SCIENTIFIC REPORTS

OPEN

SUBJECT AREAS:
SOCIAL EVOLUTION
THEORETICAL ECOLOGY

Received
26 September 2013

Accepted
9 December 2013

Published
9 January 2014

Evolutionary Significance of the Role of Family Units in a Broader Social System

Bradford R. Greening, Jr.[1] & Nina H. Fefferman[1,2]

[1]Department of Ecology, Evolution, and Natural Resources, Rutgers University, 14 College Farm Road, 1st Floor, New Brunswick NJ 08901, USA, [2]DIMACS, Rutgers University, 96 Frelinghuysen Road, Piscataway NJ 08854, USA.

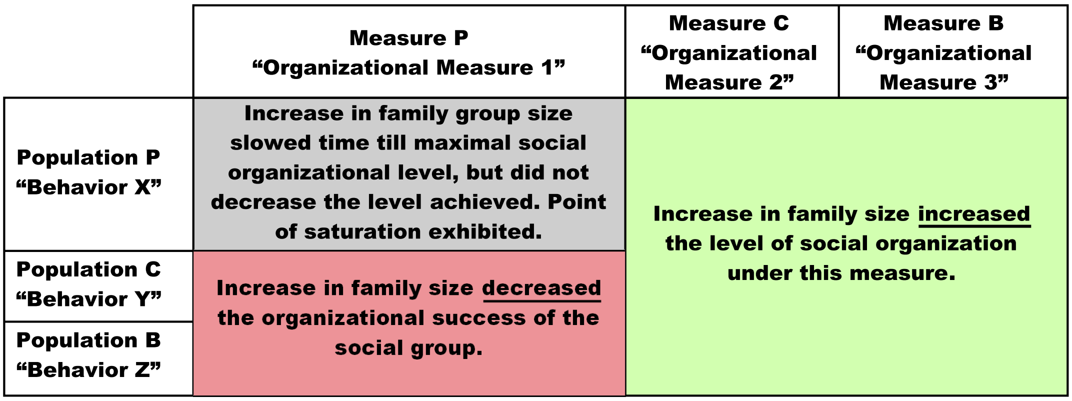
Correspondence and requests for materials should be addressed to B.R.G. (bgreening01@gmail.com) or N.H.F. (fefferman@aesop.rutgers.edu)

Indirect benefits to individual fitness in social species can be influenced by a variety of behavioral factors. Behaviors which support the fitness of kin provide indirect benefits in the form of evolutionary success of relatives. Further, individuals may obtain additional indirect benefits via participation in a well-organized social environment. Building on previous models of selfishly-motivated self-organizing societies, we explore the evolutionary trade-off between inclusion and maintenance of family groups and the ability of a population to sustain a well-organized social structure. Our results demonstrate that the interactions between Hamiltonian and organizationally-based indirect benefits to individual fitness interact to favor certain types of social affiliation traits. Conversely, we show how particular types of social affiliation dynamics may provide selective pressures to limit the size of behaviorally-defined familial groups. We present the first studies of the evolution of social complexity differentiating affiliation behavior between kin and non-kin.

Intra-population interactions among social animals are as nuanced as the diversity of systems in which they occur. These nuances may result from genetically determined behavior or behavioral plasticity in social choice, and can be influenced by external factors (e.g. seasonal changes in the environment) as well as factors internal to the population (e.g. competition for dominance). Examples from nature exhibit many multi-factored systems of determining social affiliation behaviors, such as those of the American bison (*Bison bison*), in which the males of a herd form bachelor groups featuring linear dominance hierarchies during non-mating seasons[1]. In other cases, these 'group-within-group' interactions are more stable, such as those observed in sperm whales which live in groups whose members may fluctuate, yet each individual will also have a group of 'constant companions'[2]. The natural evolutionary question then arises: do these differences in social phenotypes give rise to differences in the fitness of participating individuals in ways that could shape the evolution of social systems?

Studies have shown that dynamically shifting social associations in a system in which individuals form and abolish social affiliations in order to maximize personal benefit can have a significant impact on the stable structure of a social group and on the overall level of success of the system as a whole[3–5]. These studies showed that it is possible to evolve substantial organizational complexity in already social groups, where individuals only employ selfishly motivated behaviors. This initial study assumed that each of an individual's social contacts could be voluntarily replaced as individuals tried to make increasingly more important social connections in order to maximize their own success. Though the motivating cues for replacing affiliations may not be the same, such behaviors have been observed in nature, e.g.[6].

