

1 **A social mechanism facilitates ant colony emigrations over**  
2 **different distances**

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13 **Social control of emigrations in ants**

14  
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## 27 **Summary statement**

28 Within social systems, we often see ‘key’ individuals that are disproportionately active in various tasks. Here  
29 however, we show that the contribution of such individuals may be far from decisive.

## 30 **Abstract**

31 Behavioural responses enable animals to react rapidly to fluctuating environments. In eusocial organisms, such  
32 changes are often enacted at the group level, but may be organised in a decentralised fashion by the actions of  
33 individuals. However, the contributions of different group members are rarely homogenous, and there is  
34 evidence to suggest that certain ‘keystone’ individuals are important in shaping collective responses.  
35 Accordingly, investigations of the dynamics and structuring of behavioural changes at both the group and  
36 individual level, are crucial for evaluating the relative influence of different individuals. Here, we examine the  
37 composition of tandem running behaviour during colony emigrations in the ant species *Temnothorax albipennis*.  
38 Tandem running is modulated in response to emigration distance, with more runs being conducted when a more  
39 distant nest site must be reached. We show that certain individuals are highly active in the tandem running  
40 process, attempting significantly more work in the task. Contrary to expectations, however, such individuals are  
41 in fact no more successful at conducting tandem runs than their less active nest mates. Instead, it seems that  
42 when more tandem runs are required, colonies rely on greater recruitment of workers into the process. The  
43 implications of our study are that in some cases, even when apparently ‘key’ individuals exist within a group,  
44 their relative contribution to task performance may be far from decisive.

## 45 **Introduction**

46 Spanning a broad range of species and genera, behavioural modification constitutes an essential component of  
47 the adaptive repertoires of animals. Examples range from simple Pavlovian responses in mammals (Jenkins et  
48 al. 1978), to complex, multi-generational cultural changes in human societies (Kirk 1996; Inglehart 1997) and  
49 inter-species mutualisms in the social insects (Way 1963). Common to all of these strategies, is the advantage of  
50 rapid benefits when compared to the more gradual changes elicited by natural selection alone. Considerable  
51 effort has been invested into studying behavioural changes at both the group (Barsade 2002; Langridge et al.  
52 2004) and the individual level (Shettleworth 2001). However, the interplay between the two, especially in  
53 complex networks, is less well understood (Bornstein & Yaniv 1998; Franklin & Franks 2012; Anderson &  
54 McShea 2001; Hunt et al. 2016).

55 Social insects display complex life history characteristics, underpinned by efficient colony organisation, and  
56 thus provide excellent models for studying how group level behavioural changes are structured through the  
57 actions of individuals. This is in no small part due to their propensity for self-organisation, whereby complex  
58 processes may emerge without the need for centralised control, an ability that many human systems lack  
59 (Camazine et al. 2003). Self-organisation can lead to the formation of adaptive, but flexible group behaviours,  
60 which often confer additional benefits to colony functioning (Goss et al. 1989). Hence, such behaviours are of  
61 interest when attempting to elucidate how multi-level behavioural change is structured. Colony relocation  
62 represents one process that is regulated at both the group and individual level in social insects, and indeed, wide

63 variation exists among species in relation to how migration effort is assigned. Examples range from varying  
64 distributions of worker effort within colonies, as seen in the ant *Myrmecina nipponica* (Cronin 2015), to extreme  
65 cases where a single individual is key to overall collective organisation, such as in the queenless Ponerine,  
66 *Diacamma indicum* (Sumana and Sona 2013).

67 In the ant *Temnothorax albipennis*, emigration behaviour is regulated at the group level to best suit  
68 environmental conditions, but relies on individual contributions and information sharing (Franks & Richardson  
69 2006). Colonies of this species reside within rock cavities in a moderately heterogeneous and unstable  
70 environment, and as such, they frequently have to emigrate to potential new nest sites in order to maintain their  
71 protection from external threats (Dornhaus et al. 2004). Before an emigration can occur, however, scouting  
72 workers must accumulate within a new nest site until a ‘quorum threshold’ is reached (Pratt 2004). A key  
73 behaviour in this process is tandem running, in which workers lead their nest mates to the location of a potential  
74 nest site or food source (Franklin & Franks 2012). During a tandem run, the leading worker will maintain  
75 intermittent tactile contact between its gaster and a follower’s antennae, leading it to the desired resource via an  
76 often-tortuous journey, and thus informing it of the route (Franks & Richardson 2006). Previous work has  
77 shown that colonies of *T. albipennis* increase their rate of tandem running; defined as the total number of  
78 tandem runs in relation to colony size, during emigrations where the target nest site is further away (O’Shea-  
79 Wheller et al. 2016). This may be explained by the need to reduce emigration time and thus colony exposure  
80 during more distant emigrations (Traniello 1989), and it is elicited by a reduction in the rate of nest discovery  
81 (Pratt 2004). Despite being colony wide phenomena, tandem running responses are necessarily achieved by  
82 perception at the individual level, whereby workers determine that a quorum has not yet been met in a new nest  
83 site (Pratt 2004). As a consequence, the individual propensities of ants to engage in tandem running are likely to  
84 influence the overall structuring of the process, yet the dynamics of this remain unexplored.

85 Several potential hypotheses may explain how individuals contribute to an increase in tandem running over  
86 longer emigration distances. First, workers that would not usually be involved begin to assist in leading or  
87 following tandem runs. Second, a ‘core’ of the same highly active workers simply lead more tandem runs  
88 themselves, or third, a combination of both may occur. The relative likelihood and significance of such options  
89 is uncertain, as previous studies have shown complex and differing structures of work distribution within  
90 colonies. Much of the work conducted to date supports the concept that *T. albipennis* colonies have some  
91 ‘specialist’ workers in relation to certain task groups (Dornhaus 2008; Dornhaus et al. 2008). It has been noted  
92 that task propensities are positively correlated within groups of related tasks e.g. ‘foraging’ and ‘emigration’.  
93 Moreover, workers highly active in one task group may be less so in others (Pinter-Wollman et al. 2012),  
94 suggesting ‘situational specialisation’. Nevertheless, some workers may still be persistently active across all task  
95 groups (termed elites), though they constitute only a small proportion of individuals (Pinter-Wollman et al.  
96 2012). In addition, the extent of specialisation may vary depending on colony characteristics, for example, it has  
97 been shown that during brood carrying, smaller colonies will employ some specialist workers that are more  
98 active than others, while in larger colonies, each active individual contributes more evenly to the process  
99 (Dornhaus et al. 2008). Consequently, a greater understanding of how increased tandem running and other  
100 behavioural changes occur during more distant emigrations, should help to shed light upon the underlying  
101 processes that govern group and individual behaviour in a decentralised system.

