1   **Lay summary**

2   Sharing social information through recruitment can alter the outcome of collective decisions.

3   We show that when ants share social information through recruitment, colonies consistently

4   choose a nest site that fluctuates between being good and bad over a constantly mediocre

5   alternative, even when the latter is only good for 25% of the time. This choice contrasts with

6   previous results showing colonies can accurately assess nest sites that fluctuate in quality

7   when recruitment is infrequent.

8   **The effect of social information on the collective choices of ant colonies**

9   **Abstract**

10   In collective decision-making, groups collate social information to inform their decisions.

11   Indeed, societies can gather more information than individuals- so social information can be

12   more reliable than private information. Colonies of *Temnothorax albipennis* can estimate the

13   average quality of fluctuating nest sites when the sharing of social information through

14   recruitment is rare. However, collective decisions in *T. albipennis* are often reached with the

15   use of recruitment. We use a new experimental set-up to test how colonies react to fluctuating

16   nest sites when they use recruitment to reach a decision. When recruitment is used colonies

17   consistently choose nest sites that fluctuate between being 'good' and 'poor' over constantly

18   'mediocre' alternatives. Moreover, they do so even if the fluctuating option is only 'good' for

19   25% of the time. The ants' preference for fluctuating nest sites appears to be due to tandem

20   running. Even if a nest site is only briefly 'good', scouts that experience it when it is 'good'

21   are likely to perform tandem runs to it. However, a constantly 'mediocre' nest site is unlikely

22   to ever provoke tandem runs. Consequently, the fluctuating nest sites attracted more tandem

23   runs, even when they were only 'good' for a short time. This led to quorum attainment in

24   fluctuating nest sites rather than in constant 'mediocre' nest sites. The results of this

1

25 experiment demonstrate how sharing of social information through recruitment can change

26 the outcome of collective decisions.

Background

28 Through social means individuals can obtain information that they might not be able to

29 collect themselves. Social information is also useful as it may be more accurate than private

30 information (e.g. Surowiecki, 2004). Furthermore, individuals are known to perform better in

31 certain tasks when they have access to social information. For example, in a difficult and

32 uncertain task Wolf et al. (2013) observed that human participants made fewer false positives

33 and more true positives when they had access to social information, than when they acted

34 independently. However, in some cases social information may be poor and groups can be led

35 to bad decisions (Rieucau and Giraldeau, 2011). For example, groups of guppies (*Poecilia*

36 *reticulate*) that are initially trained to follow a long route to a food source take longer than

37 individuals that forage independently to identify a shorter route (Laland and Williams, 1998).

38 Similarly humans often use inaccurate social information (Rieucau and Giraldeau, 2011),

39 which can lead to disastrous information cascades (Bikhchandani et al., 1998). For example,

40 Helbing et al. (2000) found that in an evacuation individuals attempt to exit using the same

41 route as other people, even when other options are available. This can have disastrous effects

42 as exits become overcrowded (Helbing et al., 2000). Similarly, in elections certain individuals

43 use social information to determine which party they vote for, which can influence election

44 results (McAllister and Studlar, 1991).

45   A recent review by Grűter and Leadbeater (2014) emphasised how information

46 sharing in social insects can have both good and bad effects, depending on the situation. Here

47 we investigate the effect of information sharing, through tandem running, on the outcome of

48 collective decisions in nest site choice in the rock ant (*Temnothorax albipennis*). *T.*

49   *albipennis* is an excellent model system for the study of cooperative decision-making as they

50   are easily collected, easy to keep in the laboratory, amenable to experimentation and

51   demonstrate complex cooperative behaviors.

52   Individual *T. albipennis* ants measure the quality of potential nest-sites by

53   incorporating information from various factors such as entrance width, floor area and light

54   level (Franks et al., 2003b). If the nest site is deemed to be suitable scouts recruit others to it

55   through tandem running, which increases the rate of accumulation in the new nest (Möglich,

56   1978; Mallon et al., 2001; Franks and Richardson, 2006). In a tandem run an informed scout

57   leads a naïve follower to a particular resource by secreting a pheromone that signals to the

58   recruit to follow the leader (Möglich, 1978; Mallon et al., 2001; Franks and Richardson,

59   2006). The recruited ant may subsequently become a recruiter and through this process the

60   number of individuals in the new nest site increases. When the number of ants reaches a

61   certain threshold, known as the quorum, ants switch from tandem running to carrying nest

62   mates to the new nest site (Pratt et al., 2002). As numerous factors are considered in nest site

63   choice, colonies often migrate to a cavity that is good for certain attributes, but bad for others

64   (Franks et al., 2003b).

65   Colonies that make collective decisions are able to estimate resource quality through

66   the integration of information from a number of scouts (Robinson et al., 2009). Individuals

67   that encounter a nest site either reject it and continue searching or accept it and recruit (Pratt,

68   2005). It has been hypothesised that there is variation among individuals acceptance

69   thresholds above which they decide to recruit to a site (Robinson et al., 2009; Robinson et al.,

70   2011). Therefore, higher quality nest sites should meet the approval of more scouts, attract

71   higher rates of recruitment and, thus, be more likely to draw a quorum (Robinson et al., 2009;

72   Robinson et al., 2011). This explains how colonies are able to make accurate decisions

73   without the need for all individuals to assess all nest sites (Robinson et al., 2009; Robinson et

74   al., 2011).

75   When presented with nest cavities of fluctuating quality, house-hunting colonies of *T.*

76   *albipennis* should choose nests that are predominantly the better option, assuming rationality

77   (Edwards and Pratt, 2009; Sasaki and Pratt, 2011) and that fluctuations are not inherently

78   costly (Franks et al., 2015). This prediction has been validated by recent work that found that

79   colonies generally chose to migrate to nests that were predominantly the better option (Franks

80   et al., 2015). This study showed the ants' ability to account for fluctuations in quality when

81   measuring the attributes of a potential nest cavity and demonstrated that ant colonies are able

82   to estimate resource quality using a system that is consistent with homogenization theory,

83   which posits that fluctuations can be safely averaged to estimate the quality of a certain

84   resource (Pavliotis and Stuart, 2008; Franks et al., 2015). However, the experimental design

85   used in Franks et al. (2015) meant that tandem running was rare so positive feedback did not

86   play a role in the accumulation of ants in the new nest sites. Tandem runs rarely occur when a

87   potential new nest site is close and there are many scouts; instead a quorum is achieved by

88   scouts that independently find the cavity (Langridge et al., 2004; Franks et al., 2015). Instead,

89   the ability of colonies to choose nests that were predominantly better in Franks et al. (2015)

90   appears to have been the result of scouts spending longer in such nests. Consequently, a

91   quorum threshold was reached in higher quality nests through accumulation of ants that had

92   found the new nest site independently (Franks et al., 2015).

