

1 **TITLE PAGE**

2 **Title:** Modularity and connectivity of nest structure scale with colony size

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4 **Authors:** Julie S. Miller¹, Emma Wan¹ & Noa Pinter-Wollman¹

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6 **Author Affiliations**

7 1. Department of Ecology and Evolutionary Biology, University of California Los Angeles,
8 612 Charles E. Young Dr. East, Los Angeles, CA 90095-7246.

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10

11 **ABSTRACT**

12

13 Large body sizes have evolved structures to facilitate resource transport. Like unitary organisms,
14 social insect colonies must transport information and resources, and colonies with more
15 individuals may experience transport challenges similar to large-bodied organisms. In ant
16 colonies, transport occurs in the nest, which may consist of structures that facilitate movement.
17 We examine three attributes of nest structures that could mitigate transport challenges related to
18 colony size: (1) subdivision - nests of species with large colonies are more subdivided to reduce
19 viscosity of large crowds; (2) branching - nest tunnels increase branching in species with large
20 colonies to reduce travel distances; and (3) short-cuts – nests of species with large colonies have
21 cross-linking tunnels to connect distant parts of the nest and create alternative routes. We test
22 these hypotheses by comparing nest structures of species with different colony sizes in
23 phylogenetically controlled meta-analyses. Our findings support the subdivision and branching
24 hypotheses. The nests of species with large colonies contain more, but not larger, chambers and
25 reduce travel distances by increasing branching frequency. The similarity in how ant nests and
26 the bodies of unitary organisms respond to increasing size suggests structural solutions that are
27 common across levels of biological organization.

28

29 INTRODUCTION

30 Organisms with large body sizes are faced with the challenge of transporting nutrients, waste
31 products, and signals across greater distances compared to organisms with small bodies (Bonner
32 2004). This physical challenge has been resolved through a variety of structural features across
33 the tree of life (McMahon and Bonner 1983), including multi-cellularity (Niklas and Newman
34 2016), body plans that increase surface-area-to-volume ratios (e.g., jellyfish and sponges)
35 (Ruppert et al. 2004), branching vascular systems in animals and plants (West G. B. et al. 1997;
36 Banavar et al. 1999), and compartmentalization of specialized tissues into organs (Gould 1966).
37 Social insect colonies have frequently been compared to whole organisms (Wheeler 1910; Seeley
38 1989; Holldobler and Wilson 2009), and large colonies may experience transport challenges that
39 are similar to those of large bodied organisms (Gillooly et al. 2010). In larger colonies, the speed
40 and/or reliability with which resources or information reach disparate parts of the colony will
41 depend on transfer occurring among more individuals and across greater distances (Pacala et al.
42 1996; O'Donnell and Bulova 2007; Dornhaus et al. 2012).

43 Transport of resources and information in social insect colonies may depend on the
44 layout of their nests. Nest structure affects the routes that individuals take as they move resources
45 and information and therefore the way in which individuals interact (Pinter-Wollman et al. 2013;
46 Pinter-Wollman 2015b; Tschinkel 2015; Pinter-wollman et al. 2018; Vaes et al. 2020) and
47 behave as a collective (Burd et al. 2010; Pinter-Wollman 2015a). Having more individuals may
48 slow the delivery of resources and information, but the physical structure of the nest can promote
49 rapid or efficient movement. Here we investigate how features of the nest, including subdivision,
50 branching, and short-cuts, relate to typical colony size, i.e., the average number of individuals in
51 a colony, of different ant species.

52 Subdivision, or compartmentalization, is one way in which large systems mitigate the
53 challenges of size. For example, large cities subdivide into smaller units, such as neighborhoods
54 (Anas et al. 1998) and large multicellular organisms consist of subdivided cells and organs
55 (Kempes et al. 2012; Okie 2013). The size of the units are constrained by the costs of expanding
56 surface area-to-volume ratios (Bonner 1988; Lorenz et al. 2011). In social insect nests, larger
57 chambers can hold more individuals, but make it harder for individuals to contact each other
58 (Brian 1956; Aguilar et al. 2018). Constraining the size of nest chambers reduces the number of
59 individuals occupying each chamber while reducing the distances they need to travel to interact.
60 The “subdivision hypothesis” predicts that the nests of species with larger colony sizes will
61 consist of more chambers compared to nests of species with small colonies, while chamber sizes
62 will not differ in relation to colony size.