However, in a natural setting, some of the most highly social groups exhibit the formation of some affiliations which are more robust to replacement than others. Vance et al[7]. have shown that fission-fusion societies, such as those of African elephants, will exhibit large groups which have extremely dynamic affiliations between individuals, as well as sub-groups which are of a more permanent nature. Most frequently, these more permanent social affiliations are familial, involving mother-calf pairs interacting in groups of close relatives[8]. The traditional explanation for these familial sub-groups is that Hamiltonian kin selection leads to indirectly increased individual fitness of those maintaining these bonds. However, within the context of social complexity and dynamic self-organization, it is a reasonable hypothesis that these bonds themselves can either increase or else compromise the success of the social organization of the group. As in all studies of multi-level selection, e.g.[4,5,9], individuals may reap fitness benefits from participating in well-organized societies. Therefore, this impact to the organizational success of the group may also contribute (either positively or negatively) to the indirect fitness of participating individuals, thereby providing a selective pressure for groups operating under particular affiliation dynamics to maintain, or avoid the maintenance of, familial sub-groups.



	Measure P "Organizational Measure 1"	Measure C "Organizational Measure 2"	Measure B "Organizational Measure 3"
Population P "Behavior X"	Increase in family group size slowed time till maximal social organizational level, but did not decrease the level achieved. Point of saturation exhibited.	Increase in family size increased the level of social organization under this measure.	
Population C "Behavior Y"	Increase in family size decreased the organizational success of the social group.		
Population B "Behavior Z"			

Figure 1 | Classification of impact of family structure on organizational success. Increase in the size of family affiliations per individual fall into one of three categories dependent upon the operational affiliation preference ('behavioral strategies') and the measure used to define organizational success. We include the more generic terms 'Behavior' and 'Organizational Measure' to stress that while our computational experiment used particular mechanisms to measure these effects, our results are meant to be interpreted more generally regardless of whether or not the operating mechanism for affiliation choice is also the measure of organizational success.

While there have been studies which have focused on how various affiliation-maintenance strategies in social populations can promote the emergence and existence of cooperation between individuals via natural selection, e.g.[10–12], no work has yet explored how the inclusion of familial groups can enhance or hinder the evolution of complex social systems. Furthermore, only a few studies have given attention to the effect that the social structure as an emergent property of the group has on individuals themselves[4,5]. Building on the already existing model framework developed in Fefferman and Ng[3] and expanded upon in[4,5,13,14], we utilize measures of network centrality as proxy measures of success (namely Popularity, Closeness, and Betweenness; cf.[15], see Methods section for details) in investigating the ability of a social population to successfully self-organize. When defined at the individual level, these measures provide a spectrum from directly observable individual characteristics (and therefore quite simple, e.g. Popularity centrality), to characteristics which would be difficult or impossible to evaluate by direct observation (and therefore quite complicated, e.g. Betweenness), in totality representing a similar range of individual evaluative capabilities and complexity of social organization. The biological relevance of our population-wide measures is such that they indicate a relative success level for the social population under selective pressures that favor simple, intermediate, and complex social structures, allowing us to compare the relative fitness impact of increasing family group sizes in hypothetical evolutionary scenarios which favor each type of selective pressure. This robustness to these selective pressures may therefore confer fitness benefits to individuals participating in well-organized populations.

In order to investigate the impact of long-term versus short-term affiliations on the organizational success of a self-organizing population, we have expanded the original model system to now include two different types of social affiliations: 'friendships', defined as those which can be kept or discarded based upon individual preference, and 'familial ties', defined as permanent affiliations. (Note that it need not be the case that these affiliations are actually formed solely between related individuals; many cooperatively breeding species have been shown to form groups in which unrelated individuals will come together to rear young, e.g.[16,17].) Expanding on this model system provides a controlled experimental environment with baseline data from previous studies by which we are specifically able to attribute the changes in the social organization of the population uniquely to the addition of family units. In this way, we here present an initial examination of how the inclusion of familial ties into a scheme of selfishly motivated social behavior may have played a role in the evolution of increasingly complex social systems.

Results

It is traditionally assumed that preferential affiliation and interaction with genetically related members of a social population can have a positive fitness effect on an individual through acquisition of indirect fitness benefits owing to the propagation of related genes into future generations[18–20]. In addition, the quality of the social environment in which an individual participates can also have a positive or negative fitness impact on that individual[4,5]. Therefore when considering the evolutionary impact of family ties, it is important that we consider the tradeoff between these two factors. In light of this, the impact of the addition of a 'family tie' behavior on the level of organizational success within our simulations can be grouped into three classes of outcome dependent upon the organizing preference employed by the individuals in the population, and the centrality measure used to evaluate organizational success (See Figure 1; note slight notational change in the figure for sake of clarity).