93   Recruitment is likely to have an influence on decision-making in *T. albipennis* as it is

94   often used to reach decisions (Dornhaus et al., 2004; Franks and Richardson, 2006).

95   Furthermore, there are other examples of cases where recruitment has affected colony

96   decisions. Social insect colonies often need to choose between different food sources and

97   recruitment to such resources is common (Von Frisch, 1967; Hölldobler et al., 1974;

98   Deneubourg et al., 1987; Gottlieb et al., 2013). Recruitment to food sources appears to have a

99   strong effect on food site choice. For example, ant colonies that use trail pheromones

100   typically do not utilise two resources of equal quality in a symmetrical way; instead most

101   individuals will forage from only one of the resources (Deneubourg et al., 1986; Pasteels and

102   Deneubourg, 1987). This occurs as a consequence of one pheromone trail becoming stronger

103   causing most individuals to choose to follow the same trail (Deneubourg et al., 1986; Pasteels

104   and Deneubourg, 1987). Similarly, once a pheromone trail is established to a resource of a

105   particular quality certain colonies are often unable to switch to a higher quality resource as

106   the original trail is too strong (Pasteels and Deneubourg, 1987; Detrain and Deneubourg,

107   2006). Numerous other examples in which recruitment or positive feedback affect group

108   decisions have been observed in humans (e.g. Kirman, 1993; Hirshleifer and Teoh, 2003).

109   Clearly recruitment plays an important role in collective decision-making in many

110   systems. Therefore, it seems likely that recruitment would have an influence on the decisions

111   that ant colonies make. The earlier finding of accurate assessment of fluctuating resources in

112   the absence of tandem running, in Franks et al. (2015), provides an interesting possibility for

113   comparisons between decisions that have been influenced by tandem running and those that

114   have not. In this study we test the hypothesis that tandem running influences the outcome of

115   collective decisions made by colonies of *T. albipennis* when faced with fluctuating nest sites.

116   The reason that we suggest that this is a possibility is that the mechanism used by individuals

117   to determine whether they should contribute to a quorum by spending more time in a nest or

118   contribute to a quorum by tandem running may be different. Such differences may result in a

119   quorum being reached in different nest sites depending on whether tandem running is used or

120   not. Consequently, recruitment may influence the outcome of collective decisions in certain

121   situations.

122   **Methods**

Collection and housing of ant colonies

Thirty colonies of *T. albipennis* were collected from Dorset, UK on 27th September 2014. Colonies contained between 23 and 235 adults (mean = 116, s.d. = 57.4) and a roughly equal number of brood and adults (Franks et al., 2006a). Most, but not all, colonies contained a queen; this is not unusual for *T. albipennis* and queenless colonies have often been used for decision-making experiments (Partridge et al., 1997; Franks et al., 2006b).

Following collection colonies were housed in artificial nests (dark; cavity dimensions: 60 x 35 x 1mm; nest entrance: 4mm) and fed according to standard protocols from the day they were collected (Franks et al., 2003a). One week prior to its first trial each colony was induced to migrate into a holding nest (dark; cavity dimensions: 55 x 35 x 1.6mm; nest entrance: 4mm) with a detachable wall (Figure 1) by removing the upper nest cover of their original nest. This method of inducing emigration was used to remain consistent with the methodology of Franks et al. (2015).

Experimental design

The experimental design was identical to that in Franks et al. (2015) except for the use of larger and more complex arenas, which were employed to stimulate more tandem runs. Franks et al. (2015) did not observe many tandem runs in their experiment. This appears to be because a quorum was reached before tandem runs were performed due to the high level of independent nest-site discovery by scouts as a consequence of the small arenas used (Mallon et al., 2001; Franks et al., 2015). This is typical for experiments using small arenas and 'emergency migrations' (e.g. Langridge et al., 2004). By creating a larger arena we limited the possibility of a quorum being reached by independent scouts, which allowed time for individuals to perform tandem runs to the nests.

146   In each trial, colonies were provided with a choice between two potential nest sites.

147   One of the nest sites remained constantly 'mediocre' as it had a narrow (1mm wide) nest

148   entrance, but was light. In contrast, the other nest site had a wide (4mm) nest entrance and

149   fluctuated between being better or worse than the constant nest through the removal and

150   replacement of a dark red filter (Table 1). Disturbance caused by the removal and

151   replacement of the dark filter was controlled for, by removal and replacement of a transparent

152   filter over the constant nest at the same time. The experiment used three conditions of

153   fluctuating nest (Table 2).

154   The experimental set-up consisted of three arenas (23 x 23 x 1.7cm) connected by

155   acetate bridges (7 x 4.5cm). At the start of each trial the detachable wall was removed from

156   the holding nest. The holding nest was then placed in the central arena and the new nest sites

157   were placed in each of the peripheral arenas (Figure 2).

158   Each trial was run for 5h with the number of ants at each new nest site recorded every

159   10min. Throughout the trial, the occurrence and times of tandem runs and social carrying of

160   brood and workers to each nest site were recorded. Both the time and the number of ants in

161   each new nest site were recorded when the quorum threshold was reached. A quorum was

162   said to have been reached when the first ant or brood item was carried to either of the new

163   nests. The quorum threshold was estimated by recording the number of individuals in the nest

164   site to which social carrying was directed at the time it began. This method was used to be

165   consistent with the method used by Franks et al. (2015). Following the attainment of a

166   quorum, the number of carriers to each nest was recorded at 10-min intervals until the end of

167   5h.

168   Sixty trials were performed, with each of the 30 colonies used in two of the three

169   conditions to trade off the requirements of a balanced design with minimizing the interval

170   between trials. There was an interval of 14 days between each of the two trials for all

171   colonies. The effects of this design were accounted for in a mixed model analysis (see

172   Statistical methods).

173   **Statistical methods**

174   Analyses were performed with R (version 3.1.1) (R Core Team, 2014) and IBM SPSS 21

175   (IBM Corp, 2012). We used the Generalized Linear Mixed Model tool in IBM SPSS 21 to

176   test for effects in our data (IBM Corp, 2012). Graphs were produced using the R package

177   ggplot2 (Wickham, 2009).

178   *Nest choice*

179   We fitted a mixed binary logistic regression model with a logit link to all trials included in

180   the analysis (see Results for inclusion criteria). The response was the type of nest chosen

181   (fluctuating or constant). The fixed effects of the original model were condition as a factor,

182   colony size as a covariate and the interaction between condition and colony size. The random

183   effect built into the model was colony identity. None of the fixed predictors had a significant

184   effect (see SI, Section 1).

185   *Nest population dynamics*

186   We fitted a mixed model with a Poisson-distributed error structure and a log link to the nest

187   dynamics data (number of ants in each nest every 10min) for both fluctuating and constant

188   nests for the 41 trials included in the analysis (see Results for inclusion criteria). The

189   predictors in the model were the fixed factors condition and nest type, the covariate time and

190   all two-way and three-way interactions between them. Order was also included as a fixed

191   factor predictor. The random factor predictor in the model was colony identity.

