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Abstract
The social network structure of animal populations has major implications to survival, reproductive success, sexual selection, and pathogen transmission. Recent studies showed in various species that the structure of social networks and individuals' positions in it are influenced by individual traits such as sex, age, and social rank, and can be heritable between generations. 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 such a general model of social network structure. We consider the emergence of network structure as a result of two types of social bond formation: via 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 some of the observed properties of social networks, such as heritability of network position or assortative associations, can be understood as a consequence of social inheritance. Our results highlight the need to consider the dynamic processes that generate social structure in order to explain patterns of variation in social networks.

Disciplines
Animal Sciences | Behavior and Ethology | Biology | Evolution | Population Biology

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. Recent studies showed in various species that the structure of social networks and individuals' positions in it are influenced by individual traits such as sex, age, and social rank, and can be heritable between generations. 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 such a general model of social network structure. We consider the emergence of network structure as a result of two types of social bond formation: via 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 some of the observed properties of social networks, such as heritability of network position or assortative associations, can be understood as a consequence of social

inheritance. Our results highlight the need to consider the dynamic processes that generate social structure in order to explain patterns of variation in social networks.

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 [1] and survival [2, 3]. Sociality affects individual health and evolutionary fitness via multiple mechanisms in humans and other animals, including pathogen transmission [4–7] but also through promoting or hindering particular social behaviors [8–11]. Social bonds can both increase stress induced by competition [12], while at the same time providing buffer for individuals against stressors and their effects [13, 14]. The social structure of a population summarizes the social bonds of its members [15]. 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) [16]. The new interdisciplinary field of "Network Science" has provided 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 [17–20]. Furthermore, using SNA provided evidence for the effects of social structure on a range of phenomena, such as sexual selection [21] and cultural transmission [22, 23].

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 measurements, combined with increasingly detailed data ("reality mining" [24]) about social interactions in na-

ture, 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 influential efforts to model animal social network structure. Notably, Seyfarth [25] 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., 26] have been very influential in the study of social structure. 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.

A large body of theoretical work in network science aims to explain the general properties of social networks through simple models of how networks form. However, these models tend to focus either on networks with a fixed set of agents [e.g. 27, 28], or on boundlessly growing networks [e.g., 29, 30], with few exceptions [31, 32]. 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 [30], i.e., two individuals to be connected with each other if they are both connected to a third individual. Real-world human and animal networks exhibit significantly more clustering than random or preferential attachment models predict.

To overcome these limitations, we provide a general network formation model based on simple demographic and social processes. Despite

being extremely simplistic, we demonstrate that our model can generate networks that match both degree and local clustering distributions of real-world animal social networks 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.

1 A general model of social structure

We model social structure as a result of demographic processes (birth and death) and social processes, i.e. social inheritance and stochastic bond formation. Our departure point for this model is the model by Jackson and Rogers [30], which 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. 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 [31]. 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 many reptiles, 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

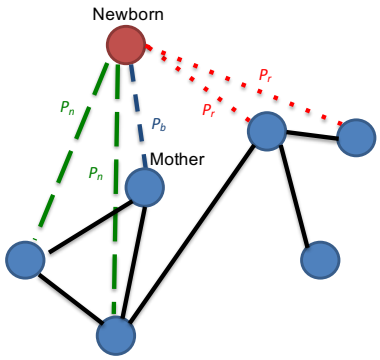

Figure 1: Graphical illustration of the model: a newborn individual is connected to its parent with probability p_b, to its parent's connections with probability p_n, and to individuals not directly connected to its parent with probability p_r.

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 [20, 33]. In the Supplementary Information (SI), we provide a mean-field approximation of the degree distribution of this model which shows an excellent fit with our simulations (see Figure 3).

