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The role of individual choice in the evolution of social complexity

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Constant re-evaluation of social affiliations and shifting social network structures can profoundly affect the adaptive fitness of individuals within a population, as well as yielding super-additive effects felt by the population as a whole. To evaluate the impact of different social affiliation choices, and the relative ability of individuals to correctly assess the success of other individuals, we have created a set of mathematical models based on network centrality measures. We choose the hypothetical measures of "popularity", "closeness" and "betweenness" to examine the resulting self-organizations of social groups. Our findings suggest that some different types of social behaviors can lead to the same levels of stability and organizational success, suggesting the possibility that complex organizations could have evolved from simpler ones without any change in the selective pressures acting on the population.

Introduction

In trying to understand the evolution of sociality, many studies have focused on the initial introduction and stability of social behaviors, such as altruism (e.g. Ligon 1983, Dugatkin 2002, Croft *et al*. 2004). While these studies lend fascinating insight into individual-level game theoretic analysis of the possible evolution from solitary into social species, very few studies have examined the subsequent evolution of social structure based on these individual actions. Additional studies have investigated the effects of different behaviors (based on individual physiological and behavioral differentiation and specialization) in populations of different sizes on the levels of operational complexity in co-operative task completion (cf. Anderson & McShea 2001). However, to the best of our knowledge, no studies have looked at the effects of individual choice motivated by a desire to secure maximal positions of social status alone (regardless of the mechanism used to evaluate the quality of such choices).

Different species have evolved incredibly diverse social structures, from the strict dominance hierarchy of the stellar jay (*Cyanocitta stelleri*; e.g. Brown 1963) to the complex social interactions of gibbons (*Hylobates lar*; territorial families with dispersal of young upon maturation; e.g. Brockelman *et al*. 1998), to the highly distributed organization of some ants (e.g. Anderson & McShea 2001). Since all of these social structures rely on underlying individual social behaviors, it is possible that different social organizations may have evolved separately, after the evolution of individual social behavior. This possibility leads to a new and different focus for investigation: the introduction and maintenance of social organization, and the stability and success of that organization, in already social groups.

Naturally, though social organization is best described as a group-level trait, it must arise collectively from the individual social behaviors of the members of the group. As can be observed in many species of birds (e.g. *Gallus gallus*; cf. Parker & Ligon 2002, Forkman & Haskell 2004), the choices of individuals regarding how to interact with others in the group are redefined and re-evaluated over time. These re-evaluations can happen constantly, due to continual challenges from individuals (cf. Parker & Ligon 2002), or periodically, due to altered environmental conditions or natural states (e.g. molting or mating seasons; cf. Belthoff *et al*. 1994). From the perspective of natural selection, a stable social structure may provide some evolutionary benefit. (Note that a stable organization does not imply an unchanging role within that organization for each individual, simply a consistency in the organization itself.) Empirical studies suggest that social instability can lead to direct, individual physiological costs (cf. Belthoff *et al*. 1994, Wikelski *et al*. 1999, Creel 2001, Lange & Leimar 2004; though these effects may not be as strong as previously suspected in some species — cf. Sloman & Armstrong 2002), and it is reasonable to suppose that there might be profound indirect costs as well. It is therefore important to isolate which sorts of individual choices lead to the greatest stability of social organization and under which conditions, and to understand the relationships/tradeoffs between stability and the level to which the desired organization is accomplished.

Even without incorporating external influences (e.g. resource limitation or predation which have been shown to affect social stability in some species; e.g. Ward & Hart 2003), population-specific characteristics may have a huge impact on the ability of individual choice to lead to population-level social stability. Group size may play an important role in the efficacy of certain choices; if individuals are not able to asses the qualities on which they are basing their social choices in all other group members, their choices may be suboptimal based on lack of complete knowledge. Naturally, this can also arise from an inability to distinguish these characteristics accurately. These types of individual sub-optimality of choice may seriously affect the stability of the group (either positively or negatively), causing a very different outcome from a situation of complete knowledge or infallible choice. Additionally, behavioral differences among individuals could easily lead to very different group stability from those arising from a group with uniform preferences. Given the complexity of selection and evolution, it may even be that there is disagreement between the proximate cues individuals use as selective criteria for their social affiliations within a group and the ultimate reasons for population stability. In order to understand how such individual choices affect the population, it is necessary to examine these effects within a variety of different population scenarios.

