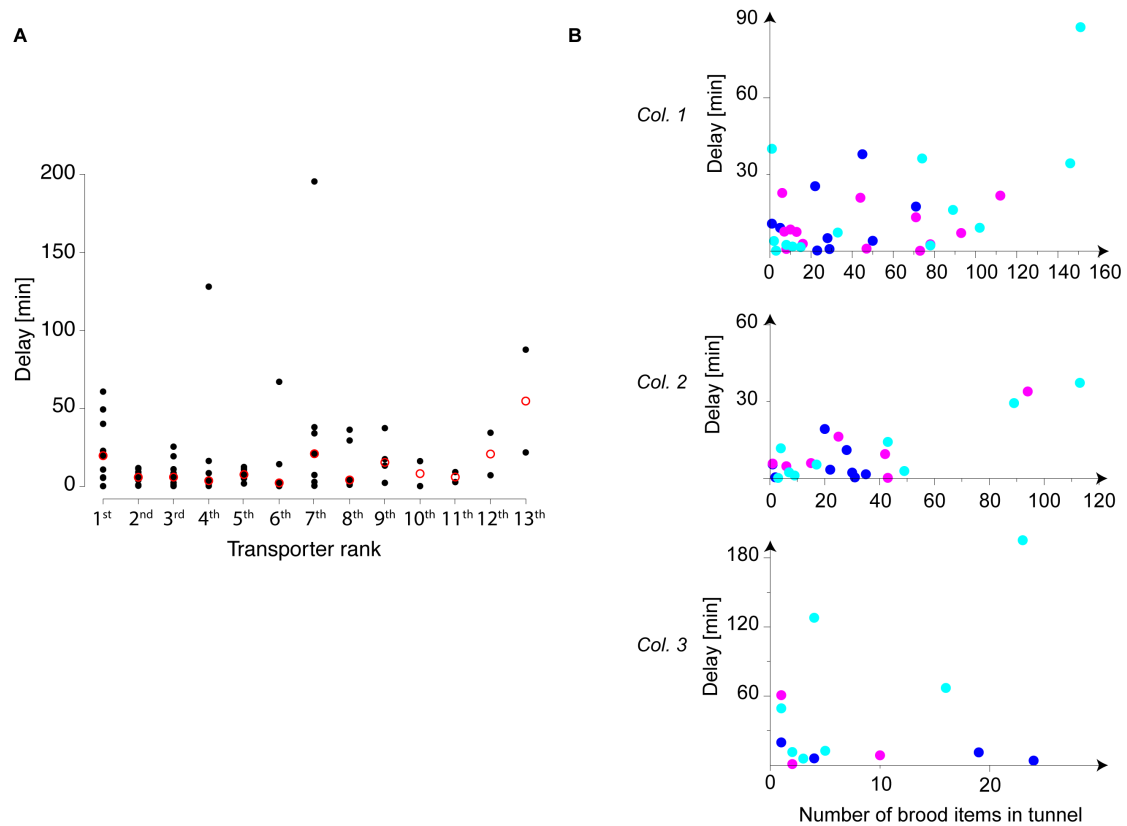
644 dots show data in the hour preceding light-off. Yellow dots show data between light-off

645 and the first transport. The black line shows the average relationship between the number

646 of ants in the nest and the number of interactions before light-off, and the red line shows

647 the same relationship in the interval between light-off and the first brood transport.

648



649

650

651 **Supplementary Figure 4. Brood accumulation in the tunnel does not speed up**

652 **transporter recruitment.** A. Each black dot shows the recruitment delay. For all but the

653 first transporter, recruitment delays are with regard to the transport start of the previous

