Furbook or Featherbook?

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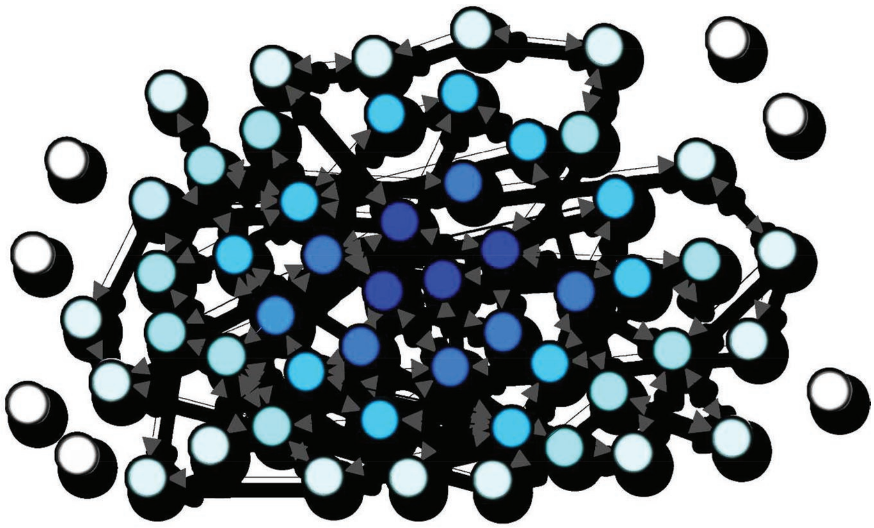
Social network analysis: Old questions, new tools

It was the study of terrorism networks that sparked the idea. Dan Blumstein was part of an interdisciplinary collaboration exploring "Darwinian security," involving security experts and academics studying evolution, ecology, human behavior, anthropology, and sociology. As Blumstein dived into the literature, learning about the statistics describing group stability in terrorism networks, he realized that the network approach could be applied to other behavioral questions. "A number of people had already begun using network thinking when studying food webs," he says. In discussion with some of them, he began thinking about the sorts of questions one could answer by applying network tools to animal behavior.



This figure depicts a rhesus macaque social network. The circles are individual monkeys. The lines connect monkeys who are grooming partners. Monkeys who are more socially connected (those in the center of the figure who have a greater number of direct and indirect connections) are darker blue. Image: Lauren Brent.

Blumstein, professor and chair of the Department of Ecology and Evolutionary Biology at the University of California, Los Angeles, was part of the first wave of researchers who began applying network thinking to animal-behavior questions. That was about a decade ago. Now, social network analysis is a flourishing research tool that is gaining momentum.

Since the early 2000s, research publications on social networks have proliferated. In June 2015, at an Animal Behavior Society symposium dedicated to the study of social networks, held in Anchorage, Alaska, Tina Wey explained that social-network structure provides a window to group living. It can help researchers understand "what the consequences are of the existence of social organization for individuals within those groups," said Wey, a former doctoral student with Blumstein and now a postdoctoral researcher at New Mexico State University. The harnessing of network thinking and analysis is allowing researchers to probe a diversity of questions about the transmission of disease, information, and culture. Social-network analysis is also a technique that provides new ways to investigate ecological processes such as dispersal.

Social-network statistics allow a variety of ways to think about how individuals are connected to one another, explains Blumstein. What does it mean to quantify a social network? As explained by Wey, Blumstein, and their colleagues in a 2008 review for *Animal Behaviour*, "Social network analysis is the study of social groups as networks of nodes connected by social ties." In designing social-network studies, "people are still asking questions about the costs and benefits of sociality," says Blumstein. But adopting the network toolkit allows precise ways of thinking about what each of those attributes of sociality might be. Social-network analysis allows the investigation of the same questions that animal-behavior researchers have been asking for decades—but in a more rigorous way.

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Social networks can be conceptualized through spider web–like network diagrams that visualize the organization of nodes (usually representing individuals) in a social context. Several review papers have summarized both the conceptual aspects and terminological aspects of creating and analyzing social networks (see the "Further reading" box). For the uninitiated, the first hurdle in embarking on social-network analyses might be the baffling abundance of social network–specific jargon. A large number of network metrics have been developed, reflecting the large number of attributes that can be investigated. These metrics fall into two main categories: those that describe the properties of individuals and those that describe the properties of the network as a whole. A recent "How To" paper in the *Journal of Animal Ecology* (2015) provides a useful primer explaining how to construct, conduct, and interpret animal social networks and includes a glossary of basic terms. As the authors explain, "The networks that biologists create are analytical representations of a combined set (or subset) of measures of true relationships." In other words, researchers can quantify "observed networks," with the hope that they represent "true" social systems.

