Synchronised brood transport by ants occurs without 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[1], prairie dogs that call

33 to warn their family of predators[2] and honeybees that use waggle dance to signal

34 a food source to nest mates[3,4]. 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[5,6,7,8,9,10]. Ants optimize foraging

44 by creating pheromone trails[11,12], 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[13]. In emergencies, ants release highly volatile

47 alarm pheromones[11]. If a nest is destroyed knowledgeable ants first lead tandem runs

48 to new nest sites before switching to brood transport[14]. 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[15] 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[9].

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[16,17,18,19,20]. 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[19,20,21].

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 [22, 23, 24, 25].

72

Results

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±6.2 minutes (mean±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±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±28.0% of

83   the time. The average time taken by a worker to transport one brood item was

84   36.7±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: ϱ=-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
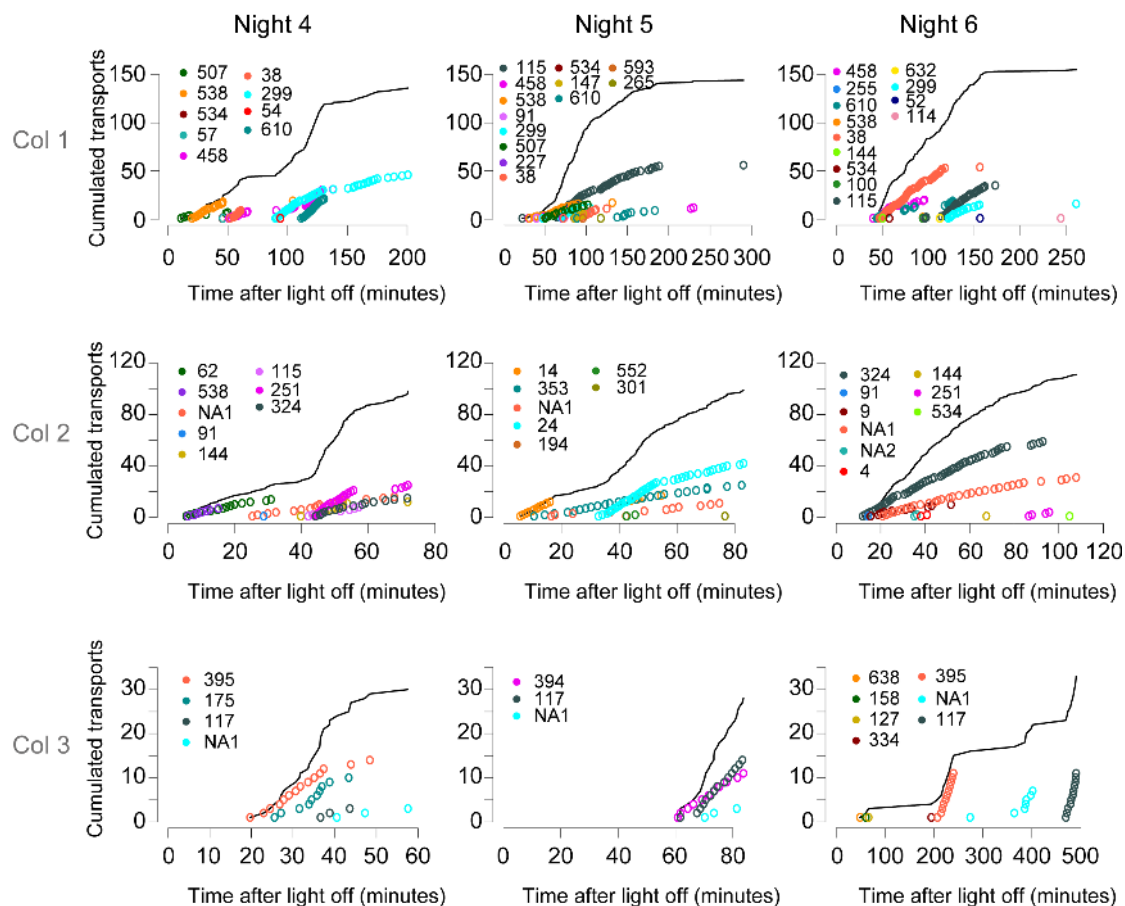
Fig 1. Brood transport dynamics on three consecutive days in three colonies. The black line indicates the cumulated number of brood transports to the tunnel of all workers. Each coloured circle represents a single brood transport event by one worker, and data are shown as cumulative transports. Different colours represent different workers.

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

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

110   contributed together to 24.8±18.7% of the transports.