102 In this study, we examined several key stages in both short and long distance emigrations at the group and  
103 individual level, in an effort to determine how behavioural changes were structured across individuals. Chiefly,  
104 we wished to determine if increases in the rate of tandem running were due to key individuals up-regulating  
105 their activity, more workers becoming involved, or indeed a mix of these two. We also tested the hypothesis that  
106 workers would alter their average tandem running return speed across emigration distances, as faster return rates  
107 would allow ants to recruit other colony members to a new nest more rapidly. Additionally, we attempted to  
108 determine if there was a link between initial scouting behaviour and a worker's subsequent propensity to  
109 become actively engaged in emigrations.

110 We addressed these questions by quantifying colony level changes, including those associated with tandem  
111 running, scouting, average return speed, and workforce mobilisation. Then, in order to dissect the processes  
112 underlying such changes, we measured distributions of individual scouting, tandem running, and movement  
113 speed, having uniquely marked all workers within each of the 10 experimental colonies. Furthermore, we  
114 identified behavioural sub-groups of workers by categorising individuals in relation to their engagement in only  
115 one, or both emigration distances. We then assessed differences in attempted and successful per capita tandem  
116 running workloads between these groups, to quantify their relative importance to the system as a whole.

## 117 **Materials and methods**

### 118 *a) Colonies*

119 We collected ten colonies of *Temnothorax albipennis* (Curtis, 1854) from the isle of Portland, Dorset on 29<sup>th</sup> of  
120 September 2015. Colonies contained between 47 and 187 workers, between 19 and 130 brood items and each  
121 had a single queen. No specific permission was required for collection, with ants being taken from a disturbed  
122 quarry area open to the public. Additionally, no collection permit was required, as *T. albipennis* is not a  
123 protected species. In order to minimise the impact of colony removal on the local population and ecology, we  
124 used an established rota to vary collection location, based on date.

125 Colonies were migrated into initial laboratory nests and allowed to acclimatise for a period of 7 days after  
126 collection. We maintained them in the laboratory under established conditions (Dornhaus et al. 2004; Franks et  
127 al. 2003), with all nests being housed in plastic Petri dishes featuring Fluon coated sides. Ants were fed weekly  
128 with *Drosophila melanogaster* (Meigen, 1830), and allowed to forage for water and honey solution *ad libitum*.

### 129 *b) Marking*

130 The ten colonies were randomly numbered in order to determine a marking sequence. For each colony in turn,  
131 we anaesthetised all workers with CO<sub>2</sub> and painted them with a unique permutation of three colours, one on the  
132 thorax and two on the gaster (fig. 1A). A mounted single-hair and microscope were used in order to apply the  
133 paint with precision. Markings corresponded to an identification key, allowing rapid determination of individual  
134 identity, in addition to total colony populations (S1, Tab1). Care was taken to ensure that CO<sub>2</sub> exposure was  
135 kept to a minimum, and there was at least a 48h interval between marking and experimental trials, as studies  
136 have shown that insect behaviour may be affected after anoxia (Poissonnier et al. 2015). Further precautions

137 were taken to ensure that paint did not cover the gaster tips of workers, as this may impair the use of chemical  
138 signalling (Stuttard et al. 2015).

139 *c) Nest design*

140 We utilised two different nest qualities in our experiment; ‘poor’ and ‘excellent’. Colonies were initially housed  
141 in ‘poor’ quality nests, and allowed to emigrate into the ‘excellent’ nests during trials. Both designs were  
142 composed of microscope-slide lids and bases with a cardboard perimeter sandwiched between the two to create  
143 an internal cavity. The area of this cavity was constant across both nest qualities, measuring 65x35mm. ‘Poor’  
144 quality nests had 1 mm high walls, a 6 mm wide entrance and a clear cover, while ‘excellent’ quality nests had 2  
145 mm high walls, a 1 mm wide entrance and a red filter cover. These differences combined to make excellent  
146 nests more spacious, more secure, and darker than ‘poor’ quality nests, and thus far superior in the ants’  
147 assessment (Franks et al. 2003).

148 *d) Emigration trials*

149 All colonies underwent emigration trials under ‘move-to-improve’ conditions, in which their original nests were  
150 left intact, allowing them to emigrate of their own accord to the superior ‘excellent’ quality nests (Dornhaus et  
151 al. 2004), at distances of 100 mm and 300 mm (fig. 1B,C). Twenty emigrations were conducted in total, over a  
152 period of 35 days, with each colony performing two emigrations in turn. In order to account for the potential  
153 experience effects of multiple emigrations (Langridge, Sendova-Franks, & Franks, 2008), using random  
154 assignment, five of the colonies underwent the 100 mm trial first, and five the 300 mm trial first.

155 Prior to the initiation of each trial, we cleaned 1000x1000 mm arenas with 70% ethanol solution, and  
156 illuminated them evenly using the laboratory lighting system (4100 Lumens, Colour rendering index: 85).  
157 Colonies housed in their original ‘poor’ nests were then transferred into the arenas and empty ‘excellent’ quality  
158 nests were placed at either 100 mm or 300 mm from them. At the initiation of experiments, the emigration  
159 process was observed and we began monitoring scout identities and numbers, tandem leader and follower  
160 identities and tandem durations, tandem run success rate at the two different distances, average ant return speed,  
161 and the total numbers of ants in the arena and nests (at 10min intervals). Additionally, HD video recording  
162 equipment (Panasonic HC-X900 series) was set up over both nest sites for the duration of emigrations, in order  
163 to facilitate further data analysis (fig. 1B, C).

164 *e) Range of assessment factors*

165 Analyses were broadly divided into investigations of the distribution of tandem running among workers, average  
166 return speeds, and the effect of scouting propensity on emigration engagement. Within these groups, we  
167 examined both colony level behaviour, and that of individual ants (via marking).

168 To quantify behavioural changes in tandem running distribution, we compared the total number of tandem runs  
169 per colony; percentage colony engagement in tandem leading or following, and the total number of tandem runs  
170 per ant. By measuring the total number of tandem runs per individual, we were able to compare the activity of  
171 ants that were involved at a single emigration distance, to those involved across both emigration distances. This  
172 division method was important for testing the hypothesis that the same key individuals would conduct  
173 significantly more tandem runs at a longer distance (i.e. those individuals comprising the ‘both’ group).

174 To achieve this, workers were divided into two groups; those actively engaged in only one emigration distance  
175 (the ‘either’ group), and those actively engaged in both emigration distances (the ‘both’ group). Engagement in  
176 an emigration was defined as workers conducting scouting, tandem running, or both.

177 We then compared the attempted and successful per capita tandem running workload of ants using the same  
178 division method, in order to account for the different sizes of these groups. Per capita tandem-running workload  
179 constituted the average amount of tandem running work (leading or following) done by each tandem-running  
180 worker, as a proportion of the total tandem running work conducted by all workers in a given emigration, and  
181 thus was a measure of individual contributions. In concert with the total absolute numbers of tandem runs  
182 conducted by workers, the use of this proportional measure allowed us to determine the relative importance of  
183 worker groups in the tandem running process at different distances. Additionally, we tested the effect of  
184 numbers of attempted tandem runs on an individual’s tandem running success.