192   *Tandem runs, quorum numbers and quorum times*

193   All tests on the effect of condition and order of presentation of the conditions on the number

194   of tandem runs, quorum number and time of quorum were performed on data from the trials

195   in which a colony chose either of the two nests and used tandem runs before reaching a

196   quorum in either of the nest sites. To test for any effect of different conditions and trial orders

197   on quorum times a linear mixed model with an identity link was fitted to the data as the

198   residuals were compatible with a normal distribution (Shapiro-Wilk normality test: $W =$

199   0.9726, $p = 0.4184$). To test for any effect of different conditions and trial orders on quorum

200   number and number of tandem runs, mixed models with poisson distributed error structures

201   and log links were fitted to the data. The initial models used condition, order, colony size and

202   all possible interaction terms as fixed factors. We then removed colony size and all

203   interactions as none had a significant effect on either response variable. Consequently, each

204   model included the predictors condition and order as fixed factors, colony identity as a

205   random factor and the respectivevariable (number of tandem runs, quorum number or time of

206   quorum attainment) as the response.

207   An additional mixed model with a negative binomial error structure and a log link was

208   fitted to the data for the number of tandem runs to each nest type before a quorum was

209   reached. The model included nest type (mediocre or fluctuating) as a fixed factor, colony

210   identity and trial identity were used as random factors and the number of tandem runs was set

211   as the response.

212   **Results**

213   **Nest choice**

214   In 41 of the 60 trials colonies migrated to one of the nest sites and performed tandem runs

215   before reaching a quorum (choices made in all trials are detailed in Table S1). Remarkably, in

216 40 of the 41 trials included in the analysis, the colonies chose to migrate to the fluctuating

217 nest (Figure 3).

Nest population dynamics

219 The preference for fluctuating nests over constant nests is further exemplified by the rate of

220 accumulation of scouts in each of the nest sites (Figure 4). Scouts accumulated at a

221 significantly higher rate in fluctuating nests over constant nests when the fluctuating nest was

222 'good' for 75% of the time (GLMM: $p<0.01$) and when the fluctuating nest was 'good' for

223 50% of the time (GLMM: $p<0.01$), but not when the fluctuating nest was 'good' for 25% of

224 the time (GLMM: $p>0.05$). There was no significant difference in the rate of accumulation

225 between the constant nests for the different conditions (GLMM: $p>0.05$), but there was a

226 lower rate of accumulation in the fluctuating nests when they were 'good' for 25% of the

227 time than when they were 'good' for 50% or 75% of the time (GLMM: $p<0.05$). Full model

228 results are detailed in Section 3 of the Supplementary Information.

Tandem runs, quorum numbers and quorum times

230 The number of tandem runs performed before a quorum was reached did not differ between

231 conditions (GLMM: $F_{2,37} = 0.485$, $p = 0.619$; Figure 5a) or between first and second trials

232 (GLMM: $F_{1,37} = 0.038$, $p = 0.846$; Figure 5b). However, there were significantly more

233 tandem runs to fluctuating nests (median = 5, I.Q.R. = 6) before quorum attainment than to

234 constant nests (median = 0, I.Q.R. = 0) (GLMM: $F_{1,65} = 82.062$ $p < 0.001$). Average quorum

235 numbers did not differ between conditions (GLMM: $F_{2,37} = 2.331$, $p = 0.111$; Figure 6a) or

236 between first and second trials (GLMM: $F_{1,37} = 0.941$, $p = 0.338$; Figure 6b). Additionally,

237 the average time taken to reach a quorum was not significantly different between conditions

238 (LMM: $F_{2,37} = 12.644$, $p = 0.121$; Figure 7a). Additionally, there was a significant difference

239 between the first (median = 210min, I.Q.R. = 95min) and second (median = 125min, I.Q.R. =

240 102.5min) trials (LMM: $F_{1,37} = 12.644$, $p < 0.005$; Figure 7b). Furthermore, the number of

241 tandem runs in the first hour of the trial was significantly higher (Wilcoxon: $W = 82.5$, $n =$

242 43, $p < 0.0001$) and the time of the first tandem run was significantly earlier (Wilcoxon: $W =$

243 369, $n = 43$, $p < 0.0001$) in the second trials compared to the first trials. This did not appear to

244 have an effect on choice as almost all colonies chose the fluctuating nest.

Discussion

246 Our results indicate a strong and consistent preference for nest sites that are at least

247 occasionally 'good', when tandem runs were used to reach a quorum. Interestingly, even

248 when a fluctuating nest site was 'poor' for longer than it was 'good' colonies still chose it

249 over a constantly 'mediocre', alternative. Franks et al. (2015) found that when tandem runs

250 were not used colonies were able to choose nests that were predominantly the best option.

251 The contrast between the findings here and those of Franks et al. (2015) is interesting as the

252 key difference between the experiments is the presence (in this study) or the absence (in

253 Franks et al. 2015) of tandem running.

254 We propose that the reason that ants chose the fluctuating nest in the present

255 experiment is determined by the acceptance threshold used by ants to decide whether to

256 perform a tandem run or not. The threshold above which an individual ant will perform a

257 tandem run is thought to vary among individuals in a colony (Robinson et al., 2009;

258 Robinson et al., 2011). Some individuals are predicted to perform tandem runs to low quality

259 nests, whilst others are predicted to only perform tandem runs to very high quality nests.

260 Such a distribution of thresholds may allow colonies to discriminate between nests of

261 different quality (Robinson et al., 2009; Robinson et al., 2011). In this experiment when a

262 nest is 'poor' or 'mediocre' it appears that it is below the tandem running threshold for most

263 ants. In contrast, when a nest is 'good' a high proportion of ants perform a tandem run to it.

11

264   Therefore, even if a nest is only 'good' for a short period of time it still induces certain

265   individuals to recruit to it. Meanwhile, a 'mediocre' nest is unlikely to evoke many tandem

266   runs as it is probably only above the tandem running threshold for few individuals. This

267   hypothesis is supported by the observed number of tandem runs performed to each nest type;

268   in most trials there were no tandem runs to constant nests before a quorum was reached

269   (median = 0, I.Q.R. = 0), whereas fluctuating nests attracted multiple tandem runs (median =

270   5, I.Q.R. = 6).

271   The most interesting finding of our experiments is that recruitment through tandem

272   running strongly influences the outcome of the collective decision made by the ants. This

273   clearly indicates a difference between the mechanisms used by scouts to determine whether

274   to tandem run to a nest and the mechanism they use to determine whether they should spend a

275   certain length of time in a nest. The ability of colonies to migrate to nests that were

276   predominantly the best option in the experiment performed in Franks et al. (2015) may have

277   been a consequence of an alternative method of assessment used when tandem running is not

278   used. It seems possible that individuals in Franks et al. (2015) spent longer in nests of higher

279   quality, resulting in colonies being able to make accurate decisions without the need for

280   recruitment. Seemingly one of the causes for a difference between the results of Franks et al.