63 Another way that large systems improve transport is by increasing their connectivity and
64 in turn, reducing travel distances. Travel distances can be reduced by branching paths. Many
65 natural systems exhibit branching structures which reduce travel distances without the addition
66 of cross-linking paths. For example, hierarchical branching structures are common in the
67 vascular networks of animals (West G. B. et al. 1997; Tekin et al. 2016) and plants (McKown et
68 al. 2010; Blonder et al. 2018). Branching structures are also common when resources enter
69 through a single site and need to be homogeneously distributed throughout the system (Dodds
70 2010). The “branching hypothesis” predicts that nests of species with larger colonies will have
71 tunnels with high branching frequency to reduce travel distances in the nest.

72 Reducing travel distances and increasing connectivity can further be accomplished by
73 adding cross-linking paths, or short-cuts, that connect distant parts of a network and create
74 alternative access routes to maintain traffic flow (Corson 2010; Katifori et al. 2010; Bullmore

75 and Sporns 2012; Blonder et al. 2018). Indeed, the frequency of cross-linking paths often
76 increases with population size and traffic flow (e.g., roads: Levinson 2012; and computer routing
77 networks: Jyothi et al. 2016). The “short-cut hypothesis” predicts that nests of species with larger
78 colonies will contain more cross-linking paths than nests of species with smaller colonies.
79 Despite the transport benefits of adding short-cuts, every additional connection has a building
80 and maintenance cost, and a highly connected nest may be structurally unsound (Monaenkova et
81 al. 2015).

82 Ants offer an ideal system to study the interaction between group size and structural
83 adjustments to size due to their large range of colony sizes (Bourke and Franks 1995) and the
84 structural diversity of their nests (Tschinkel 2015). We focus our study on ground-nesting
85 species because of all ants, they have the greatest potential to control the structure of their nests.
86 Prior studies of subterranean ant nest structure in relation to colony size have focused on single
87 species, showing that ant nests grow in volume and increase chamber size and/or number over
88 time (Tschinkel 1987, 2004, 2005, 2011, 2015). Fewer studies have examined how tunnel
89 connectivity changes with colony development (but see Buhl et al. 2004a), so branching patterns
90 in ant nests are not well understood. These studies on the ontogeny of nest structure do not
91 provide information on the evolution of nest structures in relation to their mature colony size,
92 which we examine here in a phylogenetically controlled cross-species comparison.

93 We hypothesize that if ant colonies face size-associated challenges in transport and
94 communication, analogous to other systems, then the structure of nests should relate to colony
95 size in ways that ease the movement of individuals, resources, and information throughout the
96 nest. We examine the relationship between three attributes of nest structure: (1) subdivision, (2)

97 branching and (3) and short-cuts, with colony size by comparing different ant species in
98 phylogenetically controlled meta-analyses.

99

100 **METHODS**

101 **Obtaining nest and colony size data**

102 To test our hypotheses, we gathered data on nest architecture of subterranean ant species. We
103 identified publications with graphical representations of ant nests by searching for the terms
104 “nest”, “structure”, “architecture”, “casting”, and “excavation/ed” on Google Scholar and Web
105 of Science. We identified 24 papers that contained photographs or illustrations of castings or
106 excavations of complete ant nests with distinguishable entrances, tunnels, and chambers. For the
107 subdivision hypothesis, we included data from an additional 3 papers containing tables with
108 measures of chamber size and number, even though nest images were not available (Table S1).
109 We excluded 14 publications from our dataset because interior chambers and/or tunnels were
110 obscured, nests were constructed under artificial conditions, or were from incipient colonies
111 (Table S2). Authors were contacted for additional images when parts of the nest were obscured,
112 accounting for approximately 10% of the images we used. Physical castings of unpublished nests
113 were also obtained (Table S1). When more than one nest was available for a species, we took an
114 average of all measurable nests.

115 To relate nest structure with colony size – i.e., the number of ants in a colony - we
116 searched the scientific literature and the web (AntWiki.org and AntWeb.org) for information on
117 the number of workers in a mature colony. For the majority of species, we used the average
118 colony size from the literature. When only a range (minimum - maximum) for number of ants
119 was available, we took the midpoint. Information about the number of ants in a colony at the
120 time of nest excavation or casting was available in less than half of the studies we obtained nest

121 structures from, but when available, we used the reported number of adult workers for those
122 particular nests. When colony size was not available for a particular species, or when nest
123 identity at the species level was unknown, we used colony sizes representative of the order of
124 magnitude for the genus obtained from a sister species. This approximation was necessary for
125 *Forelius sp* - in which colony size from *F. pruinosus* (10^4) was used, and for *Dorymyrmex bureni*
126 - in which colony size from *Dorymyrmex bicornis* (10^3) was used (Table S1). We excluded
127 *Pheidole oxyops* and *Acromyrmex subterraneus* nests from our analysis because colony size was
128 not available for these species, and because we could not make a reliable approximation due to
129 substantial variation in their colony size (Table S2).