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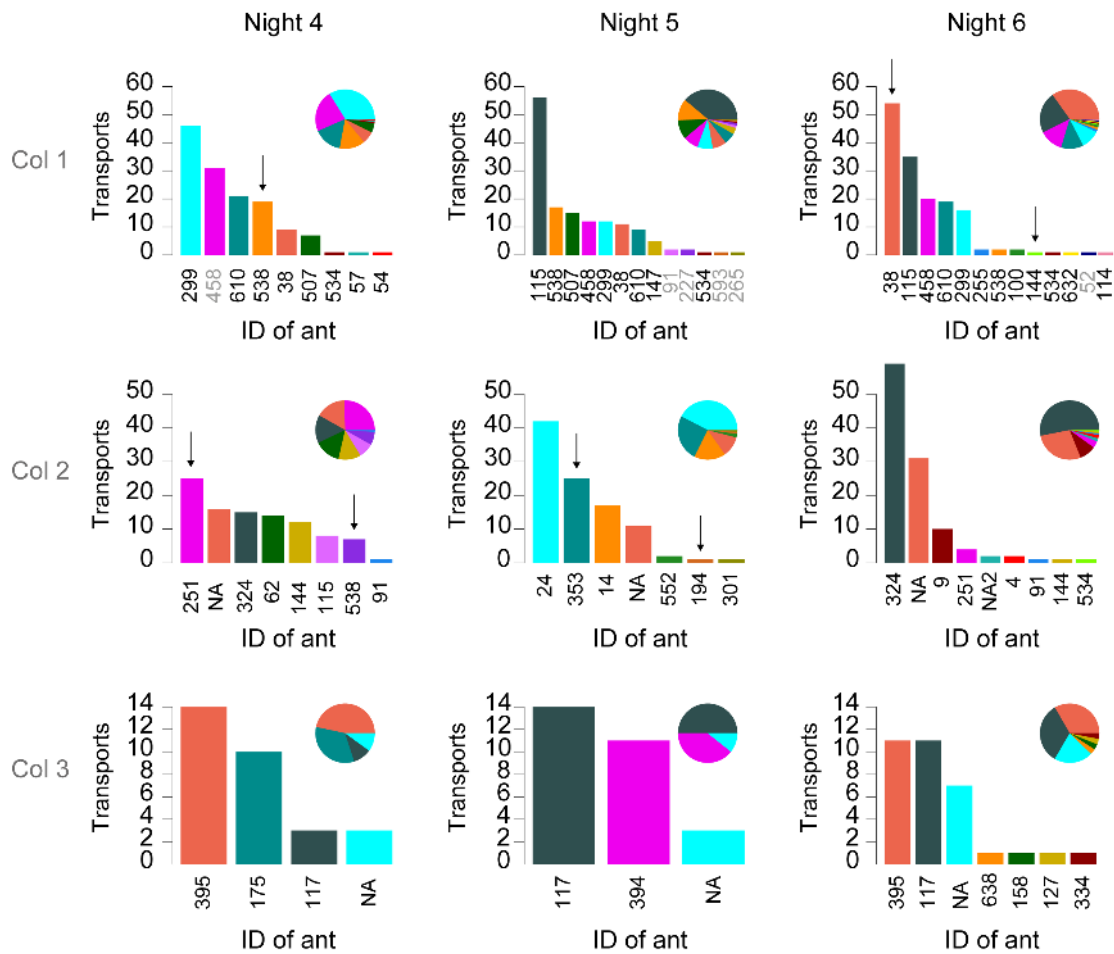
112   Color ranking based on total transports : most ... fewest

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[26] to determine the daily interaction

122   networks of workers and assign each of them to a specific social group[27]. Colonies

123   had on average 55.9%±11.3% nurses, 16.5%±4.9% cleaners and 25.1%±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: χ^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: χ^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: χ^2=0.81, p=0.37; insufficient data

132 was available to conduct similar tests for nest cleaners and foragers).