2 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

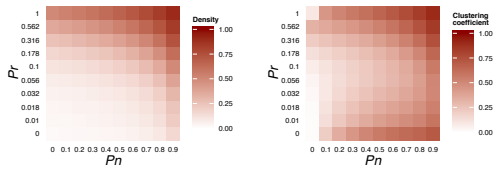

Figure 2: The dependency of social network density and clustering coefficient on social inheritance, p_n, and probability of random bonding, p_r. Parameter values: simulation steps=2000, $N = 100$.

tend to cluster together, also depends on these parameters, but not monotonically; high levels of clustering were observed in simulations with low or high p_r, but not at intermediate levels (Fig. 2).

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* [20]), rock hyrax (*Procavia capensis* [34]), bottlenose dolphin (*Tursiops* spp. [35]), and sleepy lizard (*Tiliqua rugosa* [36]). 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. 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 [30]. 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).

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

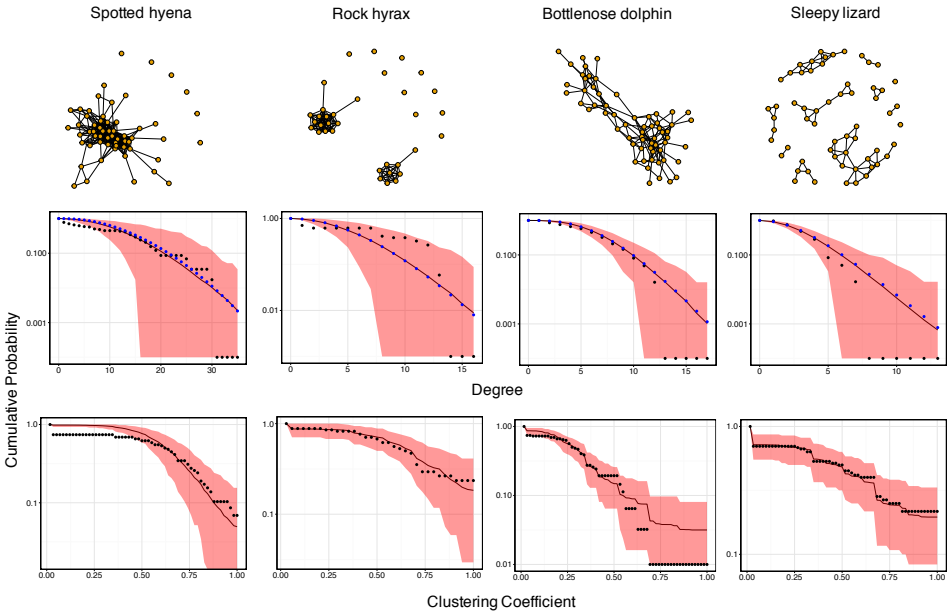

Figure 3: Comparing model output to networks of four species. Upper row: observed networks. Middle row: Cumulative degree distributions of observed and simulated networks. Lower row: Cumulative clustering coefficient distributions of observed and simulated networks. Black dots represent observed values. 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.

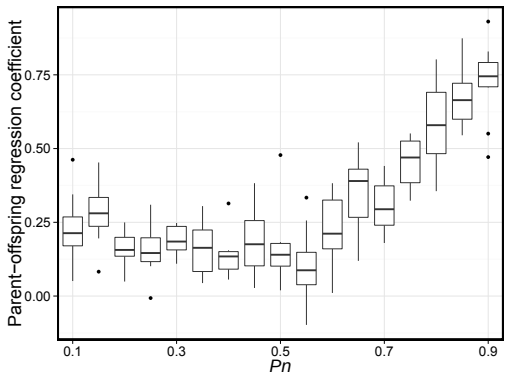

Figure 4: The regression of betweenness centrality among parents and their offspring as a function of the strength of social inheritance (p_n). The bottom and top of the box mark the first and third quartiles. The upper whisker extends from the hinge to the highest value that is within 1.5*IQR of the 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, $N = 100$, $p_r = 0.01$.

