Current Zoology, 2016, 62(3), 207–214
doi: 10.1093/cz/zow052
Advance Access Publication Date: 28 April 2016
Article

Article

Exploration of unpredictable environments by networked groups

Takao Sasaki[a,b,*], Marco A. Janssen[c], Zachary Shaffer[a], and Stephen C. Pratt[a]

[a]School of Life Sciences and Center for Social Dynamics and Complexity, Arizona State University, Tempe AZ 85287-4501, USA, [b]Department of Zoology, University of Oxford, OX1 3PS, UK, and [c]School of Sustainability and Center for Behavior, Institutions and the Environment, Arizona State University, Tempe, AZ 85287-5502, USA

*Address correspondence to Takao Sasaki. E-mail: takao.sasaki@zoo.ox.ac.uk.

Received on 17 March 2015; accepted on 30 June 2015

Abstract

Information sharing is a critical task for group-living animals. The pattern of sharing can be modeled as a network whose structure can affect the decision-making performance of individual members as well as that of the group as a whole. A fully connected network, in which each member can directly transfer information to all other members, ensures rapid sharing of important information, such as a promising foraging location. However, it can also impose costs by amplifying the spread of inaccurate information (if, for example the foraging location is actually not profitable). Thus, an optimal network structure should balance effective sharing of current knowledge with opportunities to discover new information. We used a computer simulation to measure how well groups characterized by different network structures (fully connected, small world, lattice, and random) find and exploit resource peaks in a variable environment. We found that a fully connected network outperformed other structures when resource quality was predictable. When resource quality showed random variation, however, the small world network was better than the fully connected one at avoiding extremely poor outcomes. These results suggest that animal groups may benefit by adjusting their information-sharing network structures depending on the noisiness of their environment.

Key words*:* agent-based model, collective cognition, conformity, small world networks, speed–accuracy trade-off.

Social animals often share information relevant to foraging behavior, habitat choice, and other critical decisions (Krause and Ruxton 2002; Gordon 2010; Seeley 2010; Sumpter 2010). The pattern of sharing can be modeled as a network in which nodes are group members and edges connect individuals that share information with one another (Wey et al. 2008; Krause et al. 2009; Blonder and Dornhaus 2011; Tokuda et al. 2012; Waters and Fewell 2012; Mann et al. 2012; Cantor and Whitehead 2013; Greening et al. 2015; Pinter-Wollman 2015; Brent, 2015). Sharing may occur via signals produced by natural selection to convey information (e.g., alarm calls (Hollén and Radford 2009), recruitment to food sources (Czaczkes et al. 2015), or fertility signals (Le Conte and Hefetz 2008)) or by incidental cues that animals use opportunistically to guide their behavior (e.g., imitating the actions of a successful forager (Galef and Giraldeau 2001) or responding to the movements of a fellow group member (Meunier et al. 2006; Ward et al. 2008)). The structure of an information-sharing network can affect the decision-making performance of individual members as well as that of the group as a whole (Krause et al. 2009; Sih et al. 2009; Croft et al. 2011; Bode et al. 2012; Pinter-Wollman et al. 2014). For example, harvester ant colonies *Pogonomyrmex barbatus* have a minority of workers that interact significantly more often with others in the nest (Pinter-Wollman et al. 2011). This skewed distribution of connections expedites information flow, enhancing the colony's ability to make fast and accurate decisions. Analysis of animal social networks can aid in deciphering underlying mechanisms of collective decision making (Wey et al. 2008).

Animal groups can vary in the degree to which each member is directly connected to others. For example, a group may be relatively well mixed, with all members equally likely to interact with one

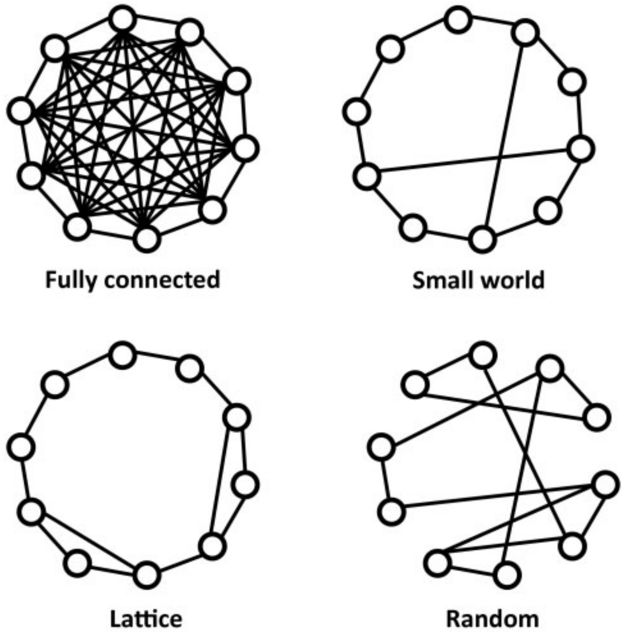

Figure 1. Examples of the 4 network structures examined. Each has 10 agents and 12 connections, except for the fully connected network, which has 45 connections. Circles and lines represent agents and connections, respectively.