130

131 **Nest Subdivision Hypothesis**

132 To test the subdivision hypothesis, we related colony size to the number and size of nest
133 chambers. We counted chambers in 296 nests from 43 species in 24 genera and measured their
134 sizes in 188 nests from 37 species in 21 genera. To quantify the size of chambers, we measured
135 the maximum width of each chamber using ImageJ (Rueden et al. 2017). We excluded nests
136 from the size analysis if images did not include a scale bar or if species identity was unknown for
137 a nest (e.g., *Forelius sp.*). We used chamber width as a proxy for chamber area because we relied
138 on 2D images of 3D structures. When we had access to physical castings, we measured chamber
139 width directly from the structures using a measuring-tape. We validated that chamber width was
140 a reliable indicator of chamber area using an independent dataset (see Supplemental Materials).

141 To allow for cross-species comparison, we standardized chamber width to worker size.
142 Worker size was measured using a standard metric of ant body size, Weber's length (Brown
143 1953), using ant profile images containing a scale bar from AntWeb.org or other publications. In

144 monomorphic species, one ant length measurement was made per species. In species with
145 continuous worker polymorphism, we took the average length from all available images. In
146 species with discrete worker polymorphism (i.e., majors and minors), we used a weighted
147 average, based on typical frequency of majors according to the literature (Brown and Traniello
148 1998; Murdock and Tschinkel 2015). Standardized widths of all chambers in each nest were
149 averaged to obtain a single standardized chamber width per nest.

150

151 **Nest Connectivity**

152 *Nests as Networks*

153 To examine nest connectivity, we depicted each nest as a network, as in (Buhl et al. 2004b; Perna
154 et al. 2008; Viana et al. 2013; Pinter-Wollman 2015a; Kwapich et al. 2018), by manually
155 assigning a node ID to each chamber, nest entrance, tunnel junction, and ends of tunnels that did
156 not reach a chamber ('end nodes') and connecting these nodes with edges depicting tunnels.
157 When quantifying nest casts as networks we excluded the "mushroom top" where the casting
158 material pools around the nest entrance when it is poured (Tschinkel 2010). We designated the
159 nest entrance as the narrowest section of the mushroom top. We obtained networks of 170 nests
160 of 38 species from 21 genera, excluding images in which the network structure could not be
161 inferred because tunnel connections were obscured or ambiguous (Table S1 & 2). We excluded
162 polydomous nests because it was not possible to calculate the network measures we used, mean
163 travel distances and number cycles (see below), without information about the structure of trails
164 connecting different nests.

165

166

167 *Branching Hypothesis*

168 To test the if branching reduces travel distances in large colonies, i.e., the ‘branching hypothesis’
169 we quantified the length of the travel paths in a nest as the mean distance of a network. Mean
170 distance of a network is the sum of the lengths of the shortest paths that connect all possible pairs
171 of nodes, divided by the number of all possible node pairs:

$$\text{Mean Distance} = \frac{1}{n(n-1)} \sum_{i=1}^n d_{ij}$$

172 where n is the number of nodes, and d is the shortest path between all node pairs i and j
173 (Newman 2018). We used the “mean_distance()” function in igraph R package (Csárdi 2020).

174 To determine if observed nests had more branching than expected based on their size,
175 i.e., the number of nodes in the network, we compared the mean distance of networks from
176 observed nests to mean distance of reference models of networks with known branching
177 properties. We evaluated how mean distance relates to nest size under different assumptions
178 about how new nodes are added to a network (i.e., generative models (Hobson et al 2021)). We
179 used three generative reference models that represent the upper and lower bounds on
180 connectivity for how nest networks might increase in size (Buhl et al. 2004b; Bebber et al. 2007;
181 Tero et al. 2010; Latty et al. 2011): (1) chain networks, in which new nodes are added to the last
182 node in a chain – i.e., no branching; (2) triangulated networks, in which new nodes are connected
183 to at least two other nodes such that they form a triangle while avoiding edge overlap. We
184 generated random triangulated networks using Delaunay triangulation with the deldir() function
185 in the ‘deldir’ R package (Turner 2020). The x,y coordinates of the nodes to connect were
186 randomly generated using the sample() function; and (3) minimum spanning trees (MSTs), in
187 which each new node is added to a terminal node to form a new branch in a hierarchical
188 structure. New nodes are added such that the total length of the network is minimized and no

189 cycles are formed. We generated MST networks by pruning the triangulated graphs generated in
190 the prior step using the ‘mst’ function in the ‘igraph’ R package (Csárdi 2020). Each of the above
191 generative processes was run for network sizes ranging from 3 to 100 nodes, in increments of
192 one node. We repeated this process 1000 times for each network size for both triangulated
193 networks and MSTs because they were probabilistic generative processes, but not for the chain
194 network generation because it has only one solution. For each generated network, we calculated
195 the mean distance to create reference distributions for comparison with the observed data
196 (Hobson et al. 2020; Figure 2B). See R code in the supplementary materials.

