1 **Ancestral state reconstruction suggests repeated losses of**

2 **recruitment communication during ant evolution (Hymenoptera:**

3 **Formicidae)**

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16

17 **Author contributions**

18 S.M.G and C.G. developed the study question. S.M.G. performed the literature

19 research, analyzed the data and wrote the primarily manuscript. S.M.G and C.G.

20 contributed critically to the drafts and gave final approval for publication.

21

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Abstract

Eusocial insects have evolved different strategies to share information about their environment and workers can recruit nestmates to food sources or new nest sites. Ants are the most species-rich social insect group and are known to use pheromones, visual and tactile signals to communicate and inform nestmates about resources. However, how these different strategies evolved and whether there was a predominant evolutionary sequence that led to present day recruitment strategies is not well understood. In our study we explored two competing hypotheses about the ancestral recruitment communication: (1) ant ancestors did not recruit nestmates and species evolved more complex recruitment strategies over time vs. (2) early ants used mass-recruitment, which was lost repeatedly in some lineages. We combined an extensive search of the scientific literature and ancestral state reconstruction to estimate the ancestral recruitment strategy, focusing on the categories (i) no recruitment, (ii) tandem running, (iii) group-recruitment and (iv) chemical mass-recruitment. Stochastic character mapping suggests that mass-recruitment was ancestral in ants (59-61%), whereas "no recruitment" was unlikely to be the ancestral condition (21%). Similarly, marginal ancestral state reconstruction suggests that mass-recruitment (44-81%) or group-recruitment (48-50%) represented the original state. Our results are consistent with the finding that early ants lived in colonies containing up to several thousand individuals, which are typically associated with mass-recruiting in ants. However, our ability to robustly identify patterns in the evolution of communication in ants remains hampered by a lack of natural history information for most ant species.

Keywords: ancestral state, communication, Formicidae, recruitment, tandem running

48   **Introduction**

49   Communication about resources is widespread in social insects and different species

50   have evolved a variety of strategies to communicate with other individuals (Czaczkes

51   et al., 2015; Franklin, 2014; Grüter & Leadbeater, 2014; Hölldobler & Wilson, 1990;

52   Leadbeater & Chittka, 2007; von Frisch, 1967; Wilson, 1971; Grüter, 2020). Senders

53   can use visual, tactile (body contact in honeybees, Grooters, 1987; antennation,

54   Hölldobler & Wilson, 1990; von Frisch, 1967) or chemical (e.g. pheromones, Czaczkes

55   et al., 2015; Hölldobler & Wilson, 1990) signals to share information about food

56   locations, nesting locations, dangers or the needs of individuals and the colony.

57   Ants (Family: Formicidae) are an extraordinarily diverse, widespread and

58   ecologically important group of social insects, containing over 13,000 extant species

59   (Reeves & Moreau, 2019). Ants probably first appeared in the early Cretaceous, more

60   than 100 million years ago, most likely from a lineage of wasps (Hölldobler & Wilson

61   2009; Moreau et al., 2006; Ward, 2014). Ants have evolved a variety of different

62   communication strategies, some of which are behaviourally highly complex

63   (Hölldobler, 1999). There are also species that employ several strategies during

64   recruitment (see below).

65   Several classification systems for recruitment behaviours have been proposed

66   (Beckers et al., 1989; Jaffe, 1984; Lanan, 2014). The most common strategies are the

67   use of pheromone trails (Czaczkes et al., 2015; Hölldobler & Wilson, 1990, 2009),

68   group-recruitment (Hölldobler, 1971; Liefke et al., 2001), tandem recruitment (Franklin,

69   2014; Glaser & Grüter, 2018; Grüter et al., 2018) or no recruitment at all

70   (solitary/individual) (Beckers et al., 1989; Jaffe, 1984). In tandem recruitment, a scout

71   with knowledge of a valuable resource recruits a single nestmate to that resource. The

72   follower maintains contact with the leader by antennating the gaster and hind legs of

73   the leader. In group-recruitment, a scout leads a group of up to thirty nestmates to a

74   resource (Beckers et al. 1989; Liefke et al., 2001). A short-lived, volatile pheromone

75   emitted by the leader helps recruited ants stay close to the leader (Möglich et al., 1974).