The concepts of *degree*, *centrality*, and *betweenness* are three of the key ideas that help unravel what types of questions can be explored by examining social-network structure. *Degree* refers to the number of other animals that the focal individual directly interacts with—that is, how many social interaction partners it has. *Centrality* is a way of denoting how connected or central an individual is in a network. *Betweenness* is a way of measuring the gatekeeping function of particular individuals—the extent to which one individual connects or "brokers" pairs of other individuals that otherwise would not be able to reach each other.

Social network studies of brown spider monkeys* (Ateles hybridus) *in Colombia are shedding new light on the costs and benefits of grooming in disease transmission. Photograph: Wikimedia Commons.

Insights into disease transmission

Scientists have long recognized the importance of social connectivity and network analysis in understanding the transmission of disease. In human public health, this approach has been especially important in the study of HIV/AIDS and other sexually transmitted diseases. But such an approach is also beginning to take hold in the study of disease in free-living animals. Thomas Gillespie applies network analysis as a tool to study intraspecies disease transmission in primates, looking for behavioral interactions that might lead to disease-transmission events. It is an approach that can be challenging, depending on the study species, explains Gillespie, a professor in the Departments of Environmental Sciences and Environmental Health at Emory University. "It's quite difficult to look at interindividual transmission events with chimpanzees, for example," says Gillespie, "because they cover huge areas and the amount of data that we can get on any given day on a certain subset of the group is minimal," he explains.

However, he and his international collaborators recently took a look at the costs of sociality for disease transmission in a population of brown spider monkeys (*Ateles hybridus*) in Colombia. Like their human cousins, these spider monkeys live in what is known as a *fission–fusion society*. That means that over the course of their daily lives, small groups of individuals coalesce into larger groups (fusion) and then disperse into smaller groups (fission) quite frequently. In quantifying the social network of these monkeys, Gillespie and his team closely observed monkey behavior to document a continuous record of the distance between individuals (proximity). They also recorded occasions when monkeys were in actual physical contact during play—grooming, biting, copulation, or communal resting. This allowed them to develop two separate networks representing proximity and contact.

As well as documenting the monkeys' social behaviors, Gillespie and his team measured the richness of gastrointestinal parasite species in each of the individuals within the network, by means of fecal sampling. "These guys are frugivores, so they're pooping all day," explains Gillespie, so carefully collecting offerings for which producers can be confidently assigned reveals an abundance of material for analysis. Increased risk of disease transmission has long been considered a cost of sociality, and previous social-network analyses on lizards and mammals had already demonstrated that highly connected individuals had a greater probability of infection by ectoparasites and bacteria. As described in a 2014 article in *Philosophical Transactions of the Royal Society B*, Gillespie and his colleagues were able to test whether the same was true for gut-dwelling endoparasites. “What we saw very clearly was that individuals who groomed other individuals had a much higher risk of becoming infected with several species of parasites that typically are soil-transmitted helminths,” he says.

To the human eye, one of the benefits of the grooming process appears to be the removal of ectoparasites such as ticks. But those ectoparasites are intermediate hosts for endoparasites, explains Gillespie, so when one animal pulls the tick or flea off the animal it is grooming, in many cases, “they are biting into them, they’re swallowing them, and in the process, potentially infecting themselves.” Additionally, physical contact between two unhygienic individuals leads to the possibility for cross-individual infection. “They don’t have anything equivalent to washing their hands after they go to the bathroom,” explains Gillespie, “so there is fecal contamination in their fur, particularly around the anus,” which is a primary point for grooming. His findings suggest a hidden cost to grooming, which has often been perceived as a beneficial cleaning activity. Hints of this previously unexplored complexity in parasite transmission are “the reason this is really exciting to us,” he says.

Photographic and acoustic sampling off the Galápagos Islands to describe the private social lives of sperm whales. Researchers use photographic records to identify individuals and with whom they interact. They also record the whales’ sounds to eavesdrop on their communication. Photograph: Theresa Kirchner.

Two female sperm whales (Physeter macrocephalus) initiate a synchronized foraging dive off the Galápagos Islands and show their fluke tails. The flukes’ unique patterns of natural markings are used to identify individuals and to track who their social companions are. Photograph: Mauricio Cantor.

