

The problem and promise of scale in multilayer networks

Alec L. Robitaille¹, Quinn M.R. Webber², Julie W. Turner¹, Eric Vander Wal^{1,2}

¹Department of Biology, Memorial University of Newfoundland, Canada; ²Cognitive and Behavioural Ecology Interdisciplinary Program, Memorial University of Newfoundland

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. Meanwhile, social processes can also scale from fine-scale interactions to co-occurrence to overlapping home ranges. Multilayer networks promise the integration of monolayer animal social networks with the complexity and importance of animal space use and movement 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 scale, e.g., grain and extent. But scale can affect multilayer network dynamics and how we build and interpret them. Here, we discuss the role of scale in the context of multilayer networks and provide a case study of caribou (*Rangifer tarandus*) to illustrate the role of social, spatial, and temporal scale on multilayer processes. We also present perspectives on future development and application of scale in multilayer networks with respect to habitat selection and space use, individual fitness and phenotypes, and movement ecology and collective movement. Effective integration of social and spatial processes, including biologically meaningful scales, within the context of animal social networks is an emerging area of research; our contribution uniquely incorporates perspectives on how the social environment and spatial processes are linked across scales in a multilayer framework. Based on social network and behavioural ecology theory as well as our case study, we demonstrate potential for interconnectedness among individual animals, their social environment, and the landscapes they occupy.

Introduction

Our inference regarding the ecological processes underlying ecological patterns are directly linked to the scale at which they are observed (Levin 1992; Allen and Hoekstra 2015). Animals are influenced across scales, through processes such as species-specific as trophic interactions and resource availability (Legendre 1993; Chave 2013) and global climate and productivity (Field et al. 2009). Multiscale ecology has been integrated into species distribution modelling (Elith and Leathwick 2009), habitat selection (Mayor et al. 2007), and food webs (Sugihara, Schoenly, and Trombla 1989). Meanwhile, in the context of animal behaviour, certain behaviours are scale dependent, for example, acoustic communication in birds occurs over variable spatial scales (Luther 2009). We posit that animal behaviour and, more specifically, the social environment that animals experience must also be scale-dependent.

Sociality exists across both temporal and spatial scales (Whitehead 2008). For example, grooming requires close spatial proximity between conspecifics and occurs over brief time periods (e.g. Carter et al. 2015), whereas social association represents shared space use by members of the same social group (Figure 1, 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 coarser 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). Thus, we define social scale as the type of social relationship observed that can be explicitly defined and measured (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, which 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 (monolayer), drastically simplifying the potential 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.

Our study is motivated by behavioural, landscape, and spatial ecology to build a conceptual and analytical framework for scale-dependent multilayer networks and we apply this framework to a 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 social scale of relationships, spatial scale of landscapes, and temporal scale of analysis influence our ability to interpret complex social systems? Second, can variation in social, spatial, and temporal improve predictions associated with biological differences in seasonal 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 social (visual and auditory perception), spatial (habitat type), and temporal (seasonal). Caribou are gregarious ungulates with fission-fusion dynamics (Lesmerises, Johnson, and St-Laurent 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 - 20 September) and winter (1 January - 17 February) based on caribou socioecology (Peignier et al. 2019).

Caribou location data

We used GPS location data collected from Fogo Island caribou in 2017 and 2018. Adult female caribou were immobilized and fitted with global positioning system (GPS) collars (Lotek Wireless Inc., Newmarket,