197 We further scaled the observed networks to the reference models to relate mean distance
198 to colony size (number of individuals) in a way that accounted for expected changes in network
199 size (number of nodes). To create scaled measures of mean distance, we divided the observed
200 mean distance by the mean value of mean distance of the reference networks (from the 1000
201 simulations) for each network size (3-100 nodes). The closer the scaled mean distance value is to
202 1, the more similar the observed network is to the reference model. Scaled values greater than 1
203 indicate that the observed network has a higher mean distance than expected according to the
204 reference model. Likewise, scaled values less than 1 indicate a smaller mean distance than
205 expected according to the reference model. We related these scaled values with colony size using
206 phylogenetically controlled comparisons as described below in Statistical Analyses (Figure 2C).

207

208 *Short-Cut Hypothesis*

209 To test if larger colonies have nests with more short-cuts, i.e., the short-cut hypothesis, we
210 quantified short cuts using the number of cycles in a network (Buhl et al. 2004b; Pinter-Wollman

211 2015a). A cycle is a path along a network that returns to its starting node after passing through at
212 least one other node (Newman 2018). The number of cycles in a nest is:

$$\text{Number of cycles} = m - n + 1$$

213 where n is the number of nodes and m is the number of edges. Cycles are a good approximation
214 of the path redundancy of a network, or presence of short-cuts, indicating how often there is
215 more than one route to any given part of the nest (Perna and Latty 2014).

216 To account for how network size affects the rate at which new cycles are added, we
217 compared the observed nests to the reference models of networks described above. Following a
218 similar procedure to the one described for network mean distance, we calculated the number of
219 cycles in triangulated networks (Figure 2E) and then scaled the number of cycles in observed
220 nests to triangulated networks of equivalent size. Because both chain and MST reference models
221 do not produce cycles, we did not include these models when we scaled the observed nests. We
222 related the scaled number of cycles in a nest with colony size using phylogenetically controlled
223 comparisons as described below (Figure 2F).

224

225 **Statistical Analyses**

226 We examined the effect of colony size on the above nest measures while controlling for
227 phylogeny. We used a pruned evolutionary tree of the ants (Formicidae) from (Blanchard and
228 Moreau 2017) and calculated the mean trait value for each species. A complete species-level tree
229 was not available for all species in our dataset, so we selected only one species per genus and ran
230 our analysis using a genus-level tree. When there were data for more than one species per genus,
231 we used the species which had the most nests in our dataset (subset 1 in Tables S3-S13). To
232 ensure this sub-setting of species did not bias our results, we re-ran each analysis with previously

233 excluded species as representatives of a genus, and report the proportion of those runs that were
234 statistically significant. See supplementary materials for results from all runs (Tables S3-13).

235 We ran phylogenetic generalized least squares (PGLS) comparing each nest trait to the
236 log of colony size. PGLS is a multiple regression that controls for the degree of similarity
237 between species based on phylogenetic distance in a co-variance matrix. We ran PGLS by
238 estimating the phylogenetic signal, lambda λ , through maximum likelihood in the “caper”
239 package v1.0.1 in R (Orme et al. 2018), with $\lambda=0$ meaning no phylogenetic signal, and $\lambda=1$
240 meaning the observations completely match phylogeny (Pagel 1999). Due to the small sample
241 size (20 - 24 genera) we could not estimate lambda with high confidence (Freckleton 2009).
242 Therefore, we further conducted PGLS for fixed lambda values (0, 1) using the “ape” package
243 v5.1 in R (Paradis et al. 2018). When our models did not meet the assumption of normality of
244 residuals we analyzed these relationships by calculating phylogenetic independent contrasts
245 (PICs) instead (Paradis et al. 2018). PIC transformed data were modeled using OLS regression,
246 with the intercept set to the origin (R Core Team 2019). Due to small sample sizes, we calculated
247 95% confidence intervals for OLS model coefficients using a bootstrap (1000 iterations).

