## Cooperation and the social brain hypothesis in primate social networks

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The social brain hypothesis states that the relative size of the neocortex is larger for species with higher social complexity as a result of evolution. Various lines of empirical evidence have supported the social brain hypothesis, including evidence from the structure of social networks. Social complexity may itself positively impact cooperation among individuals, which occurs across different animal taxa and is a key behavior for successful group living. Theoretical research has shown that particular structures of social networks foster cooperation more easily than others. Therefore, we hypothesized that species with a relatively large neocortex tend to form social networks that better enable cooperation. In the present study, we combine data on brain and body mass, data on social networks, and theory on the evolution of cooperation on networks to test this hypothesis in primates. We have found a positive effect of brain size on cooperation in social networks even after controlling for the effect of other structural properties of networks that are known to promote cooperation.

# I. INTRODUCTION

The social brain hypothesis posits that the relative size of the neocortex in the brain is positively correlated with social complexity [1]. The hypothesis has obtained quantitative support in terms of various indices of social complexity for primates and other taxa [2]. Social networks are a key aspect of social complexity [3–5]. In fact, various social network measures have been related to the social brain hypothesis. The original study in this area showed that group size is correlated with neocortex size in primates [6]. Further work demonstrated that the number of contacts an individual has, which is called the degree of the node in network analysis, is positively correlated with relative neocortex size in primate species [7] and the size of the amygdala and some other

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brain regions in human individuals [8–10]. Other network indices such as the so-called complexity of the network [8], edge connectivity and two-clans [11], and global efficiency [4] have also been shown to be correlated with the size of the neocortex [4, 11] or amygdala [8] of primates including humans.

Social networks have functions. Focusing on the animal kingdom, the structure of social networks affects, for example, the speed of diffusion of information and diseases, mating behavior, predator avoidance, communication efficiency, and group movement [4, 12–14]. However, social networks also have costs. For example, network structure determines disease transmission potential and epidemic outcomes in populations, because a pathogen can only spread if the relevant form of contact exists between two individuals. Networks with high degree heterogeneity (i.e. high variation in the number of contacts among individuals) have increased transmission potential due to the presence of superspreaders which cause rapid, explosive outbreaks of disease in a population [15]. Animal social networks that we observe today may therefore be a result of evolutionary processes in which more advantageous network structures have proliferated at the expense of less advantageous structures under restrictions imposed by the environment and trade-offs between different objectives.

One function for which social networks are particularly relevant is cooperation. Individuals of various animal species cooperate with each other, even cooperating with non-kin and in social dilemma situations in which non-cooperation is more lucrative than cooperation [16–19] (but see [20]). Although cooperation under social dilemmas is an evolutionary puzzle, theoretical research has suggested various mechanisms enabling cooperation [21, 22]. Network reciprocity, or the effect of the network structure, is one mechanism to promote cooperation [22–26]. Specifically, a relatively small node degree (i.e., the number of neighboring individuals per individual) [27, 28] and heterogeneity among individuals in the network in terms of the degree [29, 30] can both promote cooperation compared to well-mixed populations depending on the assumptions underlying the evolutionary process models.

In the present study, we extend the social brain hypothesis to the domain of cooperation. We ask whether species with a large neocortex size form social networks that foster cooperation to a greater extent than networks for other species. While cooperation occurs in various animal taxa [17, 19], here we focus on primates because neocortex data are available for many primate species and various indices that correlate with neocortex size have been documented for primates, as we reviewed above. Recently developed mathematical theory enables us to quantify the ease of cooperation for networks with arbitrary structure [28]. We use this theory and look for significant

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determinants of cooperation as a function of the neocortex size and other key properties of the network structure including those which are known to affect cooperation.