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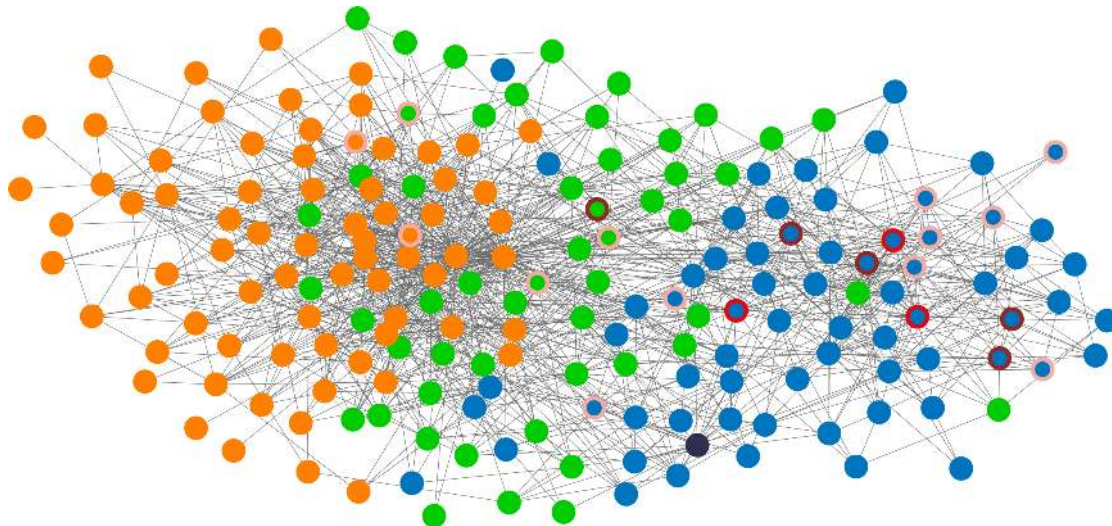
134

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%±2.9% of all workers and 37.8%±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[24,25]. 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: χ^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[28]— was similar after interacting

173   with a privately informed or an uninformed ant (Kruskal-Wallis: χ^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±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: ϱ=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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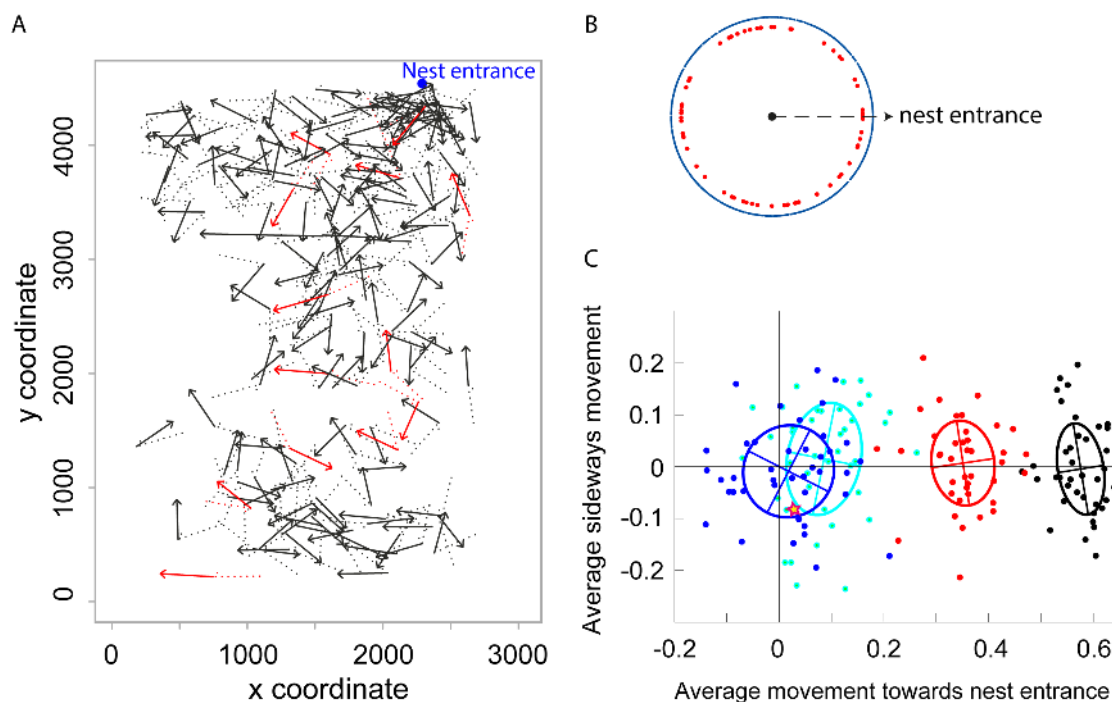
Fig 4. No evidence for communication between workers. (A) Changes of trajectory following the first interaction with a privately informed ant. Arrows indicate the trajectories after the first interaction with a privately informed ant and the dotted lines the trajectories just before this interaction. Transporter trajectories are in red and those of other ants in black. The blue circle indicates the nest entrance. Data shown are those of colony 1 on day 5. (B) Distribution of directions after the first interaction with a privately informed ant. Each dot represents the direction relative to the nest entrance of a single worker on a given day. Red dots indicate transporters and blue dots (forming a ring) indicate other ants. The arrow indicates the direction of the nest entrance. (C) Expected change in direction from simulated data in which 0% (blue), 10% (cyan), 50% (red) or 90% (black) of the ants understood a message. Each dot is the average movement towards the nest entrance of 66 simulated transporters. The cross and ellipse show the average and the standard deviation across 40 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.

