

Disease implications of animal social organization and network structure - a quantitative analysis

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Summary

1. Previous studies examining the disease costs of sociality have largely focused on the link between group size and transmission. However, infectious disease spread is driven by the structure of infection-spreading interactions between individuals.

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2. We used statistical tools to review the organization of the interaction networks of 47 species, including mammals, birds, reptiles, fish and insects by categorizing each species into one of four social systems, *relatively solitary*, *fission-fusion*, *gregarious* and *socially hierarchical*. Additionally, using computational experiments of infection spread, we determined the disease costs of each social system.
3. Our analysis predicts consistent structural differences across social systems, regardless of species or interaction type. We find that solitary species have large variation in numbers of interactions, that socially hierarchical species are the least clustered in their interactions, and that fission-fusion species tend to be the most fragmented. However, these structural differences are primarily driven by low weighted edges, which suggests that different social systems have evolved unique strategies to organize weak ties.
4. Disease simulations show that the organization of interaction networks can mitigate the disease costs of group living for certain social systems under certain conditions. In particular, the low clustered and fragmented interactions networks of socially hierarchical species are expected to cause frequent outbreaks of lowly transmissible pathogens, but a reduced risk of epidemic outbreaks of fast spreading infections. In contrast, the network structure of fission-fusion and gregarious species predict frequent and prolonged epidemic outbreaks of highly transmissible pathogens.
5. By evaluating the implications of network organization across social systems, our finding offers new perspective on the debate about the disease costs of group living. Additionally, this study demonstrates the scope of meta-

analytic methods in social network analysis, which in future could be used to test ecological and evolutionary hypotheses on cooperation, group-living, communication, and resilience to extrinsic pressures.

Keywords

animal social network, contact network, epidemiology, infectious disease dynamics, meta-analysis, social behaviour, social complexity, wildlife disease

Introduction

1 Host social behaviour plays an important role in the spread of infectious diseases.
2 Socially complex species from honeybees to primates live in large groups and are
3 considered to have elevated costs of pathogen transmission due to high contact
4 rates (Loehle, 1995; Altizer *et al.*, 2003). Previous studies, therefore, have tested
5 hypotheses on the disease costs of sociality by associating group size with infection
6 transmission (Rifkin, Nunn & Garamszegi, 2012; Patterson & Ruckstuhl, 2013).
7 Beyond a simple dependence on group size, however, recent work in the field of
8 network epidemiology has shown that infectious disease spread largely depends on
9 the organization of infection-spreading interactions between individuals (Godfrey
10 *et al.*, 2009; White, Forester & Craft, 2015; Craft, 2015; VanderWaal & Ezenwa,
11 2016). Indeed, when interactions between individuals are assumed to be homo-
12 geneous, the expectation of higher disease costs of group-living has been mixed
13 (Arnold & Anja, 1993; Rifkin, Nunn & Garamszegi, 2012; Patterson & Ruckstuhl,
14 2013).

15 The advantage of social network analysis is that it integrates heterogeneity
16 in interaction patterns at individual, local and population scales to model global
17 level processes, including the spread of social behaviour and infectious diseases.
18 A fundamental individual-level characteristic relevant to the spread of social or
19 biological contagion in networks is the number of direct social partners, associates
20 or contacts, capturing the interaction necessary for transmission. In recent years,
21 network analysis tools have allowed for rapid advances in our understanding of
22 how individual interaction rates are related to the risk of infection. For example,
23 Otterstatter & Thomson (2007) demonstrated that the contact rate of a bumble
24 bee is a significant predictor of *Crithidia bombi* infection risk from an infected
25 nestmate. Leu, Kappeler & Bull (2010) showed that lizards that frequently visited
26 neighbouring refuges had higher tick loads. While much attention has been focused
27 on disease implications of individual sociality, the implications of species' social
28 system (henceforth also referred to as *species sociality*), ranging from solitary to
29 ones with stable and hierarchical group composition, remains unclear.

30 By quantifying group-level metrics that describe global structures in interac-
31 tion patterns, the network approach provides a unique opportunity to examine
32 the disease costs of species sociality. The role of higher-order network structures
33 such as degree heterogeneity, network fragmentation, modularity and global clus-
34 tering coefficient on infectious disease spread is complex, but is relatively well
35 understood (Keeling, 2005; Meyers *et al.*, 2005; Sah *et al.*, 2017). For example,
36 as degree heterogeneity in a network increases, the epidemic threshold (i.e., the
37 minimum pathogen transmissibility that can cause large outbreaks) approaches
38 zero. However, outbreaks are less likely to reach epidemic proportions in highly
39 degree heterogeneous network than in the other networks (Meyers *et al.*, 2005).

40 Network clustering and modularity measures the tendency of nodes to form cliques
41 and subgroups, respectively (Fig. 1). Although the dynamics of infectious disease
42 spread remain largely unaffected in networks with moderate levels of clustering
43 and modularity, extreme levels of these metrics in networks reduce outbreak size
44 and prolong epidemic outbreaks (Keeling, 2005; Sah *et al.*, 2017).

45 Recent mathematical models predict that the network structure of socially
46 complex species can serve as a primary defence mechanism against infectious dis-
47 ease by lowering the risk of disease invasion and spread, without requiring an
48 additional increase in physiological immunocompetence or behavioural avoidance
49 (Hock & Fefferman, 2012). It remains unproven, however, whether the structure
50 of interaction networks naturally observed in less-complex social systems mediates
51 infectious disease risk and transmission. A systematic examination of the dis-
52 ease costs associated with species sociality requires a comparative approach that
53 isolates unique structural characteristics of interaction patterns, while controlling
54 for population size, data collection methodology and type of interaction recorded.
55 However, comparing networks across different taxonomic groups has proven to
56 be a difficult task, with only a few cross-species network comparisons (Faust &
57 Skvoretz, 2002; Faust, 2006).