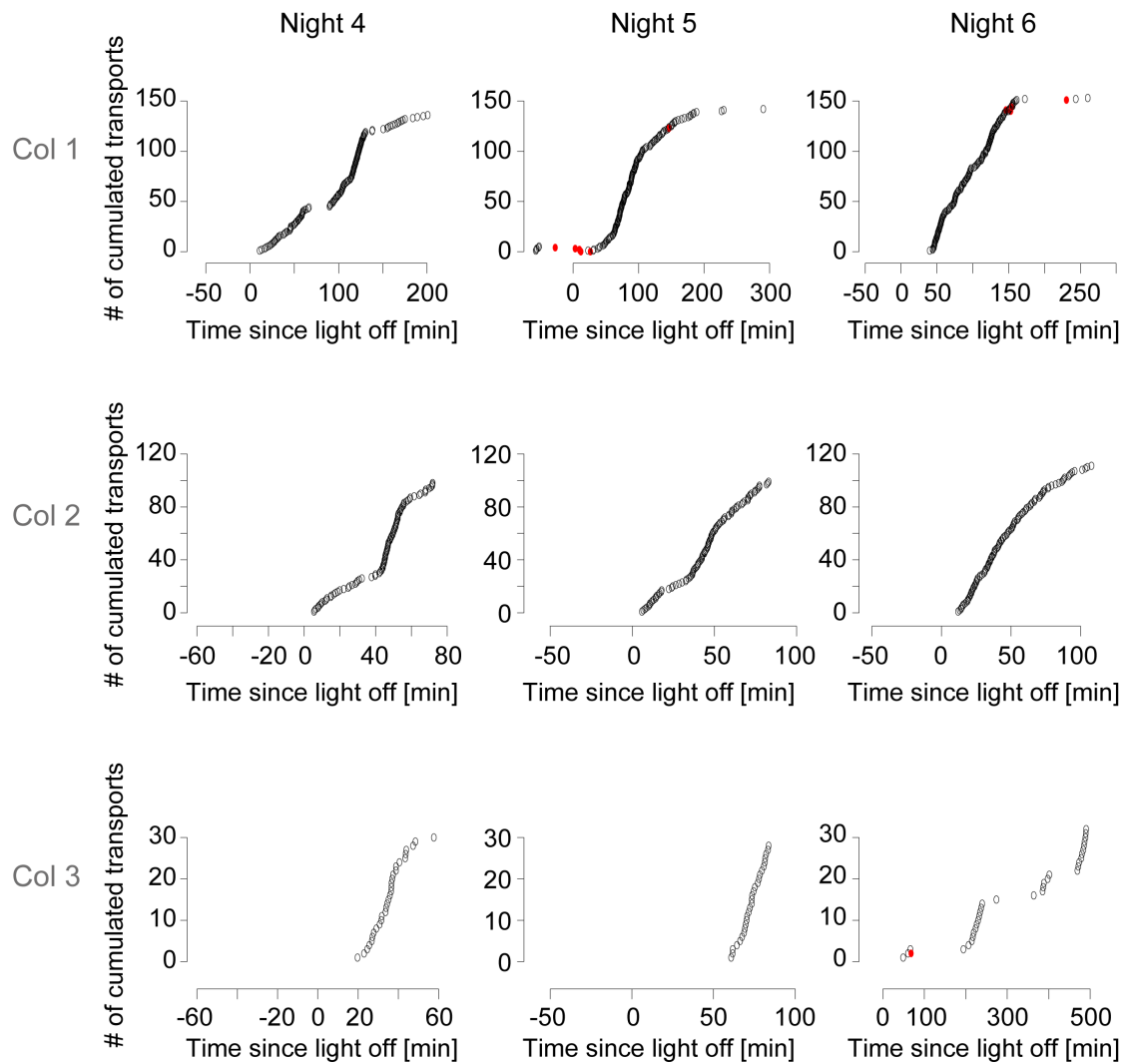
654 transporter. For the first transporter, recruitment delays are with regard to light-off. Red

655 circles indicate the median recruitment delay for each transporter rank. B. The recruitment

656 delays are the same as in A. Blues dots show data for night 4, magenta dots data for night

657 5, and cyan dots data for night 6. Data are shown separately for each colony.

658



659

660

661 **Supplementary Figure 5. Workers transport almost exclusively from the nest to the**

662 **tunnel.** Grey dots show transports from the nest to the tunnel. Red dots show transports

663 from the tunnel to the nest.

664

665

Interval length for speed estimate (s)	#interactions excluded due to missing speed data(%)	Speed increase after an interaction with a privately informed ant (mm/s);mean±std	Speed increase after an interaction with a non privately informed ant(mm/s); mean±std	Kruskal-Wallis Chi2	p-value
5	79 (12.9)	0.89±2.3	0.26±3.1	3.25	0.071
10	50 (10.2)	0.25±2.8	0.15±2.9	2.77	0.096
20	20 (6.3)	0.23±1.8	0.07±2.3	3.09	0.079

666

667 **Supplementary Table 1. Speed change after an interaction with a privately informed**

668 **ant.**

669

670

671 **Supplementary Video 1. Worker transporting brood.** Worker 62 transports brood to the  
672 tunnel. At 16s in the video, ant 62 takes brood directly from another worker without this  
673 worker changing its behaviour. Data is from colony 2 and the frame rate is accelerated 5  
674 times. The green line shows the worker's trajectory in the previous minute.

675

676 **Supplementary Video 2. Targeted queen recruitment to the tunnel.** Worker 632 (in  
677 pink) approaches the queen, pulls on her mandibles, and then returns to the tunnel with  
678 the queen (in blue) following her. The data are from colony 1.

679

680 **Supplementary Video 3. Recruitment of two non-transporters to the tunnel.** Worker  
681 458 (in green) interacts with workers 607 (in blue) and 278 (in cream), and both then follow  
682 worker 458 to the tunnel. The trajectories are shown for all three workers after the  
683 interactions finished. The data are from colony 1.