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METHODS PAPERS

Using an agent-based model to inform sampling design for animal social network analysis

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Abstract

Producing accurate and reliable inference from animal social network analysis depends on the sampling strategy during data collection. An increasing number of studies now use large-scale deployment of GPS tags to collect data on social behaviour. However, these can rarely capture whole populations or sample at very high frequencies. To date, little guidance exists when making *prior* decisions about how to maximise sampling effort to ensure that the data collected can be used to construct reliable social networks. We use a simulation-based approach to generate a functional understanding of how the accuracy of various network metrics is affected by decisions along three fundamental axes of sampling effort: coverage, frequency and duration. Researchers often face trade-offs between these three sampling axes, for example due to resource limitations, and thus we identify which axes need to be prioritised as well as the effectiveness of different deployment and analytical strategies. We found that the sampling level across the three axes has different consequences depending on the social network metrics that are estimated. For example, global metrics are more sensitive than local metrics to the proportion of the population tracked, and that among local metrics some are more sensitive to sampling duration than others. Our research demonstrates the importance of establishing an optimal sampling configuration for drawing relevant and robust inferences and presents a range of practical advice for designing GPS based sampling strategies in accordance with the research objectives.

Keywords Animal social network analysis · GPS tag · Sampling coverage · Sampling duration · Sampling frequency · Sampling strategy

Introduction

Social network analysis is a valuable tool for animal studies, providing insights into the structure, dynamics, and functioning of social relationships within animal com- munities (Krause et al. 2007; Croft et al. 2008; Farine and Whitehead. 2015; Shizuka et al. 2021; Sosa et al. 2021). A challenge for studies using SNA is the ability to collect sufficient data to construct the network (Hoppitt and Farine. 2018; Silk. 2018; Smith et al. 2022; Gilbertson et al. 2021; Kaur et al. 2024). Collating social data ideally involves observing many or all individuals in a group or population at once. However, the cost and effort required to do so, especially in free-ranging populations, is often prohibitive (Hebblewhite and Haydon. 2010; Krause et al. 2013; Jung et al. 2018). Insufficient spatial coverage or biased sampling locations can lead to incomplete, inaccurate, or biased network representations (James et al. 2009; Smith and Moody 2013; Davis et al. 2018). The duration and intensity of sampling efforts also impact the completeness and reliability of social network data, as short

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observation periods may underestimate overall network connectivity and dynamics (Lusseau et al. 2008; Perreault. 2010; Cross et al. 2012; Fründ et al. 2015; He et al. 2022). Moreover, biases in sampling, such as preferentially observing certain individuals or groups over others, provide an inaccurate picture of social interactions and network structure, affecting the reliability of inferences obtained from the data (Voelkl et al. 2011; Cross et al. 2012; Davis et al. 2018; Espín-Noboa et al. 2018). While these potential problems are well established, previous work provides little guidance on how to overcome sampling limitations. Yet, there are likely to be some general principles that can be followed (He et al. 2022).

Most studies face trade-offs when determining the most appropriate sampling effort. These include sampling more broadly to increase the proportion of the population sampled versus sampling fewer individuals more often (Wey et al. 2008; Smith and Moody 2013; Silk et al. 2015; Davis et al. 2018). This issue is increasingly resolved by using automated tracking methods that can substantially increase the capture of data at the individual level (Aplin et al. 2015; Strandburg-Peshkin et al. 2015; Alarcón-Nieto et al. 2018). In wild populations, telemetry methods, in particular GPS tracking, are becoming increasingly used to study social behaviours (He et al. 2022). However, GPS tracking also involves a number of trade-offs. For example, tags can increase sampling frequency (more points per unit of time) at the cost of sampling duration. Further, because of their high cost, decisions also need to be made about which individuals to deploy GPS trackers onto. Here again there are trade-offs, such as between sampling more intensively within a focal subset of the population versus spreading GPS devices more evenly across the population (Smith and Moody 2013; Smith et al. 2017).

An issue for empiricists is that realistic sampling recommendations for wildlife contact networks are lacking, and little research has explored the impact of telemetry location frequency on network estimation (Costenbader and Valente 2003; Cross et al. 2012; Gilbertson et al. 2021). One challenge with generating guidelines for how to sample wild populations is that we typically do not have a real baseline against which to evaluate our dataset. One approach has been to subsample large and intensively collected data (e.g. Davis et al. (2018)). However, such datasets are not yet available for species where sampling challenges are most exacerbated, notably in species where there is continuous formation and dissolution of social groups (i.e. fisson-fusion dynamic, Aureli et al. (2008)). One solution is to simulate population-level data, from which we can test different sampling strategies. Gilbertson et al. (2021) used simulations of individual movement trajectories to outline best practices for telemetry sampling, in particular for network studies of infectious disease in wildlife. Gilbertson et al. (2021) suggested prioritizing local network metrics and increasing sampling frequency to enhance accuracy, particularly in situations of low sampling coverage. However, it is unclear how general these findings are across taxa, and whether they are influenced by non-random or geographically biased telemetry sampling. Additionally, the simulations assumed that individuals move independently. Yet we know that many animals also make social movements, which could also affect network inference. Further investigation is needed to understand sampling strategies and how association behaviours among individuals affect networks inferred using telemetry methods.

Therefore, in this paper we developed and used an ABM that incorporates both social and non-social factors affecting animal movements and interactions. Our objective was to understand the trade-offs associated with collecting empirical data using animal telemetry. Here we focused on the accuracy of social network metrics estimates when moving along the three axes of sampling efforts, specifically (Gilbertson et al. 2021; He et al. 2022):

- Sampling coverage: The number and allocation of GPS devices among individuals in one or more social groups.
- Sampling frequency: The number of times per day in which GPS devices record data.
- Sampling duration: The total amount of time over which devices collect data.

