

The problem and promise of scale in multilayer networks

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Abstract

Scale remains a seminal concept in ecology. Spatial scale, for instance, has become a central consideration in the way we understand landscape ecology and animal space use. Multilayer networks promise the integration of monolayer animal social networks with the complexity and importance of animal movement and space use in heterogeneous landscapes. Despite the complex interplay between social networks and how animals use space, there remains an important biological and methodological gap in our understanding of an animal's perception of spatial scale, e.g., grain and extent, can affect multilayer network dynamics. Here, we test how multilayer network metrics (e.g., versatility, multi-degree, similarity) are sensitive to variation in an animal's perception of scale. We will simulate animal movement data coupled with emergent social networks on increasingly heterogeneous landscapes across spatial scales. Furthermore, we review specific examples of spatially explicit data types to include in multilayer networks and explore the relevant nuances of these data. *Our simulations will highlight the need to carefully select scales for measuring spatial processes and appropriately weight layers and edges representing different types of data.* Effective integration of spatial processes, including biologically meaningful scales, within the context of animal social networks is an emerging area of research; our contribution will uniquely incorporate landscape ecology theory as a way to link different scales of social and spatial processes in a multilayer network. Based on social network and landscape ecology theory as well as our simulations we demonstrate potential for interconnectedness among individual animals and the landscapes they occupy.

Introduction

Our understandings of ecological pattern and process are directly linked to the scale at which they are observed (Levin 1992; Allen et al. 2015). Animals and landscapes are influenced across scales processes as global as climate and productivity (Field et al. 2009), and species-specific as trophic interactions and resource availability (Legendre 1993; Chave 2013). The effect of scale in ecology has been explored through species distribution modelling (Elith et al. 2009), habitat selection (Mayor et al. 2007), and food webs (Sugihara et al. 1989). Scale can be considered throughout ecology, including animal behaviour and the social environment that animals experience.

Sociality exists across scales (Whitehead 2008). For example, grooming and mating relationships require close proximity between conspecifics and occur over brief time periods (e.g. Carter et al. 2015), whereas social association represents shared space use by members of the same social group (Franks et al. 2010). Further, for social interactions or associations to occur individuals must share space, and thus have overlapping home ranges. In the context of the social environment, home range overlap is a relatively coarse scale of sociality across which individuals share space over larger spatial and temporal scales (e.g. Piza-Roca et al. 2018). Although the social environment clearly scales spatially and temporally, it remains unclear whether coarser scales of sociality, including social association and home range overlap, vary predictably with social interaction (Castles et al. 2014; Farine 2015). Here, we define *social scale* as the type of social relationship observed that can be explicitly defined and measured in social network analyses (see Glossary; Farine et al. 2015).

Animal social network analysis is a well-developed tool used to measure the relationships of individuals and organization of social systems (Krause et al. 2009; Wey et al. 2008; Croft et al. 2008). Social network analysis provides insight into the structure of social communities and social network properties can influence population dynamics and evolutionary processes (Pinter-Wollman et al. 2014; Kurvers et al. 2014). Despite the widespread use and innovation of traditional social network analysis (Webber & Vander Wal 2019), it typically considers a single scale of sociality in a given network, drastically simplifying the complexity of animal social systems (Finn et al. 2019).

Unlike traditional *monolayer* social networks, multilayer networks explicitly consider social systems across contexts, including scale-dependent contexts (Pilosof et al. 2017). Multilayer networks are made up of multiple layers, each representing different classes of individuals (e.g. male or female), types of behaviours (e.g. grooming, travelling, or foraging), spatial areas (e.g. local or regional), or temporal windows (e.g. daily or seasonal) (Kivela et al. 2014; Porter 2018). Multilayer networks are relatively novel to studies of animal behaviour (Finn et al. 2019; Silk et al. 2018), although they have been used to describe multidimensional human social systems, complex transportation networks, and neural networks (Silk et al. 2018). The role of scale within multilayer social networks remains unexplored but provides a unique opportunity to develop novel understanding of variation in the temporal or spatial scales associated with social systems.