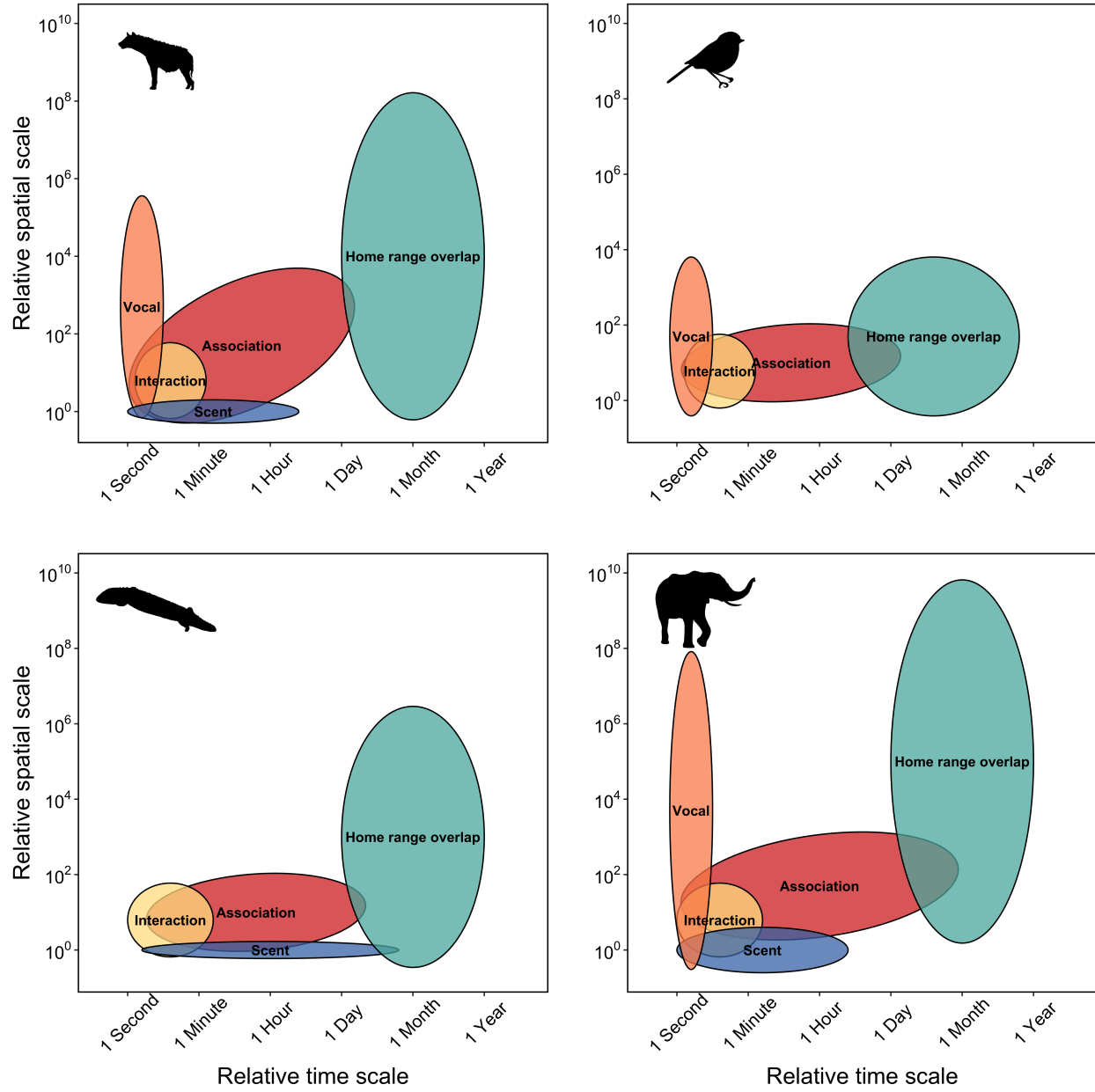


Figure 1: Space-time diagram displaying variation the spatial and temporal extent required for different social processes across a range of taxa.
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ON, Canada, GPS4400M collars, 1,250 g) as described by Schaefer and Mahoney (2013). Collars were programmed 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

Landcover data were provided by the Newfoundland and Labrador Wildlife Division. Available landcover classification included nine habitat types at 10m resolution. We reclassified the landcover types into three categories: foraging habitat, open habitat, and forest habitat. Foraging habitat consisted of lichen habitat, open habitat consisted of wetland, rocky barrens, and anthropogenic habitat types, while forest 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 a multilayer social network consisting 16 individual nodes and two aspects (season and landcover). Two season elementary-layers (winter and summer) and three landcover elementary-layers (open, forest and lichen) combined for a total of six layers. Layers were the social association network generated in each season and landcover combination. Proximity-based social network layers were generated using the R package `spatsoc` (Robitaille, Webber, and Wal 2019) in R version 3.6.1 (2019-07-05) (R Core Team 2019).

Within each layer, we assumed individuals were associating if simultaneous GPS fixes (i.e., recorded within 5 minutes of each other) were within a given spatial 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, Webber, and Wal 2019). Group assignment based on the chain rule has previously been applied to caribou at a distance of 50m (Peignier et al. 2019; Lesmerises, Johnson, and St-Laurent 2018). In all networks, nodes represented individuals, intralayer edges represented associations between individuals in a given habitat type and season, and interlayer edges represented connections between the same individuals across contexts.

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 and Whitehead 2015). Social groups were designated if two or more individuals occurred within a given distance of one another at any given time point.

Network metrics For each multilayer network, we calculated four metrics. These included: multidegree, graph strength, redundancy/relevance, and layer similarity.

- Multidegree
- 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.
- Graph strength
- 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.
- layer similarity

Varying scale in multilayer networks

Social scale We altered social scale based on visual (short distance) and auditory (long distance) sensory modalities of caribou . Specifically, we modified the spatial 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, individuals within 500m of one another were considered in the same group.

