Animal Social Networks

Edited by: Jens Krause, Richard James, Daniel W. Franks, and Darren P. Croft

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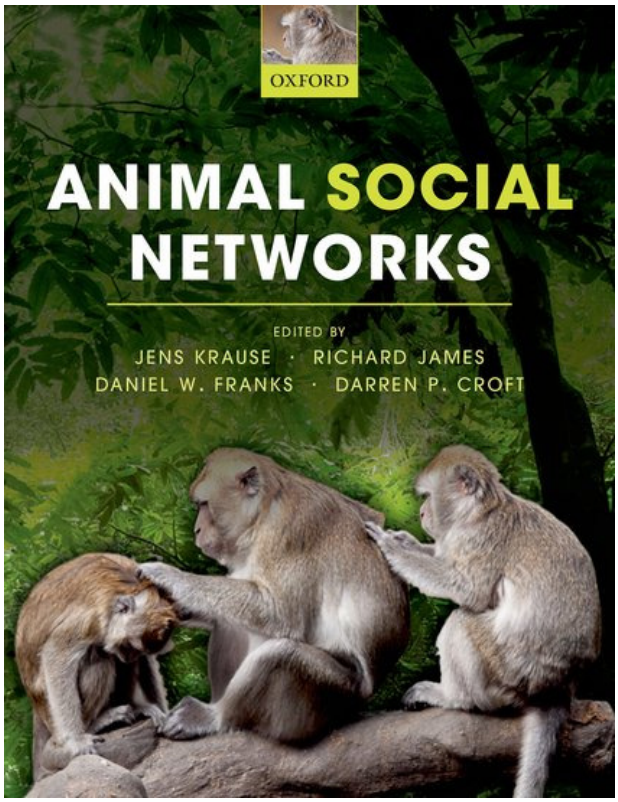

According to www.wearesocial.com, there are approximately 2.3 billion active social media users, representing an astounding 31% of the world's human population. Thus, interest in social networks is very strong among human primates. The term social networking has taken on a life of its own, almost to the point that it has become passé in everyday parlance. It was for this reason I think that, at first, I was not very excited about the use of social networking to study non-human organisms. It seemed to me like a fad that was jumping on the bumper of the proverbial bandwagon. Or, so I thought.

Fast forward to June 2015 to the Animal Behavior Society meeting in Anchorage, Alaska. As outgoing ABS president, Dan Rubenstein had organized a full-day Presidential Symposium on Social Networks. Wait a minute, if the esteemed Dan Rubenstein is hopping a ride on the social networking bumper, maybe I needed to give this subject a second look. I attended the full day symposium and became a convert. Thus, I was interested in reading more about the field in Animal Social Networks.

This edited volume includes 19 chapters with a mix of newcomer and veteran authors. Interestingly, three of the four editors published a similarly themed book in 2008, *Exploring Animal Social Networks* (Princeton University Press) but the present authors indicate that the first book was more focused on methodologies, whereas the new book examines the biology of taxa and a synopsis of what new ground has been discovered since social network theory was applied to the study of animal behaviour.

This edited volume is divided into four unequal sections. Section 1, *Introduction to Animal Social Networks*, consists of one main chapter that provides a primer of networkology, largely for those unfamiliar with terms used in this field. Section 2 of the book features nine chapters that use a conceptual approach to examine patterns and processes common to network theory. Section 3 consists of seven chapters that cover taxon-specific summaries (primates, cetaceans, fishes, insects, birds, ungulates, and lizards), emphasizing unique characters or challenges associated with each taxonomic group. The final section is merely a conclusion that discusses new analytical as well as methodological advances that will likely form the backbone of future network approaches.

Despite network theory being applied as early as the 1950s, animal behaviorists were not introduced to reviews on the topic until 2007-2008. The editors argue that network analysis is now "firmly embedded in behavioural biology". They define a social network as any number of individuals interconnected via social ties between them. Advocates argue that group dynamics will affect individuals and thus studies at the individual level will not reveal group-level phenomena, and thus a network approach is needed.

James' chapter (*ch 2, A networks primer*) describes networks as directed/undirected with weighted/ unweighted edges. These networks can be depicted diagrammatically or as matrices. Networks can be characterized by either node-based or network-level measures of structure. He goes on to provide other details on communities and model networks and network models.

Croft et al. (*ch 3, Assortment in social networks and the evolution of cooperation*) discuss the evolution of cooperation and relate it to Hamilton's rule. While cooperation among kin has been examined in detail, this chapter attempts to look at dynamic social groups where individuals interact with both kin and non-kin. Game theory has a long tradition of examining cooperation among non-kin and has resulted in numerous reciprocity models. This chapter's main focus is on mechanisms that determine the structure of social networks and how this structure relates to the evolution and maintenance of cooperation. The authors examine how individuals often assort themselves within populations to facilitate cooperation.

