Spatial point locations explain a range of social network positions in a wild ungulate

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Abstract

The structure of wild animal social systems governs many eco-evolutionary processes, and is determined by a complex combination of intrinsic and extrinsic drivers. Spatial structuring is a key determinant of sociality, but quantifying spatial components alongside multiple other drivers remains difficult due to data scarcity and analytical complexity. We used a 43-year dataset detailing a wild red deer population to investigate how individuals' spatial behaviours drive social network positioning, while simultaneously assessing other potential contributing factors. Using Integrated Nested Laplace Approximation (INLA) multi-matrix animal models, we demonstrate important roles of space sharing, two-dimensional point locations, and especially annually varying spatiotemporal locations, alongside reduced but detectable impacts of demography, genetics, and individual-level traits. Interestingly, spatial patterns and other drivers differed considerably among different social network metrics. These results indicate strong, multifaceted spatiotemporal structuring, emphasising the importance of considering multiple components of spatial behaviour when investigating the causes and consequences of sociality.

Introduction

Social behaviour is an integral component of an animal's phenotype, driving processes including disease transmission, mating, learning, and selection (Croft *et al.* 2008; Krause *et al.* 2015; Firth *et al.* 2018; Sah *et al.* 2018; Firth 2020). Due to its generality and flexibility, social network analysis has recently become an important method for studying wild animal social systems (Krause *et al.* 2015; Webber & Vander Wal 2019). Contemporary studies of animal behaviour often use social networks to derive individual-level traits (i.e. social network positions), under the notion that between-individual variation in network positioning is indicative of between-individual variation in social behaviour (Krause *et al.* 2015). However, social networks are also shaped by many extrinsic factors: demography determines population structure and the available individuals to interact with (Shizuka & Johnson 2019)**,** while the environment governs resource distributions, movement corridors, and emergent patterns of space use, all of which will influence the architecture of the social system (Firth & Sheldon 2016; Webber & Vander Wal 2018; Farine & Sheldon 2019; He *et al.* 2019). As such, when assessing individual-level social network positions and associated eco-evolutionary consequences, it is important to consider the population's environmental context and individual space use as factors that may affect association patterns. Such analyses can provide insights into the extent to which intrinsic *versus* extrinsic processes contribute to social network positioning (Lusseau *et al.* 2006), and can reveal how social preferences and space use interact (Firth & Sheldon 2016; Spiegel *et al.* 2016; Webber & Vander Wal 2018), indicating underlying forces governing behavioural and social processes.

Several frameworks have been proposed to facilitate the untangling of spatial and social processes in wild animals (Jacoby & Freeman 2016; Silk *et al.* 2018, 2019; Webber & Vander Wal 2018; Mourier *et al.* 2019). To date, associated statistical methodology focusses on incorporating spatial activity into the node-and-edge structure of network data, including e.g. null network permutations (Firth & Sheldon 2016), spatially embedded networks (Daraganova *et al.* 2012), and nested super-networks composed of movement trajectories (Mourier *et al.* 2019). Many such analyses involve reducing movement patterns into some form of spatial network based on home range overlap or spatial proximity between dyads (Mourier *et al.* 2019). For example, statistical models named "animal models" can examine spatial variation by fitting such matrices as variance components, potentially alongside other dyadic similarity matrices, to quantify genetic and non-genetic contributions to individuals' phenotypes (Kruuk 2004; Stopher *et al.* 2012b; Regan *et al.* 2016; Thomson *et al.* 2018; Webber & Vander Wal 2018). However, movement paths are highly multivariate, and dyadic home range overlaps represent just one aspect of spatial behaviour (Mourier *et al.* 2019;

Pasquaretta *et al.* 2020). As such, controlling for structuring using space sharing alone potentially risks missing important variation.

On the one hand, there is now much evidence supporting the intuitive concept that spatial proximity and social activity are aligned: that is, individuals that share more space are more likely to associate or interact, for elk (Vander Wal *et al.* 2014), raccoons (Robert *et al.* 2012), foxes (Sanchez & Hudgens 2015), great tits (Firth & Sheldon 2016), and myriad other systems. However, while important, this concept is subtly distinct from fine-scale spatial assessment of heterogeneity in social behaviour – i.e., whether different areas of the landscape encourage different social network structures. For instance, if environmental gradients across a study system alter individuals' behaviour, then this will alter local social network structure, so that individuals will exhibit different social network traits depending on their locations in space – independent of their pairwise space sharing. Most notably, resource distributions are often extremely heterogeneous, altering habitat selection, aggregation in space, and therefore social network structure (Webber & Vander Wal 2018). Consequently, individuals living in high-resource areas may (for example) have many social partners. This phenomenon can have far-reaching consequences, for example by enhancing disease exposure in resource-supplemented populations (Becker *et al.* 2015). Notably, due partly to the analytical challenges, few studies of spatial-social structuring have examined the effect of point locations (i.e., where an animal is on a landscape) compared to space sharing (i.e., how much a pair of animals overlap in an unspecified space), and/or compared their influence to individual-level phenotypic traits.