another, or it may be subdivided into clusters based on relatedness, age, or sex, with members more likely to interact within than across clusters (Krause et al. 2014). Methods of communication may also vary from broadcast signals that rapidly spread information throughout the group (e.g., Blumstein and Daniel 2004), to more local signals detected by only one or a few members (e.g., Richardson et al. 2007). The resulting differences in network structure are likely to affect how well individuals gather accurate information about their environment. Insofar as individuals benefit from the rapid spread of important information, we might expect the best network structure to be a fully connected one, in which each member can directly transfer information to all other members. Such a network, however, would also rapidly spread inaccurate information that can result from individual assessment errors, leading group members to make suboptimal choices. Thus, an optimal network should balance sharing of currently available knowledge with opportunities to gather new information for a more accurate assessment of the environment. In fact, computer simulations show that less connected network structures can collectively outperform more connected ones in complex environments where the best option is hard to discover (Lazer and Friedman 2007; Mason et al. 2008; Mason and Watts 2012). This is because a fully connected network allows the rapid spread of information about easily discovered suboptimal options, settling everyone's choice before the best option becomes known. In contrast, slower information spread in sparser networks makes them less likely to get stuck on suboptimal local peaks before finding the global optimum. These results suggest that the relative performance of different network structures depends highly on the environment.

In this study, we examined how social network structure affects a group's ability to discover resource peaks. We tested idealized structures that differ in features important to real animal social networks, particularly the degree of local clustering and the number of fellow group members directly contacted by each individual (Pinter-Wollman et al. 2014; Krause et al. 2014). Our goal was to explore the effects of these general network attributes on a group's ability to thoroughly explore its environment. Although we did not model a specific biological context, the problem we examined is similar to that faced by a social group looking for food, water, nesting sites, or other resources that are distributed unevenly in the environment.

In addition to resource distribution, we further explored the role of resource predictability. If animals make error-prone assessments of resource quality, or if the environment varies randomly over time, then an individual's assessment of current gains may have limited ability to predict future gains. For example, consider 2 foraging areas, one of which is more profitable than the other. When future gains are perfectly predicted by current experience, it is relatively easy to differentiate them, because gains at one area always exceed those at the other. When gains are less predictable, however, it becomes hard to discriminate between sites because the inferior one can sometimes be more profitable than the superior one. This could affect the value of information sharing and thus the efficacy of different network structures in maximizing resource acquisition. To test this possibility, we manipulated environmental predictability and investigated how it affected the performance of different network structures. We first measured collective performance of 4 distinct network structures exploring 3 different payoff distributions in a perfectly predictable environment. We then repeated the same analysis in an environment made less predictable by the addition of assessment error.

Materials and Methods

Model description

We follow the Overview, Design concepts, and Details (OOD) protocol, a standard format for describing agent-based models (Grimm et al. 2006; 2010). Models were created in Netlogo (version 5.1.0) (Wilensky 1999) and are available at OpenABM (https://www.openabm.org/model/4581/version/1/view).

Purpose

The purpose of this study was to explore the relative performance of different network structures in situations where group members receive unreliable information about their environment. Our model was based on the self-, social-, and exploration-based choices (SSEC) model developed by Goldstone et al. (2008) and Mason et al. (2008). Our methods (described below) followed theirs, except where noted.

Network types

We used 4 types of networks: fully connected, small world, lattice, and random (Figure 1). In the fully connected network, every agent was connected to every other agent. In the small world and lattice networks, all agents were connected to their immediate 2 neighbors, and some agents were also connected to a third agent at either a far distance (small world) or a close distance (lattice). In the random network, agents were connected randomly. Each network had 10 agents and a total of 12 connections, except the fully connected network, which had 45 connections.

