Social inheritance can explain the structure of animal social networks

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Abstract

The social network structure of animal populations has major implications to survival, reproductive success, sexual selection, and pathogen transmission. But as of yet, no general theory of social network structure exists that can explain the diversity of social networks observed in nature, and serve as a null model for detecting species and population-specific factors. Here we propose a simple and generally applicable model of social network structure. We consider the emergence of network structure as a result of social inheritance, in which newborns are likely to bond with maternal contacts, and via forming bonds randomly. We compare model output to data from several species, showing that it can generate networks with properties such as those observed in real social systems. Our model demonstrates that important observed properties of social networks, including heritability of network position or assortative associations, can be understood as a consequence of social inheritance.

1   Introduction

The transition to sociality is one of the major shifts in evolution, and social structure is an important and ever-present selective factor, affecting both reproductive success Silk et al. (2003) and survival (Silk et al., 2010; Barocas et al., 2011) and ecological dynamics (Packer et al., 2005). Sociality affects individual health, ecological dynamics, and evolutionary fitness via multiple mechanisms in humans and other animals, such as pathogen transmission (e.g. Hamede et al., 2009; Mossong et al., 2008) and promoting or hindering of particular social behaviors (Ohtsuki et al., 2006; Santos et al., 2008; Rand et al., 2014). Social bonds can both increase stress induced by competition (Kappeler et al., 2015), while at the same time providing buffer for individuals against stressors and their effects (Cohen and Wills, 1985; Kikusui et al., 2006). The social structure of a population summarizes the social bonds of its members (Hinde, 1976). Hence, understanding the processes generating variation in social structure across populations and species is crucial to uncovering the impacts of sociality.

Recent years have seen a surge in the study of the causes and consequences of social structure in human and animal societies, based on theoretical and computational advances in social network analysis (SNA) (Wey et al., 2008). The new interdisciplinary network science provides many tools to construct, visualize, quantify and compare social structures, facilitating advanced understanding of social phenomena. Researchers studying a variety of species, from insects to humans, have used these tools to gain insights into the factors determining social structure (Fewell, 2003; Lewis et al., 2012; Aplin et al., 2013; Ilany et al., 2015). Using SNA provided evidence for the effects of social structure on a range of phenomena, such as sexual selection (Oh and Badyaev, 2010) and cultural transmission (Aplin et al., 2015; Allen et al., 2013).

At the same time, most applications of SNA to non-human animals have been at a static and descriptive level, using various computational methods

to quantify features of social structure. These methods, combined with increasingly detailed data ("reality mining" Krause et al., 2013) about social interactions in nature, provided valuable insights about the complex effects of social interaction on individual behaviors and fitness outcomes. Yet, we still lack a comprehensive theory that can explain the generation and diversity of social structures observed within and between species. There have been only a few efforts to model animal social network structure. Notably, Seyfarth (1977) used a generative model of grooming networks based on individual preferences for giving and receiving grooming, and showed that a few simple rules can account for complex social structure. This model and related approaches (e.g., Sterck et al., 1997) have been very influential in the study of social structure and continue to drive empirical research. At the same time, they mostly focused on primates and were geared towards specific questions such as the effects of relatedness, social ranks, or ecological factors in determining social structure.

Independently, a large body of theoretical work in network science aims to explain the general properties of human social networks through simple models of how networks form. Yet these models tend to focus either on networks with a fixed set of agents (e.g. Skyrms and Pemantle, 2000), or on boundlessly growing networks (e.g., Jackson and Rogers, 2007), with few exceptions (Moore et al., 2006; Ghoshal et al., 2013). These network formation models therefore have limited applicability to animal (and many human) social groups where individuals both join (through birth of immigration) and leave (through death or emigration) the network. Furthermore, most work in network science concentrates on the distribution of number of connections individuals have (the degree distribution). Models that fit the degree distribution of real-world networks tend to be a poor fit to other important properties, notably the tendency of social connections to be clustered (Jackson and Rogers, 2007), i.e., two individuals to be connected with each other if they are both connected to a third individual.

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Real-world human and animal networks exhibit significantly more clustering than random or preferential attachment models predict.

To overcome these limitations, we provide a generally applicable network formation model based on simple demographic and social processes. Our model assumes a neutral demographic process (birth and death), and focuses on a central social process that is in operation in many social species: the "inheritance" of social connections from parents. This central component of our model is based on the observation that in many species with stable social groups, individuals interact with the social circle of their parents. This is essentially the case in all mammals, where newborns stay close to their mothers until weaning, but also common in other taxa, such as birds, fish, and insects. After positively interacting with the parents' social contacts, young individuals are likely to form social bonds with these conspecifics.

Despite being extremely simplistic, we demonstrate that our model can generate networks that match both the degree and local clustering distributions of real-world animal social networks, as well as their modularity, using only two parameters. We also show that social heritability of connections can result in the appearance of genetic heritability of connectivity traits, as well as assortativity in the absence of explicit assortative preferences. Our approach highlights commonalities among groups, populations, and species, and uncover general principles underlying variation in social structure.

2 Methods

2.1 A general model of social structure

Our departure point is the model by Jackson and Rogers (2007), which is based on role models introducing their new contacts to their other con-
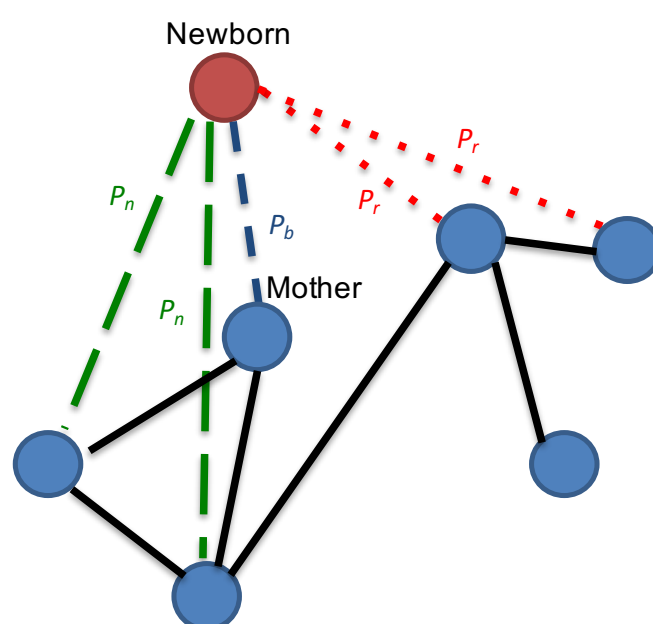
Figure 1: Graphical illustration of the model: a newborn individual is connected to its parent with probability p_b, to its parent's connections with probability p_n, and to individuals not directly connected to its parent with probability p_r.

tacts, and can reproduce many attributes of large-scale human social networks. However, Jackson and Rogers' model is based on a constantly growing network with no death or emigration of agents and their results hold asymptotically for very large networks. Since we are interested in small-scale animal networks that do not grow unboundedly, we model a population where existing individuals die and get replaced at an equal rate with newborn individuals (Moore et al., 2006). We model binary undirected, implicitly cooperative networks, but our model can be extended to weighted networks that describe the strength of each social bond, and directed ones, such as agonistic networks.

