

The problem and promise of scale in multilayer animal social networks

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Contents

1	Abstract	2
1.1	Keywords	2
2	Introduction	3
3	Scale in multilayer networks: a case study	5
3.1	Caribou socioecology	5
3.2	Caribou location data	5
3.3	Landscape data and habitat classification	5
3.4	Caribou multilayer social networks	5
3.5	Varying scale in multilayer networks	6
4	Scale in multilayer networks in practice: case study results and discussion	8
5	Perspectives to advance multilayer networks	9
5.1	Phenotypes and Individual fitness	9
5.2	Movement ecology and collective movement	16
5.3	Habitat selection and space use	17
6	Conclusions	18
7	Acknowledgements	18
8	References	19

1 Abstract

Scale remains a foundational 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. Here we discuss the role of scale in the context of multilayer networks and provide a social ungulate case study 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; phenotypes and individual fitness; 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, as such our contribution incorporates perspectives on how the social environment and spatial processes are linked across scales in a multilayer context.

1.1 Keywords

Social network analysis, Landscape ecology, Movement ecology, Space use

2 Introduction

Our inference regarding the ecological processes underlying ecological patterns are directly linked to the scale at which they are observed [Levin_1992; Allen_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_2009]. Multiscale ecology has been integrated into species distribution modelling [Elith_2009], habitat selection [Mayor_2007], and food webs [Sugihara_1989], among others. Meanwhile, in the context of animal behaviour, certain behaviours are scale-dependent; for example, acoustic communication in birds varies with spatial scales [Luther_2009]. We posit that it is important to consider that animal behavior within the social environment will 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_2015], whereas social association represents shared space use by members of the same social group [Figure 1, Franks_2009]. Further, for social interactions or associations to occur individuals must share space, and thus have overlapping home ranges [VanderWal_2014]. In the context of the social environment, home range overlap is an example of how animals 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_2014; Farine_2015a]. Thus, we define social scale as the type of social relationship observed that can be explicitly defined and measured [Farine_2015a].

Animal social network analysis is a well-developed tool used to measure the relationships of individuals and organization of social systems [Krause_2009; Wey_2008; Croft_2011]. 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_2013; Kurvers_2014]. Despite the widespread use and innovation of traditional social network analysis [Webber_2019], it typically considers a single scale of sociality in a given network (monolayer), drastically simplifying the complexity of animal social systems [Finn_2019].

Unlike traditional monolayer social networks, multilayer networks explicitly consider social systems across contexts, including scale-dependent contexts [Pilosof_2017]. Multilayer networks are made up of multiple layers, each representing (i) different classes of individuals, e.g. male or female; (ii) types of behaviours, e.g. grooming, travelling, or foraging; and (iii) spatial areas, e.g. local or regional, or temporal windows, e.g. daily or seasonal [Kivela_2014; Porter_2018]. Multilayer networks are relatively novel to studies of animal behaviour [Silk_2018; Finn_2019], although they have been used to describe multidimensional human social systems, complex transportation networks, and neural networks [Silk_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 examinations 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_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 the social, spatial, and temporal scale 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 phenotypes and individual fitness [Webber_2018], movement ecology and collective movement [Jolles_2019], and habitat selection and space use .

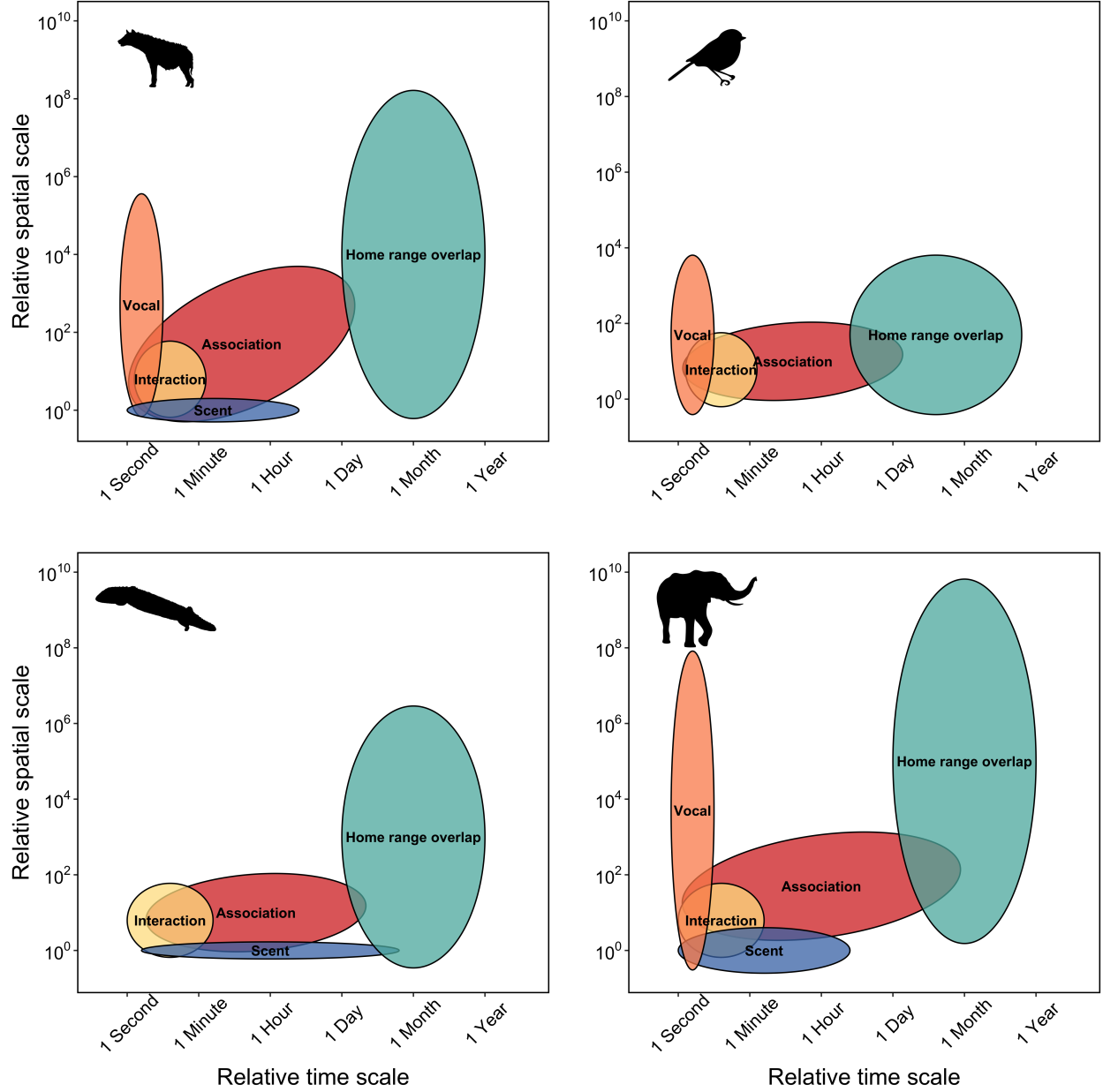


Figure 1: Space-time diagram displaying variation the relative spatial and temporal extent required for different types of social and communication processes for four species, including hyaena, passerine birds, sleepy lizards, and elephants. Spatial and temporal extent for social interactions, e.g. mating, grooming, or aggression, are similar for most species because physical contact between two individuals is required for most social interactions. The logical extension is that spatial and temporal extent for social interaction is hierarchically nested within the spatial and temporal extent for social association because individuals must share space to interact. By contrast, different species have potential for greater spatial and temporal extents, for example, temporal extent for vocal communication is similar for most species because most vocal calls only persist in the environment for seconds, but spatial extent for vocal communication is highly variable with elephant calls extending the great distance and passerine calls extending the shortest distance.