### II. METHODS

## A. Threshold benefit-to-cost ratio for cooperation

We assume a network with N nodes that is connected, undirected, and weighted. On the given network, we consider the gift-giving game, which is a simple variant of the prisoner's dilemma game. In the gift-giving game, one player, called the donor, decides whether or not to pay a cost  $c \ (> 0)$  to benefit another player, called the recipient. If the donor pays c, which we refer to as cooperation, then the recipient gains b (> c). If the donor does not, which we refer to as defection, then the recipient gains nothing. The donor receives a higher payoff by defecting than cooperating. However, the average payoff over the players in the network is larger when the donor cooperates rather than defects. We assume that the gift-giving game occurs twice on each edge of the network by swapping the roles of the donor and recipient in a single round of the evolutionary dynamics. The payoff of each player i in each round is given as the weighted average of the payoff that iobtains over all *i*'s neighbors, where the weight for averaging is proportional to the edge weight. For updating the strategy of the players in each round of evolutionary dynamics, we assume the death-birth process with selection on birth, which is known to foster cooperation under certain conditions [27, 28]. In the death-birth process with selection on birth, one first selects a node i to be replaced uniformly at random. Then, one selects a parent to reproduce with the probability proportional to its fitness among the neighbors of i. The fitness of each player is assumed to be linearly but only weakly depending on the payoff, which is the regime called the weak selection.

Under this setting, without mutation, all players will eventually become either cooperators (i.e., fixation of cooperation) or defectors (i.e., fixation of defection). We use the recently developed random-walk-based theory that enables one to calculate the fixation probability for cooperation for arbitrary network structure [28]. We assume that just one node, selected uniformly at random, is initially a cooperator and the other N - 1 nodes are defectors. If the fixation probability for cooperation [27, 28, 31]. Under the weak selection limit, Allen et al. showed the expression for the threshold benefit-to-cost ratio, denoted by  $(b/c)^*$ , such that the fixation probability for cooperation is larger than 1/N when  $b/c > (b/c)^*$ , i.e., Eq. (2) in Ref. [28]. If  $(b/c)^*$  is smaller, the network supports

cooperation more strongly because natural selection favors cooperation for relatively small values of b/c.

We calculated  $(b/c)^*$  for each network using our in-house code in Python 3.10, which implements the procedures described in [28].

## B. Data

The data for this study come from the Animal Social Network Repository (ASNR) [32, 33]. The ASNR contains 770 non-human social networks from eight animal classes and 69 species. For each network in this data set, nodes represent an individual animal. Edges represent a specific type of contact between two animals, such as grooming in primates and trophallaxis in ants, as well as more general contact such as group membership and spatial proximity.

There are 114 primate social networks in the ASNR, including 60 grooming networks, 31 spatial proximity networks, 10 mating networks, and 13 networks with other contact types. Most sampled populations are free-ranging (84), with some captive (18) and some semi-ranging (7) populations, as well as five populations for which the type was not recorded. There are 99 catarrhine primate networks, 13 platyrrhine networks, and 2 strepsirrhine networks. Sampling of the different contrasts represented in the ASNR is thus somewhat unbalanced but reflects the sampling effort present in the literature.

To test our hypothesis we require that, to the best extent possible, the edges represent prosocial contacts between individuals. Other contact types, such as dominance or mating, may reflect motives that are not relevant to the spread of cooperative behaviors, and proximity-based networks may reflect individuals who are co-located by chance or interest in a common resource rather than for social interaction. We therefore used the ASNR networks with the interaction types labeled "grooming", "physical contact", and "overall mix"; the "overall mix" category captures one additional network that recorded grooming behavior. We thus obtained 67 possible networks, which we regarded as undirected weighted networks.

Thirteen out of the 67 networks yielded negative  $(b/c)^*$  values, which imply that spiteful behavior evolves instead of cooperation [28, 34]. We discarded these networks because we are interested in cooperation under social dilemma situations. Additionally, we discarded one network that was composed of two disconnected dyads and used the remaining 53 connected networks for our analysis. Most species had a single network in the repository. The exceptions were *P. cynocephalus* (which had 23 networks), *M. fascicularis* (2), *M. fuscata* (4), *M. mulatta* (9), and *M. radiata* (2). For these species we took the median for  $(b/c)^*$  and for the network-based explanatory variables explained in Section II C to prevent a few species, such as *P. cynocephalus* and *M. mulatta*, from dominating the set of networks to be analyzed. In this manner, we reduced the 53 networks to observations on 17 species for further analysis.