76   In mass-recruitment, successful scouts lay pheromone trails between the nest and the

77   resource, which is followed and strengthened by nestmates. Some species use a

78   particular strategy in one context but not in another. For example, *Neoponera* or

79   *Diacamma* species perform tandem runs when they relocate to a new nest site, but

80   when they are foraging for prey they do so solitarily (Fresneau, 1985; Kaur et al., 2017).

81   Furthermore, recruitment communication can depend on the type of food source that

82   is collected. When collecting small prey, ants often do not recruit nestmates as they

83   can carry home the food item by themselves, but use recruitment communication when

84   finding larger resources, like honey dew-secreting aphid colonies or large prey items

85   (Czaczkes et al., 2011; Czaczkes & Ratnieks, 2012; Detrain & Deneubourg, 2008;

86   Lach, 2005). These examples highlight that the use of recruitment communication

87   often depends on the ecological context.

88   Species with small colonies (<1000 individuals) often do not use recruitment or they

89   perform tandem runs, whereas medium size colonies (up to a few thousand individuals)

90   tend to recruit nestmates by group-recruitment or by pheromone trails and large

91   colonies use mainly pheromone trails (Beckers et al., 1989). Recruitment *via*

92   pheromone trails requires colonies to have a minimum number of foragers to deposit

93   pheromones in order to maintain the trail (Beekman et al., 2001). The link between

94   colony size and recruitment strategy is not rigid, however, and species with similar

95   colony sizes can differ in the strategies they employ (Beckers et al., 1989).

96   This diversity in recruitment strategies raises the question how these strategies

97   evolved and whether certain forms of recruitment tend to precede other methods. One

98   hypothesis is that recruitment communication increased in complexity over

99   evolutionary time. According to this scenario, early ants would have foraged solitarily,

100   like many present-day ponerine ants (Beckers et al., 1989; Maschwitz & Schönegge,

101   1983; Villet, 1990). Subsequently, small-scale communication mechanisms evolved,

102   like tandem-running and group-recruitment. From these forms of communication,

103   mass-recruitment with longer-lasting chemical trails may have evolved (Beckers et al.,

104   1989; Hölldobler & Wilson, 1990; Traniello, 1989). Hingston (1929) and Wilson (1959),

105   for instance, suggested that tandem running is an ancestral form of communication

106   that was used by early ants. Short-lived pheromones released by the tandem leader

107   play a potentially important role for the cohesion between the leader and follower in a

108   tandem run (Basari et al., 2014). It would then have been a small evolutionary step to

109   produce longer lasting trail pheromones that allowed mass-recruitment in species with

110   larger colony sizes. The hypothesis of an increase in scale – from small-scale to large-

111   scale recruitment – has recently been supported by Reeves & Moreau (2019) who

112   suggest solitary foraging as the ancestral recruitment strategy.

113   A phylogenetic analysis by Burchill & Moreau (2016), on the other hand, suggested

114   that early ant species had medium colony sizes, with colonies containing up to several

115   thousand individuals, which is typically associated with mass-recruitment in extant ants

116   (Beckers et al., 1989). This suggests that mass-recruitment may have been a more

117   likely strategy used by early ants. Following this argument, recruitment would have

118   been lost over time in some lineages as ant species with small colony sizes evolved

119   (Burchill & Moreau 2016). The antiquity of tandem running has also been questioned

120   by the fact that this behaviour is found in species that are considered more derived,

121   such as in *Temnothorax* and *Leptothorax* (Planque et al. 2010). This suggests that

122   tandem running may be a derived behaviour, at least in some groups.

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123   The main aim of our study was to estimate the ancestral state of recruitment

124   communication of the Formicidae. While Reeves & Moreau (2019) focused on

125   recruitment communication during foraging, we also considered whether species use

126   recruitment during emigrations. We included these cases because numerous ant

127   species do not communicate during foraging but use recruitment communication in

128   other ecological situations (Fresneau, 1985; Grüter et al., 2018; Kaur et al., 2017). The

129   value of communication in foraging depends on the foraging ecology of a species, such

130   as the kind of food that is exploited and food source distribution (Anna Dornhaus et al.,

131   2006; I'Anson Price et al., 2019; Sherman & Visscher, 2002). Thus, the strategies used

132   during foraging reflect foraging ecology and provide an incomplete picture of the

133   recruitment strategies used by a species. To better understand the evolution of

134   recruitment communication mechanisms, it is instructive to consider whether a species

135   uses recruitment communication, irrespective of the type of resource that is exploited.