Consider a social group of size N. Suppose that each time step, an individual is born to a random mother, and one individual is selected to die at random. With probability p_b, the newborn will meet and connect to its mother (generally, p_b will be close to one, but can be low or zero in species such as some insects, where individuals might not meet their mothers). A crucial component of our model is the general assumption that the likelihood of a newborn A connecting with another individual B depends on the relationship between A's mother and B: the probability A will connect to B is given by p_n if A's mother is connected to B, and p_r if not (Figure 1). Hence, p_n is the probability an offspring "inherits" a given connection of its parent. If $p_n > p_r$, the population exhibits a tendency for clustering, a well-established and general phenomenon in social networks (Lusseau, 2003; Ilany et al., 2015).

2.2 Mean-field approximation of the model

Despite being based on a simple process, most aspects of the dynamics our model are analytically intractable, so we use simulations to study them. We can however, characterize the expected degree distribution in our networks from a mean-field approximation. To characterize the expected dynamics of the degree distribution, consider a focal individual that has degree d at

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time period t. In period $t+1$, the probability that this individual increases its degree by one, p_d^+, is:

$$p_d^+ = \frac{(N-1-d)}{N}\frac{d p_n + (N-d-2)p_r + p_b}{N-1} \, .$$ (1)

The first fraction in (1) is the probability that an individual not connected to the focal individual is selected to die, while the second fraction is the average probability that the newborn individual becomes connected to the focal individual.

The probability of a focal individual's degree d (> 0) going down by one, p_d^-, is likewise given by

$$p_d^- = \frac{d}{N}\left(1 - \frac{(d-1)p_n + (N-d)p_r + p_b}{N-1}\right) \, ,$$ (2)

which is simply the probability one of the focal individual's connections dies times the newborn individual does not connect to the focal individual.

Denoting by ϕ_d[1] the probability that a randomly selected individual in the population has degree d, we can write the following rate equation for the mean-field dynamics of the degree distribution (Moore et al., 2006):

$$\frac{d\phi_d}{dt} = b_d(\boldsymbol{\phi}) + p_{d-1}^+ N\phi_{d-1} + p_{d+1}^- N\phi_{d+1} - (p_d^+ + p_d^-)N\phi_d - \phi_d \, ,$$ (3)

where $b_d(\boldsymbol{\phi})$ is the probability that a newborn is born with d connections (itself a function of the degree distribution $\boldsymbol{\phi}$), and the last term in (3) is the probability that a degree d individual dies, reflecting our assumption that death occurs randomly with respect to degree. If we assume $p_b = 1$, so that the newborn always connects to its parent, then $b_d(\boldsymbol{\phi})$ is given by

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[1]for $0 \le d \le N-1$, with the convention that $p_{-1}^+ = p_0^- = 0$

(for $d \geq 1$; $b_0 = 0$ in that case):

$$b_d(\boldsymbol{\phi}) = \sum_{l=0}^{N-1} \phi_l \sum_{i=0}^{\text{Min}(l,d-1)} \binom{l}{i} p_n^i (1 - p_n)^{l-i} \binom{N - 2 - l}{d - 1 - i} p_r^{d-1-i} (1 - p_r)^{N-1-l-d+i}$$

(4)

where the inner sum is the probability that an offspring of a parent of degree l is born with degree d, and the outer sum takes the expectation over the degree distribution. Equation (3) is of an approximate nature, since it assumes that death and birth events are uncorrelated between different degrees. Our simulations suggest that the approximation is good except in very dense networks. Setting equation (3) equal to zero for all d and solving the resulting N equations, we can obtain the stationary degree distribution. We were unable to obtain closed-form solutions to the stationary distribution, but numerical solutions display good agreement with simulation results (see Figure 3). It is worth noting that although the p_k^+ and p_k^- terms are similar to models of preferential attachment with constant network size (e.g. Moore et al., 2006), these models assume that each new addition to the network has exactly the same degree, whereas in our model, the number of links of a newborn is distributed according to equation (4). Furthermore, the degree distribution does not capture the clustering behavior of preferential attachment models, which generate much less clustering than our model for a similar mean degree (results not shown), consistent with results in growing networks (Jackson and Rogers, 2007).

2.3   Data

We compared the output of our model with observed animal social networks of four different species. For this analysis we used data from published studies of spotted hyena (*Crocuta crocuta* (Ilany et al., 2015)), rock hyrax (*Procavia capensis* (Ilany et al., 2013)), bottlenose dolphin (*Tursiops*

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spp. (Lusseau et al., 2003)), and sleepy lizard (*Tiliqua rugosa* (Bull et al., 2012)).

The Hyena social network was obtained from one of the binary networks analyzed by (Ilany et al., 2015), where details on social network construction can be found. Briefly, the network is derived from association indexes based on social proximity in a spotted hyena clan in Maasai Mara Natural Reserve, Kenya, over one full year (1997). Similarly, the hyrax network was described by (Ilany et al., 2013), and is based on affiliative interactions in a rock hyrax population in the Ein Gedi Nature Reserve, Israel, during a five-months field season (2009). The dolphin network was published in (Lusseau et al., 2003), and is based on spatial proximity. The lizard social network was published by (Bull et al., 2012), and is also based on spatial proximity, measured using GPS collars. To get a binary network, we filtered this network to retain only social bonds with association index above the 75% quartile.