We used the species-level neocortex ratio (NCR) estimate from [7] for all but one species, *Colobus guereza*; a species-level NCR estimate was not available in [7], so we used the genus-level NCR estimate from [6]. Additionally, we used the total brain mass and body mass data from [35] for all species except *Papio papio*, for which the data is not present. For *Papio papio*, we used the data of the closely related species *P. cynocephalus* [36]. We included brain and body size as simpler measures of species' anatomical and physiological complexity that may also correlate with sociality [37]. These three measures (i.e., brain mass, body mass, and NCR) are highly correlated with each other (see Section III).

### C. Analysis

Data analysis was conducted in R 4.2 [38]. We used the "MuMIn" package [39] to implement the model selection procedure described below. Code in R and Python to reproduce these analyses is available at https://github.com/ngmaclaren/cooperation-threshold.

We used generalized linear models (GLMs) to test whether NCR and other variables were associated with the ease of cooperation,  $(b/c)^*$ . We considered eight explanatory variables: NCR, brain mass in grams, body mass in grams, and five network indices some of which are known to influence  $(b/c)^*$ . The five network indices are the number of nodes in the network (denoted by N), the average degree over the N nodes (denoted by  $\langle k \rangle$ ), the average node strength (i.e., the average of the weighted degree over the N nodes), denoted by  $\langle s \rangle$ , the average clustering coefficient (denoted by C), i.e., the average over all nodes of the number of complete triangles divided by the number of possible triangles involving each node [40, 41], and the average weighted clustering coefficient (denoted by  $\tilde{C}_w$ ), which is calculated similarly to the unweighted version except that it uses the geometric mean of the edge weights instead of a count of edges [42]. Because brain mass, body mass,  $\langle s \rangle$ , and  $\tilde{C}_w$  are positive and obey right-skewed distributions, we used the natural logarithm transform of each of these variables.

We began our modeling process from a position of relative ignorance, including these eight explanatory variables as predictors. By design, our outcome variable,  $(b/c)^*$ , is positive and continuous, suggesting a model with gamma-distributed errors. To test our choice, we built five different models, each with all eight explanatory variables, with different error models and link functions (i.e., gamma and Gaussian distributions with both inverse and log links, and a quasi-Poisson model) and calculated the deviances of each [43]. As expected, the gamma models fit well  $(\chi^2 \text{ test with } d.f. = 8; p = 0.942 \text{ and } 0.986 \text{ for the inverse and log links, respectively}), whereas the$ other models did not (<math>p < 0.001 for each). The residual deviances associated with both gammabased models are small (inverse link: 2.87, log link: 1.81), further suggesting good fit [43]. We chose the inverse link because it is the canonical link function for the gamma distribution [43] and because it improves interpretability in this analysis.

The number of explanatory variables (i.e., eight) is relatively large given the number of observations (i.e., 17). Therefore, we evaluated all possible models with only up to five explanatory variables and calculated the AICc for each model. AICc is a modification of the Akaike Information Criterion (AIC) that is preferred for model selection when data sets are relatively small [44].

Because we use the inverse link function, a positive coefficient implies that the inverse of the outcome variable,  $(b/c)^*$ , increases as the explanatory variable increases. In other words, positive coefficients suggest that an increase in the explanatory variable decreases  $(b/c)^*$  on average, promoting cooperation in the network.

# III. RESULTS

There were 206 models, or combinations of the explanatory variables, with five or fewer explanatory variables for predicting  $(b/c)^*$ . We show the sorted AICc values for these models in Fig. 1. The three best models in terms of the AICc have similar AICc values compared to the other models, with  $\Delta$ AICc < 1, where  $\Delta$ AICc is the difference between the AICc for a model and that for the model minimizing the AICc. The fourth and fifth best models have  $\Delta$ AICc  $\approx 2$ . All the other models have  $\Delta$ AICc > 3, forming a series of models with few obvious cut-points until the poorest models. Therefore, we focus on the five models with  $\Delta$ AICc < 3; we show these five models in Table I.