Studies across ecological disciplines are increasingly using Integrated Nested Laplace Approximation (INLA) models to control for spatial autocorrelation in a multitude of contexts (Lindgren *et al.* 2011; Lindgren & Rue 2015; Zuur *et al.* 2017). This approach uses individuals' point locations to model 2-dimensional spatial patterns in the response variable, thereby controlling for and estimating spatiotemporal variation associated with fine-scale positioning within the landscape (Albery *et al.* 2019). Neither animal models nor INLA have yet been used to examine how spatial processes shape social network positions, despite their enormous potential for doing so. Further, although animal models can be fitted using INLA (Holand *et al.* 2013), there has been no exploration of how dyadic space sharing and individual point locations can be fitted simultaneously within animal models, how these factors compete with each other, and what insights this framework can provide.

As with spatial behaviour, sociality can be summarised using a range of different metrics (Krause *et al.* 2015; Sosa *et al.* 2020). Social network measures can represent individuals' own social connections, such as 'degree' (their number of social ties), or 'average strength' (the mean strength of their associations); alternatively, more complex network metrics may represent individuals' positions within the wider network, including 'betweenness' (the extent to which they bridge different social groups), 'Eigenvector centrality' (the centrality of their associates), and 'clustering' (the propensity for their associates to be connected to one another). These diverse metrics can provide insights into different aspects of social behaviour, while arising from different spatial movement syndromes: for example, individuals that consistently inhabit densely populated locations may commonly reoccur with the same individuals and thus experience high average strength, while individuals that move around various locations or inhabit restricted movement corridors may connect otherwise disconnected social groups together, thereby exhibiting high betweenness centrality (Firth *et al.* 2017). Further, different metrics can also provide insights into various consequences of sociality: for instance, while spreading a highly contagious disease may depend heavily on an animal's degree (unique number of partners), their influence on the spread of a learned behaviour may depend more on local clustering (Firth 2020). Because few studies use multiple spatial behaviour metrics (as outlined above) and few include other potential drivers in the same models, it is unclear how spatial factors compare to other individual-level and demographic factors in shaping sociality, and whether different spatial behaviours are important for determining different social network metrics.

The Isle of Rum red deer (*Cervus elaphus*) study population is an unmanaged wild population with a fission-fusion social system (Clutton-Brock *et al.* 1982). They exhibit spatial autocorrelation in a number of important phenotypes: individuals with greater home range overlap have more similar behavioural and life history traits (Stopher *et al.* 2012b), and those in closer proximity have more similar parasite burdens (Albery *et al.* 2019); further, as with other matrilineal mammalian systems, closely related individuals frequently associate (Clutton-Brock *et al.* 1982) and live closer together (Stopher *et al.* 2012b). Individuals have highly repeatable home ranges (Stopher *et al.* 2012b) which decline in size over their lifetimes, predicting declining survival probability (Froy *et al.* 2018). As such, the deer comprise an ideal system for assessing spatial-social relationships in the wild.

To assess how individuals' spatial behaviours translate to social network positions, we constructed fine-scale social networks from 43 years of censuses describing social groupings across the study population. We derived 8 different individual-level network positioning measures of varying complexity which are often proposed to be important to different social processes (Krause *et al.* 2015; Sosa *et al.* 2020). Using multi-matrix animal models in INLA (Thomson *et al.* 2018), we examined whether spatial locations and home range overlap explained variation in network position metrics, alongside a range of individual-, temporal-, and population-level factors. Additionally, we investigated how various spatiotemporal autocorrelation structures compared in determining social behaviour. We expected that a) locations on the landscape would determine a substantial proportion of social network positioning, comparable or greater than space sharing and other individual-level drivers; b) that this influence would be temporally varying; and c) that different social network metrics would exhibit different spatial patterns and vary in their relationship to the other drivers. We furthermore predicted that the spatial gradient in population density would have a strong effect on social network structure. This not only comprises a large-scale empirical examination of the factors shaping social network positions in this extensively monitored wild mammal, but also provides a methodological advancement in developing powerful, flexible new methods (INLA-based multi-matrix animal models) with broad potential for examining spatial-social processes in this and other systems.

Methods

Study system and censusing

This study was carried out on a long-term study population of red deer on the Isle of Rum, Scotland (57°N,6°20′W). We focussed on females aged 3+ years, as these individuals have the most complete associated census data. Individuals are monitored from birth, providing substantial life history and behavioural data, and >90% of calves are caught and tagged, with tissue samples taken (Clutton-Brock *et al.* 1982). The population thus has comprehensive genomic data, allowing high-powered quantitative genetic analyses: most individuals born since 1982 have been genotyped at >37,000 SNPs, distributed throughout the genome (e.g. Huisman, Kruuk, Ellis, Clutton-Brock, & Pemberton, 2016). Census data were collected for the years 1974-2017, totalling 423,070 census observations. Deer were censused by field workers five times a month, for eight months of the year, along one of two alternating routes (Clutton-Brock *et al.* 1982). Individuals' identities, locations (to the nearest 100M), and group membership were recorded. Grouping events were estimated by seasoned field workers according to a variant of the "chain rule" (e.g. Castles et al., 2014), where individuals grazing in a contiguous group within close proximity of each other (under ~10 metres) were deemed to be associating. Our dataset totalled 3356 annual observations among 532 grown females, with mean 112 groups observed per individual (Figure 1).