Within the populations organizing under the Popularity affiliation preference (hereafter *P*-population), inclusion of increasingly many family ties slowed the time until maximum organizational success was achieved under the Popularity centrality measure. However, only the inclusion of so many family ties that all non-family individuals were constantly replaced, the "point of saturation", caused any deviation from the ultimate levels of organizational success to which the population converged (Figure 2a, 2b, 2c). (Naturally, once saturation had been achieved, the population's organizational success was only as good as that seen in the Random population, since all non-family must constantly be replaced, obviating any actual affiliation preferences.) For the same *P*-populations, however, the organizational success achieved under either the measure of Closeness or Betweenness centrality was increased by the inclusion of familial ties (Figures 3a, and 4a). Therefore, for a *P*-population, there is no scenario in which the inclusion of familial behavior (up until the point of saturation) harmed the ultimate organizational success of the population. Further, if complex social structures are more successful under the current operational selective pressure, increasing the number of family ties per individual in the *P*-populations would therefore have a positive net effect. We can therefore make the case that, whether or not the evolutionary origin of familial behavior was rooted in Hamiltonian kin selective benefit, the inclusion of such social behaviors as part of a self-organizing affiliation principle to determine social structure would have benefited those populations in which the selective pressures had shifted from requiring only a basic social structure to requiring a more complex social organization to achieve sufficient fitness.

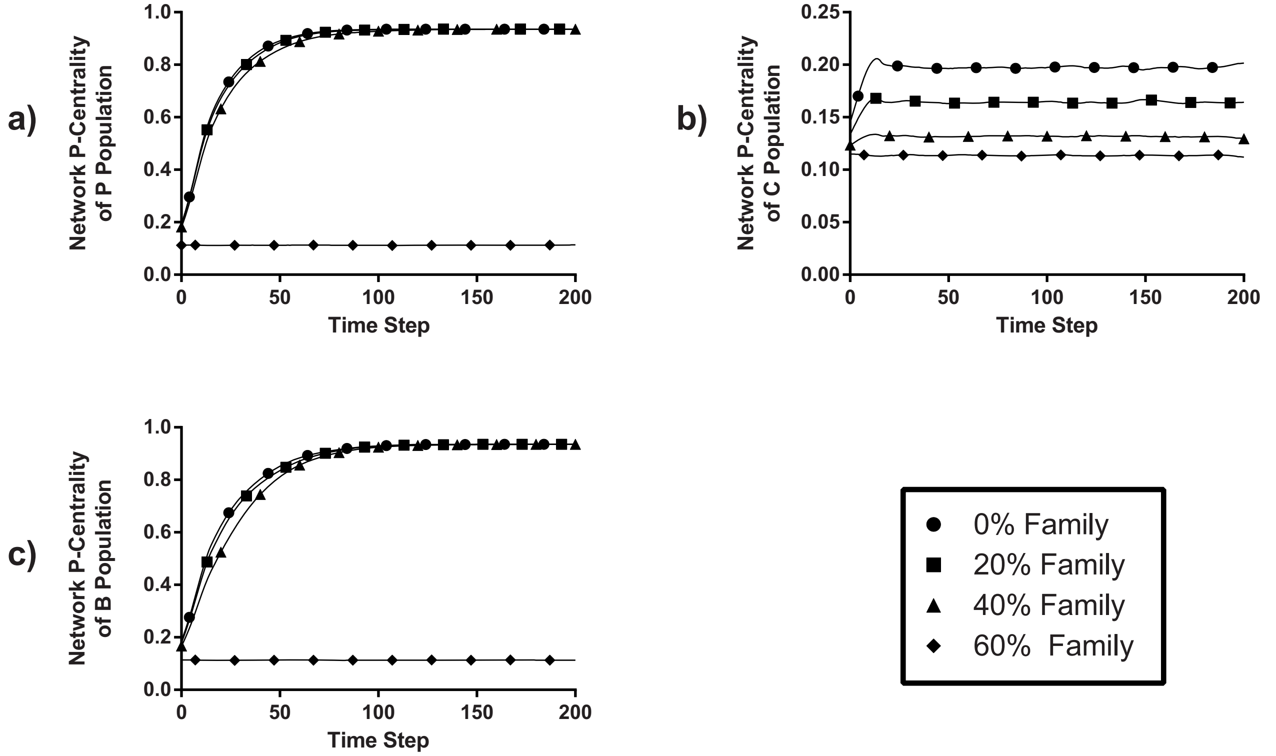


Figure 2 | **(a,b,c) - Organizational success measured by Popularity.** These 3 figures show the organizational success of the P, C, and B populations respectively, as measured by the population-wide Popularity criteria. We can see here through cross comparison of the graphs that the P-populations will do the best, and that adding a family structure onto these behaviors will still allow achievement of the same levels of success, although it does raise the time required to make it to that level. More importantly, we can see it does not pay to add family structure for any type of adopted behaviors under the Popularity criteria for success.