185 We quantified average worker return speed across the two emigration distances, pooled by colony. When  
186 returning to their old nest, workers take a direct route between sites (Franks & Richardson 2006), and thus speed  
187 was calculated as a function of distance over time. To assess the effect of prior scouting on an individual’s  
188 propensity to engage in emigrations, we measured scouting effort (defined as the numbers of ants exploring  
189 outside the nest over time) across colonies, and the effect of prior scouting experience (defined as leaving the  
190 nest to explore) on a worker’s subsequent involvement in tandem running. New-nest discovery time, percentage  
191 colony involvement in emigrations and quorum attainment time were also analysed.

#### 192 *f) Statistical analysis*

193 For all colony-level data, we used Shapiro-Wilk tests to check for normality, and hence to inform the application  
194 of appropriate statistical tests. Where the data were found to be normally distributed, we conducted either paired  
195 or independent t-tests. For measures in which the data were not normally distributed, we used a combination of  
196 Wilcoxon signed-ranks tests and Independent Sample Mann-Whitney U tests. As non-parametric tests are less  
197 powerful than parametric ones, when the significance level was between 0.05 and 0.1, we double-checked  
198 results by applying parametric methods to transformed data. In all such cases, the significance of the tests was  
199 unaltered.

200 When individual data were used, we employed Generalised Linear Mixed Models to account for the effect of  
201 colony and worker ID. All GLMMs included at most, two fixed predictor variables. Model selection was based  
202 on AIC and always began with the full model, involving interaction. The fit of all GLMMs was validated via  
203 analyses of Pearson residuals. All statistical analyses were performed in SPSS (Release versions 21.0.0.0,  
204 23.0.0.0, IBM Corporation and other(s) 1989, 2012, 2016).

#### 205 *Tandem running at colony level*

206 We used a combination of paired-sample t-tests for measures with normally distributed data, and Wilcoxon  
207 signed-ranks tests for measures where the data were not normally distributed.

208

209

210 *Individual tandem running distribution*

211 GLMMs assessing the effect of the number of leading and following attempts on successes of leading and  
212 following, used leading or following success/failure as the binomial response variables with a logit link, distance  
213 (100 mm or 300 mm) as a fixed factor predictor, number of attempted leads or follows as a covariate, and  
214 colony ID as a random factor. Worker ID was redundant, as no repeated measures were taken for any of the  
215 individuals. The GLMM assessing the number of attempted tandem runs by workers across emigration  
216 involvement groups used the total number of attempted tandem runs as a normal response variable with a log  
217 link, distance (100 mm or 300 mm) and involvement in either or both emigrations as fixed factor predictors, the  
218 interaction between the two, and colony ID and worker ID nested within colony ID as random factors. The  
219 GLMM assessing attempted per capita tandem running workload used per capita attempted workload as a  
220 normal response variable with a log link, distance (100 mm or 300 mm) and involvement in either or both  
221 emigrations as fixed factor predictors, the interaction between the two, and colony ID as a random factor. The  
222 GLMM assessing per capita successful tandem running workload used successful workload per capita as the  
223 normal response variable with a log link, distance (100 mm or 300 mm) and involvement in either or both  
224 emigrations as fixed factor predictors, the interaction between the two, and colony ID and worker ID nested  
225 within colony ID as random factors.

226 We used paired t-tests to compare the percentage of individuals involved at both emigration distances to those  
227 involved at only one distance for each colony.

228 *Average worker return speeds*

229 A Wilcoxon signed-ranks test was employed to determine differences in the average return speed of workers  
230 between the two distances.

231 *Scouting propensity and emigration engagement*

232 The difference in the number of active scouts between distances was tested using a Wilcoxon signed-ranks test.  
233 To calculate the tandem running propensity of workers based on previous scouting activity, we measured the  
234 numbers of ants engaging in tandem runs as a proportion of the total population in each scouting category (the  
235 two scouting categories were individuals previously involved in scouting, and individuals not previously  
236 involved in scouting), within colonies. This was assessed using a combination of Mann-Whitney U tests  
237 (leading) and independent sample t-tests (following). Differences between the two distances were quantified  
238 with a Mann-Whitney U test.

239 *Discovery times and quorum attainment*

240 Distance-based differences in the time of quorum attainment were tested with a paired-sample t-test, while  
241 differences in new nest discovery time were assessed with a Wilcoxon signed-ranks test.

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244

## 245 **Results**

### 246 *a) Tandem running at colony level*

247 Under the longer-distance emigration treatment, colonies on average employed a higher number of tandem runs  
248 (Wilcoxon signed-ranks tests,  $U=2.194$ ,  $n=10$ ,  $\text{median}_{100}=8.5$ ,  $\text{median}_{300}=14$ ,  $P=0.028$ , fig. 2A). By contrast, the  
249 percentage of successful tandem runs was reduced, on average, at the longer emigration distance, although this  
250 was not statistically significant (Paired-sample t-test,  $t=1.032$ ,  $df=9$ ,  $P=0.329$ , fig. 2B). Additionally, at the  
251 longer emigration distance, colonies utilised a greater percentage of their potential workforce in both tandem  
252 running (Paired-sample t-test,  $t=48.00$ ,  $df=9$ ,  $P=0.037$ ), and the emigration process *in toto* (scouting and tandem  
253 running) (Paired-sample t-test,  $t=-3.214$ ,  $df=9$ ,  $P<0.001$ ) (fig. 2C,D).

### 254 *b) Individual tandem running distribution*

255 Across both emigration distances, an individual's probability of leading a tandem run successfully, significantly  
256 increased with the number of leading attempts made (GLMM, odds ratio=1.422,  $df=140$ ,  $P=0.017$ ), independent  
257 of colony ID (Colony random effect:  $Z=0.918$ ,  $P=0.359$ ). Furthermore, in agreement with the colony-level data,  
258 tandem leaders had a higher probability of success when leading at the shorter distance (GLMM, odds  
259 ratio=2.100,  $P=0.030$ ). However, the number of following attempts had no significant impact on the probability  
260 of following success (GLMM, odds ratio=0.216,  $df=189$ ,  $P=0.735$ ), independent of the random factor (Colony  
261 random effect:  $Z=0.775$ ,  $P=0.439$ ). The probability of following success was higher, but not statistically  
262 significantly so, at the shorter distance (GLMM, odds ratio=1.284,  $P=0.427$ ).