Here, we discuss and integrate variation in temporal and spatial scales within a multilayer network framework. We borrow from behavioural, landscape, and spatial ecology to build a conceptual and analytical framework for scale-dependent multilayer networks and we apply this framework to a fission-fusion social system case study of caribou (*Rangifer tarandus*) in Newfoundland, Canada (Peignier et al. 2019). We use this case study to address two principal questions associated with scale-dependent multilayer networks. First, to what degree does the spatial scale of landscapes, temporal windows of analysis, and social scale of relationships, influence our ability to interpret complex social systems? Second, can variation in spatial, temporal, and social scale improve predictions associated with seasonal differences in resource availability and social association? We conclude with perspectives for further development and application of scale in multilayer networks with respect to landscape ecology (Schneider 2009), individual fitness and phenotypes (Webber & Vander Wal 2018), and movement ecology and collective movement (Jolles et al. 2019).

Scale in multilayer networks: a case study

Caribou socioecology

Here, we use caribou as a case study to develop scale-dependent multilayer networks based on temporal (seasonal), spatial (habitat type), and social (visual and auditory perception). Caribou are gregarious ungulates with fission-fusion dynamics (Lesmerises et al. 2018) that display temporal (Peignier et al. 2019) and spatial (Webber et al. unpublished data) variation in social networks. In winter, caribou dig holes in the snow, termed craters to access forage (Bergerud 1974). As a result, caribou tend to occupy and re-use craters once they are established and there is considerably less access to forage than when the landscape is snow-free. Importantly, craters exist on the landscape at multiple scales: the crater scale (a single crater), the feeding area scale (multiple craters in close proximity), and the winter range scale (all craters within an individual’s range) (Mayor et al. 2009). The distribution of forage for caribou is therefore seasonally heterogeneous, with greater access in snow-free seasons compared to winter as well as spatially heterogeneous in winter because the distribution of craters on the landscape varies meaning that access to vegetation in winter is highly variable for caribou. We therefore partitioned data into two discrete seasons: summer (3 August - 17 October) and winter (1 January – 16 March) based on caribou socioecology (Peignier et al. 2019).

Caribou location data

We used GPS location data collected from Fogo Island caribou in 2018. Adult female caribou were immobilized and fitted with global positioning system (GPS) collars (Lotek Wireless Inc., Newmarket, ON, Canada, GPS4400M collars, 1,250 g) as described by Schaefer and Mahoney (2013). Collars were programmed to collect location fixes every 2 hours. Prior to analyses, we subset GPS fixes into a discrete removed all erroneous and outlier GPS fixes following Bjørneraas et al. (2010). We did not collar all female caribou in the herd; however, we assumed that our sample of collared animals was random.

Landscape data and habitat classification

Landscape classification data were provided by the Newfoundland and Labrador Wildlife Division. Available landcover classification included nine habitat types at 30 x 30m resolution. We distilled the landcover types

into three broad categories: foraging habitat, open habitat, and closed habitat. Foraging habitat consisted of lichen habitat, open habitat consisted of wetland, rocky barrens, and anthropogenic habitat types, while closed habitat consisted of coniferous forest, conifer scrub, broadleaf forest, and mixed-wood forest habitat types. Water habitat was excluded from all subsequent analyses.

Caribou multilayer social networks

Network types and construction (defining layers for the multilayer network)

We generated seasonal multilayer social networks consisting of habitat-specific monolayers. Each layer was the social association network generated in one of three habitat types (lichen, open, and closed). For habitat-specific networks, all GPS relocations were assigned to the corresponding habitat type and proximity-based social network layers were generated using the R package *spatsoc* (Robitaille et al. 2019) in *R version* (R Core Team 2020).

Within each habitat-specific monolayer network, we assumed individuals were associating if simultaneous GPS fixes (i.e., recorded within 5 minutes of each other) were within a given distance of one another. Typically for ungulates and other gregarious mammals, the ‘chain rule’ is applied for group assignment. For GPS data, the chain rule is applied if discrete spatiotemporal GPS fixes buffered by a given distance formed a contiguous buffer for two or more individuals, even if some individuals within the buffer were not within the given distance of one another (Robitaille et al. 2019). Group assignment based on the chain rule has previously been applied to caribou at a distance of 50m (Peignier et al. 2019; Lesmerises et al. 2018). To assess the role of social scale in multilayer networks, we varied the threshold distance for group assignment between 5-500m (see *Social scale* section below). In all networks, nodes represented individuals, intralayer edges represented associations between individuals in a given habitat type, and interlayer edges represented **XXXX** [ALEC??].