With the populations organizing under the Closeness and Betweenness affiliation preferences (hereafter *C*-, and *B*-populations respectively), not only did the inclusion of increasingly many family ties have a substantial impact on the organizational success achieved by the population, but whether that impact was positive or negative depended on the centrality measure used to evaluate population-level success (Figures 2–4, Panels B and C, respectively). Under the popularity measure of network success, the inclusion of familial ties decreased the success of both the *C*- and *B*-populations (Figures 2b and 2c). However, under both the closeness and betweenness centrality measures of network success, the inclusion of familial ties increased the success of both the *C*- and *B*-populations (Figures 3b and 4b, and 3c and 4c, respectively). While the mechanisms behind these observations are easily explained by the familial ties compromising a universal convergence to the same *F* individuals, and therefore increasingly approximating the success achieved for each measure by the Random network[3] (in which no affiliation preferences are present), the biological interpretation is far more interesting: this demonstrates the possibility that selective pressures that are best alleviated by highly organized social endeavors could act via indirect benefits to increase individual fitness by alleviating those pressures at the expense of the indirect fitness benefits which would have been achieved by instead maintaining familial ties with kin. In other words, networks under pressure to self-organize under simple metrics may select for the dissolution of large family groups, but select to maintain them if the pressures are to organize into complex societies. The inclusion of an already existing familial behavior (due either to Hamiltonian pressures, or some other mechanism) could therefore prime a population for a behavioral shift towards more complex self-organizing social affiliation preferences.

Interestingly, the concept of a point of saturation implies an endogenous limit on the size of family groups. We are therefore able to hypothesize that populations observed to organize under affiliation principles that are compromised in their success by exceeding saturation should exhibit smaller family units (relative to their total number of affiliations in the population) than should populations organizing under more complex affiliation strategies. This would be contrary to a prediction made by a purely Hamiltonian point of view, in which, so long as additional affiliations are assumed to provide fitness benefits to the recipients, individuals should always prefer to affiliate with relatives, thereby gaining an indirect fitness benefit from the success of their kin, rather than limit familial affiliation in favor of associating with non-kin.

Discussion

Studies of social networks, affiliation dynamics and individual behavior, cf.[21–23], have shown that highly complex behaviors of systems in biology can be produced by very simple, local rules acted upon by individuals comprising the system[24]. Within even this narrow, initial, theoretical investigation, our models have demonstrated the interplay between the evolution of highly-organized social structures and the ability of individuals to maintain family structures. We have shown that contrary to traditional Hamiltonian predictions, under certain selective pressures, family units of restricted size may be selected for, rather than a simple binary selection for or against the inclusion of family units. As family group size increases, we can expect increasing trade-offs in benefits between the average indirect fitness increase shared within the related group (a function of the relatedness coefficient within that group) and the distributed individual benefits from participating the well-organized broader social structure. These concepts can act in concert, or involve carefully balanced trade-offs, increasing individual fitness only within certain environments, providing very specific selective pressures.