281   (2015) and those in this paper are a consequence of the rating systems in each being of

282   differing levels of continuity. The mechanism proposed by Franks et al. (2015) is continuous,

283   whereby the length of time an individual spends in a nest is a linear function of nest quality.

284   In contrast, the mechanism that we propose the ants use in this experiment is discrete,

285   whereby individuals perform a tandem run when they observe a 'good' nest, but not when

286   they observe a 'poor' or 'mediocre' nest. Consequently, colonies in this experiment were not

287   able to discriminate between 'mediocre' and 'poor' nests, whereas in Franks et al. (2015)

288   they were.

289   It appears that the information transmitted by tandem leaders resulted in colonies

290   always selecting a nest that was occasionally 'good', over one that was consistently

291   'mediocre'. Examples of recruitment altering colony behaviors have been observed in both

292   social insects (Deneubourg et al., 1986; Pasteels and Deneubourg, 1987; Detrain and

293   Deneubourg, 2006; Sasaki et al., 2013) and humans (Kirman, 1993; Hirshleifer and Teoh,

294   2003). However, the difference between this case and others is that the extent of positive

295   feedback observed in this experiment was small with an average of only 5 tandem runs per

296   trial (median = 5, I.Q.R. = 6). This demonstrates the influence that a few important events can

297   have on collective decisions and shows how even low levels of positive feedback can alter

298   decision accuracy.

299   Negative feedback mechanisms are important in preventing positive feedback causing

300   incorrect choices in collective decision-making systems (Camazine et al., 2003). However, in

301   certain systems the occurrence of uncontrolled positive feedback is generally observed in

302   experimental scenarios that are presumably rare in nature (e.g. Deneubourg et al., 1986;

303   Pasteels and Deneubourg, 1987; Detrain and Deneubourg, 2006). Negative feedback

304   mechanisms have been identified in *Temnothorax* species (e.g. Sasaki et al. 2014; Stroeymeyt

305   et al. 2014). Furthermore, there is evidence for negative feedback mechanisms to prevent

306   mistaken recruitment in honey-bees (Kietzman and Visscher 2015). However there is no

307   known negative feedback mechanism that acts against misdirected tandem running. This

308   appears to be the case in this experiment as extreme fluctuations in light levels are probably

309   not common in the rock crevices *T. albipennis* generally inhabit. This could be the reason that

310   *T. albipennis* has not adapted to avoid the effects of positive feedback through tandem

311   running. Never the less, experiments that present subjects with such manipulations are a

312   useful method for investigating how mechanisms of behavior work as they allow researchers

313   to examine such mechanisms in detail..

314   The reason that the ants behave in this way may give us an indication of the

315   conditions under which colonies live in the wild. Colonies of this species are found at high

316   densities in the wild (Partridge et al., 1997) and competition between colonies for living

317   space is probably important. Therefore, responding to the discovery of a good potential nest

318   site quickly by tandem running could be essential to a colony finding somewhere to live.

319   The results of this experiment show improvement in emigration speed over time

320   (Figure 7b). Langridge et al. (2004) found that colonies are able to increase migration

321   efficiency with experience, but only when the previous migration was within the past 6 days.

322   In this experiment there was an interval of 14 days between trials and there were still signs of

323   improvement (Figure 7b). One possible cause for this difference might be the presence of

324   tandem running; which rarely occurred in Langridge et al. (2004) because the use of small

325   arenas and 'emergency' migrations, in which the current nest is made uninhabitable. Here,

326   faster decision-making seems to be the result of earlier tandem running in subsequent trials;

327   tandem runs were observed earlier and more frequently in the first hour in subsequent trials.

328   Individuals that performed tandem runs in the first experiment may be better at retaining

329   information regarding the layout of the arena or scenario, which could have prompted them to

330   tandem run earlier. Alternatively, colonies that have previously migrated in a 'move-to-

331   improve' scenario, as in the present experiment, could be able to improve migration

332   efficiency over longer time periods than those that have migrated in an 'emergency' scenario,

333   as in Langridge et al. (2004). Regardless of the mechanism, this result indicates that the

334   findings of Langridge et al. (2004) may be restricted to certain situations. However, further

335   investigation of this effect is required before a full conclusion can be drawn.

336   This study shows a strong effect of tandem running on the way that colonies make

337   decisions. The high standard of nest required to induce tandem running is probably important

338   in preventing wasteful recruitment to poor quality nests. However, in this scenario it led

339   colonies to migrate to a nest that was poorer than an alternative nest for the majority of the

340   time. This demonstrates how influential social information can be in collective decision-

341   making systems. These results also show the power of tandem running in influencing colony

342   decisions and the mechanisms by which ant colonies are able to respond to a high quality nest

343   site rapidly.

344 **Data accessibility**

345 All data are available from XXXX

346 **References**

347   Bikhchandani S, Hirshleifer D, Welch I, 1998. Learning from the behavior of others:

348   Conformity, fads, and informational cascades. Journal of Economic Perspectives 12:151-

349   170.

350   Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E, 2003. How

351   self-organization works. Self-organization in biological systems NJ, USA: Princeton

352   University Press.

353   Deneubourg J-L, Aron S, Goss S, Pasteels JM, 1987. Error, communication and learning

354   in ant societies. European Journal of Operational Research 30:168-172. doi:

355   10.1016/0377-2217(87)90093-2.

356   Deneubourg J-L, Aron S, Goss S, Pasteels JM, Duerinck G, 1986. Random behaviour,

357   amplification processes and number of participants: How they contribute to the foraging

358   properties of ants. Physica D-Nonlinear Phenomena 22:176-186. doi: 10.1016/0167-

359   2789(86)90239-3.

360   Detrain C, Deneubourg J-L, 2006. Self-organized structures in a superorganism: do ants

361   "behave" like molecules? Physics of Life Reviews 3:162-187. doi:

362   10.1016/j.plrev.2006.07.001.

363   Dornhaus A, Franks NR, Hawkins RM, Shere HNS, 2004. Ants move to improve:

364   colonies of Leptothorax albipennis emigrate whenever they find a superior nest site.

365   Animal Behaviour 67:959-963. doi: 10.1016/j.anbehav.2003.09.004.

366   Edwards SC, Pratt SC, 2009. Rationality in collective decision-making by ant colonies.

367   Proceedings of the Royal Society B-Biological Sciences 276:3655-3661. doi:

368   10.1098/rspb.2009.0981.

369   Franks NR, Dornhaus A, Best CS, Jones EL, 2006a. Decision making by small and large

370   house-hunting ant colonies: one size fits all. Animal Behaviour 72:611-616. doi:

371   10.1016/j.anbehav.2005.11.019.