248

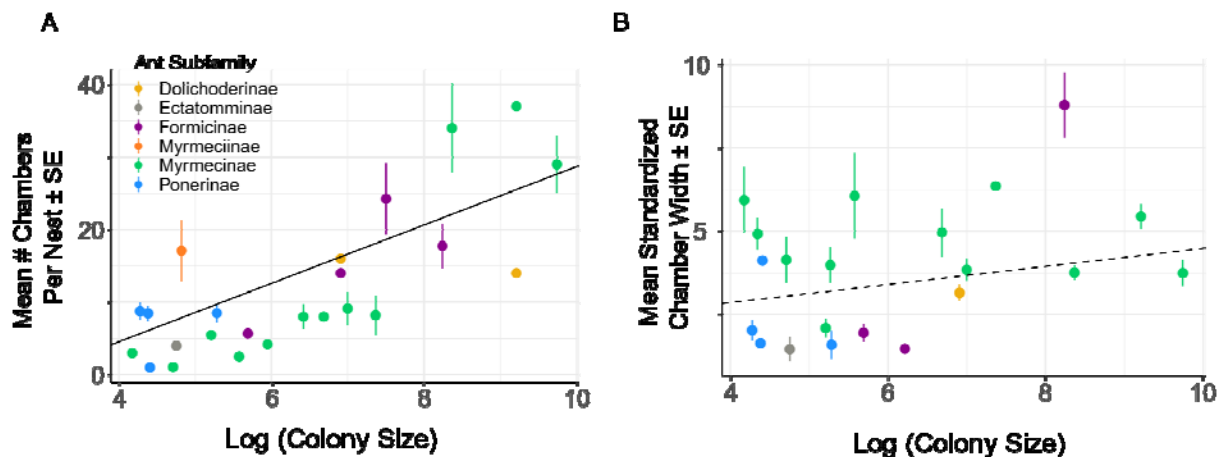
249 **RESULTS**

250 **Subdivision Hypothesis**

251 Both predictions of the subdivision hypothesis, that chamber number would be larger in species
252 with large colony sizes and that chamber size would not relate to colony size, were supported.

253 We found a statistically significant positive relationship between number of chambers per nest
254 and colony size (Figure 1A; N= 24 genera, OLS of PIC: $\beta = 4.024$, 95% CI = 2.014, 6.292, $R^2 =$
255 0.560, $p < 0.0001$; Table S3). The effect size of this relationship was large ($3.7 < \beta < 4.3$ across

256 all data subsets) and statistically significant in all species subsets (19/19 datasets). We did not
257 find a statistically significant relationship between the average standardized chamber width and
258 colony size (Figure 1B; N=21 genera, OLS of PICs: $\beta = 0.325$, 95% CI = -0.086, 0.932, $R^2 =$
259 0.102, $p = 0.15$; Table S4) in the majority of the species subsets (14/15 datasets). This lack of
260 statistical significance could be attributed to low statistical power (power < 0.4 from a post-hoc
261 power analysis based on N=21 genera, effect size = 0.1, and alpha = 0.05).
262



263
264 **Figure 1:** Relationship between the log of colony size (number of ants in a colony) and (A)
265 average number of chambers per nest or (B) average standardized chamber width. Each data
266 point represents a mean value for a single species, whiskers indicate standard errors when
267 multiple nests were sampled. Colors represent ant subfamilies. Lines are fits from the PGLS
268 ($\lambda=1$) with a statistically significant fit as a solid line and a relationship that is not statistically
269 significant is a dashed line.