McDonald and Pizzari (*ch 4, Mating behaviour: sexual networks and sexual selection*) examine the

relationship between social network theory and sexual selection, referred to as sexual networks. Structuring of mating networks has obvious implications for selection on sexual traits. Nightingale et al (*ch 5, Quantifying diffusion in social networks: a Bayesian approach*) describes a Bayesian approach to quantifying social transmission of information. Most typically, social transmission involves the process by which behavioural traits spread through groups. The transmission of the behavioural trait can be measured as the time of acquisition or the order of acquisition. The authors offer up an alternative to using random effects under maximum likelihood. Rather, they argue for including random effects within a Bayesian framework by using Markov chain Monte Carlo methods.

Wilson and Krause (*ch 6, Personality and social network analysis in animals*) discuss animal personalities, otherwise known as consistent differences among individuals in their behavioural responses to ecological stimuli. Rather than focusing on simplistic dyad associations, the authors argue for the utility of a network approach. This theme is repeated throughout the book. McDonald and Dillon (*ch 7, Temporal changes in dominance networks and other behaviour sequences*) focus on the temporal sequence of events and how they relate to dominance states. They compare among ten algorithms used to assess ranks among individuals. But, the most important message I took away from their chapter was their comment that social network studies are often descriptive and without hypothesis driven tests or novel insights into social dynamics. They caution against making too much out of spurious patterns that may emerge, particularly if they are not relevant to the biology of the species.

Bode et al (*ch 8, Group movement and animal social networks*) relate group movement patterns to animal social networks. Collective motion is used to reference synchronized motion of groups of organisms. But, these collective motions are likely a function of local interactions. Local interactions are mediated through interaction networks that structure the flow of information between individuals. They extend this to individual, group, and population levels and discuss how social and interaction networks typically function at different timescales.

McGregor and Horn (*ch 9, Communication and social networks*) introduce the reader to communication networks and argue that these types of networks are not the same as social networks. Communication networks are typically several individuals within signalling and receiving range of one another. The authors also discuss the role of eavesdroppers and corresponding audience effects, topics that have received much attention in recent years.

Drewe and Perkins (*ch 10, Disease transmission in animal social networks*) comment on how disease transmission networks were one of the first networks to be studied. They focus on parasite transmission processes to illustrate this point. The two main elements in disease transmission include the probability of acquiring infection and the contact rate between infectious and susceptible hosts. Of course, many pathogens are transmitted in the absence of parasites and the presence of this intermediate vector likely changes the contact rate compared with other transmission not involving parasites.

Beisner and McCowan (*ch 11, Social networks and animal welfare*) provide a chapter on animal welfare. They divide their treatment of this subject into physical and psychological/social well being. There was some overlap with the previous chapter in their discussion of disease transmission. They discuss how these factors are exacerbated when animals are held in captivity. Likewise, stress can lead to illness and reduced immune function. Much of the discussion uses examples from the non-human primate literature, likely due to publication bias of primate studies and associated animal welfare.

Macdonald and Voelkl (*ch 12, Primate social networks*) comment on the 370 species of primates and how the study of non-human primates differs from what social scientists study in humans, mainly due to the fact that self-reporting is not available for non-human primates. Gero and Rendell (*ch 13, Oceanic societies: studying cetaceans with a social networks approach*) focus on how cetaceans are widely known for their cognitive abilities, rivalling or even exceeding those of primates. The authors point out that acoustic environments in aquatic conditions favour lower frequencies, travel costs are typically lower with little evidence of territoriality, and cetaceans operate at larger spatial and temporal scales. Strangely lacking from this chapter was any comment on the 33 species of pinniped taxa, a large group of mostly oceanic mammalian vertebrates that have been well studied.

Krause et al. (*ch 14, The network approach in teleost fishes and elasmobranchs*) reveal that there are over 25,000 species of fishes yet social network analysis has only been applied to a small number of taxa (the authors list ten species). Some of the most well studied taxa include model organism such as guppies or sticklebacks. Of course, insect taxa far exceed those of fishes and as Naug (*ch 15, Social networks in insect colonies*) indicates, the social structure of many insect species have been studied in detail. Ironically, however, network approaches are relatively rare among insects. Naug argues that this is due to technical and statistical challenges associated with studying large colonies.

Garroway et al (*ch 16, Perspectives on social network analyses of bird populations*) speak of the paucity of data on individual interactions in birds. Of those investigators that have attempted to follow individual birds, the usual methods include colour bands, PIT tags, or some form of telemetry. Of particular note are newer technologies that allow tags to communicate with one another. But, strikingly, there are not very many examples of social network theory being used in birds. Similarly, Rubenstein (*ch 17, Networks of terrestrial ungulates: linking form and function*) indicates that only a handful of ungulate taxa have been studied in a manner conducive to network analysis. Of those taxa that have been studied, Rubenstein argues that four important conclusions have been reached: individual social systems are adapted to particular features of the environment, hierarchical societies have strong bonds at lower levels

but are more plastic at higher ones, dynamic social structure analyses do a better job than static methods when attempting to define a community, and societal structure shapes function.