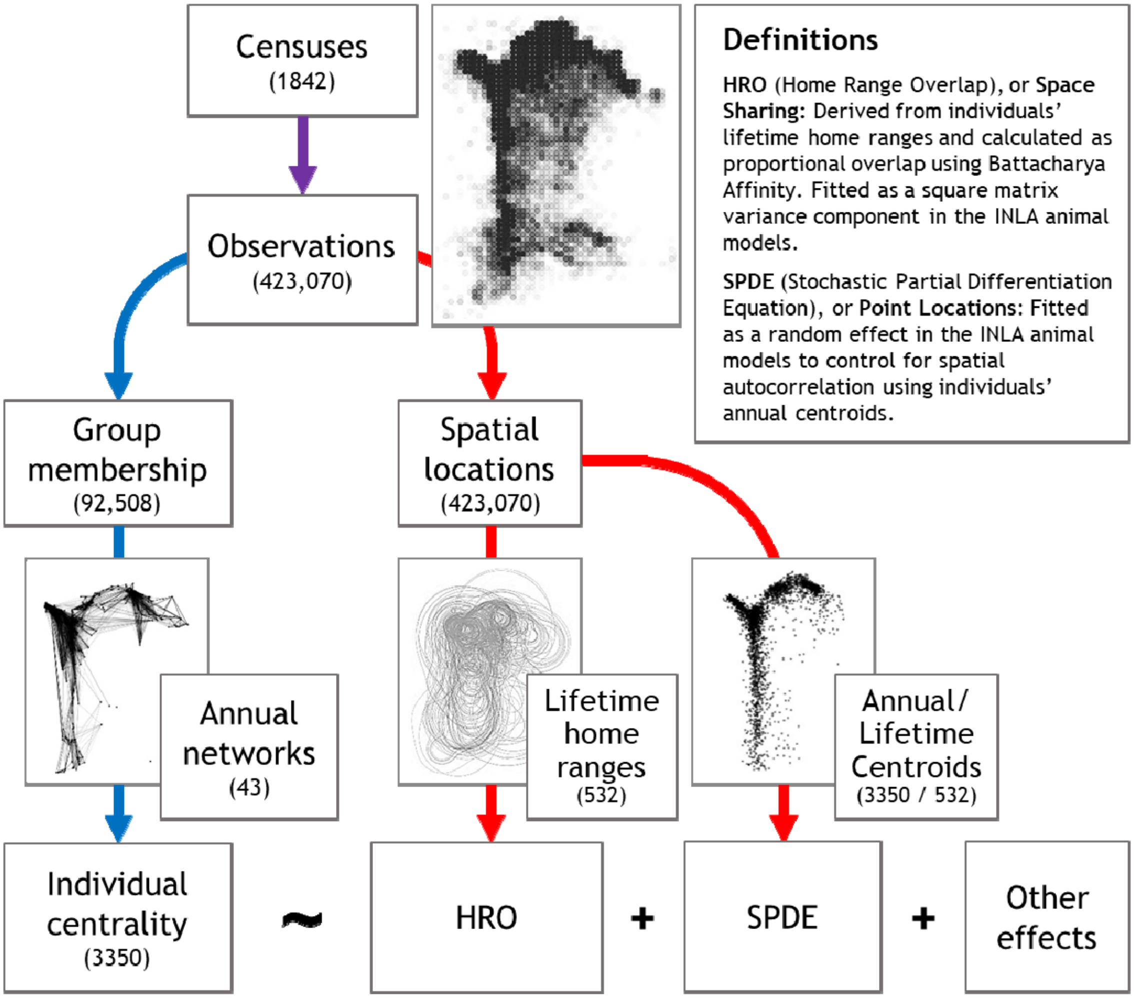
In this system, female reproduction imposes substantial costs for immunity and parasitism (Albery *et al.* 2020), and for subsequent fitness (Clutton-Brock, Albon, & Guinness, 1989; Froy, Walling, Pemberton, Clutton-Brock, & Kruuk, 2016). If a female reproduces, she produces 1 calf per year in the spring, generally beginning in May; the "deer year" begins on May 1 for this reason. Here, reproductive status was classified into the following four categories using behavioural observations: True Yeld (did not give birth); Summer Yeld (the female's calf died in the summer, before 1st October); Winter Yeld (the female's calf died in the winter, after 1st October); and Milk (calf survived to 1st May the following calendar year).

Generating spatial and social matrices

All code is available online at https://github.com/gfalbery/INLA_N_Out. We constructed the HRO matrix using the R package AdeHabitatHR, following previous methodology (Stopher *et al.* 2012b; Regan *et al.* 2016; Froy *et al.* 2018). First, using a kernel density estimation method, we derived lifetime home ranges for each individual with more than five census observations. We used lifetime home ranges to fit one value per individual in the animal models; individual ranges (and range sizes) correlate strongly from year to year (Stopher *et al.* 2012b; Froy *et al.* 2018). We derived proportional home range overlap (HRO) of each dyad using Bhattacharya Affinity (following Stopher *et al.* 2012b), producing values between 0-1 (i.e. no overlap to complete overlap).