136   In addition, we explored whether tandem running was indeed an early recruitment

137   strategy that preceded group- and mass-recruitment (Hingston, 1929; Wilson, 1959).

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Material & Methods

Literature research for recruitment strategies

141   Data were collected on the recruitment strategies used by extant ant species *via* an

142   extensive search of the published scientific literature (from October 2019 to March

143   2020). For many ant species, information about recruitment was collected from reviews

144   or articles about recruitment (Beckers et al., 1989; Jaffe, 1984; Silvestre et al., 1999).

145   Furthermore, we searched in Google Scholar using the search terms (ant species or

146   genus in combination with "recruit", "forag", "prey", "individual", "solitary", "tandem",

147   "group", "trail", "pheromone"). We included species-level information when the

148   recruitment strategy was described based on observations or collected in controlled

149   experiments. Data were coded as discrete character traits. Each species was allocated

150   to one of four different recruitment strategies, similar to Jaffé (1984), Beckers et al.

151   (1989) and Lanan (2014): no recruitment, tandem running, group-recruitment and

152   mass-recruitment (Table 1). Reeves & Moreau (2019) found that the different

153   classification systems led to very similar outcomes in their ancestral state

154   reconstruction.

Table 1. Recruitment classifications and definitions, largely based on Jaffé (1984).

Recruitment strategy	Definition
Solitary/individual	No recruitment, no information transfer between nestmates
Tandem running	A single ant (scout) attracts a single nestmate using antennal contact and then physically leads a nestmate to the goal. Physical contact is often maintained between scout and nestmate, chemical signals may be used
Group-recruitment	A scout recruits "up to thirty nestmates" and leads them to the goal. Chemical signals are often used for short-distance attraction but physical contact between scout and the group is also used
Mass-recruitment	Groups are guided via chemical trails alone. Large numbers of ants can be recruited by a small number of recruiters. Chemical trails are laid on the substrate.

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156   The literature search highlighted that there is a relative scarcity of detailed information

157   about foraging strategies in the ant literature (see also Reeves & Moreau 2019). There

158   are numerous examples of studies that mention recruitment of nestmates, but without

159   providing details of the strategy and the context when this was observed. These studies

160   were not included in our analysis. If possible, we also collected and compared the

161   recruitment data to Reeves and Moreau (2019), who collected data on ant foraging

162   strategies. In some cases, we were unable to recover the information from the cited

163   primary literature (e.g. *Buniapone amblyops*, *Mayaponera constricta* or *Megaponera*

164   *analis*). *Tetramorium caespitum* uses both group and mass-recruitment (Collignon &

165   Detrain, 2010). We considered this to be a mass-recruiting species for our analysis.

166   Additionally, we used a subset that included only ant species that perform tandem runs

167   and analysed if recruitment to nest sites or food sources was more likely to be the

168   ancestral state.

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170   *Phylogenetic comparative methods*

171   We modified the phylogenetic tree of Branstetter et al. (2017), which contains ~1000

172   ant species and is a phylogram based on molecular data. In our literature research we

173   found information for 161 species, 82 genera and 11 sub-families (Table S1) that were

174   also present in the phylogenetic tree. Overall, the species included in our study

175   represent 25% of genera and 65% of sub-families. Species with no recruitment data

176   available were removed from the dataset with the *drop.tip* function in the R package

177   "ape" (Paradis & Schliep, 2019).

178   We performed marginal ancestral state reconstructions (ASR) for the dataset, using

179   the functions *fitMk* and *ace* from the R package "phytools" (Revell, 2012) and "ape"

180   (Paradis & Schliep, 2019) to estimate the transition rates and the ancestral states for

181   our tested character using a maximum likelihood (ML) approach. The *fitMk* function

182   assumes that the probability to change from one state to another depends only on the

183   current state and not on the state that has come before. Furthermore, every character

184   state is equally likely to change to one of the other states. The *ace* function utilizes

185   marginal reconstruction and returns the marginal ancestral state likelihood of all nodes

186   within a phylogeny.