Spreading culture: Dolphins, blue tits, marmots

In addition to allowing scientists insights into the spread of harmful parasites and pathogens, social-network analysis opens windows into the spread of information and culture. The interplay between information flow and the structure of relationships in the context of a network is the research quest of Mauricio Cantor at Dalhousie University, in Nova Scotia, Canada. Cantor has examined the spread of *culture*—defined as “group-specific behavior transmitted by social learning”—in dolphins and whales. As in any system in which the goal is to identify the structure of a social network, individuals must be uniquely identifiable. The bottlenose dolphins (*Tursiops aduncus*) Cantor and his collaborators studied, for example, are photo identified by dorsal-fin markings. The researchers then look at the time these dolphins spend together, as obtained from long-term data sets of individuals observed in proximity. Unlike primates, whose specific interactions can often be observed and documented, cetaceans “tend to do all of the cool stuff underwater, so it’s hard to see,” says Cantor.

Nevertheless, by amassing observations collected over many years, Cantor has analyzed the transmission of a unique feeding tactic in dolphins in parts of Brazil where these animals cooperate with artisanal fishermen. Dolphins herd fish schools toward a barrier of fishermen, who then cast their nets when the dolphins signal the right moment. Both dolphins and fishermen catch more and bigger fish by cooperating, but not all dolphins have adopted the strategy. Over time, the behavior spread through the dolphin social network, in a way that could be predicted by diffusion analysis, explains Cantor. “When you map who interacts with whom, and how many individuals adopt the new behavior, you can determine whether the animals are learning from each other or learning by themselves,” he explains.

With his doctoral advisor, Hal Whitehead, Cantor is also investigating the spread of different dialects in sperm whales (*Physeter macrocephalus*) in waters near the Galápagos Islands. Recently published findings in *Nature Communications* suggest that cultural transmission via social networks can lead to different patterns of communication. Modeling different possible modes of transmission for the vocal repertoire of sperm-whale clicks, which form stereotyped patterns known as *codas*, Cantor and his colleagues discovered from their 18-year data set that it is not only in human societies that complex but predictable cultural transmission can create divergence in dialect. Over time, cultural transmission through their social networks has caused the segregation of these whales into “vocal clans.”

Cultural transmission has been anecdotally invoked in the spread of bird behavior by great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) that learned to open the foil lids of milk bottles to steal the rich cream on top. The behavior began in the south of England in the 1920s and, over a period of 20 years, spread over most of Britain. That presumed cultural transmission intrigued Lucy Aplin at the Edward Grey Institute at Oxford University. With an international team of colleagues, she designed an experiment that began in 2012 to cleverly explore the process by which traditions can spread.

***Social network studies on great tits* (Parus major) *in Oxford’s Wytham Woods are facilitated by the microchip tags in their leg bands that allow the continuous automatic tracking of their movements. Photograph: Francis Franklin* [Wikimedia Commons].**