58 In this study, we conduct a quantitative analysis across 47 species based on
59 666 interaction networks to investigate the relationship between network com-
60 plexity and the disease costs for different species sociality. This is achieved in
61 three steps. First, we use phylogenetically-controlled Bayesian MCMC models to
62 identify network structures which are predictive of species sociality. Second, we
63 perform computational model-based disease experiments to determine the role of
64 various global network metrics in curbing the invasion of a novel pathogen and

65 limiting the spread of infectious diseases. Finally, we identify the relative costs of
66 disease transmission for each social system as mediated by their network structure.
67 We hypothesized that social species organize their network structure to mitigate
68 pathogen transmission associated with group living. However, we expected the
69 presence of alternate disease defence mechanisms in socially complex species to
70 also play an important role: social insects, for example, could rely on social im-
71 munity as a primary strategy to minimize disease transmission risk, allowing these
72 species to organize their interactions to maximize information transfer.

73 Our analysis, by broadening the scope of network analysis from species-specific
74 analysis to meta-analytic approach, offers new perspective on how social structure
75 strategies mediate the disease costs of group living. A better understanding of the
76 association between network structure and different social systems, in the future,
77 can facilitate investigations on other evolutionary and ecological hypotheses, in-
78 cluding the ones on group living, social complexity, communication, population
79 robustness and resilience to extrinsic population stressors.

80 **Materials and methods**

81 **Dataset**

82 We first conducted electronic searches in *Google Scholar* and popular data reposi-
83 tories, including *Dryad Digital Repository* and *figshare* for relevant network datasets
84 associated with peer-reviewed publications. We used the following terms to per-
85 form our search: "social network", "social structure", "contact network", "interac-
86 tion network", "network behaviour", "animal network", "behaviour heterogeneity"

87 and "social organization". Only studies on non-human species were considered in
88 our primary search. Network studies not reporting interactions (such as biological
89 networks, food-web networks) were excluded. By reviewing the quality (i.e.,
90 whether enough information was provided to accurately reconstruct networks) of
91 published networks datasets, we selected 666 social networks spanning 47 animal
92 species and 18 taxonomic orders. Edge connections in these networks represented
93 several types of interactions between individuals, including dominance, grooming,
94 physical contact, spatial proximity, direct food-sharing (i.e. trophallaxis), foraging,
95 and interactions based on the asynchronous use of a shared resource. Fig.
96 2 summarizes the species, the number of networks and the reported interaction
97 types contributed by each taxonomic order represented in the study.

98 **Classifying species sociality**

99 Developing a definition of sociality that encompasses the spectrum of social systems
100 across diverse taxonomic groups is challenging. Consequently, we followed
101 Slater & Halliday (1994) to classify species into four broad categories of sociality
102 based on the degree of association between adults during activities such as foraging,
103 travelling, sleeping/resting and rearing offspring. *Relatively solitary* species
104 were defined by infrequent aggregation or association between adults outside of the
105 breeding period. Examples of *relatively solitary* species in the database include
106 the desert tortoise (*Gopherus agassizii*), wild raccoons (*Procyon lotor*), and the
107 Australian sleepy lizard (*Tiliqua rugosa*). Recent studies suggest that the social
108 structure of a species traditionally considered as solitary can be complex (Sah
109 *et al.*, 2016; Prange *et al.*, 2011). We therefore categorized the three species as *rel-*

110 *actively solitary* and not solitary. Species that aggregate for one or more activities,
111 but have unstable group composition and do not have a hierarchical social orga-
112 nization were classified as *fission-fusion*. Examples of fission-fusion species in our
113 database include bottlenose dolphins (*Tursiops truncatus*), bison (*Bison bison*),
114 Indiana bats (*Myotis sodalis*), Asian elephants (*Elephas maximus*), and guppies
115 (*Poecilia reticulata*). Species characterized by a permanent or temporary social
116 hierarchy where individuals form stable associations were classified as *socially hi-*
117 *erarchical*. Examples of socially hierarchical species include carpenter ants (*Cam-*
118 *ponotus fellah*), yellow baboons (*Papio cynocephalus*), elephant seals (*Mirounga*
119 *angustirostris*) and spotted hyenas (*Crocuta crocuta*). Finally, all species that
120 demonstrated behavior of colonial breeding, communal roosting or aggregating
121 behavior during foraging that were not classified as *socially hierarchical* or *fission-*
122 *fusion* were categorized as *gregarious*. Examples of gregarious species represented
123 in our database include field voles (*Microtus agrestis*), sociable weavers (*Philetairus*
124 *socius*) and golden-crowned sparrows (*Zonotrichia atricapilla*).

125 **Identifying unique network structures of species sociality**

126 To examine the structure of interaction networks associated with our four classified
127 social systems, we used a Bayesian mixed-model approach using the *MCMCglmm*
128 package in R (Hadfield, 2010), with species sociality as the response. The fol-
129 lowing network measures were included as predictors in the model (see Table S1
130 in the Supplementary Information for definitions): degree heterogeneity, degree
131 homophily, global clustering coefficient, weighted clustering coefficient, transitiv-
132 ity, average betweenness centrality, weighted betweenness centrality, average group

133 size, network fragmentation, group cohesion, relative modularity and network di-
134 ameter. Network fragmentation (i.e., the number of groups within the largest
135 connected component of the interaction network) and Newman modularity was
136 estimated using the Louvain method (Blondel *et al.*, 2008). Relative modular-
137 ity was then calculated by normalizing Newman modularity with the maximum
138 modularity that can be realized in the given interaction network (Sah *et al.*, 2014,
139 2017). We included the number of nodes and edges in the network to provide a
140 statistical control for dependence of global network metrics on network size and
141 density, and average edge weight was included to control for data sampling design.
142 To control for phylogenetic relationships between species, a correlation matrix
143 derived from a phylogeny was included as a random factor. The phylogenetic re-
144 lationship between species was estimated based on NCBI taxonomy using phyloT
145 (<http://phylot.biobyte.de>). We also controlled for repeated measurements within
146 groups, animal species, the type of interaction recorded, and edge weighting cri-
147 teria by including *group*, *taxa*, *interaction type* and *edge weight type* as random
148 effects in the analysis. The random effect of *interaction type* consisted of 10 levels,
149 including: dominance, foraging, grooming, group membership, non-physical social,
150 physical contact, non coincident resource use, spatial proximity, trophallaxis, and
151 mixed interactions (Fig. 2). The *edge weight type* random effect was categorized
152 into 6 levels: frequency, duration, half weight index, simple ratio index, twice
153 weight index, and unweighted.