3 Scale in multilayer networks: a case study

3.1 Caribou socioecology

Here, we use caribou as a case study to develop scale-dependent multilayer networks based on predicted social (visual and auditory perception), spatial (habitat type), and temporal (seasonal) scales. Caribou are gregarious ungulates with fission-fusion dynamics [Lesmerises_2018] that display temporal and spatial variation in social networks [Peignier_2019]. In winter, caribou dig holes in the snow, termed craters, to access forage [Bergerud_1974]. Cratering is presumed to be a costly behaviour and 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_2009]. The distribution of forage for caribou is therefore seasonally heterogeneous because the distribution of craters on the landscape varies meaning that access to vegetation in winter is highly variable for caribou. Caribou therefore have greater access to forage in snow-free seasons. We partitioned data into two discrete seasons: summer (3 August - 20 September 2017) and winter (1 January – 17 February 2018) based on caribou socioecology [Peignier_2019].

3.2 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, ON, Canada, GPS4400M collars, 1,250 g) as described by [Schaefer_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 [BJ_RNERAAS_2010]. We did not collar all caribou in the herd; however, the proportion of marked adult females was ~10% of all adult females and ~5% of all individuals in the herd. We assumed these individuals were randomly distributed throughout the population.

3.3 Landscape data and habitat classification

Landcover data were provided by the Newfoundland and Labrador Wildlife Division [Integrated_2013]. Available landcover classification included nine habitat types at 30 m resolution. We reclassified the landcover types into three categories: foraging habitat, open habitat, and forest habitat using the R package `raster` [Hijmans_2019]. 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. Water habitat was excluded from all subsequent analyses.

3.4 Caribou multilayer social networks

3.4.1 Network types and construction

We generated a multilayer social network consisting 14 individual nodes and two aspects (season and landcover). Two season elementary-layers (winter and summer) and three landcover elementary-layers (forest, forage, and open) combined for a total of six layers. Layers were composed of individuals represented as nodes and social associations represented as edges, for each season and landcover combination. Proximity-based social network layers were generated using the R package `spatsoc` [Robitaille_2019] in R version 3.6.2 (2019-12-12) [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_2019]. Group assignment based on the chain rule has previously been applied to caribou at a distance of 50 m [Peignier_2019; Lesmerises_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 seasons and within habitat classes (Figure 2).

We weighted edges of social networks by the strength of association between caribou using the simple ratio index (SRI, Cairns and Schwaeger 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_2015]. Social groups were designated if two or more individuals occurred within a given distance of one another at any given time point.

3.4.2 Network metrics

We used a series of metrics to characterize the multilayer networks, focusing on the role of individuals, importance of individual layers and the similarity of different layers. To measure the role of individuals, we calculated degree centrality and graph strength. Degree centrality is the number of direct connections an individual has to other individuals in a network layer. Graph strength is the degree weighted by the strength of association, in this case SRI, in each layer-specific season and landcover context. Extending degree centrality, we calculated multidegree, the sum of degree centrality across layers, and neighbourhood, the sum of unique neighbours to each individual [Berlingiero_2012; Kivela_2014]. We evaluated the relevance and redundancy of layers by combining the multidegree and neighbourhood to calculate connective redundancy and layer relevance. Connective redundancy is the proportion of neighbours repeated in multiple layers, and layer relevance is the proportion of neighbours present in each layer compared to the neighbourhood for each individual [Berlingiero_2012]. Finally, we calculated the similarity of layers between seasons, across landcover classes (e.g. winter open compared to summer open) using the Pearson correlation coefficient [Br_dka_2018]. Network metrics were calculated using the R packages `igraph` [Csardi_2006], `asnipe` [Farine_2019] and `data.table` [Dowle_2019].

3.5 Varying scale in multilayer networks

3.5.1 Social scale

We modified the spatial distance threshold required for group assignment using `spatsoc` [Robitaille_2019] (see above) and re-assigned groups at incremental distances between 5 - 500 m. For example, at the finest social scale, only individuals within 5 m of one another were considered in the same group, whereas at the coarsest social scale, individuals within 500 m of one another were considered in the same group. We assumed these scales represented visual (short distance) to auditory (long distance) sensory modalities of caribou.

3.5.2 Spatial scale

To assess the influence of spatial scale on multilayer networks, we aggregated our landcover raster at varying scales relevant to caribou ecology. We aggregated the 30 m landcover raster using the R package