Table I indicates that no model among the best five models has more than three explanatory variables. Therefore, adding more explanatory variables would not be useful in better explaining  $(b/c)^*$  across the different networks. The two network features, i.e., average degree and the weighted clustering coefficient, have consistently negative coefficients, with average degree appearing in each of the best five models and the weighted clustering coefficient appearing in all but one model. The present result that a smaller average degree promotes cooperation is consistent with the previous

Model 1	Coef.	SE	p
Intercept	-0.344	0.176	0.072
$\langle k  angle$	-0.009	0.003	0.020
$\ln(\tilde{C}_{\mathbf{w}})$	-0.057	0.025	0.043
$\ln(\text{Body mass})$	0.039	0.020	0.075
$\Delta AICc$	0.00		
Model 2	Coef.	SE	p
Intercept	-0.295	0.163	0.093
$\langle k  angle$	-0.008	0.003	0.020
$\ln(\tilde{C}_{\mathrm{w}})$	-0.059	0.025	0.036
$\ln(\text{Brain mass})$	0.064	0.036	0.095
$\Delta AICc$	0.13		
Model 3	Coef.	SE	p
Intercept	-0.201	0.127	0.137
$\langle k  angle$	-0.010	0.004	0.019
$\ln(\tilde{C}_{\rm w})$	-0.047	0.028	0.115
NCR	0.097	0.059	0.121
$\Delta AICc$	0.69		
Model 4	Coef.	SE	p
(Intercept)	-0.021	0.105	0.845
$\langle k  angle$	-0.009	0.004	0.055
$\ln(\tilde{C}_{\rm w})$	-0.067	0.040	0.114
$\Delta AICc$	1.83		
Model 5	Coef.	SE	p
(Intercept)	-0.182	0.124	0.165
$\langle k  angle$	-0.009	0.003	0.015
NCR	0.138	0.054	0.024
$\Delta AICc$	1.95		

TABLE I. The best five models, i.e., the models with  $\Delta AICc < 3$ . A positive coefficient suggests that variable is associated with a smaller  $(b/c)^*$ , i.e., easier evolution of cooperation. SE stands for the standard error. We remind that  $\langle k \rangle$  and  $\tilde{C}_w$  represent average degree and the weighted clustering coefficient, respectively.



FIG. 1. AICc for all possible GLMs with between zero and five explanatory variables.

findings [27, 28]. Body mass and brain mass, which are highly correlated with each other (with Pearson correlation coefficient r = 0.953), are each the third predictor in the best two models, which are nearly indistinguishable in terms of the AICc;  $\Delta$ AICc for Model 2 = 0.13. Compared to these best two models, the third best model uses NCR in place of body or brain mass as the third explanatory variable. Note that NCR is also highly correlated with body mass (r = 0.81) and brain mass (r = 0.84), partly because we are only analyzing primates. The fourth best model only contains the average degree and the weighted clustering coefficient. We note that the number of nodes N, average weighted degree  $\langle s \rangle$ , and the unweighted clustering coefficient C did not appear among the best five models.

In each of best five models in which a brain size variable (i.e., brain mass or NCR) appears (i.e., Models 2, 3, and 5), the coefficient for the brain size variable is positive. This result suggests that social networks for primates with a larger brain size tend to better accommodate cooperative behavior if the average degree and the clustering coefficient (i.e., abundance of triangles) are the same. We visualize this relationship in Fig. 2. However, formally, either brain mass or NCR only satisfies p < 0.05 for Model 5 (p = 0.024); brain mass and NCR yield p = 0.095 in Model 2 and p = 0.121 in Model 3, respectively. We visualize in Fig. 3 the coefficient values and associated 95% confidence intervals for each explanatory variable for each of the best five models. In Fig. 3, a circle's position and the span of the line segment in the horizontal direction indicate the value of the estimated coefficient and its 95% confidence interval, respectively. The figure shows that,