Payoff distributions

In each round, an agent chose a number between 0 and 100. Each number was associated with a specific payoff according to 1 of 3 continuous payoff distributions: unimodal, trimodal, and needle (Figure 2). Each distribution had a single global maximum, and thus

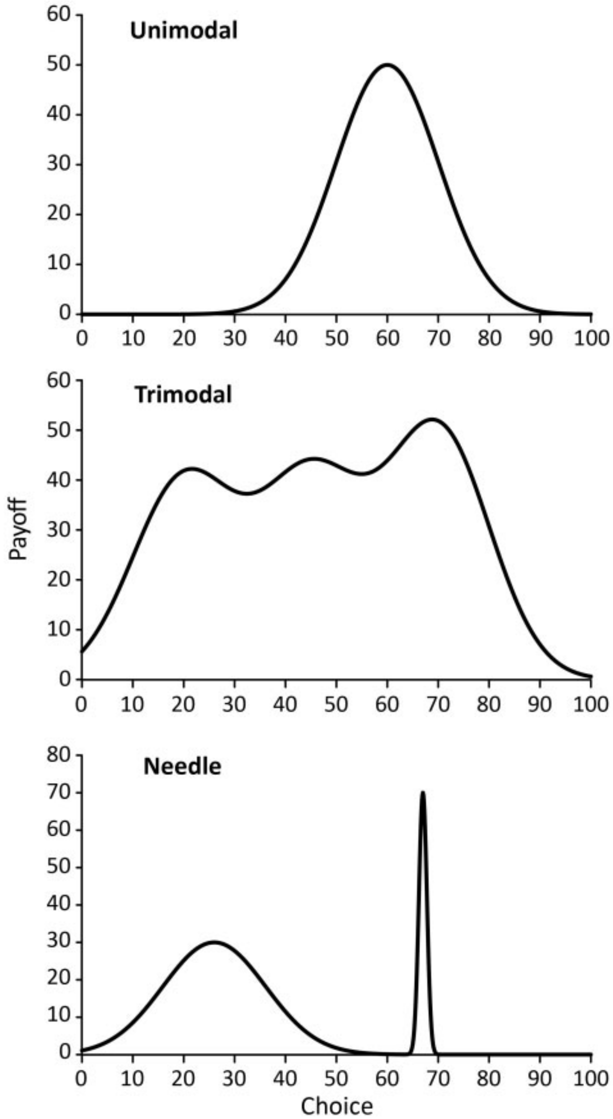

Figure 2. The 3 payoff distributions used in simulations. All are described by Equation 1, using different parameter values (given in Table 1).

1 "correct" choice, but the trimodal and needle distributions had additional lower peaks. All 3 distributions can be mathematically described as:

$$f(x) = a_1 \exp\left(-(b_1(x-c_1))^2\right) + a_2 \exp\left(-(b_2(x-c_2))^2\right) + a_3 \exp\left(-(b_3(x-c_3))^2\right) \quad (1)$$

The parameter values for each distribution are summarized in Table 1. The unimodal, trimodal, and needle payoffs represent successively greater challenges to discovery of the best resource: for the unimodal distribution, agents will find the peak as long as they move up a gradient of performance. For the trimodal distribution, they face the risk of getting stuck on a local peak and missing the global maximum. For the needle distribution, the global maximum is still harder to find because it is much narrower than the competing local maximum.

In the first experiment, the payoff function determined the exact payoff received by an agent choosing value x. In the second experiment, the function's output was added to a noise term drawn from a normal distribution with mean zero and standard deviation 10. This random component modeled resource unpredictability resulting from assessment noise or environmental change over time.

Table 1. Parameters used in Equation 1 to produce the 3 payoff distributions

Distribution	a_1	a_2	a_3	b_1	b_2	b_3	c_1	c_2	c_3
Unimodal	50	0	0	0.07	0	0	60	0	0
Trimodal	40	40	50	0.07	0.07	0.07	20	45	70
Needle	30	70	0	0.07	0.9	0	26	67	0

Parameters a_i, b_i, and c_i determine, respectively, the payoff for peak i, the variance around the peak, and its position. Parameter b is inversely related to variance, so larger values indicate narrower peaks.

Agent strategies

On every round, each agent probabilistically chose 1 of 3 strategies:

Stay: The agent chooses the same number it did on the previous round.

Best: The agent chooses the number that paid the most among its directly connected neighbors in the previous round.

Random: The agent chooses a number randomly.

In the first round, all agents used the random strategy. As the simulation progressed, agents updated their probabilities of choosing each strategy according to their own payoff history. That is, the higher the payoffs previously earned using a given strategy, the more likely that strategy was to be used again. Probabilities were calculated from a baseline of 45% for each of the first 2 strategies and 10% for the third.