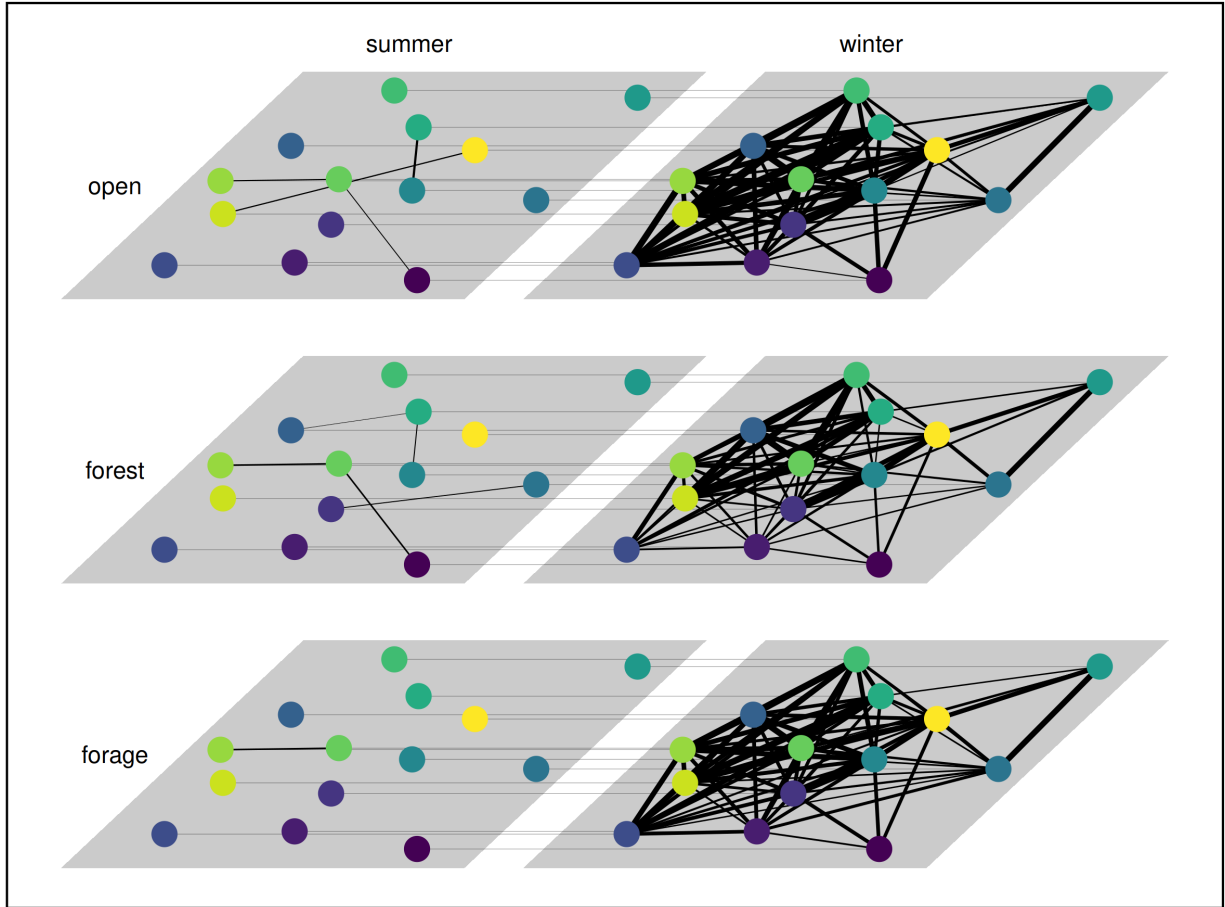


Figure 2: Visualization of multilayer network for social ungulate case study representing social association of caribou (*Rangifer tarandus*) on Fogo Island, Newfoundland in summer 2017 and winter 2018. Individual caribou ($n = 14$) are shown as nodes and each individual is represented by a unique color. Six layers represent combinations of two seasons (winter and summer) and three habitat classes (open, forest and forage). Intralayer edges connect pairs of individuals that associated according to spatial and temporal thresholds described above, and are scaled in line thickness according to strength of association (SRI). Interlayer edges connect individuals to themselves across seasons and within habitat classes (eg. individual “A” in summer, forest and individual “A” in winter, forest).

grainchanger [Graham_2019] at five scales: 100 m, 250 m, 500 m, 750 m and 1000 m. Aggregation occurred using a modal moving window method using a circular window corresponding to the above scales [Graham_2019a]. We assume 30 m and 100 m represents fine-scale decision making for caribou during foraging, while re-sampling at 500 m, 750 m and 1000 m represents the scale at which caribou tend to select and avoid habitat (Bastille-Rousseau et al. 2017).

3.5.3 Temporal scale

3.5.3.1 Time window length and position We altered the temporal scale of multilayer networks by varying the length and position of the time window used to define seasons. The length of the time window varied from 40-100 days using a fixed start day for winter (starting at 1 January) and summer (starting at 3 August). The position of the time window was shifted by 1-48 days, using a fixed time window length of 48 days. These new time windows were iteratively used to partition data into two discrete seasons (winter, summer) and generate multilayer networks.

3.5.3.2 Number of observations 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_2018; Weber_2019]. For example, GPS data is commonly collected at a fixed rate, eg. every x minutes or hours, continuously throughout the study period. We investigated the influence of the number of observations on resulting multilayer networks. We randomly selected 500 timesteps and iteratively included 25 additional observations, regenerating the multilayer network and calculating associations of individuals. Subsequent iterations included the previous set of observations to mimic collection of observational data.

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

In general, individuals in multilayer networks became more connected as social scale increased; however, this relationship varied by habitat type and season. As social scale increased, graph strength for winter networks increased rapidly between 5 m and 50 m thresholds, followed by a plateau, while graph strength for summer networks did not change as the social threshold increased (Figure 3a). Layer relevance increased for winter networks between 5 and 50 m social thresholds, then did not change for any habitat types which suggests the winter habitat layers captured most, if not all, of the potential connections an individual would have across these networks (Figure 3b). Layer similarity (Figure 3c) and connective redundancy (Figure 3d) were relatively stable across social thresholds. Taken together, these results suggest the optimal social scale at which groups should be assigned is likely somewhere between ~20 - 100 m based on the rate at which network metrics stabilized. For ungulates, groups are often assigned based on 50 m threshold (Lingle 2003; Lesmeries et al. 2018; Peignier et al. 2019), suggesting that given similar quantities of data, ~50 m is likely an appropriate social scale for generating social networks in caribou and similar species.

Increasing landcover resolution resulted in a decreased proportion of forage, a rare and patchy habitat, and corresponding low connectivity of individuals in these habitats. Mean graph strength increased consistently in winter forest and open habitats. Mean graph strength in winter forage varied across landcover resolutions with an increase at 250 m and decrease at 500 m. Individuals in summer layers had consistent weak connections. Layer relevance was stable in winter for open and forest habitats but decreased for forage habitats (Figure 4b). Layer relevance was stable for all habitat classes in summer layers. Layer similarity was stable for forest and open, except for a sharp decrease in layer similarity in open at 100 m and 250 m (Figure 4c). Layer similarity was not possible to calculate between winter and summer forage because, at all landcover resolutions greater than 30 m, there were no individuals connected in the network layers. Individuals still used forage habitats but given a lower availability due to increasing landcover resolution, at a much lower rate. Connective redundancy slightly decreased as landcover resolution increased (Figure 4d). These results indicate the importance of matching landcover resolution to scale of selection as well as

ensuring the landcover product used has a resolution fine enough to detect landscape features and habitats relevant to study species.

As the number of observations used to generate multilayer networks increased, individuals became more connected and metrics appeared to stabilize. Mean graph strength varied in winter layers at low number of observations, becoming stable at ~ 75 observations and was consistently weak in summer layers (Figure 5a). Layer relevance in winter layers increased between ~ 10 m and ~ 100 m observations, remaining stable with additional observations (Figure 5b). Like coarse landcover resolution (Figure 4), low numbers of observations were not sufficient for capturing individuals in all contexts and therefore layer similarity could not be calculated below ~ 30 observations for forest, approximately ~ 80 observations for open (Figure 5c). Layer similarity was not possible to calculate for forage layers because there were no connected individuals in summer forage. Once sufficient observations were obtained, layer similarity was relatively stable for forest and open layers. Connective redundancy increased dramatically between ~ 10 m and ~ 50 m observations before stabilizing with all new observations included (Figure 5d). Given the observed trend of these multilayer metrics stabilizing after a certain number of observations are included, the results suggest this sensitivity method could be useful for determining the number of observations necessary for sufficiently describing social dynamics across contexts.

Moving window positions defining seasons showed an increase in connectivity of individuals in summer layers. Graph strength increased at time window position ~ 20 for summer and winter layers and, while summer layers continued to increase, winter layers showed a decrease in graph strength at time window position ~ 35 (Figure 7a). Layer relevance increased across moving window positions for summer layers and was relatively stable for winter layers (Figure 7b). These results indicate slight decreasing connectivity and increased connectivity in summer layers at shifted winter time windows. Layer similarity was relatively stable across moving window positions except for a sharp decline at window position ~ 28 in forage and open layers (Figure 7c). Connective redundancy showed a marginal increase with increasing window position (Figure 7d). Similar to window length, changing the position of the time window in this case results in a mismatch between expected periods of resource seasonality and corresponding sociality, highlighting the importance of carefully selecting temporal scale of analysis.