We weighted edges of social networks by the strength of association between caribou using the simple ratio index (SRI, Cairns and Schwager 1987):

$$SRI = \frac{x}{x + y_{AB} + y_A + y_B}$$

where x is the number of fixes where individuals A and B were within a given distance of each other, y_A is the number of fixes from individual A when individual B did not have a simultaneous fix, y_B is the number of fixes from individual B when individual A did not have a simultaneous fix, and y_{AB} is the number of simultaneous fixes from individuals A and B that were separated by more than the given distance (Farine & Whitehead 2015). Social groups were designated if two or more individuals occurred within a given distance of one another at any given time point.

For each multilayer network, we calculated XXX metrics. These included four neighborhood-based metrics: degree centrality, multidegree, degree deviation, and neighbours as well as two multilayer [need better term here?] metrics: connective redundancy and relevance (see Glossary for definitions). GOING TO NEED MORE HERE (SEE SMITH-AGUILAR ET AL 2019 PAPER FOR REFERENCE ON EXPLAINING THESE).

We generated all networks Right now, we calculate mostly degree/neighborhood based metrics.

Reference for extending degree centrality to multilayer, neighbors, connective redundancy and relevance: Berlingerio 2011 “Foundations of multidimensional. . .”

- Degree centrality
- Multidegree
- Degree deviation: standard deviation of degree across layers
- Neighbors/neighborhood (number of unique actors directly connected to each focal)

Neighbors = degree within a network layer But across a multilayer network with multiple layers, some neighbors are repeated.

So the difference between neighbors and degree is the basis for

- Connective redundancy: $1 - (\text{neighborhood} / \text{degree})$ When connective redundancy is 0, all edges on all layers are necessary to preserve the social ties
- Relevance: neighborhood of specific layer / neighbourhood of full ml net. This is the proportion of neighbors present on the layer of focus. Comparing across, it tells you which layers are most important for each individual.

Then there will be some layer similarity. Right now it's just a correlation of each season's asnipe SRI matrix
Finally, some weighted variables:

- eigenvector centrality, summed across layers as described in Boccaletti, Stefano, et al. "The structure and dynamics of multilayer networks." *Physics Reports* 544.1 (2014): 1-122.

Scale in multilayer networks

Temporal scale

We altered the temporal scale of multilayer networks using a moving time-window approach to define seasons.

1. time window length

Varying length of time window (used to define seasons). From 75 to 150 right now. Fixed start julian day for winter is day 1 and for summer is 215. Network layers for winter and summer are calculated for each window length.

1. time window position Varying position of time window (used to define seasons). Fixed length at 75. Window positions starting at 1, to + 75. So 1-75 is first iteration for winter and 75-150 is second iteration for "winter". Same for summer, starting at 215. Network layers for each season are constructed.

Spatial scale

To assess the influence of spatial scale on multilayer networks, we re-sampled our landcover classification map at varying scales. Specifically, we selected scales relevant to caribou ecology. We re-sampled landcover using the **grainchanger package** (Graham 2019) at **five** scales: 100m, 250m, 500m, 1000m, 2500m. Sampling at 100 and 250m represents fine-scale decision making for caribou during foraging (REF), while re-sampling at 1000m and 2500m represents the scale at which caribou tend to select and avoid habitat (Bastille-Rousseau et al. 2017). Resampling occurred based on a modal moving window method, where **XXXXX**. **[ALEC YOU'RE GOING TO HAVE TO ADD DETAIL HERE]**

For each landcover (the original resolution and modal resampled resolutions), seasonal network layers are combined in a multilayer network

Altering social scale

We altered social scale based on visual (short distance) and auditory (long distance) sensory modalities of caribou (REF?). Specifically, we modified the distance threshold required for group assignment (see above) and re-assigned groups at incremental distance between 5-500m. For example, at the finest social scale, only individuals within 5m of one another were considered in the same group, whereas at the coarsest social scale, only individuals within 500m of one another were considered in the same group.

Altering observational scale

Studies of social network analysis vary in the number and frequency of observations as well as the data collection technique used to generate networks (Davis et al. 2018; Webber and Vander Wal 2019).

Randomly select max number of observations - timegroups - (right now 750). For each iteration, include n observations for each season for all individuals. Subsequent iterations include nstep more (right now 25), along with previously included to remove stochasticity. Parallels with observation data.