We here present an initial investigation into the stability and organizational success of different social organizations based on individual choice. The study of social networks provides a natural characterization from which to begin these investigations (cf. Wasserman & Faust 1994, Scott 2000, Carrington *et al*. 2005) and from these we borrowed three different strategies for individual social choice. The first two: (1) **Popularity**: choosing to affiliate with those who are the most 'popular', and (2) **Closeness**: choosing to affiliate with those who are most closely connected to all other individuals within the group, are rather basic strategies, based on the hypothesized inherent capabilities of social species. The third strategy was chosen to represent a more 'complicated' (and therefore possibly more evolved) evaluation of the social structure of the group as a whole: (3) **Betweenness**: choosing to affiliate with those who function as necessary intermediates between other individuals.

It is natural to suppose that individuals of any species may observe the affiliations of others and therefore naturally quantify the "popularity" of others, whether the ultimate mechanism causing the popularity is something as simple as individual body size (e.g. Owen-Smith 1993) or as complicated as predator-attracting color displays (e.g. sexually selected traits; Promislow *et al.* 1992). Regardless of mechanism, this sort of quorum sensing of the choices of others has been observed in decision making in a number of social species (e.g. Pratt *et al.* 2002) and it is only natural to apply it to individual social choices. Similarly, evaluating how closely connected other individuals are to the rest of the group may easily represent something as simple as recognition of genetic relatedness (which some species have been shown capable of evaluating in others; Ward & Hart 2003, Gamboa 2004). The final strategy, however, implies an ability to understand 'network flow', not only as a current facet of social organization, but as it would be without the contribution of each other individual. This level of third-person evaluation may, in fact, not occur in natural environments, but was included to investigate whether or not stability was more or less difficult to attain under more complicated types of individual choice. These measures are by no means the only available. Social network theory provides many different measures, each capturing a different aspect of the social organization of a population. In choosing to examine only these three measures, we do not mean to suggest that these are the only such measures of possible importance, merely that they represent a sufficient diversity of possible complexity in individual evaluative capability as to provide an initial point for investigation.

The mathematical tools for quantitative evaluation of both individual- and group-level organizations can be borrowed directly from the fields of applied graph theory and social network theory. While these tools have traditionally been applied only to static networks, more recent studies have focused on dynamic or evolving networks (cf. Snijders 1997, Doreian 2006). By allowing dynamic choices to alter the social affiliations over time based on these measures, we can begin to examine the impact these choices have on the stability of social structures. This work provides a first look at the evolution of social organization in species where social behavior has already evolved.

Model

In order to examine the impact of individual affiliation choices, we are concerned with directed relationships from one individual to another (i.e. if u chooses to become affiliated with v, that is not the same as the case in which v chooses to become affiliated with u). It should be noted that our definition of "social affiliation" may be thought of as "preferential attachment" (the attachment of individuals to others based on individual selection criteria in a growing network; cf. Barabási & Albert [1999]) in which an attachment may be removed without necessarily altering either involved individual's status within the graph. To create a mathematical model of this affiliation network, we created a *directed graph* (or *digraph*) consisting of a set of n individuals (or *vertices*) in a social population called $V = \{v_1,v_2,...,v_n\}$ individuals, and a set of directed lines (or *arcs*) called A, where $(v_i,v_j) \in A$ represents an arc between the pair of individuals v_i and v_j going from v_i to v_j. For ease of notation, we say that v_i is *adjacent to* v_j and v_j is *adjacent from* v_i. Additionally, we say that (v_i,v_j) is an *out-arc* of v_i in G and v_j is an *out-neighbor* of v_i. (Note: we assume that no individual is allowed to affiliate with itself and that each pair (v_i,v_j) can occur at most once within the graph, meaning that A is a set of at most $n(n - 1)$ arcs.)

The *distance* between v_i and v_j is denoted by $d(v_i,v_j)$ = the length of a shortest path between v_i and v_j. In the event that there is no path from v_i to v_j, we set $d(v_i,v_j)$ = to the number of vertices in the digraph ($|V|$). The *indegree* of a vertex v_i, $d_{\text{in}}(v_i)$, is the number of vertices that are adjacent to v_i. Similarly, the *outdegree* of v_i, $d_{\text{out}}(v_i)$, is the number of vertices that are adjacent from v_i (cf. Chartrand & Lesniak 2004).

We then borrow three widely used social evaluation measures (first introduced by Freeman 1979) defined as follows:

a. The **Popularity** measure of a vertex v_i, $P(v_i)$, is defined as

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

This measure is basically the proportion of all vertices in G that are adjacent to v_i.