263 Across colonies, the percentage of individuals involved (scouting or tandem running) in emigrations at both  
264 distances was smaller than the percentage involved at just one distance (Paired-sample t-test,  $t=-4.039$ ,  $df=9$ ,  
265  $P=0.001$ , fig. 3). The interaction between distance and involvement group was significant in its effect on the  
266 total number of tandem runs attempted per individual (GLMM, effect of interaction:  $F_{1,262}=4.455$ ,  $P=0.036$ , fig.  
267 4), indicating that worker group was important within distances. Specifically, the 'both' engagement group  
268 attempted more tandem runs per individual than the 'either' group at 300 mm (GLMM, Bonferroni post-hoc  
269 test:  $t=5.098$ ,  $df=262$ ,  $P<0.001$ ,  $\text{mean}_{\text{either}}=1.281$ ,  $\text{mean}_{\text{both}}=2.000$ ), but not at 100 mm (GLMM, Bonferroni post-  
270 hoc test:  $t=1.143$ ,  $df=262$ ,  $P=0.254$ ,  $\text{mean}_{\text{either}}=1.145$ ,  $\text{mean}_{\text{both}}=1.316$ ), suggesting a greater role for this group at  
271 the longer distance.

272 Following on from this, the per capita attempted tandem running workload of ants in the 'both' group was  
273 significantly higher than that in the 'either' group across both emigration distances (GLMM, effect of group:  
274  $F_{1,292}=18.327$ ,  $P<0.001$ ;  $\text{mean}_{\text{either}}=0.579$ ,  $\text{mean}_{\text{both}}=0.750$ ). The attempted per capita tandem running workload  
275 of the ants was lower at 300 mm than at 100mm, regardless of their involvement in either or both emigrations  
276 (GLMM, effect of distance:  $F_{1,292}=15.149$ ,  $P<0.001$ ,  $\text{mean}_{100}=0.741$ ,  $\text{mean}_{300}=0.586$ , fig. 5A). However, the  
277 interaction between distance and involvement group was very close to the threshold of significance (GLMM,  
278 effect of interaction:  $F_{1,292}=3.817$ ,  $P=0.052$ ). This may be explained by the per capita workload performed by the  
279 'both' group being significantly higher than for the 'either' group at 300 mm (GLMM, Bonferroni post-hoc test:



280  $t=4.026$ ,  $df=292$ ,  $P<0.001$ ,  $mean_{either}=0.486$ ,  $mean_{both}=0.708$ ), but not at 100 mm (GLMM, Bonferroni post-hoc  
281 test:  $t=1.762$ ,  $df=292$ ,  $P=0.079$ ,  $mean_{either}=0.691$ ,  $mean_{both}=0.795$ ).

282 Interestingly, when only successful tandem running workload was examined, these differences were somewhat  
283 diminished; per capita tandem running workload was still lower at 300 mm than at 100 mm across both  
284 involvement groups, (GLMM, effect of distance:  $F_{1,292}=4.831$ ,  $P=0.029$ ,  $mean_{100}=0.737$ ,  $mean_{300}=0.591$ , fig.  
285 5B). Ants in the ‘both’ group also still had a significantly higher successful per capita tandem running workload  
286 than those involved in the ‘either’ group across both distances (GLMM, effect of group:  $F_{1,292}=6.037$ ,  $P=0.015$ ,  
287  $mean_{either}=0.582$ ,  $mean_{both}=0.748$ , fig. 5B), however, the interaction between distance and whether ants were  
288 involved in either or both emigrations was not significant (GLMM, effect of interaction:  $F_{1,292}=0.012$ ,  $P=0.915$ ).  
289 This was due to a lack of difference within distances at both 100mm (GLMM, Bonferroni post-hoc test:  $t=1.774$ ,  
290  $df=292$ ,  $P=0.077$ ,  $mean_{either}=0.654$ ,  $mean_{both}=0.831$ ) and 300mm (GLMM, Bonferroni post-hoc test:  $t=1.677$ ,  
291  $df=292$ ,  $P=0.097$ ,  $mean_{either}=0.519$ ,  $mean_{both}=0.673$ ).

### 292 c) *Average worker return speeds*

293 The average return speed of workers across colonies was significantly higher for longer emigration distances  
294 (Wilcoxon signed-ranks test,  $U=-3.92$ ,  $n=10$ ,  $P<0.001$ , fig. 6).

### 295 d) *Scouting propensity and emigration engagement*

296 Before emigrating over the longer distance, on average, colonies employed significantly greater numbers of  
297 scouts (Wilcoxon signed-ranks test,  $U=2.253$ ,  $n=10$ ,  $P=0.024$ ,  $mean_{100}=16$ ,  $mean_{300}=25$ ). In any given  
298 emigration, previously scouting significantly increased a worker’s propensity both to lead (Mann-Whitney, U  
299 test,  $U=3.250$ ,  $n_{scouted}=10$ ,  $n_{not-scouted}=10$ ,  $P<0.001$ ,  $median_{scouted}=0.176$ ,  $median_{not-scouted}=0.040$ ), and to follow  
300 (Independent-sample t-test,  $t=-3.680$ ,  $df=9$ ,  $P=0.002$ ,  $mean_{scouted}=0.172$ ,  $mean_{not-scouted}=0.084$ ), tandem runs, and  
301 this trend was not significantly different between emigration distances (Mann-Whitney U test, leading:  
302  $U=0.338$ ,  $n_{100}=10$ ,  $n_{300}=10$ ,  $p=0.738$ ,  $median_{100}=0.071$ ,  $median_{300}=0.084$ ; following:  $U=1.826$ ,  $n_{100}=10$ ,  $n_{300}=10$ ,  
303  $p=0.068$ ,  $median_{100}=0.073$ ,  $median_{300}=0.137$ ), however, it should still be noted that the median for following  
304 was much higher at 300mm.

### 305 e) *Discovery times and quorum attainment*

306 The time of quorum attainment was significantly later in emigrations over longer distances (Paired-sample t-test,  
307  $t=-3.565$ ,  $df=9$ ,  $P=0.006$ ,  $mean_{100}=39.41$  min,  $mean_{300}=94.22$  min). However, though later in the distant  
308 treatment, nest discovery time was not significantly affected (Wilcoxon signed-ranks test,  $U=9.811$ ,  $n=10$ ,  
309  $P=0.114$ ,  $median_{100}=13.37$  min,  $median_{300}=31.54$  min, checked with a paired t-test after log<sub>10</sub> transformation,  
310  $P=0.087$ ), likely in part due to the increased rate of scouting.

## 311 Discussion

312 Our results show that in *T. albipennis* colonies, tandem running activity is redistributed across individuals in  
313 response to differing emigration distances. In agreement with previous work (Pratt et al. 2002; Pratt 2004;  
314 O’Shea-Wheller et al. 2016), we found that the incidence of tandem running rose significantly with longer  
315 emigration distances (fig. 2A,C, 4). Tandem success tended to decrease with distance, although this result was

316 statistically significant only for leaders. It was not significant either for followers, or colonies as a whole (fig.  
317 2B). Furthermore, a significantly larger proportion of each colony was engaged in emigrations and tandem  
318 running at 300mm, and average worker return speeds were higher (fig. 2C,D, fig. 6). Crucially, we observed that  
319 a small minority of individuals attempted a greater workload (leading or following tandem runs) at the longer  
320 emigration distance in comparison to their nest mates (fig. 5A). However, the relative importance of these ants  
321 dwindled when only successful workload was considered (fig. 5B). In concert, our data show that while colonies  
322 use multiple processes to adjust emigration dynamics over longer distances, an increase in the number of active  
323 individuals is likely the key driver behind increased tandem running (fig. 2C,D).