372   Franks NR, Dornhaus A, Fitzsimmons JP, Stevens M, 2003a. Speed versus accuracy in

373   collective decision making. Proceedings of the Royal Society B-Biological Sciences

374   270:2457-2463. doi: 10.1098/rspb.2003.2527.

375   Franks NR, Dornhaus A, Metherell BG, Nelson TR, Lanfear SAJ, Symes WS, 2006b. Not

376   everything that counts can be counted: ants use multiple metrics for a single nest trait.

377   Proceedings of the Royal Society B-Biological Sciences 273:165-169. doi:

378   10.1098/rspb.2005.3312.

379   Franks NR, Mallon EB, Bray HE, Hamilton MJ, Mischler TC, 2003b. Strategies for

380   choosing between alternatives with different attributes: exemplified by house-hunting

381   ants. Animal Behaviour 65:215-223. doi: 10.1006/anbe.2002.2032.

382   Franks NR, Richardson T, 2006. Teaching in tandem-running ants. Nature 439:153-153.

383   doi: 10.1038/439153a.

384   Franks NR, Stuttard JP, Doran C, Esposito JC, Master MC, Sendova-Franks AB, Masuda

385   N, Britton NF, 2015. How ants use quorum sensing to estimate the average quality of a

386   fluctuating resource. Scientific Reports. Advance online publication. doi:

387   10.1038/srep11890.

388   Gottlieb D, Phillips BB, Sendova-Franks AB, Franks NR, 2013. Individual and social

389   information gathering are fine-tuned to the internal state of the group. Animal Behaviour

390   85:1479-1484. doi: 10.1016/j.anbehav.2013.03.046.

391   Gruter C, Leadbeater E, 2014. Insights from insects about adaptive social information

392   use. Trends in Ecology & Evolution 29:177-184. doi: 10.1016/j.tree.2014.01.004.

393   Helbing D, Farkas I, Vicsek T, 2000. Simulating dynamical features of escape panic.

394   Nature 407:487-490. doi: 10.1038/35035023.

395   Hirshleifer D, Teoh SH, 2003. Herd behaviour and cascading in capital markets: A review

396   and synthesis. European Financial Management 9:25-66. doi: 10.1111/1468-036X.00207.

397   Hölldobler B, Möglich M, Maschwitz U, 1974. Communication by tandem running in the

398   ant *Camponotus sericeus*. Journal of Comparative Physiology 90:105-127. doi:

399   10.1007/BF00694481.

400   Kietzman PM, Visscher PK, 2015. The anti-waggle dance: use of the stop signal as

401   negative feedback. Frontiers in Ecology and Evolution. 3: 14. doi:

402   10.3389/fevo.2015.00014.

403   Kirman A, 1993. Ants, rationality, and recruitment. Quarterly Journal of Economics

404   108:137-156. doi: 10.2307/2118498.

405   Laland KN, Williams K, 1998. Social transmission of maladaptive information in the

406   guppy. Behavioral Ecology 9:493-499. doi: 10.1093/beheco/9.5.493.

407   Langridge EA, Franks NR, Sendova-Franks AB, 2004. Improvement in collective

408   performance with experience in ants. Behavioral Ecology and Sociobiology 56:523-529.

409   doi: 10.1007/s00265-004-0824-3.

410   Mallon EB, Pratt SC, Franks NR, 2001. Individual and collective decision-making during

411   nest site selection by the ant Leptothorax albipennis. Behavioral Ecology and

412   Sociobiology 50:352-359. doi: 10.1007/s002650100377.

413   Mallon EB, Pratt SC, Franks NR, 2001. Individual and collective decision-making during

414   nest site selection by the ant Leptothorax albipennis. Behavioral Ecology and

415   Sociobiology 50:352-359. doi: 10.1007/s002650100377.

416   McAllister I, Studlar DT, 1991. Bandwagon, underdog, or projection - opinion polls and

417   electoral choice in Britain, 1979-1987 Journal of Politics 53:720-741. doi:

418   10.2307/2131577.

419   Möglich M, 1978. Social-organization of nest emigration in Leptothorax (Hym form).

420   Insectes Sociaux 25:205-225. doi: 10.1007/bf02224742.

421   Partridge LW, Partridge KA, Franks NR, 1997. Field survey of a monogynous

422   leptothoracine ant (Hymenoptera, Formicidae): Evidence of seasonal polydomy? Insectes

423   Sociaux 44:75-83. doi: 10.1007/s000400050031.

424   Partridge LW, Partridge KA, Franks NR, 1997. Field survey of a monogynous

425   leptothoracine ant (Hymenoptera, Formicidae): Evidence of seasonal polydomy? Insectes

426   Sociaux 44:75-83. doi: 10.1007/s000400050031.

427   Pasteels JM, Deneubourg J-L, 1987. Self-Organization Mechanisms in Ant Societies (I)

428   Trail Recruitment to Newly Discovered Food Sources. In: Pasteels JMD, J.-L., editor.

429   From Individual to Collective Behaviour in Social Insects Basel: Birkhauser. p. 155-175.

430   Pavliotis G, Stuart A, 2008. *Multiscale Methods: Averaging and Homogenization.*

431   Springer

432   Pratt SC, 2005. Quorum sensing by encounter rates in the ant Temnothorax albipennis.

433   Behavioral Ecology 16:488-496. doi: 10.1093/beheco/ari020.

434   Pratt SC, Mallon EB, Sumpter DJT, Franks NR, 2002. Quorum sensing, recruitment, and

435   collective decision-making during colony emigration by the ant Leptothorax albipennis.

436   Behavioral Ecology and Sociobiology 52:117-127. doi: 10.1007/s00265-002-0487-x.

437   R Core Team 2014. R: A language and environment for statistical computing. Vienna: R

438   Foundation for Statistical Computing

439   Rieucau G, Giraldeau L-A, 2011. Exploring the costs and benefits of social information

440   use: an appraisal of current experimental evidence. Philosophical Transactions of the

441   Royal Society B-Biological Sciences 366:949-957. doi: 10.1098/rstb.2010.0325.

442   Robinson EJH, Franks NR, Ellis S, Okuda S, Marshall JAR, 2011. A simple threshold

443   rule is sufficient to explain sophisticated collective decision-making. Plos One 6. doi:

444   10.1371/journal.pone.0019981.

445   Robinson EJH, Smith FD, Sullivan KME, Franks NR, 2009. Do ants make direct

446   comparisons? Proceedings of the Royal Society B-Biological Sciences 276:2635-2641.

447   doi: 10.1098/rspb.2009.0350.

448   Sasaki T, Granovskiy B, Mann RP, Sumpter DJT, Pratt SC, 2013. Ant colonies

449   outperform individuals when a sensory discrimination task is difficult but not when it is

450   easy. Proceedings of the National Academy of Sciences of the United States of America

451   110:13769-13773. doi: 10.1073/pnas.1304917110.