We first quantified how increasing sample coverage, frequency, and duration con- tribute to a reduction of errors in different network metrics, spanning from the individual to the population. Next, we examined more directly the trade-off between sampling more intensively versus sampling for a longer duration. This allowed us to determine which sampling approach delivers the best estimations for a given amount of data. Finally, we examined the effect of different decisions with regards to sampling coverage. Specifically, we tested how selecting individuals that were more densely connected versus randomly selecting individuals across the broader population affected conclusions about the population network structure (He et al. 2022). We achieve these three tasks with the help of a custom ABM designed in software R (R Core Team 2022). Our model was inspired by ungulate movement, thus allowing us to portray the intricacies of the data collection process and answer such questions for this well-studied group. However, our results are also adaptable to all species that live in societies with fission–fusion dynamics. The software and method have the potential to extend to more complex dynamics, for example by including seasonal variation effects on the social or feeding parameters, migration events, sex-specific behaviors, incorporation of real vegetation cover data, etc. We provide

our source code to facilitate such extensions in Code Availability below.

Materials and methods

Model scope and conceptual design

Our model structure follows the "Overview, Design concepts and Details" (ODD) criteria proposed by Grimm et al. (2020) for ABMs. The model presented here is based on some fundamental assumptions that have allowed us to simplify the representation of complex animal decisions while capturing vital aspects of the movement process, and thus the drivers of encounters among individuals. These specific assumptions are:

1. Each animal is represented as an agent that is capable of making decisions and interacting with its environment based on internal states and external stimuli.
2. The grid space is inhabited by a single type of agent.
3. Interactions between animals primarily occur within a local neighborhood defined by the grid structure.
4. Resources required for survival are limited and unevenly distributed across the environment.
5. The resource quantity or quality is not affected by the time of the year. It remains constant throughout the whole cycle of simulations.
6. Agents do not reproduce or exhibit any life history traits.
7. Agent movement patterns are uniform across the simulations, i.e. there is no concept of day and night.

Environment representation

We simulated an environment in the form of a grid structure. Figure 1 depicts the spatial organisation of the environment consisting of a two-dimensional 40 by 40 grid. Each cell in the grid represented a location where agents occur and denoted a distance unit (1 unit = 10 m). The total area represented by this 40 by 40 grid is 16 hectares. The environment is also heterogeneous, with resource density varying across the grid. Each cell in the grid had a resource quality index value, which ranged from 0 to 1, with 0 indicating no availability of resources and 1 indicating maximum resource amount.

Agent definition

Our model consisted of 500 individuals, or agents (Fig. 1). An individual's initial state could be one of two: foraging or resting. Each individual could be foraging or resting with a probability of 0.7 and 0.3. If an individual was in a foraging mode, they walked one unit each time point across the grid.

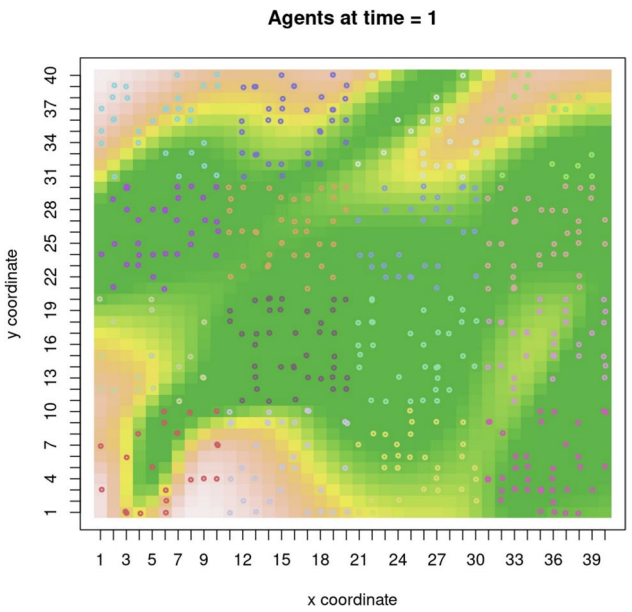


Fig. 1 Simulated environment and agents. The simulated environment consists of a 40×40 grid cells. At time point 1, individuals' locations are randomly distributed. The color of a grid cell represents its resource quality. The greener the cell, the better the resource available at that cell

If they were resting, remained in the same cell until their state changed. Each individual was also given an energy level at the start of the simulation. An individual's energy level could range from 0 to 1, with 0 indicating the lowest energy level and 1 indicating the highest level of energy possible. We also defined connections among the individuals within the population, resulting in 16 sets of individuals that exhibited social preferences towards each other. The size of these social sets ranged from 19 to 41 animals. In each social set, a pair was assigned a connection with a probability of 0.9.

Behavioural rules

Resting state

If an individual was in resting state, they remained in the same cell and there was no movement. Their energy in the resting state lowered by 0.05 units per unit time.

Foraging state

At each time point, an individual in the foraging state moved to one of the nine immediate surrounding cells (including the current cell) as shown in Fig. 2a. An individual's movement and the choice of next cell was based on their current energy level and the presence of socially preferred conspecifics in the neighbouring cells.

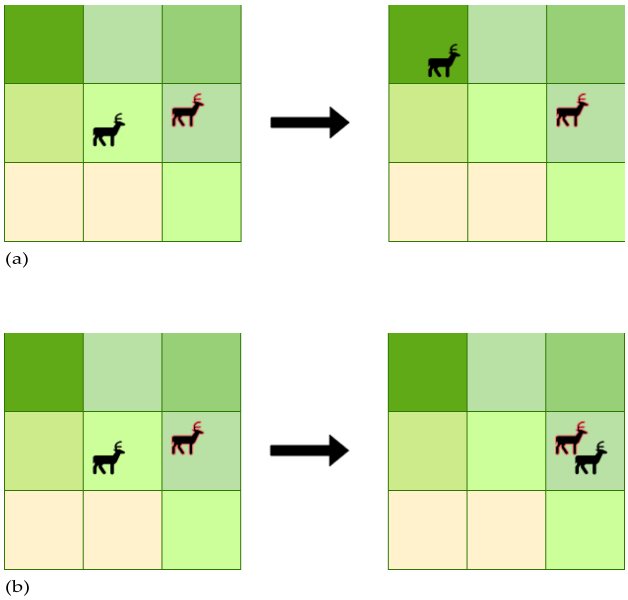


Fig. 2 An individual's movement decisions under two different scenarios. **a** An individual in foraging state with an energy level lower than the social threshold. The greenest cell is more likely to be chosen for movement at the next time point. **b** An individual in foraging state with an energy level greater than the social threshold. Presence of another individual (here in resting state) affects the choice of next cell