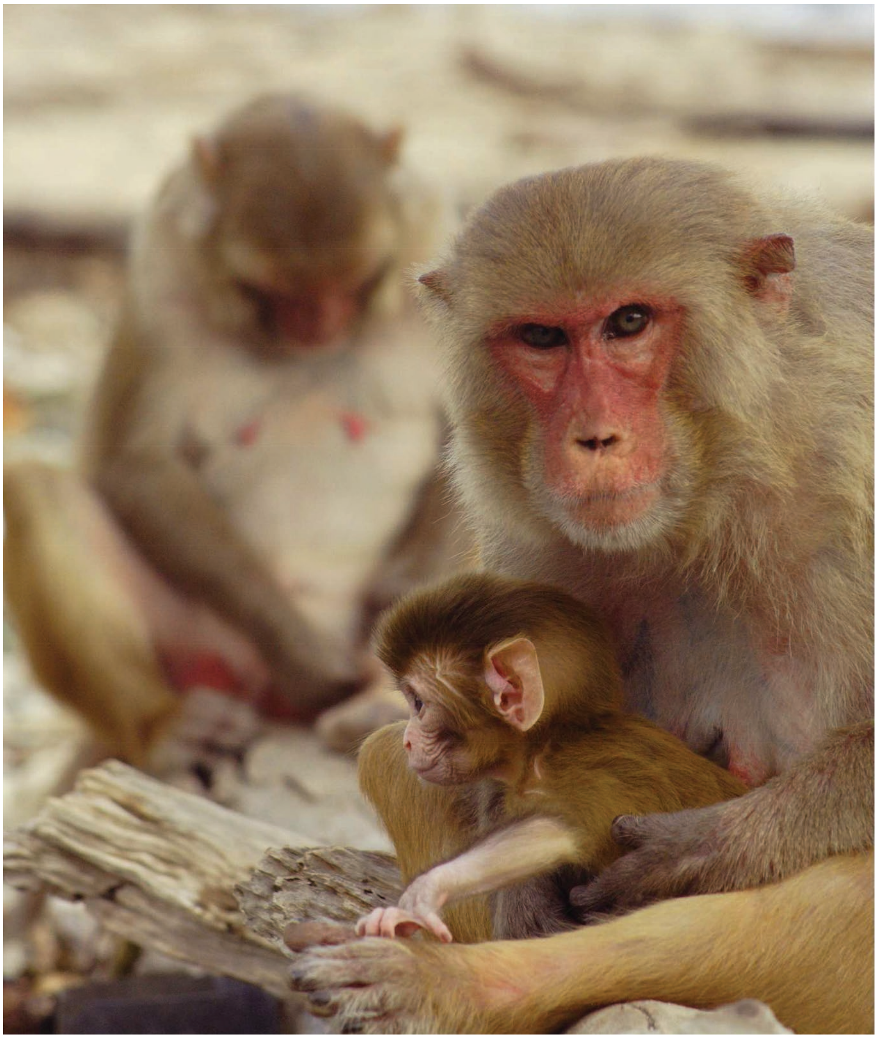
Designing a puzzle that had to be solved in order for great tits to extract food from a box, she captured two males from each of five different populations and gave them an opportunity to learn to open the puzzle box by means of sliding a red or blue door. Once successfully trained, these “demonstrators,” as well as two untrained control males taken from three additional populations, were released back at their sites of capture. Meanwhile, researchers had placed in the woods several puzzle boxes, each with a red door and a blue door, which provided equally rewarding treats (mealworms) when opened. Because at least 90 percent of the great tits in this study location—Oxford’s Wytham Woods—have microchip tags in bands on their legs to allow the continuous automatic tracking of their movements via antennae, Aplin and her colleagues were able to track the cultural diffusion of this novel behavior through the social network. Puzzle boxes logged the identity of each visitor and each successful red or blue door opening.

What Aplin’s team discovered only 20 days after release was that in populations without trained demonstrators, up to half of the population had learned through innovation to open the puzzle box on their own. “In the control populations, it was on average 10 days before an individual innovated,” says Aplin, adding, “From this point, we assume that most subsequent individuals learned by social learning from these innovators.” Meanwhile, in the five populations with knowledgeable demonstrators, an average of 75 percent of individuals were successfully solving the food puzzles. A close look at the social network indicated that in comparison with naive associates, if one individual was capable of solving the puzzle, its “friends” were 12 times more likely to learn it, too. Interestingly, although the rewards were the same for using their bill to slide the red or blue doors, these tits were cultural conformists: During learning, naive birds were significantly more likely to adopt the color solutions of their trainers, leading to different schools of problem solving. Finally, following up, the scientists found that cultural transmission persisted over time, and cracking the puzzle "became increasingly entrenched over two generations."

Another United Kingdom–based scientist who has been probing the influence of social networks on animals is the University of Exeter's Lauren Brent. Her fascination with human social behavior led her to ponder whether in animals, too, it is not just our friends that matter but also friends of friends. This has been recognized and capitalized on in human social networks such as LinkedIn, where friends of friends can be important in accessing career opportunities, but Brent discovered that these indirect relationships had rarely been explored in animals. Examining both the direct and indirect connections within a social network of rhesus macaques (*Macaca mulatta*), she found that "reproductive output was best predicted by how indirectly connected these individuals are rather than their direction connections." Both direct and indirect connections mattered, she found, but in terms of reproductive success, indirect connections seemed to matter more.

Some primatologists have been skeptical about the value of social-network analysis, suggesting that it is "a fancy term for something we've always done, basically accusing me of pulling some newfangled technical wool over their eyes," Brent laughs. Her answer to the skeptics has always been that network analysis allows researchers to look not just at direct connections but also at indirect connections. Nevertheless, only recently has the potential importance of those indirect connections been recognized, and not just in primatology.

"Marmots are not primates," notes Dan Blumstein, referring to the fact that under observation, their social interactions are relatively infrequent. Nevertheless, social-network analyses have allowed Blumstein to examine the ecological process of dispersal with a completely fresh approach. Studying yellow-bellied marmots (*Marmota flaviventris*) in the East River Valley, in Colorado, he and his colleagues,



Social network analysis has been used by Lauren Brent (right) to gain quantitative insights into the social life in these rhesus macaques* (Macaca mulatta) *in Puerto Rico and the importance of friends of friends. Photographs: Lauren Brent.

including Wey, used the network approach to look at which individuals within a population disperse versus stay put. In their study population, all of the individuals have fur marks that can be seen from a distance. So to quantify their social-network structure, his team recorded marmot interactions such as foraging in close proximity; grooming; displacements (when one leaves when another arrives); chases; bites; and, rarely, fights. Blumstein's group also recorded play behavior, such as chasing, fleeing, tumbling, play fighting, boxing, and wrestling.