Scale in multilayer networks in practice: case study results

Perspectives to advance multilayer networks

Landscape ecology

Individual fitness and phenotypes

Social network positions are frequently used to represent the social environment that an individual experiences or their social phenotype. Social phenotypes are increasingly linked to important fitness for individuals of various species, including primates (e.g. Brent, Ruiz-Lambides, & Platt, 2017; Thompson, 2019), dolphins (e.g. Stanton & Mann, 2012; Stanton, Gibson, & Mann, 2011), and birds (e.g. McDonald, 2007; Royle, Pike, Heeb, Richner, & Kolliker, 2012). The effect of scale on the relationship between an individual's social network position and fitness may depend on the hypotheses being tested and logistical constraints. Two scales that are important for understanding fitness consequences in the context of social network positions are temporal and social scales (Almeling, Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer, 2016; Berger, Lemaître, Allainé, Gaillard, & Cohas, 2015; Brent et al., 2017).

Social network structure depends on the timeframe of observation, which can make networks difficult to compare (Castles et al., 2014). Furthermore, social network structure can vary seasonally and indicate social environments that an individual experiences (e.g. Brent, MacLarnon, Platt, & Semple, 2013; Hamede, Bashford, McCallum, & Jones, 2009; Holekamp, Smith, Strelloff, Van Horn, & Watts, 2012), or they can be consistent across time, which can be used to reflect social phenotypes (Aplin et al., 2015; Stanley, Mettke-Hofmann, Hager, & Shultz, 2018). Seasonal fluctuations have the potential to have disease transmission and fitness effects for individuals (Balasubramaniam et al., 2019; Chen et al., 2014). **[QW: I'm not sure what this paragraph adds - I think if we need to save space we could cut it]**

In long-lived species, social phenotypes can change over their lifetimes in ways that can affect fitness (Berger et al., 2015; Brent et al., 2017). These findings highlight the necessity to carefully consider the temporal scale that is meaningful for the proposed hypotheses, especially for understanding the relationship between an individual's social phenotype and fitness. Further complicating the issue, social phenotypes can change over stages of ontogeny, although it is important to note that individuals progress through development at different rates (Tarka, Guenther, Niemelä, Nakagawa, & Noble, 2018). This variation can make defining appropriate temporal scales for testing the fitness implications of an individual's social phenotype over different stages of ontogeny even more difficult. However, considering fine temporal scales may provide insight across development stages that may otherwise be missed (CITE-myself??). Multilayer networks provide a framework to test hypotheses linking social phenotypes and fitness across temporal scales. Because of the non-independent nature of social interactions and associations, especially over time, it is hard to test hypotheses about social dynamics with a suitable null control (Farine, 2017; Proskurnikov & Tempo, 2017). Using the framework of multilayer networks, making layers of different temporal periods provides a way to make appropriate null models to test questions about the dynamics of an individual's social network position over multiple aggregated time periods.

Social scale is another major consideration for social network analysis, especially in the context of different types of interactions and associations in the same analysis (Carter, Lee, & Marshall, 2015; Castles et al., 2014; Farine, 2015). It is a common trope that individuals must be associating to interact and most studies therefore assume that proximity is proxy for interacting (Farine, 2015). For instance, baboons need to be in proximity

in order to groom each other, but this trope highlights human bias toward interactions that can be readily observed in the field. Animals have certain interactions that do not require proximity such as long-distance vocalization and olfactory signals (Carter et al., 2015). With the advancement of bio-logging technology, we have the ability to record social interactions that do not require proximity, particularly long-distance communication networks with devices like microphone arrays (Snijders & Naguib, 2017). The multilayer network framework further enables researchers to examine the relationship between social phenotypes and fitness across social scales and to test how good social proximity is as a proxy for social interactions in a holistic way.

These different social scales can have different fitness repercussions for individuals. Rhesus macaques (*Macaca mulatta*) that had stronger, more stable social associates and grooming partners, but not more social partners, had higher survivorship than those who did not (Ellis, Snyder-Mackler, Ruiz-Lambides, Platt, & Brent, 2019). This finding highlights the need to investigate the effect of temporal and social scales on the relationship between social network positions and fitness. Multilayer networks provide an avenue to do so considering the whole social system rather than just one type of social interaction at a time, which is what has been done under most circumstances but is not very realistic.

Multilayer networks further provide unique challenges and opportunities for understanding the social phenotypes and environments of individuals and their fitness outcomes. Picking the proper temporal scale is important but a challenge because all layers in the multilayer network should reflect the same time period, and the period should be long enough for each layer to have enough data for robust networks (Farine, 2017). These considerations may be limiting factors when answering questions that require timeframes that are relevant to different individuals. On the other hand, multilayer network metrics provide an opportunity to simplify statistical models. Interactions that happen meters apart, proximity associations, and long-distance interactions can be encapsulated in a single multilayer network, and a single metric can be used to describe the various social scales of an individual’s network position. This multilevel network metric could be used to assess the relationship between an individual’s social phenotype and fitness. It would also be a meaningful simplification of many network metrics that could help simplify statistical analyses and deal with the frequent correlations between social network metrics in different types of networks (Castles et al., 2014).