Process overview and scheduling

Each simulation started with creation of 1 of the 4 network types. It then progressed through 15 rounds, during which each agent in the network chose a decision strategy and then used it to make a choice. After each round, the agents updated their strategy probabilities according to the outcome of their choice. After every 15-round session, a new network was generated and all the parameters were re-initialized. For each network structure, 500 15-round simulations were run for each of the 3 payoff distributions.

At the end of each simulation, we measured the group's performance by counting the number of agents that came within a specified distance of the global maximum. This distance was 8 for the unimodal and trimodal distributions and 4 for the needle distribution.

We conducted 2 experiments. In the first experiment, there was no noise, and we measured performance of all 4 network types for all 3 payoff distributions. In the second experiment, we added noise and similarly measured network performance.

Statistical analysis

Data were analyzed via Kruskal–Wallis, Nemenyi, Mann–Whitney–Wilcoxon, and χ^2 tests, as detailed in the results. The statistical package R (v. 3.1.1) was used for all analyses.

Results

In the absence of noise, the fully connected network outperformed the other networks for the unimodal and trimodal distributions and performed statistically indifferently for the needle distribution (Figure 3A). That is, agents in the fully connected network reached

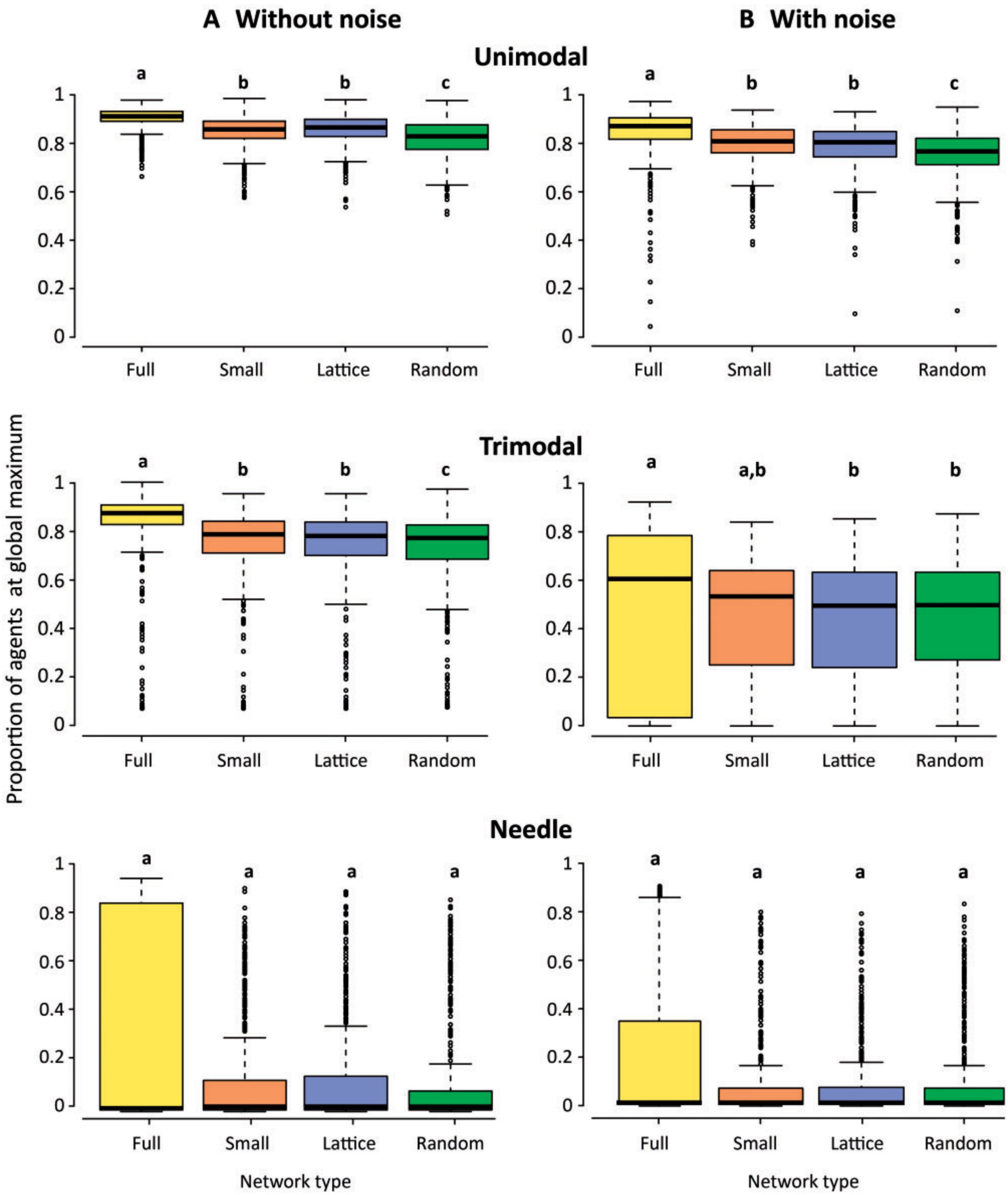

Figure 3. Performance of each network for 3 payoff distributions in environments where noise was absent (A) or present (B). In the noise-free environment, the fully connected network (labeled "Full") outperformed the others in the unimodal and trimodal distributions, and tied the others in the needle distribution. In the noisy environment, the fully connected network similarly outperformed the others, except in the trimodal payoff distribution, where the small world network did as well, on average. Different letters indicate significant differences between networks (Kruskal–Wallis test followed by multiple comparisons using Nemenyi tests, $P < 0.05$). Boxes indicate the lower and upper quartiles. Horizontal lines within boxes indicate the median, whiskers extend to the 1.5 interquartile range from the box, and open circles are outliers.