154 All continuous fixed-effects were centered (by subtracting their averages) and
155 scaled to unit variances (by dividing by their standard deviation) to assign each
156 continuous predictor with the same prior importance in the analysis (Schielzeth,
157 2010). Since network measures can be highly correlated to each other, variance

158 inflation factor (VIF) was estimated for each covariate in the fitted model, and
159 covariates with VIF greater than 5 were removed to avoid multicollinearity. We
160 used a weakly informative Gelman prior for fixed effects and parameter-expanded
161 priors for the random effects to improve mixing and decrease the autocorrelation
162 among iterations (Gelman, 2006). Specifically, a χ^2 distribution with 1 degree of
163 freedom was used as suggested by Hadfield (2014). We ran three MCMC chains
164 for 15 million iterations, with a thinning interval of 1000 after burn-in of 50,000.
165 Convergence of chains was assessed using the Gelman-Rubin diagnostic statistic
166 (Gelman & Rubin, 1992) in the *coda* package (Plummer *et al.*, 2006).

167 Groups of certain species in our database were represented with multiple net-
168 works, each summarizing a set of interactions occurring in a discrete time period.
169 To ensure that such animal groups were not over-represented in the original anal-
170 ysis, we performed a cross-validation of our analysis by random sub-sampling.
171 Specifically, we repeated the analysis 100 times with a random subset of the data
172 composed of (randomly selected) single networks of each unique animal group in
173 our database. An average of coefficient estimates across the multiple subsamples
174 was then calculated and compared to the coefficient estimate of the full dataset.

175 **Evaluating the role of weak ties in driving structural differences in** 176 **species sociality**

177 The analysis described in the previous section assumes equal importance of all
178 edges recorded in an interaction network. To examine the role of weak ties in
179 driving the structural differences between the four social systems, we removed
180 edges with weights lower than a specified threshold. Three thresholds were exam-
181 ined in detail: 5%, 10% and 20% of highest edge weight. In particular, all edges

182 with weights below the specified cut-off point were removed to obtain filtered in-
183 teraction networks. Next, the phylogenetically controlled Bayesian mixed model
184 analysis was performed to determine the structural difference between the filtered
185 interaction networks of the four social systems. We ran three separate models,
186 each with one of the three specified cutoff points.

187 **Disease implications of structure and species sociality**

188 We consider the disease costs of species sociality with synthetic experiments based
189 on a computational disease model, and follow up with statistical analysis of the
190 results.

191 **Disease simulations**

192 We performed Monte-Carlo simulations of the discrete-time susceptible-infected-
193 recovered (SIR) model of infection spread through each network in our database.
194 For disease simulations, we ignored the weights assigned to social interactions be-
195 tween individuals, because the impact of weight (whether they represent contact
196 duration, frequency or intensity) on infection transmission is generally unclear and
197 is usually context-dependent. Transmissibility of the simulated pathogen was de-
198 fined as the probability of infection transmission from an infected to susceptible
199 host during the infectious period of the host. Assuming infection transmission to
200 be a Poisson process and a constant recovery probability, the pathogen transmis-
201 sibility can be calculated as $T = \frac{\beta}{\beta + \gamma}$, where β and γ is the infection and recovery
202 probability parameter, respectively. Each disease simulation was initiated by in-
203 fecting a randomly chosen individual in the social group. At subsequent time steps

204 every infected individual(s) in the population could either transmit infection to a
205 susceptible neighbour with probability parameter β or recover with probability γ .
206 The disease simulation were terminated when there were no remaining infected
207 individuals in the network. We performed simulations of pathogens with a wide
208 range of trasmissibility values (0.025 to 0.5). Disease simulations for each value of
209 pathogen transmissibility and social network were summarized using three mea-
210 sures: (a) epidemic probability, the likelihood of an infectious disease invasion
211 turning into a large epidemic (i.e., outbreaks that infect at least 15% of the indi-
212 viduals in the population), (b) epidemic size, the number of individuals infected
213 in the population, and (c) epidemic duration, the duration of infectious disease
214 spread.

215 **Evaluating disease outcomes of structure and sociality**

216 Three separate multivariate Bayesian-MCMC models, one corresponding to each
217 outbreak measure (epidemic probability, epidemic size and epidemic probability),
218 were fit to establish disease costs of network measures associated with species
219 sociality. Outbreak measures across different pathogen transmissibility were en-
220 tered as multivariate response variables. To evaluate the role of network structure
221 on the probability of large outbreaks, network measures investigated in the final
222 model of the previous analysis were included as predictors (Table1). We repeated
223 the analysis with species sociality as predictor to directly estimate the vulnerabil-
224 ity of different social systems towards disease transmission. In both the models,
225 the effective number of nodes (i.e., the number of individuals with degree greater
226 than zero), network density and the size of the largest connected component of
227 the network were also included as predictors. (Average edge weights were not in-

228 cluded because disease simulations were performed over unweighted networks). As
229 before, phylogenetic correlations, group identification, animal species, interaction
230 type and edge weight type were included as random effects in the analysis. To
231 make posthoc comparisons within the models, we performed pairwise comparisons
232 between the four social systems with a Tukey adjustment of p values, using the
233 *lsmeans* R package (Lenth, 2016).