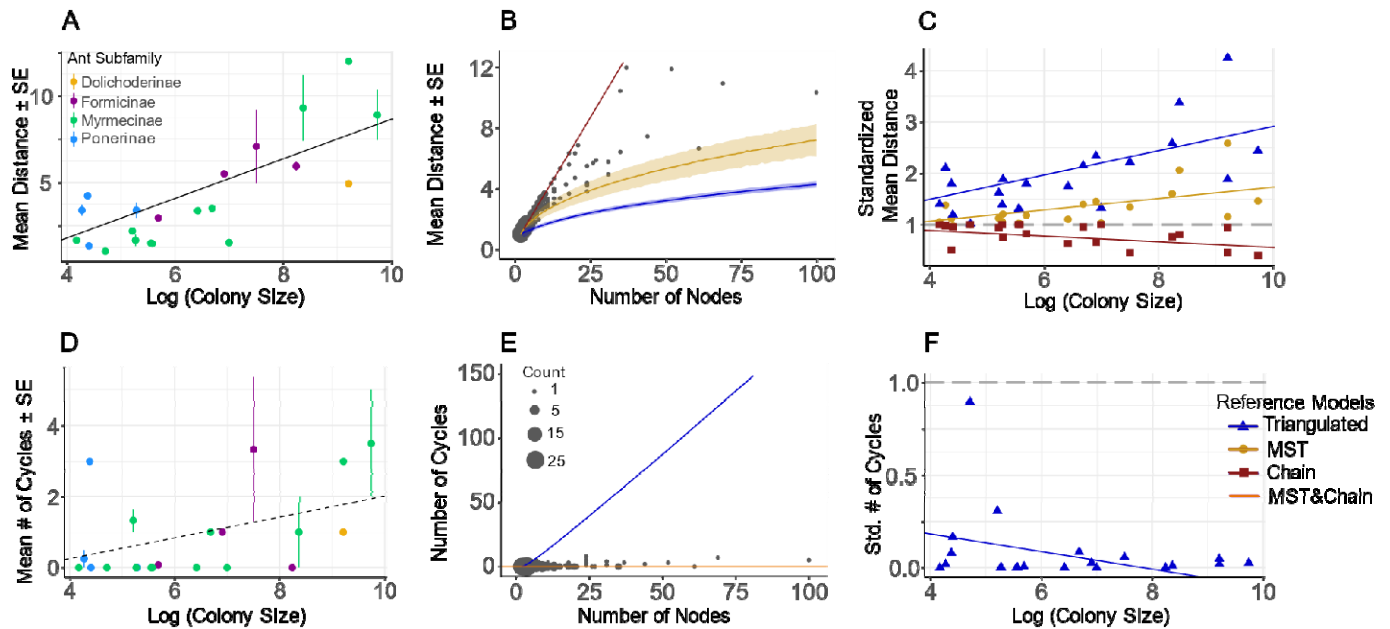
270

271 **Branching Hypothesis**

272 The “branching hypothesis”, that branching would reduce travel distances in nests of species
273 with large colonies, was supported. Raw, unscaled, mean distance of nests significantly increased
274 with colony size (Figure 2A; $N = 21$ genera, PGLS $\lambda = \text{MaxLL}$: $\beta = 1.36 \pm 0.247$, $\lambda = 0.585$, $R^2 =$
275 0.615 , $p = 0.0007$; $\lambda = 1$: $\beta = 0.844 \pm 0.227$, $p = 0.0015$; $\lambda = 0$: $\beta = 1.013 \pm 0.251$, $p < 0.0001$; Tables
276 S5-S7). In the chain network reference models, mean distance increased fastest and linearly with
277 network size (i.e., number of nodes; Figure 2B). In the triangulated reference models, mean
278 distances were smallest and increased nonlinearly, slowing their rate of increase with increasing
279 network size. In the MST reference models, mean distances were intermediate between the
280 values expected from the chain and triangulated reference models, and also increased nonlinearly
281 (Figure 2B). The mean distances of empirically observed nests were between the expected
282 values for chain and MST reference models (Figure 2B). When we scaled the observed mean
283 distance with the expected mean distance based on each of the three reference models, we found
284 that the relationship between scaled mean distance and colony size differed across the three
285 models (Figure 2C). Mean distances scaled to chain networks declined with colony size and the
286 relationship was statistically significant in almost all data subsets (15/16 datasets; PGLS $\lambda = 1$: β
287 $= -0.055 \pm 0.024$, $p = 0.031$; 16/16 datasets; $\lambda = 0$: $\beta = -0.061 \pm 0.024$, $p = 0.018$; Tables S8 & S9).
288 In contrast, mean distances scaled to triangulated networks increased significantly with colony
289 size in almost all the data subsets (15/16 datasets; OLS of PIC: $\beta = 0.236$, 95% CI = 0.055,
290 0.466, $R^2 = 0.348$, $p = 0.0048$; Table S10). Mean distances scaled to MSTs also increased
291 significantly with colony size (15/16 species subsets), but the effect size was smaller than for
292 triangulated networks (OLS of PIC: $\beta = 0.11$, 95% CI = -0.022, 0.240, $R^2 = 0.281$, $p = 0.013$;
293 Table S11).
294

295 **Short-cut Hypothesis**

296 The “short-cut hypothesis,” that nests from species with larger colonies would contain more
297 cycles, was not supported. The relationship between the number of cycles in a nest had a positive
298 relationship with colony size, but this trend was not statistically significant in the majority of the
299 data subsets (Figure 2D; 15/16 subsets; $N = 21$ genera, OLS of PIC: $\beta = 0.293$, 95% CI = -0.089,
300 0.528, $R^2 = 0.160$, $p = 0.072$; Table S12). The triangulated reference networks showed a steep
301 increase in the number of cycles as a function of network size, and far exceeded the number of
302 cycles in observed nests given their networks’ size (Figure 2E). However, the number of cycles
303 in observed nests was similar to that expected from the chain and MST reference networks,
304 which do not produce cycles at any network size (Figure 2E). The measure of cycles scaled to
305 the triangulated reference models significantly decreased with colony size in all species subsets
306 (16/16 subsets; Figure 2F; OLS of PIC: $\beta = -0.048$, 95% CI = -0.102, -0.015, $R^2 = 0.090$, $p =$
307 0.186; Tables S13).



