Forum: Can multilayer networks advance animal behavior research?

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Abstract: Interactions among individual animals — and between these individuals and their environment — yield complex, multifaceted systems. The development of multilayer network analysis offers a promising new approach for studying animal social behavior and relating it to eco-evolutionary dynamics.

Social systems are complex and multi-faceted

Ecological, evolutionary, and behavioral processes arise from interactions among individuals from the same or from different species. The study of these processes and their underlying interactions has benefited from advances in network science that have provided essential computational and analytical tools (1).

Investigating animal social systems using networks has uncovered novel insights into the roles of social structure for transmitting information (2) and infection (3), the roles of particular individuals in maintaining social stability (4), and many other features. However, social systems have multiple facets, as they incorporate multiple types of social interactions that occur at different times and locations and which are linked to physical networks that connect important habitats (Fig. 1). Traditional network analysis typically ignores crucial interdependencies when studying such interconnected or multirelational systems. Despite the potential importance of analyzing the full range of interdependencies and facets of behavioral systems in an integrated framework, few tools have been available to conduct such studies until recently, and these have been employed to examine animal social behaviors on scarce occasions (see review in (5)).

What is a multilayer network?

Multilayer networks have emerged as a novel methodology in network science (6). A multilayer network combines multiple networks, called "layers", into one mathematical object. Analyzing such networks can uncover ways in which different layers interact and impact one another. There are two main types of multilayer networks. ***Multiplex networks***, which are used to model multirelational systems, possess edges between layers that connect nodes representing the same entity across different layers. For example, in a primate social system, a multiplex network can include layers for aggressive interactions, grooming interactions, play interactions, and so on (7). A common simplifying assumption is that each layer in a multiplex network encompasses the same individuals, but not all individuals need to be involved in all types of interactions. Studying multiplex networks enables the examination of individuals' roles in a society by simultaneously considering multiple modes of interaction (5, 6, 8). ***Interconnected networks***, which can model connections between different subsystems, can include interlayer edges that connect either identical entities or different ones. In contrast with multiplex networks, in interconnected networks, interlayer edges can connect different entities to each other (Fig. 1). Therefore, layers in interconnected networks often represent different types of nodes. One example is networks with both social and spatial behavior, which combine social interactions with networks of spatial locations and can provide insights into how ecological environment shapes animal social systems (Fig. 1) (6).

Capturing the multiple facets of group living

Multilayer network analysis offers considerable potential to advance the study of key questions in animal behavior (Box 1). For example, because there is typically an interplay between different social contexts (4) and because interactions encompass both multiple contexts and temporal changes, using a multilayer framework can provide better understanding than monolayer analyses of the roles that individuals play in their society. Such interdependencies among different types of interactions can influence fitness (5). The transmission of information and disease, two key ecological processes that help shape animal societies, can depend on multiple types of behavioral interactions, and taking an increasingly holistic view of intra-group interactions can reveal how interactions might help regulate transmission.

Novel methodology that incorporates relationships and interdependencies between layers have been developed for quantifying multilayer network structure and its effects on dynamical processes (6), and a few specific approaches have been suggested for examining various research questions in ecology (8). Moreover, many common network tools have been generalized for multilayer networks (6). For example, the extension of various centrality measures into "versatility" measures facilitates identification of the roles of an individual in a multilayer network (9). Such versatility measures can help improve understanding of the roles that individuals play in groups by examining questions that relate social-network position(s) to phenotypic traits or measures of fitness. Mesoscale structures, such as motifs and communities, now have multilayer analogs (10), which can reveal social organization that is not apparent if single interaction types are considered independently. Finally, the study of dynamical processes (e.g., disease or information transmission) has been extended to multilayer networks (6, 11), providing valuable insights into both the spreading dynamics of multiple infections and interdependencies between disease and information transmission.

Integrating behavioral and ecological networks across scales

The advances that multilayer network analysis offers animal behavior research span all levels of biological organization, from interactions among molecules to inter-specific interactions that affect evolutionary processes. A multilayer approach can integrate physiological, behavioral, and ecological explanations for social behavior to help disentangle the mechanistic and adaptive processes that shape sociality. For example, a multilayer network in which social interactions and physiological processes (such as hormone interactions, cell-to-cell communication, and neural networks) are intertwined has the potential to greatly advance the study of integrative connections that impact behavioral interactions.

Multilayer network analysis offers a way to link animal social behavior with physical environments. The connectivity of suitable habitats and resources within those habitats influence animal movement patterns, which in turn influence multiple types of social interactions (such as competition or mate choice) and how they change over time. Integrating such spatial, temporal, and social dynamics using multilayer networks can uncover novel ecological impacts on social behavior (Box 1; Fig. 1). Applying a multilayer perspective can help reveal how ecological changes influence the evolutionary dynamics of social decision-making or how social species respond to human-induced environmental changes.

Conservationists and wildlife managers must inevitably consider interactions between multiple species, often including humans. Using interconnected networks, or other types of multilayer networks, can help inform conservation actions by simultaneously considering both human and wildlife social structures. For example, multilayer networks can help reveal how human interactions directly and indirectly alter wildlife social structures, and how they impact wildlife population dynamics, by combining human social–ecological networks (e.g., (12)) and socio-spatial networks of animals. Further, management actions aimed at preventing the spread of infection in wildlife populations can incorporate multiple types of social interactions. Such integration of interaction types can aid identification of individuals whose removal will have the largest impact on population stability (13) or whose vaccination might best mitigate disease transmission.