Defined in this way, the maximum value of $P(v_i)$ is 1 and this occurs when v_i is adjacent from all other vertices in G. We then defined a **population-wide Popularity** measure to evaluate the overall Popularity of individuals in a population as a whole in the following way. Let $P^* = \max\{d_{\text{in}}(v_i)|i = 1,...,n\}$, then the network Popularity measure of G is

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

This provides us with a population-wide measure of the success of the organizational strategy (i.e. how well the population does as a whole at being organized according to the Popularity measure of individuals).

b. The **Closeness** measure of a vertex v_i, $C(v_i)$ is defined as

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

Note that for some j, $d(v_i,v_j)$ may not be defined if v_j is not reachable in G from v_i. As before, we then set $d(v_i,v_j) = n$ to reflect the relative difficulty in reaching v_j from v_i as compared to other vertices v_k where $d(v_i,v_k)$ is defined. The closeness measure of v_i attains the maximum value of 1 when v_i is adjacent to all other vertices in G. We defined the **population-wide Closeness** success measure of G as

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

c. The **Betweenness** measure of v_i, $B(v_i)$ is defined as

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

where S = set of all shortest paths between *all* pairs of vertices v_i,v_j, and for every vertex v_i, count(v_i) = number of shortest paths in S that passes through v_i. (Note that if a shortest path P in S originates or terminates at v_i, P is not counted in count(v_i).)

Since $(n - 1)(n - 2)$ is the total number of ordered pair of vertices (v_j,v_k), $k,j \neq i$, $B(v_i)$ gives the average number of shortest paths per ordered pair of vertices that contains v_i along the path. We defined the **population-wide Betweenness** success measure of G as

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

The vertex affiliation preference for each v_i was determined at the outset of computation, either assigning the same preference to all vertices, or else assigning approximately 1/3 of the vertices to each type. Once assigned, an individual kept that affiliation preference throughout the simulation. To model the constantly changing affiliation dynamics of any social group, each vertex v_i was created with affiliations to five other individuals at random. Each vertex then changed the set of vertices to which it is adjacent in each iteration of the model's computation by keeping three of its existing out-arcs while dropping the other two and replacing them with new ones. Which of the existing out-arcs were dropped depended on the measure guiding v_i's affiliation choice. For example, if v_i was designated to prefer Popularity as a measure for social affiliation, it would compare the Popularity measures of its out-neighbors and then remove the out-arcs to the two out-neighbors with the least Popularity measure themselves. In this case, we say that v_i is 'a P-vertex', or else is 'of type P'. In addition to these three experimental preferences, a null-model in which vertices dropped two affiliations at random (rather than according to a ranked order by any of the measures) was run to show the comparative stability and success values.

To represent the incomplete knowledge of individuals, the choice of these two new out-neighbors was made randomly from among the rest of the population excluding the two individuals with whom the affiliation was just dropped. However, to investigate the effect of having complete knowledge of the status of others on the population outcome, scenarios were modeled where the two new affiliations were made, rather than at random, to the two individuals (from the entire population) with the best measure of the preferred type (no longer excluding the two just dropped).

During each iteration, t, in all scenarios (*see* Table 1) $P(v_i)$, $C(v_i)$ and $B(v_i)$ were computed for each v_i, and $P(G_t)$, $C(G_t)$ and $B(G_t)$ were computed for the entire population G_t. Each model was run for 200 iterations to allow the $P(G_t)$, $C(G_t)$ and $B(G_t)$ values to stabilize. To ensure accuracy of the result despite the inherent stochasticity of the dynamic system, each scenario was then computed under Monte Carlo simulation (until the point at which the variance in the result had decreased to less than 1/1000* (value of measure at stabilization), which always occurred within 50 simulations) and the average value at each iteration, across all Monte Carlo simulations for each scenario, was recorded.

Results and discussion

Zero-knowledge

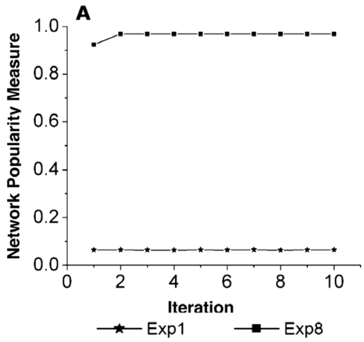
The Random scenarios (experiment 1) set a baseline expectation for both stability and success in the absence of any affiliation preference (Fig. 1). If the measure of organizational success was Popularity, having no knowledge resulted in a much lower level of success than that achieved when complete-knowledge was available (Fig. 1A). However, under the organizational measures of Closeness and Betweenness, the relationship of knowledge to success was inverted, yielding greater success when less knowledge was available (Fig. 1B and C). Since individual choices were made in these scenarios using no information about any other individuals within the population, we can think of this as our initial condition, prior to the evolution of complex social organization. In this case, individuals behave socially, still forming affiliations with each other, but doing so without any particular preferences. (An equivalent alternative interpretation would involve individuals having affiliation preferences, but being unable to evaluate others to determine how to express those preferences.) In order, then, to evolve a social organization, the correct expression of individual preferences would be expected to provide some benefit to the fitness of that individual. While this benefit could be achieved in conflict with the greater fitness of the group, it could also be that selfish individual decisions also benefit the population as a whole, providing a super-additive fitness benefit to particular social affiliation preferences.