2.4   Network measures

To study the networks produced by our model and compare them to observed networks, we used a number of commonly used network measures. Network density is defined as $D = \frac{T}{N(N-1)}$ where T is the number of ties (edges) and N the number of nodes. The global clustering coefficient is based on triplets of nodes. A triplet includes three nodes that are connected by either two (open triplet) or three (closed triplet) undirected ties. Measuring the clustering in the whole network, the global clustering coefficient is defined as

$$C = \frac{\text{closed triplets}}{\text{triplets}} \tag{5}$$

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The local clustering coefficient measures the clustering of each node:

$$C_i = \frac{\text{number of edges among node i's contacts}}{\text{number of possible ties among node i's contacts}} \tag{6}$$

The betweenness centrality of a node v is given by

$$g(v) = \frac{2 \sum\limits_{s \neq v \neq t} \frac{\sigma_{st}(v)}{\sigma_{st}}}{(N-1)(N-2)} \tag{7}$$

where σ_{st} is the total number of shortest paths from node s to node t and $\sigma_{st}(v)$ is the number of those paths that pass through v.

Finally, we used modularity to measure the strength of a division of the networks into modules, also called groups or communities. The modularity of a given partition to c modules is

$$Q = \sum_{i=1}^{c} (e_{ij} - a_i^2) \tag{8}$$

where e_{ij} is the fraction of edges connecting nodes in two different modules, and a_i^2 is the fraction of edges connecting nodes in the same module. We computed network modularity for partitions given by the walktrap community detection method (Pons and Latapy, 2005).

3   Results

We simulated social network dynamics to test how social inheritance and stochastic social bonding affect network structure, heritability, and assortativity. For all of our results, we assume $p_b = 1$. As expected, the network density (the number of edges out of all possible edges) depends on p_n and p_r. The global clustering coefficient, a measure of the extent to which nodes tend to cluster together, also depends on these parameters, but not mono-
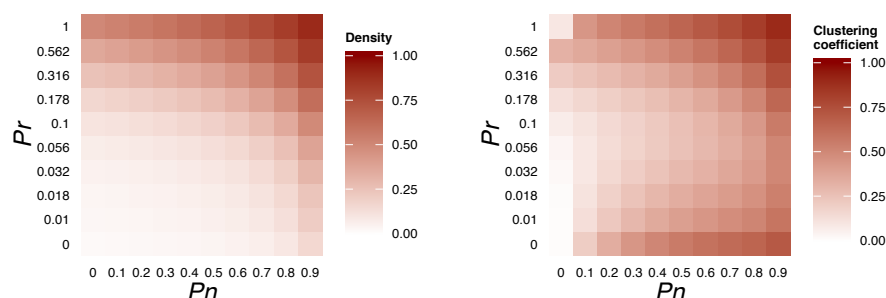
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Figure 2: The dependency of social network density and clustering coefficient on social inheritance, p_n, and probability of random bonding, p_r. Parameter values: simulation steps=2000, $N = 100$.

tonically; high levels of clustering were observed in simulations with low or high p_r, but not at intermediate levels (Fig. 2). We also tested how changes in network size affected its properties. These tests did not provide a general conclusion, suggesting that the network structure might be sensitive to its size in some cases (see Supporting Information).

We then compared the output of our model with observed animal social networks of four different species. We found species-specific values of p_n and p_r that could generate networks similar to those observed with respect to the degree and local clustering coefficient distributions, as well as the network modularity. Figure 3 illustrates that our model of social inheritance can produce networks with realistic social structure. In particular, the good match of local clustering distributions is an advance over network growth models based on preferential attachment (Jackson and Rogers, 2007). Furthermore, our model generated networks with realistic modularity values (see SI, figure S4). The values we found suggest that social inheritance is stronger in hyena and hyrax than in dolphins and sleepy lizards (Table 1). We also solved for the stationary distribution of the mean-field dynamics of the degree distributions (Figure 3).
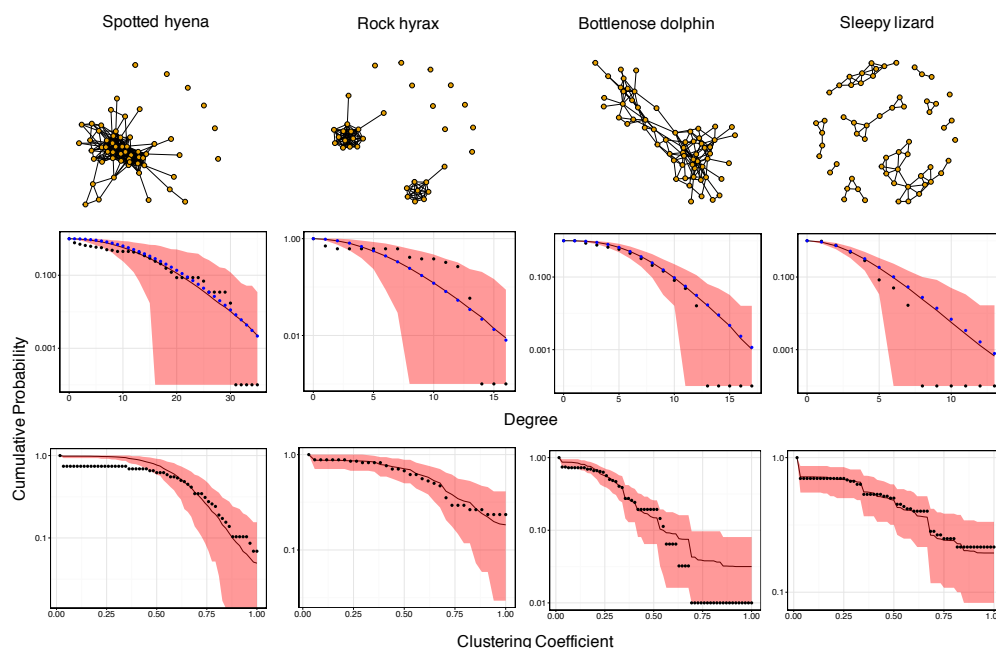
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Figure 3: Comparing model output to networks of four species. Upper row: observed networks. Middle row: Cumulative degree distributions of observed and simulated networks. Lower row: Cumulative clustering coefficient distributions of observed and simulated networks. Black dots represent observed values. Blue dots depict mean-field estimation (available only for degree distribution). Red line notes mean values for 500 simulated networks with the same species-specific p_n and p_r values (given in Table 1), whereas light red area depicts 95% confidence intervals.

Species	p_n	p_r
Spotted hyena	0.90	0.010
Rock hyrax	0.80	0.009
Bottlenose dolphin	0.53	0.033
Sleepy lizard	0.57	0.005

Table 1: Parameter values used in the simulations for each species in Figure 3.