452   Sasaki T, Hölldobler, Millar JG, Pratt SC, 2014. A context-dependent alarm signal in the

453   ant Temnothorax rugatulus. Journal of Experimental Biology 217: 3229-3236.

454   10.1242/jeb.106849

455   Sasaki T, Pratt SC, 2011. Emergence of group rationality from irrational individuals.

456   Behavioral Ecology 22:276-281. doi: 10.1093/beheco/arq198.

457   Stroeymeyt N, Jordan C, Mayer G, Hovsepian S, Giurfa M, Franks NR, 2014. Seasonality

458   in communication and collective decision-making in ants. Proceedings of the Royal

459   Society B-Biological Sciences 281: 20133108. doi: 10.1098/rspb.2013.3108

460   Surowiecki J, 2004. The wisdom of crowds. New York: Doubleday.

461   Von Frisch K, 1967. The dance language and orientation of bees. Harvard: Harvard

462   University Press.

463   Wickham H, 2009 ggplot2: elegant graphics for data analysis. Springer New York,

464   Wolf M, Kurvers RHJM, Ward AJW, Krause S, Krause J, 2013. Accurate decisions in an

465   uncertain world: collective cognition increases true positives while decreasing false

466   positives. Proceedings of the Royal Society B-Biological Sciences 280. doi:

467   10.1098/rspb.2012.2777.

468

469

470

471

Figure legends

Figure 1. Holding nest before (left) and after the removable wall has been detached at the start of the experiment (right)

Figure 2. Experimental set up used in all trials.

Figure 3. Choices between the fluctuating and constant nest for trials in which colonies performed tandem runs before reaching a quorum. The percentage of time a nest was good corresponds to 10 min periods of fluctuations (i.e. 25% good was good for 2.5min and bad for 7.5min in every 10 min for the duration of the experiment).

Figure 4. Changes over time in the number of ants in each potential nest until a quorum was reached. Colonies which did not migrate, split or did not perform tandem runs were excluded. Each colour represents a colony for both fluctuating and mediocre nests in each condition. The percentage of time a nest was good corresponds to 10 min periods of fluctuations (i.e. 25% good was 'good' for 2.5 min and 'poor' for 7.5 min for the duration of the experiment).

Figure 5. A: Number of tandem runs before a decision was reached for different conditions B: Number of tandem runs before a decision was reached for first and second trials. The percentage of time a nest was good corresponds to 10 min periods of fluctuations (i.e. 25% good was 'good' for 2.5 min and 'poor' for 7.5 min for the duration of the experiment).

Figure 6. A: Quorum number for each condition B: Quorum number for first and second trials. The percentage of time a nest was good corresponds to 10 min periods of fluctuations (i.e. 25% good was 'good' for 2.5 min and 'poor' for 7.5 min for the duration of the experiment).

Figure 7. A: Time taken to reach a quorum for each condition; B: Time taken to reach a quorum for first and second trials. The percentage of time a nest was good corresponds to 10

495   min periods of fluctuations (i.e. 25% good was 'good' for 2.5 min and 'poor' for 7.5 min for

496   the duration of the experiment).

497

498

499

500   **Tables**

501   **Table 1.** Parameters of nests of different quality. All nests had an inner cavity with the

502   dimensions 55mm x 30mm x 1.6mm

Nest quality	Nest entrance width (mm)	Light level
Poor	4	Light
Mediocre	1	Light
Good	4	Dark

503

504

505   **Table 2.** Quality of each nest type over 10min periods for each of the conditions

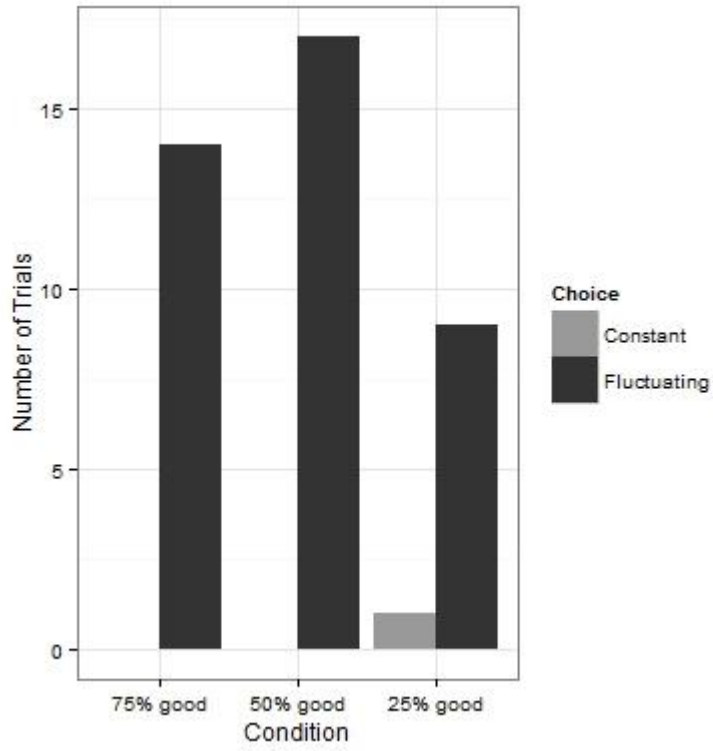| Condition	Constant nest	Fluctuating nest
75% good	Mediocre	Good for 7.5min/ bad for 2.5min
50% good	Mediocre	Good for 5min/ bad for 5min
25% good	Mediocre	Good for 2.5min/ bad for 7.5min

506

507

508

509   Fig 1

2cm

Removable   Fluctuating   Acetate   Holding   Constant   Removable
red filter   nest   bridge   nest   nest   transparent filter