To control for individuals' two-dimensional point locations we used a Stochastic Partial Differentiation Equation (SPDE) effect, in which distance between points is used to calculate spatial autocorrelation using Matern covariance (Lindgren *et al.* 2011). This random effect used individuals' annual centroids (mean easting and northing in a given year) or lifetime centroids (mean easting and northing across all observations) as point locations to approximate spatial variation in the response variable (Lindgren *et al.* 2011; Albery *et al.* 2019). We used a genomic relatedness matrix (R_{GRM}) using homozygosity at 37,000 Single Nucleotide Polymorphisms, scaled at the population level (Yang *et al.* 2011; for a population-specific summary, see Huisman *et al.* 2016). This matrix is well-correlated with pedigree-derived relatedness metrics (Huisman *et al.* 2016). Home range overlap was well-correlated with distance between lifetime centroids (i.e., closer individuals tended to share more range), and both were weakly but significantly correlated with genetic relatedness (Supplementary Figure 1).

We constructed annual social networks using "gambit of the group," where individuals in the same grouping event (as described above) were taken to be associating (Franks *et al.* 2010). Dyadic associations were calculated using the 'simple ratio index' (Cairns & Schwager 1987) derived as a proportion of total sightings (grouping events) in which the focal individuals were seen together: $\text{Sightings}_{A,B}/(\text{Sightings}_{A}+\text{Sightings}_{B}-\text{Sightings}_{A,B})$, or $\text{Intersect}_{A,B}/\text{Union}_{A,B}$. In this dyadic matrix, 0=never seen together and 1=never seen apart. We constructed a series of 43 annual networks constructed only from census records in each May-December period, from which we derived annual social network position measures as response variables (Figure 1-2). We elected to investigate this seasonal period because it stretches from the spring calving period until the beginning of the mortality period, simplifying network construction and avoiding complications arising from mortality events.



Definitions

HRO (Home Range Overlap), or **Space Sharing:** Derived from individuals' lifetime home ranges and calculated as proportional overlap using Battacharya Affinity. Fitted as a square matrix variance component in the INLA animal models.

SPDE (Stochastic Partial Differentiation Equation), or **Point Locations:** Fitted as a random effect in the INLA animal models to control for spatial autocorrelation using individuals' annual centroids.

Figure 1: Data processing and analysis pipeline, demonstrating how behavioural census data were collected, used to derive social and spatial behavioural traits, and fitted in INLA animal model GLMMs. Numbers in brackets represent sample sizes, and only include females aged 3+ years. Blue arrows represent social behaviour; red arrows represent spatial behaviours. See methods for the fixed and random effects. The text box displays the definitions for the different spatial effects.

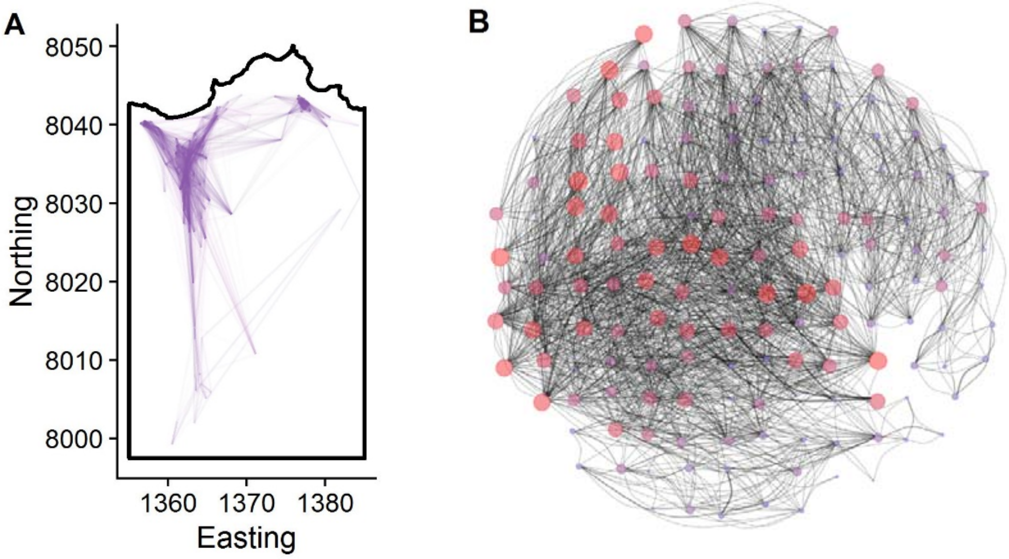


Figure 2: Spatial structuring of the 2016 social association network as a representative example. A: the spatial locations (centroids) of individual deer, connected by their social associations. Line opacity and width are weighted by connection strength. Ten axis units = 1KM. B: the same social network expanded into an even, circular grid according to their nearest spatial positions in A). The points' (i.e. nodes') sizes and colours show individuals' strength centrality (large and red=high strength; small and blue=low strength). Thickness of the lines (i.e. edges) connecting them shows dyadic association strength between individuals.