Intermediate knowledge

In investigating the effects of individual social choices on group stability and societal organization, it became immediately clear that some types of behaviors caused societal organizations to centralize over time (e.g. Popularity, experiment 4). By the measure of Popularity, over time, all individuals came to agree on (and therefore affiliate themselves with) a central group of three most popular individuals (Fig. 2). This not only caused the group to be highly stable, but also highly successful (by the definition of group success for Popularity). By each individual acting selfishly to maximize their own benefit from

Table 1. The experimental models.

Experiment	Vertex affiliation preference	Knowledge	Total number of vertices	Number of B vertices	Number of C vertices	Number of P vertices
1	Random	None	100	NA	NA	NA
2	Betweenness	Incomplete	100	100	0	0
3	Closeness	Incomplete	100	0	100	0
4	Popularity	Incomplete	100	0	0	100
5	Heterogeneous	Incomplete	100	33	34	33
6	Betweenness	Complete	100	100	0	0
7	Closeness	Complete	100	0	100	0
8	Popularity	Complete	100	0	0	100
9	Heterogeneous	Complete	100	33	34	33



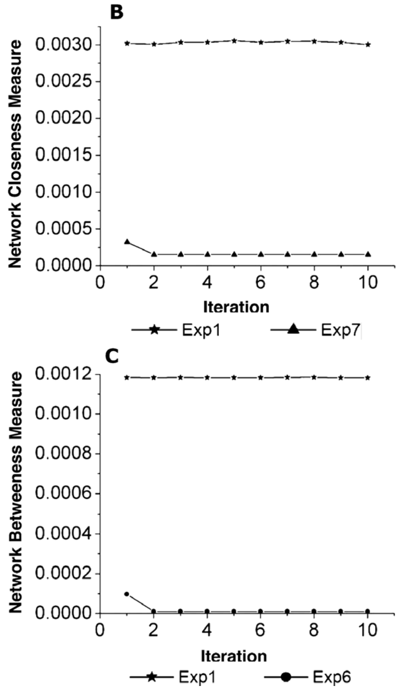


Fig. 1. The success and stability of the zero-knowledge *vs.* complete-knowledge experiments. For the Network Popularity measure (panel **A**), the lack of knowledge (or affiliation preference) resulted in a much lower level of success of the social organization achieved by the population than was achieved when complete-knowledge was available. The exact opposite is seen for both the Network Closeness and Betweenness measures (panels **B** and **C**).

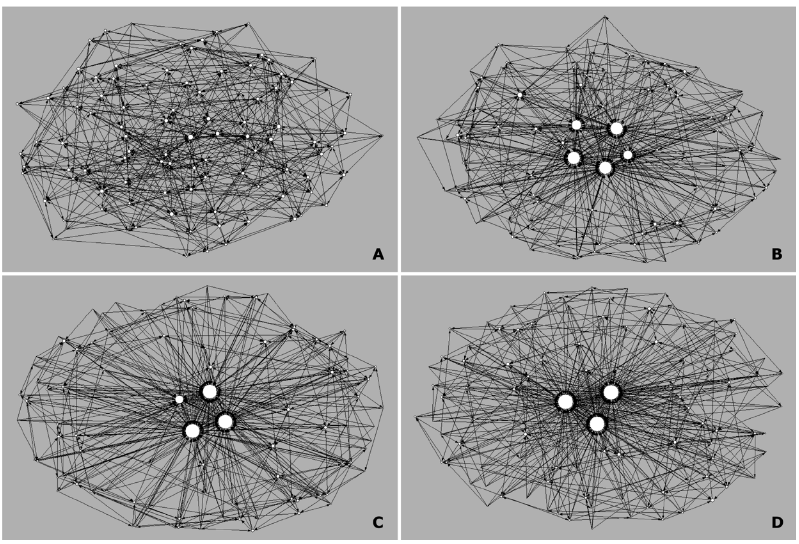
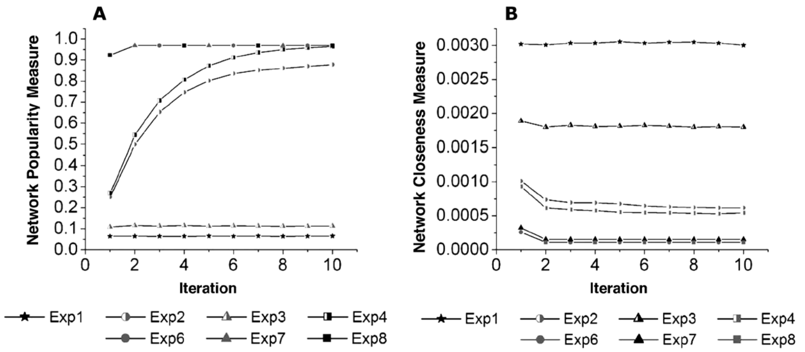