Spatial scale To assess the influence of spatial scale on multilayer networks, we aggregated our landcover classification map at varying scales relevant to caribou ecology. We aggregated the 10m landcover raster using the R package **grainchanger** (L. Graham 2019) at five scales: 100m, 250m, 500m, and 1000m. Aggregation occurred using a modal moving window method using a circular window corresponding to the above scales (L. J. Graham et al. 2019). 10m and 100m represents fine-scale decision making for caribou during foraging , while re-sampling at 500m and 1000m represents the scale at which caribou tend to select and avoid habitat (Bastille-Rousseau et al. 2017).

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

1. time window length

Varying length of time window (used to define seasons). Starting with a window of day 1-40 and using a moving window to go to day 1-100. 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 48 Window positions starting at 1, to + 48 So 1-48 is first iteration for winter and 48-96 is second iteration for “winter”. Same for summer, starting at 215. Network layers for each season are constructed.

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 - . For each iteration, include n observations for each season for all individuals. Subsequent iterations include nstep more , along with previously included to remove stochasticity. Parallels with observation data.

Scale in multilayer networks in practice: case study results and discussion

Each metric's interpretation

- Multidegree: sum of degree across layers. High multidegree = connected to many individuals across layers. Low multidegree = not connected to many individuals across layers.
- Degree deviation: deviation of degree across layers. High degree deviation = large difference between degree for an individual across layers. Low degree deviation = individuals are similarly connected across layers.
- Graph strength: weighted version of degree. High graph strength = highly connected. Not summed in this case across layers.
- Neighbours: number of unique individuals adjacent to each actor. Considered in a single layer, this is equal to the degree.
- Neighbourhood: number of unique individuals across all layers. High neighbourhood = a high number of unique individuals connected to an actor.
- Relevance: layer centric metric, corresponding to the number of neighbours on a layer divided by the total neighbourhood for each actor. High relevance means that the layer is highly relevant to the individuals connections. A low relevance means this layer does not contribute many neighbours to an individuals overall neighbourhood.
- Connective redundancy: the total multilayer neighbourhood divided by the multidegree. High connective redundancy indicates a multilayer network that has many repeated edges across layers between an actor and its neighbours. Low connective redundancy indicates that each layer is important for preserving all social ties.
- Layer similarity: how similar each layer is (Brodka 2018). Pearson's correlation coefficient of degree vectors for each layer, comparing each landcover across seasons.

Figure captions and brief interpretations

- decreasing availability of patchy lichen = no edges in these layers, though some small proportion of relocations still exist in those layers
- decreasing connective redundancy because through resolution because lichen decreased in connectivity and landcovers became more homogeneous (?)
- decreasing winter lichen relevance because the degree + number of edges decreased
- increasing layer relevance as more individuals are connected with increasing buffer size
- decrease in connective redundancy due an increase in summer forest degree at the last (500m) social threshold
- increasing graph strength consistent with increasing strength in winter
- increasing window length = increasingly similar layers and increasingly redundant edges. more individuals have the opportunity to interact
- increasing window length also leads to increasing similarity between seasons because seasons are less well defined/include more shoulder seasons
- decreasing graph strength at the upper end of window length in winter showing again inclusion of more shoulder season