Statistical Analysis

We derived eight individual-level network metrics from the annual social networks for use as response variables in INLA Generalised Linear Mixed Models (GLMMs) with a Gaussian family specification. In increasing order of complexity, our measures included four direct metrics: 1) Group Size – the average number of individuals a deer associated with per sighting; 2) Degree – the number of unique individuals she was observed with; 3) Strength – sum of all their weighted social associations to others; 4) Mean Strength – the average association strength to each of the unique individuals she was observed with (equivalent to strength divided by degree). We also included four more complex "indirect" metrics: 5) Eigenvector centrality – akin to the sum of her unique associates' degrees; 6) Weighted Eigenvector – akin to the sum of her associates' strengths weighted by their association to her; 7) Betweenness – the number of shortest paths that pass through the focal individual to traverse the whole network; 8) Clustering (local) – the tendency for an individual's contacts to be connected to one another, forming triads. The raw, untransformed correlations were assessed for all metrics (Supplementary Figure 2); when modelling them as response variables, to approximate normality, all social metrics were square root-transformed apart from eigenvector centralities (which were left untransformed), group size (which was cube root-transformed), and betweenness (which was log-transformed). Each social network metric was fitted as a response variable in a separate model set (as outlined conceptually in Figure 1). We ensured that all models followed the same base structure. Random effects included individual identity and year (categorical), as well as the genetic relatedness matrix. Fixed effects included Age (continuous, in years), Reproductive Status (four categories: True Yeld; Summer Yeld; Winter Yeld; and Milk), and Number of observations (continuous, log-transformed), as well as year-level continuous factors including Year (continuous) and that year's study Population Size (log-transformed). All continuous response and explanatory variables were standardised to have a mean of zero and a standard deviation of 1.

To investigate the divergent effects of different spatial behaviours, we iteratively added different combinations of spatial random effects to the base model, in increasingly complex formulations. First, we added the HRO (space sharing) matrix. Next, we added an INLA Stochastic Partial Differentiation Equation (SPDE or point location) spatial effect based on lifetime centroids, to investigate whether point locations and space sharing behaved similarly when at the same timescale (i.e., across individual lifetimes). Next, to investigate whether finer temporal scales improved our inference of spatial effects, we altered the SPDE effect to use annual rather than lifetime centroids. Finally, we fitted the annual centroids in a spatiotemporal model structure, allowing entirely different (uncorrelated) spatial fields for the SPDE effect for each year. Only one of the SPDE random effects was fitted at once, and the best-fitting model was identified using changes in Deviance Information Criterion (DIC). A conservative change of 10ΔDIC was used to differentiate between competing models – i.e., any variable that decreased DIC by more than 10 was deemed significant.

To compare the variance accounted for by all fixed and random effects, we examined the model's predicted values and their correlations with the observed values. We used the model to predict each social behaviour metric, and iteratively held each explanatory variable's predictions at the mean, one at a time. We then assessed the squared correlations of these values with the observed values (i.e., R^2), relative to those of the full model. Variables with greater effects in the model produced less accurate predicted values when held constant. Animal models generally extract the variance components (random effects) of genetic and non-genetic contributors to quantify heritability (Kruuk 2004). However, in INLA models, the SPDE variance components are hard to estimate where the range parameter is large; as such, predicting using the model is a preferred approach for our purposes (Finn Lindgren, pers. comms.). Nevertheless, the variance components were found to largely mirror our results when inspected.