308

309 **Figure 2: Nest Connectivity: branching (A-C) and short-cut (D-F) hypotheses. (A, D)**

310 Relationship between colony size (average number of ants in a colony) and (A) network mean

311 distance and (D) mean number of cycles in nests. Each data point represents a mean value for a

312 single species, whiskers indicate standard errors around the mean when multiple nests were

313 sampled for a given species, colors represent ant subfamily (see legend in A). Dashed line is the

314 regression fit for PGLS when $\lambda=1$, solid when statistically significant and dashed when not

315 statistically significant; (B, E) The mean distance (B) or number of cycles (E) according to

316 network size (number of nodes). Networks from observed nests are plotted as grey dots, sized

317 according to sample size. In (B) lines are mean distances as a function of number of nodes for

318 chain (red), MST (yellow) and triangulated (blue) reference networks, with 95% confidence

319 intervals from 1000 simulation runs shown as shading around the lines; in (E) Blue line is the

320 number of cycles in triangulated networks as a function of number of nodes. Orange line depicts

321 the number of cycles for both MSTs and chain networks, which contain zero cycles at all

322 network sizes; (C, F) Relationship between colony size (average number of ants in a colony) and
323 scaled mean distance (C) and scaled number of cycles (F). Mean distance (C) is scaled to chain
324 (red), MST (yellow) and triangulated (blue) networks. Cycles (F) are only scaled to triangulated
325 networks (blue). Each point represents a mean of scaled values from the nests of each species.
326 Grey dashed line at $y=1$ represents values at which observed nests contain the same value as
327 expected from the reference model. Values below the dashed line indicate networks that have
328 lower values than expected by the reference model. Values above the dashed line indicate
329 networks which have values greater than expected according to the reference model. Solid
330 colored lines indicate statistically significant regression fits for PGLS ($\lambda=1$).

331

332 **DISCUSSION**

333 Our results support the hypothesis that nest architecture mitigates the challenges of larger colony
334 sizes, i.e., more individuals in a colony. Our comparative analysis found that nests of species
335 with larger colonies are more subdivided and reduce travel distances through increased
336 branching. Overall, we did not find a strong effect of phylogeny.

337 As predicted by the subdivision hypothesis, the number of chambers was greater in species
338 with larger colonies and chamber size was not related to colony size (Figure 1). These results
339 suggest that nests of species with large colonies are divided into more sub-units than nests of
340 species with small colonies, and that the size of those sub-units does not increase proportionately
341 to colony size. Similar patterns of increased spatial subdivision with body size are the
342 cornerstone of multi-cellularity (Bonner 1998), and also characterize subdivision as the brain
343 (Kaas 2000) and cities (Anas et al. 1998) increase in size. Given our correlational findings, it
344 remains unclear if subdivision in nests serves a similar function as it does in these other systems.

345 Further data are needed on the distribution of individuals throughout nest chambers to determine
346 if ants utilize chambers in a way that is consistent with subdivision (e.g. Tschinkel 1999;
347 Murdock and Tschinkel 2015). Nest subdivision may facilitate division of labor through spatial
348 segregation of tasks (Tofts and Franks 1992; Richardson et al. 2011; Mersch et al. 2013), and
349 slow down the spread of disease (Pie et al. 2004; Stroeymeyt et al. 2014, 2018). However, the
350 only direct test of the benefit of nest subdivision showed that subdivision does not increase brood
351 rearing efficiency (Cassill et al. 2002; Tschinkel 2018). Limits on chamber size may also be
352 imposed by physiological processes, such as gas exchange or temperature regulation (Jones and
353 Oldroyd 2006), or by structural constraints, because large chambers may collapse. Thus, the
354 causes and consequences of nest sub-division remain to be tested.