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Next, we tested if social inheritance can generate heritability of indirect network traits in social networks. Direct network traits, such as degree, will by definition be heritable when p_n is high and p_r low. To see if this also holds for emergent network traits, we measured the correlation between parent and offspring betweenness centrality for a set of social inheritance (p_n) values. As Fig. 4 shows, high probability of social inheritance (when $p_n > 0.5$) results in a pattern of heritability. In other words, when individuals are likely to copy their parents in forming social associations, the resulting network will suggest heritability of centrality traits, although the only heritability programmed into the model is that of social inheritance and stochastic bonding. Similar patterns obtain for local clustering coefficient and eigenvalue centrality (results not shown).

Finally, we tested the effect of social inheritance on assortativity, i.e. the preference of individuals to bond with others with similar traits. We simulated networks where each individual had one trait with an arbitrary value between 0 and 1. Newborns inherited their mother's trait with probability $1 - \mu$, where μ is the mutation rate. Individuals followed the same rules of the basic model when forming social bonds. Hence, individuals did not explicitly prefer to bond with others with the same trait value. Nevertheless, the rate of assortativity was significantly higher than in random networks, in which the trait values were re-assigned randomly (Figure 5).

As an alternative model generating assortativity, we considered an explicit assortativity model, in which newborns explicitly prefer bonding with those with similar traits. Although this model generated networks with high assortativity, as expected, it failed to reconstruct other important features of observed networks, such as high clustering and modularity (Supporting Information, figures S5 and S6). This result further suggests that although assortativity is a feature of observed networks, in some cases it is probably a byproduct of social inheritance rather than a driving force of social network structure.
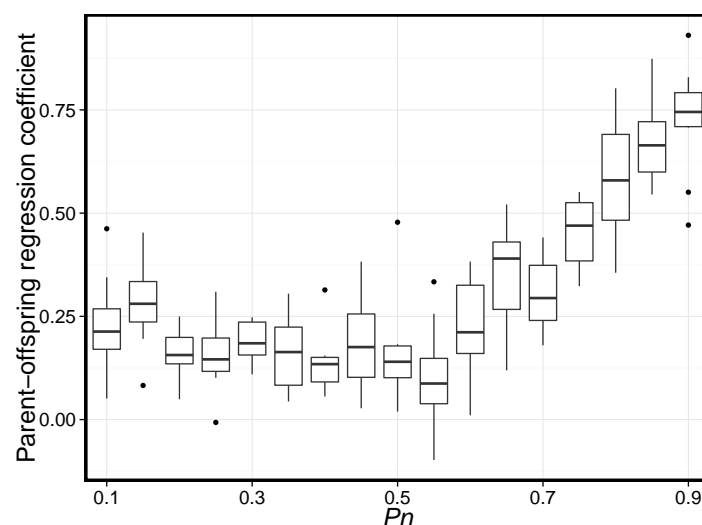
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Figure 4: The regression of betweenness centrality among parents and their offspring as a function of the strength of social inheritance (p_n). The bottom and top of the box mark the first and third quartiles. The upper whisker extends from the hinge to the highest value that is within 1.5*IQR of the hinge, where IQR is the inter-quartile range, or distance between the first and third quartiles. The lower whisker extends from the hinge to the lowest value within 1.5*IQR of the hinge. Data beyond the end of the whiskers are outliers and plotted as points. Ten replications were run for each p_n value. Parameter values: simulation steps=2000, $N = 100$, $p_r = 0.01$.
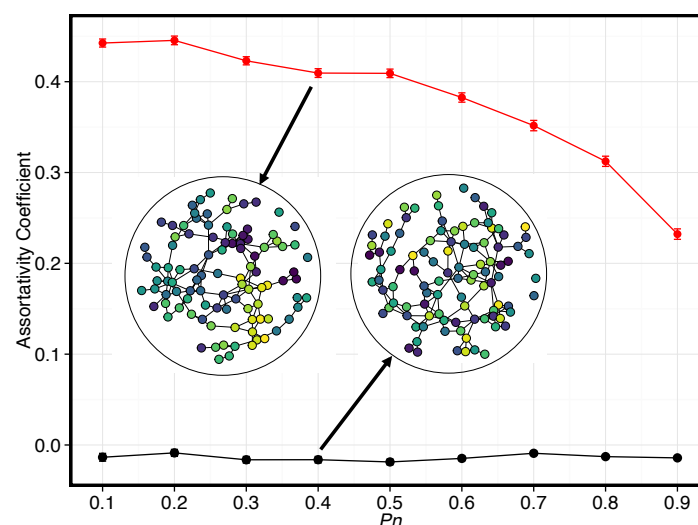
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Figure 5: Illustration of assortativity without explicit assortative preference. Dots and notches note assortativity coefficients and standard errors, respectively, for model networks (red), and shuffled networks, where trait values were reassigned randomly. Inset networks illustrate examples from the two groups. Circle colors represent arbitrary continuous trait values. Lines represent social bonds between individuals. Parameter values are the same as in 4, with mutation probability $\mu = 0.05$

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4   Discussion

Our model provides a step towards a general theory of social structure in animals, and incorporates two main processes shaping social networks: 1) demography, which influences social structure as individuals gain contacts when others join the population and lose contacts when individuals die or leave; 2) "social inheritance" of connections, where individuals are more likely to bond with individuals already connected to their parents than to the rest of the population. This second process is crucial to the formation of cohesive clusters in social networks. Notably, social inheritance usually depends on the mother-offspring unit, long viewed as the base of social structure (Kummer, 1971). We showed that in four different species it is possible to identify parameter values to generate networks that are similar in structure to the observed social networks, with respect to both the degree distribution and modularity, and markedly also the clustering coefficient distribution, in contrast to most studies of social network formation.

Clustering is an important feature of social networks, that distinguishes them from other types of networks, such as transportation networks and the internet Newman and Park (2003). Theory predicts that clustered networks are more conducive to cooperation (Cavaliere et al., 2012), and empirical studies document a tendency to close triads (Ilany et al., 2013, 2015), suggesting that it might be a generally adaptive feature of social structure. Nevertheless, most previous models of sociality and network formation do not explicitly account for clustering. For example, whereas preferential attachment can reconstruct the degree distribution of social networks, it fails to reconstruct their high degree of clustering (Jackson and Rogers, 2007).

Our work shows that clustering can result from social inheritance, which requires a behavioral mechanism that facilitates introduction of newborns to their mother's social partners. As in many species young individuals tend to follow their mothers, it is easy to think about such a passive mechanism: young individuals are introduced to other individuals by spend-

ing time with their mother's partners. Moreover, in many species group members show active interest in newborns (Kinnaird, 1990), promoting the initiation of a social bond between newborns and their mother's partners. Further work could test if initial interest in newborns later translates to stronger social bonds with individuals reaching adulthood.