324 The upregulated investment in tandem running over longer emigration distances may be explained by the lower  
325 independent discovery rate of more distant nests (O'Shea-Wheller et al. 2016; Pratt, 2004). This is because to  
326 commit to a new nest colonies must achieve a quorum threshold, which may be attained by ants individually  
327 discovering a new nest, or being recruited to it via tandem running (Pratt, 2004). Consequently, a decrease in  
328 individual discovery rate seems to require an increase in tandem running to reach such a quorum (fig. 2A).  
329 Interestingly, average worker return speed also increased, and the explanation for this likely arises from the  
330 properties of ant locomotion; it has been shown that for any given movement, the longer the duration, the higher  
331 the average speed (fig. 6) (Christensen et al. 2015). However, while every movement is bracketed by an  
332 initiation and termination phase, these phases comprise a constant percentage of the overall movement,  
333 suggesting that ants determine movement duration before initiating a journey (Christensen et al. 2015).  
334 Consequently, this indicates that ants up-regulate their speed when planning to move over longer distances  
335 (Hunt et al. 2016). Previous studies have found that this speed-distance rule applies to short discrete movements,  
336 yet the majority of journeys are made up of many such movements. Here, to our knowledge for the first time, we  
337 show that it is also applicable to longer, compound movements, indicative of a consistent overarching  
338 mechanism.

339 Differences at the colony level were underpinned by variation in individual behaviour between emigration  
340 distances. The finding that individual tandem running workload (leading and following tandem runs) decreased  
341 with the number of ants actively engaged (fig. 5A,B, fig. 2D) is consistent with observations in analogous  
342 systems, and constitutes a commonly observed phenomenon in insect societies (Karsai & Wenzel 1998;  
343 Dornhaus et al. 2008). Principally, the decrease in individual contributions when more ants are engaged may be  
344 explained by the reduced need for workers to be involved in a task, and the concomitant reduction in task  
345 stimuli (Pinter-Wollman et al. 2012). Furthermore, for longer emigrations, although more tandem runs may be  
346 required due to a reduced encounter rate (O'Shea-Wheller et al. 2016, Pratt 2004), colonies of *T. albipennis* use  
347 quorum thresholds relative to their total population (Dornhaus & Franks 2006). As such, the quorum threshold  
348 required by a colony of any given size should remain constant, and thus the task of attaining it would potentially  
349 be distributed over more workers at longer emigration distances, creating a dilution of individual effort  
350 (Dornhaus & Franks 2006).

351 The changes in numbers of tandem runs between distance treatments might largely be attributed to the greater  
352 numbers of workers engaging in more distant emigrations. However, in concert with this, some ants that were  
353 involved in multiple emigrations conducted many more tandem runs at 300 mm than the rest of the actively  
354 engaged worker population (fig. 4). This suggested that there were certain individuals specialising in the task, as

355 is the case for other task groups in this species (Robinson et al. 2009; Pinter-Wollman et al. 2012). As such,  
356 there was the potential for these individuals to contribute significantly to the tandem running process, via task  
357 threshold differences and reinforcement processes (Sendova-Franks et al. 2002; Sendova-Franks & Franks  
358 1995). The idea of task reinforcement was supported further by the finding that more leading attempts did  
359 correlate with a higher success rate, and so we investigated the relative contributions of worker groups actively  
360 engaged in emigrations, in an effort to isolate a specialist faction.

361 We defined actively engaged workers as those conducting scouting, leading or following of tandem runs, or  
362 both. This definition was adopted as previous scouting activity significantly increased an individual's propensity  
363 to either lead or follow tandem runs, a trend that remained constant across both distances, although was more  
364 probable at 300mm. We separated actively engaged workers into two groups; workers actively engaged across  
365 both distances, and workers actively engaged at only one distance. This division method allowed us to  
366 determine how individuals recurrently involved in emigrations contributed to the process. This latter group  
367 formed a minority of the total population of actively engaged workers (fig. 3), but interestingly, attempted a  
368 significantly greater number of tandem runs per individual (fig. 4). Furthermore, ants in this group attempted a  
369 significantly greater workload per individual than those in the 'either' group, when migrating over the longer  
370 distance (fig. 5A). However, the data for successful workload performed per individual did not differ  
371 significantly between the two groups, at any distance (fig. 5B).

372 Our data suggest that some individuals are indeed disproportionately active in the tandem running process,  
373 specifically attempting more tandem runs per ant overall (fig. 4), and a greater per capita workload when the  
374 new nest is further away (fig. 5A). However, they do not perform a greater successful workload per capita  
375 within distances (fig. 5B), and as such, the relative importance of these 'elite' workers (Hölldobler & Wilson  
376 1990) in shaping emigration dynamics is debatable. Instead, it appears that the majority of changes in tandem  
377 running at the colony level are achieved via increased recruitment of workers into the process, rather than by  
378 reliance on key individuals (fig 2C,D, 5B). Such findings are also supported by previous work, showing that the  
379 ability to utilise a larger workforce negates the need for specialists (Dornhaus et al. 2009). This highlights an  
380 interesting contradiction; it suggests that although some workers are highly active and conform to the definition  
381 of 'elites', they may not actually be that effective at their task, despite investing more effort than their nest  
382 mates. Hence, in this case at least, the usefulness of the term 'elite' is debatable. Indeed, a recent study, also in  
383 the *Temnothorax* genus, found that reliance on specialists in the face of dynamic environments may be  
384 disadvantageous (Jongepier & Foitzik 2016), highlighting another case in which the contribution of 'elites' is far  
385 from decisive.

386 The presence of inactive or 'lazy' workers has received some attention in social insects (Dornhaus et al. 2008;  
387 Beshers & Fewell 2001) and may be accounted for proximately by task thresholds, as inactive individuals are  
388 likely to be those that require a higher level of stimulus before they engage in a given task (Robinson et al.  
389 2009). However, here we see a case of active but ineffective workers in a task that is moderately difficult to  
390 complete (only 65% of all tandem runs were successful). While the exact mechanisms underlying this are as yet  
391 unknown, there are several potential causes. One possibility, is that workers attempting a greater number of  
392 tandem runs were doing so as a compensatory reaction to failing more often. This is plausible, as interruptions  
393 to tandem runs were common in our experiment, as in others (Franks et al. 2009). It is also likely that highly

394 active individuals made a significant contribution by leading only partially successful tandem runs. This is  
395 because, as demonstrated in previous experiments (Franks et al. 2010), even when tandem runs end prematurely,  
396 they may still be effective in directing naive workers to a new nest (Franks et al. 2010; Pratt 2008). However,  
397 while both of these factors provide viable explanations, their relative importance will likely require further  
398 investigation.