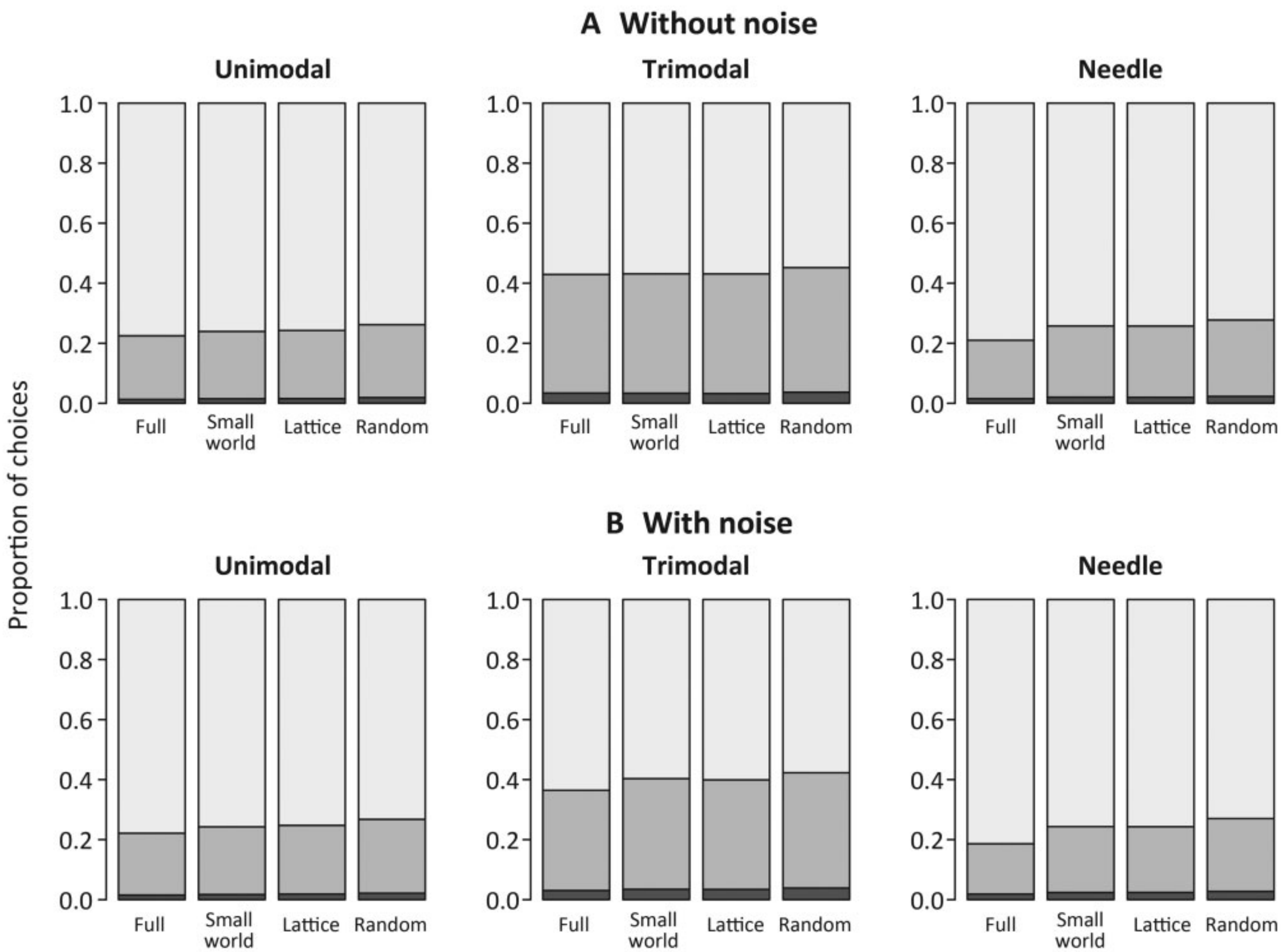

Figure 4. Decision strategies used by agents in environments where noise was absent (A) or present (B). Bar heights show the proportion of all decisions made according to the Best (light gray), Stay (medium gray), and Random (dark gray) strategies, for each combination of payoff distribution and network type. For each combination, the number of times each strategy was used was summed over all agents, rounds, and runs and the proportion of each strategy was calculated. The first round (when all agents were required to use the Random strategy) was not included in the calculation.

the global payoff maximum at least as often as agents in the other networks, regardless of the distribution. As expected, performance varied across payoff distributions, with the highest proportion of agents finding the peak in the unimodal distribution, a somewhat lower proportion doing so in the trimodal distribution, and a much lower proportion succeeding in the needle distribution. Agents most often used the Best strategy, and very few used the Random strategy (Figure 4A). Payoff distribution had little effect on strategy choice, except that agents were more likely to choose the Stay strategy under the trimodal distribution. Strategy choice varied little among the different network types (Figure 4A).

We performed the second experiment to determine whether the dominance of the fully connected network would persist in a noisy environment. The results showed that it did, except for the trimodal payoff distribution, where the small world network did about as well (Figure 3B). Looking more closely at the trimodal case, the 2 network types had the