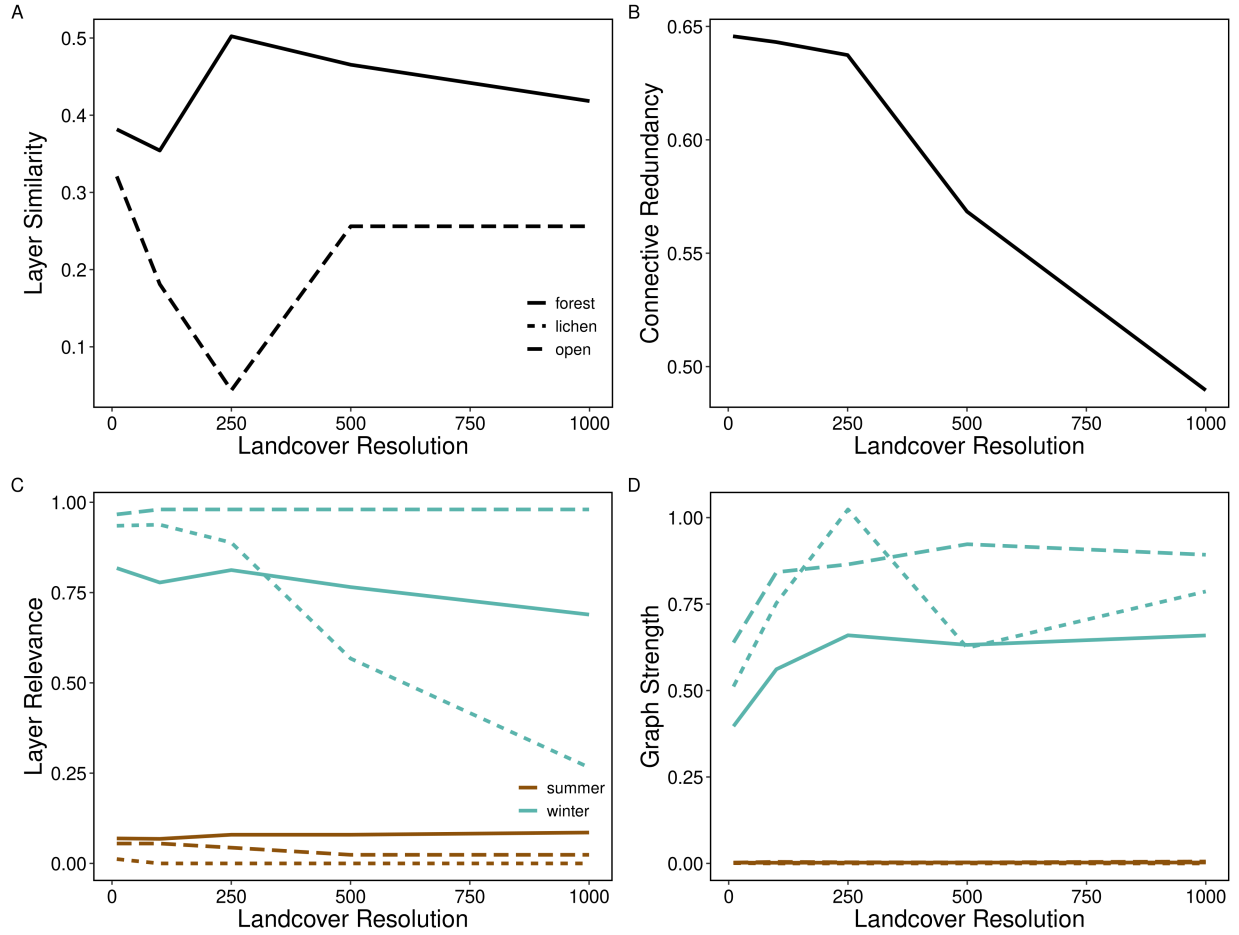


Figure 2: varying scale in landcover resolution. For each landcover resolution (10m, 100m, 250m, 500m and 1000m), multilayer networks were constructed for each landcover class (open, forest and lichen) across two seasons (winter and summer) and four network metrics calculated. A) Similarity of landcover network layers between seasons (e.g.: open summer compared to open winter) showed different responses to changing landcover scale with an increase in similarity for forest layers at 250m and decrease in similarity for open layers at 