An individual could opt to make social movements if one of their preferred conspecifics was present in a neighbouring cell or to go to a cell with a higher resource quality index. This decision was made based on their current level of energy and the social threshold. We defined the social threshold (set to 0.5) as the energy level below which individuals made movements exclusively based on food resources. Above this threshold, individuals moved preferentially towards strong social contacts. When making social movements, individuals' energy decreased by 0.1 units per time point. When foraging, individuals either consumed resources or searched to find better quality food, depending on the habitat quality in the current cell and on their current energy level. If the current energy level was lower than the cell's resource quality index, the individual used the resource and gained energy, otherwise they searched for a better resource (reducing their energy decreased by 0.1 unit per time point). Finally, foraging reduced the resource quality index of each cell, which was depleted following an exponential function of the current resource quality. The depletion function is given by:

$$\frac{e^{3x}}{2e^{3}}$$

where x is the current resource quality index of the cell. The amount of resource quality depleted by an individual's foraging was equal to the amount of energy acquired by that individual through resource consumption. See section Decision making process of an individual for a flowchart summary of the decision-making process of an individual in the model.

In cases where multiple connections were present in different neighbouring cells, the decision was based on a two-step process. See Agent's movement when multiple connections are present in multiple neighbouring cells for more details on this process. This two-step decision process is performed simultaneously for each agent in the simulation at each time point. The decision process of an agent in foraging state with energy level greater than the social threshold is decided in this way. The decisions are influenced by the presence of all of their connections in the neighbourhood, regardless of their state.

Parameter settings

For an ABM to be realistic, a good set of parameters is necessary to demonstrate the target behavior in a realistic way (Tan and Bora 2019). In this model, there were several parameters that were needed to be tuned such that the model would reflect the nuances of the environment and social effects on movement. The model was assessed over multiple set of parameters. For details, see section Model calibration in appendix, which details calibration over values of replenish value, social threshold, energy depleted when moving, energy depleted when resting, minimum resting threshold, searching span, and movement span.

Model implementation and data collection

After setting up the grid, we performed the simulations for 4380 time points. Each time point in the simulation spanned two hours. This would depict the movement of animals recorded throughout a year, with observations made every two hours. The dataset consisted of 4380 time points, with each time point containing information on individual positions on the grid (given as (x,y) coordinates), their energy level, and their activity state (either foraging or resting).

As the goal is to understand how sampling levels affect the network metric accuracy, we sampled at different values spanning the three fundamental axes of sampling effort—sampling coverage, sampling frequency and sampling duration (Fig. 3). The values of sampling coverage ranged from 25 to 100% where we analysed the networks obtained from a random selection of 125, 250, 375 and 500 individuals. For sampling duration, we analysed the data collected over 91 days, 182 days, 274 days and 365 days. This represented one quarter, one half, three quarters, and an entire year of observation. In terms of sampling frequency, networks were generated by recording the observations at different

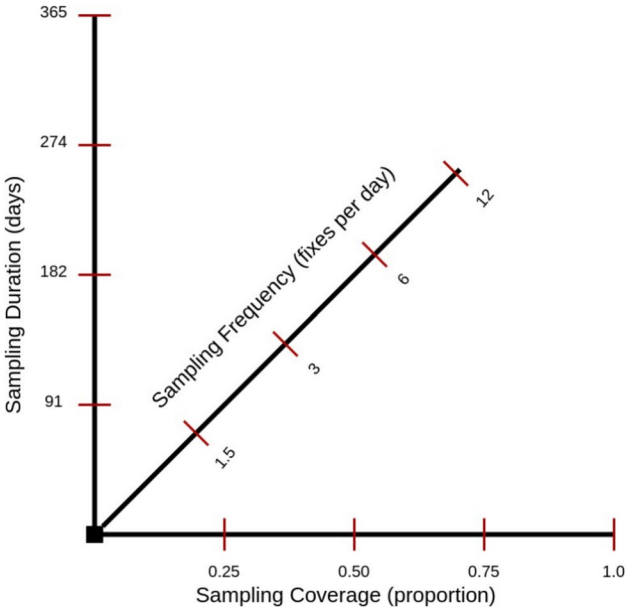


Fig. 3 Sampling points along the three axes of sampling. Sampling along these points produced 64 networks. The sample obtained corresponding to the point (1.00, 12, 365) produced the network with highest accuracy

sampling frequencies. Sampling frequencies were 12 fixes, 6 fixes, 3 fixes and 1.5 fixes per day corresponding to fix intervals between subsequent observations of 2 h, 4 h, 8 h and 16 h respectively. In this way, 64 samples were selected to obtain 64 network structures.

In a similar way, for the third aspect of the analysis, we sampled individuals with a coverage of 25% and 50% but whole sets of individuals were sampled. For example, for a sampling coverage of 25%, 125 individuals were chosen belonging to just 5 groups as compared to all 16 groups in random sampling.

Consideration of GPS error in data collection

In the process of gathering empirical data through GPS fixes, various sources of positional error may arise (He et al. 2022). To ensure greater realism in our simulated model, we incorporated these nuances into the data collection procedure. We used empirical data gathered by He et al. (2022) and generated a distribution of error magnitudes while taking a GPS fix. Specifically, we fit a cumulative density function to the real GPS error data shown in Fig. 2(a) of He et al. (2022) which depicts a Johnson SU distribution of errors. We then use this empirical distribution to generate random samples of GPS errors which we add to the underlying true exact position of each agent at each stage of our simulation. In our simulation, as each cell in the grid comprised of a 10 m X 10 m region, an error value of magnitude less than 10 m did not displace the individual. However, if an error value was between 10 and 20 m, the recorded location would shift by one cell randomly in any direction and so on. Therefore, for each recording location of an individual in the simulation, there was a possibility of its position being wrongly recorded. The empirical distribution of GPS errors places 96.7% of observations within the correct cell, 2.6% in an adjacent cell, and decreasingly small proportions in cells farther away.

