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.

Introduction

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

Quantifying a complex social environment can represent a challenge, but can be achieved through the suite of tools available in social network analysis. A network approach is useful as social relationships are an emergent property of the interactions of multiple individuals, and there is increasing evidence that indirect connections among individuals within animal populations are important (Brent, 2015). In the last decade social network analysis, originally developed in the social and physical sciences, has become a pervasive tool in the study of animal behaviour (Krause et al., 2014; Pinter-Wollman et al., 2013). As well as directly modelling social relationships, it can be integral to understanding other 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     $P(N) = ce^{\theta_1 z_1(\text{N}) + \theta_2 2 z_2(\text{N}) + \cdots + \theta_n z n z_n(\text{N})}$

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 strucutre 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,

for example, node-based covariates could be used to model which sex formed

more (or stronger) edges, and additionally whether intra-sex edges were more

likely than inter-sex ones (i.e. males tending to interact with other males, and

females with females). Node-based covariates for continuous traits can also

include a difference term, for example: are edges more likely when the attributes

of two individuals are more similar? This might be expected in situations such as

dominance hierarchies where interactions are more likely if two individuals are

more closely matched (e.g. Dey & Quinn, 2014).

b) Dyadic covariates model how other relationships among individuals in a network

affect edge values. For example, with animal social networks, where space use is

often an important component of social structure, a matrix of the distances

between individual home ranges or refuges might be a valuable dyadic covariate.

Another example might be genetic relatedness, if social relationships within a

group are thought to be influenced by kinship (e.g. Carter et al., 2013; Godde, et

al., 2015; Wolf et al., 2007).

c) Structural covariates are aspects of network topology that might be expected to

affect edge formation, and can occur at several levels of complexity (Fig. 1). The

most basic structural term would be a measure of edge density, somewhat

equivalent to having an intercept within a generalised linear model. This models

the general tendency for individuals to be connected to other individuals, and is

typically negative in social networks as individuals tend not to be connected to all

other individuals. Increasingly complex structural terms can be incorporated, and

these define the dependency structure used within the model to understand

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   Aikaike 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

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

263

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 el. (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

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

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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

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717
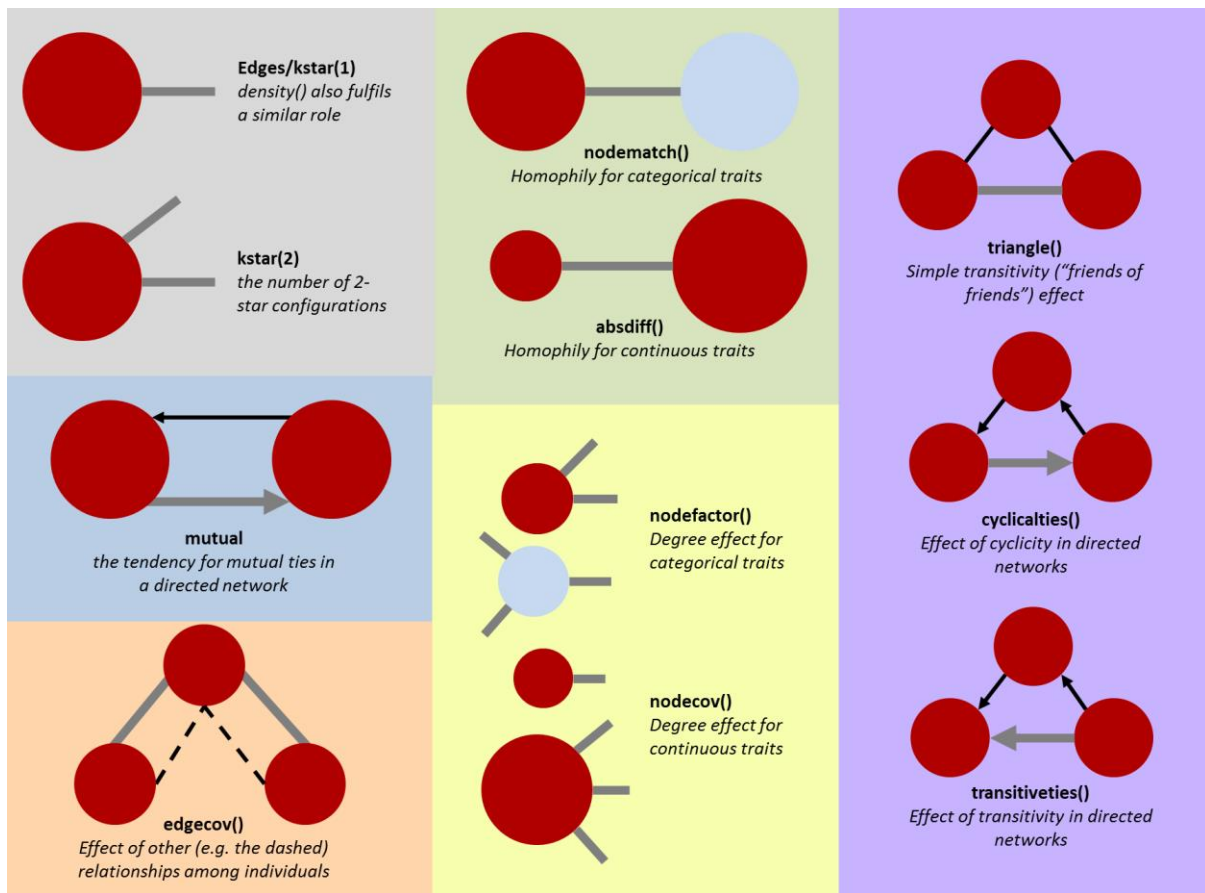
Figures