234 Results

235 Unique network structures of species sociality

236 The final model (after removing collinear predictors) consisted of seven global net-
237 work measures - degree heterogeneity, degree homophily, global betweenness cen-
238 trality, global clustering coefficient, group cohesion, network fragmentation and
239 network diameter (Fig. 1, Table 1). Of the four social systems (relatively soli-
240 tary, fission-fusion, gregarious and socially hierarchical), the interaction networks
241 of solitary species demonstrated high degree heterogeneity, or large variation in
242 the number of individual social partners (Table 1). On the contrary, variation
243 in individual degree was much lower in socially hierarchical species as compared
244 to other social systems. In addition, socially hierarchical species experience a
245 local social environment that is not as well inter-connected; this is evident by
246 the low global clustering coefficient of their interaction networks as compared to
247 other social systems. In terms of network fragmentation (which was calculated
248 on the largest connected component of a network), the interaction networks of
249 fission-fusion species were the most subdivided into socially cohesive groups. The

250 interaction networks of solitary species were less fragmented, or had fewer socially
251 cohesive groups as compared to gregarious species (Table1). No statistically signif-
252 icant differences were observed between the social systems with respect to degree
253 homophily, betweenness centrality, group cohesion and network diameter. Table
254 S2 reports the average coefficient estimates of all seven global network metrics
255 from the cross-validation analysis; all estimates were within the 95% confidence
256 interval of the effect sizes reported in the full model (Table 1).

257 **Role of weak ties in driving structural differences in species sociality**

258 When the weakest 5% edges were removed from all weighted networks, the struc-
259 tural differences between the four social systems were observed mainly in two
260 network metrics - degree heterogeneity and network fragmentation. Similar to
261 the unfiltered networks (Table 1), the 5% filtered interaction networks of soli-
262 tary species had the highest variation in individual degree as compared to other
263 social systems; and 5% filtered networks of fission-fusion species were more frag-
264 mented compared to solitary and socially hierarchical species (Table S3). When
265 the weakest 10% and 20% edges were removed, the global network measures across
266 all social systems were similar to each other, except for one important difference.
267 Both 10% and 20% filtered networks of social species (fission-fusion, gregarious
268 and socially hierarchical) demonstrated a statistically significant higher global be-
269 tweenness centrality, or higher global connectivity than solitary species (Table S4,
270 S5). This difference was not observed in unfiltered or 5% filtered networks.

271 The reason behind why filtering out 10% and 20% weak edges removed most
272 structural differences lies in the organization of weak edges within the four social
273 systems. In solitary species, the weakest edges are disproportionately distributed

274 between individuals in a network. Removal of lowest 5% edges therefore increased
275 the degree heterogeneity and reduced the local and global connectivity in these
276 species as compared to the unfiltered networks (Fig. S1).

277 In contrast to solitary species, large structural changes were observed in other
278 social systems (fission-fusion, gregarious, socially hierarchical) only when 10% and
279 20% of the weakest edges were removed from their interaction networks (Fig. S1).
280 In particular, the degree heterogeneity of 10% and 20% filtered networks were com-
281 parable across all social systems. The decrease in global betweenness centrality in
282 social species, however, was minor as compared to solitary species. Consequently,
283 the global connectivity of social species in 10%-20% filtered networks was signifi-
284 cantly higher than solitary species.

285 **Disease costs of interaction structure and species sociality**

286 Our previous analysis revealed important differences in the structure of interaction
287 networks in relatively solitary, fission-fusion, gregarious and socially hierarchical
288 species. Do these topological differences then mediate differential disease costs of
289 sociality among the four social systems? To answer this question, we first exam-
290 ined how degree heterogeneity, clustering coefficient and network fragmentation
291 influence outbreak risk and transmission of low, moderate and highly transmissi-
292 ble pathogens (Fig. 3; see Fig. S2 in Supporting Information for the results on an
293 extended range of pathogen transmissibility values). High variation in individual
294 sociality (i.e., high degree heterogeneity) in interaction networks was predictive
295 of a reduced risk of frequent epidemic outbreaks; outbreaks that did reach epi-
296 demic proportion were shorter and infected a lower proportion of the population

297 (Fig. 3). The presence of cliques in interaction networks (high global clustering
298 coefficient), and the subdivision of networks into socially cohesive groups (high
299 fragmentation) was associated with a reduced risk of lowly transmissible infec-
300 tions becoming large epidemics. Conversely, highly contagious pathogens caused
301 frequent epidemic outbreaks in networks with higher global clustering coefficient
302 and network fragmentation. In terms of disease transmission, network clustering
303 and fragmentation was associated with smaller but prolonged epidemic outbreaks,
304 but the effect was more prominent at low pathogen transmissibility (Fig. S2).

305 Consequently, the risk of epidemic outbreaks due to low transmissible pathogen
306 was higher in socially hierarchical species than fission-fusion and gregarious social
307 systems. This effect reversed for highly transmissible infections: socially hierarchi-
308 cal species experienced significantly fewer epidemic outbreaks from highly conta-
309 gious pathogens as compared to other social (fission-fusion and gregarious) species.
310 The reason behind this can be explained in terms of how network fragmentation
311 and clustering influence epidemic risk. Interaction networks of socially hierarchi-
312 cal species are less clustered than the networks of gregarious and fission-fusion
313 species, and are less subdivided than gregarious species (Table 1). For low trans-
314 missible pathogens, network fragmentation and clustering reduce the probability
315 of large outbreaks, but for highly transmissible pathogen both network metrics are
316 associated with higher epidemic probability (Fig. 3).

317 Low clustered networks of socially hierarchical species also experienced large
318 epidemic outbreaks of moderately transmissible pathogens as compared to gre-
319 garious species (epidemic size; Fig. 4). No statistical difference was observed in
320 terms of outbreak size of low and highly transmissible pathogens, probably due to
321 high variation between networks within each social systems. However, moderately

322 contagious infections persisted longer in gregarious species than in solitary species,
323 and highly transmissible outbreaks died out quickly in solitary species than both
324 fission-fusion and gregarious social systems (epidemic duration; Fig. 4). This is
325 because interaction networks of fission-fusion and gregarious are highly subdivided
326 as compared to solitary species (Fig. 1), and fragmentation of interaction networks
327 prolongs disease spread (Fig. 3).