Analysis

We obtained 64 network structures from the 64 samples that were generated as described above. We analysed these networks with respect to three global and three individual-level network metrics. The global network metrics used for analysis were edge density, assortativity, and transitivity and the individual-level metrics used for analysis were degree, strength, and betweenness.

Edge density (binary) is the ratio of the number of edges present to the maximum number of edges that the network can contain. Assortativity measures preference for the nodes of a network to connect to other nodes that are similar in some way (Farine 2014). In this simulation, we had initialised individuals belonging to one of the 16 pre-defined sets of strongly connected individuals. Therefore, assortativity provided a measure of tendency of individuals were in the same location (i.e. inferred to be associated) with their preferential associates versus other individuals. We calculated assortativity using the assortnet package (Farine 2016) in R. The assortativity value for the fully observed network was 0.8541. Transitivity of a network measures the probability that the connections of a node are also connected with each other.

The correlation analysis included three individual-level network metrics: degree, strength, and betweenness. The degree of a node represents the number of connections it has in the network. The strength of a node is equal to the sum of all the edge weights connecting to it. It is often referred to as weighted degree. The betweenness of a node is the number of times it appears on the shortest path between two other nodes in the network. Nodes with high betweenness values act as bridges connecting different parts of a network. Nodes in a network can be ranked according to their values of degree, strength, or betweenness. The agent base model was designed in R (R Core Team 2022) where all analyses were carried out. We used the R package aniSNA (Kaur 2024) to easily compute network metrics and analyse network structures.

Accuracy

Our goal was to quantify three factors that impact accuracy. First, we looked at how the accuracy of projected network metrics changes as we moved along the three sample axes. We calculated the absolute relative error between the estimated values of the global network metrics and the observed value acquired from the full network as it provides a standardized measure that is independent of the scale or magnitude of the network metrics being compared. Full network refers to the network obtained from the fully simulated population and corresponds to the point (1.00, 2, 365) on the 3-dimensional sampling space (Fig. 3). Absolute relative error is defined as the absolute difference between the true value and the estimated value, normalized by the true value and is calculated as follows:

$$\left| \frac{True\ value - Estimated\ value}{True\ value} \right|$$

To determine the accuracy with respect to individual-level network metrics, we calculated the Pearson correlation coefficients between the network metric values of the sampled networks and the fully observed network. This analysis allowed us to acquire an understanding of how well the original ranks of the nodes were preserved in the sampled networks.

Secondly, we considered the trade-offs between sampling duration and frequency, as one often comes directly at the cost of the other. At each of the 16 levels of sampling (4 for sampling duration times 4 for sampling frequency), we calculated the total number of recorded observations as follows:

$$N = Sampling\ duration\ (in\ days) \times frequency\ (number\ per\ day),$$

where N is the Number of observations.

We analysed this trade-off for the lowest level of coverage i.e., 25%. Observing 25% of animals over 91 days with a frequency of 1.5 fixes per day resulted in 136 recorded observations. In contrast, a 365-day sample with 2 h between fixes yielded 4380 recorded observations. Furthermore, several samples with various settings produced approximately the same number of observations. For example, the three samples obtained by (0.25, 4, 91), (0.25, 8, 182) and (0.25, 16, 365) configurations generated 546 to 548 observations. Therefore, we used our data to examine what the best strategy is if we have a constraint on the number of observations that may be captured.

Thirdly, we analysed how the accuracy of network metrics is affected when the sampling is done randomly as compared to when it is done group-wise. So for this analysis, we compared the error and the correlation coefficient when the coverage was random versus when whole sets of individuals were sampled. We performed this analysis for 25% and 50% of sampling coverage. As for higher coverage proportions, the two sampling techniques would lead to a similar selection of animals and the differences would be negligible.

Results

Error in the values of global network metrics

Error in edge density was most affected by sampling duration and sampling frequency, and least affected by sampling coverage (Fig. 4). The lowest error was found at the highest sampling duration and highest sampling frequency, even when the coverage was only 25%.

Overall, assortativity had little error across whole of sampling space (Fig. 4). We did find error to be slightly elevated with lower sampling coverage (from 0.0113 at 100% coverage and lowest values for duration and frequency to 0.0222 at 75% coverage and highest frequency and duration). However, these errors remain very small, suggesting that assortativity is highly robust to subsampling.

Error in transitivity was significantly influenced by sampling frequency, followed by sampling duration and was least affected by sampling coverage (Fig. 4). The error rose over 0.5 when the sampling frequency was decreased to 1.5 fixes per day hours from 12. However, the error was just 0.008 when the coverage was dropped to 25%. At each level of frequency and duration, the error remained approximately the same regardless of the coverage values. This analysis suggested that the best combination of coverage, frequency and duration depends on the specific network metric being investigated in relation to the research question.

Correlation coefficient values for node-level network metrics

The joint impact of the three levels of sampling is summarised in Fig. 5, which shows that the network metric degree was most affected by sampling duration, followed by sampling coverage and was least affected by sampling frequency. The correlation values dropped below 0.4 when the sampling duration was reduced to 91 days even with full coverage and highest frequency. In contrast, the correlation was over 0.7 with a high sampling duration of 365 days and a full coverage, regardless of the observation frequency. Therefore, to get high correlation for the network metric degree, higher sampling duration was the most critical factor as achieving a correlation above 0.5 (or equivalently a value of 1 minus the correlation below 0.5) was only achieved when duration was above the minimum value considered, whereas higher values of correlation of degree could be achieved when the minimum values of frequency (1.5 fixes per day) or coverage (0.25) were used and duration was over more than 91 days.