Fig. 2. The convergence of the social network towards stability in a homogeneous population of type P individuals (experiment 4). The size of each node represents the relative popularity measure of the individual and the progress of the convergence is shown through iterations 1 (panel **A**), 50 (panel **B**), 100 (panel **C**) and 200 (panel **D**).

social affiliation, the population self-organized into a stable and successful structure. Benefits of individual action may therefore be super-additive, yielding greater individual benefit by increasing the fitness of the entire group through the coincident, unorganized, individually selfish behavior of its members.

However, this success was seen to be affiliation-behavior specific. Populations of type C individuals stabilized most rapidly (experiment 3, Fig. 3), indicating a possible trade-off between rapidity in achieving stability and the level of organizational success ultimately achieved. Further, the success of populations of type B within its own metric actually declined over time, though the decrease was gradual (experiment 2, Fig. 3C), indicating that this metric did not lead to Betweenness measure stability within the 200 iterations of



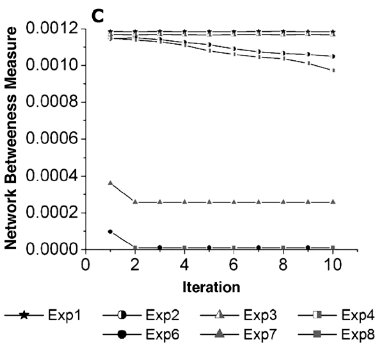


Fig. 3. Resulting population-wide organizational success measures for homogeneous populations (experiments 1–4, 6–8). Each measure is shown for all experiments (hence, for all population types). While the level of organizational success of populations of type P under the corresponding Network Popularity measure increased (panel **A**, experiment 4), the success of populations of type C, under the Network Closeness measure remained relatively stable after an initial decrease (panel **B**, experiment 3), and the success of populations of type B, under the Network Betweenness measure decreased over time (panel **C**, experiment 2). Experiments with complete knowledge (experiments 6–8) out-perform their incomplete-knowledge counterparts under the Popularity measure but not under the Closeness or Betweenness measures.

the model computation. This would imply that any population operating under selective pressure to achieve high organizational success under the Betweenness measure would actually have a lesser chance of survival over time as individuals continued to alter their affiliations based on maximizing the status of their affiliations under the Betweenness metric. Interestingly, in both the B and C preference populations (experiments 2 and 3, respectively), the measure success of the populations by the same preference measure was lesser than that achieved by the Random type population (experiment 1, Fig. 3), indicating that populations in which individuals act appropriately based on either B or C preferences are actually less successful at achieving a successful social organization by those same measures. This would seem to indicate that these preferences may not have been adaptive via the mechanism of improving group-level organizational success. Of course, one possibility is that the random social structure never existed and that social groups evolved at the same time as a basic social affiliation preference of one type or another (perhaps of a sort not considered in these models).

However, there are a number of possibilities which would still have led to the evolution of such a preference system despite this seeming detriment. Perhaps the average (probabilistic) expectation of gain to individual fitness achieved by having either preference outweighed the communal costs of living within a less successful social structure. In order to determine whether or not this might have been the case, it becomes necessary to look at the individual-level affiliations within the population over time and track whether or not particular individuals become and remain more successful over time than others. (Preliminary investigations into this expansion of our models have begun.) Perhaps, in fact, none of these organizational success metrics have enough of an effect to be the primary force shaped by selection during the evolution of social complexity. Or perhaps the success measure under selection is incidentally achieved by these preferences causing selection to favor them for reasons other than organizational success.

Looking carefully at the Popularity success measures (*see* Fig. 3A), it becomes clear that populations of type B individuals (experiment 2) achieve nearly the same levels of organizational success as do the populations of type P individuals (experiment 4) and that stability is achieved just as rapidly. Therefore a population under selective pressure to achieve organizational success under the Popularity measure would be expected to survive equally well if the population was comprised of individuals of type P as if the population was comprised of individuals of type B. Similarly, by the Betweenness success measures (*see* Fig. 3C), populations of type C individuals (experiment 3) have a greater success, with greater organizational stability than populations of type B (experiment 2). Therefore, if a population were under selective pressure to increase their organizational success as measured by Betweenness, it would be most effective for individuals to make their affiliation choices based on Closeness. This leads to the intriguing possibility that more and more complex social structures could have evolved, based not on their own organizational success, by being favored by (or at least able to withstand) selection due to an ability to closely mirror the fitness success of simpler measures.