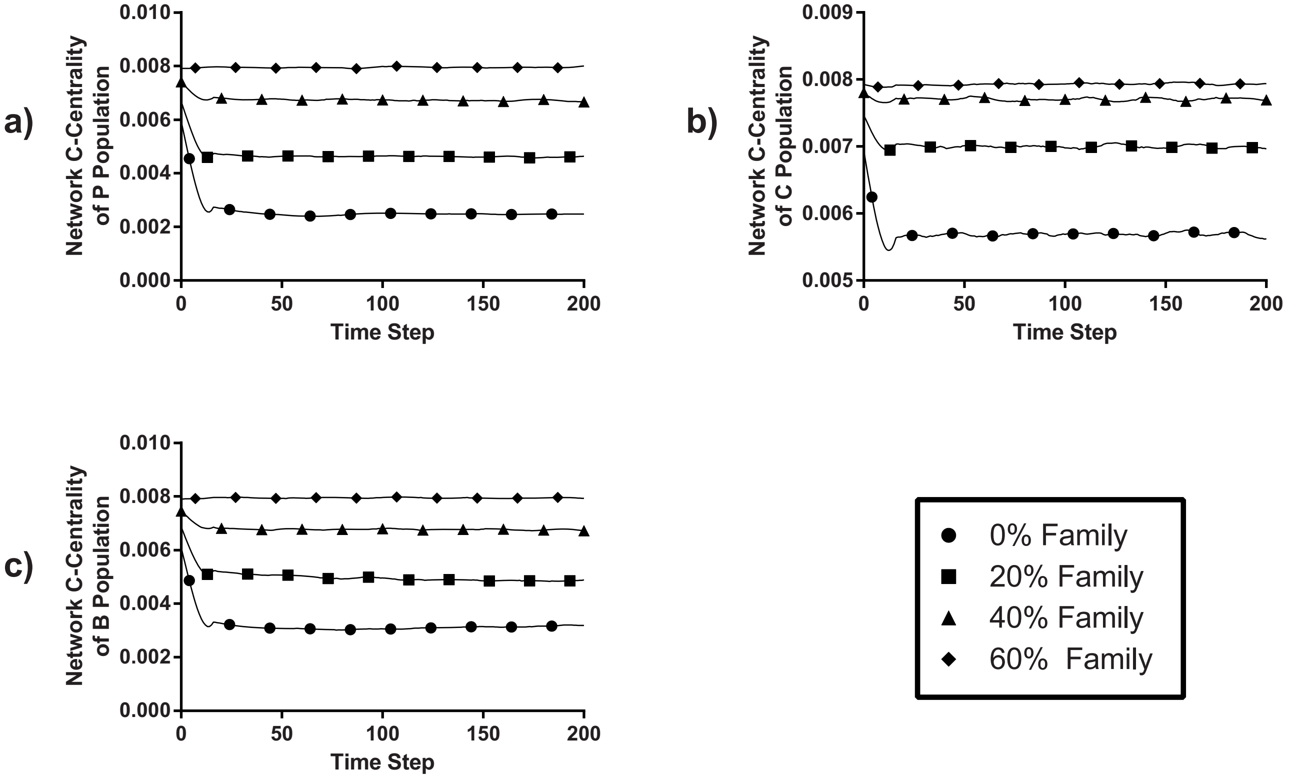


Figure 3 | (a,b,c) - Organizational success measured by Closeness. These 3 figures show the organizational success of the P, C, and B populations respectively, as measured by the population-wide Closeness criteria. We can see here that the 60% family levels (i.e. the Random networks) will do the best regardless of the population's affiliation preference. More importantly, we can see it pays to add family structure for any type of affiliation preference under the Closeness criteria for success.

Kin groups have been traditionally studied through the lens of Hamiltonian inclusive fitness. The results presented here show that the introduction and maintenance of family structures into a social population can have a clear impact on the evolution of more general social behaviors, highlighting the importance of examining family structures not only via Hamiltonian thought, but also in terms of the broader social context. Though our results involved only the model systems of three different affiliation preferences, we believe that they form a basic framework from which more carefully tailored theoretical and empirical studies of the evolution of social complexity and kin-selection in particular natural systems may be launched.

Methods

We define our network as a directed graph G consisting of n individuals and a set of directed edges E, where the edge $(v_i, v_j) \in E$ indicates the directed edge from v_i to v_j. We can then refer to v_j as an out-neighbor of v_i. The out-degree of an individual v_i, $d_{out}(v_i)$, is the number of individuals that are adjacent to v_i, and similarly, the in-degree of v_i, $d_{in}(v_i)$, is the number of individuals for which v_i is an out-neighbor (cf.[25]). We then refer to the distance $d(v_i, v_j)$ between individuals v_i and v_j as being equal to the length of a shortest path between them. It is important to note that in a directed network, $d(v_i, v_j)$ may not be the same as $d(v_j, v_i)$.

To measure the "success" of our population, we borrow from 3 widely used measures of network centrality, cf.[15], namely Popularity centrality (also sometimes referred to as "preferential attachment" in growing networks; cf.[26]), Closeness centrality, and Betweenness centrality, cf.[27–29]. As with the earlier models, we assume that individuals themselves use similarly-named but separately defined measures to evaluate the quality of their affiliations and thereby make decisions about whether or not to replace friendships based on the relative quality of their current friends. Each of these measures can be defined at the individual level and at the population-wide level as follows:

Popularity (or degree) centrality.

$$P(v_i) = \frac{d_{in}(v_i)}{n-1}$$

This measure reflects the proportion of individuals which have v_i as an out-neighbor. Note that by this definition, the maximum value of $P(v_i)$ is 1, which occurs when every other individual in the network has v_i as an out-neighbor. To define the population-wide Popularity measure of the network G, let $P^* = max\{d_{in}(v_i)|i = 1, 2, \ldots, n\}$, then

$$P(G) = \frac{\sum_{i=1}^{n} [P^* - d_{in}(v_i)]}{(n-1)(n-2)}$$

Closeness centrality.