250m. Note that lichen layer similarity is not shown because individuals did not interact in lichen habitats greater greater than 10m landcover resolution. B) Mean connective redundancy across individuals showed a decreasing trend with increasing landcover resolution. C) Mean layer relevance and D) mean graph strength across individuals showed sparse connectivity in summer compared to winter networks and a decrease in winter lichen layer relevance at higher landcover resolutions.

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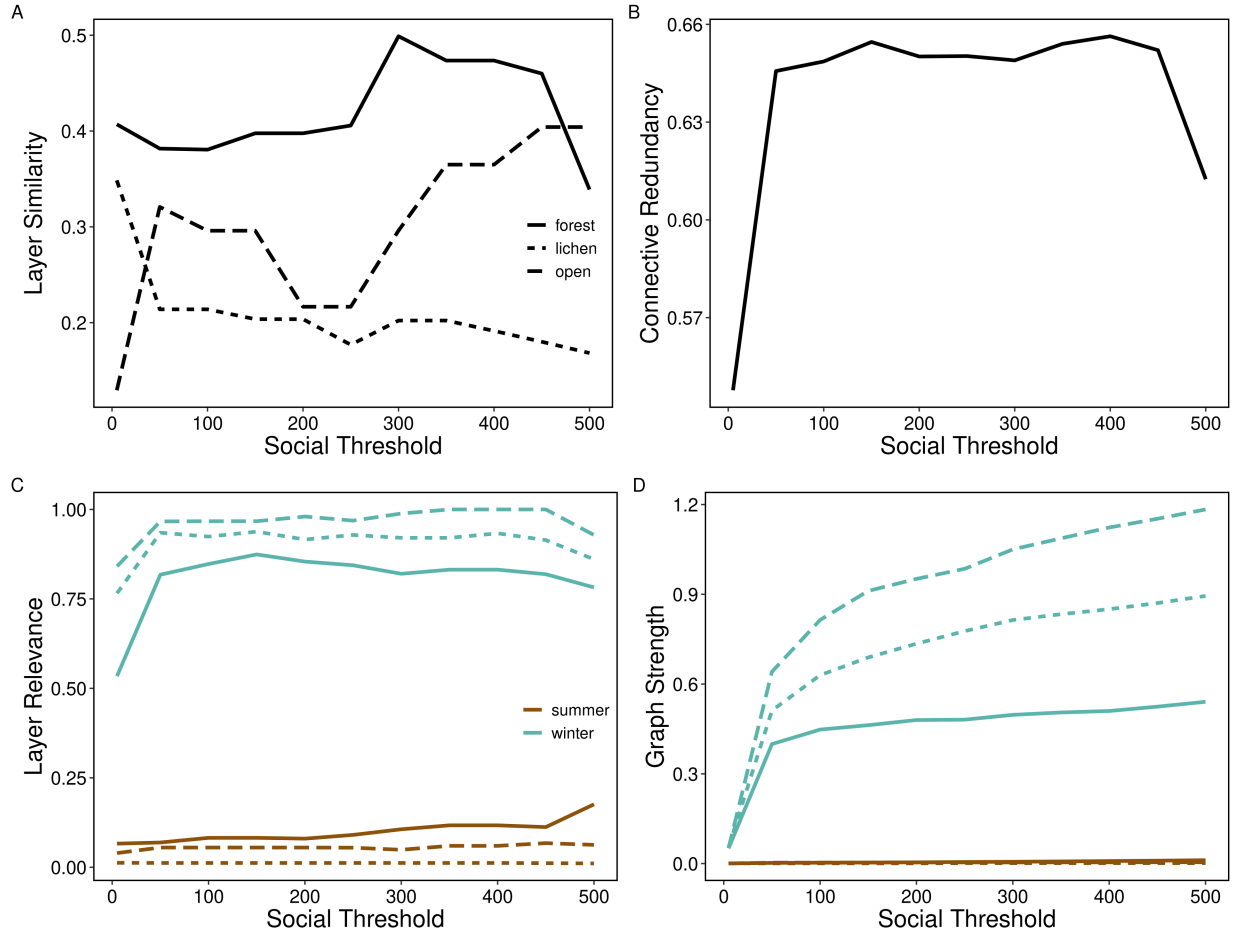