328 Discussion

329 Disease has long been proposed as a major cost to social living, though few studies
330 have explicitly examined how the structure of social systems may affect vulner-
331 ability to disease transmission. It is also becoming increasingly clear that the
332 impact of an infectious disease on a population depends on the structure of in-
333 teraction networks, not just group size. This has critical implications for un-
334 derstanding evolutionary tradeoffs between social systems and disease dynamics.
335 However, network comparisons are not straightforward, making it difficult to per-
336 form meta-analysis across taxonomic groups and sampling schemes (James, Croft
337 & Krause, 2009; Castles *et al.*, 2014; Farine & Whitehead, 2015). By employing
338 phylogenetically-controlled Bayesian mixed effects models, we demonstrate how
339 comparative methods can be applied to social network analysis. This study, to
340 our knowledge, is the first attempt to utilize an extensive database of animal so-
341 cial networks to understand the disease costs of species sociality mediated by the
342 structure of their interaction networks.

343 Our analysis compared global structural features associated with interaction
344 networks of species classified into four social systems: relatively solitary, fission-

345 fusion, gregarious and socially hierarchical. The evidence that we present here
346 suggests that, at the least, solitary, fission-fusion, and higher social organizations
347 can be distinguished from each other based on *(i)* degree of variation among so-
348 cial partners (i.e. degree heterogeneity), *(ii)* local connectivity, as indicated by
349 the presence of cliques within the interaction networks (i.e, global clustering co-
350 efficient), and *(iii)* the extent to which the interaction network is divided into
351 cohesive social groups (i.e., fragmentation). Remarkably, these differences exist
352 between social systems in spite of differences in network size, number of interac-
353 tions recorded, data collection methodology, type of interaction recorded and the
354 interaction weighting criterion. Other global network metrics analysed (degree as-
355 sortativity, global betweenness centrality, group cohesion and network diameter)
356 could be dependent on data collection methods, and therefore no difference was
357 observed between the social systems after controlling for sampling designs (Fisher,
358 Silk & Franks, 2017).

359 Social species are typically assumed to have a skewed degree distribution (for
360 e.g. bottlenose dolphins Lusseau *et al.* (2003), wire-tailed manakins Ryder *et al.*
361 (2008)), which implies that a small proportion of individuals have a large num-
362 ber of social partners. Our results, however, show that degree heterogeneity in
363 relatively solitary species can be much higher than social species. Large variation
364 in the number of social connections in solitary species may simply arise due to a
365 high variation in spatial behavior as compared to social species (Pinter-Wollman,
366 2015; Sah *et al.*, 2016). Conversely, interaction networks of socially hierarchical
367 species, such as ants and savanna baboons demonstrated the least variation in
368 individual sociality, and the lowest global clustering coefficient. A homogeneous
369 network structure as observed in these species allows for efficient and equitable

370 information transfer to all individuals, while low global clustering coefficient in-
371 creases network resilience and stability in dealing with crisis, including removal or
372 death of individuals (Krause *et al.*, 2014).

373 Our results also show that the interaction networks of fission-fusion species are
374 the most subdivided into cohesive social groups followed by gregarious species.
375 The presence of many but small, socially cohesive groups within interaction net-
376 works of fission-fusion species can be explained based on the behavioural tendency
377 to frequently switch affiliative partners; as a result, individuals form consistent
378 social bonds with a small number of individuals (Rubenstein *et al.*, 2015). Many
379 social species form groups based on sex or age class, kinship and functional roles
380 (Kanngiesser *et al.*, 2011), and modular subdivisions has been shown in theoretical
381 models to promote behavioural diversity and cooperation (Whitehead & Lusseau,
382 2012; Gianetto & Heydari, 2015). Gregarious and fission-fusion species may there-
383 fore limit group size to maximize benefits of cooperation, making their interaction
384 networks subdivided (Marcoux & Lusseau, 2013).

385 Previous studies have typically focused on group size as the key parameter im-
386 pacting disease transmission and group living costs. While this might be an easy
387 parameter to measure, it does not capture the complex spatio-temporal dynamics
388 of most animal societies. Our analysis shows that the unique strategy of how in-
389 teractions are organized across different social systems has important impact on
390 disease transmission patterns. We find that socially complex species with tempo-
391 rary or permanent hierarchical social organization experience frequent epidemics
392 of lowly contagious pathogens, and larger epidemic size of moderately transmissi-
393 ble infections, as compared to non-hierarchical gregarious species. This is because
394 socially hierarchical species have low variation in the number of interactions and

395 low local connectivity as compared to other social and solitary species.

396 Networks with high degree heterogeneity have a larger proportion of low de-
397 gree individuals compared to homogeneous networks, and have a minority of high
398 degree nodes. As the proportion of high degree individuals is rare, an infectious
399 disease outbreak rapidly depletes these superspreaders and must infect low de-
400 gree individuals in order to propagate through the entire network, where the risk
401 of stochastic extinction is higher. It follows that typical disease outbreaks dis-
402 sipate sooner in degree heterogeneous. In contrast, homogeneous networks with
403 the same edge density have a higher proportion high degree nodes, and therefore
404 local depletion of highly connected nodes occurs more slowly, leading to larger and
405 more persistent disease outbreaks (Meyers *et al.*, 2005; Kiss, Green & Kao, 2006).
406 High global clustering coefficient in an interaction network creates redundant paths
407 between individuals which makes it harder for infections to encounter new sus-
408 ceptible individuals and percolate throughout the network (Newman, 2003). In
409 contrast to frequent and larger epidemics of low and moderately contagious infec-
410 tion, socially hierarchical species experience reduced disease burden from highly
411 contagious pathogens than other social species. We postulate that the conflicting
412 efficiency of interaction networks towards infection spread in socially hierarchical
413 species reflects the trade-off between maximizing information flow and minimizing
414 pathogen spread. Social insects, for instance, have sophisticated group-level de-
415 fences (including sanitary behaviors, allogrooming and the use of antimicrobials)
416 that may serve as primary defence mechanism against low to moderately spread-
417 ing infections. The organization of interaction networks in these species, therefore,
418 may have evolved to maximize information flow, while relying on social immunity
419 to reduce the spread of low to moderately spreading infections.