$$C(v_i) = \frac{n-1}{\sum_{j \neq i} d(v_i, v_j)}$$

This measure provides a way to characterize the average distance in the network from individual v_i to all other individuals. Note that for some (v_i, v_j) pairs, $d(v_i, v_j)$ may not be defined if v_i is not reachable from v_j in the network. If this is the case, we set $d(v_i, v_j) = n$, showing the relative hardness of traveling from v_i to v_j. By this definition, the maximum possible value for $C(v_i)$ is 1, and occurs when all other individuals in the network are out-neighbors of v_i. The population-wide Closeness measure of G can then be defined as

$$C(G) = \frac{\sum_{i=1}^{n} C(v_i)}{(n-1)(n-2)}$$

Betweenness centrality.

$$B(v_i) = \frac{2[count(v_i)]}{(n-1)(n-2)}$$

Let S be a set consisting of all shortest paths between all pairs of individuals in G, then count(v_i) is the number of paths in S that contain individual v_i as an intermediate individual. This measure characterizes the proportion of shortest paths between all pairs of other individuals which contain v_i, and as such, it gives an indication of how critical the individual v_i is to the flow of information through the network. By this definition, the maximum value of $B(v_i)$ is attained when the individual v_i is contained in all shortest paths of the network (excepting those shortest paths for which v_i is an end-point). We then defined the population-wide Betweenness measure as

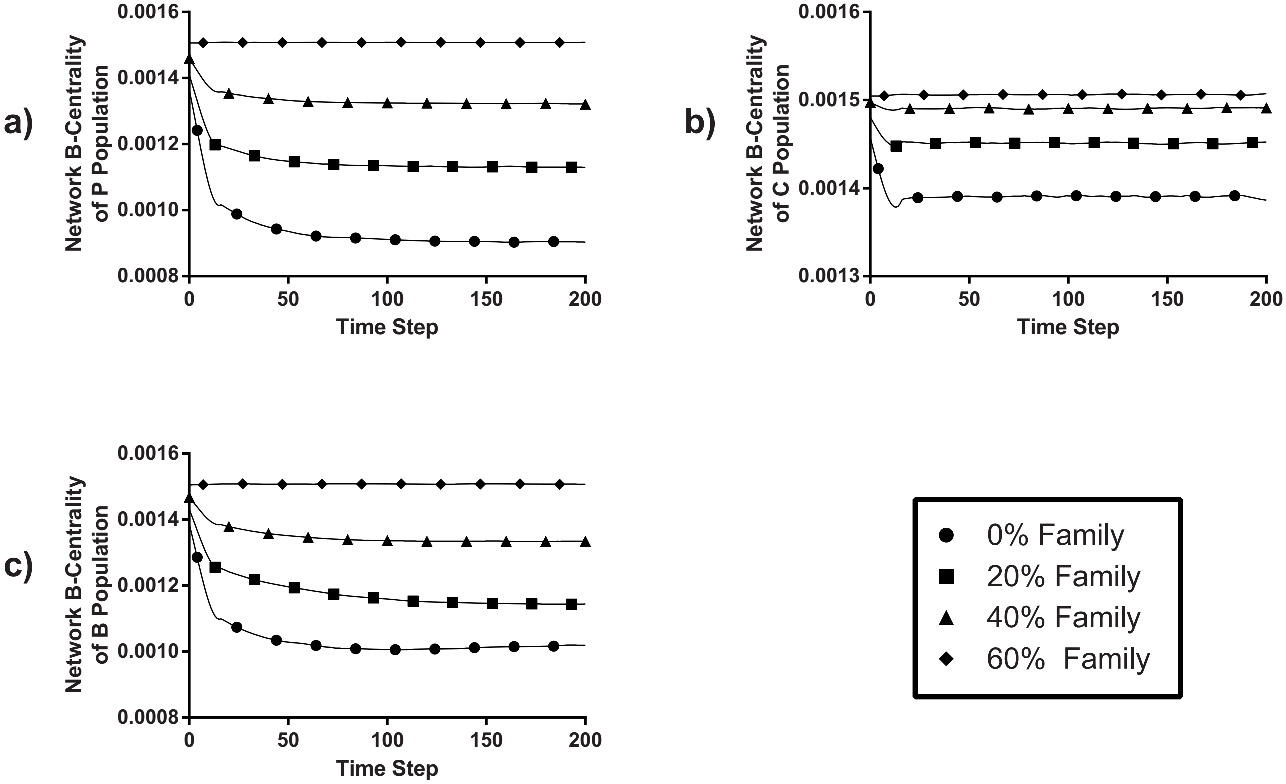


Figure 4 | (a,b,c) – Organizational success measured by Betweenness. These 3 figures show the organizational success of the P, C, and B populations respectively, as measured by the population-wide Betweenness criteria. We can see here that the 60% family levels (i.e. the Random networks) will do the best regardless of the population's affiliation preference. More importantly, we can see it pays to add family structure for any type of affiliation preference under the Betweenness criteria for success.

