Exploration of unpredictable environments by networked groups

Takao Sasaki\textsuperscript{a,b,*}, Marco A. Janssen\textsuperscript{c}, Zachary Shaffer\textsuperscript{a}, and Stephen C. Pratt\textsuperscript{a}

\textsuperscript{a}School of Life Sciences and Center for Social Dynamics and Complexity, Arizona State University, Tempe AZ 85287-4501, USA, \textsuperscript{b}Department of Zoology, University of Oxford, OX1 3PS, UK, and \textsuperscript{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.

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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 \textit{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
In this study, we examined how social network structure affects 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...
1 “correct” choice, but the trimodal and needle distributions had additional lower peaks. All 3 distributions can be mathematically described as:

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

(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.

### 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 \(\chi^2\) 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

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**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.
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.
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: $\chi^2 = 211.0, df = 9, P < 0.01$) (Figure 5B). The fully connected network often performed very well—in one-third of simulations over 80% of agents reached the 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
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.

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References
Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC, 2012. Social networks predict patch discovery in a wild population of songbirds. Proc R Soc B: Biol Sci 279:4199–4205.
Blonder B, Dornhaus A, 2011. Time-ordered networks reveal limitations to information flow in ant colonies. PLoS ONE 6:20298.
Blumstein DT, Daniel JC, 2004. Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to calls from juveniles. Ani Behav 68:1257–1265.
Bode NW, Wood AJ, Franks DW, 2012. Social networks improve leaderless group navigation by facilitating long-distance communication. Carr ZooL 58:329–341.
Brent LJN, 2015. Friends of friends: Are indirect connections in social networks important to animal behaviour? Ani Behav 103:211–222.
Brent LJN, MacLarnon A, Platt ML, Semple S, 2013. Seasonal changes in the structure of rhesus macaque social networks. Behav Ecol Sociobiol 67:349–359.
Cantor M, Whitehead H, 2013. The interplay between social networks and culture: Theoretically and among whales and dolphins. Phil Trans R Soc B: Biol Sci 368:20120340.
Croft DP, Madden JR, Franks DW, James R, 2011. Hypothesis testing in animal social networks. Tren Ecol Ecol 26:502–507.
Czaezkes TJ, Gruter C, Ramnieks FLW, 2015. Trai pheromones: An integrative view of their role in social insect colony organization. Ann Rev Entomol 60:581–599.
De Silva S, Ranjeewa ADG, Kryazhimskiy S, 2011. The dynamics of social networks among female Asian elephants. BMC Ecol 11:17.
Galef BG, Girardeau L-A, 2001. Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. Ani Behav 61:3–15.
Godfrey SS, Sih A, Bull CM, 2013. The response of a sleepy lizard social network to altered ecological conditions. Ani Behav 86:763–772.
Goldstone RL, Roberts ME, Mason W, 2008. Collective search in concrete and abstract spaces. In: Kugler T, Smith JC, Connolly T, Son Y-J, editors. Decision Modeling and Behavior in Complex and Uncertain Environments. Berlin: Springer, 277–308.
Gordon DM, 2010. Ant Encounters. Princeton: Princeton University Press.
Greening BR, Pinter-Wollman N, Fefferman NH, 2015. Higher-order interactions: Understanding the knowledge capacity of social groups using simplicial sets. Carr ZooL 6:114–127.
Grimm V, Berger U, Bastiansen F, Elsassen S, Ginot V et al., 2006. A standard protocol for describing individual-based and agent-based models. Ecol Model 198:115–126.
Grimm V, Berger U, DeAngelis DL, Polhill JG, Goske J et al., 2010. The ODD protocol: A review and first update. Ecol Model 221:2760–2768.
Hollen LL, Radford AN, 2009. The development of alarm call behaviour in mammals and birds. *Ani Behav* 78:791–800.

Kacelnik A, El Mouden C, 2013. Triumphs and trials of the risk paradigm. *Ani Behav* 86:1117–1129.

Krause J, James R, Franks N, Croft D, 2014. *Animal Social Networks*. Oxford: Oxford University Press.

Krause J, Lusseau D, James R, 2009. Animal social networks: An introduction. *Behav Ecol Sociobiol* 63:967–973.

Krause J, Ruxton GD, 2002. *Living in Groups*. Oxford: Oxford University Press.

Lazer D, Friedman A, 2007. The network structure of exploration and exploitation. *Admin Sci Quart* 52:667–694.

Le Conte Y, Hefetz A, 2008. Primer pheromones in social Hymenoptera. *Ann Rev Entomol* 53:523–542.

Lusseau D, 2007. Evidence for social role in a dolphin social network. *Evol Ecol* 21:357–366.

Mann J, Stanton MA, Patterson EM, Bienenstock EJ, Singh LO, 2012. Social networks reveal cultural behaviour in tool-using using dolphins. *Nat Comm* 3:980.

Mason WA, Jones A, Goldstone RL, 2008. Propagation of innovations in networked groups. *J Exp Psych: Gen* 137:422–433.

Mason W, Watts DJ, 2012. Collaborative learning in networks. *Proc Nat Acad Sci* 109:764–769.

Meunier H, Leca JB, Deneubourg J-L, Petit O, 2006. Group movement decisions in capuchin monkeys: The utility of an experimental study and a mathematical model to explore the relationship between individual and collective behaviours. *Behaviour* 143:1511–1527.

Pinter-Wollman N, 2015. Persistent variation in spatial behavior affects the structure and function of interaction networks. *Curr Zool* 61:98–106.

Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D et al., 2014. The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behav Ecol* 25:242–255.

Pinter-Wollman N, Wollman R, Guetz A, Holmes S, Gordon DM et al., 2011. The effect of individual variation on the structure and function of interaction networks in harvester ants. *J R Soc Int* 8:1562–1573.

Richardson TO, Sleeman PA, McNamara JM, Houston AI, Franks NR, 2007. Teaching with evaluation in ants. *Curr Biol* 17:1520–1526.

Seeley TD, 2010. *Honeybee Democracy*. Princeton: Princeton University Press.

Sih A, Hanser SF, McHugh KA, 2009. Social network theory: New insights and issues for behavioral ecologists. *Behav Ecol Sociobiol* 63:975–988.

Smith JE, Van Horn RC, Powning KS, Cole AR, Graham KE et al., 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behav Ecol* 21:284–303.

Sumpter DJT, 2010. *Collective Animal Behavior*. Princeton: Princeton University Press.

Tokuda M, Bouli JP, Izar P, Strier KB, 2012. Social cliques in male northern muriquis *Brachyteles hypoxanthus*. *Curr Zool* 58:342–352.

Ward AJW, Sumpter DJT, Couzin ID, Hart PB, Krause J, 2008. Quorum decision-making facilitates information transfer in fish shoals. *Proc Nat Acad Sci* 105:6948–6953.

Waters JS, Fewell JH, 2012. Information processing in social insect networks. *PLoS ONE* 7:e40337.

Wey T, Blumstein DT, Shen W, Jordán F, 2008. Social network analysis of animal behaviour: A promising tool for the study of sociality. *Ani Behav* 75:333–344.

Wilensky U, 1999. *NetLogo*. Evanston: Center for Connected Learning and Computer-Based Modeling, Northwestern University.