FIG. 2. Threshold for cooperation,  $(b/c)^*$ , as a function of the NCR for Model 3. Each circle represents a primate species. The solid line represents the predicted  $(b/c)^*$ . The dotted lines indicate twice the standard error of prediction.

although some 95% confidence intervals for the brain size variables include zero, the value and sign of the coefficient estimates are consistent, and the confidence intervals only marginally cross zero. As expected, the coefficients for the average degree and weighted clustering coefficient are consistently negative. We thus conclude that our data analysis provides evidence in favor of our hypothesis: brain size, measured in two different ways, is positively associated with the ease with which cooperation spreads in primate social networks, albeit not strongly.

## IV. DISCUSSION

Consistent with network reciprocity, animal social networks foster cooperation in terms of fixation probability [45]. Advancing this finding one step further, we found positive support for the social brain hypothesis in terms of network reciprocity in primates. In reaching our conclusion, we controlled for major network properties that affect cooperation, such as the average degree and the clustering coefficient, as well as the size of the entire group. We point out that the average degree, i.e., average number of others one individual contacts, is also a major outcome variable that the social brain hypothesis aims to explain in terms of brain size. Therefore, the present results are orthogonal to these previous ones. Exploration of network properties that covary with both brain



FIG. 3. Coefficient estimates for the best five models. The circles represent the coefficient values. The lines represent the 95% confidence intervals. NCR: neocortex ratio,  $\langle k \rangle$ : average degree,  $\tilde{C}_{w}$ : average weighted clustering coefficient.

size and  $(b/c)^*$  and finding generative mechanisms of such network properties warrant future work.

We found that the weighted clustering coefficient negatively contributes to evolution of cooperation and that the unweighted clustering coefficient does not have effect, at least for the best five models. This result is apparently inconsistent with spatial reciprocity, which dictates that high clustering in networks promotes cooperation [22, 46, 47]. In fact, these results have been derived for the fraction of cooperators in the quasi-stationary state of evolutionary dynamics in relatively large networks rather than the fixation probability for the cooperator strategy; we examined the latter quantity in this study. The effect of clustering on the fixation probability for cooperation is not systematically known. For example, some numerical simulations suggest that clustering, which is present in most empirical networks, does not facilitate the fixation of cooperation [27, 48]. Therefore, our results are in fact not contradictory to the known results for spatial reciprocity, and fixation of cooperation in clustered networks remains to be investigated.

Cooperative group living is often advantageous in the animal kingdom because it can provide protection from predators and increase the efficiency of foraging tactics [18, 49]. However, one of the most commonly cited disadvantages to cooperative group living is the increase in disease transmission potential [49, 50]. In fact, previous work suggests that the average degree is the most important aspect of network structure in determining the transmission potential for pathogens on a network [51]. Our results show that average degree is negatively associated with the evolution of cooperation, a finding supported by previous theoretical work [27]. Given that small average degrees are beneficial for both enhancing cooperation and reducing pathogen transmission opportunity, cooperation and protection against disease transmission potential might have coevolved through a decrease in the average degree of social networks. Maintaining contacts is also costly for individuals. However, a large average degree helps robustness of networks against node and edge failures [14, 52]. We may be able to further discussion of the evolution of network structure and social brain hypotheses by simultaneously taking into account multiple functions of animal society such as cooperation, protection against infection, robustness, and communication efficiency.

The present work also opens avenues for further work to explore intersection between social brain hypothesis, networks, and cooperation. Investigation of social networks of species other than primates is worthwhile. Additional study of important contrasts within the primates—such as between catarrhine and platyrrhine primates, or between captive and wild groups—can also be informative. We are also aware that most of the social networks we used are grooming networks. Network structure may vary according to the type of prosocial contact even for the same group of animals [51], which is worthy of investigation. Although further comparative work along these lines is currently limited by available data [32], various technological and algorithmic developments of automatic data collection [14, 53] are expected to allow us to access more data and explore these topics in a near future.

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