Godfrey (*ch 18, Linking lizards: social networks in reptiles*) states that reptiles are not typically thought of as social taxa and thus network theory has rarely been used in their study. In fact, only ten studies on four taxa (a skink, a tuatara, and two lizards) have been published, as of the writing of this book.

The editors conclude by stating that the application of network theory to animal social systems is not new - primatologists and epidemiologists were using such methods in the 1950s. The last decade though has really seen an increase in quantitative approaches to network analyses. The major finding being that network structures are non-random and dynamic. With the development of complex dataloggers and other means of mass data collection, methods of analyses are becoming much more complex. Individuals can be recognized and tracked as never before.

So, who is the audience for this book? The back cover suggests that it is for graduate students and researchers. I would agree that it is a good "first blush" treatment of network theory and its application to animal behaviour. For those looking for a "how to" guide to network analysis, they won't find it in this volume. But, with over 1200 references provided, an interested reader will have plenty of fodder to go forth. If you are interested in social network theory, this edited volume is a must have.

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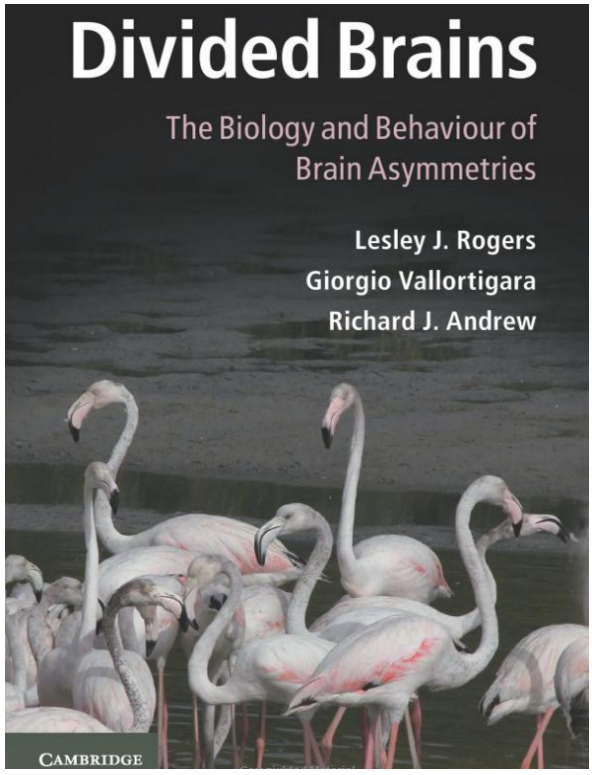
BOOK REVIEW

Divided Brains: The Biology and Behaviour of Brain Asymmetries

By Lesley J. Rogers, Giorgio Vallortigara, and Richard J. Andrew.

Cambridge University Press, 2013. 229 pp.



As I learned through Larry Dill, behaviors sort into the 4 F's: feeding, fleeing, fighting, and reproduction (see Pribram 1960, Ydenberg & Dill 2015). *Divided Brains* details how all of these sorts of behaviors are influenced by asymmetries in the brain. As a rule for vertebrates, search for food is more effective with the right eye and detection of predators more effective using their left eye using their right eye. Vertebrates are also more likely to attack a rival when they see it with their left eye. Finally, social interactions often show a bias toward left eye, including face recognition and processing of novel and emotional information.

Across the careers of the authors, they have played leading roles in documenting evidence for asymmetries in brains and behaviors. Feeling that vast published results were scattered and not fully appreciated, they wrote this book to provide a framework for understanding the vast literature on such asymmetries.

The organization for the book is straightforward and attractive to students of animal behavior: Sandwiched between introductory and concluding sections, the authors use the perspective of Tinbergen's four questions to organize the heart of the book into chapters on *Function, Evolution, Development,* and *Causation*. As expected from using Tinbergen's four questions, study organisms and behaviors are often revisited from different perspectives in different chapters.

The chapter on *Function* is most obviously important to behavioral ecologists. Here both individual asymmetry and the population distribution of asymmetries deserve attention. Individual asymmetry may function to allow specialization on different aspects of sensory tasks, either at the level of information gathering or at the level of information processing. For example, it may be hard to carefully measure differences in brightness between neighboring points within view of an eye and to quickly detect changes in average brightness across the field of view. Although it would seem that having one eye specialized for detecting attacks would be a disadvantage for attacks coming from the "wrong" side, evidence shows that escape responses are faster for fish with more asymmetric brains. I am still pondering these results as both speed and direction can matter for escaping.

Given an individual advantage to asymmetry, what mix of asymmetric individuals should we expect in the