Figure 1. A diagrammatic guide to the key terms that can be used in ERGMs. Grey box (top left): Basic structural terms estimating the tendency for the number of edges and multi-edge configurations in a graph. Blue box (middle left): the tendency to form mutual ties, a dyadic structural terms specific to directed networks. Orange box (bottom right): dyadic covariates on the tendency to form edges (i.e. as a result of other relationships between the individuals). Green box (top centre): Individual or nodal terms for effects of homophily. Yellow box (bottom centre): Individual or nodal terms for effects on the number of edges formed. Purple box (right): Basic triadic effects for undirected (triangle, top) and directed networks.
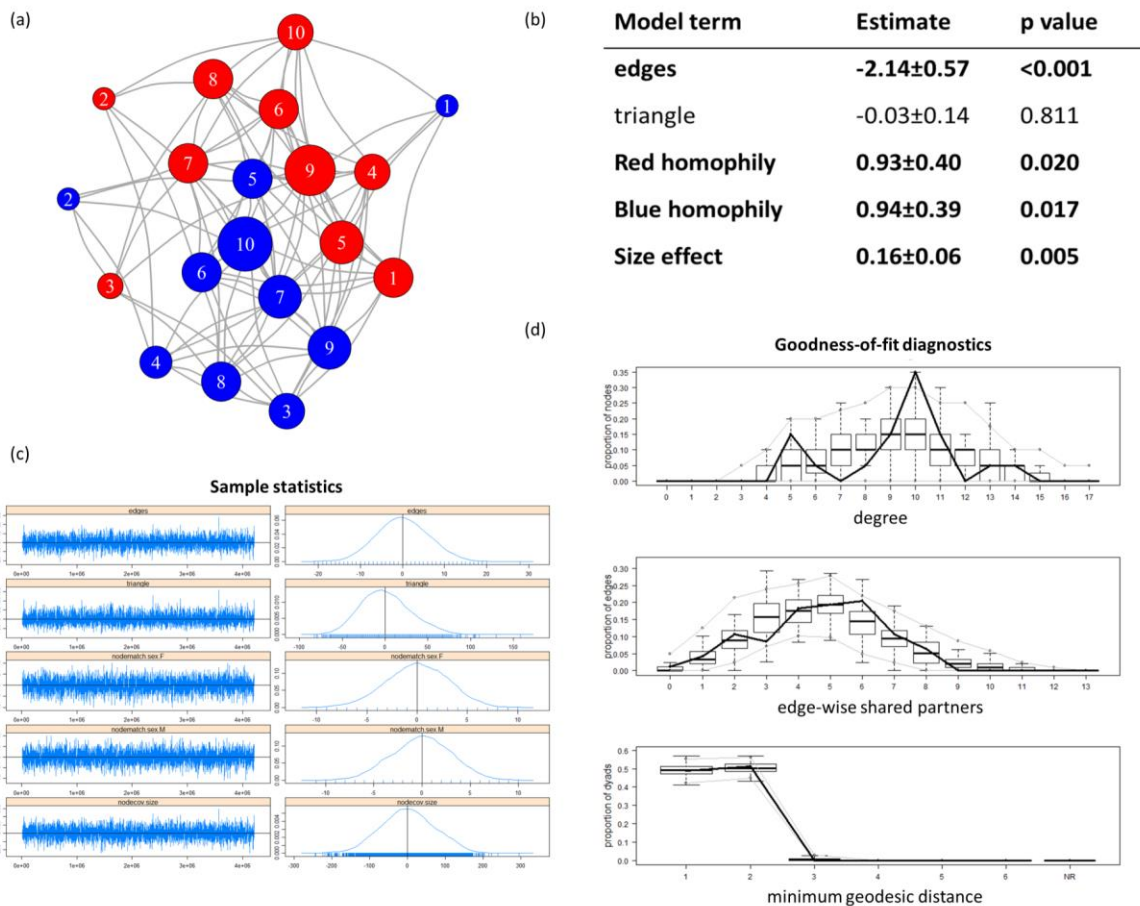
Figure 2. The fitting of an ERGM to a toy dataset consisting of two types of individual (red and blue) that additionally vary in size (white node labels). a) Shows the network that the ERGM is fitted