Complete knowledge

While experiment 1 provides a zero-knowledge baseline for comparison with these incomplete knowledge models (experiments 2–4), experiments 6–8 provide a baseline for the other extreme: complete knowledge (*see* Figs. 1 and 3). In these experimental scenarios, individuals were able to evaluate all other individuals, regardless of whether or not they were affiliated to them, and make their affiliation choices based on this complete understanding of all others. Biologically, this could be interpreted as living within a small enough group size that sufficient contact is likely among all members of the group for all such evaluations to be possible. This allows us to examine the possibility that affiliation preferences can produce different relative levels of stability and/or success in groups of different sizes. These levels of knowledge clearly greatly affect the centrality of the social organization after the population has stabilized. As the level of knowledge increased, a central few individuals were chosen as affiliates by more and more of the population until at last, under complete knowledge, all of the rest of the population affiliated themselves with these few central individuals only (*see* Fig. 4). Naturally, achieving this kind of network structure had different effects on the organizational success achieved under each of the three measures (*see* Fig. 3). For populations of type P individuals, measured by the Popularity metric, complete knowledge (experiment 8) allows the population to reach the same level of organizational success achieved in the incomplete knowledge scenario (experiment 4). Moreover, the time until the population reaches stability at a maximal level of success vastly decreases, converging by the twentieth iteration to the same level achieved by the incomplete scenario (experiment 4) only during the last twenty iterations of the model (iterations 180–200) (*see* Fig. 3A). This means that, as measured by the Popularity metric, smaller populations would be expected to achieve higher organizational success more rapidly than larger populations, though both would ultimately converge to the same level. In contrast, the availability of complete knowledge greatly decreased the organizational success via measures of Betweenness and Closeness, regardless of the population type (*see* Fig. 3B and C).

Under these complete knowledge conditions, a population of type P individuals (experiment 8) had the same success and stability as a population of type B individuals (experiment 6) when evaluated under the Betweenness measure (*see* Fig. 3C). Interestingly, as with the incomplete knowledge scenarios, a population of type C (experiment 7) yielded a higher level of success (though the same level of stability) under the Betweenness measure (*see* Fig. 3C). For both Popularity and Closeness measures, it did not matter which affiliation preference was employed by the population (experiments 6–8; *see* Fig. 3A and B). This would imply (for example) that a population under selective pressure to achieve organizational success according to either the Popularity or Closeness measure could as easily evolve as a population of type B, C or P individuals, so long as the group was small enough to provide complete knowledge. For Popularity, this leads to a potential trade-off between group size and group success,