$$B(G)=\frac{\sum_{i=1}^{n}B(v_i)}{(n-1)(n-2)}$$

These centrality measures were used to define the affiliation preferences for each individual, (determined at the beginning of each simulation) such that the affiliation preference for all individuals in the network was identical and unchanging throughout the course of the simulation. We then notate a network made up of individuals having an affiliation preference of Popularity as a *P*-network; similarly a *C*-network (resp. *B*-network) is a network comprised of individuals having the Closeness (resp. Betweenness) centrality preference. Each network was constructed having 50 individuals, such that each individual v_i was initially assigned 5 out-neighbors at random, of which a uniform, constant number, *F*, were designated to be "family members", that is, out-neighbors with whom the affiliation could not be broken throughout the course of the simulation. (Note that, by this definition, each individual had at least *F* family members, but family ties from others would also be interpreted as permanent family structure; i.e. direction of the family tie did not affect whether or not it was a permanent affiliation.) The affiliations with those individuals not designated as family were able to be actively maintained or broken throughout the course of the simulation, dependent upon v_i's affiliation preference, in the following way: At each time step *t*, each individual v_i ranked its non-family affiliations according to its affiliation preference, dropping the two existing out-neighbors which were ranked lowest, and choosing 2 new out-neighbors at random (mirroring the established protocol from[3]). Note that these dynamics place an upper-bound on the number of possible family members, such that each individual can have at most 3 out-neighbors designated as family. Note too that the case of 3 family members approximates the Random network in that all non-family members will be replaced at each time step, regardless of ranking or of the affiliation preference of v_i. As described in[3], the Random network is generated by the same conditions given for the experimental network and features ongoing dynamics according to the same algorithm, except that the choice of which current affiliations to switch at each time step is done by random lottery.

Each simulation had a total of 200 time steps, and each experimental setup ($F = \{0, \ldots, 3\}$) was repeated 300 times. In all networks, at each time step *t*, $P(v_i)$, $C(v_i)$, and $B(v_i)$ were recorded for all v_i, and $P(G_t)$, $C(G_t)$, and $B(G_t)$ were recorded for the network at that time *t*. We also computed the average value for each of these measurements at each time step *t* across all repetitions of each respective experimental setup. (It is important to note that although, due to their definitions, direct comparison of the actual values of the networks by these different metrics is meaningless, the relative levels of success by each type of population within each single measure can provide valuable insight).

1. Roden, C., Vervaecke, H. & Van Elsacker, L. Dominance, age and weight in American bison males (Bison bison) during non-rut in semi-natural conditions. *Appl. Anim. Behav. Sci.* **92**, 169–177, doi:10.1016/j.applanim.2004.10.005 (2005).
2. Whitehead, H., Waters, S. & Lyrholm, T. Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. *Behav. Ecol. Sociobiol.* **29**, 385–389, doi:10.1007/bf00165964 (1991).
3. Fefferman, N. H. & Ng, K. L. The role of individual choice in the evolution of social complexity. *Ann. Zool. Fenn.* **44**, 58–69 (2007).
4. Hock, K. & Fefferman, N. H. Extending the Role of Social Networks to Study Social Organization and Interaction Structure of Animal Groups. *Ann. Zool. Fenn.* **48**, 365–370, doi:10.5735/086.048.0604 (2011).
5. Hock, K., Ng, K. L. & Fefferman, N. H. Systems Approach to Studying Animal Sociality: Individual Position versus Group Organization in Dynamic Social Network Models. *PLoS One* **5**, e15789, doi:10.1371/journal.pone.0015789 (2010).
6. Parker, T. & Ligon, D. Dominant male red junglefowl (*Gallus gallus*) test the dominance status of other males. *Behav. Ecol. Sociobiol.* **53**, 20–24, doi:10.1007/s00265-002-0544-5 (2002).
7. Vance, E., Archie, E. & Moss, C. Social networks in African elephants. *Comput. Math. Organ. Th.* **15**, 273–293, doi:10.1007/s10588-008-9045-z (2009).
8. Wittemyer, G. & Getz, W. M. Hierarchical dominance structure and social organization in African elephants, Loxodonta africana. *Anim. Behav.* **73**, 671–681, doi:10.1016/j.anbehav.2006.10.008 (2007).
9. Fewell, J. H. Social Insect Networks. *Science* **301**, 1867–1870, doi:10.1126/science.1088945 (2003).
10. McNamara, J. M., Barta, Z., Fromhage, L. & Houston, A. I. The coevolution of choosiness and cooperation. *Nature* **451**, 189–192, doi:10.1038/nature06455 (2008).
11. Santos, F. C. & Pacheco, J. M. Scale-Free Networks Provide a Unifying Framework for the Emergence of Cooperation. *Phys. Rev. Lett.* **95**, 098104 (2005).
12. Santos, F. C., Pacheco, J. M. & Lenaerts, T. Cooperation prevails when individuals adjust their social ties. *PLoS Comput. Biol.* **2**, 1284–1291: e1140, doi:10.1371/journal.pcbi.0020140 (2006).
13. Hock, K. & Fefferman, N. H. Violating Social Norms when Choosing Friends: How Rule-Breakers Affect Social Networks. *PLoS One* **6**, e26652, doi:10.1371/journal.pone.0026652 (2011).