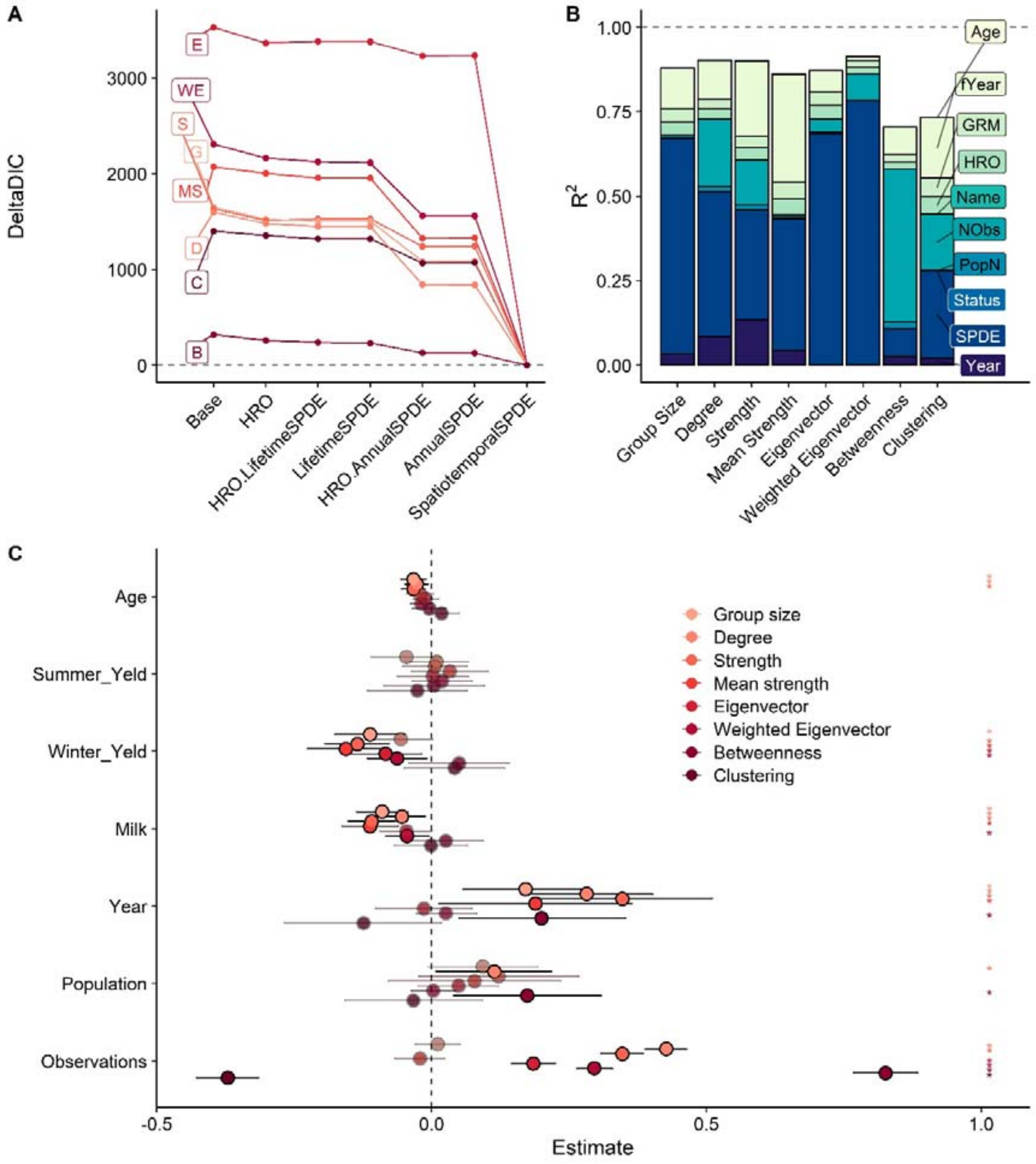


Figure 3: Model outputs demonstrating strong effects of spatial and non-spatial drivers on social network positions. A: DIC changes associated with addition of different spatial components, for all eight social network centrality measures. Models are arranged in order of model fit, and the rank order varied little among response variables. Different colours correspond to different network centrality response variables, with the same colour key as panel C. The SPDE models are differentiated into those using individuals' lifetime centroids ("LifetimeSPDE") and annual centroids ("AnnualSPDE") and the spatiotemporally varying annual spatial fields ("SpatiotemporalSPDE"). B: Variance accounted for by each variable for all eight network position measures, expressed as contribution to R^2 in the annual model (squared correlation between observed and predicted values). Different shades correspond to different variables. fYear = year as a categorical random effect. GRM = Genomic

Relatedness Matrix. HRO = home range overlap. Name = individual identity. NObs = number of observations (i.e., sampling bias). PopN = population size. Status = reproductive status. SPDE = point location effects estimated using the Stochastic Partial Differentiation Equation effect in the INLA models. For all response variables, individual level effects (Age, Reproductive Status, Name) had a negligible effect. C: Fixed effect estimates for the models. Fixed effects are grouped into individual factors (age and three reproductive status effects), annual factors (continuous time in years since study began, and annual population size), and sampling factors (observation number). Reproductive status effects are separated into four levels: did not reproduce (the intercept); calf died in the first few months of life (“Summer Yeld”); calf died during the winter (“Winter Yeld”); and calf survived to May the following year (“Milk”). Different colours correspond to different network centrality response variables. Points represent the posterior mean; error bars denote the 95% credibility intervals for the effects. Asterisks denote significant variables (i.e., those whose estimates did not overlap with zero). Significant variables are fully opaque, while non-significant ones are transparent.

Results

Spatial behaviours were extremely important in determining all eight individual-level social network position measures. The non-spatial model was by far the worst-fitting for all eight response variables, and the DIC changes associated with adding spatial components were substantial (Figure 3A). Notably, point location-based SPDE effects tended to improve model fit more than space sharing HRO effects, even when conceptualised at the same timescale (i.e., across the individual’s lifetime; Figure 1A). Investigating the R^2 components of the models containing only HRO (i.e., without SPDE effects) revealed that in general spatial overlap accounted for more variation than the genetic matrix (Supplementary Figure 3), but comparing these with the other models revealed that the point location effects contributed more than either of these matrices (Figure 3B). Annually varying centroids further improved model fit, and allowing the spatial field to vary between years in our spatiotemporal models improved models even more (Figure 3A). Although the space sharing and genomic relatedness matrices had similar sized impacts on the full models (Figure 3B), removing the SPDE effect resulted in a substantial increase in the HRO effect, but with very little impact on the GRM’s R^2 (Supplementary Figure 3). These findings were relatively consistent across all metrics (Figure 3A-B), although the SPDE effect was notably smaller for betweenness (Figure 3B). Taken together, these results reveal that lifetime space sharing was good at accounting for variation in social behaviour, but that its effect was surpassed by increasingly complex temporal formulations of point location effects.

We compared the importance of all fixed and random effects by predicting selectively from the model, revealing overwhelmingly strong effects of spatiotemporal factors (Figure 3B). Our models fit well and explained a substantial amount of variation in social network centrality (>70%), and the majority of the model’s fit was lent by the INLA SPDE effect (Figure 3B). Observations also had a notable impact for Degree, Betweenness, and

Clustering, and the categorical random effect for year had a substantial effect across all response variables (Figure 3B). Fixed effects for year and observation numbers were generally strong and significantly positive across metrics, except in the case of clustering, which was significantly negative (Figure 3B). There were also small positive effects of population size on betweenness and degree centrality (Figure 3B).