5 Perspectives to advance multilayer networks

The integration of behavioural and ecological theory has shown the value of considering the importance of various ecological disciplines to better understand and predict animal social networks, including demography [Shizuka_2019], evolutionary and quantitative genetics [Fisher_2017], disease ecology [Silk_2017], and animal personality [Sih_2018]. While the number of studies integrating social network theory into a broader array of behavioural and ecological sub-disciplines is impressive, only recently has the role of animal space use been considered in describing the causes and consequences of the social environment in the context of (1) phenotypes and individual fitness [Webber_2018], (2) movement ecology and collective movement [Bode_2011], and (3) habitat selection and space use [He_2019]. Importantly, much of the work linking space use and the social environment has been theoretical and empirical studies are lacking [but see Peignier_2019; Strandburg_Peshkin_2015; Strandburg_Peshkin_2017]. Here, we discuss the role multilayer networks within the emerging integration of social and spatial ecology within the behavioural ecology literature.

5.1 Phenotypes and Individual fitness

Social network positions are frequently used to represent the social environment that an individual experiences or their social phenotype. Multilayer networks provide a way to bridge these different scales so that we can examine social phenotypes in more holistic ways rather than looking at each scale separately as has traditionally been done. From a monolayer network perspective, social phenotypes are increasingly linked to important fitness for individuals of various species, including primates [Brent_2017; Thompson_2019], dolphins [Stanton_2012; Stanton_2011], and birds [McDonald_2007; Royle_2012]. Both

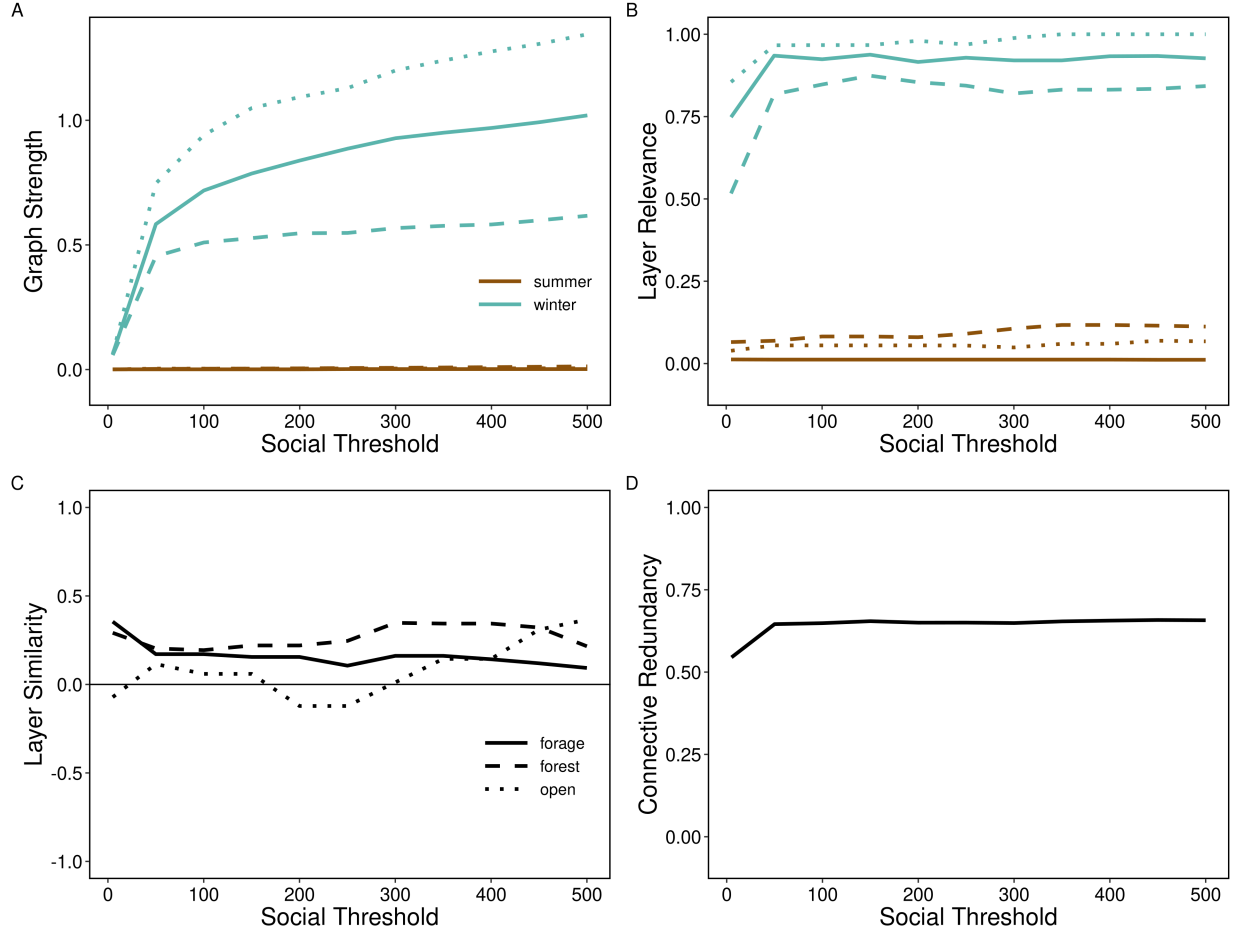


Figure 3: Varying scale in social threshold. For each social threshold, multilayer networks were constructed of caribou social associations (*Rangifer tarandus*, $n = 14$) on Fogo Island, Newfoundland in summer 2017 and winter 2018 across three habitat classes (forest, forage, and open). A) Mean graph strength across individuals showed an increase for winter network layers while summer network layers had consistently weak connections. B) Mean layer relevance was increased for winter layers between 5 m and 50 m, otherwise stable for all social thresholds >50 m for winter and all social thresholds for summer. C) Similarity of network layers across seasons and within habitat classes (e.g. open summer compared to open winter) was relatively stable for all habitat class layers. D) Mean connective redundancy across individuals showed an increase between 5 m and 50 m before remaining stable through all other social thresholds.