5cm
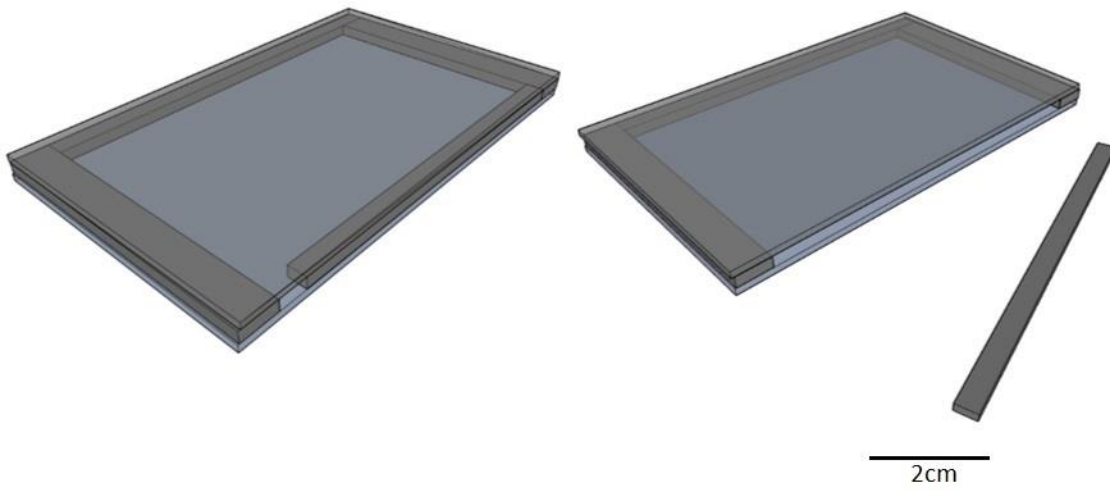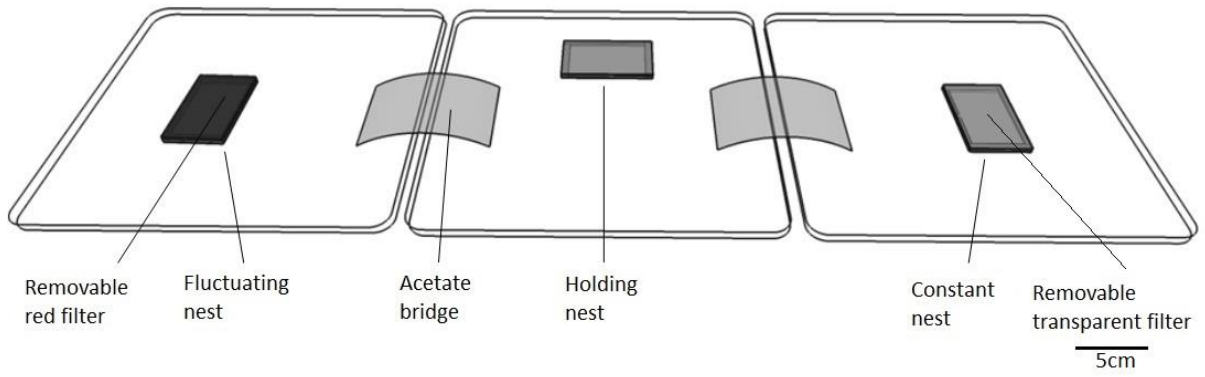
510

511   Fig 2

512

513   Fig 3

514

515

516

517

518
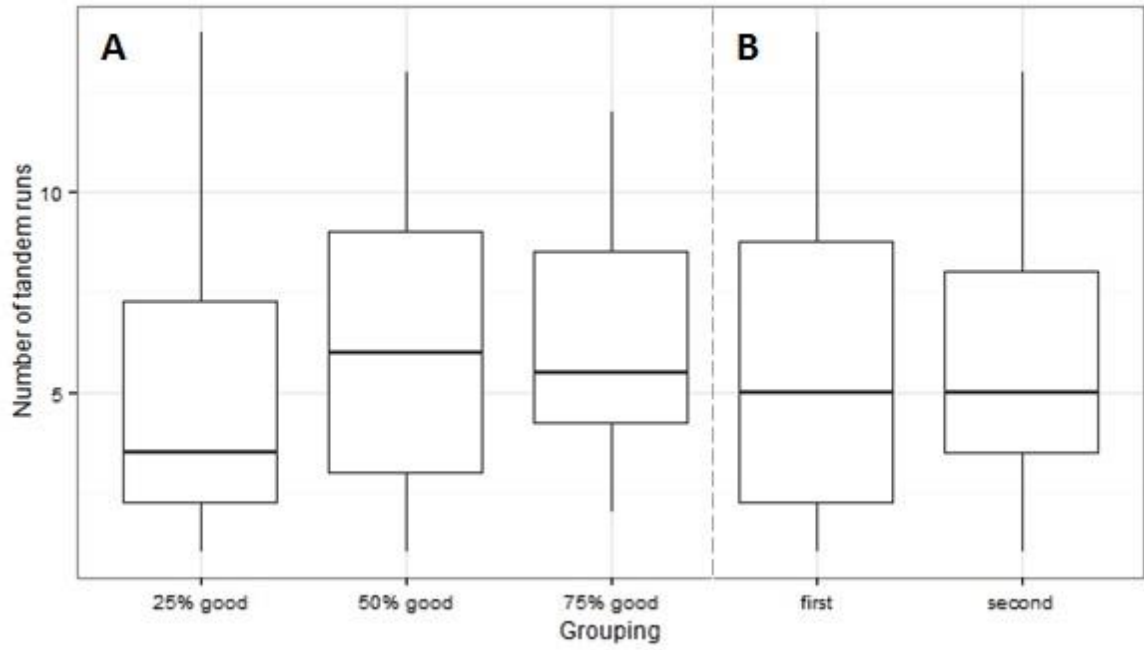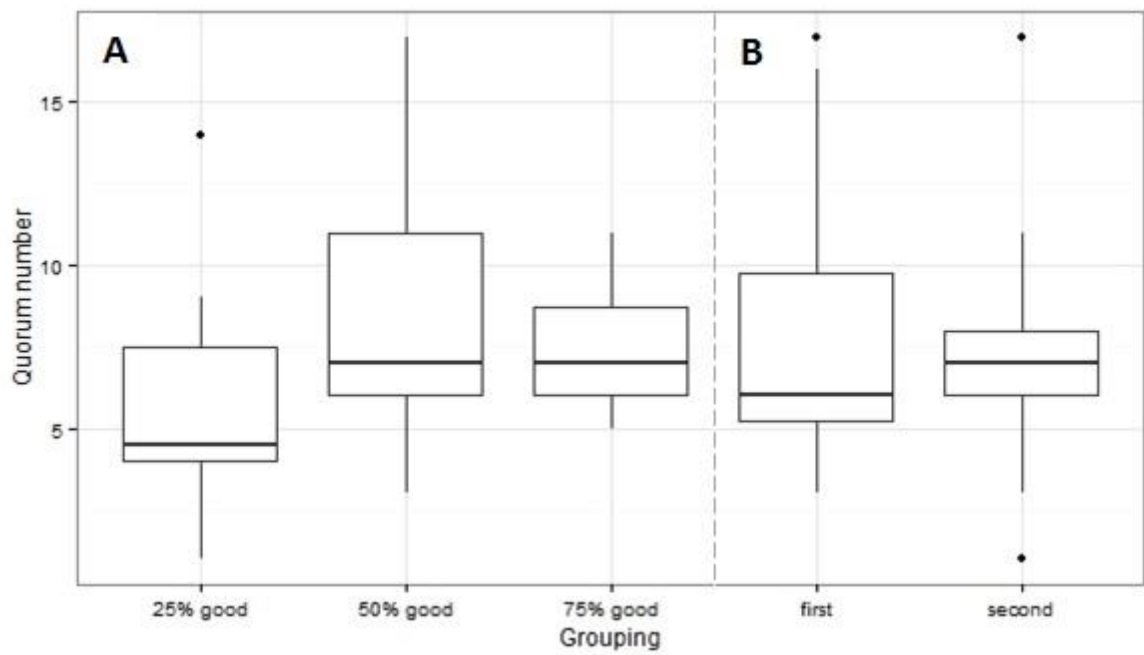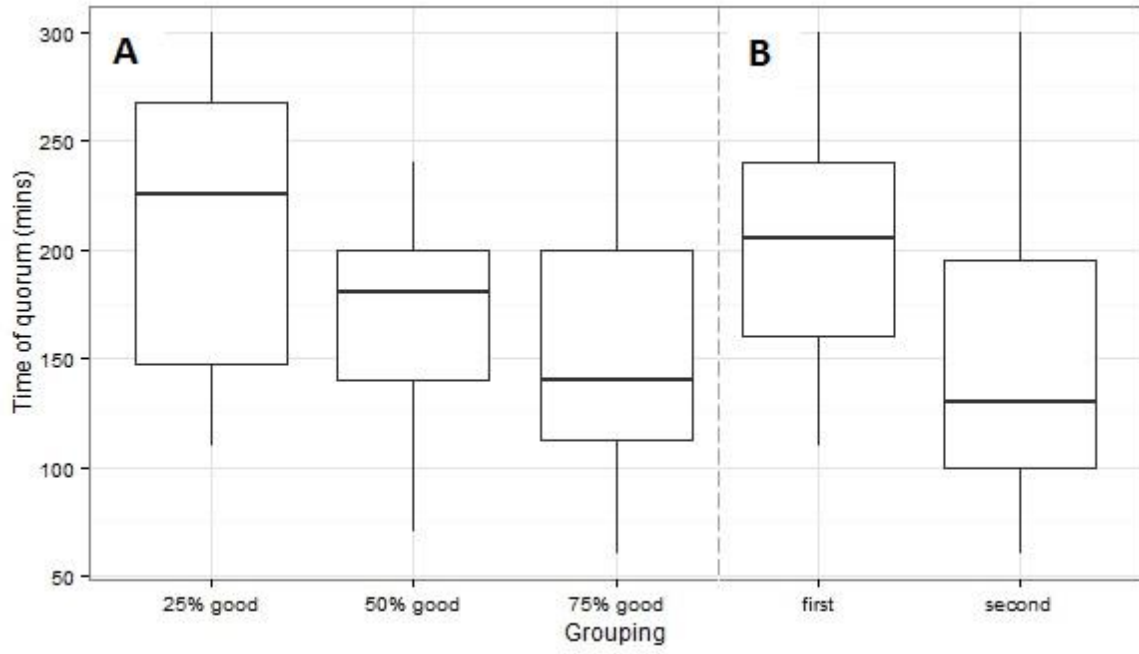
519