14. Hock, K. & Fefferman, N. H. Social organization patterns can lower disease risk without associated disease avoidance or immunity. *Ecol. Complex.* **12**, 34–42, doi:10.1016/j.ecocom.2012.09.003 (2012).
15. Freeman, L. C. Centrality in social networks conceptual clarification. *Soc. Networks* **1**, 215–239 (1979).
16. Starks, P. T. Natal nest discrimination in the paper wasp, Polistes dominulus. *Ann. Zool. Fenn.* **40**, 53–60 (2003).
17. Griesser, M. *et al.* Influence of Winter Ranging Behaviour on the Social Organization of a Cooperatively Breeding Bird Species, The Apostlebird. *Ethology* **115**, 888–896, doi:10.1111/j.1439-0310.2009.01678.x (2009).
18. Smith, J. M. Group selection and kin selection. *Nature* **201**, 1145–1147 (1964).
19. Hamilton, W. D. The genetical evolution of social behaviour. II. *J. Theor. Biol.* **7**, 17–52 (1964).
20. Hamilton, W. D. The evolution of altruistic behavior. *Am. Nat.* **97**, 354–356 (1963).
21. Doreian, P. Actor network utilities and network evolution. *Soc. Networks* **28**, 137–164, doi:10.1016/j.socnet.2005.05.002 (2006).
22. Jeanson, R., Kukuk, P. F. & Fewell, J. H. Emergence of division of labour in halictine bees: contributions of social interactions and behavioural variance. *Anim. Behav.* **70**, 1183–1193, doi:10.1016/j.anbehav.2005.03.004 (2005).
23. Snijders, T. A. B. Stochastic actor-oriented models for network change. *J. Math. Sociol.* **21**, 149–172 (1996).
24. Camazine, S. *Self-organization in biological systems.* (Princeton University Press, Princeton, NJ, 2001).
25. Chartrand, G., Lesniak, L. & Zhang, P. *Graphs and digraphs.* 5th edn, (CRC Press, Boca Raton, FL, 2011).
26. Barabasi, A. L. & Albert, R. Emergence of scaling in random networks. *Science* **286**, 509–512 (1999).
27. Carrington, P., Scott, J. & Wasserman, S. *Models and methods in social network analysis.* (Cambridge University Press, Cambridge [England]; New York, 2005).
28. Scott, J. *Social Network Analysis.* (Sage, Los Angeles, CA, 2013).
29. Wasserman, S. & Faust, K. *Social network analysis: methods and applications.* (Cambridge University Press, Cambridge [England]; New York, 1997).

Acknowledgments

We thank the National Science Foundation (NSF) for funding to the Center for Discrete Mathematics and Theoretical Computer Science (DIMACS) as well as for NSF #1049088 EaSM providing funds to the Fefferman Lab. We also thank the Department of Homeland Security (DHS) for funding to the Control, Command, and Interoperability Center for Advanced Data Analysis (CCICADA), where this work was jointly completed. We also thank Dr. Kah Loon Ng and Erin Mulder for their assistance with the computer programming required to perform our simulations. We finally thank the audience at Morgan State University for helpful suggestions when an early version of this work was presented at the CCICADA Semi-Annual Research Summit.

Author contributions

B.R.G. and N.H.F. contributed equally to the design, model implementation, and analysis of the data gathered from the model, as well as to the writing and revision of the manuscript. All authors have seen and approved of the final manuscript.

Additional information

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Greening Jr, B.R. & Fefferman, N.H. Evolutionary Significance of the Role of Family Units in a Broader Social System. *Sci. Rep.* **4**, 3608; DOI:10.1038/srep03608 (2014).