Our model makes a number of simplifying assumptions such as no individual heterogeneity, or age- or stage-structure in our demography. We also do not treat sex-specific dispersal, a mechanism that results in different social environments for the two sexes. We do not argue that these assumptions necessarily hold in nature. However, we argue the fact that we can produce realistic-looking networks using this very simple model indicates that the social inheritance of connections is likely to be an important factor structuring social networks. Our model can therefore serve as a departure point to test the effect of additional factors. For example, after fitting the model to an observed social network, one could test whether personality can explain the variance not explained by social inheritance and stochasticity. This can be attained by adding personality to the agent-based model as a factor that influences individual bonding decisions.

Our model also has implications for how positions in social networks can be inherited, which has important implications for social dynamics. For example, Fowler et al. (2009) found that in humans, network traits such as degree and transitivity were heritable. In non-human primates, it was suggested that indirect network traits such as betweenness are more heritable than direct ones in rhesus macaques, (*Macaca mulatta*, Brent et al., 2013). In contrast, a study of yellow-bellied marmots, *Marmota flaviventris*, presented evidence for heritability of social network measures based on direct interactions (Lea et al., 2010), but not indirect interactions. Taken together, these studies suggest network position can be heritable, but have not been able to elucidate the mechanism of inheritance. Our model suggests that much of the inheritance of network position might be social (as

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opposed to genetic), from individuals copying their parents (or other role models). Therefore, studies aiming to get at genetic inheritance specifically need to control for social inheritance.

Another robust finding in network science and animal behavior is that individuals tend to connect to others with traits similar to themselves (e.g., (Croft et al., 2005; Lusseau and Newman, 2004; Wolf et al., 2007)). This assortativity is crucial for social evolutionary theory, as the costs and benefits of social interactions depend on partner phenotypes. Nevertheless, recent work (Xie et al., 2015) has found that assortative mating can arise without assortative preferences, as a result of dynamic processes in a closed system. Our model provides another general mechanism, social inheritance, that can lead to high assortativity in the absence of explicitly assortative preferences for social bonding. Indeed, an alternative model based on explicit assortativity failed to reconstruct topological features of observed networks. Empirically, our results call for a careful assessment of networks with apparent phenotypic assortment, and controlling for social inheritance. This will be difficult to do with only static network data, but will be feasible for species with long-term data on the network dynamics.

There are several interesting avenues to be explored in future research. First, we used binary networks to describe the strength of social bonds that are inherently on a continuous scale (Croft et al., 2011; Farine, 2014). Whereas our model could generate networks similar in structure to observed networks, weighted networks that can describe the delicate differences in the strength of social bonds between individuals would be more relevant in some cases. It would be straightforward to replace our binary bond generation with a distribution of bond strength though that will come at the cost of additional model complexity and parameters. Therefore, such an extension might be best attempted in conjunction with a more mechanistic approach to how social bonds are formed and maintained. Second, even though our model is extremely simplistic, most of its mathemat-

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ical properties (including probability distributions over network measures such as the degree distribution) are analytically intractable, which makes model-fitting a challenge. Methods such as approximate bayesian computation (Marjoram et al., 2003), coupled with dimensionality reduction techniques (Wegmann et al., 2009) can be used to develop algorithms for estimating parameters of the model and also incorporate more information about individual variation and environmental effects. Additionally, long-term datasets on social network dynamics can allow estimation of the social inheritance and random bonding parameters p_n and p_r directly. Lastly, our model does not consider changes in social bonds after these were established. Although this assumption is supported by empirical findings concerning bond stability in some species (Ilany et al., 2015; Shizuka et al., 2014), future models in which this assumption is relaxed should be developed. We also assume a single type of bond between individuals, whereas in nature, different social networks exist for different kinds of interactions (e.g., affiliative, agonistic, etc.). Such "multiplex networks" represent an important future direction.

In conclusion, the theory we present here is based on the idea that any snapshot of a social network should be regarded and analyzed as the result of a dynamic process (Pinter-Wollman et al., 2014). A social network is emergent in its nature, and its structure depends on environmental, individual, and structural effects (Ilany et al., 2015) and as such, it can only be understood in the context of past events, within a demographic framework.

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Supporting Information

SI 1   The effect of varying network size

Population size might influence social structure in unknown ways. To test how changes in population size affect the resulting network, we simulated networks that grow or shrink in size. We then compared measures of the networks to those of stable networks, where the network size was kept constant. In a shrinking network model, we started the simulation with 200 individuals and ran it for the first 1000 time steps as a constant size network (one born and one dead at each time step). After 1000 steps we set the probability of each individual to die at any time step at 0.05, corresponding to an expected mortality of 10 individuals per time step initially. We kept the number of individuals born at each time step at one. We kept running the simulation until population size fell to 100 individuals, and compared network characteristics to a parallel simulation where the population size started out with $N = 100$ and held constant throughout. Similarly, in a growth model we started with 100 individuals for the first 1000 steps, and then changed the probability of each individual to die at a given time step to 0.001 (instead of 0.01 in a stable network size). We stopped the simulation when the network size increased to 200. Again, we compared these networks to networks that started out with $N = 200$ were kept constant throughout. We present results for two series of parameter sets: 1. the four sets of parameter values, as fitted to the four species we tested (see Table 1). 2. Another 15 parameter sets, where p_n varied between 0.5 and 0.9 (5 values) and p_r was one of 0.01, 0.05, and 0.1. For each parameter set, we ran 100 replicate pairs of shrinking (or growing) and constant size networks. Tables S1 and S2 compare the network measures of stable to shrinking and growing networks, respectively, for the sets of fitted values.

 The effect of shrinking the network size was not consistent for all pa-

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Network density

Parameter set	Mean±SD for stable N	Mean±SD for shrinking N
Hyena	0.084 ± 0.022	0.092 ± 0.013
Hyrax	0.041 ± 0.009	0.049 ± 0.007
Dolphin	0.065 ± 0.006	0.066 ± 0.005
Lizard	0.011 ± 0.003	0.012 ± 0.002

Clustering coefficient

Parameter set	Mean±SD for stable N	Mean±SD for shrinking N
Hyena	0.092 ± 0.043	0.092 ± 0.026
Hyrax	0.054 ± 0.036	0.054 ± 0.022
Dolphin	0.073 ± 0.015	0.069 ± 0.013
Lizard	0.021 ± 0.040	0.016 ± 0.030

Modularity

| Parameter set	Mean±SD for stable N	Mean±SD for shrinking N
Hyena	0.381 ± 0.095	0.348 ± 0.046
Hyrax	0.524 ± 0.068	0.458 ± 0.049
Dolphin	0.339 ± 0.027	0.326 ± 0.025
Lizard	0.773 ± 0.062	0.776 ± 0.056

SI Table 1: Network measures of simulated networks, comparing simulations of constant network size to those with shrinking networks. Parameter sets indicate the values of p_n and p_r used, taken from Table 1. Clustering coefficient is the global clustering coefficient. P values were calculated from t tests.