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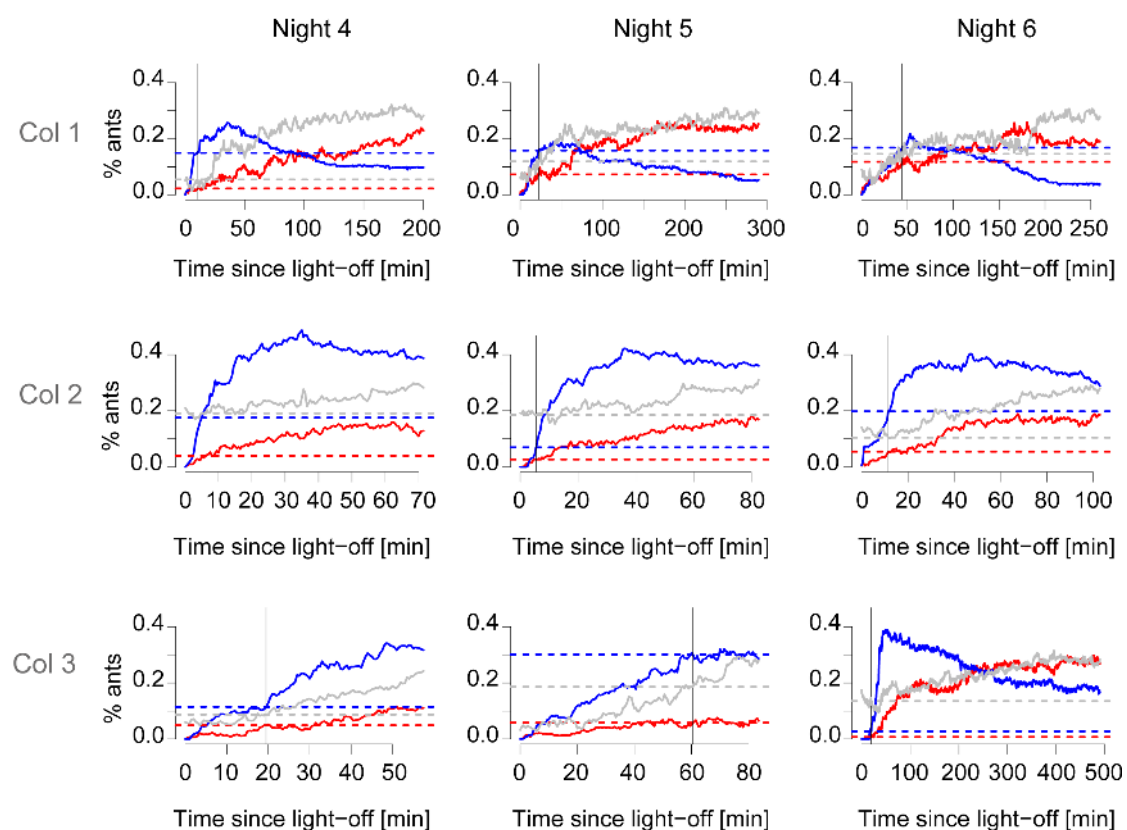
223   **Fig 5. No evidence for a quorum threshold triggering brood transport.** Each line shows
224   the percentage of ants: privately informed ants in red, socially informed ants in blue, ants in
225   the tunnel in grey. The vertical line indicates when the first transport occurred, and the dashed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

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[13]. 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[29]. Ants

265   have a limited ability to convey a message through tactile communication alone[28, 30,31].