to. b) Shows the summary of the model output, revealing significant homophily and a positive effect of size on the number of interactions. c) Shows the model convergence plots produced by running mcmc.diagnostics(), with the left column of panels showing that the parameters have converged and so only vary around a stable point, while the right column of panels shows the distribution of estimates for the parameters is approximately normal in each case. d) shows the model goodness-of-fit produced by the function gof().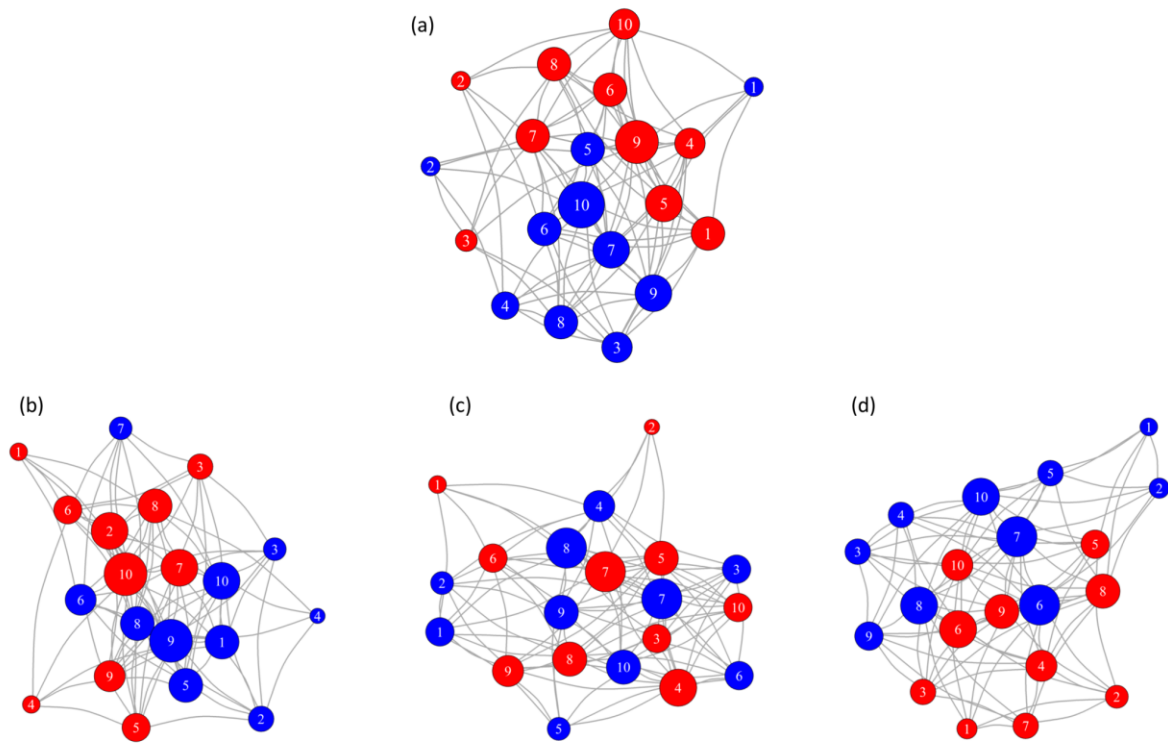 Goodness-of-fit for degree (top), edge-wise shared partners (middle) and minimum geodesic distance (bottom) are shown, with the range of values in the simulated models (box plots) generally showing the same pattern as the observed network (black line). Full R code is provided in the supplementary information.

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).

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