Figure 3: varying scale in social threshold. For each social threshold (5m, 50m, 100m, 150m, 200m, 250m, 300m, 350m, 400m, 450m, 500m), multilayer networks were constructed for each landcover class (open, forest and lichen) across two seasons (winter and summer) and four network metrics calculated. A) Similarity of landcover network layers between seasons (e.g.: open summer compared to open winter) showed different responses to changing landcover scale with an overall increase in similarity for open layers and decrease in similarity for lichen layers. B) Mean connective redundancy across individuals increased rapidly between 5m and 50m reaching a plateau around 0.65 before decrease between 400m and 500m. C) Mean layer relevance was relatively stable across social thresholds for each season and landcover layer. D) Mean graph strength across individuals showed an increase for winter network layers at 50m through 500m while summer network layers remained consistently sparse.

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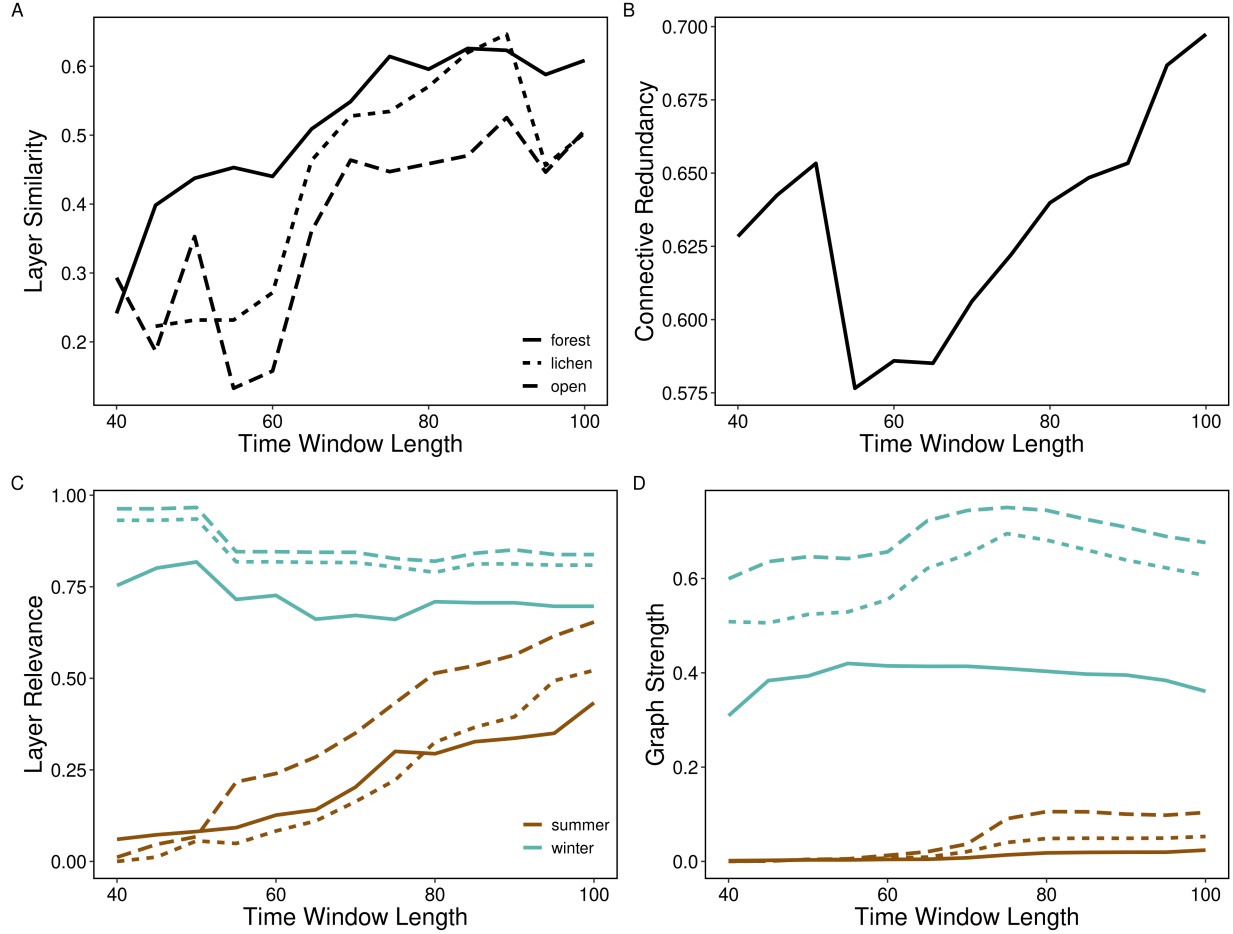