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 beneficial if the time needed for successful recruitment is short,

271   and if recruitment occurs early on (see Figure 6).
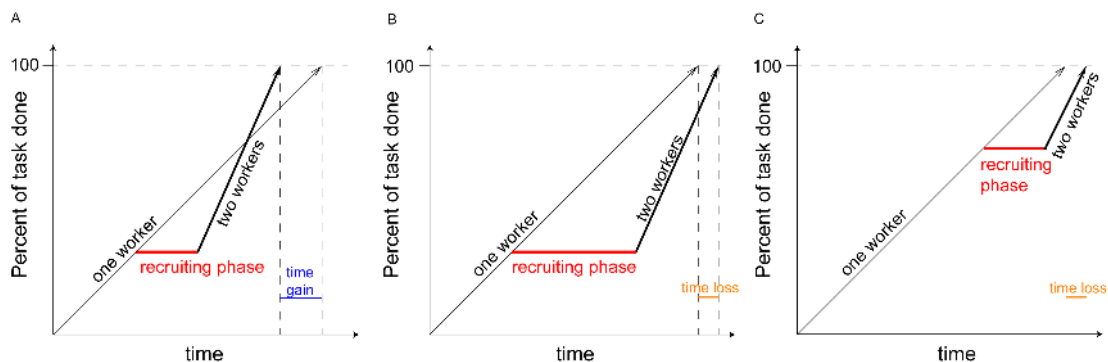
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273   **Figure 6. Cost and benefit of successful recruitment.** The time invested in recruiting help is
274   indicated in red. The time gained from recruiting a helper is shown in blue, and the time lost
275   due to recruiting help in orange. (A) 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[32,33]. 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[34,35]. 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[36]. 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[9,14]. In contrast,
310   synchronization without communication is optimal when reliable communication is
311   expensive, hard to achieve, or when perfect synchrony is not needed[29,37]. 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[38], bats and starlings that converge at seasonal feeding
316   and sleeping spots[39,40] and Mormon crickets, who migrate in masses in search for salt
317   and proteins[41]. In ants simulations further suggest that food choice during foraging
318   could be achieved without communication through individual learning and
319   preference[42].

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*[43]. 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[44] during the brood displacement.

331   Similar specialization has been reported for foraging, brood care, stone

332   collection[45,46,47] and could result from inherent and consistent differences between

333   workers, for example in motivation, physiology, or sensory threshold[48,49]. 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[50].

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[51,52].

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[53].

351

357

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

Material and Methods

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

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

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

During the night, workers transported the brood to the tunnel and brought it back to the nest at dawn, presumably because they prefer to keep the brood in a confined environment rather than an open environment when both are dark. We tracked the 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-transports, 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)[27]. 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[26] 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±29.9 s *vs*. 10.3±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°

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 (≈ 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 α_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 $-$

449   π and π. 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)[56]. 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

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469

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626

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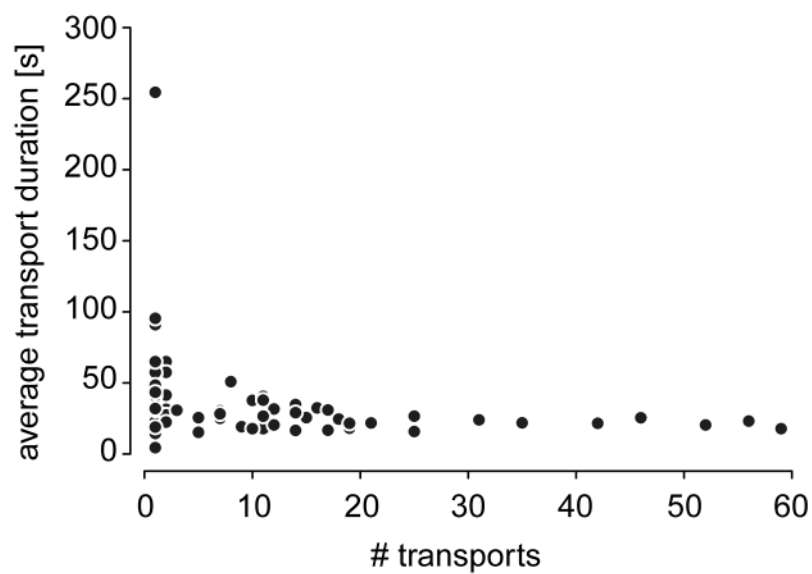
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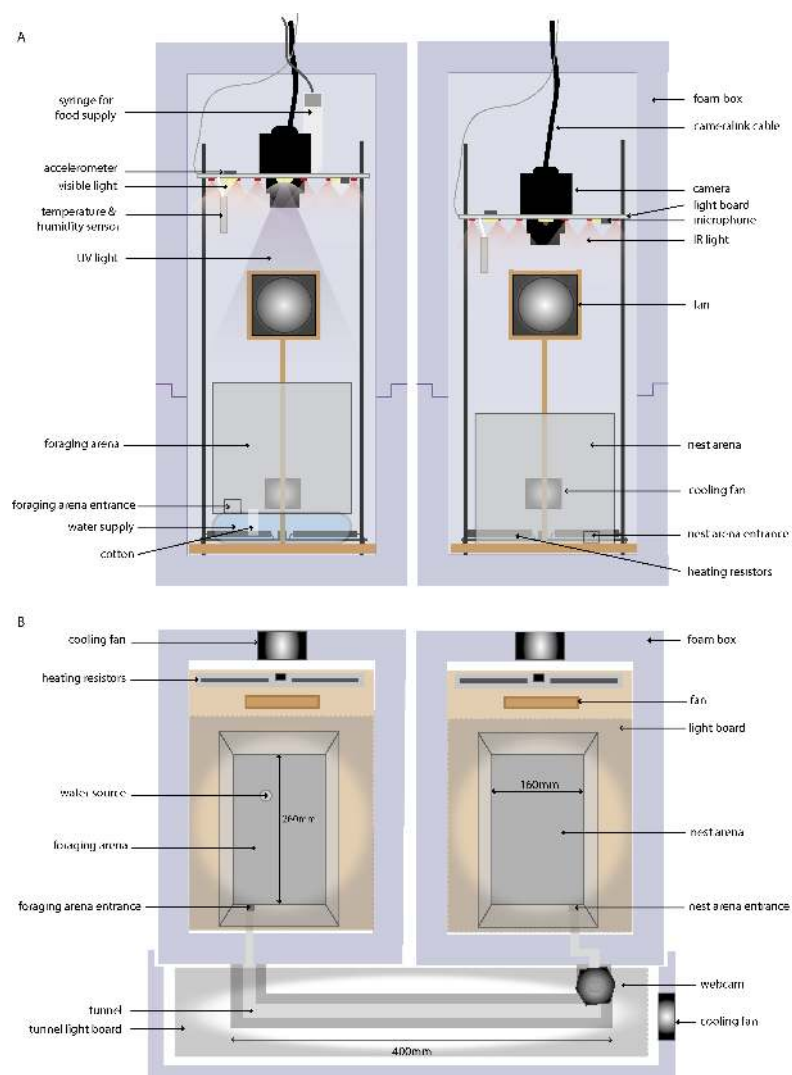
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631   **Supplementary Figure 1:** Tracking setup (A) Lateral view (B) Top view; reproduced with