187   Additionally, we performed a stochastic character mapping (SCM) by using

188   *make.simmap* from the R package "phytools". For the stochastic reconstructions of

189   character states we used an MCMC approach, to explore the posterior probabilities of

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190   all nodes and provided the number of changes between the character states (1000

191   simulations performed).

192   Three commonly used transition rate models were analysed for the ancestral state

193   reconstructions: "equal rates" (ER), "symmetrical rates" (SYM) and "all rates different"

194   (ARD) with names referring to transition rates between each state. We used the Akaike

195   information criterion (AIC) values corrected for small sample sizes (AICc values) for

196   the three transition rates. We calculated the AIC-weights which standardize the AIC

197   scores of the fitted models and measured the relative weight of evidence for the three

198   models used in our data (Harmon, 2019). We visualized the results by mapping the

199   ancestral state on the phylogeny with the function *plotTree*.

200

201   **Results**

202   *Evolution of recruitment strategy*

203   The ancestral state reconstruction results were mapped to our phylogeny (Fig. 1). The

204   log-likelihood values, AIC values, AICc values and the number of free parameters per

205   model are presented in Table 2. We compared the AIC and AICc values, which

206   revealed that simple ER models were inferior and, thus, were rejected. A "symmetric

207   model" and "all-rates-different model" best explained our transition between

208   recruitment states. Thus, both transition models were used to analyse the ancestral

209   state of recruitment strategies in ants.

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Figure 1. Ant phylogeny including recruitment strategy and (**A**) marginal ancestral state reconstruction or (**B**) stochastic character mapping. Nodes provide estimates based on Markov chain models. The phylogeny is based on Branstetter et al. (2017).

Table 2. Results of the transition rate models. Log likelihoods, Akaike information criterion values, number of free parameters and Akaike-weights are shown.

Model	LogL	AIC	AICc	free parameters	AICcW
ER	-170.0	336.9	342.0	1	0.03
SYM	-161.4	331.6	335.4	6	0.45
ARD	-155.7	331.4	337.6	12	0.52

Marginal ancestral state reconstruction analyses and stochastic character mapping both suggest that mass-recruitment is the most probable strategy at the root of the phylogeny (71.2% and 60.2%, respectively) (Table 3). Also, internal nodes (lineage splitting events) were dominated by high probabilities for the mass-recruitment category. Mass-recruitment was the most likely ancestral state in both the Poneroids and the Formicoids (Figure 1). The stochastic character mapping revealed that there were an estimated 81.3 changes between recruitment strategies (Table 4). The most common transitions were from mass-recruitment to solitary/individual behaviour (33.7%) or to group-recruitment (18.5%) (Figure 2). Furthermore, there were transitions from no recruitment to tandem running (14.8%) or mass-recruitment (12.7%). Tandem running evolved several times independently in the subfamilies Ponerinae, Pseudomyrmecinae, Formicinae and Myrmecinae. Furthermore, it seems that recruitment was lost at least once in all subfamilies, except in the Dorylinae (army ants). Similarly, we found group-recruitment in nearly all included sub-families, except in the Paraponerinae. The Myrmeciinae were the only group without species that perform mass-recruitment.

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Table 3. Ancestral character estimation using marginal ancestral state reconstruction and stochastic character mapping. Values represent likelihoods of recruitment strategies at the root.