Network density

Parameter set	Mean±SD for stable N	Mean±SD for growing N
Hyena	0.089 ± 0.012	0.086 ± 0.019
Hyrax	0.043 ± 0.005	0.043 ± 0.008
Dolphin	0.065 ± 0.003	0.065 ± 0.003
Lizard	0.011 ± 0.001	0.012 ± 0.002

Clustering coefficient

Parameter set	Mean±SD for stable N	Mean±SD for growing N
Hyena	0.097 ± 0.022	0.098 ± 0.033
Hyrax	0.050 ± 0.015	0.055 ± 0.024
Dolphin	0.070 ± 0.006	0.071 ± 0.007
Lizard	0.015 ± 0.013	0.018 ± 0.016

Modularity

| Parameter set	Mean±SD for stable N	Mean±SD for growing N
Hyena	0.292 ± 0.060	0.313 ± 0.098
Hyrax	0.407 ± 0.034	0.432 ± 0.050
Dolphin	0.238 ± 0.013	0.245 ± 0.014
Lizard	0.681 ± 0.041	0.679 ± 0.050

SI Table 2: Network measures of simulated networks, comparing simulations of constant network size to those with growing networks. Parameter sets indicate the values of p_n and p_r used, taken from Table 1. Clustering coefficient is the global clustering coefficient. P values were calculated from t tests.
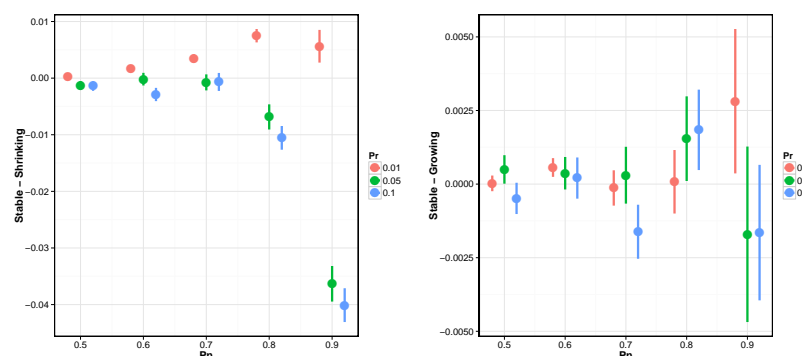
SI Figure 1: The difference in network density of simulated networks from our model between stable and shrinking (left) or growing (right) networks. Points and lines represent the mean difference and standard error, respectively
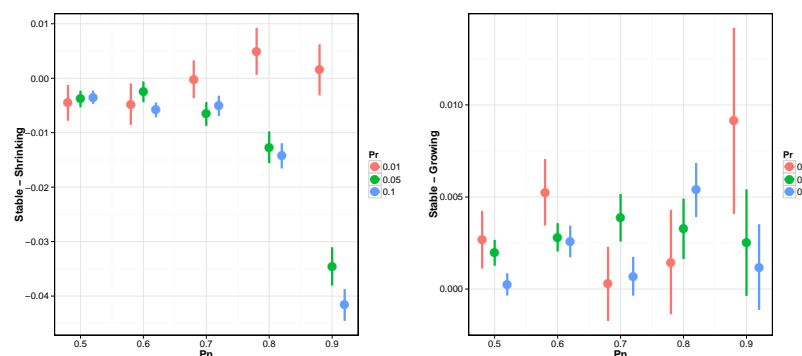

SI Figure 2: The difference in global clustering coefficient of simulated networks from our model between stable and shrinking (left) or growing (right) networks. Points and lines represent the mean difference and standard error, respectively.
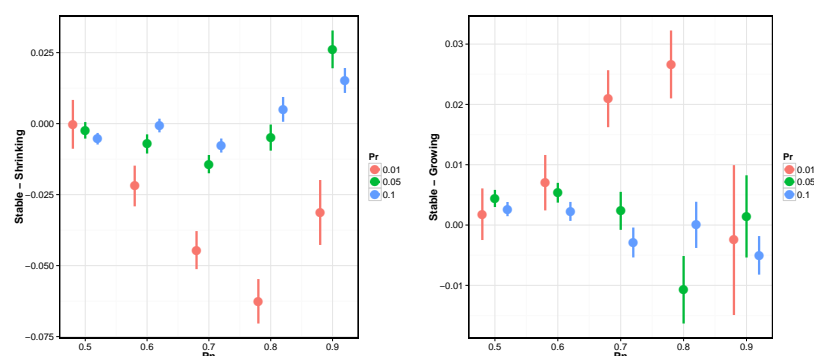
SI Figure 3: The difference in network modularity of simulated networks from our model between stable and shrinking (left) or growing (right) networks. Points and lines represent the mean difference and standard error, respectively.

rameter sets. Nevertheless, shrinking networks tended to be denser in ties and less modular than networks of constant size for low p_r. In a similar fashion, the effect of growing network size was not consistent for all parameter sets.

We conclude that the effect of changes in population size on network structure is unpredictable, and depends on the bonding probabilities. Future work should explore many interesting questions about the interaction of population size and social structure.