Although individual-level drivers (reproduction, age, and individual identity) had a negligible impact on all variables' R2 (Figure 3B), many had a significant effect (i.e., their 95% credibility intervals did not overlap with zero; Figure 3C). Individuals whose calves lived to the winter and then either died before the 1st May ("Winter Yeld") or survived ("Milk") were generally less central than those that did not give birth ("True Yeld") or whose calf died before 1st October ("Summer Yeld"). Similarly, there were minor age-related decreases in network centrality for the direct metrics (Group Size, Degree, and Strength; Figure 3C).

To investigate spatial patterns of sociality, we projected the annual SPDE random effect in two-dimensional space (Figure 4; Supplementary Figures 5-12). As expected, the spatial distributions of network centrality metrics were highly variable, but generally peaked in the central north area of the study system and decreased outwards (Figure 4). Mean Strength was an exception, being lowest in the high-density areas and increasing outward (Figure 4D); Clustering was patchily distributed, such that no clear pattern was evident (Figure 4H); and Betweenness was slightly offset, being highest in the north-northeast of the study area rather than in the central north (Figure 4G). The range of autocorrelation also varied among metrics; Betweenness and Clustering had notably shorter ranges than the other metrics (Supplementary Figure 4). We also plotted the spatial fields through time, revealing substantial variation in the spatial fields across the study period (Supplementary Figures 5-12).

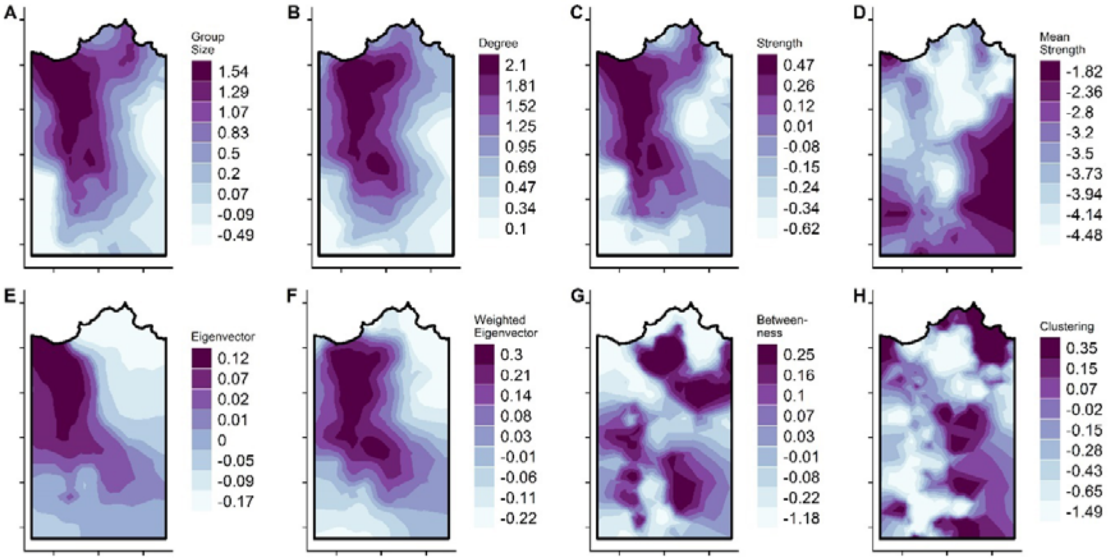


Figure 4 (Previous page): Spatial fields for the SPDE random effect for each response variable, taken from the INLA animal models and based on annual centroid point locations. Metrics can be conceptualised as simpler dyadic "direct" metrics (top row) and more complex "indirect" metrics (bottom row). Darker colours correspond to greater values. Each axis tick corresponds to 1km; for the values associated with the Easting and Northings, see Figure 1.

Discussion

The role of spatial behaviour in driving social network positions

The position individuals occupy within their social networks can affect many aspects of their ecology and evolution (Krause *et al.* 2015; Firth *et al.* 2018; Sah *et al.* 2018), and our results confirm the powerful role of fine-scale spatial activity in shaping such traits (e.g. Farine & Sheldon, 2019; Mourier et al., 2019; Webber & Vander Wal, 2018). Although pairwise home range overlap was important in determining social centrality measures, point locations were substantially more important, and allowed us to more easily account for spatiotemporal variation. Inter-annual variation in spatial effects proved especially influential in our models, across increasingly sophisticated spatiotemporal model formulations. While point locations were superior to home range overlaps even at the same coarse timescale (i.e., across lifetimes), our models universally revealed benefits of incorporating temporally varying spatial behaviours. Moreover, the autocorrelation range and the importance of different behavioural components differed notably across centrality measures, suggesting that different spatial processes play a role in determining different network positions. As such, we propose that social network studies should more regularly incorporate both space sharing and (temporally varying) point locations in their statistical approaches to anticipate these effects. This practice will help to buffer for the fact that the spatial environment not only correlates with social proximity, but can alter the fabric of the network itself.