399 In conclusion, we find that several factors contribute to the acceleration of emigrations over longer distances,  
400 and that both highly active individuals, and the regulation of total worker involvement play a role. Crucially, we  
401 show that the greater number of active workers employed over longer emigrations is the strongest factor linked  
402 to increased tandem running, having a greater influence than the utilisation of ‘elite’ workers. Overall, our  
403 results indicate that although key individuals have their place in the tandem running process, it is the  
404 mobilisation of the masses that likely makes the real difference when emigrating over greater distances.

## 405 **Competing interests**

406 The authors declare that they have no competing interests.

407

## 408 **Author contributions:**

409 TAOW and NRF conceived the study and wrote the manuscript; TAOW, DKWA and DEE conducted all  
410 experimental work; TAOW and ABSF carried out the statistical analysis. All authors gave final approval for  
411 publication.

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413 This work received no specific funding.

## 414 **Data availability**

415 **Table S1.** Raw data from the experiment.

## 416 **Ethical standards statement**

417 All applicable institutional and/or national guidelines for the care and use of animals were followed.

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## 502 **Figure legends**

503 **Figure 1.** Marked *Temnothorax albipennis* workers, though some are missing paint marks, the numbering  
504 system was robust to this (A), experimental arena setup for 100 mm trial (B), and 300 mm trial (C). Dimensions  
505 indicate actual arena sizes, figure is for illustrative purposes only, and is not to scale.

506 **Figure 2.** Total number of tandem runs at colony level  $n_{100}=10$ ,  $n_{300}=10$ ,  $P=0.028$ , (A), and percentage of  
507 successful tandem runs out of those attempted  $n_{100}=10$ ,  $n_{300}=10$ ,  $p=0.329$  (B), percentage of colony engaged in  
508 tandem running  $n_{100}=10$ ,  $n_{300}=10$ ,  $p=0.037$  (C), and percentage of colony engaged in the emigration process as a  
509 whole (scouting, tandem leading or following)  $n_{100}=10$ ,  $n_{300}=10$ ,  $P<0.001$  (D), for the two emigration distances.  
510 Coloured lines indicate individual colony changes in tandem running over distance, palette is chosen for clarity.  
511 Outliers (further than 1.5 times the interquartile range from the median) are indicated with circles.

512 **Figure 3.** Number of workers involved in tandem running at one, or both, emigration distances, as a percentage  
513 of the total number of workers actively engaged for both groups. Actively engaged workers are those involved  
514 in scouting, tandem leading or following  $n_{100}=10$ ,  $n_{300}=10$ .

515 **Figure 4.** Total number of attempted tandem runs per ant. Boxplots are divided by emigration distance, and  
516 within each distance, by individuals actively engaged at only that distance; the ‘either’ group (flat boxes), or  
517 both emigration distances; the ‘both group’ (grey boxes),  $n=296$ , ( $n_{100\text{either}}=76$ ,  $n_{100\text{both}}=53$ ,  $n_{300\text{either}}=114$ ,  
518  $n_{300\text{both}}=53$ ). Asterisked lines highlight significant differences within distances (Bonferroni post-hoc test,  
519  $P<0.05$ ). Outliers (further than 1.5 times the interquartile range from the median) are indicated with circles.

520 **Figure 5.** Per capita attempted (A), and successful (B), workload per ant. Boxplots are divided by emigration  
521 distance, and within each distance, by individuals actively engaged at only that distance; the ‘either’ group  
522 (white boxes), or both emigration distances; the ‘both group’ (grey boxes),  $n=296$ , ( $n_{100\text{either}}=76$ ,  $n_{100\text{both}}=53$ ,  
523  $n_{300\text{either}}=114$ ,  $n_{300\text{both}}=53$ ). Asterisked lines highlight significant differences within distances (Bonferroni post-  
524 hoc test,  $P<0.05$ ), outliers (further than 1.5 times the interquartile range from the median) are indicated with  
525 circles.

526 **Figure 6.** Mean return speed of workers within colonies for the two distances  $n_{100}=101$ ,  $n_{300}=114$ ,  $p<0.001$ ,  
527 inlay displays changes in mean return speed of individuals tracked across both emigration distances, coloured

528 lines indicate each individual's change in mean return speed  $n_{100}=20$ ,  $n_{300}=20$ . Outliers (further than 1.5 times  
529 the interquartile range from the median) are indicated with circles.  
530



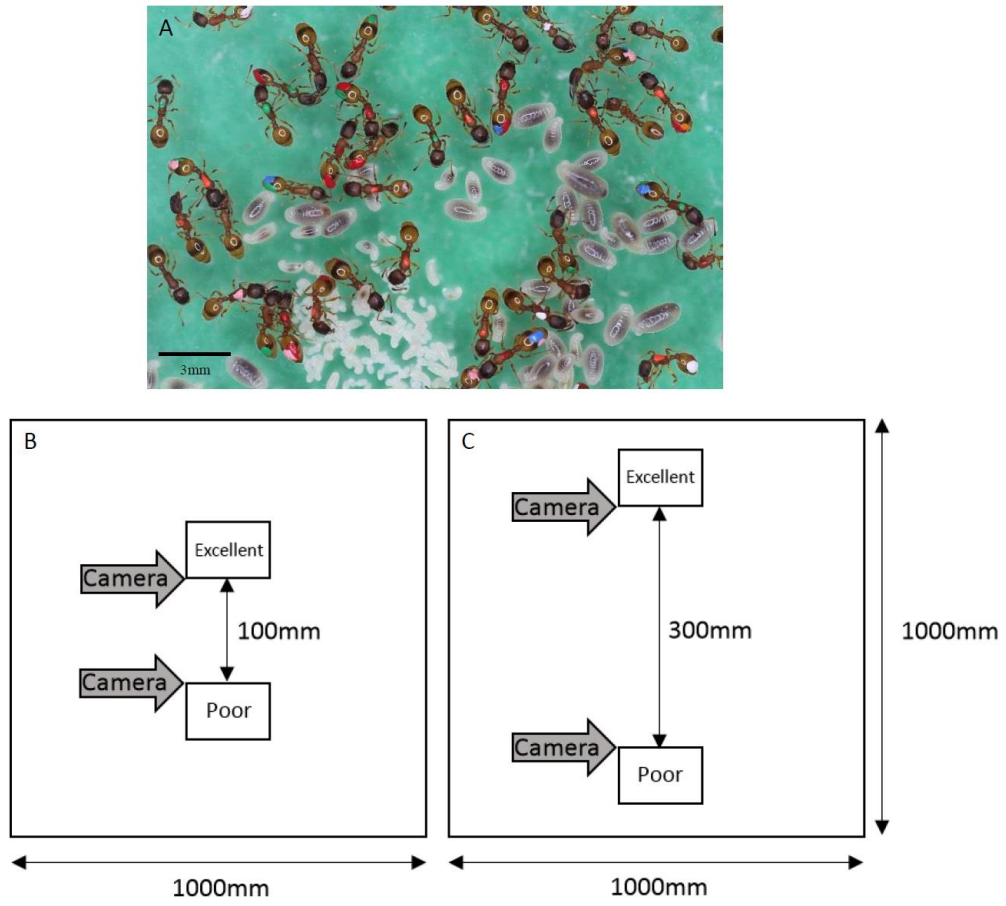


Figure 1.