SI 2   Modularity of model networks

Social networks feature higher modularity than random networks. That is, social networks can usually be partitioned into subgroups of individuals (communities in network jargon), more densely connected within than between those subgroups. To test another aspect of our model, we calculated the modularity of simulated networks after identifying the community (subgroup) structure. Modularity measures the strength of division

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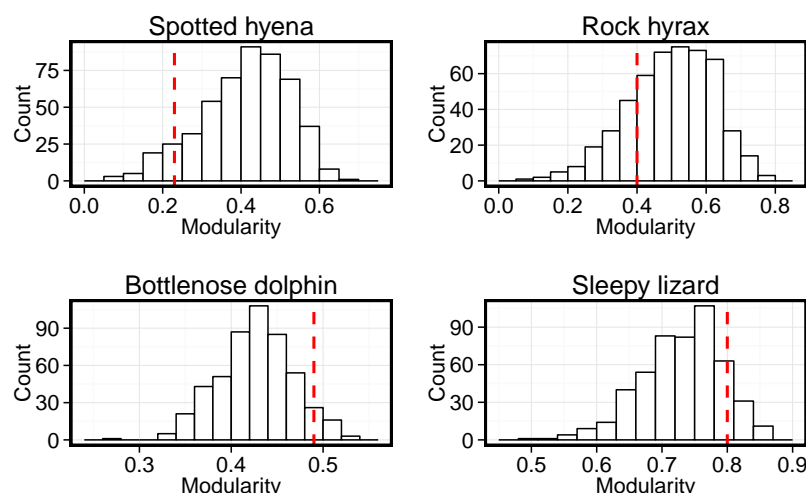
SI Figure 4: The network modularity of simulated networks from our model (distribution), compared to modularity of observed networks (red line). Modularity was calculated after partitioning the network to communities using the Walktrap algorithm. In all four species, the observed modularity could be generated by the model, i.e. was not an outlier.

into communities, where high modularity indicates dense connection between individuals within communities and sparse connections between individuals across communities. We used the Walktrap community finding algorithm, based on the idea that short random walks on a network tend to stay in the same community (Pons and Latapy, 2005). In all four tested networks (see main text), the modularity of the observed network was not an outlier in the distribution of modularity values of simulated networks. Thus, we could not reject the null hypothesis that the observed network belongs to the family of simulated networks, when considering their modularity (Figure S4).

SI 3   An alternative assortativity model

We constructed an alternative model of social network dynamics, focused on preference to form social bonds with other individuals with similar traits. The purpose of this model is to test the notion that explicit assortativity is the main factor determining network structure, as suggested empirically in various species. In this alternative model, newborns still bond their mother with probability p_b, but then form bonds with all others with probability proportional to the similarity of an arbitrary trait value. The trait is inherited from the mother in the same manner as in the main model (see main text). Specifically, the probability of a new born to connect with any other individual was defined as $\frac{e^x - e^{(-1)}}{3}$, where x is the absolute difference in trait values of the newborn and a candidate individual. This term ensures the connection probability to be in a realistic range, resulting in networks with similar density to the mean density of the four observed networks (0.123, see main text).

Unsurprisingly, simulations of the explicit assortativity model (2000 time steps, 100 individuals, 500 repeats) resulted in networks with high assortativity (Figure S5). However, the resulting networks failed to reconstruct other important topological features of the observed networks, namely the global clustering coefficient and modularity. The only exception was the spotted hyena, where modularity values, but not global clustering coefficient, matched modularity levels of the explicit assortativity model.

To conclude, a model of social structure where individuals base their social bonding almost exclusively on assortativity fails to reconstruct the topological features of observed networks in the tested species.
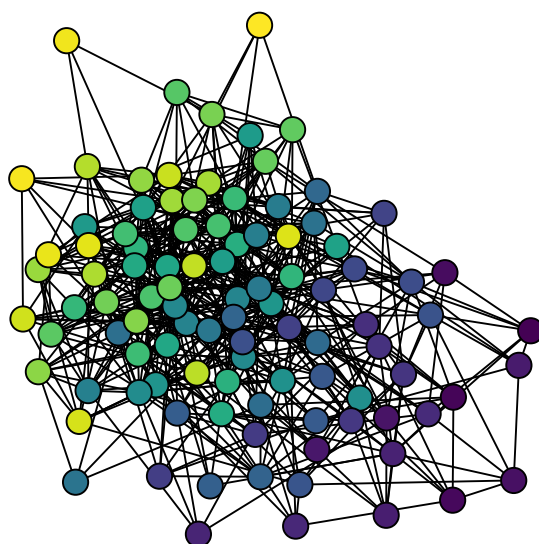
SI Figure 5: An example of a social network resulting from the explicit assortativity model, in which newborns are more likely to connect with similar individuals. Colors represent the values of an arbitrary trait, considered when forming bonds. See test for model definition and simulation parameters.
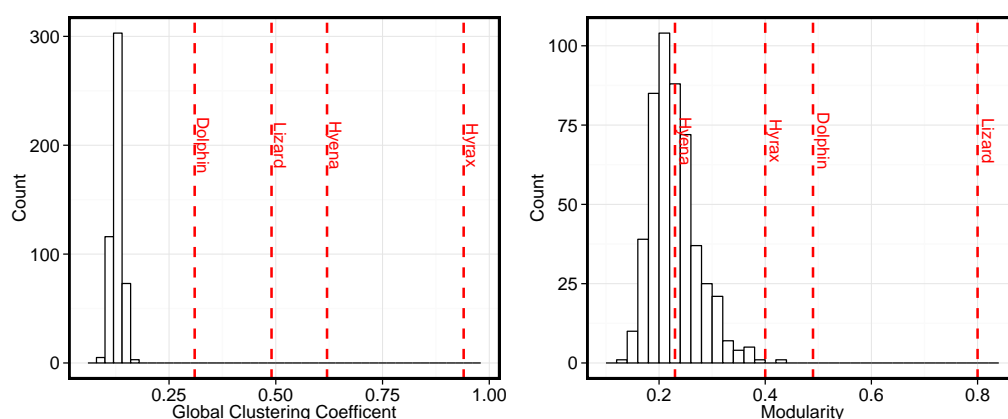
SI Figure 6: A comparison of the global clustering coefficient and modularity of 500 networks resulting from the explicit assortativity model (see text for details) to the values of observed networks of four species. Distributions show value of network measures for model networks. Red line show values for observed networks. The global clustering coefficient of all model networks is much lower than that of observed networks. Similarly, the modularity of model networks is lower than observed networks, except for the spotted hyena.

SI 4   Fitting the model to data

## SI 4.1   Partial least square regression

To obtain estimates of parameter values p_n and p_r from observed network, we used a dimensionality reduction approach that incorporates information about degree and local clustering distributions from the observed networks. For each empirically observed network, we ran the model with 10000 random values of p_n and p_r between 0 and 1, and the network size was set to match the observed network. We then used partial least squares regression, using the R package *pls* (version 2.4-3), to obtain a regression of the network degree and clustering coefficient distributions on p_n and p_r. Based on the regression formula, we predicted the values of p_n and p_r. The values predicted by the regression were sufficient to simulate networks that were usually close in their degree and clustering coefficient distributions to the observed network, but manual refinement was required in some cases to achieve better fit. The values given in Table 1 are the result of the manual refinement. They are meant to demonstrate the ability of the model to generate realistic looking networks, and do not constitute a real fitting of the model to data.