	Character states	Scaled root likelihood (fitMk)	Scaled root likelihood (ace)	Stochastic charac mapping (make.simmap)
SYM	No recruitment	0.15	0.16	0.21
	Tandem running	0.01	0.01	0.10
	Group-recruitment	0.02	0.02	0.07
	Mass-recruitment	0.81	0.81	0.61
ARD	No recruitment	0.05	0.06	0.21
	Tandem running	0.01	0.01	0.09
	Group-recruitment	0.50	0.48	0.12
	Mass-recruitment	0.44	0.45	0.59

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Table 4. Changes from stochastic character mapping. GR = group-recruitment, MS = mass-recruitment, NR = no recruitment, TR = tandem running
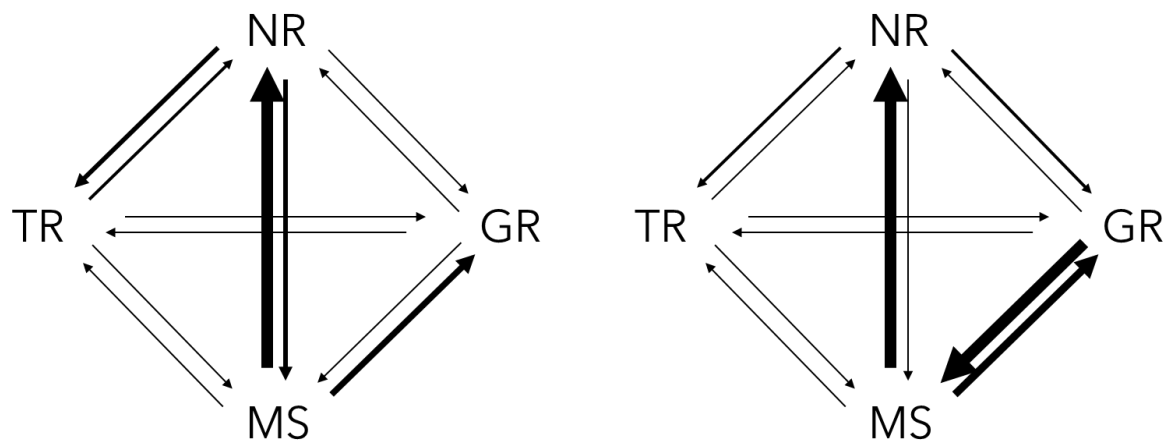
	SYM		ARD	
Total changes	75.783		104.472	
Type	Number	Percentage	Number	Percentage
GR → MS	3.44	4.5%	32.013	30.6%
GR → NR	0.595	0.7%	0	0%
GR → TR	1.224	1.6%	0	0%
MS → GR	14.902	19.7%	23.572	22.6%
MS → NR	26.57	35.1%	27.514	26.3%
MS → TR	0.489	0.6%	0.952	0.9%
NR → GR	1.412	1.9%	7.409	7.1%
NR → MS	10.061	13.3%	0	0%
NR → TR	9.8	12.9%	9.572	9.2%

| TR → GR	2.626	3.4%	3.44	3.3%
TR → MS	0.117	0.2%	0	0%
TR → NR	4.547	6.0%	0	0%

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Figure 2. Transitions between states from stochastic character mapping for the methods SYM and ARD. The thickness of the arrow reflects the relative commonness of a transition. GR = group-recruitment, MS = mass-recruitment, NR = no recruitment, TR = tandem running

Evolution of tandem running

Twenty-one species included in our study perform tandem runs. For some species it is not known if they recruit to food sources and during nest relocations. For other species it is known that they perform tandem runs to new nest sites, but forage solitarily for food sources (*Neoponera*, *Diacamma* or *Paltothyreus*) (Table S1).

After mapping the recruitment strategy onto the phylogenetic tree (Figure 3), we found that all species that can perform tandem runs do so during colony emigrations to new nest sites. Several species (43%) that use recruitment via tandem running do not do so during foraging.