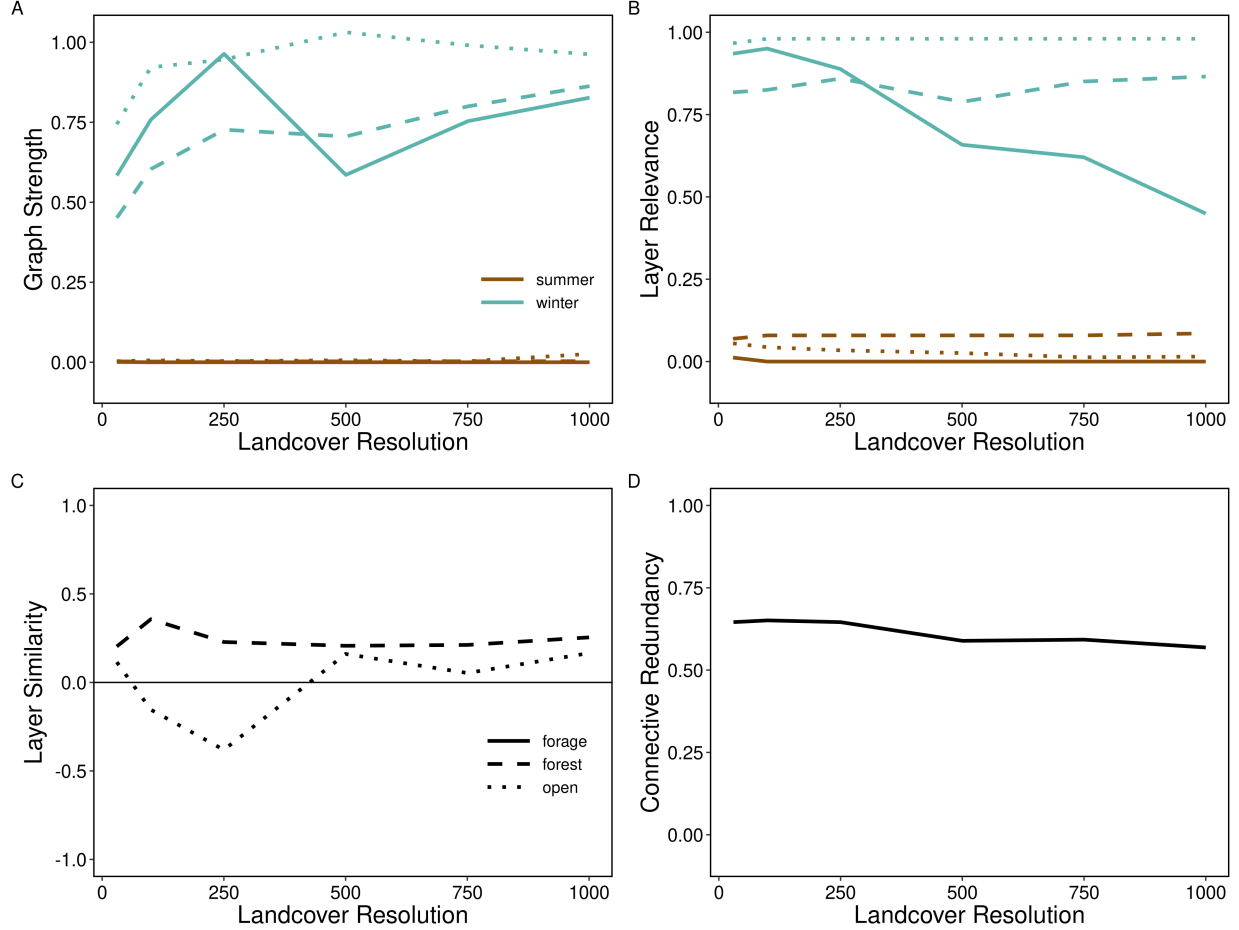


Figure 4: Varying spatial scale in landcover resolution. For each landcover resolution, multilayer networks were constructed of caribou social associations (*Rangifer tarandus*, $n = 14$) on Fogo Island, Newfoundland in summer 2017 and winter 2018 across three habitat classes (forest, forage, and open). A) Mean graph strength of individuals in winter forest and open habitats increased consistently while winter forage varied with a peak at 250 m and valley at 500 m. Individuals in summer layers had consistent weak connections. B) Mean layer relevance showed sparse connectivity in summer compared to winter networks and a decrease in winter forage layer relevance at higher landcover resolutions. C) Similarity of landcover network layers between seasons (e.g. open summer compared to open winter) was relatively stable for forest and open, except for a sharp decrease in open at 100 m and 250 m. Note that layer similarity in summer forage is not shown because individuals did not interact at landcover resolutions greater than 30 m and therefore layer similarity could not be calculated. D) Mean connective redundancy across individuals showed a slight decreasing trend with increasing landcover resolution.