same median performance (Nemenyi test: $q = 1.9$, $P = 0.20$), but a significantly different distribution of performance (Chi-squared test: $\chi^2 = 211.0$, $\mathrm{df} = 9$, $P < 0.01$) (Figure 5B). The fully connected network often performed very well—in one-third of simulations over 80% of agents reached the global maximum. However, it also often missed the peak completely—in another one-third of simulations fewer than 10% of agents reached the peak. In contrast, the small world network rarely performed at either extreme. Instead, in over two-thirds of simulations 50–80% of agents reached the peak. These distributions are different from those seen in the environment without noise, where both network types showed similar left-skewed frequency distributions (Figure 5A). Strategy choice followed the same pattern seen in the absence of noise (Figure 4).

For the noisy environment, we also looked at how performance changed over 15 rounds. With the unimodal payoff distribution (Figure 6A), all networks showed improved performance over time, with the fully connected network improving more rapidly at first but reaching a plateau after 5–6 rounds. The small world network eventually caught up in performance, and the lattice and random networks lagged somewhat behind. A similar pattern was seen with the trimodal distribution, but the plateau was lower and was reached more slowly (Figure 6B). For the needle network, all networks started at a low level of performance and declined similarly over the 15 rounds (Figure 6C).

Discussion

The principal result of this study is that a fully connected network is always at least as good as other network structures at maximizing