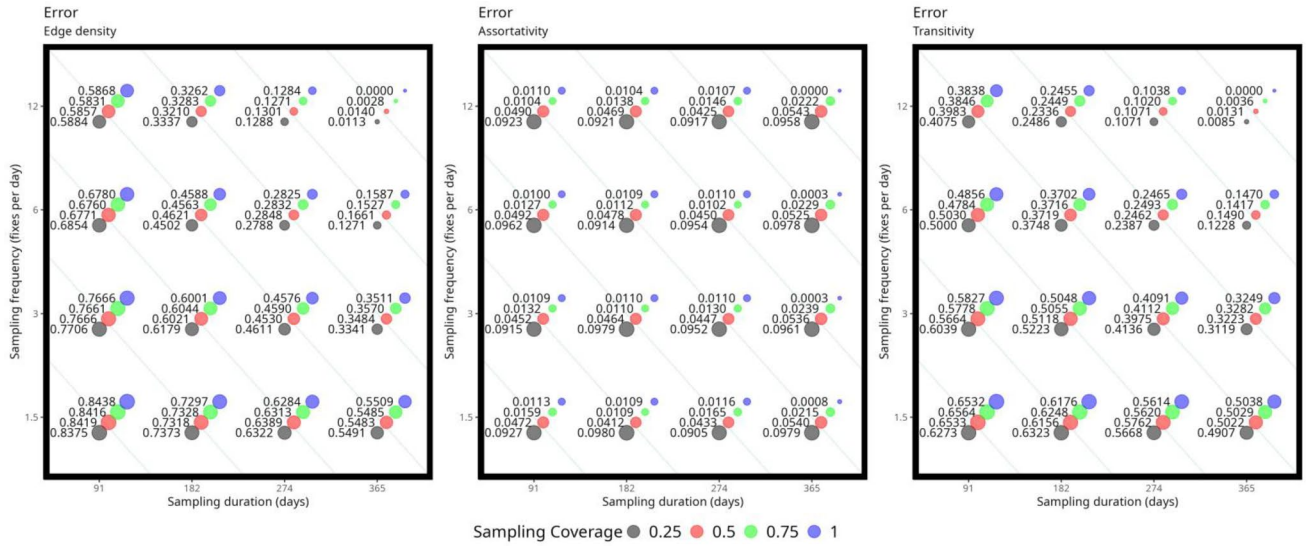


Fig. 4 The error in the three global network metrics—edge density, assortativity, and transitivity. The x-axis denotes sampling duration, y-axis denotes frequency in fixes per day and the colour of the circles in each plot correspond to a sampling coverage value. The size of the circles corresponds to the magnitude of the error. Note that the top right value in each plot is zero as it corresponds to the observed network obtained from complete observations of the population

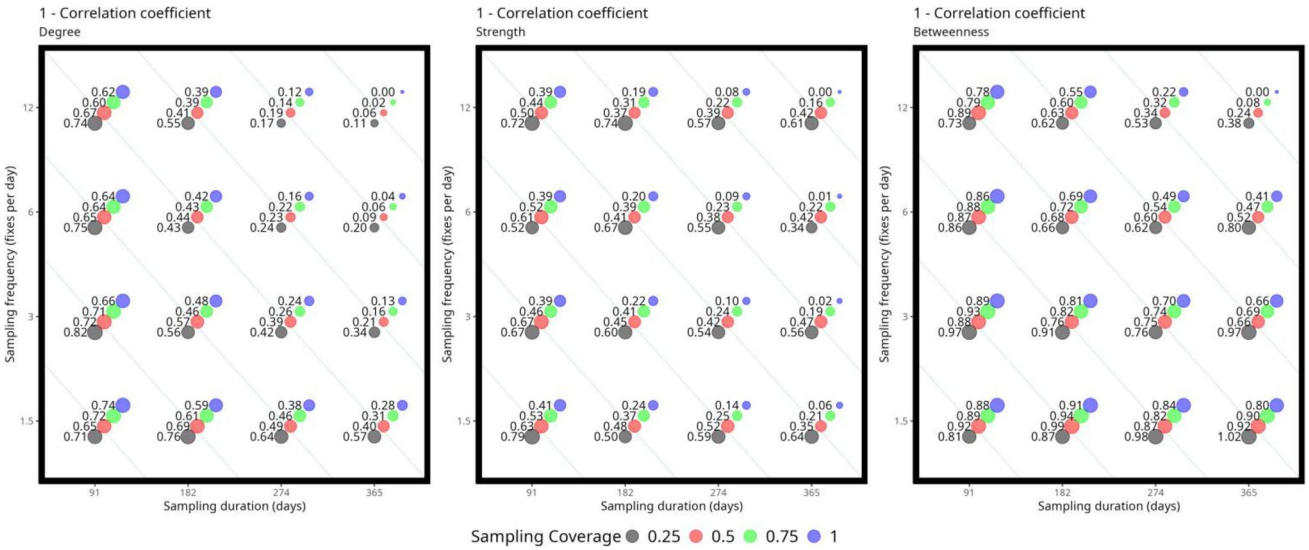
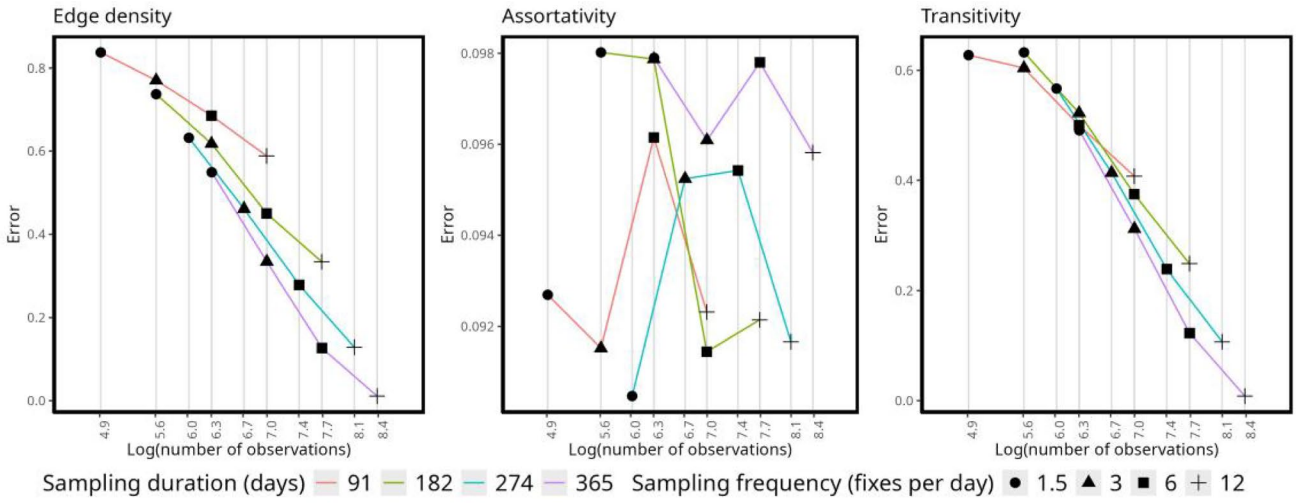