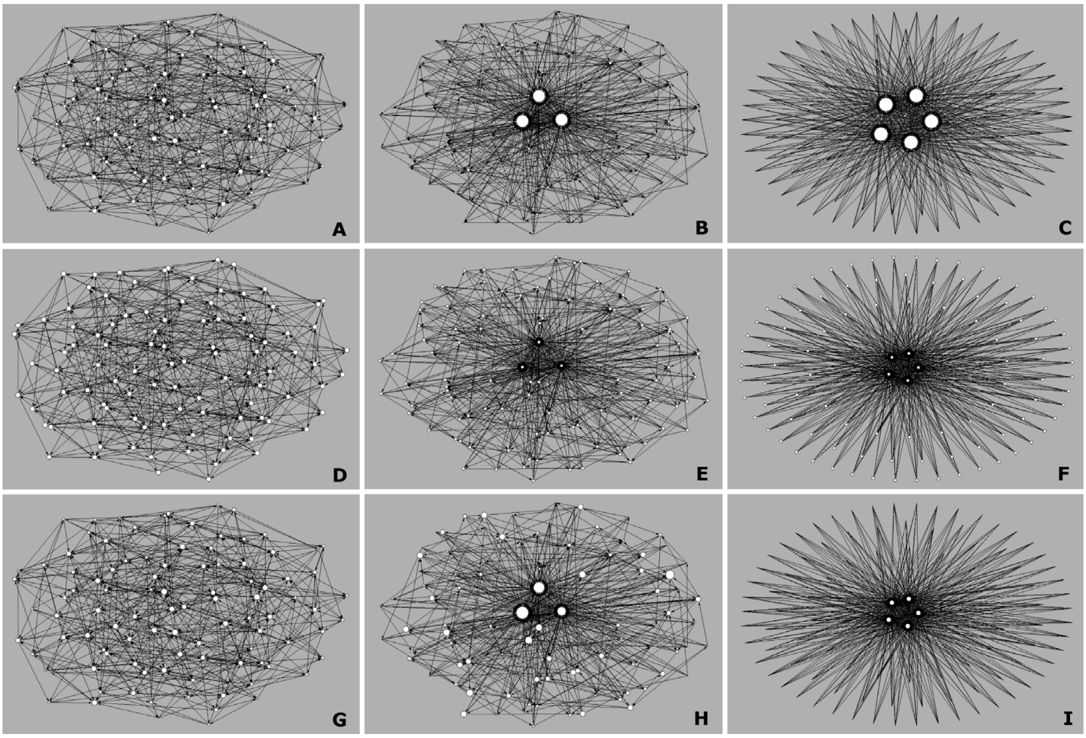


Fig. 4. Comparing the effects "knowledge" (none / incomplete / complete) on the structure of the network emerging at iteration 200 (close to stability) of a population of type P. The progression of the figures from left to right for each of the three rows shows the convergence of the structure as the level of information available to individuals making affiliation choices rises from zero-knowledge (left-most panels **A**, **D** and **G**), to incomplete knowledge (middle panels **B**, **E** and **H**), to complete knowledge (**C**, **F** and **I**). In each, the relative size of the individual node represents its individual success under the measure corresponding to the affiliation preference governing choice (Popularity, Closeness and Betweenness, in rows 1, 2 and 3 respectively). These graphs together show that the centrality of the network increases with the level of knowledge, though the relative success of individuals varies greatly across the different measures.

potentially (so long as stability had not been achieved) limiting the size to which a population could grow and possibly even leading to cycles in population size (similar to those seen in density dependent feedback models). For Closeness, this would lead to a very different effect, causing the population to "escape" the limitation imposed on its organizational success by complete knowledge. If a population were to grow sufficiently to make complete knowledge impossible, we would expect the organizational success of the population to grow towards the greater level achieved by the incomplete scenario. This level of success would then, again, be different for the populations of individuals of different types. Therefore, while a sufficiently small population would feel no difference in selective force based on the affiliation preference, as the population grew, a population of type C would become much more organizationally successful than a population of type B, which would in turn be slightly more successful than a population of type P.

Diversity in social preference

In each of these experiments, the populations examined have been comprised of individuals with the same affiliation preference. However, it is equally possible during the course of the evolution of social organization, that the same population could foster individuals with different affiliation preferences. Either these different preferences could be the result of phenotypic

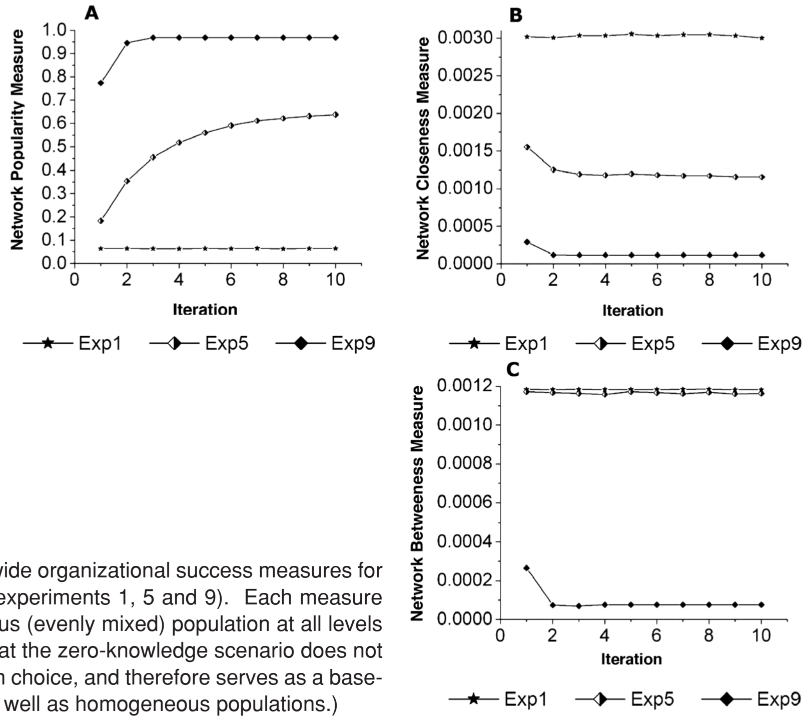


Fig. 5. Resulting population-wide organizational success measures for heterogeneous populations (experiments 1, 5 and 9). Each measure is shown for the heterogeneous (evenly mixed) population at all levels of knowledge. (Again, note that the zero-knowledge scenario does not involve any informed affiliation choice, and therefore serves as a baseline for the heterogeneous as well as homogeneous populations.)

plasticity in the expression of a single genetic basis for social affiliation preference, or else new mutations might arise over time, altering the preference measure used to make such choices. Regardless of how it came about, it is possible that the need for, or the capability of, achieving more complicated social organizations stemmed from a diversity of social preference within single populations.