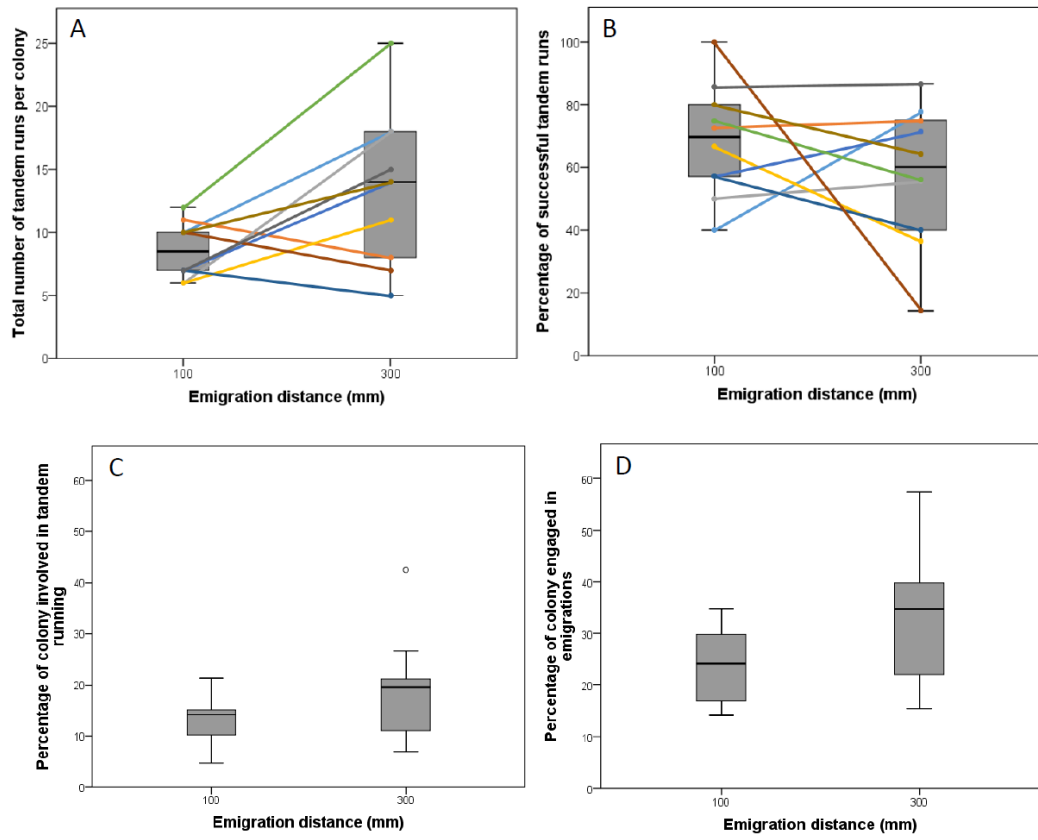


Figure 2.

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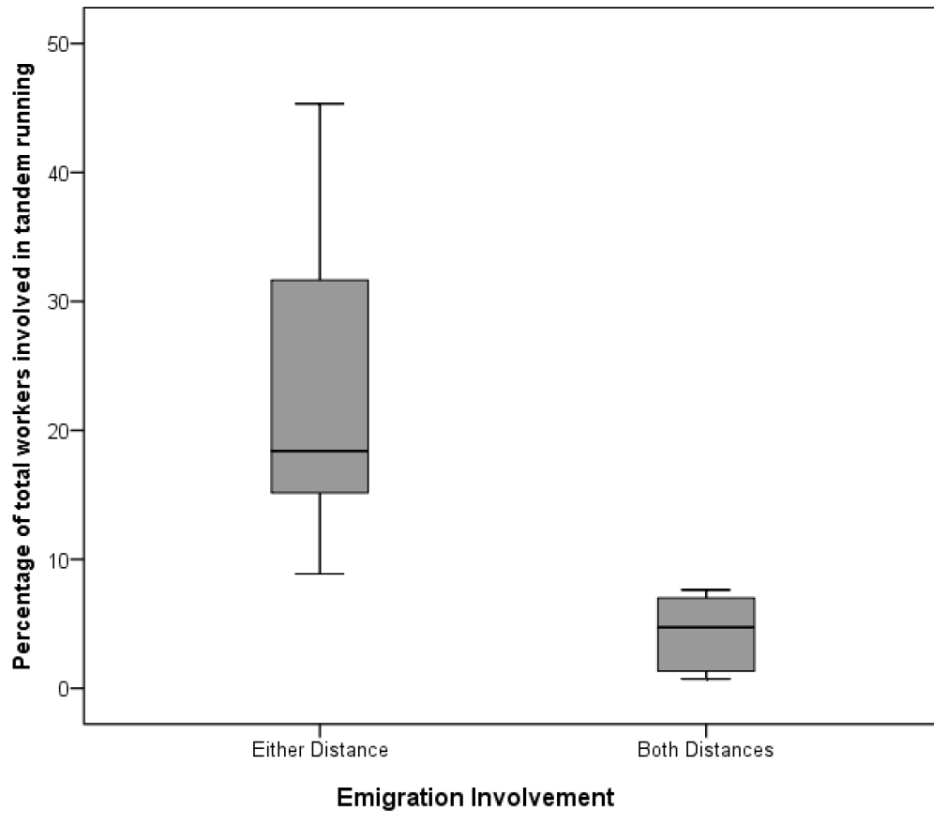


Figure 3.