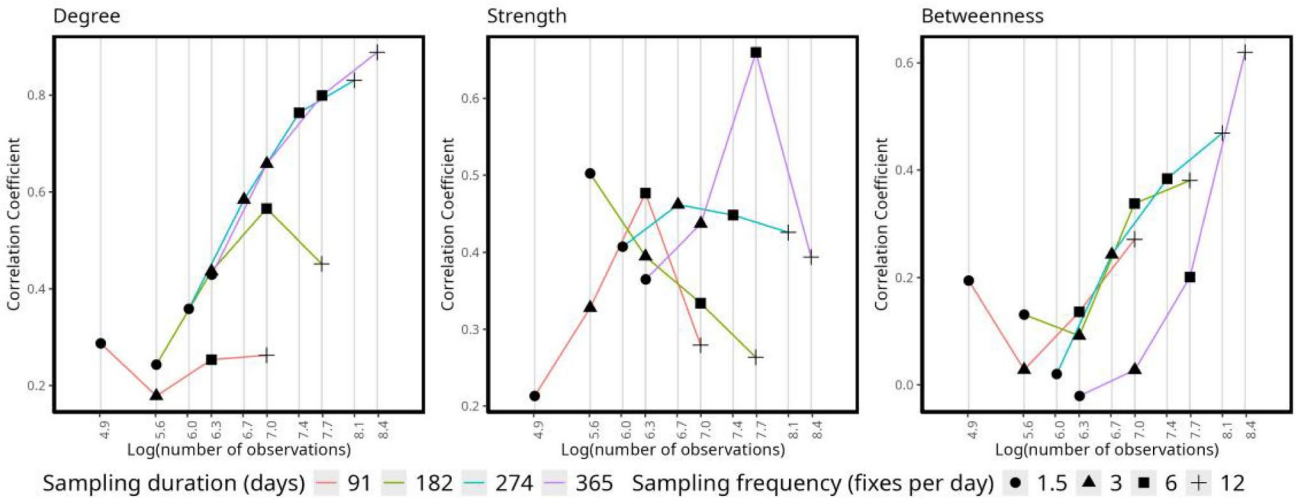
Fig. 5 1 minus the correlation coefficient between node-level metric values from sampled networks and the fully observed network based on complete observations of the full population. The x-axis represents sampling duration, the y-axis represents frequency in fixes per day, and the colour of the circles in each plot corresponds to the sampling coverage value. The size of the circles represents the 1 minus the correlation, with smaller circles therefore corresponding to more agreement between sampled and full networks. Note that the top right value in each plot is zero as it corresponds to 1 minus the correlation for the observed network obtained from full observations of the population

Sample coverage had a significant impact on correlation values for network metric strength, followed by sampling duration. After observing individuals for 365 days with a high sampling frequency of 2 h, the correlation coefficient was as low as 0.39 when just 25% of the population was sampled. In comparison, the correlation coefficient was over 0.75 when the sampling duration was merely 182 days, frequency was 1.5 fixes per day, and coverage was 100%. Hence, selecting higher values for coverage and duration was crucial for capturing correlations in strength.

The network metric betweenness was least affected by sampling coverage. However, the correlation values dropped



(a) Error for global network metrics.



(b) Correlation coefficient for node-level network metrics.

Fig. 6 Trade-offs in the two axes of sampling, sampling duration and sampling frequency. In each plot, the x-axis denotes the log of total number of observations in the sample configuration. The y-axis denotes the values for error in (**a**) and correlation coefficients in (**b**). The color of the lines connecting the points represent sampling duration in days and the shape of the points represent sampling frequency in fixes per day network metric, with some metrics requiring more sampling coverage than others to obtain comparable levels of accuracy. We discuss how each of the sampling axes influences the accuracy of estimated network metrics based on the network properties that they represent, and provide recommendations for efficient configurations for the three sampling axes

quickly as the values were lowered on each of the three axes (Fig. 5). A sampling duration of less than 274 days, frequency of under 12 fixes per day and coverage less than 50% lead to correlations dropping below 0.7. The network metric of betweenness demonstrated the greatest sensitivity to incomplete sampling.

Trade-offs between the three axes of sampling

For the network metrics edge density and transitivity, we found that for a given number of samples, it was typically better to increase sampling duration at the cost of sampling frequency as opposed to increasing sampling frequency at the cost of duration (Fig. 6a). For example, there were three configurations, resulting in a log (number of observations) of 6.3. Out of these three configurations, for 25% coverage, the lowest error was achieved when the frequency was 1.5 fixes per day and a sampling duration of 365 days. The overall error in assortativity remained minimal, less than 0.1 across all configurations. Nevertheless, it was noted that favoring an increase in sampling frequency over sampling duration yielded better results for a fixed number of samples.

While prioritizing sampling duration over sampling frequency provided better correlation for the individual-level

network metric degree with a fixed number of samples, no distinct trend was evident for the network metrics strength and between- ness (Fig. 6b). The correlation values were under 0.7 for all configurations at 25% sampling coverage for strength and betweenness, indicating the significance of higher sampling coverage in achieving improved correlations for these two network metrics.

Random vs group-wise sampling

For the global network metrics, edge density, assortativity and transitivity, the difference in the error as a function of deployment strategy was largely imperceptible (see Fig. D in appendix section Plots for random versus group-wise sampling). However, a close inspection indicated that the error magnitude was mostly lower when the sampling was done groupwise for the network metrics edge density and transitivity. In contrast, random sampling mostly produced a lower error for network measure assortativity.