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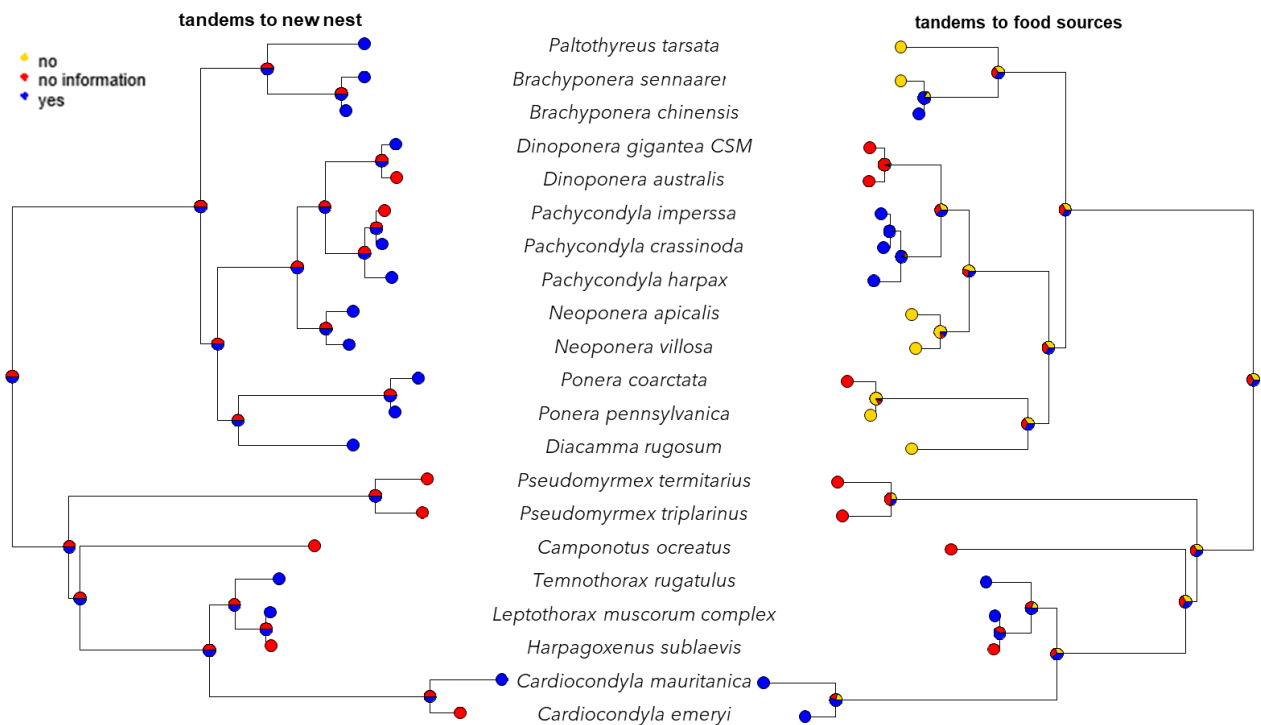
Figure 3. Ancestral state reconstruction for ant species that perform tandem running to either new nest sites, food sources or both. Nodes provide estimates based on Markov chain models.

Discussion

Our ancestral state analyses indicate that mass-recruitment or group-recruitment were likely used for recruitment by the last common ancestor of present-day ants. During the course of their evolutionary history, all included subfamilies show switches from mass-recruitment to other recruitment strategies. Strikingly, most transitions occurred from mass recruitment to group or no recruitment. The repeated loss of communication seems puzzling, but probably coincided with the emergence of lineages with small colony sizes (e.g. in Amblyoponinae, Myrmeciinae, Ponerinae, Pseudomyrmecinae) (Burchill & Moreau 2016), where communication is less beneficial (Beckers et al. 1989). Transitions between mass- and group-recruitment were also more frequent than between tandem running and no recruitment. Tandem running evolved independently

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268   in 4 of 11 subfamilies. Furthermore, there were several transitions from no recruitment

269   to tandem running or mass-recruitment. These findings highlight that recruitment

270   strategies are an evolutionarily flexible and reversible trait.

271   Many lineages appear to have lost the ability to recruit nestmates. The putative

272   loss of chemical mass-recruitment seems puzzling at first, but could be explained by

273   the constraints of living in a small colony (Beckers et al., 1989; Dornhaus et al., 2012)

274   and/or a switch to a diet or foraging strategy that does not require pheromone trails.

275   Smaller colonies tend to exploit resources solitarily or they use tandem running. One

276   reason could be that smaller colonies do not have sufficiently large colonies to maintain

277   pheromone trails (Beckers et al., 1989; Beekman et al., 2001; Planqué et al., 2010). A

278   recent study has suggested that the ancestral Formicidae had medium colony sizes

279   containing up to several thousand individuals (Burchill & Moreau, 2016). These

280   findings in combination with the findings that medium sized colonies often use group

281   or mass-recruitment (Beckers et al. 1989) are consistent with our results that the best-

282   supported ancestral recruitment strategy was mass- or group-recruitment.