Analyzing their data quantifying the marmot social-network structure, they tested the "social-cohesion hypothesis," an idea proposed in 1977 that suggests that individuals that are more socially connected—those engaged in more social interactions—are the ones least likely to disperse beyond their natal ranges. In yellow-bellied marmots, most males, but only half of females, disperse away from where they were born, as yearlings. So if the social-cohesion hypothesis explains patterns of marmot dispersal, Blumstein's team predicted that social relationships would be more important predictors of dispersal for females than for males. That is exactly what they found. Female yearlings that were more socially embedded, and those that interacted with more individuals, were less likely to disperse. And just as the team predicted, dispersal was relatively unaffected by network structure in males.

But in investigating the likelihood of dispersal, or any other ecological correlate, does it matter whether those social relationships are nice or nasty? That's something that intrigues Blumstein, because studying aggressive relationships is easier to do in nonhumans. Aggressive relationships may have different consequences or be correlated with different things from cooperative relationships, he suggests. And since much of the human network analysis in public health and medicine focuses on "nice" relationships, he suggests that there is a huge opportunity for looking at nasty networks, too.

In Colorado's East River Valley, Dan Blumstein's team is studying social networks in yellow-bellied marmots (**Marmota flaviventri**). *Shown here are two siblings playing near their mother. Photograph: Ben Hulsey.*

Further reading.

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Challenges ahead

With so many ecological, evolutionary, and behavioral hypotheses that can be explored using social-network analysis, network data can be analyzed in a diversity of ways. But "because there are so many different ways to quantify a network, it can be a real challenge to pick meaningful measurements," cautions Ralf Kurvers, a researcher at the Centre for Adaptive Rationality at the Max Planck Institute for Human Development. Kurvers is first author of a 2014 review paper in *Trends in Ecology and Evolution*, examining emerging issues in the evolutionary and ecological consequences of animal social networks.

Although people are excited about the idea of investigating social networks, "often, there is a divide between the modelers and the people who really understand what's happening on the ground, in the field," says Gillespie. There is a tendency, he says, for people to use data that may not be good enough in models.

Kurvers agrees. Despite these "fancy techniques," says Kurvers, "we still actually need to understand what's going on [behaviorally] at that moment in space and time, and sometimes that seems to be neglected," he suggests. Technologies such as the Global Positioning System (GPS) and passive integrated transponder tags allow a "reality mining" approach, with continuous data mining of the entire environment of multiple individuals at the same time. That makes for rich data sets, he says, but it is still "important to know what you want to know."

In considering the possibility of diving into this new research subdiscipline, are the analytical techniques needed to quantify and analyze social networks difficult to master? Blumstein suggests not. The real challenge, he says, "is thinking clearly about the questions and thinking clearly about what the variables mean," because "it's really easy to come up with nonsense analyses."

"It's very easy to calculate these things," he says, and to come up with post hoc explanations. What is hard, Blumstein suggests, is coming up with a priori predictions. He also suggests a need for some standardization of metrics and methods. "There are still people publishing in really good places, asking questions using their own metrics that aren't social-network metrics." Blumstein also sees the need for more experiments, because much of the work so far, with a few notable exceptions, such as the work of Aplin, is correlative.

On the wish list for future social-network analyses is the examination of fitness consequences and the heritability of social relationships. Heritability of interactions and social dominance is an area that Blumstein has studied and continues to explore in marmots.

As for the overall promise of social-network analysis, "I think everyone should be skeptical," notes Blumstein. "I've always been an enthusiast, a skeptic, and a critic simultaneously," he adds, recognizing the tremendous promise of social-network analysis. "Just because you can calculate something," he explains, "doesn't mean you should or doesn't mean that it's going to be useful."

Lesley Evans Ogden is a science-writer producer based in Vancouver, Canada. A field ecologist turned journalist, her social network includes an eclectic mix of scientists, writers, producers, curious minds, and creative geniuses providing invaluable material for a story well that never runs dry. Say hello on Twitter at @ljevanso or via her website at www.lesleyevansogden.com.

Erratum

In a recent BioBriefs (*BioScience* 65: 1196, doi:10.1093/biosci/biv149), the affiliation of Ben Dantzer was misstated. He is at the University of Michigan.

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