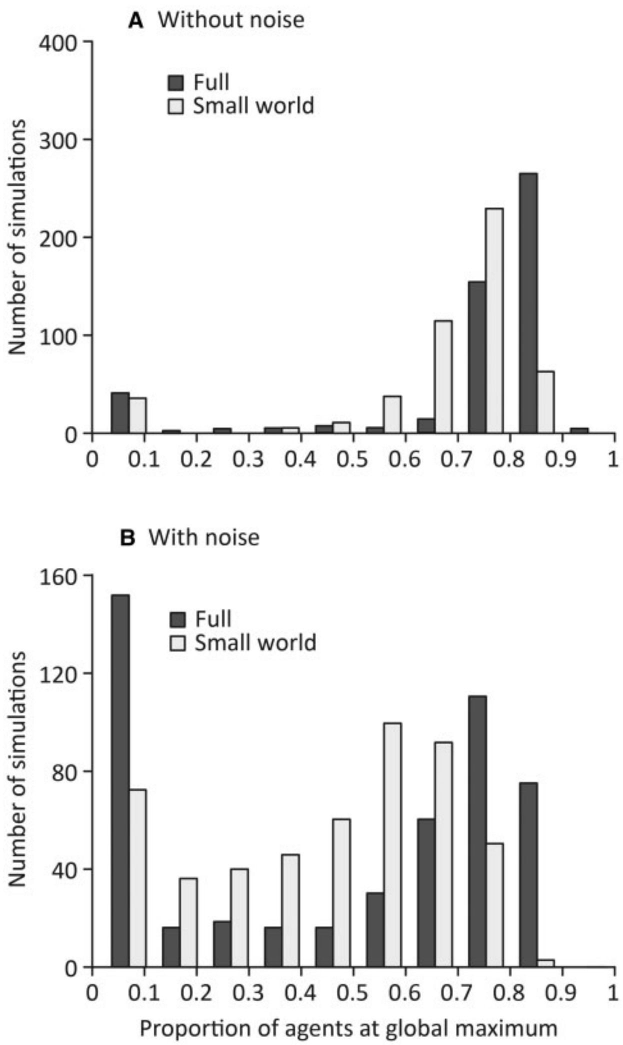

Figure 5. Frequency distribution of performance (i.e., proportion of agents at the global maximum) when noise was absent (A) or present (B). When noise was absent, both the fully connected and small world networks showed left-skewed frequency distributions, though the patterns were different ($\chi^2_9 = 244.0$, $P < 0.01$). When the noise was present, however, the fully connected network showed a bimodal distribution, with peaks at very high and very low performance. In contrast, the small world network showed a single peak at moderately high performance ($\chi^2_9 = 211.0$, $P < 0.01$).

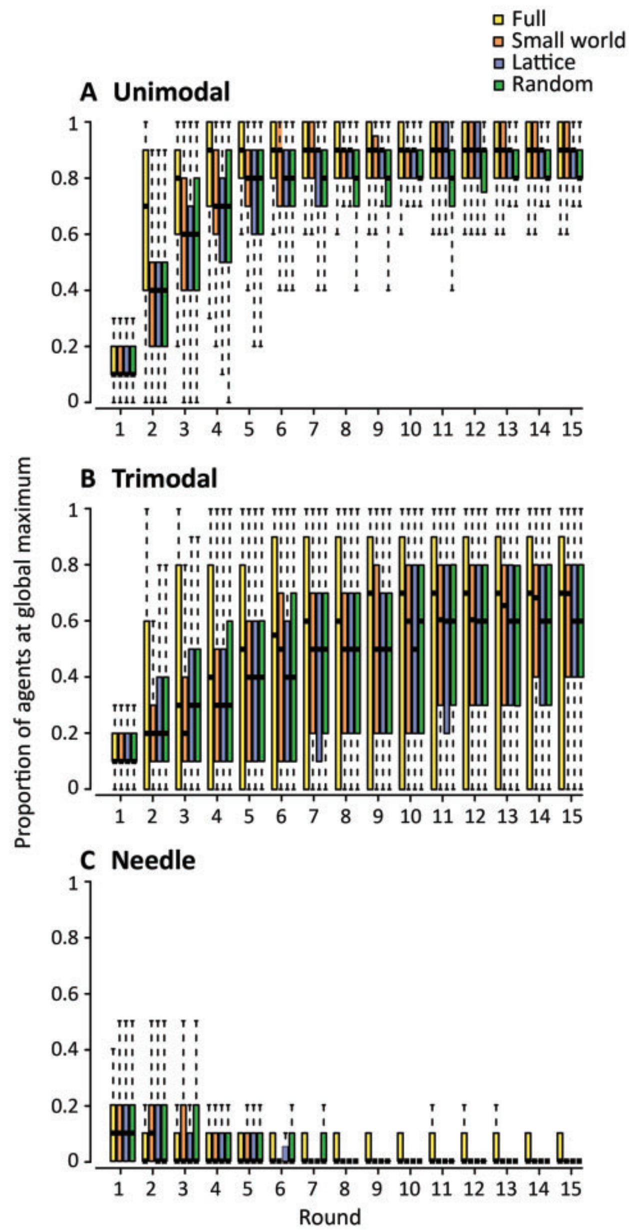

Figure 6. Performance of the 4 network structures over 15 rounds of search in a noisy environment, for 3 different payoff distributions: (A) unimodal, (B) trimodal, and (C) needle. For the unimodal and trimodal distributions, the fully connected network initially performed better, but the small world network eventually caught up. In the trimodal distribution, however, the small world network showed less variation in performance than did the full network. For the needle distribution, all networks performed similarly, and declined in performance over time. Boxes indicate the lower and upper quartiles, and horizontal lines within boxes indicate the median. Brackets indicate the range, except for outliers (omitted for clarity).

