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 heterogenous 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 (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 intra-specific interactions and the structure of social communities and social network properties can influences 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 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 organismal 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 (Ref), 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.

### Caribou location data

We used GPS location data collected from Fogo Island caribou in winter 2018 (1 January – 16 March). 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. Although associations between collared and uncollared animals were unrecorded, we assumed that our networks (see below) were unbiased representations of the relative degree of social association among all caribou.

### Landscape data and habitat classification

### Social network analysis

We used R package spatsoc (Robitaille et al. 2019) in *R version* (R CITATION) to generate proximity-based social networks (PBSN) from GPS telemetry data. We generated social networks for each herd in each season based on proximity of GPS fixes for individual caribou: we assumed association between two individuals if simultaneous GPS fixes (i.e., recorded within 5 minutes of each other) were within 50 m of one another (Lesmerises et al. 2018). We represented individuals in our networks by nodes and associations between individuals were represented by edges.

We applied the ‘chain rule’, where each discrete spatiotemporal GPS fix was buffered by 50 m and we considered individuals in the same group if 50 m buffers for two or more individuals were contiguous, even if some individuals within the buffer were not within 50 m of one another. Group assignment based on the chain rule has commonly been applied to gregarious mammals, including caribou (Peignier et al. 2019; Lesmerises et al. 2018). We weighted edges of social networks by the strength of association between dyads of caribou using the simple ratio index (SRI, Cairns and Schwager 1987):

where x is the number of fixes where individuals A and B were within 50 m of each other, yA is the number of fixes from individual A when individual B did not have a simultaneous fix, yB is the number of fixes from individual B when individual A did not have a simultaneous fix, and yAB is the number of simultaneous fixes from individuals A and B that were separated by >50 m (Farine & Whitehead 2015). Social groups were designated if two or more individuals occurred within 50 m of one another at any given time point. We generated social networks with the igraph package in R, version 1.2.2 (Csárdi & Nepusz 2006). For each network, we calculated graph strength, defined as the sum of the edge weights for each individual in each network. We considered graph strength generated from PBSNs as an index of sociality (i.e., social strength).

## Scale in multilayer networks in practice: case study results

## Perspectives to advance multilayer networks

### Landscape ecology

### Individual fitness and phenotypes

### 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 and is related to an individual’s space use as well as the resources consumed within their home range (Van Moorter et al. 2016). Collective movement can reduce group-level predation via detection-dilution trade-offs, while it can also improve information transfer about the quality or location of resources (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 handful of studies. In gunieafowl (*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 networks of locations, which are connected in a network when individuals move between locations. For example, spatial networks were applied to monitor movement of sharks (*Carcharhinus amblyrhynchos* and *Carcharhinus melanopterus*) between 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 collective, or dyadic, 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) as well as at a fine (i.e. minute-to-minute: Cleasby et al. 2019) or coarse (global migration: Flack et al. 2018) scales. Another potential application would be to generate social networks during times when animals are engaged in different behaviours, including moving, interacting, or foraging (e.g. Muller et al. 2018; Finn et al. 2019) and construct a multilayer networks based on behaviour-specific monolayer networks (e.g. Smith-Aguilar et al. 2019) In contrast to spatial networks, movement networks could assimilate dyadic movement metrics into a network representing the continuous and simultaneous movement trajectories of animals. 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), while movement to, from, or within habitat patches can also contribute to the formation of the social environment (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 insight into the effects of habitat configuration on the formation of the social environment (He et al. 2019).