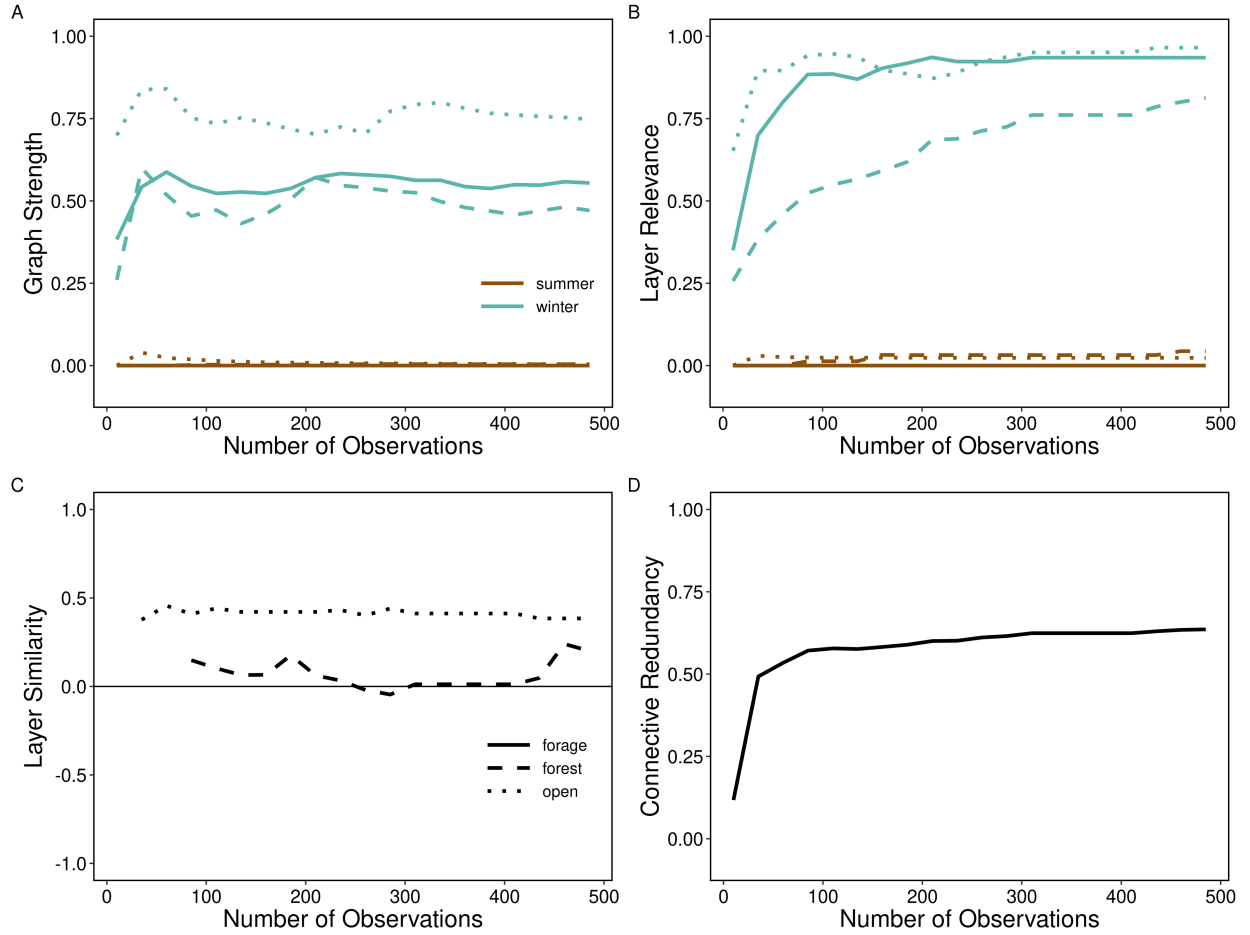


Figure 5: Varying scale in number of observations. For each iteration, a number of observations (10-485 observations in steps of 25) were selected from the complete data set to construct multilayer networks of caribou social associations (*Rangifer tarandus*, $n = 14$) on Fogo Island, Newfoundland in summer 2017 and winter 2018 across three habitat classes (forest, forage, and open). A) Mean graph strength across individuals varied for winter layers becoming relatively stable at 100 observations and remained weak throughout for summer layers. B) Mean layer relevance across individuals increased sharply for winter layers between ~ 10 m and ~ 50 m observations before stabilizing. Summer layers had consistent low layer relevance. C) Similarity of network layers across habitat classes and between seasons (e.g. open summer compared to open winter) was relatively consistent across number of observations for forest and open habitats. Note, forage habitats are not shown given no individuals interacted in the summer forage layer. D) Mean connective redundancy across individuals increased rapidly between ~ 10 m and ~ 50 m observations and then remained constant.

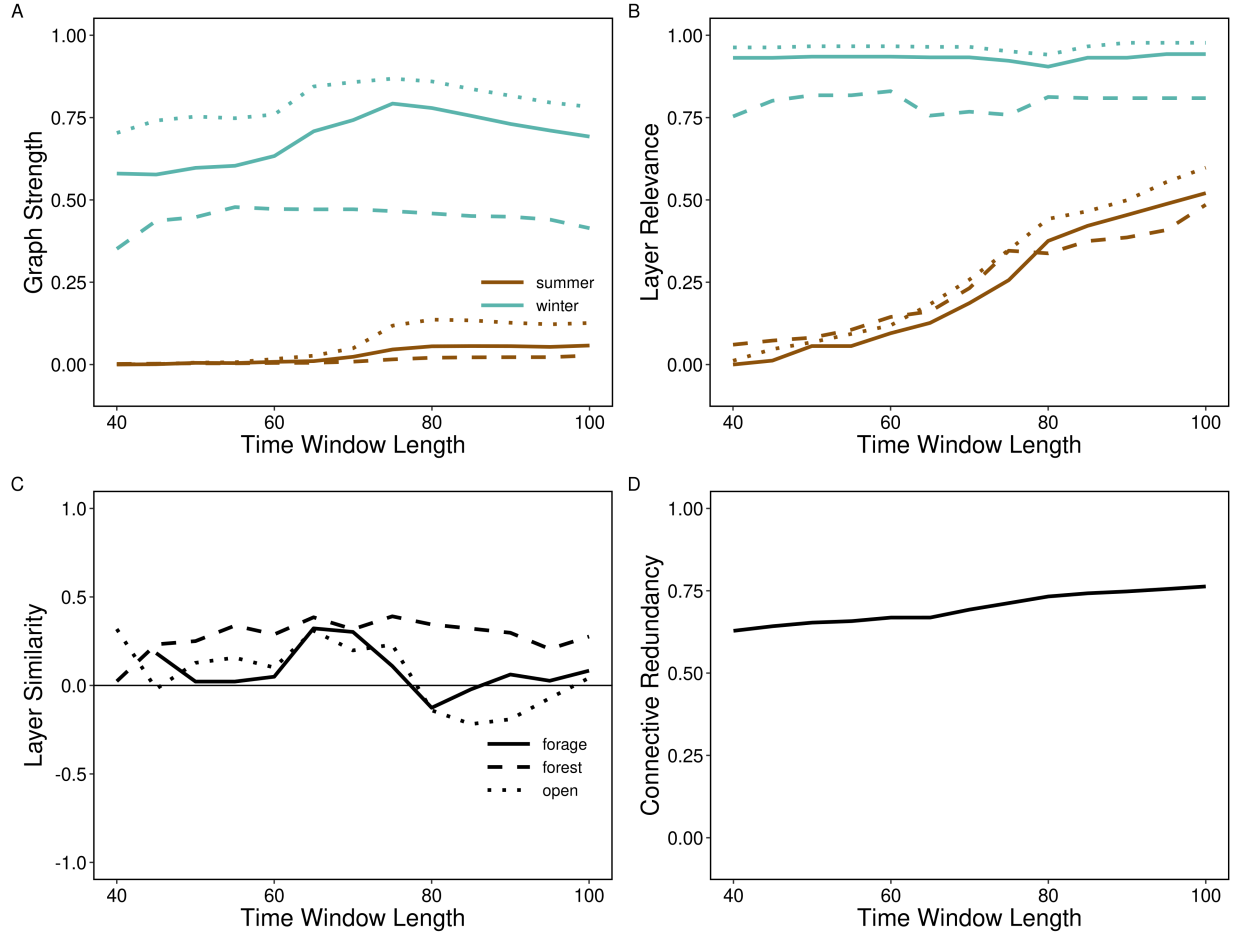


Figure 6: Varying temporal scale in time window length. For each time window length (40 to 100 days in length increasing by 5 days in sequence), multilayer networks were constructed of caribou social associations (*Rangifer tarandus*, $n = 14$) on Fogo Island, Newfoundland in summer 2017 and winter 2018 across three habitat classes (forest, forage, and open). A) Mean graph strength across individuals was relatively stable over increasing time window lengths for winter layers, though there was more variation in strength between landcover types as window length increased. Summer layers an increase in strength for open and forage habitats. B) Mean layer relevance was stable for winter layers and increased for summer layers across habitat classes. C) Similarity of layers across habitat classes and between seasons (e.g. open summer compared to open winter) was relatively stable. D) Mean connective redundancy across individuals increased marginally with increasing window length.