Methodological considerations and developments

There are many important methodological questions that still need to be addressed. For example: *How can existing methods in multilayer network analysis be implemented in the study of animal sociality? Can animal behavior inspire novel multilayer network measures, tools, and analyses?* A particularly important consideration is one of scales (8). For example, it is not always clear how to weight interactions of different types relative to each other in a multilayer framework. For networks that incorporate physiological and/or ecological networks alongside behavioral interactions, this scaling issue can be especially acute, as these interactions are measured using different units. While methods are being developed to systematically examine differences in scale, it will be important to carefully select appropriate weightings and test the robustness of conclusions to these choices. Additionally, although multilayer network analyses are burgeoning (6, 8), many current ideas have been implemented as ‘proofs of concept’, and often only in multiplex networks. Generalizing relevant approaches for interconnected networks, and other types of multilayer networks, will be extremely valuable for behavioral ecology research (5).

Conclusions

The application of multilayer methods offers a valuable opportunity to gain new insights into animal sociality, both through integrating different interactions and relationships within the same analytical framework and by providing substantive links between behaviors and the ecological, physiological, and evolutionary processes that shape them. Multilayer network analysis will allow behavioral ecologists to extend the scope of their research questions by considering interactions between networks that represent different behaviors and processes. Employing multilayer approaches will provide important new perspectives on the inherently complex social lives of animals.

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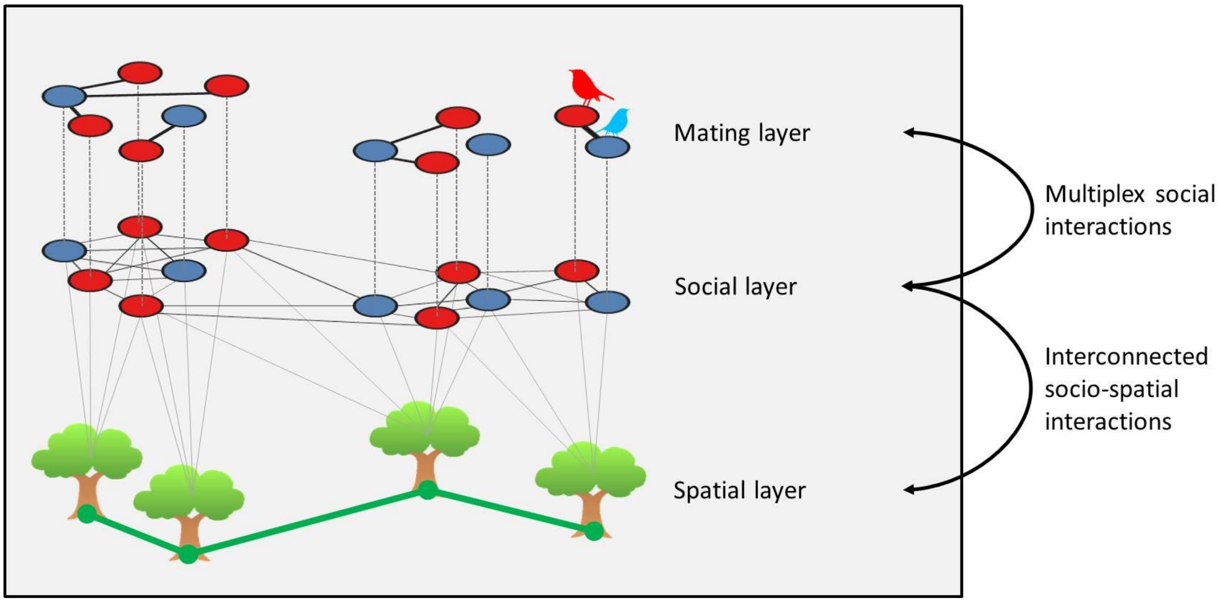
Figure 1. A multilayer socio-spatial network can integrate data from animal movement and social interactions. The top layer represents a mating network (based, e.g., on either observations or genetics), the middle layer represents a network of observed social interactions, and the bottom layer represents a spatial network of connected habitat patches. The thickness of intralayer edges represents the strengths of interactions. Interlayer edges between the social and spatial layers connect individuals to habitat patches that they have visited. Interlayer edges

between the social and mating layers connect the same individual to itself. Red nodes are females, and blue nodes are males.



Box 1: Multilayer questions in animal behavior research

We highlight some of the diverse questions in behavioral ecology and evolution that multilayer network analysis can help advance.

Multiplex networks offer a promising approach for uncovering how social relationships in animal groups emerge from the interdependencies of multiple types of behavioral interactions:

- How do affiliative (e.g., grooming) and agonistic (e.g., dominance) interactions combine to determine social relationships and patterns of collective behavior in animal groups?

- Can integrating different behavioral interactions better explain the social status, reproductive success, or fitness of an individual than studying it independently in each constituent network?
- What types (or combinations) of behavioral interactions are important for intra-group transmission of information or infection? Can some behavioral interactions have an indirect effect on transmission?

Interconnected networks facilitate considerations of animal social systems within their broader ecological context:

- How do changes in habitat and movement networks over time influence the social structure of populations? What are the implications of these changes for disease or information transmission?
- How do heterospecific interactions shape conspecific social relationships and social roles? Are keystone individuals in conspecific networks important (e.g., for disease transmission) when one also considers heterospecific interactions?