payoff, regardless of how resources are distributed in the environment. This differs from the findings of earlier studies that used the same network topologies and payoff distributions examined by us (Goldstone et al. 2008; Mason et al. 2008). Those studies reported that groups are better at finding obscure global peaks when their information-sharing networks have high levels of local connectivity: i.e., clusters of individuals that are well connected with each other but weakly connected to members of other clusters. This clustering is argued to enhance exploration by dividing the group into relatively independent subsets that more effectively search the space of possible solutions. That is, each subset has time to find distinct solutions rather than being rapidly converted to the first local peak that is found. Thus, according to these studies, the fully connected network performs best for the unimodal payoff, in which the single peak can be easily found with relatively little exploration. The more clustered small world network does best for the more challenging trimodal distribution, whereas the highly clustered lattice network does best for the needle distribution, where the hard-to-find global maximum places a premium on thorough exploration.

Our simulations did not replicate the pattern seen in these previous studies (Goldstone et al. 2008; Mason et al. 2008). Instead we found that the fully connected network, on average, performed as well as or better than the other networks for all distributions. We saw a similar pattern to the earlier studies for the unimodal case, but a very different outcome for the needle distribution, where all network types performed at a similarly low level. For the trimodal case, we saw some advantage for the small world network, but different from that seen in the previous work, which found that the small world network rose in performance more rapidly in early rounds. In our simulations, the median performance of the small world network did not exceed that of the fully connected network at any point. Instead, we found that it achieved a lower variance in performance, consistently achieving a moderately good outcome without either of the extremes that were common for the fully connected network. In short, the fully connected network achieved the best average performance for all distributions, but the small world network showed lower variance in performance for a more challenging payoff distribution (trimodal).

We attribute the difference between our results and those of Goldstone et al. (2008) and Mason et al. (2008) to their use of different distributions of local and global maxima for different networks. Specifically, they placed the global maximum for the small world network in the middle of 2 local maxima and relatively close to them. Therefore, when agents reached the local maxima, they could easily move on to the global maximum. In contrast, the peak for the fully connected network was far from the local maxima. Agents were therefore more likely to get stuck at the isolated local peak. Because we used the same payoff distribution for all networks, our results did not confound network effects with distribution effects.

Despite the difference between our results and those of the earlier studies (Goldstone et al. 2008; Mason et al. 2008), our findings also support some advantage of greater clustering in environments that reward exploration. When local maxima were present, the fully connected network performed very badly a significant proportion of the time. This can be interpreted as too-rapid propagation of the discovery of a local peak, cutting short the group's search and preventing discovery of the best solution (Lazer and Friedman 2007). This effect was most obvious for the trimodal distribution. An even more pronounced effect might have been expected for the needle distribution, with its better-hidden global maximum. This was not the case, but this may have been due to the extremely low performance of all networks for this distribution, making it difficult to distinguish relative performance.

Besides the interaction between payoff distribution and network structure, our other major finding was the importance of assessment noise. In the absence of noise, the small world network showed clearly inferior performance, meaning that groups gained no advantage from the more thorough exploration afforded by highly local connections. High locality comes at the cost of slower propagation, because each agent has limited connectivity with agents outside its local group, and thus cannot rapidly learn if an outsider finds the best solution. When assessments are not obscured by noise, groups do better to rapidly share information in a fully connected network, regardless of payoff distribution.

Our finding of a strong influence of assessment noise implies that animal groups face context-dependent trade-offs in the best way to share information. When assessment noise is low, thorough information sharing over a dense network may be best. When noise is high and getting trapped on a suboptimal local maximum is a danger, then a less-connected, small world network may be better rewarded. The latter may be especially the case when poor outcomes are disproportionately costly, making it better to reduce variance of outcomes, even at the cost of sometimes falling short of the very best performance (Kacelnik and El Mouden 2013).

If the best network structure depends on environmental context, then we predict that animal groups may adaptively change their behavior to achieve different structures according to their current circumstances. Several species show evidence of different network structures across years or seasons (Smith et al. 2010; de Silva et al. 2011; Brent et al. 2013; Godfrey et al. 2013). It is not clear whether these changes have anything to do with information sharing, but there is evidence that an individual's place within a social network can influence its ability to acquire new information about its environment (Lusseau 2007; Aplin et al. 2012; Brent 2015). Our results suggest that future research would benefit from considering how network structure as a whole influences information gathering, and whether this structure varies adaptively according to environmental predictability.

Funding

This work was supported by the National Science Foundation (Grant 1012029).

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