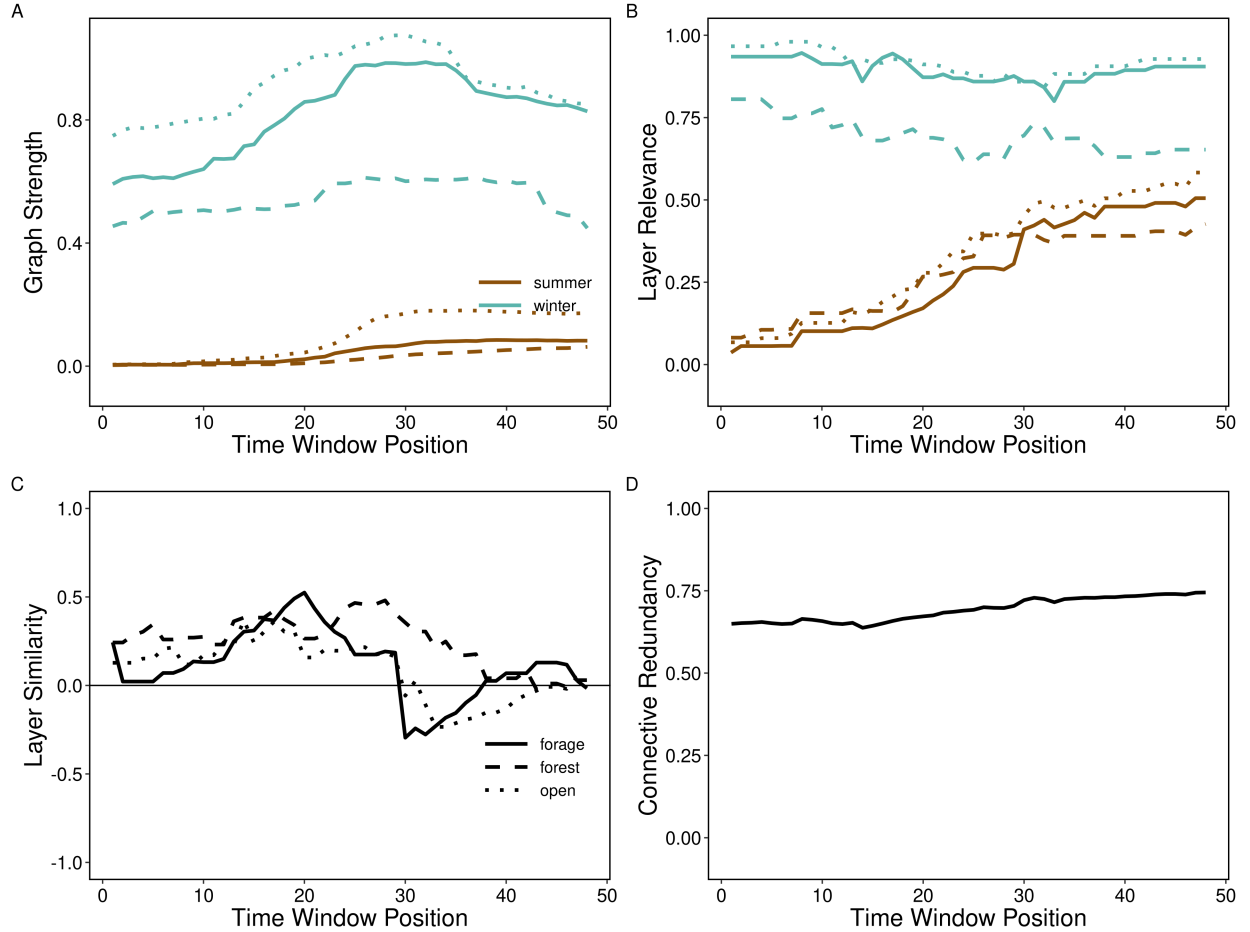


Figure 7: Varying temporal scale in time window position. For each time window position (shifting the start date of the time window used to define seasons 1 to 48 days from the original), multilayer networks were constructed of caribou social associations (*Rangifer tarandus*, $n = 14$) on Fogo Island, Newfoundland in summer 2017 and winter 2018 across three habitat classes (forest, forage, and open). A) 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. B) Mean layer relevance slightly decreased for winter layers and increased for summer layers. C) Similarity of layers across habitat classes and between seasons (e.g. open summer compared to open winter) was relatively stable until window position ~ 28 where forage and open layer similarity decreased. D) Mean connective redundancy across individuals increased marginally with advancing time window position.

social scales, types of interactions, and temporal, seasons and stages of life, have emerged as important for understanding fitness consequences in the context of social network positions [Almeling_2016; Berger_2015; Brent_2017; Holekamp_2011].

For instance, social scale is major consideration for social network analysis, especially in the context of different types of relationships, such as grooming and association, that are typically examined separately while answering a single question [Castles_2014; Carter_2015; Farine_2015a]. Furthermore, it is a common trope that individuals must be associating to interact, and many studies therefore assume that proximity is proxy for interacting [Farine_2015a]. For instance, baboons need to be in proximity to groom each other. However, animals have certain interactions that do not require proximity such as long-distance vocalization and olfactory signals [Carter_2015]. With the advancement of biologging 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_2017]. Using relocation data, our case study results indicate that there are different social patterns in different habitat types, likely indicating different types of interactions. When the social threshold is greater than approximately 50 m during the winter, individuals demonstrate dramatically different graph strength (Figure 3) in different habitat types, having higher graph strength in forage and open habitats where they can likely see each other and still interact with visual cues than in forest habitats. Varying social scales can have different fitness repercussions for individuals. Rhesus macaques (*Macaca mulatta*) had higher survivorship when they had fewer but stronger, more stable social associates and grooming partners rather than simply more associates [Ellis_2019]. This finding highlights that different qualities of social scales have lasting consequences. Multilayer networks provide the opportunity to address these types of questions involving social scale with all the individual layers of interaction integrated in a holistic way.

Temporal scale is also important for understanding the repercussions of social phenotypes. Varying the time window length and position for caribou, we found there was a lot of variation in the multilayer network metrics (Figure 6, Figure 7). These changes in the outcome depending on how the time window is defined highlight how critical it is to properly define the time window appropriately to address the questions and hypotheses of interest. For instance, social phenotypes can change over ontogeny in ways that can affect fitness [Berger_2015; Brent_2017]. Thus, it is critical to carefully consider the temporal scale that is meaningful for the proposed hypotheses. Further complicating the issue of selecting suitable time scales across ontogeny, individuals progress through development at different rates [Tarka_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 when they vary by individual. However, considering fine temporal scales provide insight across developmental stages that may otherwise be missed [Turner_2017]. Defining temporal scales is a challenge in multilayer networks just as in monolayer networks; however, multilayer networks provide metrics that enable researchers to look at similarities and differences in separate layers representing different stages of ontogeny, or seasons as in our case study, which can be difficult to detect.

Multilayer networks provide unique opportunities and challenges, linking these various scales, for understanding the social phenotypes and environments of individuals and their fitness outcomes. The multilayer network framework enables researchers to examine these different social scales simultaneously rather than individually, which is what has been done under most circumstances, but is not very realistic. Metrics from multilayer networks provide an opportunity to simplify statistical models. Interactions that happen side-by-side, 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 reduction 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_2014]. Furthermore, 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_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.

Conversely, 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, for instance. In both mono- and multilayer networks, the effect of scale on the relationship between an individual’s social network position and fitness need to be considered based on the hypotheses being tested and logistical constraints.

5.2 Movement ecology and collective movement

Social processes, movement decisions, and space use are inextricably linked and multilayer networks represent a potential analytical framework for linking these processes [Mourier_2019]. Movement as a collective group can reduce per capita predation risk via detection-dilution trade-offs and improve information transfer about the quality or location of resources to other group members [Jolles_2019]. In our case study, we integrate proximity based social networks that inherently rely on animal collective movement and, in general, we found that movement is likely an important mechanism driving social network connectivity within and between habitat types.