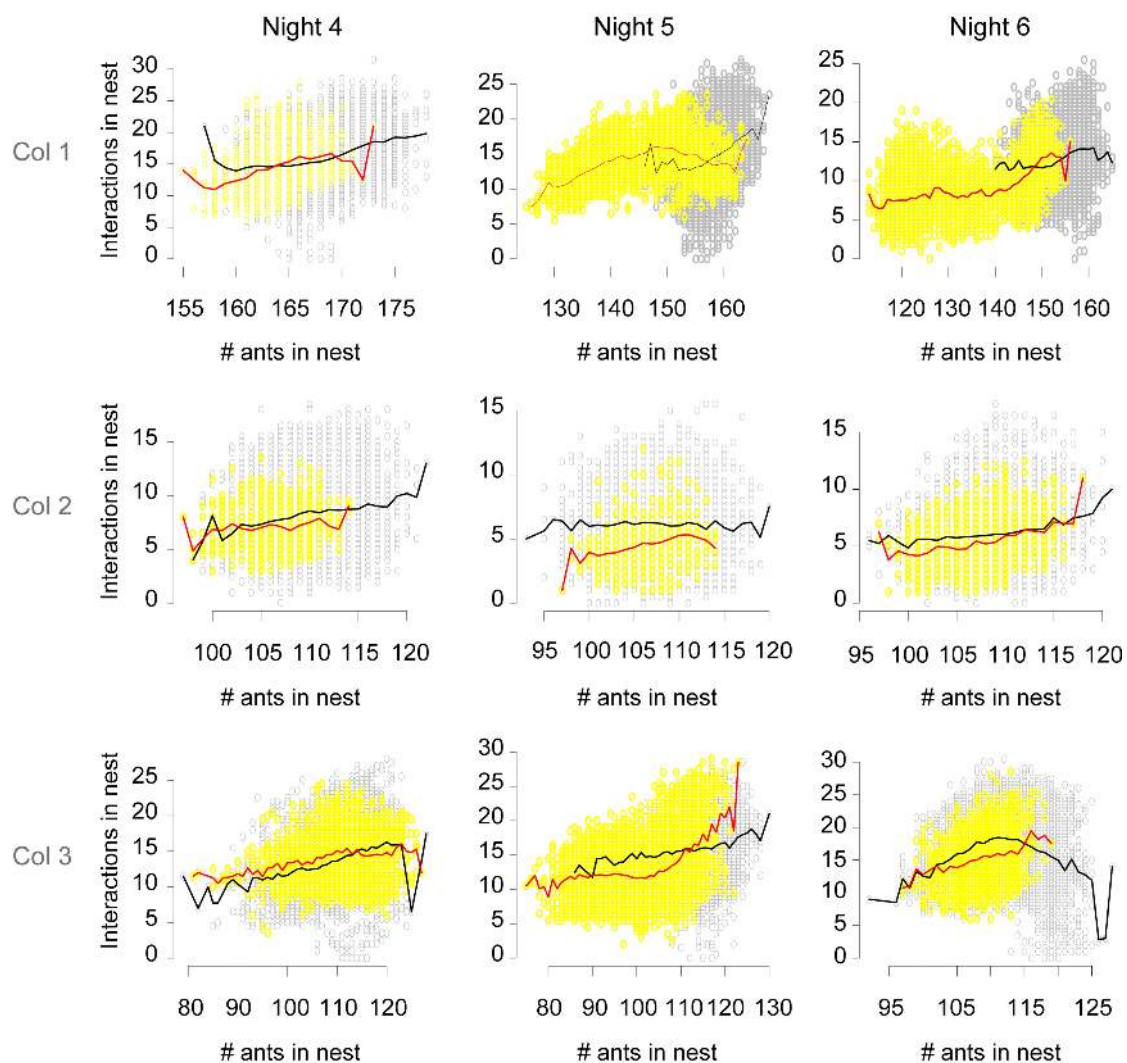632   permission from Mersch *et al.* (2013)[27]