Figure 4: varying scale in time window length. For each time window length (of a sequence from 40 to 100 by 5), multilayer networks were constructed for each landcover class (open, forest and lichen) across two seasons (winter and summer) and four network metrics calculated. A) Similarity of landcover network layers between seasons (e.g.: open summer compared to open winter) showed increasing similarity consistent across landcover layers with increasing window length. B) Mean connective redundancy across individuals increased rapidly between 5m and 50m reaching a plateau around 0.65 before decrease between 400m and 500m. C) Mean layer relevance was relatively stable across social thresholds for each season and landcover layer. D) Mean graph strength across individuals showed an increase for winter network layers at 50m through 500m while summer network layers remained consistently sparse.

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- layers are more similarly relevant at high window length
- common, though at different points - more observations until stabilizing
- we don't see the stabilizing/full plateau for connective redundancy but appears to be coming..
- still some variability, especially for graph strength because individuals are differently connected but broad strokes - they stabilize with more observations

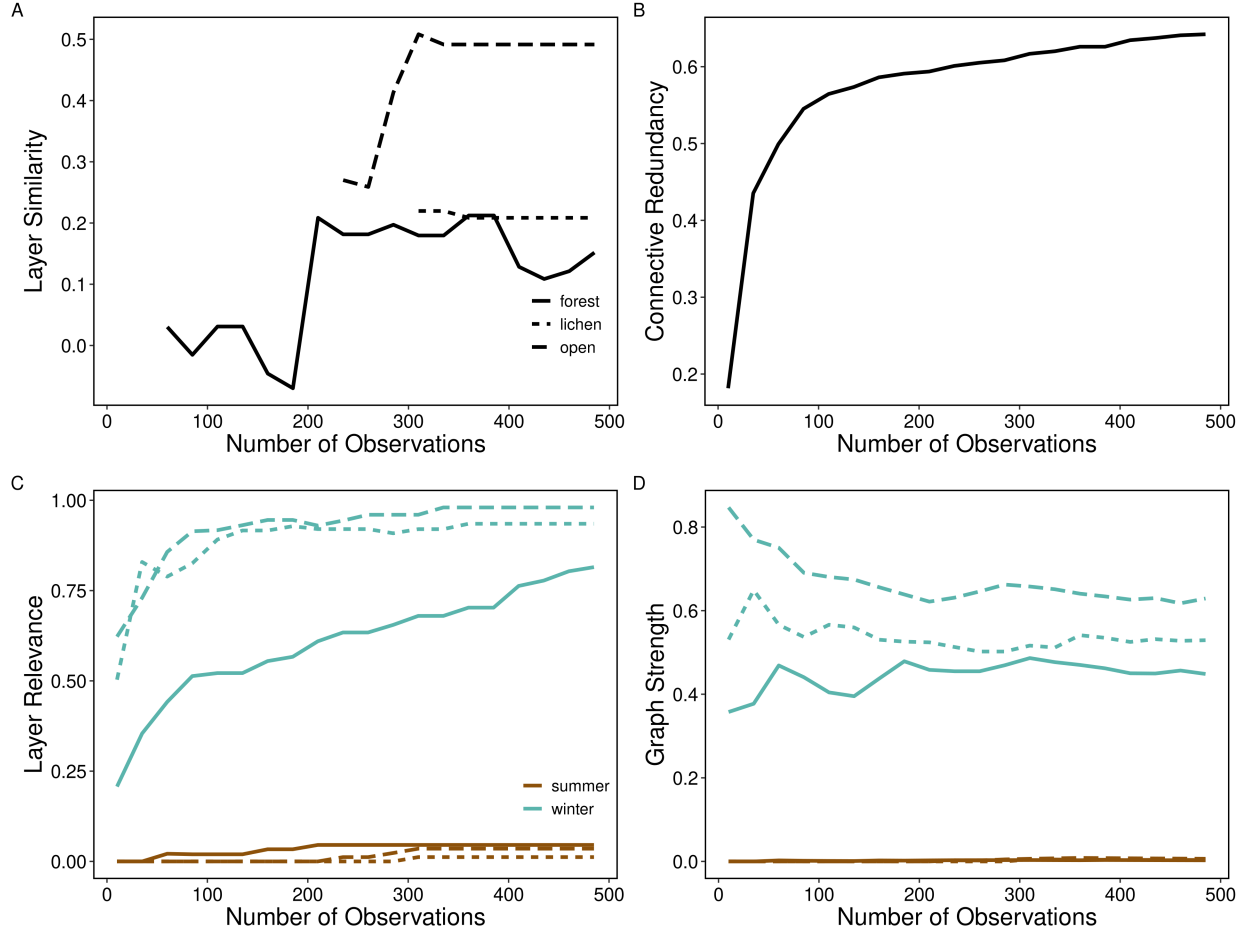


Figure 5: varying scale in number of observations. For each iteration, a number of observations (10-485 observations in steps of 25) were selected from the complete data set to construct multilayer networks with layers defined by each landcover class (open, forest and lichen) across two seasons (winter and summer) and four network metrics calculated. A) Similarity of landcover network layers between seasons (e.g.: open summer compared to open winter) showed a stabilizing layer similarity at 200 observations for forest and 300 observations for lichen and open. B) Mean connective redundancy across individuals increased with increasing number of observations, with a decreasing rate of increase around 100 observations. C) Mean layer relevance across individuals increased for winter layers and slightly increased for summer layers. D) Mean graph strength across individuals varied for winter layers becoming relatively stable at 200 observations and remained sparse throughout for summer layers.

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- increasing network connectivity in summer when the window position is moved - these seasons are more similar than the original window position

- same theme shown in the connective redundancy
- quite variable layer similarity, not sure what to pull out of that one
- increased graph strength for winter down the middle, with generally increasing summer layers - again where the season is including more shoulder season potentially