Although multilayer animal social networks are relatively novel [Silk_2018], movement behaviour within multilayer networks has been considered. 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_2019]. Although movement between fixed arrays is inherent, networks are not constructed based on continuous measures of dyadic or collective movement [Long_2014]. Our case study builds on the work of Mourier et al. (2019) and explicitly integrates continuous and simultaneous measures of animal movement through space and time as layers of a multilayer social network.

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. In a recent study of vulturine guinea fowl (*Acryllium vulturinum*), GPS movement data were used to generate monolayer association networks within a multilayer network [Papageorgiou_2019]. However, despite potential to generate networks in different spatial or social contexts, layers in the multilayer network represented social associations within and between groups. 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_2015; Strandburg_Peshkin_2017] and across scales. A collective movement layer could constitute similarity in movement for dyads [Long_2014] or groups [Bode_2011]. This movement layer could be made at a fine [i.e. minute-to-minute: Cleasby_2019] or coarse scale [global migration: Flack_2018]. Our case study integrates variation in temporal and spatial scale to assess the role of scale in predicting multilayer networks. As one might expect, we found increasing spatial scale results in saturation of potential social connections (Figure 3), while increasing temporal scale had little effect on habitat-specific networks (Figure 5). Another potential application would be to generate social networks during times when animals are engaged in different potential behaviours, including traveling, interacting, or foraging [Muller_2018; Finn_2019] and construct a multilayer network based on behaviour-specific monolayer networks [e.g. Smith_Aguilar_2019].

Importantly, the key to incorporating movement in multilayer networks across scales is the technological advancements available to overcome previous limitations [Hughey_2018]. Biologging and wildlife tracking technology has advanced to the point where relocations can be programmed to occur as frequently as each second [Börger_2016], a practice which has been applied to questions of collective movement [e.g. Strandburg_Peshkin_2015]. Meanwhile, remote sensing technology, including unmanned aerial vehicles and satellites, can be used to track the fine-scale movements of groups over large distances and time scales [Torney_2018]. Using technology to infer behaviour has therefore become standard operating procedure

for many species in many systems. Our ability to collect and process remotely sensed data and infer social processes based on animal movement provides an opportunity to use multilayer social network analysis to answer complex questions about animal socioecology.

Given the existing framework for constructing multilayer networks from behavioural layers [e.g. @Smith_Aguilar_2019], monolayer networks that explicitly quantify movement parameters could be integrated. For example, edges could represent measures of dyadic or collective movement based on dynamic interaction metrics [Long_2014]. Integrating movement layers with habitat-specific social association layers could further illuminate the role of movement as a driver of the social and spatial environments an individual experiences [Webber_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_2008]. Movement to, from, or within habitat patches or territories can also contribute to the formation of the social environment [Spiegel_2016]. For example, in sleepy lizards (*Tiliqua rugosa*) males interacted primarily at home range edges, presumably driving territorial behaviour [Spiegel_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_2019; Webber_2018].

5.3 Habitat selection and space use

Social structure and habitat selection are intimately linked: individuals must share space to interact and the distribution of resources influences group dynamics and home range size [Webber_2018]. Social structure is influenced by resource availability and seasonality [Peignier_2019], configuration [He_2019] and fragmentation [Banks_2007]. Habitat selection, the disproportionate use of available resources or landscape features by animals [Manly_1993; Boyce_1999], is a scale-dependent process [Mayor_2009]. Multilayer networks represent a novel framework for considering the influence of habitat selection and space use on sociality across scales.

Habitat selection depends on the scale at which it is measured and a singular scale is insufficient for generalizing across scales [Mayor_2009]. Habitat selection is measured using resource selection functions (RSFs), based on the proportion of used and available resources for an animal [Manly_1993; Boyce_1999]. Johnson (1980) identified four orders of habitat selection: the geographical range of a species, the home range of an individual, the habitat patches within the home range and specific resources within a habitat patch. Moving past this hierarchical perspective, Mayor (2007) emphasized the importance of considering a broad continuum of scales to reveal scale-dependent selection and avoid the bias of predefined scales assumed to be associated with certain behaviors.

Then to Mayor 2009

Despite this, still not widely adopted McGarigal 2016

For example, Mayor_2007 showed caribou select for shallow snow at all scales and by using a continuum of scales, .

The emergent relationship between habitat and sociality has been explored by the distribution and phenology of resources and use of social information. Cougar (*Puma concolor*) home ranges overlapped more in regions with high hunting opportunity, a proxy for resource richness [Elbroch_2016]. Caribou (*Rangifer tarandus*) sociality differed between seasons, where social associations were stronger in winter and contrastingly low in summer when resource availability are more homogenous [Peigner_2019]. Bison (*Bison bison*) showed stronger habitat selection in larger groups and avoidance of predation risk was a main factor contributing to their habitat selection [Fortin_2009]. These examples, comparing sociality and habitat selection across temporal or spatial contexts, are implicitly multilayer analyses.

Multilayer networks explicitly consider habitat selection and sociality across scales. Animal social systems can be parsed by spatial contexts, defined, for example, by habitat types as in Figure 4. The effect of resource phenology can be directly measured by differences in habitat selection and sociality across temporal layers. Habitat selection can be explicitly integrated using network layers defined by similarity of selection coefficients between individuals. These explicit integrations of habitat selection and sociality across social, spatial and temporal scales highlight the potential for novel insights from multilayer networks.

6 Conclusions

Multilayer networks remain a nascent but powerful tool in animal behavioural ecology. We demonstrate the potential novel analyses that vary social, spatial, and temporal scale within a multilayer framework. In our caribou case study, we show that (1) multilayer social networks can be, but are not always, scale-dependent, and (2) the use of multilayer networks could be useful for identifying habitat or season-specific social processes. Our analyses of social, spatial, and temporal scales in a multilayer network framework highlight the potential to identify scales at which different properties of layers within a multilayer network show the most variability. Furthermore, we discuss the potential integration of individual phenotypes and fitness, collective movement, and habitat selection for future analyses considering spatial ecology using multilayer networks.

Multilayer networks are complicated in that they can incorporate data as varied as social interactions, landscape features, and seasons, all of which exist at different scales and units of measurement. Our analysis of caribou multilayer networks incorporated high resolution GPS telemetry data and spatial landcover data is grounded in the context of observed animal social networks, as the scales we chose to explore, e.g., number of observations, sociality across space and time, are ones that can be observed as has traditionally been done in ethology. Thus, we highlight ways in which scale ought to be considered for both observed and remotely-sensed data when building social networks. Furthermore, GPS telemetry data provides a link between large scale landscape properties and fine scale social interactions as animal movement occurs across the landscape, and when taken into account with multiple individuals can indicate association patterns. Thus, a layer incorporating relocation data could be a great boon linking spatial and social layer in multilayer networks.

Silk et al. (2018) summarized some key multilayer questions in animal behaviour research. While these questions are important for linking animal behaviour and multilayer networks, we summarize our perspectives on the future of multilayer networks with an additional set of questions posed through the lens of spatial ecology that are relevant to the promise and problem of scale in multilayer networks:

1. How do social phenotypes vary across social, temporal, and spatial scales and at which scale might these influence fitness? Are some 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? 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?

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8 References