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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

639

640

**Supplementary Figure 3. No change in interaction frequencies after light-off.** Grey dots show data in the hour preceding light-off. Yellow dots show data between light-off and the first transport. The black line shows the average relationship between the number of ants in the nest and the number of interactions before light-off, and the red line shows the same relationship in the interval between light-off and the first brood transport.
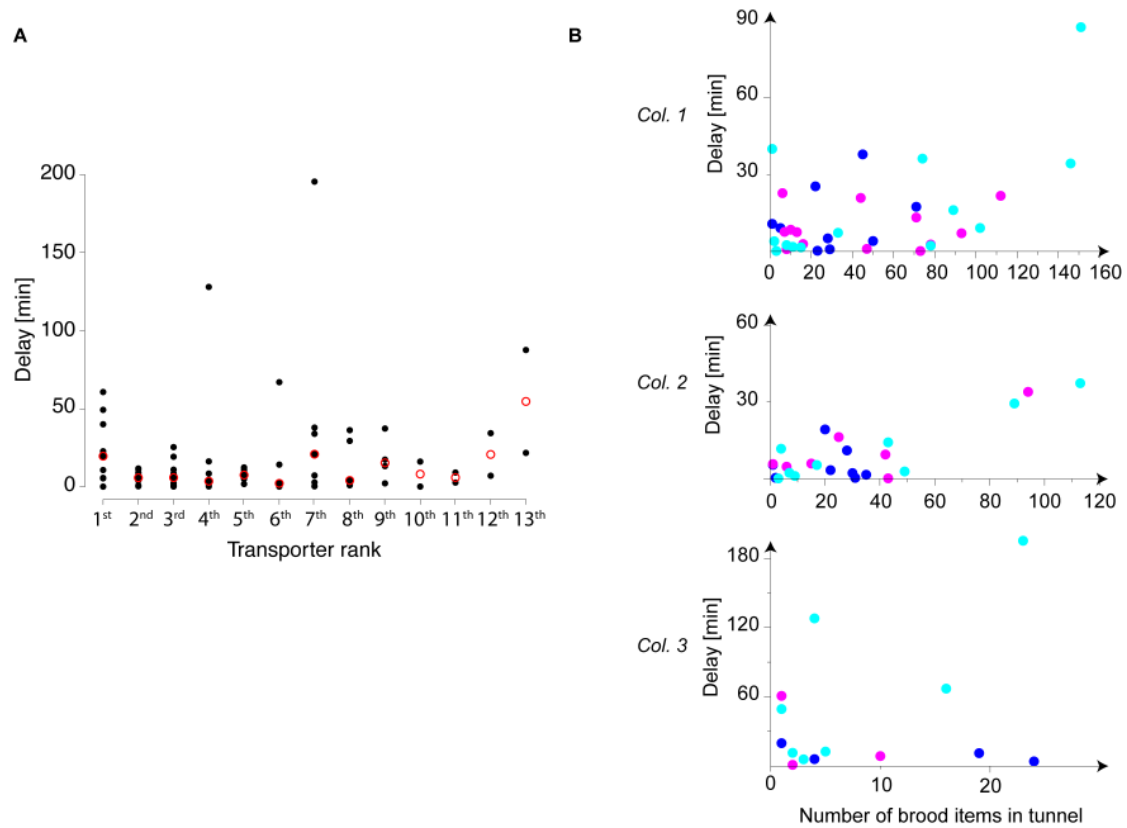
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650