The landscape of sociality

Spatial patterns were quite varied among metrics but were nevertheless amenable to interpretation. Most notably, the spatial distributions of direct metrics (group size, degree, and strength) were very similar and likely attributable to the concentration of resources in the form of high quality grazing, which peaks in the central north study area (Clutton-Brock *et al.* 1982). Individuals' resource selection behaviours increase local density in this area (Clutton-Brock *et al.* 1982), and will increase social connectivity as a result (Ostfeld *et al.* 1986; Sanchez & Hudgens 2015; Webber & Vander Wal 2018). This comprises strong evidence for density-related increases in social contact frequency, and accentuates the vital importance of considering resource distribution, habitat selection, and population structure when examining social network correlates (Spiegel *et al.* 2016; Webber & Vander Wal 2018; Farine & Sheldon 2019; He *et al.* 2019). For these simpler, direct metrics, it is possible that a measure of local spatial population density (e.g. Coulson *et al.* 1997) could be fitted to control for and estimate spatial-social confounding. In contrast, betweenness peaked in the north-northeast of the system, likely because the northeastern community is slightly isolated from the rest of the population (Figure 2), so that many 'social paths' that traverse the population (the criteria for betweenness centrality) go through individuals in this intermediate area. The causes of the spatial distribution of clustering remain unresolved, but the pattern highlights areas where individuals are connected together in triads or tight cliques, and appears to be negatively correlated with betweenness (Figure 4). For these traits, it is unlikely that a simpler explanatory variable could be formulated to quantify the spatial-social processes at play.

Regardless of the causes of the spatial patterns, such fine-scale variation across the landscape holds important eco-evolutionary consequences, particularly for the more complex network metrics. For instance, the areas of high clustering may act as 'incubator' areas where cliques can develop new socially influenced behaviours (Firth 2020) such as cooperative behaviours (Rand *et al.* 2011). The high contact rates in the northern central areas might sustain high local burdens of directly transmitted diseases (Cote & Poulin 1995), while individuals inhabiting the high-betweenness intermediate areas may be important for transmitting novel diseases across the population as a whole (VanderWaal *et al.* 2014). Without using the SPDE effect (i.e., relying only on generalised pairwise space sharing rather than accounting for specific two-dimensional spatial patterns), these insights into these patterns would not have been possible.

Analytical benefits of INLA animal models

Analyses using multiple layers of different behaviours are well-suited to extricating space and sociality in wild animal systems (Silk *et al.* 2018; Webber & Vander Wal 2018; Finn *et al.* 2019), and there is increasing conceptual and analytical overlap between movement-based and network-based approaches (Jacoby & Freeman 2016; Mourier *et al.* 2019; Pasquaretta *et al.* 2020). Notably, many spatial-social studies suffer from the necessity to reduce complex movement patterns into simpler metrics, which risks losing important information in the process. As such, recent studies have pushed for researchers to incorporate movement trajectories themselves into complex network data structures (Mourier *et al.* 2019). Our approach allows incorporation of multiple dyadic and non-dyadic behavioural measures, and with several analytical timescales, offering an alternative workaround to this problem. Although other methods can control for point locations (e.g. using autoregressive processes and row/column effects; Stopher *et al.* 2012b), INLA models allow greater precision, fit quickly, and allow easy incorporation of spatiotemporal structuring. Furthermore, plotting the SPDE effect in two dimensions, as in Figure 4, gives an easily interpretable and intuitive portrayal of network traits in space that can be hard to visualise using other methods. For these reasons, we highly recommend further exploration of INLA animal models as a flexible method with which to extricate individual, demographic, spatial, and temporal contributors to sociality where sample sizes are sufficient (Thomson *et al.* 2018; Webber & Vander Wal 2018). In addition to carrying out network-level manipulations (Daraganova *et al.* 2012; Davis *et al.* 2015; Firth & Sheldon 2016; Farine 2017), researchers concerned about spatial confounding could implement relatively familiar linear models of social behaviour, but with additional spatial components such as SPDE random effects and similarity matrix variance components, with trustworthy and interpretable results (Albery et al., in review).

Our approach also allowed us to quantify the impacts of multiple non-spatial drivers of network centrality and compare them with spatial behaviour. Although space accounted for an overwhelming amount of variation, many other factors had substantial effects. The categorical random effect for interannual variation was substantial, and there were detectable linear annual effects and population size effects, as expected given the important roles of demography in structuring social networks (Shizuka & Johnson 2019). Individual-level factors had weaker contributions to model fit and smaller effect sizes: most notably, genetic and individual random effects were negligible when spatial autocorrelation was accounted for, confirming the importance of considering space when assessing heritability independently of space in this population (Stopher *et al.* 2012a). Notably, previous analyses in this system revealed that accounting for space substantially reduced heritability estimates for spatial behaviour (home range size), but less so for life history characteristics (Stopher *et* *al.* 2012a). We impress that the finding of extreme spatial dependence in social behaviour does not necessarily imply that other traits will be subject to a similar reduction in heritability, although incorporating point locations may be similarly revealing about the non-spatial drivers of such traits.

Nevertheless, individual-level effects were encouragingly still detectable and significant, particularly for simpler “direct” metrics. It is possible that more complex social network positions are less determined by individual social behaviours, particularly for animals with relatively strong fission-fusion dynamics (i.e., heavy mixing) such as the deer; this hypothesis could be tested using similar spatial-social analyses in a number of other systems. This finding demonstrates that even when spatial structuring plays a vital role in determining social network structure, controlling for this structuring analytically can reveal important, conservative individual-level effects. Future analyses within this population, and potentially other long-term studies, could take advantage of this framework by including environmental drivers such as food availability and climatic factors to explain patterns of social connectivity, while further unpicking the causes of the individual-level trends that we observed.

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