520

521

522

523
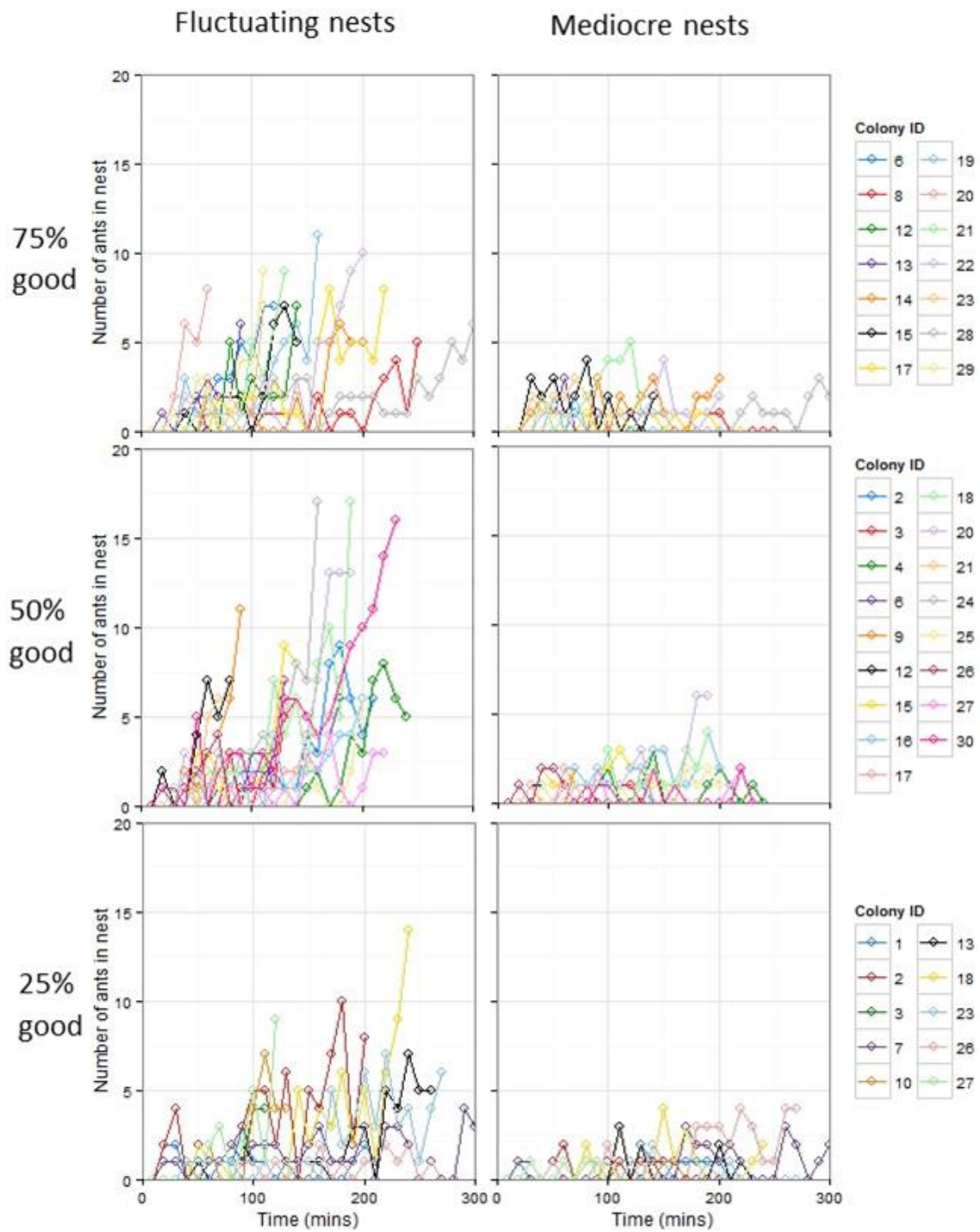
524

525   Fig 4

526

527

528

529

530   Fig 5

531

532   Fig 6

533

534
535   Fig 7