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
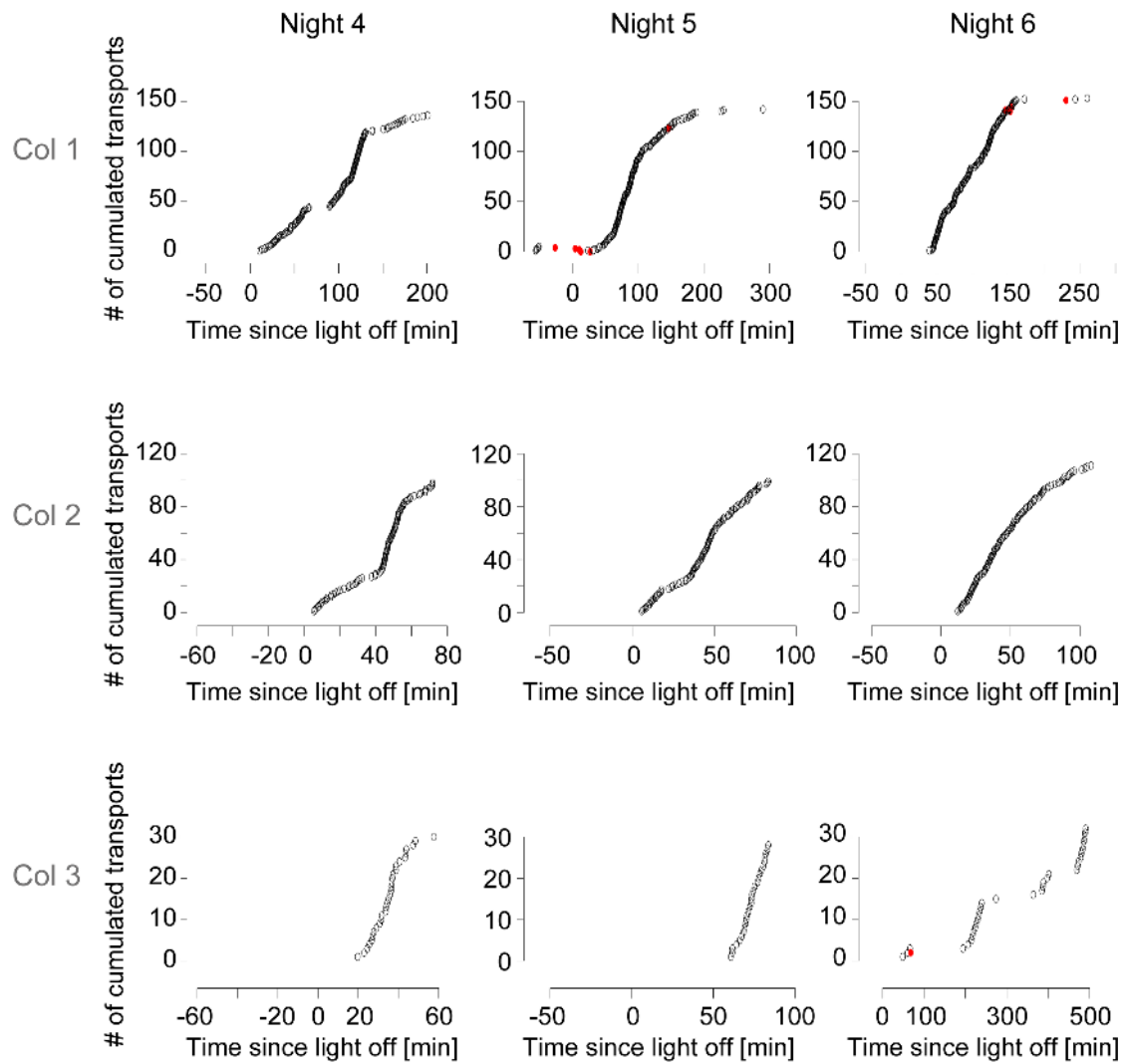
Supplementary Figure 5. Workers transport almost exclusively from the nest to the tunnel. Grey dots show transports from the nest to the tunnel. Red dots show transports from the tunnel to the nest.

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

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

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.