(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 ex-

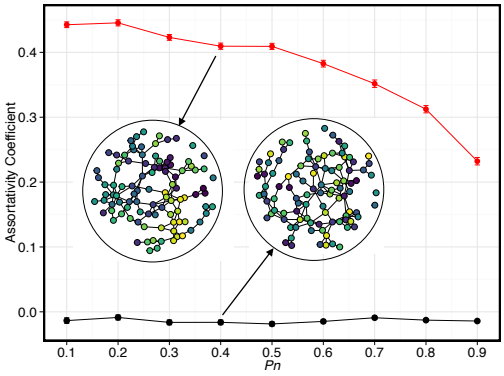

Figure 5: Illustration of assortativity without explicit assortative preference. Dots and notches note assortativity coefficients and standard errors, respectively, for model networks (red), and shuffled networks, where trait values were reassigned randomly. Inset networks illustrate examples from the 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 $\mu = 0.05$

plicitly 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).

3 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 [37]. 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 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 [38]. Theory predicts that clustered networks are more conducive to cooperation [39, 40], and empirical studies document a tendency to close triads [20, 34], 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 [30].

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 spending time with their mother's partners. Moreover, in some species current group members show active interest in newborns [41], 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 as-

sumptions actually 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. [42] 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* [43]. In contrast, a study of yellow-bellied marmots, *Marmota flaviventris*, presented evidence for heritability of social network measures based on direct interactions [44], 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 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., [45–47] for examples in animal behavior). This assortativity is crucial for social evolutionary theory, as the costs and benefits of social interactions depend on partner phenotypes. This is in line with other recent work [48] that 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. 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 future 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 [49, 50]. 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 mathematical 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 [51, 52], coupled with dimensionality reduction techniques [53] 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 [20, 54], 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 [55]. A social network is emergent in its nature, and its structure depends on environmental, individual, and structural effects [20] and as such, it can only be understood in the context of past events, within a demographic framework.

4 Methods

4.1 Data

The Hyena social network was obtained from one of the binary networks analyzed by [20], 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 [34], 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 [35], and is based on spatial proximity. The lizard social network was published by [36], 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.

4.2 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

$$C = \frac{\text{closed triplets}}{\text{triplets}} \tag{1}$$

The local clustering coefficient measures the clustering of each node:

$$C_i = \frac{\text{number of edges among node i's contacts}}{\text{number of possible ties among node i's contacts}} \tag{2}$$

The betweenness centrality of a node v is given by

$$g(v) = \frac{2 \sum_{s \neq v \neq t} \frac{\sigma_{st}(v)}{\sigma_{st}}}{(N-1)(N-2)} \tag{3}$$

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.

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Supplementary Information

SI 1 Mean-field approximation of the model

To characterize the expected dynamics of the degree distribution, consider a focal individual that has degree d at time period t. In period t+1, the probability that this individual increases its degree by one, p_d^+, is:

$$p_d^+ = \frac{(N-1-d)}{N} \frac{dp_n + (N-d-2)p_r + p_b}{N-1} \,. \tag{4}$$

The first fraction in (4) 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

$$p_d^- = \frac{d}{N}\left(1 - \frac{(d-1)p_n + (N-d)p_r + p_b}{N-1}\right), \tag{5}$$

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 [31]:

$$\frac{d\phi_d}{dt} = b_d(\boldsymbol{\phi}) + p_{d-1}^+ N\phi_{d-1} + p_{d+1}^- N\phi_{d+1} - (p_d^+ + p_d^-)N\phi_d - \phi_d\,, \tag{6}$$

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

$$b_d(\boldsymbol{\phi}) = \sum_{l=0}^{N-1} \phi_l \sum_{i=0}^{\mathrm{Min}(l,d-1)} \binom{l}{i} p_n^i (1-p_n)^{l-i} \binom{N-2-l}{d-1-i} p_r^{d-1-i} (1-p_r)^{N-1-l-d+i} \tag{7}$$

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 (6) is of an approximate nature, since it assumes that death and birth events are uncorrelated between different

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

degrees. Our simulations suggest that the approximation is good except in very dense networks. Setting equation (6) 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).