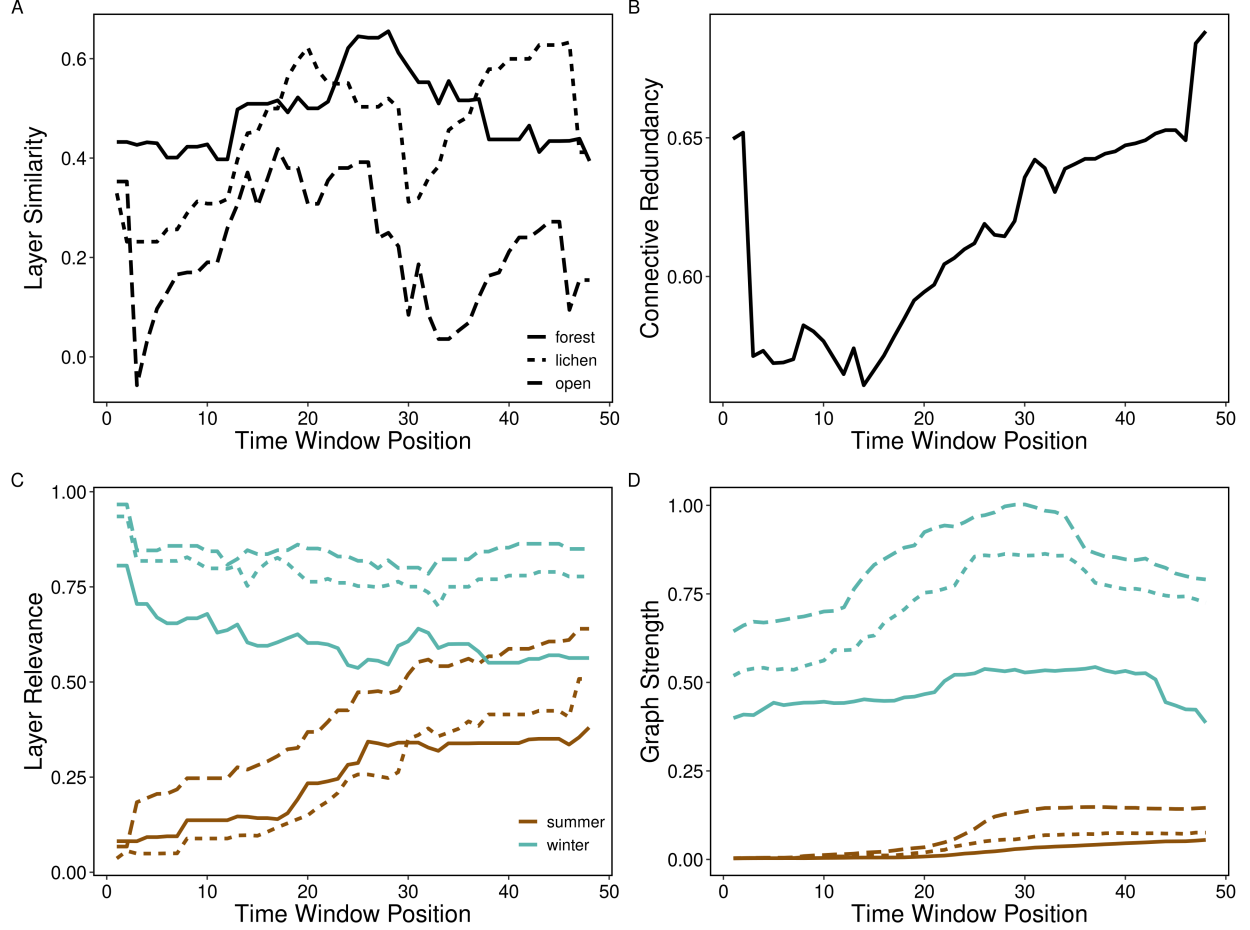


Figure 6: varying scale in time window position. For each time window position (of a sequence from 1 to 48), the time window used to define seasons was shifted and multilayer networks were constructed for each landcover class (open, forest and lichen) across two seasons (winter and summer) and four network metrics calculated. A) Similarity of landcover network layers between seasons (e.g.: open summer compared to open winter) showed increasing similarity consistent across landcover layers with increasing window length. B) Mean connective redundancy across individuals increased between window position 12 through 48 due to increased connectivity in the summer network layers. C) Mean layer relevance decreased for winter layers and increased for summer layers, showing greater connectivity in summer layers at later window positions. D) Mean graph strength across individuals increased in summer network layers at window position 25 and increased between window position 20 and 40 for winter network layers.

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Results and interpretation of temporal scale

Results and interpretation of spatial scale

Perspectives to advance multilayer networks

Habitat selection and space use

- Mayor et al. 2009 paper
- MRSF Laforge paper
- van Beest et al. 2014 scale paper
- 1st/2nd/3rd order selection
- Habitat–performance relationships: finding the right metric at a given spatial scale Jean-Michel Gaillard^{1,*}, Mark Hebblewhite², Anne Loison³, Mark Fuller⁴, Roger Powell⁵, Mathieu Basille^{1,6} and Bram Van Moorter¹
- Multi-scale habitat selection modeling: a review and outlook

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).

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 an individual’s social environment (Strandburg-Peshkin et al. 2015). Movement is a dynamic process that is related to the resources an individual consumes within their home range and the space that they 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 inextricably linked and multilayer networks represent a potential analytical framework for linking these processes (e.g. Mourier et al. 2019).

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 (edges). For example, spatial networks were applied to monitor movement of sharks (*Carcharhinus amblyrhynchos* and *Carcharhinus melanopterus*) between fixed location autonomous arrays. In this example, 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).

In contrast to spatial networks, where nodes represent spatial locations that are fixed in space, movement networks can represent continuous and simultaneous movement trajectories of multiple animals. Continuous

collection of animal relocation data using GPS technology can be used to measure how groups of animals make collective 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 scale (global migration: Flack et al. 2018). Another potential application would be to generate social networks during times when animals are engaged in different behaviours, including traveling, interacting, or foraging (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 or territories can also contribute to the formation of the social environment (Spiegel et al. 2016). For example, in sleepy lizards (*Tiliqua rugosa*) males interacted primarily at home range edges, presumably driving territorial behaviour (Spiegel et al. 2018). 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. How, and why, does the spatial scale of perception influence, e.g. auditory, visual, or chemotaxis, influence the social environment across scales? What is the role of memory, and by extension social and spatial cognition, as animals navigate their environment and make decisions about where to move next?

Acknowledgements

We thank all members of the Wildlife Evolutionary Ecology Lab, including K. Kingdon, S. Boyle, C. Prokopenko, I. Richmond, J. Hogg, and L. Newediuk for their comments on previous versions of this manuscript as well as D. C. Schneider for inspiration and helpful discussions about scale. Funding for this study was provided by a Vanier Canada Graduate Scholarship to QMRW and a NSERC Discovery Grant to EVW.

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