Indeed, in a (nearly) evenly mixed population (~1/3 of each individual type; experiment 5), the organizational successes achieved under the measures of Closeness and Popularity were substantially less (by ~1/3) than the successes achieved under the same measures in the homogeneous populations (experiments 3 and 4, respectively), and only ~2/3 and ~1/3 (respectively) of the highest success achieved (in experiment 1, the zero-knowledge Random scenario, or experiment 8, the complete-knowledge scenario in populations of type P; *see* Fig. 3A and B as compared with Fig. 5A and B). Recall that these two measures represented the "simpler" affiliation choice metrics.

In contrast, Betweenness, the measure chosen to represent a more complex, and therefore potentially more evolved, affiliation choice metric, performed better in a heterogeneous population than it did in a homogeneous population. Not only did the social organization stabilize immediately (within the first 20 iterations), but the level of organizational success achieved was nearly that achieved by the zero-knowledge Random scenario, outperforming the declining success of its homogeneous counterpart (*see* Fig. 5C). Therefore, if selective pressure was acting to maximize organizational success under either the Closeness or Betweenness measures, and the population had been purely of either type P or type B individuals, the evolution of new affiliation preferences could have increased the population's success without requiring a shift in the selective pressure. Additionally, if the population had been of type C, the shift towards a heterogeneous population would not have lowered the Betweenness measure success of the social organization, though it would have lowered success of the population under the Closeness measure. In the analogous cases of selective pressure acting to maximize organizational success under the Popularity measure, if the original populations had been of type C, it would also be the case that the move towards a heterogeneous population would increase organizational success. This result reveals how the evolution of different social choice behaviors could have been favored, or at very least been transparent to, selective pressure.

Lastly, incorporating complete knowledge into a heterogeneous population (experiment 9) showed no difference in behavior from homogeneous populations according to the Popularity and Closeness measures, but did slightly improve the success under the Betweenness measure (*see* Fig. 5). This may reflect a trade-off between knowledge-level and uniformity of preference within the population. The order of the height of the organizational success achieved by each of these experimental scenarios (*see* Table 2) provides a first glimpse into how these trade-offs might have affected the evolution of social organization. Further studies investigating many of these effects by altering the proportion of individuals of each type within population are now in the early stages of completion.

Summary and conclusions

Each of these scenarios provides a different level of insight into the processes of evolutionary progress towards the incredible complexity of social groups. From the zero-knowledge experiments, we can infer how social groups may have organized prior to the evolution of individual social choice. From the complete-knowledge experiments, we can see how the impact of this sort of newly evolved behavior could have affected smaller populations. From the incomplete-knowledge experiments we can see how the growth of a population to larger sizes can affect the organization of individuals with social preferences. Lastly, from the heterogeneous populations, we can see how more complex social preferences could have evolved from an initially simple set of individual-level choices. Further work is needed to analyze the individual-level success of particular affiliation choices within each of the experimental scenarios studied. These future investigations will reveal whether or not individual fitness is acting in concert with or contrary to organizational success and stability.

Table 2. The resulting ranks of the organizational success achieved under each measure by each of the experiments. (Ranked from highest to lowest, with experiments yielding equivalent success assigned the same ranks.) Notice that the experiments in which the population's organizational success was highest under the Betweenness or Closeness measures yielded the lowest successes under the Popularity measure, and vice versa.

Experiment	Popularity measure ranks	Closeness measure ranks	Betweenness measure ranks
1	6	1	1
2	3	4	4
3	5	2	3
4	2	5	5
5	4	3	2
6	1	7	7
7	1	6	7
8	1	7	7
9	1	7	6

It has long been known that highly complex behaviors of systems in biology, from the molecular to the ecosystem level, can be produced by very simple, local rules applied to individuals comprising the system (cf. Camazine *et al.* 2003). While it is obvious that the evolution of such local rules must have been the result of selective pressures acting on individuals, it is possible that the system-wide effects impacted the individual fitness of the system's members, either positively or negatively, and may therefore also have played an important part in the evolution of these behaviors. While these three measures may, of course, not have been the social affiliation metrics involved in such evolution, these scenarios provide a first understanding of how such complex social organizations may have been favored by selection after the initial evolution of social groups had already occurred. We feel that this focus on the evolution of organizational complexity within already social groups can make a valuable contribution to the fundamental understanding of the evolutionary progression in sociobiology.

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