283   Another reason for the loss of mass-recruitment could be that recruitment by

284   pheromone trails can have disadvantages in changing foraging landscapes.

285   Pheromone trails can persist for relatively long periods (up to several hours), which

286   can make it difficult for the colony to re-allocate workers to a newly available higher-

287   quality resource due to the strong positive feedback created by a pheromone trail

288   (Beckers et al., 1989; Grüter et al. 2012; Czaczkes et al., 2015; I'Anson Price et al.,

289   2016). This makes recruitment less flexible and colonies are more likely to miss out on

290   new food sources when the environment changes.

291   Reeves & Moreau (2019) found evidence that solitary foraging, rather than mass

292   recruitment, represented the original state in terms of recruitment strategies. Our and

293 their results are not necessarily contradictory. In our study, we considered whether a

294 species uses recruitment communication during colony emigrations and/or during

295 foraging. It is well known that foraging strategies in ants strongly depend on the

296 foraging ecology (Davidson, 1977; Dejean et al., 2012; Dornhaus et al., 2006;

297 Hölldobler & Wilson, 1990; Lanan, 2014). For example, in many ant species, foragers

298 follow a solitary foraging strategy when collecting insect prey, but they use recruitment

299 communication when the colony emigrates to a new nest-site (Lanan, 2014). In other

300 words, these species possess the ability to recruit, but foragers do not perform

301 recruitment because this would not be an adaptive strategy given their foraging

302 ecology.

303   The observation that numerous species recruit to new nest sites, but do not use

304 recruitment communication during foraging (e.g. *Neoponera* or *Diacamma* species,

305 Fresneau, 1985; Grüter et al., 2018) raises the question if recruitment communication

306 evolved first to help colonies during emigrations rather than to communicate the

307 location of food sources, as has also been suggested in the case of the honeybee

308 waggle dance (Beekman et al. 2008; I'Anson Price & Grüter, 2015). This seems

309 plausible given that during nest relocations of cavity nesting species, nest locations

310 have to be communicated very precisely. If the old nest is damaged or destroyed, a

311 fast and precise relocation is critical (Dornhaus et al., 2004; Franks et al., 2003). During

312 foraging, on the other hand, communication might often be less important. Especially

313 when food sources are abundant and evenly distributed, communication might not

314 provide benefits or even be disadvantageous due to time costs (Dechaume-

315 Moncharmont et al., 2005; Dornhaus et al., 2006; Goy et al., 2021; I'Anson Price et al.,

316 2019). The hypothesis that recruitment evolved first in colony emigrations and was co-

317 opted by some species in a foraging context is also supported by our results suggesting

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318   group- or mass-recruitment as the ancestral state and those of Reeves & Moreau

319   (2019) who suggested solitary foraging as the ancestral condition.

320   It has been suggested that tandem running is a "primitive" recruitment strategy

321   (*i.e.* ancestral) (Hingston 1929; Hölldobler et al., 1974; Schultheiss et al., 2015; Wilson,

322   1959). Our results do not support this view. We found that tandem running evolved

323   repeatedly and independently in the subfamilies Ponerinae, Pseudomyrmecinae,

324   Formicinae and Myrmecinae. Transitions to tandem running occurred most often from

325   no recruitment and, more rarely, from mass or group-recruitment. One benefit of

326   tandem running is that it allows small colonies to defend resources against competitors

327   when competition for nest sites or food sources is intense(Glaser et al., 2021).

328   In summary, our results suggest that mass or group-recruitment were the most

329   likely recruitment strategies used by the last common ancestor of present-day ants.

330   There were repeated, independent transitions to different strategies, such as tandem

331   running or no recruitment, but also transitions back to group or mass-recruitment. It

332   should be noted that our analysis is restricted to a small proportion of ant species and

333   we currently lack information about recruitment behaviours for the majority of species

334   (see also Reeves & Moreau 2019). We echo the call of Reeves & Moreau (2019) to

335   pay more attention to ant behaviour and ecology as this will allow us to better

336   understand the links between different traits of ant behaviour, ecology and natural

337   history.

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