355 The connectivity of nests changed according to colony size, but only one of our hypotheses
356 about nest connectivity was supported. The nests of species with larger colonies had reduced
357 travel distances due to their branching structure, consistent with the branching hypothesis. In the
358 nests of species with small colonies (i.e., up to ~1000 workers in nests containing up to ~10
359 nodes), mean distances tended to match the values expected for chain networks, and indeed the
360 nests of many small colony species were chains. In the nests of species with large colonies, mean
361 travel distances were shorter than would be expected for chain networks but greater than
362 expected for MSTs, and far greater than expected for triangulated networks (Figure 2B, C).
363 These findings indicate that the nests of species with large colonies have increased branching
364 (i.e., are more tree-like) relative to the nests of species with smaller colonies. By increasing the
365 frequency of branching large colonies may curb rising travel distances as their nests increase in
366 size (i.e., contain more chambers). Networks cannot simultaneously minimize travel distances
367 (i.e., be highly interconnected) and minimize their number of edges (i.e., minimize infrastructure

368 costs). Increased branching is a common way for biological transport networks to balance this
369 trade-off (e.g., ant foraging trails: Buhl et al. 2009; slime molds: Tero et al. 2010; neural
370 networks: Raj and Chen 2011; plant growth forms: Conn et al. 2017), especially as body size, or
371 population size, increases (Ringo 1991; Banavar et al. 1999; Ercsey-Ravasz et al. 2013; Cabanes
372 et al. 2015). Branching is thus a low-cost way for biological transport networks, including ant
373 nests, to maintain connectivity as they increase in size.

374 The short-cuts hypothesis, that nests from species with larger colonies will have more cross-
375 linking paths or cycles, was not supported. Although the number of cycles in a nest increased
376 with colony size, this increase was not statistically significant (Figure 2D). Cycles were added at
377 a slower rate than expected for a triangulated network (Figure 2E), which is not surprising given
378 that triangulations represent the maximum rate at which new cycles could be added with
379 increasing network size (for 2D networks). This finding lends further support to the conclusion
380 that the increase in connectivity with colony size is due to increased branching and not the
381 addition of short-cuts. However, we caution that our analysis conservatively excludes nests that
382 might have the most cycles because we could not accurately infer the topology of the most
383 convoluted nests. Our inability to detect a significant increase in the number of cycles with
384 colony size could be due to this bias in our dataset. More refined imaging techniques could
385 provide a solution to this issue and expand future work on nest architecture in general.

386 The scarcity of cycles in the nests we measured suggest that the benefits of having
387 alternative access routes, which help maintain movement (Corson 2010; Katifori et al. 2010;
388 Blonder et al. 2018, Jyothi et al. 2016) and facilitate forager recruitment (Pinter-Wollman 2015),
389 might not outweigh the potential costs of additional tunnels. For instance, there are costs to
390 building and maintaining tunnels (da Silva Camargo et al. 2013; Monaenkova et al. 2015) and

391 there may be negative consequences of many cross-linking paths, including structural instability
392 or heightened exposure to risks, like pathogens (Scovell 1983; Viana et al. 2013; Stroeymeyt et
393 al. 2014, 2018), parasites (Scovell 1983), or predators (Jeanne 1975; LaPolla et al. 2002). Nests
394 are multi-purpose structures that have other functions, like thermoregulation, humidity control or
395 ventilation (Jones and Oldroyd 2006; King et al. 2015), which might suffer when nests have
396 many cycles. In systems where the costs of cross-linking paths are low, like the plasmodia of
397 slime molds, the mycelia of fungus, or the pheromone trails of ants, cycles are ephemeral and
398 created for exploration, yet they are pruned once resources are discovered (Bebber et al. 2007;
399 Buhl et al. 2009; Tero et al. 2010; Latty et al. 2011). Conversely, when the benefits to movement
400 are very high, as in some man-made networks like urban roads or computer routing networks,
401 cycles become more common as size increases (Levinson 2012; Jyothi et al. 2016). Future
402 investigation into the building costs of tunnels and the functional consequences of interconnected
403 nest structures will help reveal why ant nests do not contain more short-cuts, or cycles.

404 As with any meta-analysis, our dataset is constrained by the available literature. Many of
405 the nests we found in the literature were built in sandy soils, and so our analysis has an over-
406 representation of species adapted to the climate and ecology of sandy soils (Table S1). Fungus
407 growers are highly-represented in our analysis, and constraints imposed by requirements to
408 maintain healthy fungus gardens could have influenced our findings. Additionally, because we
409 do not have data on the size or age of the colonies that built the majority of nests in our meta-
410 analysis, we might have included immature colonies that have not reached their full size. Further
411 work could investigate whether nest connectivity changes throughout development within a
412 species in natural environments (e.g., Tschinkel 1987, 2004, 2005, 2011) or whether there are
413 species-specific connectivity patterns that can be found at different ages.

414 In conclusion, we show that ant nests exhibit modular and efficient structures in species
415 with larger colonies. The similarity in how ant nests and the bodies of unitary organisms respond
416 to increasing size suggest that their shared architectural features, branching transportation
417 networks and compartmentalization, provide common solutions to the challenges created by
418 large size across the tree of life.

419

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