420 Challenges and opportunities

421 Sociality of animal species has been traditionally classified based on qualitative
422 phenotypes and life history traits, and the classification typically differs between
423 the taxonomic groups. While this categorization scheme is convenient, it does not
424 capture the true continuum of social behavior. As a step forward, recent studies
425 have proposed quantitative indices of sociality (Silk, Altmann & Alberts, 2006;
426 Aviles & Harwood, 2012). Our study provides insights towards the potential use
427 of network structure as a means of quantitatively defining social complexity across
428 taxonomic boundaries. However, we need to overcome several challenges before
429 robust comparative analysis can be performed on interaction networks to address
430 such issues. First, comparing network structure across taxonomic groups where
431 data is aggregated over different spatio-temporal scales is challenging. Aggregat-
432 ing interactions over small time-periods may omit important transient interactions,
433 whereas aggregating data over long time-periods may lead to a saturated network
434 where distinguishing social organization may be difficult. In addition, spatial con-
435 straints and environmental heterogeneity can impose a considerable influence on
436 the interaction network structure (Davis *et al.*, 2015; Leu *et al.*, 2016). Future com-
437 parative studies should therefore consider standardizing data over time and spatial
438 scales. The second challenge lies in defining a social group that is consistent across
439 species and social systems. This is difficult because the general rules of defining
440 groups in social species (including definitions of spatial and temporal coherence)
441 do not hold true for solitary and fission-fusion species. Network size correlates to
442 sampling intensity in many cases, and is therefore a poor proxy to group size. In
443 this study, we use community detection algorithm that utilizes the organization

444 of network structure to infer the number and composition of social groups (mod-
445 ules) within the interaction network. The third challenge for comparative studies
446 of networks lies in utilizing data-sources published in inconsistent formats. At
447 minimum the network datasets should be accompanied with the following details
448 to facilitate data-reuse: location of the data collection, type of population moni-
449 tored (captive, semi-captive, free-ranging), edge definition, edge weighting criteria,
450 node attributes (such as demography), temporal resolution of data, temporal and
451 spatial aggregation of the data, proportion of animals sampled in the area, and
452 population density.

453 In conclusion, we note that there is an enormous potential of adopting a com-
454 parative approach to study the commonalities and differences in the interaction
455 networks across a wide range of across taxonomic groups and social systems. Al-
456 though we limit our discussion to the disease implications of animal sociality and
457 social network structure, comparative network approaches can be used to quan-
458 titatively test several other evolutionary and ecological hypotheses, including the
459 ones on group living, social complexity, information transfer, and resilience to
460 population stressors.

461 **Acknowledgements**

462 We thank Stephan T. Leu for feedback on a previous version of this manuscript.
463 This work was supported by the National Science Foundation Ecology and Evolu-
464 tion of Infectious Diseases grant 1216054.

465 Data accessibility

466 The data for all animal interaction network measures used in the study, and ref-
467 erences where the actual network can be accessed, is available through the Bansal
468 Lab Dataverse at (link).

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594 Table captions

595 **Table 1.** Effect size estimates of the Bayesian generalized linear mixed models
596 (by MCMCglmm) examining the characteristics of interaction network structure
597 among the four social systems: *relatively solitary*, *fission-fusion*, *social* and *socially*
598 *hierarchical*. Shown are the posterior means of the expected change in log-odds
599 of being in focal social system (column headers), as compared to the base social
600 system (row headers), with one-unit increase in the network measure. The 95%
601 confidence intervals are included in brackets. Significant terms with $p_{\text{MCMC}} <$
602 0.05 are indicated in bold, where p_{MCMC} is the proportion of MCMC samples
603 that cross zero.

604 **Figure captions**

605 **Figure 1.** A stylized illustration of the global network measures used (in the final
606 model) to identify the structural differences in the interaction networks among
607 different social systems. (A) Degree heterogeneity, measured as the coefficient
608 of variation (CV) of the frequency distribution of the number of social partners
609 (known as the *degree distribution*). Shown is the degree distribution of a homoge-
610 nous network ($CV \ll 1$), and an exponential degree distribution of a network with
611 large variation in individual degrees ($CV = 1$). (B) Degree homophily (ρ), or the
612 tendency of social partners to have a similar degree. Shown is an example of a
613 disassortative network, where high degree individuals tend to associate with low
614 degree individuals ($\rho < 0$), and assortative degree networks, where high degree indi-
615 viduals tend to form social bonds with each other ($\rho > 0$). (C) Global betweenness
616 centrality, that measures the tendency of nodes to occupy central position within
617 the interaction network. Shown is an example of a network with low global be-
618 tweenness centrality and a network with high global betweenness centrality. Node
619 colors represent the betweenness centrality values - nodes with darker colors oc-
620 cupy more central positions within the network. (D) Group cohesion measures the
621 tendency of individuals to interact with members of own group. The network to
622 the left has three low cohesive social groups, while the network to the right has
623 highly cohesive social groups where most of the interactions occur within (rather
624 than between) groups. (E) Network fragmentation, measured as the log-number
625 of the social groups (modules) present within the largest connected component
626 of an interaction network. Shown is an example of low (left) and highly (right)
627 fragmented network. (F) The global clustering coefficient measures the ratio of

628 (closed) triplets in versus the total number of all possible triplets in the networks.
629 (G) Network diameter is the longest of all shortest paths between pairs of nodes in
630 a network. Shown is an example of a network with low network diameter (longest
631 of shortest paths = 3) and a similar network with network diameter of 5, indicated
632 by coloured edges.

633

634 **Figure 2.** Phylogenetic distribution of animal species represented in the in-
635 teraction network dataset used in this study. Numbers next to the inner ring
636 denote the total networks available for the particular species. The inner and
637 the middle ring is color coded according to the taxonomic class and the social
638 system of the species. The colors in the outer ring indicates the type of in-
639 teraction represented in the network. The tree was constructed in the Inter-
640 active Tree Of Life (<http://itol.embl.de/>) from the NCBI taxonomy database
641 (<http://www.ncbi.nlm.nih.gov/Taxonomy/>).