To verify the usage of partial least squares (PLS) regression to fit our model to observed networks, we simulated networks using known parameter values and tested the predictions of PLS regression. Specifically, we simulated 10,000 networks from our basic model over 2000 time steps, using random P_n and P_r values. We then used PLS regression to fit the degrees and clustering coefficients to parameter values. We then simulated set of 100 networks each using a given set of parameter values ($P_n = 0.6$ to 0.9, $P_r = 0.014$) and checked whether the PLS regression fit could predict those values. For example, in SI Figure 7 we plot the distribution of predicted P_n and P_r values compared to the real values used to simulate the networks. SI Figure 8 shows the distribution of predictions for ten different
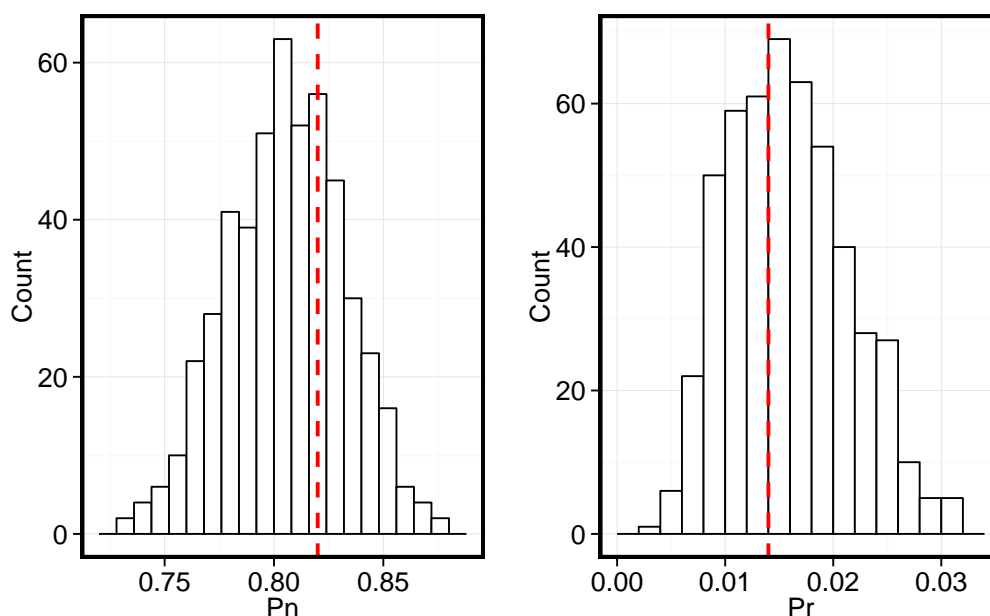
SI Figure 7: Example of how PLS regression predicts simulated network parameters. The distributions of predicted P_n (left) and P_r (right) values for 500 networks simulated using $P_n = 0.82, P_r = 0.014$ are plotted, along with the real values (red dashed line).

values of P_n, whereas P_r was fixed at 0.014.
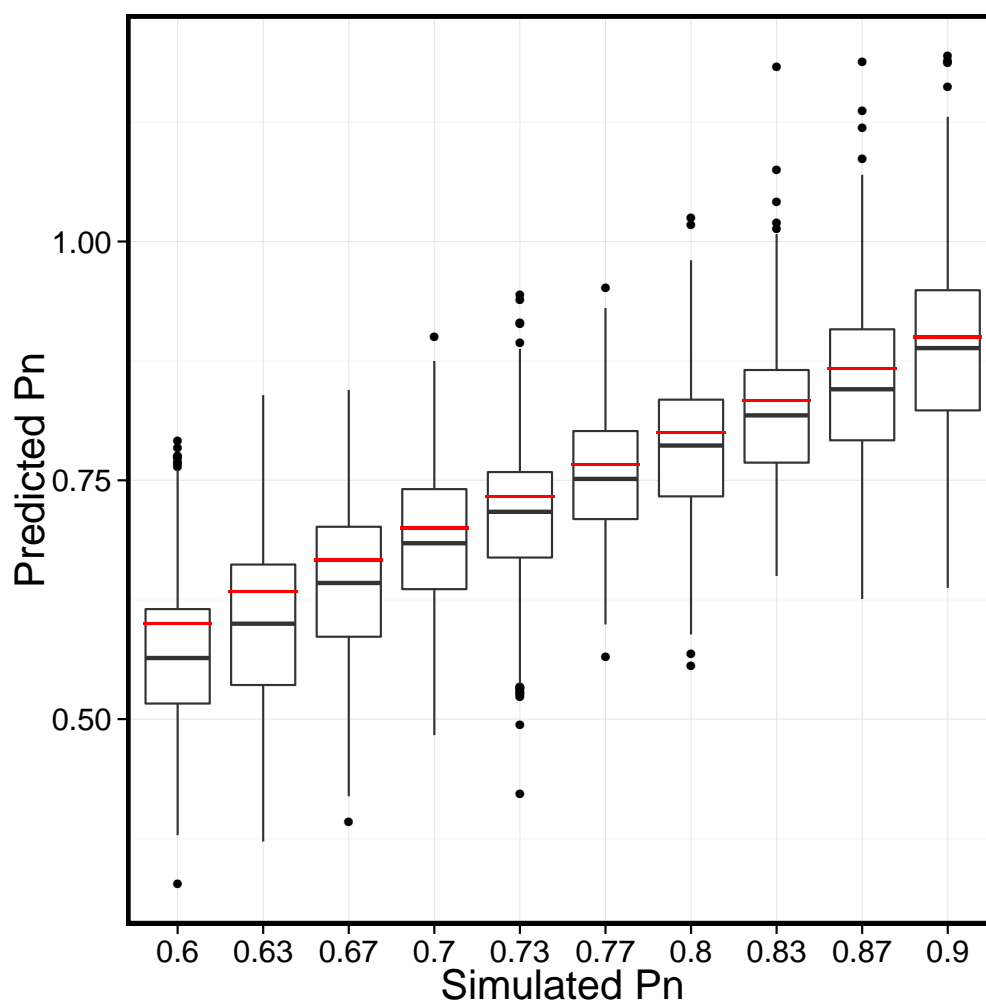
SI Figure 8: Distributions of predicted P_n values (box plot), compared to simulated values (red line). The predictions were generated after fitting a PLS regression to degrees and clustering coefficients of simulated networks. Thus, it is possible to predict the model parameter values when given an observed network.