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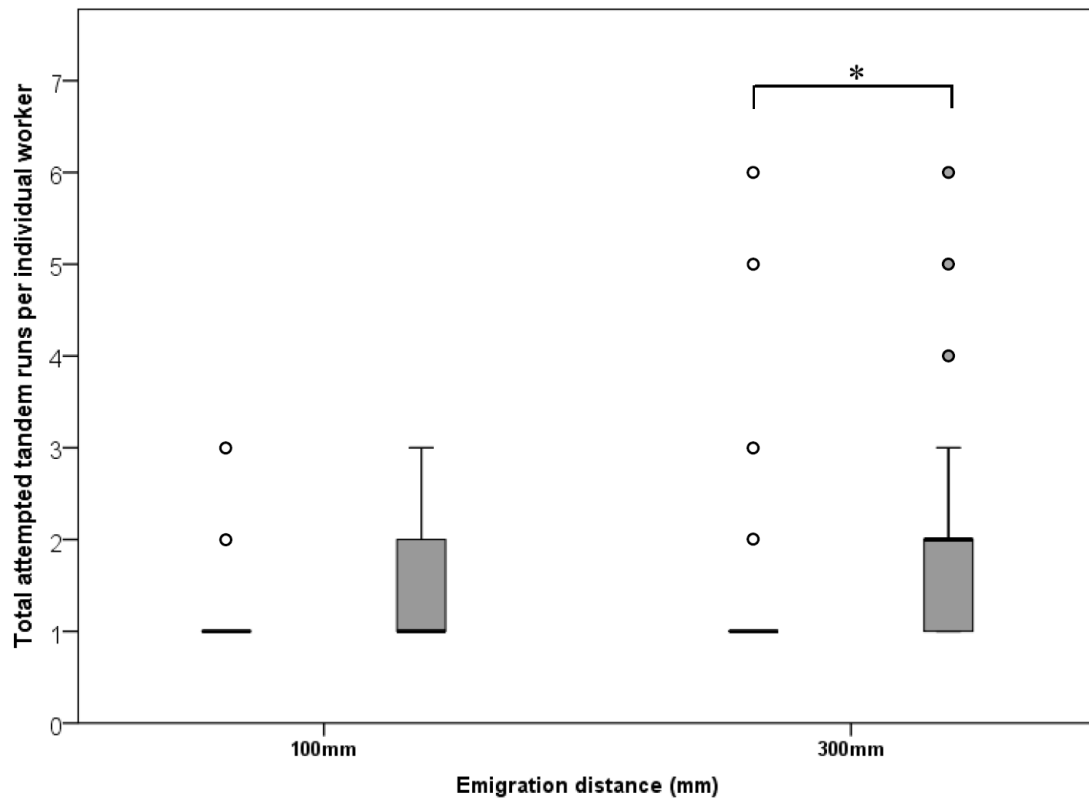


Figure 4.

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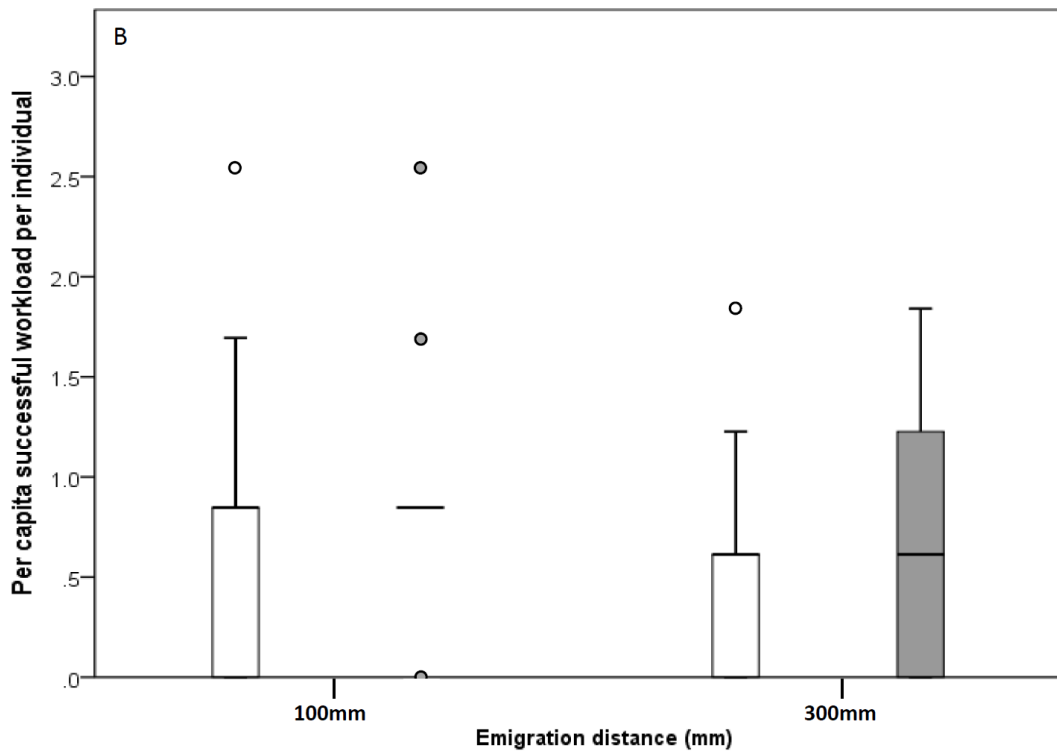
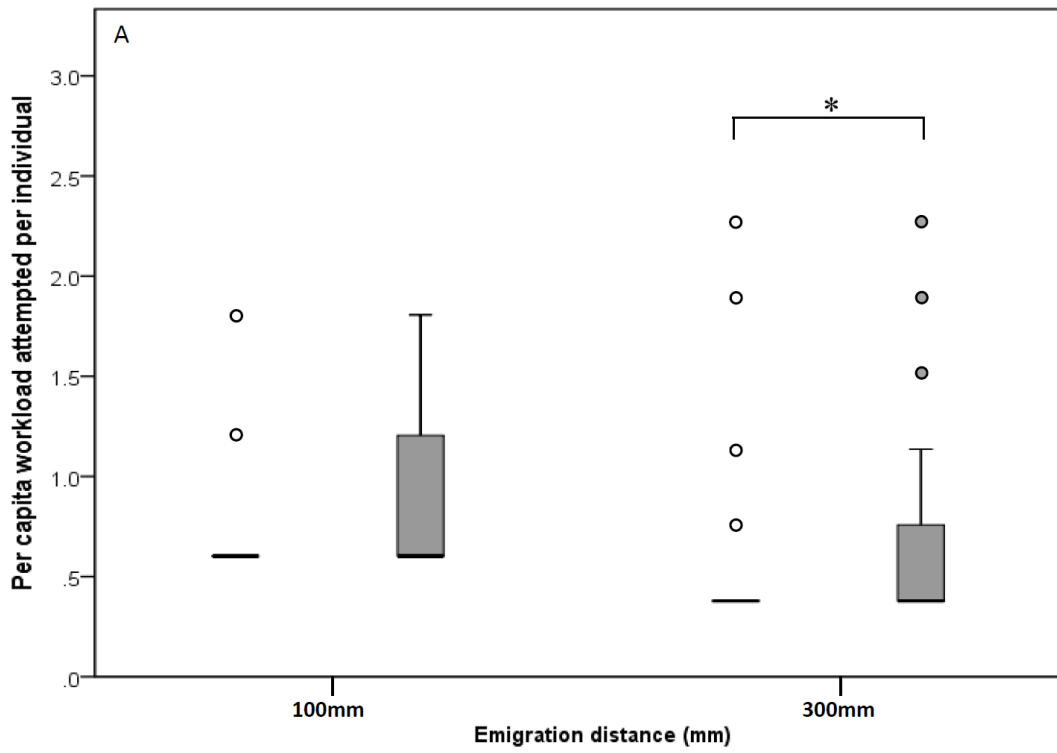


Figure 5.