642

643 **Figure 3.** Role of network structures in influencing disease transmission summa-
644 rized as epidemic probability (likelihood of large outbreaks infecting at least 15%
645 of individuals in the network), average outbreak size (proportion of individuals
646 infected in the interaction network), average outbreak duration (time to disease
647 extinction) for low (=0.05), moderate (=0.15) and highly (=0.45) transmissible
648 pathogen. The three global network measures shown are the ones that were found
649 to differ among the four social systems (Table 1). DH, degree heterogeneity; CC,
650 average clustering coefficient; NF, network fragmentation. Error bars represent
651 95% confidence intervals. Confidence intervals that do not include zero suggest
652 significant association with disease transmission (red = significant effect, black =

653 non-significant effect)

654

655 **Figure 4.** Disease costs of social systems due to interaction network structure.

656 Disease cost has been quantified in terms of epidemic probability, average epidemic

657 size and average epidemic duration for low ($=0.05$), moderate ($=0.15$) and highly

658 ($=0.45$) transmissible pathogen. Error bars represent standard errors, and different

659 letters above the bars denote a significant difference between the means ($P < 0.05$)

660

Table 1:

Degree heterogeneity	Focal		Solitary	Fission-fusion	Gregarious	Socially hierarchical
	Base					
	Solitary			-6.45 [-11.79, -1.32]	-6.36 [-11.58, -1.52]	-12.76 [-19.48, -5.79]
	Fission-fusion				-0.50 [-5.17, 4.11]	-6.27 [-11.76, -0.80]
	Gregarious					-6.23 [-11.94, -0.69]
Degree homophily	Focal		Solitary	Fission-fusion	Gregarious	Socially hierarchical
	Base					
	Solitary			0.37 [-1.48, 2.19]	-0.344 [-1.93, 1.15]	-1.82 [-4.21, 0.49]
	Fission-fusion				-0.74 [-2.56, 1.22]	-1.93 [-4.37, 0.38]
	Gregarious					-1.34 [-3.37, 0.76]
Global betweenness centrality	Focal		Solitary	Fission-fusion	Gregarious	Socially hierarchical
	Base					
	Solitary			-3.38 [-8.87, 1.97]	1.27 [-2.24, 4.91]	1.37 [-2.67, 5.48]
	Fission-fusion				3.12 [-1.56, 7.88]	3.39 [-1.32, 8.12]
	Gregarious					1.12 [-1.83, 4.63]
Global clustering coefficient	Focal		Solitary	Fission-fusion	Gregarious	Socially hierarchical
	Base					
	Solitary			-0.57 [-3.68, 2.20]	-0.08 [-2.81, 2.61]	-4.21 [-8.10, -0.76]
	Fission-fusion				0.02 [-2.55, 2.65]	-3.23[-6.98, -0.25]
	Gregarious					-3.39 [-6.30, -0.54]
Group cohesion	Focal		Solitary	Fission-fusion	Gregarious	Socially hierarchical
	Base					
	Solitary			-0.82 [-3.89, 2.44]	-0.58 [-3.22, 1.79]	-1.25 [-4.46, 1.82]
	Fission-fusion				0.48 [-1.75, 2.72]	0.04 [-2.77, 2.83]
	Gregarious					-0.06 [-2.46, 2.30]
Network fragmentation	Focal		Solitary	Fission-fusion	Gregarious	Socially hierarchical
	Base					
	Solitary			8.12 [3.67, 12.73]	3.43 [0.22, 6.79]	0.28 [-3.74, 4.44]
	Fission-fusion				-3.38 [-6.50, -0.26]	-6.19[-9.94, -2.51]
	Gregarious					-2.40 [-5.71, 0.81]
Network diameter	Focal		Solitary	Fission-fusion	Gregarious	Socially hierarchical
	Base					
	Solitary			-3.85 [-9.08, 1.31]	-1.34 [-4.73, 1.89]	0.73 [-4.22, 5.91]
	Fission-fusion				1.95 [-1.72, 5.95]	4.06[-0.58, 8.87]
	Gregarious					0.99 [-2.69, 4.57]

Figure 1:

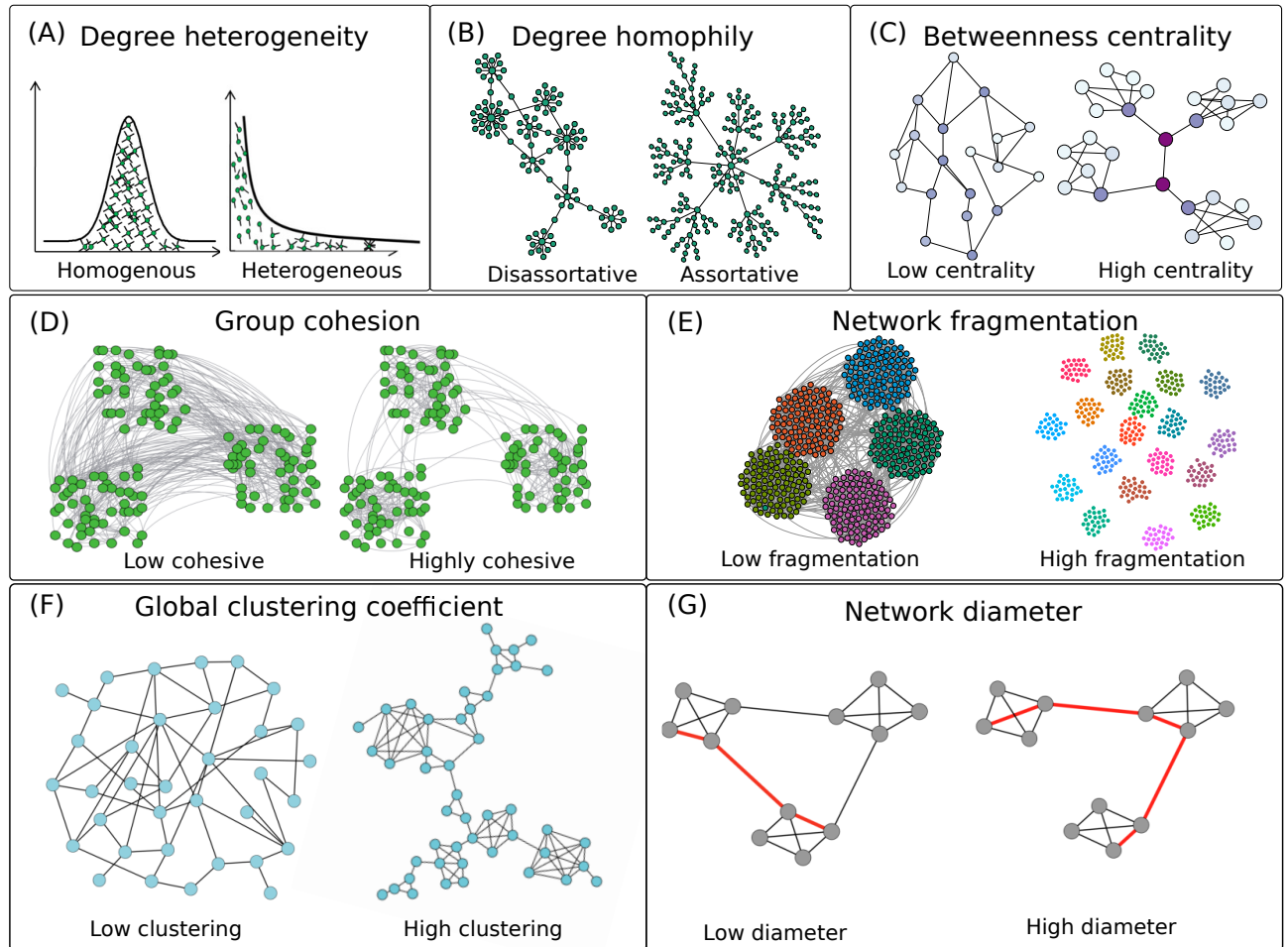


Figure 3:

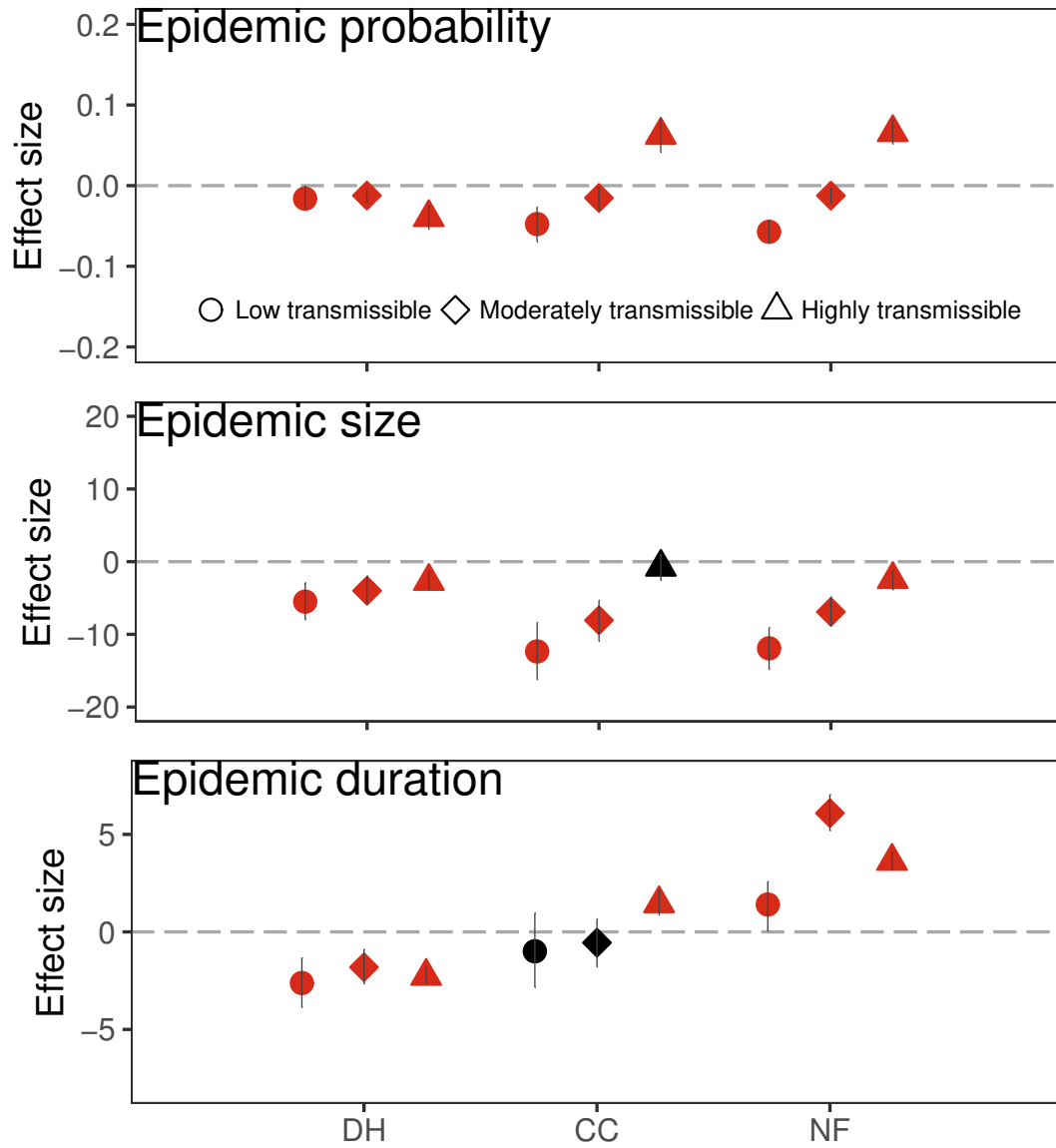


Figure 4:

