

1 **Understanding animal social structure: exponential random graph models in**

2 **animal behaviour research**

3

4 **Abstract**

5 The social environment is a pervasive influence on the ecological and evolutionary dynamics
6 of animal populations. Recently, social network analysis has provided an increasingly
7 powerful and diverse toolset to enable animal behaviour researchers to quantify the social
8 environment of animals and the impact that it has on ecological and evolutionary processes.
9 However, there is considerable scope for improving these methods further. We outline an
10 approach specifically designed to model the formation of network links, exponential random
11 graph models (ERGMs), which have great potential for modelling animal social structure.
12 ERGMs are generative models that treat network topology as a response variable. This
13 makes them ideal for answering questions related directly to how and why social
14 associations or interactions occur, from the modelling of population-level transmission,
15 through within-group behavioural dynamics to social evolutionary processes. We discuss
16 how ERGMs have been used to study animal behaviour previously, and how recent
17 developments in the ERGM framework can increase the scope of their use further. We also
18 highlight the strengths and weaknesses of this approach relative to more conventional
19 methods, and provide some guidance on the situations and research areas in which they can
20 be used appropriately. ERGMs have the potential to be an important part of an animal
21 behaviour researcher's toolkit and fully integrating them into the field should enhance our
22 ability to understand what shapes animal social interactions, and identify the underlying
23 processes that lead to the social structure of animal populations.

24 **Keywords:** network analysis, dominance hierarchy, transmission, social relationships,
25 assortative behaviour, transitivity

26

27 **Introduction**

28 Most animals engage in interactions with conspecifics, and these interactions form
29 the social environment that is fundamental to ecological and evolutionary processes
30 operating within these populations (Krause et al., 2014; Kurvers et al., 2014; Pinter-Wollman
31 et al., 2013). For example, social interactions influence an animal's risk of infection (Silk et
32 al., 2017a; White et al., 2015), modulate the collective behaviour of groups (Bode et al.,
33 2011; Farine, et al. 2016; Rosenthal et al. 2015; Strandburg-Peshkin et al. 2013; Sueur et al.,
34 2011), and may form an axis of individual personalities (Aplin et al., 2013; Croft et al., 2009;
35 Wilson et al., 2013). These interactions are often complex, varying over space and time,
36 being comprised of behaviours ranging from affiliative to agonistic, and showing
37 considerable variation among individuals (Croft et al. 2008).

38 Quantifying a complex social environment can represent a challenge, but can be
39 achieved through the suite of tools available in social network analysis. A network approach
40 is useful as social relationships are an emergent property of the interactions of multiple
41 individuals, and there is increasing evidence that indirect connections among individuals
42 within animal populations are important (Brent, 2015). In the last decade social network
43 analysis, originally developed in the social and physical sciences, has become a pervasive
44 tool in the study of animal behaviour (Krause et al., 2014; Pinter-Wollman et al., 2013). As
45 well as directly modelling social relationships, it can be integral to understanding other
46 behaviour in the context of its social environment. For instance, networks have been used in

47 the study of the social and spatial components of dispersal behaviours (Blumstein et al.,
48 2009; Fletcher et al., 2011).

49 The statistical analysis of social networks is complicated by the non-independence of
50 individuals within a population that results from linking individuals together within a
51 network (Croft et al., 2011; Farine & Whitehead, 2015). This confounds the use of the
52 conventional statistical approaches used in ecology such as the linear model and linear
53 mixed model, as these methods assume independence of the residuals, which is an invalid
54 assumption for individuals that are linked in a network. In light of this, numerous statistical
55 methodologies have been developed to analyse social network structure. Typically, the
56 analysis of animal social networks has revolved around randomisation-based approaches to
57 significance testing (Croft et al., 2011; Farine & Whitehead, 2015). The data used to
58 construct networks is permuted to generate uncertainty around the null hypothesis (e.g.
59 social interactions are assorted by a phenotype of interest), with permutations typically
60 constrained to produce biologically plausible null models. For example, if researchers are
61 studying how body size relates to social network connections in a population spread over
62 several sites, they would randomise interactions with respect to body size, but constrain the
63 randomised network connections according to the site use of that individual.

64 Randomisation-based analyses have many strengths, especially in animal social
65 network studies in which complex sampling issues often have to be controlled for (Farine &
66 Whitehead, 2015). However, using this approach controls for, rather than models, the
67 biological processes, such as site use, that generate network structure. Often these
68 processes can be directly of interest, yet treating them as a nuisance factor prevents us
69 from more fully understanding the role they play in shaping animal social systems.
70 Furthermore, randomisation-based approaches generate uncertainty around the null

71 hypothesis, rather than the observations, yet it is the observations that truly are observed
72 with error. Finally, null models are often user-defined and system-specific as the validity of
73 the comparison is sensitive to the way in which null models are constructed. As a result, it is
74 not always the best option available.

75 There are also several social network modelling frameworks developed within the
76 social sciences, some of which are now increasingly being employed in studies of animal
77 social networks. Many of these modelling frameworks are designed specifically to analyse
78 network data, and so have no requirement for independence. Further, some are generative
79 models, with the underlying processes that govern interactions explicitly modelled, with the
80 local network topology as a response variable (Cranmer et al., 2016; Silk et al., 2017b). This
81 is extremely useful for researchers specifically aiming to explain the social interactions that
82 occur among individuals, and the observed structure of the entire network, a very common
83 topic of research in animal behaviour (e.g. Best et al., 2014; Carter et al., 2013; VanderWaal
84 et al., 2014). However, the general applicability of these approaches to the study of animal
85 social behaviour has not yet been discussed or assessed.

86 In this article we review the use of one of the more highly developed and flexible of
87 these statistical network approaches, exponential random graph models (ERGMs) (Lusher et
88 al., 2013; Robins et al., 2007). We start by providing a basic verbal description of the
89 modelling approach, illustrating some of the key aspects of model fitting with a toy
90 example. We then describe the previous uses of these models in the study of animal social
91 behaviour, before going on to discuss its strengths and weaknesses as a method to model
92 animal social networks and how these models can be extended to understand more
93 complex network datasets that are increasingly used to study animal behaviour (temporally
94 dynamic, bipartite and multilayer networks). Finally, we set an agenda for future research:

95 highlighting the importance of both simulation modelling studies to better understand when
96 ERGMs may represent an appropriate tool, and determining research areas that this method
97 is best suited to. Our aim is not to displace the use of randomisation-based approaches, but
98 to describe an alternative tool that can be applied in many situations. This will give animal
99 behaviour researchers a wider array of options than are currently in use.

100

101 **Model description**

102 ERGMs are models of network topology that enable hypotheses about the processes driving
103 local network structure and edge formation to be tested (Lusher et al., 2013; Robins et al.,
104 2007). They model potential edges between individuals as stochastic variables within an
105 adjacency matrix. The response variable is the probability of matching the observed
106 network, with the explanatory variables representing various possible structural features of
107 the network. They fit broadly within the same exponential family of statistical models as
108 conventional linear and generalised linear modelling approaches. A mathematical
109 representation of the model is:

110

$$111 \quad P(N) = ce^{\theta_1 z_1(N) + \theta_2 z_2(N) + \dots + \theta_n z_n(N)}$$

112

113 *Where $P(N)$ is the probability of a given network and each z is a different network statistic or*
114 *property of the network. The effect of each z is weighted by a parameter (θ) in a similar*
115 *manner to a generalised linear model. In this equation c is a normalising constant.*

116

117 Note that this is for a single network; ERGMs were originally developed for the analysis of
118 static networks, although recent developments have made the analysis of dynamic

119 networks possible (see below). Initially, *potential edges* (regardless of whether they exist or
120 not) could only be modelled as binary (present or absent), however recent generalisations
121 of the ERGM framework now enable models of weighted edges (Desmarais & Cranmer,
122 2012; Krivitsky, 2012; Wilson et al., 2017). These models for weighted edges are likely to
123 often be preferred, as edge weights carry a majority of the information on social structure in
124 many animal networks, and filtering networks by threshold edge weights can affect analysis
125 (Franks et al. 2010, Farine 2014). Alternatively, researchers can capture repeated
126 interactions through temporal ERGMs, where the change in the network structure over time
127 is considered. We discuss these two extensions (and others) of the basic ERGM below.
128 Ultimately, the decision on whether to use binary or weighted, static or temporal networks
129 will be question, and to some extent data, driven (Carter et al. 2015).

130 Network edges are modelled in response to attributes of the nodes that they
131 connect, and the value of other edges within the network. The latter possibility means that
132 the ERGM framework accounts for the fact that edge values can be dependent on the values
133 of neighbouring edges or some other aspect of network topology, making the network
134 structure locally emergent and therefore directly dealing with non-independence related to
135 this (Lusher et al., 2013). Crucially, unlike randomisation-based methods, this approach
136 directly models the behaviours that lead to social associations or interactions, and so social
137 network structure.

138 A guide to the types of term that can be included within ERGMs is provided in Figure
139 1. From a practical perspective terms fit into three broad categories: a) node-based
140 covariates, b) dyadic covariates and c) structural covariates.

141 a) Node-based covariates explain differences in edge values as outcomes of the
142 attributes of the nodes themselves. Taking the case of sex-related differences,

143 for example, node-based covariates could be used to model which sex formed
144 more (or stronger) edges, and additionally whether intra-sex edges were more
145 likely than inter-sex ones (i.e. males tending to interact with other males, and
146 females with females). Node-based covariates for continuous traits can also
147 include a difference term, for example: are edges more likely when the attributes
148 of two individuals are more similar? This might be expected in situations such as
149 dominance hierarchies where interactions are more likely if two individuals are
150 more closely matched (e.g. Dey & Quinn, 2014).

151 b) Dyadic covariates model how other relationships among individuals in a network
152 affect edge values. For example, with animal social networks, where space use is
153 often an important component of social structure, a matrix of the distances
154 between individual home ranges or refuges might be a valuable dyadic covariate.
155 Another example might be genetic relatedness, if social relationships within a
156 group are thought to be influenced by kinship (e.g. Carter et al., 2013; Godde, et
157 al., 2015; Wolf et al., 2007).

158 c) Structural covariates are aspects of network topology that might be expected to
159 affect edge formation, and can occur at several levels of complexity (Fig. 1). The
160 most basic structural term would be a measure of edge density, somewhat
161 equivalent to having an intercept within a generalised linear model. This models
162 the general tendency for individuals to be connected to other individuals, and is
163 typically negative in social networks as individuals tend not to be connected to all
164 other individuals. Increasingly complex structural terms can be incorporated, and
165 these define the dependency structure used within the model to understand
166 how the presence/absence of edges influences the presence/absence of nearby

167 edges. For example, this might include configurations of multiple edges from a
168 node, or measures of transitivity. The former consists of “*k-star*” terms which
169 estimate the frequency of edge configurations from a node with *k* completed
170 edges (e.g. *3-star* measures the frequency of three completed edges connected
171 to a node). Measures of transitivity model how the likelihood or value of an edge
172 between *i* and *j* changes if both *i* and *j* are also already connected to *k* (a
173 consideration of “*friends-of-friends*” effects). For directed networks these
174 dependencies can include directionality as well, for example, reciprocity might be
175 hypothesised to be a strong underlying process driving network structure in
176 some social systems. Similarly, edges completing triads can be either transitive
177 ($i \rightarrow j$, $i \rightarrow k$ and $j \rightarrow k$) or cyclical ($i \rightarrow j$, $j \rightarrow k$ and $k \rightarrow i$), and these different properties
178 might be integral to the structure of some networks, such as linear dominance
179 hierarchies where cyclical triads would be expected to be much *less* common
180 than otherwise expected (Shizuka & McDonald, 2012).

181 The distinction between node-based and dyadic covariates is somewhat artificial, and in
182 some cases, a variable could be intuitively considered as either. For example, if individuals
183 more similar in size are expected to interact more, one could fit difference in size as a node-
184 based covariate or include it directly as a difference matrix. Our recommendation here is
185 that dyadic covariates should be used when the variable only exists as a function of the two
186 individuals (e.g. their genetic relatedness), while individual covariates should be used when
187 the variable can be considered a trait of that individual alone (as for the example with size).

188 Model fitting and selection differs somewhat from the fitting of generalised linear
189 models. Full models are typically built up in a stepwise manner from simple models
190 consisting of structural terms, through to the final models designed to test the hypotheses

191 of interest. This is because some more complex models may not be able to be estimated
192 due to combinations of parameters leading to degeneracy (the model placing most of the
193 probability on only a few of the complete set of possible networks, often those that are
194 either completely devoid of edges or completely connected). At each stage, parameter
195 fitting is achieved by simulating networks and comparing them with the observed network.
196 Parameter estimation requires the use of Markov Chain Monte Carlo (MCMC). From an
197 initial starting graph an edge is added or removed at random (in the case of binary ERGMs).
198 If the new configuration of the graph is closer to the observed data then the new graph is
199 taken as the next graph in the sequence, and if it is not then it is only taken as the next
200 graph in the sequence with a low, fixed probability. The MCMC chain is considered to have
201 converged when it has settled into a pattern centred around a particular combination of
202 parameter values. This maximum likelihood estimation of each parameter is calculated by
203 generating values for all parameters that centre the distribution of each parameter fitted on
204 the observed network data (Lusher et al., 2013). Parameter estimation is conditionally-
205 dependent on other covariates included in the model (Lusher et al., 2013). This allows one
206 to assess the importance of particular variables (e.g. the tendency for reciprocity) while
207 accounting for other variables (e.g. shared space use). Estimated values for parameters
208 provide an indication of likelihood of that network configuration, given the other effects in
209 the model (Lusher et al. 2013).

210 Once each model has converged, then goodness-of-fit can be assessed by comparing
211 measures calculated from networks simulated using the fitted model with equivalent
212 measures from the observed network (Lusher et al., 2013). This typically involves measures
213 such as the degree distribution (a frequency distribution of the number of connections that
214 individuals possess), geodesic distances (the length of paths through the network that link

215 individuals) and triad censuses (the frequency of triads – groups of three individuals - with
216 0, 1, 2 and 3 completed edges). However, any combination of network measures can be
217 used as long as they haven't been fitted in the model, preferably either those that provide a
218 good general measure of network structure (such as the three default goodness-of-fit tests
219 detailed above), or measures chosen specifically to capture features of interest to the
220 researcher. As more complicated models are fitted it is important to check that goodness-
221 of-fit improves. Terms that worsen the goodness-of-fit should not be retained, although
222 terms that do not greatly influence goodness-of-fit either way may be retained if they are
223 relevant to particular hypotheses. More formal testing of hypotheses can also be
224 conducted. For example, it is possible to perform backwards stepwise deletion to choose a
225 final model once the full model has been constructed (e.g. Snijders et al., 2006), using
226 approximate Wald tests to indicate whether particular terms in the model are statistically
227 significant (Lusher et al. 2013). In addition, it is possible to compare fitted models with
228 Akaike information criteria (AIC) or Bayesian information criteria (BIC) to allow the most
229 parsimonious model to be selected. This could allow the comparison of multiple competing
230 models (assuming convergence) that test different combinations of hypotheses, in a process
231 akin to multimodel inference. It is also possible to use methods of Bayesian model selection
232 such as reversible jump MCMC (Caimo & Friel 2013).

233 ERGMs can be implemented within R (R Development Core Team, 2017) and in the
234 standalone java based software PNet (Wang et al., 2009). In R there are number of packages
235 within the statnet (Handcock et al., 2008) and xergm (Leifeld et al., 2016) suites of packages
236 that enable the fitting of ERGMs (see Table 1). Basic ERGMs, including for bipartite
237 networks, can be fitted using the package ergm (Handcock et al., 2015; Hunter et al., 2008).
238 We provide an example demonstrating the model output, convergence diagnostics and

239 goodness-of-fit tests of basic ERGM fitted to a toy dataset in Figure 2 (network depicted in
240 Fig. 2a). In this example, there is homophily according to the “colour” of individuals (red or
241 blue), and a continuous effect of a “size” variable (indicated by the white node labels) on
242 the likelihood to form connections (Fig. 2b). Model estimates in binary ERGMs are
243 conditional log-odds estimates. In our example model the (intercept) log-odds estimate for
244 an edge existing is approximately -2.14. However, for every increase in size by unit 1 this
245 increases by ≈ 0.16 , and if the edge links to individuals of the same colour this increases by
246 ≈ 0.94 (with minimal difference for red-red and blue-blue). Trace plots of each Markov chain
247 and density plots for each variable (normal distributions centred on the estimate) show that
248 this basic model converges (Fig. 2c), while the goodness-of-fit plots show that it matches the
249 observed data well, although is unable to replicate a high frequency of individuals with a
250 degree of 10 (Fig. 2d). The R code for this example is provided in the supplementary
251 information. The package `ergm.count` (Krivitsky, 2015) permits the fitting of ERGMs to
252 weighted networks, in which edge weights are integer count values. Additionally, a recent
253 development has been the extension of ERGM fitting to all weighted networks with the
254 package `GERGM` (Denny et al., 2016). In these models edge weights are converted to a value
255 between zero and one through a number of user-selected functions. A further extension to
256 the ERGM framework is the fitting of hierarchical ERGMs, that enable the incorporation of
257 local rather than global dependency structures, in the package `hergm` (Schweinberger et al.,
258 2016). Finally, it is also possible to fit ERGMs to temporally dynamic networks in R, either
259 using the package `tergm` (Krivitsky & Handcock, 2016) or `btergm` (Leifeld et al., 2016). These
260 allow the ERGM framework to be used to model longitudinal network data arranged as a set
261 of network snapshots (from a single point in time) or aggregated static networks (a static
262 depiction of interactions over a predefined time interval).

263

264 **How have exponential random graph models been used before?**

265 ERGMs have been used previously to answer diverse questions related to animal
266 social behaviour. Ilany et al. (2013) used ERGMs to investigate “structural balance” in
267 directed networks of rock hyrax *Procavia capensis* interactions. They found that structural
268 balance, where individuals take on a similar set of social relationships as their current
269 contacts, was a feature of these social groups, and that there was a non-significant tendency
270 for more newly arrived individuals to feature in triads (sets of three individuals) that lacked
271 structural balance. Edelman and McDonald (2014) used ERGMs to show that cooperative
272 relationships in male long-tailed manakins *Chiroxiphia linearis* tend to be transitive and
273 stable over time. They also exploited the ERGM framework to model the impact of spatial
274 distribution of individuals, a potentially widely applicable technique which we discuss in
275 later sections.

276 ERGMs have also been used to calculate tendencies of individuals to initiate or
277 receive interactions in social groups of yellow-bellied marmots *Marmota flaviventris*, for use
278 in further analyses that related networks of affiliative interactions to age and kinship (Wey
279 & Blumstein, 2010). Two further studies have used ERGMs to model dominance
280 relationships within animal groups. For example, Dey and Quinn (2014) used ERGMs to
281 demonstrate that pukekos *Porphyrio melanotus melanotus* had linear dominance
282 hierarchies. They are also demonstrated that the type of dominance interactions (display or
283 physical aggression) differed between the sexes, were driven by differences in status signals
284 (the size of the bill shield) and showed sexual homophily. Dey et al. (2015) also investigated
285 dominance hierarchies, and observed that the dominance networks of cooperatively

286 breeding cichlids *Neolamprologus pulcher* were stable between parental care and non-
287 reproductive periods.

288 Finally, two studies to date have used ERGMs to model population social structure.
289 Fisher et al. (2016) compared networks of interactions in field crickets *Gryllus campestris*
290 and demonstrated that social structure remained similar over time. More specifically, it was
291 possible to predict network structure between years, especially when the populations were
292 similar in size. Meanwhile, Reynolds et al. (2015) used ERGMs to simulate raccoon *Procyon*
293 *lotor* contact networks to model the dynamics of rabies transmission.

294 These diverse applications demonstrate that ERGMs can be used to model affiliative
295 and antagonistic networks, to analyse differences within and among-populations, and to
296 understand dyadic and whole network-level processes. Moreover, they can be used in both
297 free-living and captive animals, and can be applied across a range of taxa. However, the
298 applicability of the ERGM framework will very much depend on the questions being
299 addressed and any constraints of the data being analysed, and we highlight the most
300 important of these considerations below.

301

302 **ERGM advantages and drawbacks**

303 **Advantages**

304 An important strength of the ERGM framework is that it explicitly incorporates the
305 dependence structures that are integral to many animal social networks (Krause et al., 2014;
306 Pinter-Wollman et al., 2013), and represent a difficulty with using conventional linear
307 modelling approaches (Croft et al., 2011; Farine & Whitehead, 2015). ERGMs are particularly
308 valuable as it is possible to directly test hypotheses related to the role of emergent network
309 properties, such as transitivity, in structuring interactions (Dey & Quinn, 2014; Ilany et al.,

310 2013). Even in other modelling frameworks designed to be implemented specifically in social
311 networks, such as latent space models and multiple regression quadratic assignment
312 procedures, it is not possible for these to be estimated (Cranmer et al., 2016).

313 A second advantage of ERGMs is that they model network topology as a response
314 variable, so are ideally suited for questions related to interactions or social relationships
315 themselves, as well as any questions for which the structure of the network is of primary
316 interest. The former could include questions related to homophily (are within-sex
317 interactions more likely to occur than between-sex ones?), or alternatively the number of
318 social relationships (do bold individuals form more interactions than shy individuals?). There
319 is also an important role for questions about network structure in studies investigating the
320 emergent group-level properties of individual social interactions, for example the transitive
321 nature of dominance interactions (Dey & Quinn, 2014; Shizuka & McDonald, 2012). In
322 randomisation-based approaches one would compare an observed metric, such as
323 transitivity in the above example, to the range of values generated by the null model, and
324 conclude that an observed network is more or less transitive than expected given the null
325 processes. This however makes it difficult to assess to what extent transitivity is an
326 emergent property of other predictors of network formation (which may covary with
327 transitivity), rather than a fundamental process driving network structure (as transitivity and
328 cyclicity may well be in dominance hierarchies). Such information is available if correctly
329 specified generative models of network structure such as ERGMs are used.

330 ERGMs can also be used as generative models of network structure, which offer
331 great potential as tools in animal social network analysis. Once parameters for the model
332 have been estimated, new networks can be simulated using these values. This makes it
333 possible to generate uncertainty around the observed network structure, and facilitates the

334 comparison of network structure between different populations. For example, simulating
335 social network structure for a population using the parameters for the network structure
336 from a *different* population would allow you to compare the fundamental network structure
337 between these populations, controlling for differences in population size or composition
338 (e.g. Fisher et al., 2016). This might provide a promising solution to the problems in
339 comparing networks between populations and species (Faust & Skvoretz, 2002).

340

341 **Drawbacks**

342 There are, however, also drawbacks in the application of ERGMs to animal networks,
343 as well as some more general issues that might impact on their use to study animal social
344 behaviour. First, ERGMs have been developed in the social sciences where there is greater
345 confidence that edges within a network represent true social ties. Therefore, the ability to
346 extend them to studying animal social relationships is uncertain in situations where social
347 relationships are inferred rather than observed, for instance from spatio-temporal co-
348 occurrences. This applies principally to association-based networks calculated by converting
349 a bipartite network of individuals and groups to a social network using the “gambit of the
350 group” assumption (Whitehead & Dufault, 1999), which has been widely used to construct
351 animal social networks (Farine & Whitehead, 2015). In general, ERGMs may not be
352 appropriate for analysing such networks, at least in the absence of further work to
353 determine the impact that the sampling issues and data structure imposed by these
354 methods has on model outputs.

355 One possible solution to this is to use ERGMs to model the bipartite networks that
356 links individuals and groups directly, and make inferences about the socio-spatial behaviour
357 of individuals in this manner. In situations where networks have been constructed for pre-

358 defined behavioural interactions (e.g. dominance interactions), there is not the same issue
359 with network ties being inferred. However, care still needs to be taken in incorporating
360 individuals with differing observation times. One solution may be to fit nodal covariates for
361 time spend under observation, or dyadic covariates for time spent jointly under observation,
362 within the ERGM. Alternatively, social relationships may need to be converted to rates of
363 interaction (Whitehead, 2008), or generalised affiliation indices (Whitehead & James, 2015)
364 before being modelled.

365 A second potential issue with the application of ERGMs (or other statistical network
366 models) to studying animal social networks are issues related to missing nodes (incomplete
367 sampling of individuals) or edges (not observing all social interactions). The impact of
368 missing nodes and edges on network analysis has received some research focus in a range of
369 fields (Silk et al., 2015; Smith & Moody, 2013; Smith et al., 2017), although much of this has
370 focussed on the calculation of network metrics rather than any impacts on hypothesis
371 testing methods (Silk et al., et al., 2017b). Shalizi and Rinaldo (2013) suggested that ERGMs
372 would not be able to accurately estimate structural parameter estimates in sub-sampled
373 networks, however they made no comment on their ability to test hypotheses related to
374 differences in individual behaviour in these situations. Although the inferences made about
375 individual differences in behaviour are reliant on relative differences rather than being able
376 to precisely parameterise the full network, ERGMs should be used with caution in systems
377 where high proportions of individuals or interactions are not recorded.

378 Finally, there are two disadvantages more generally to the ERGM framework that
379 animal behaviour researchers should be aware of; computationally intensive parameter
380 estimation and degeneracy. The former occurs as a result of exact parameter inference
381 typically being intractable, and therefore relying on Monte Carlo methods. Practically, this

382 limits the size of networks that ERGMs can be used on to networks with 10s or a few 100s of
383 nodes (depending on the model being fitted), rather than the large networks generated in
384 some studies of social animals. Degeneracy is a well-established issue in the fitting of ERGMs
385 (Handcock et al., 2003; Lusher et al., 2013), and means that for certain combinations of
386 parameters the Markov chain Monte Carlo estimation rarely converges or does not
387 converge. In these situations, it can be difficult to fit models in a stepwise fashion. Structural
388 terms involving triads (modelling transitivity within the network) are often especially likely
389 to result in instability and lead to model degeneracy. One possible solution is to attempt
390 fitting hierarchical ERGMs (using the R package hergm) with local rather than strong
391 dependence structures (which restrict dependencies within particular regions of the
392 network), which can reduce problems with model degeneracy, especially in larger networks
393 (Handcock et al., 2003; Schweinberger, 2011; Schweinberger & Handcock, 2015).

394

395 **Potential future applications**

396 As discussed previously, ERGMs offer a flexible framework for testing hypotheses
397 related to edge formation and network topology. As a result they could be useful in
398 answering a wide range of questions related to animal social network analysis. We focus on
399 a few key areas here, for which ERGMs are likely to be useful but have rarely been applied.

400

401 **Generating uncertainty for modelling transmission processes**

402 As previously highlighted, a major advantage of the ERGM modelling framework is
403 that it is possible to simulate networks using the parameters fitted to the originally
404 observed network. This can be used to generate a set of networks that are similar but not
405 identical to the original network (e.g. Fig. 3). Almost all animal social networks are a sub-

406 sample of the full set of interactions that occur, and the subsequent simulation of dynamic
407 processes on these networks may be subject to error. Therefore, being able to simulate
408 networks fitted with the same set of parameters, that are important in generating the
409 observed network but without its exact structure, offers an important route to robust
410 conclusions when testing hypotheses relating to network topology, such as the factors
411 influencing information and disease transmission within animal populations. For example,
412 Reynolds et al. (2015) fitted ERGMs to contact networks of raccoons in different seasons,
413 and used the generated networks to apply simulation models of rabies spread to
414 demonstrate seasonality in disease dynamics caused by changes in contact network
415 structure. The ability to use ERGMs in this way also facilitates comparison in transmission
416 dynamics between species by quantifying differences in network structure between them,
417 and making it possible to simulate dynamic processes more broadly than on the single
418 observed network. A caveat to this is that the usefulness of the simulated networks depends
419 on the goodness-of-fit of the model; poorly fitting models will generate networks that show
420 transmission dynamics unlike the observed one.

421

422 **Hypotheses related to social dominance**

423 One area where ERGMs have been employed particularly successfully in studying
424 animal social behaviour is in studies of social dominance (Dey & Quinn, 2014; Dey et al.,
425 2015). Existing measures of dominance hierarchies seek to estimate the linearity of
426 hierarchies (De Vries et al., 2006; Douglas et al., 2017), and operate in the absence of other
427 variables. ERGMs can be used alongside these approaches to provide a useful quantification
428 of the linearity of hierarchies arising as an emergent property of network structure. For
429 example, the terms estimating the importance of transitive and cyclical interactions in an

430 ERGM provide a direct quantification of how tendencies for transitive and cyclical triads
431 contribute to the linearity of a hierarchy (Shizuka & McDonald, 2012). Importantly, these
432 effects can be tested alongside the influence of phenotypic traits such as body size, age and
433 sex, as well as dyadic covariates such as relatedness, which may be expected to play a
434 substantial role in many systems. In addition, the fact that parameters are estimated with
435 standard error while controlling for other possible effects facilitates comparisons of
436 hierarchies between different behaviours (e.g. ritualised dominance behaviours versus
437 agonistic behaviours), or between different species, and offers a great opportunity for
438 effective cross-species comparisons.

439 The use of ERGMs also enables a very natural extension to considering dominance
440 interactions as temporally dynamic. The use of temporal ERGMs makes it possible to
441 determine the stability of hierarchical interactions over time, which is likely to influence the
442 benefits of hierarchy formation and therefore have important implications for individuals
443 living in groups. Further, it would additionally be possible to consider how changes in traits
444 influence hierarchical interactions, for example whether dominance interactions are more
445 likely to change as individuals get closer in body weight or condition.

446

447 **Hypotheses related to differences in network structure**

448 ERGMs quantify network structure by providing parameter values that describe the
449 structure of the network. While these parameters are context specific (i.e. they depend
450 closely on the other parameters included in the model), they do offer a great opportunity to
451 test for differences in network structure between populations or for different types of
452 behavioural interaction within a population. In particular, comparisons of social networks
453 between populations are complicated by many network measures being influenced by the

454 size of the network (Croft et al., 2008). Cross-species comparisons of network structure
455 using a standardised approach would allow an improved understanding of the more general
456 evolutionary processes and constraints shaping animal sociality. The application of an ERGM
457 framework would enable this to be done while considering system-specific effects that are
458 known to be important by researchers. For example, an analysis exploring the impact of
459 relatedness on the tendency for within-group behavioural interactions could be completed
460 while controlling for differences between species in how males and females interacted, or
461 the age-structure of within-group interactions. The resulting estimate for the effect of
462 relatedness could then be compared across populations or species.

463

464 **Hypotheses related to network stability over time**

465 Temporal ERGMs have not been used in animal behaviour research. There are other
466 methods available to study dynamic networks (Fisher et al., 2017; Silk et al., 2017b; Tranmer
467 et al., 2015), and the choice of model should be driven by the data available and questions
468 of interest (Silk et al. 2017b). Temporal ERGMs are somewhat similar to stochastic actor-
469 oriented models (SAOMs) as both are based on an ERGM-type framework, however each
470 take different approaches to modelling network change. Temporal ERGMs have the
471 advantage of being able to accommodate more complex temporal dependencies, thereby
472 not requiring linear change in network structure over time (Silk et al. 2017b). Relational
473 event models (REMs) in contrast model temporally explicit interaction data, so are less
474 focussed on network structure (focussing instead on the temporal dynamics of interactions
475 themselves, albeit in a social context) (Tranmer et al. 2015). The stability of animal social
476 interactions or relationships is a topic of great interest (Pinter-Wollman et al., 2013), and in
477 many species long-term stable associations or alliances are likely to be beneficial (Brent et

478 al., 2015; Gomes et al., 2009; McComb et al., 2001). Temporal ERGMs offer an excellent
479 framework to test the stability of social relationships within animal groups. Edelman and
480 McDonald (2014) used an approach similar to that of a temporal ERGM, by using the
481 previous year's network as a dyadic covariate for the current year's network in male long-
482 tailed manakins. They found that the previous year's network was a significant predictor of
483 the current network, indicating that cooperative relationships between males persisted over
484 time. Further, it is possible to use temporal ERGMs to model network change over time
485 according to a user-specified function, allowing the incorporation of non-linear rates of
486 change. Within this, parameters for the rate of change in social relationships can be linked
487 with dyadic covariates, so that it is possible to test hypotheses that relationships between
488 particular types of individuals are likely to change faster than others.

489

490 **Outstanding issues**

491 The use of ERGMs in animal behaviour research would benefit from simulation-
492 modelling studies that can provide greater evidence for when their use (and the use of
493 other similar models) is likely to be appropriate. In particular, exploring the impact of
494 subsampling network interactions on hypothesis testing in networks will be especially useful
495 (Silk et al., 2017b). This is ideally suited to simulation modelling approaches in which "real"
496 scenarios (e.g. realistic levels of missing data) can be generated and then sampled.
497 Theoretical work has suggested that parameter estimates for structural terms are unlikely to
498 accurately reflect the true properties of the unsampled network in these cases (Shalizi &
499 Rinaldo, 2013), however hypothesis testing may still be appropriate when relative
500 differences are important. A simulation-modelling approach could also reveal whether it is
501 appropriate to apply ERGMs to association-based networks of animals, and if so how this

502 might be achieved. Two possibilities seem most likely here: (1) using ERGMs of bipartite
503 networks linking individuals and groups, and (2) including terms that can control for biases
504 introduced by the method of data collection (e.g. effects of gregariousness, number of times
505 observed etc.) and ensuring that this can result in accurate parameter estimation and low
506 statistical error rate.

507

508 **Conclusions**

509 Exponential random graph models have received relatively limited use to study
510 animal behaviour, but have provided some interesting insights. This is despite animal
511 behaviour researchers only exploiting some of the more basic approaches within this
512 flexible network modelling framework. We have provided an outline of the strengths and
513 weaknesses of using ERGMs to study animal behaviour, and have used this to highlight both
514 some research areas where they offer real potential, and where further simulation
515 modelling work is required to test their appropriateness in testing hypotheses about animal
516 network structure. Together, this information should provide an important guide to
517 researchers hoping to extend the application of ERGMs in the study of animal social
518 networks, and contribute to developing our understanding of the underlying processes
519 driving animal social relationships.

520

521 **References**

522 Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C.
523 (2013). Individual personalities predict social behaviour in wild networks of great tits
524 (*Parus major*). *Ecology Letters*, *16*(11), 1365–1372.

525 Best, E. C., Dwyer, R. G., Seddon, J. M., & Goldizen, A. W. (2014). Associations are more
526 strongly correlated with space use than kinship in female eastern grey kangaroos.
527 *Animal Behaviour*, *89*, 1–10.

528 Blumstein, D. T., Wey, T. W., & Tang, K. (2009). A test of the social cohesion hypothesis:
529 interactive female marmots remain at home. *Proceedings of the Royal Society of*
530 *London B: Biological Sciences*, *276*(1669), 3007–3012.

531 Bode, N. W. F., Wood, A. J., & Franks, D. W. (2011). The impact of social networks on animal
532 collective motion. *Animal Behaviour*, *82*(1), 29–38.

533 Brent, L. J. N. (2015). Friends of friends: are indirect connections in social networks
534 important to animal behaviour? *Animal Behaviour*, *103*, 211–222.

535 Brent, L. J. N., Franks, D. W., Foster, E. A., Balcomb, K. C., Cant, M. A., & Croft, D. P. (2015).
536 Ecological knowledge, leadership, and the evolution of menopause in killer whales.
537 *Current Biology*, *25*(6), 746–750.

538 Caimo, A. & Friel, N. (2013). Bayesian model selection for exponential random graph
539 models. *Social Networks*, *35*(1), 11-24.

540 Carter, A.J., Lee, A.E.G. & Marshall, H.H. (2015). Research questions should drive edge
541 definitions in social network studies. *Animal Behaviour*, *104*, e7-e11.

542 Carter, K. D., Brand, R., Carter, J. K., Shorrocks, B., & Goldizen, A. W. (2013). Social networks,
543 long-term associations and age-related sociability of wild giraffes. *Animal Behaviour*,
544 *86*(5), 901–910.

545 Cranmer, S. J., Leifeld, P., McClurg, S. D., & Rolfe, M. (2016). Navigating the range of
546 statistical tools for inferential network analysis. *American Journal of Political Science*
547 *61*(1), 237-251.

548 Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton

549 University Press.

550 Croft, D. P., Krause, J., Darden, S. K., Ramnarine, I. W., Faria, J. J., & James, R. (2009).
551 Behavioural trait assortment in a social network: patterns and implications. *Behavioral*
552 *Ecology and Sociobiology*, *63*(10), 1495–1503.

553 Croft, D. P., Madden, J. R., Franks, D. W., & James, R. (2011). Hypothesis testing in animal
554 social networks. *Trends in Ecology & Evolution*, *26*(10), 502–507.

555 De Vries, H., Stevens, J. M. G., & Vervaecke, H. (2006). Measuring and testing the steepness
556 of dominance hierarchies. *Animal Behaviour*, *71*(3), 585–592.

557 Denny, M. J., Wilson, J. D., Cranmer, S. J., Desmarais, B. A., & Bhamidi, S. (2016). GERGM:
558 Estimation and Fit Diagnostics for Generalized Exponential Random Graph Models. R
559 package version 0.10.0. <https://cran.r-project.org/package=GERGM>

560 Desmarais, B. A., & Cranmer, S. J. (2012). Statistical inference for valued-edge networks: the
561 generalized exponential random graph model. *PLoS One*, *7*(1), e30136.

562 Dey, C. J., & Quinn, J. S. (2014). Individual attributes and self-organizational processes affect
563 dominance network structure in pukeko. *Behavioral Ecology*, aru138.

564 Dey, C. J., Tan, Q. Y. J., O'Connor, C. M., Reddon, A. R., Caldwell, J. R., & Balshine, S. (2015).
565 Dominance network structure across reproductive contexts in the cooperatively
566 breeding cichlid fish *Neolamprologus pulcher*. *Current Zoology*, *61*(1), 45–54.

567 Douglas, P. H., Ngomo, A.-C. N., & Hohmann, G. (2017). A novel approach for dominance
568 assessment in gregarious species: ADAGIO. *Animal Behaviour*, *123*, 21–32.

569 Edelman, A. J., & McDonald, D. B. (2014). Structure of male cooperation networks at long-
570 tailed manakin leks. *Animal Behaviour*, *97*, 125–133.

571 Farine, D. R. (2014). Measuring phenotypic assortment in animal social networks: weighted
572 associations are more robust than binary edges. *Animal Behaviour*, *89*, 141-153.

573 Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal
574 social network analysis. *Journal of Animal Ecology*, *84*(5), 1144–1163.

575 Farine, D. R., Strandburg-Peshkin, A., Berger-Wolf, T., Ziebart, B., Brugere, I., Li, J., Crofoot,
576 M. C. (2016). Both nearest neighbours and long-term affiliates predict individual
577 locations during collective movement in wild baboons. *Scientific Reports* *6*(1), 27704.

578 Faust, K., & Skvoretz, J. (2002). 8. Comparing networks across space and time, size and
579 species. *Sociological Methodology*, *32*(1), 267–299.

580 Fisher, D. N., Rodríguez-Muñoz, R., & Tregenza, T. (2016). Wild cricket social networks show
581 stability across generations. *BMC Evolutionary Biology*, *16*(1), 151.

582 Fisher, D. N., Ilany, A., Silk, M. J., & Tregenza, T. (2017). Analysing animal social network
583 dynamics: the potential of stochastic actor-oriented models. *Journal of Animal Ecology*,
584 *86*(2), 202–212.

585 Fletcher, R. J., Acevedo, M. A., Reichert, B. E., Pias, K. E., & Kitchens, W. M. (2011). Social
586 network models predict movement and connectivity in ecological landscapes.
587 *Proceedings of the National Academy of Sciences*, *108*(48), 19282–19287.

588 Franks, D. W., Ruxton, G. D., James, R. (2010). Sampling animal association networks with
589 the gambit of the group. *Behavioral Ecology and Sociobiology*, *64*(3), 493-503.

590 Godde, S., Côté, S. D., & Réale, D. (2015). Female mountain goats, *Oreamnos americanus*,
591 associate according to kinship and reproductive status. *Animal Behaviour*, *108*, 101–
592 107.

593 Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild
594 West African chimpanzees. *Proceedings of the Royal Society of London B: Biological
595 Sciences*, *276*(1657), 699–706.

596 Handcock, M. S., Robins, G., Snijders, T. A. B., Moody, J., & Besag, J. (2003). Assessing

597 degeneracy in statistical models of social networks. *Journal of the American Statistical*
598 *Association* 76, 33-50.

599 Handcock, M. S., Hunter, D. R., Butts, C. T., Goodreau, S. M., & Morris, M. (2008). statnet:
600 Software tools for the representation, visualization, analysis and simulation of network
601 data. *Journal of Statistical Software*, 24(1), 1548.

602 Handcock, M. S., Hunter, D. R., Butts, C. T., Goodreau, S. M., Krivitsky, P. N., & Morris, M.
603 (2015). ergm: Fit, Simulate and Diagnose Exponential-Family Models for Networks. The
604 Statnet Project. <http://cran.r-project.org/package=ergm>

605 Hunter, D. R., Handcock, M. S., Butts, C. T., Goodreau, S. M., & Morris, M. (2008). ergm: A
606 package to fit, simulate and diagnose exponential-family models for networks. *Journal*
607 *of Statistical Software*, 24(3), nihpa54860.

608 Ilany, A., Barocas, A., Koren, L., Kam, M., & Geffen, E. (2013). Structural balance in the social
609 networks of a wild mammal. *Animal Behaviour*, 85(6), 1397–1405.

610 Krause, J., James, R., Franks, D. W., & Croft, D. P. (2014). *Animal social networks*. Oxford
611 University Press.

612 Krivitsky, P. N. (2012). Exponential-family random graph models for valued networks.
613 *Electronic Journal of Statistics*, 6, 1100.

614 Krivitsky, P. N. (2015). ergm.count: Fit, Simulate and Diagnose Exponential-Family Models
615 for Networks with Count Edges. <http://cran.r-project.org/package=ergm.count>

616 Krivitsky, P. N., & Handcock, M. S. (2016). tergm: Fit, Simulate and Diagnose Models for
617 Network Evolution Based on Exponential-Family Random Graph Models. The Statnet
618 Project (URL: <http://www.statnet.org>). R package version 3.4.0. [http://cran.r-](http://cran.r-project.org/package=tergm)
619 [project.org/package=tergm](http://cran.r-project.org/package=tergm)

620 Kurvers, R. H. J. M., Krause, J., Croft, D. P., Wilson, A. D. M., & Wolf, M. (2014). The

621 evolutionary and ecological consequences of animal social networks: emerging issues.
622 *Trends in Ecology & Evolution*, 29(6), 326–335.

623 Leifeld, P., Cranmer, S. J., & Desmarais, B. A. (2016). xergm. Extensions for Exponential
624 Random Graph Models. R package version 1.7.0. [https://cran.r-](https://cran.r-project.org/web/packages/xergm/index.html)
625 [project.org/web/packages/xergm/index.html](https://cran.r-project.org/web/packages/xergm/index.html)

626 Lusher, D., Koskinen, J., Robins, G., Lusher, D., Koskinen, J., & Robins, G. (2013). *Exponential*
627 *random graph models for social networks*. Structural analysis in the social sciences.
628 Cambridge University Press, New York.

629 McComb, K., Moss, C., Durant, S. M., Baker, L., & Sayialel, S. (2001). Matriarchs as
630 repositories of social knowledge in African elephants. *Science*, 292(5516), 491–494.

631 Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S.,
632 Waters, J. S., Prager, S. D., Sasaki, T., Wittemyer, G., Fewell, J., McDonald, D. B. (2013).
633 The dynamics of animal social networks: analytical, conceptual, and theoretical
634 advances. *Behavioral Ecology*, 25(2), 242-255.

635 R Development Core Team, R. (2017). R: A Language and Environment for Statistical
636 Computing. (R. D. C. Team, Ed.), *R Foundation for Statistical Computing*. R Foundation
637 for Statistical Computing. <https://doi.org/10.1007/978-3-540-74686-7>

638 Reynolds, J. J. H., Hirsch, B. T., Gehrt, S. D., & Craft, M. E. (2015). Raccoon contact networks
639 predict seasonal susceptibility to rabies outbreaks and limitations of vaccination.
640 *Journal of Animal Ecology*, 84(6), 1720–1731.

641 Robins, G., Pattison, P., Kalish, Y., & Lusher, D. (2007). An introduction to exponential
642 random graph (p^*) models for social networks. *Social Networks*, 29(2), 173–191.

643 Rosenthal, S. B., Twomey, C. R., Hartnett, A. T., Wu, H. S., Couzin, I. D. (2015). Revealing the
644 hidden networks of interaction in mobile animal groups allows prediction of complex

645 behavioral contagion. *Proceedings of the National Academy of Sciences*, 112 (15), 4690-
646 4695.

647 Schweinberger, M. (2011). Instability, sensitivity, and degeneracy of discrete exponential
648 families. *Journal of the American Statistical Association*, 106(496), 1361–1370.

649 Schweinberger, M., & Handcock, M. S. (2015). Local dependence in random graph models:
650 characterization, properties and statistical inference. *Journal of the Royal Statistical*
651 *Society: Series B (Statistical Methodology)*, 77(3), 647–676.

652 Schweinberger, M., Handcock, M. S., & Luna, P. (2016). hergm: Hierarchical Exponential-
653 Family Random Graph Models with Local Dependence. R package version 3.1-0.
654 <https://cran.r-project.org/web/packages/hergm/index.html>

655 Shalizi, C. R., & Rinaldo, A. (2013). Consistency under sampling of exponential random graph
656 models. *Annals of Statistics*, 41(2), 508.

657 Shizuka, D., & McDonald, D. B. (2012). A social network perspective on measurements of
658 dominance hierarchies. *Animal Behaviour*, 83(4), 925–934.

659 Silk, M. J., Croft, D. P., Delahay, R. J., Hodgson, D. J., Boots, M., Weber, N., & McDonald, R. A.
660 (2017a). Using social network measures in wildlife disease ecology, epidemiology, and
661 management. *BioScience*, 67(3), 245–257.

662 Silk, M. J., Croft, D. P., Delahay, R. J., Hodgson, D. J., Weber, N., Boots, M., & McDonald, R. A.
663 (2017b). The application of statistical network models in disease research. *Methods in*
664 *Ecology and Evolution*.

665 Silk, M. J., Jackson, A. L., Croft, D. P., Colhoun, K., & Bearhop, S. (2015). The consequences of
666 unidentifiable individuals for the analysis of an animal social network. *Animal*
667 *Behaviour*, 104, 1–11.

668 Smith, J. A., & Moody, J. (2013). Structural effects of network sampling coverage I: Nodes

669 missing at random. *Social Networks*, 35(4), 652–668.

670 Smith, J. A., Moody, J., & Morgan, J. H. (2017). Network sampling coverage II: The effect of
671 non-random missing data on network measurement. *Social Networks*, 48, 78–99.

672 Snijders, T. A. B., Pattison, P. E., Robins, G. L., & Handcock, M. S. (2006). New specifications
673 for exponential random graph models. *Sociological Methodology*, 36(1), 99–153.

674 Strandburg-Peshkin, A., Twomey, C. R., Bode, N. W.F., Kao, A. B., Katz, Y., Ioannou, C. C.,
675 Rosenthal, S. B., Torney, C. J., Wu, H. S., Levin, S. A., Couzin, I. D. (2013). Visual sensory
676 networks and effective information transfer in animal groups. *Current Biology* 23 (17),
677 R709-R711.

678 Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C. M.,
679 Williams, L., Zinner, D., Aureli, F. (2011). Collective decision-making and fission–fusion
680 dynamics: a conceptual framework. *Oikos*, 120(11), 1608–1617.

681 Tranmer, M., Marcum, C. S., Morton, F. B., Croft, D. P., & de Kort, S. R. (2015). Using the
682 relational event model (REM) to investigate the temporal dynamics of animal social
683 networks. *Animal Behaviour*, 101, 99–105.

684 VanderWaal, K. L., Atwill, E. R., Isbell, L., & McCowan, B. (2014). Linking social and pathogen
685 transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*).
686 *Journal of Animal Ecology*, 83(2), 406–414.

687 Wang, P., Robins, G., & Pattison, P. (2009). PNet: program for the simulation and estimation
688 of exponential random graph models. Melbourne School of Psychological Sciences, The
689 University of Melbourne.

690 Wey, T. W., & Blumstein, D. T. (2010). Social cohesion in yellow-bellied marmots is
691 established through age and kin structuring. *Animal Behaviour*, 79(6), 1343–1352.

692 White, L. A., Forester, J. D., & Craft, M. E. (2015). Using contact networks to explore

693 mechanisms of parasite transmission in wildlife. *Biological Reviews* 92(1), 389-409.

694 Whitehead, H. (2008). *Analyzing animal societies: quantitative methods for vertebrate social*
695 *analysis*. University of Chicago Press.

696 Whitehead, H., & Dufault, S. (1999). Techniques for analyzing vertebrate social structure
697 using identified individuals: review and recommendations. *Advances in the Study of*
698 *Behavior*, 28.

699 Whitehead, H., & James, R. (2015). Generalized affiliation indices extract affiliations from
700 social network data. *Methods in Ecology and Evolution*, 6(7), 836–844.

701 Wilson, A. D. M., Krause, S., Dingemanse, N. J., & Krause, J. (2013). Network position: a key
702 component in the characterization of social personality types. *Behavioral Ecology and*
703 *Sociobiology*, 67(1), 163–173.

704 Wilson, J. D., Denny, M. J., Bhamidi, S., Cranmer, S. J., & Desmarais, B. A. (2017). Stochastic
705 weighted graphs: Flexible model specification and simulation. *Social Networks*, 49, 37–
706 47.

707 Wolf, J. B. W., Mawdsley, D., Trillmich, F., & James, R. (2007). Social structure in a colonial
708 mammal: unravelling hidden structural layers and their foundations by network
709 analysis. *Animal Behaviour*, 74(5), 1293–1302.

710

711

712 **Tables**

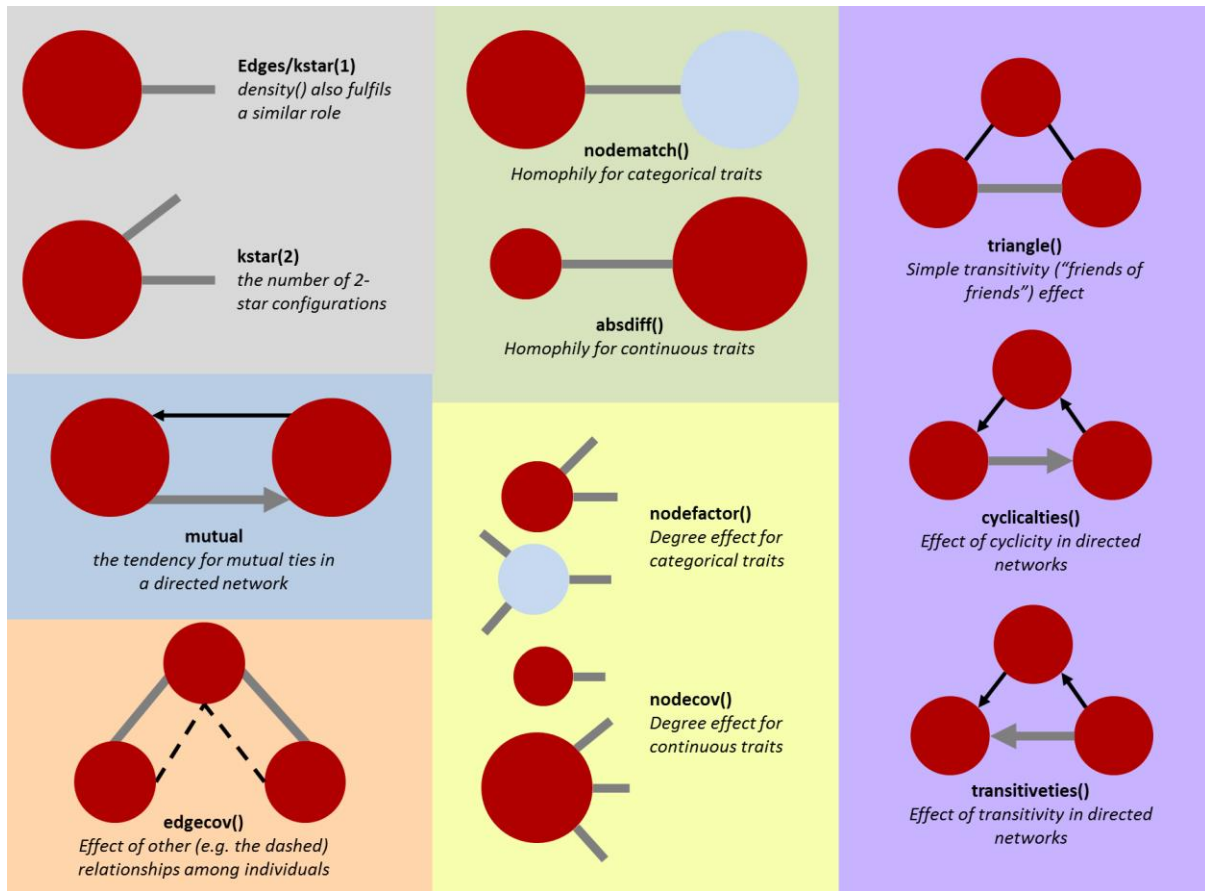
713 Table 1. A list of the different software packages available to analyse ERGMs, and their
 714 respective capabilities i.e. the types of network data (beyond static and binary networks)
 715 that they can be used to analyse

Software	Platform	Capabilities	Source / reference
PNet	Windows (Java based)	Binary, Hierarchical (local dependency structures)	http://www.melnet.org.au/pnet/ Wang et al., 2009
MPNet	Windows (Java based)	Bipartite, Two-layer	http://www.melnet.org.au/pnet/
ergm	R	Bipartite	https://cran.r- project.org/web/packages/ergm/index.html Handcock et al., 2015; Hunter et al., 2008
ergm.count	R	Weighted (positive integers only)	https://cran.r- project.org/web/packages/ergm.count/index.html Krivitsky, 2015
GERGM	R	Weighted	https://cran.r- project.org/web/packages/GERGM/index.html Denny et al., 2016
hergm	R	Hierarchical (local dependency structures)	https://cran.r- project.org/web/packages/hergm/index.html Schweinberger et al., 2016
tergm	R	Temporally dynamic	https://cran.r- project.org/web/packages/tergm/index.html Krivitsky & Handcock, 2016
btergm	R	Temporally dynamic	https://cran.r- project.org/web/packages/btergm/index.html Leifeld et al., 2016

716

717

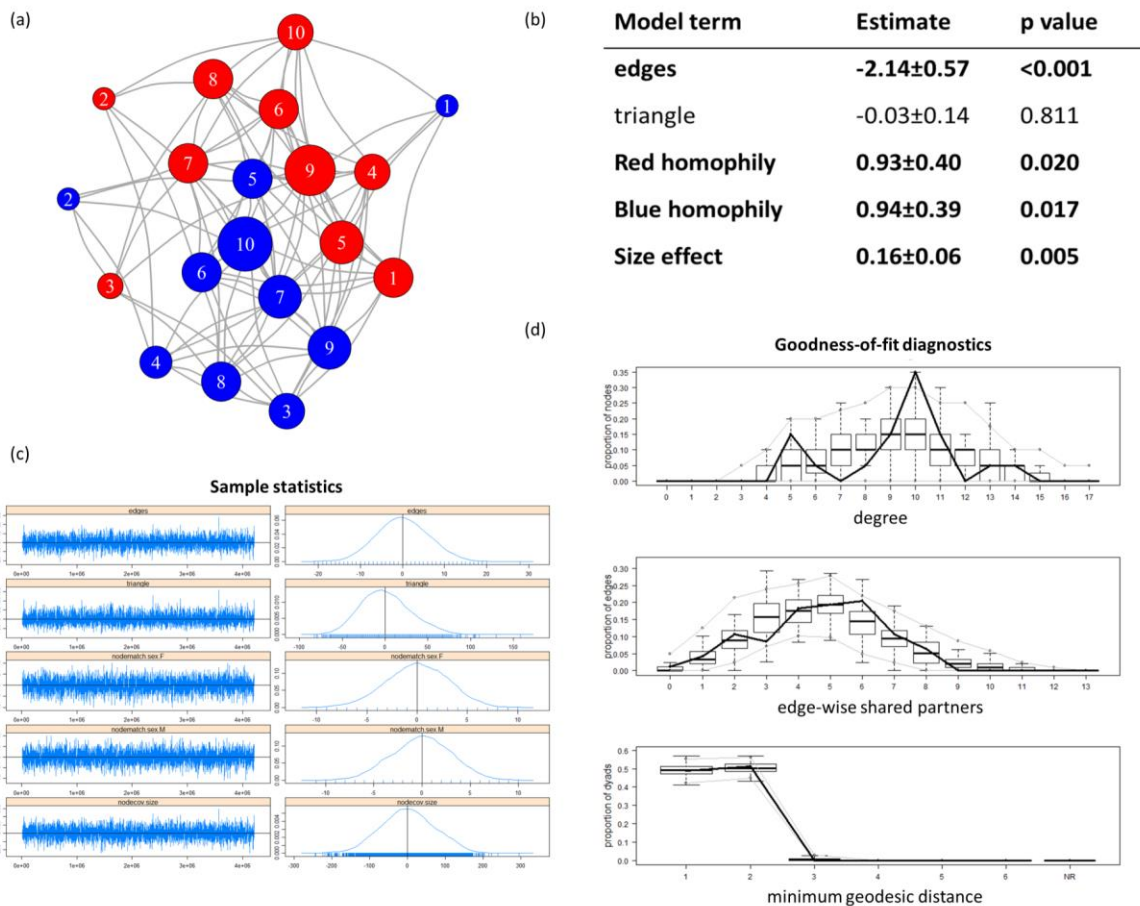
718 **Figures**



719

720 Figure 1. A diagrammatic guide to the key terms that can be used in ERGMs. Grey box (top left):
 721 Basic structural terms estimating the tendency for the number of edges and multi-edge
 722 configurations in a graph. Blue box (middle left): the tendency to form mutual ties, a dyadic
 723 structural terms specific to directed networks. Orange box (bottom right): dyadic covariates on the
 724 tendency to form edges (i.e. as a result of other relationships between the individuals). Green box
 725 (top centre): Individual or nodal terms for effects of homophily. Yellow box (bottom centre):
 726 Individual or nodal terms for effects on the number of edges formed. Purple box (right): Basic triadic
 727 effects for undirected (triangle, top) and directed networks.

728



729

730 Figure 2. The fitting of an ERGM to a toy dataset consisting of two types of individual (red and blue)

731 that additionally vary in size (white node labels). a) Shows the network that the ERGM is fitted to. b)

732 Shows the summary of the model output, revealing significant homophily and a positive effect of

733 size on the number of interactions. c) Shows the model convergence plots produced by running

734 `mcmc.diagnostics()`, with the left column of panels showing that the parameters have converged and

735 so only vary around a stable point, while the right column of panels shows the distribution of

736 estimates for the parameters is approximately normal in each case. d) shows the model goodness-

737 of-fit produced by the function `gof()`. Goodness-of-fit for degree (top), edge-wise shared partners

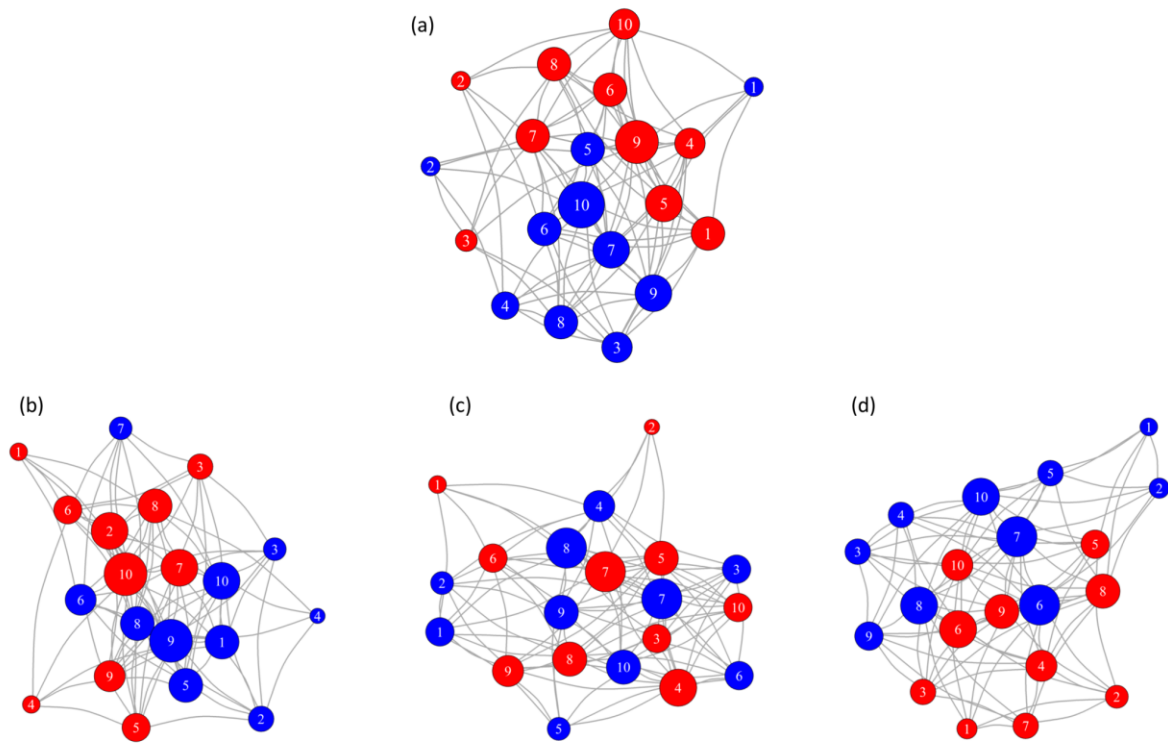
738 (middle) and minimum geodesic distance (bottom) are shown, with the range of values in the

739 simulated models (box plots) generally showing the same pattern as the observed network (black

740 line). Full R code is provided in the supplementary information.

741

742



743
 744 Figure 3. The original toy network used in our simple example of ERGM fitting (a) compared to three
 745 networks simulated using the fitted ERGM (b-d).

746

747

748