Movement ecology and collective movement

Animal movement undoubtedly affects the social environment (Strandburg-Peshkin et al. 2015), and multilayer networks are no exception (Mourier et al. 2019). Movement is a dynamic process that is related to the resources an individual consumes within their home range and their general space use (Van Moorter et al. 2016). Collective movement can reduce group-level predation via detection-dilution trade-offs and improve information transfer about the quality or location of resources to other group members (Jolles et al. 2019). Social processes, movement decisions, and space use are therefore inextricably linked.

Although multilayer animal social networks are relatively novel (Silk et al. 2018), movement behaviour within multilayer networks has already been considered in a couple studies. In vulturine guinea fowl (*Acryllium vulturinum*), GPS movement data were used to generate *monolayer* association networks within a multilayer network (Papageorgiou et al. 2019). In addition, *spatial networks* are physical locations (nodes) which are connected in a network when individuals move between said locations (ties). For example, spatial networks were applied to monitor movement of sharks (*Carcharhinus amblyrhynchos* and *Carcharhinus melanopterus*) between fixed location autonomous arrays, where nodes represent locations within the array, *intralayer edges* represent individual movement frequency, and *interlayer edges* represent contact probability among individuals at a given node (Mourier et al. 2019). While both studies integrate movement in some capacity, neither generate networks based on continuous measures of dyadic or collective movement (Long et al. 2014).

Continuous collection of animal relocation data using GPS technology can be used to measure how groups of animals make movement decisions in the context of their local environment (Strandburg-Peshkin et al. 2015, 2017) and across scales. A collective movement layer could constitute similarity in movement for dyads (Long et al. 2014) or groups (Bode et al. 2011). This movement layer could be made at a fine (i.e. minute-to-minute: Cleasby et al. 2019) or coarse (global migration: Flack et al. 2018) scale. In contrast to spatial

networks, movement networks could assimilate dyadic movement metrics into a network representing the continuous and simultaneous movement trajectories of animals. Another potential application would be to generate social networks during times when animals are engaged in different behaviours, including traveling, interacting, or foraging [**JWT: these are not mutually exclusive behaviors, which may not matter here**] (e.g. Muller et al. 2018; Finn et al. 2019) and construct a multilayer network based on behaviour-specific monolayer networks (e.g. Smith-Aguilar et al. 2019). Importantly, the key to incorporating movement in multilayer networks across scales is the technological advancements available to overcome previous limitations (see Hughey et al. 2018).

Given the existing framework for constructing multilayer networks from behavioural layers (e.g. Smith-Aguilar et al. 2019), movement layers could be integrated with interaction or association layers. Integrating movement layers with habitat-specific social association layers could further shed light on the role of movement as a driver of the social and spatial environments an individual experiences (Webber and Vander Wal 2018). In our case study, we generated multilayer networks based on habitat-specific monolayers. Coordinated movement of dyads, or groups, could vary based on habitat, and the approach we outline could be used to explore mechanisms linking the social and spatial environments. For example, social processes may be an emergent property of the landscape because animals aggregate at resources, such as waterholes (Chamaillé-Jammes et al. 2008). Movement to, from, or within habitat patches can also contribute to the formation of the social environment [**JWT: how? I think it would help to clarify the example**] (Spiegel et al. 2016). Incorporating movement ecology within a multilayer network framework is a logical next step for a burgeoning field. In particular, when association networks are habitat-specific, we suggest the integration of movement and space use in multilayer networks provides novel insights into the effects of habitat configuration on the formation of the social environment (He et al. 2019).

Conclusions

something something blah blah.

Silk et al. (2018) presented some key multilayer questions in animal behaviour research. While these questions represent an important starting point for multilayer networks, we present an additional set of questions relevant to the promise and problem of scale in multilayer networks:

- 1) How do social phenotypes across scales differently influence fitness? Are some temporal or social scales better predictors for different fitness metrics?
- 2) Why do individuals associate more strongly with certain conspecifics in some habitats? What, if any, is the role of movement in the context of habitat networks?
- 3)