The differences in the correlation values were comparatively more apparent for the individual-level network metrics degree, strength and betweenness (Fig. E in appendix section Plots for random versus group-wise sampling). Degree values tend to correlate better when the sampling is done randomly and the network metric strength correlated better when the sampling was performed group-wise for lower coverage proportions. This held true for nearly all of the 32 samples. Betweenness values for groupwise sampling procedure declined as the sampling efforts were reduced along each of the three sampling axes. This is analogous to the case in which sampling was done at random. However, random sampling yielded better correlation for lowest sampling coverage with higher frequency and longer duration.

Discussion

Using an ABM provides us with sufficient flexibility to design a constrained and controlled environment, allowing us to compare several scenarios and analyse the effect of sampling levels across the three axes. It has allowed us to capture individual and environmental heterogeneity by modeling agent characteristics, for example, their energy levels and change in state that directly influenced their individual decision- making processes. In addition, it has made it possible to simulate social contacts efficiently using precise principles. This has enabled us to investigate the complex social phenomena and network features that emerge when animals are attracted to, and move with, preferred conspecifics, revealing insights into the fundamental group structures that evolve from bottom-up interactions. Agent-based modeling has also served as a computational platform for hypothesis testing in this paper, allowing us to manipulate model parameters and experiment with different thresholds to test hypotheses about different sampling regimes and the effects of changes in sampling on the accuracy of measured network metrics. This has in turn enabled us to identify critical thresholds that influence the social dynamics and the inferences that we obtain by forming a network structure from the sample.

Our ABM, combined with strategic subsampling, highlighted that sampling decisions can have a substantial impact on data collecting results, and hence the suitability of a data set for answering questions about group and individual behaviour (Fragaszy et al. 1992; Davis et al. 2018; Gilbertson et al. 2021; He et al. 2022). Our findings suggested that the influence of each of these three axes varies depending on the social.

Optimizing sampling strategies for accurate assessment of social network metrics

We examined three aspects of the global network—edge density, assortativity, and transitivity—as well as three aspects of individual-level rankings within the population—degree, strength, and betweenness. Our goal was to identify optimal configurations for the three sampling axes values to minimize error and maximize correlations while keeping a fixed number of total samples. We found that the global network metrics of edge density and transitivity were most significantly impacted by most by sampling frequency and then duration as evidenced by a greater variation in error by frequency than by duration. Conversely, assortativity was overall much less sensitive with an error always below 0.1, mostly impacted by sampling coverage. At the node level, both degree and strength were particularly affected by decreasing sampling duration, particularly for higher coverage. Duration needed to be 274 days or above to achieve greater than 0.6 correlation in either of these metrics. Sampling coverage had a pronounced effect on strength and betweenness metrics compared to degree, with correlations in both below 0.4 when the log of the number of observations is below 5.6. Interestingly, betweenness was heavily influenced by all three sampling axes values.

High sampling coverage is an important factor while calculating such network metrics whose values are not just dependent on a localised part of the network but are influenced by the network as a whole for example, assortativity, and betweenness. Some other network metrics falling into this category are eigenvector centrality, modularity, homophily and closeness centrality. These results are in-line with the conclusions made by Davis et al. (2018) and Gilbertson et al. (2021) that such measures of association were more sensitive to insufficient sampling. Sampling coverage would also play a crucial role while collecting the samples for research objectives consisting of community detection algorithms in

the network. In such research studies, if the sampling coverage is insufficient, observing animals for prolonged periods of time with high frequency will have no positive effect on the estimated values of social network metrics.

High sampling duration and high frequency appears to be necessary for obtaining low error rates in network metrics that are highly dependent on the localised regions of a network, for example, edge density, transitivity, strength, and degree. The accuracy of these network metrics is directly proportional to the comprehensiveness of the monitoring regimes. As a result, monitoring animals with high frequency over an extended period helps to reduce error rates. However, these network metrics are resilient to low sampling coverage since they do not capture information on overall connectivity patterns or clustering within the network, as well as a node's centrality and influence. These findings align with the study by Silk et al. (2015), which found that tracking as few as 30% of individuals can still accurately represent their relative positions in the social network, suggesting that collecting more samples per dyad should be prioritised over collecting more individuals (see also Davis et al. (2018)).

Trade-offs in the three sampling axes

To attain a comparable level of accuracy for edge density and transitivity, lowering the sampling frequency required increasing the sampling duration and coverage while keeping the total number of observations constant. To acquire an error value less than 0.2, more sampling effort was required, as low error values were only attained with a large number of total observations. However, for assortativity, achieving low error rates did not require a large number of observations.

Previous analyses suggested the impact of better sampling duration on the network metrics degree and strength (Voelkl et al. 2011; Silk et al. 2015; Davis et al. 2018). Yet 'better sampling' can be achieved via any of the three axes duration, frequency, and coverage. Having a high frequency and high coverage at the same time was not required to produce satisfactory values for correlation coefficients; rather, at least one of these axes should be high. High frequency sampling was the primary need for achieving favourable values for betweenness, resulting in a large number of observations.

Overall, these findings underscored that it is possible to obtain a desired level of accuracy in the network metric estimates with a reduced sampling effort, if the sampling strategies and the configurations of the three sampling axes are carefully chosen. This choice should always be derived by the properties of the chosen social network metrics along with a careful consideration of which aspects of the network do they capture. However, a challenge is that different axes are better for different network metrics, so which metric should be prioritised will often come down to the research question.

Optimizing sampling coverage: Insights from random and groupwise coverage

We analysed the differences in the network metric estimates for random and groupwise sampling for lower levels of sampling coverage of 25% and 50%. The network metric assortativity was better estimated for random sampling coverage in contrast to the rest of the two network metrics. This was logical, as assortativity requires both within-type and between-type edges. Therefore, if the research objective centers around assessing assortativity, then the sampling approach should prioritize capturing a representative sample of individuals across various types (e.g. social group, as what we simulated here, or according to traits Farine (2014)).

The node-level network metrics degree and strength showed opposite behaviours to each other with degree performing better with random sampling coverage. A striking difference in the patterns for degree and strength indicates the importance of groupwise connections that contribute significantly towards the total strength of a node in the network. The strength of a node represents the overall intensity and frequency of interactions that a pair of nodes have within the network, where degree just represents the number of individuals a node encounters without considering the intensity of those encounters. Therefore, degree rankings were better preserved in randomly selected network, whereas preserving strength rankings of individuals required more individuals with strong inter-individual preferences. Another way of putting this is that having fewer preferred associates marked will substantially impact an individual's strength estimate. Therefore, to maximise the accuracy of strength requires sampling sets of more strongly interconnected individuals. Surprisingly, no such pattern was observed for the network metric betweenness, indicating that substantial sampling coverage is necessary for betweenness and that for low levels, it makes no difference whether the coverage is random or groupwise.

This has once again demonstrated the significance of having a well-planned sampling approach that is consistent with the research question and the relevant network metric. The prior selection of a social network metric should guide the sampling coverage criteria.

Limitations and future directions

The approach of using ABMs in general all suffer from the same potential limitation: namely that the behaviour of the agents or the simulated environment in which they are embedded are not quite realistic enough. Fortunately, ABMs are an active area of development, but despite the increasing number and complexity of available tools, we

have identified a need for a model that focusses on social network behaviors. For this, we require (i) multiple interacting agents (ii) that interact at socially relevant scales. Careful consideration of these issues has the potential to greatly inform empirical studies. In this paper we have presented one such case study, demonstrating how our ABM can inform decisions around the competing resources of sampling frequency, duration, and coverage for GPS tagging when the research goal is accurate inference of social network structure. There are a number of possible extensions in order to make our method more generally applicable. By combining social network data with demographic models, researchers may predict how changes in social structure, connectivity, or network topology will affect population dynamics, dispersal patterns, disease transmission, and conservation outcomes (Ellers et al. 2010; McLane et al. 2011; Salgado and Gilbert 2013; Khazaii 2016).

While our simulation model at a conceptual level may not fully capture the complexity of real animal behavior (Jonker and Treur 2004), it can be refined with more specific on-the-ground knowledge from a given population (which itself can be informed from real tracking data). Thus, the ABM presented here can be made more realistic by adding additional layers of movement constraints and decision making processes at the level of individuals in an iterative fashion (Cristiani et al. 2010; Tang and Bennett 2010; Thiele et al. 2012; Bernardi and Scianna 2020; Gochanour et al. 2023). Individual-specific gregariousness, sex and age-specific behaviours can readily be added, again by drawing from distributions estimated from real data relevant to the particular study species of interest. Seasonal variation, such as a breeding period or migration events can also be added via time-varying social and movement parameters. In addition to these refinements, the modeling framework presented in this paper operated under several simplifying assumptions whose primary objective was to compare the sampling strategies on social network metrics. While these assumptions constrained the model's applicability to more complex, dynamic scenarios, they did not impact the simulations' ability to answer our specific research questions. However, for the model to be applied to other purposes, these assumptions would need to be adapted or relaxed. The discussion of these limitations is crucial for refining and enhancing the model's capabilities in future iterations.

Our model assumed static social preferences between agents, meaning that the social preferences between agents did not change over time. This assumption may not capture the dynamic formation or dissolution of groups that takes place in animal societies. The movement decisions made by agents at each time point were based on fixed rules of trade-offs between social preference and resource quality, with no consideration of complex, individual-specific behaviours, learning, or memory. Additionally, our model used a constant rate for resource regeneration, and depletion occurred using a simple exponential function. This did not account for the spatial variability or interactions that might occur between different types of resources available. The movement of agents across the grid assumed equal energetic costs, ignoring potential variability in terrain or habitat barriers. The uniform grid environment lacked barriers or distinct habitat types, limiting its use for habitat connectivity or landscape-level movement studies.

Due to these simplifying assumptions, the model presented here may not be appropriate for systems where social connections are dynamic or are influenced by external factors, such as seasonal changes or dominance hierarchies. The model also did not account for individual foraging strategies or their metabolism, making it unsuitable for studies requiring precise energy budgets. Furthermore, for studies involving disease transmission, the model would need additional layers of complexity, including precise contact rates, interaction durations, and indirect contacts if pathogens have indirect modes of transmission.

An important feature of ABMs in general is in providing meaningful environmental layers. Adding environmental barriers, such as impassable terrain or physical hurdles, can be used to test certain hypotheses (He et al. 2019) and vegetation cover based on real data can be readily embedded in our grid. Furthermore, resource availability can be made more flexible by programming it to include multiple sorts, such as food and water. At the individual level, behaviours can be adjusted and developed to include more complicated elements that influence their decision-making processes, foraging methods, social dominance, metabolic rates, and other characteristics (Anderson et al. 2017). Individuals may also have factors such as stress, reproductive status, and changing preferences for particular types of social affiliations. Another complicated component might be integrating learning processes that allow individuals to adjust their behaviours based on previous experiences, and environmental feedback. For example, the ABM presented by Perez et al. (2021) simulated animal movements that were governed by learning and memory in a dynamic landscape and provided insights into how bears use previously acquired landscape data to maximize use of high-quality areas within a heterogeneous landscape. Therefore, by thoroughly considering the features, behaviours, and decision-making processes of species agents in an ABM, realistic simulations that reflect the dynamics of animal behaviour, ecology, and population dynamics within complicated settings (de Almeida et al. 2010; Diaz et al. 2021; Hoegh et al. 2021) may be developed using our approach. Our results are particularly applicable to fission–fusion social systems and further work is required to assess how this might be extended to other systems.

Conclusions

In conclusion, our research has highlighted the importance of carefully designing sampling strategies aligned with the research question and the specific network metrics relating to the research objectives. The choice of social network metric should guide the criteria for sampling coverage, frequency, and duration, ensuring that the collected data are suitable for addressing questions about the social network structure of the concerned population. Our findings revealed the varying influence of each sampling axis on different network metrics, highlighting the need for tailored sampling approaches to achieve accurate metric estimates.

Moreover, our analysis provided valuable insights into the trade-offs involved in optimizing sampling strategies for social network metric estimation. We identified con- figurations that yielded minimum error and maximum correlations while constraining on the total number of observations. In particular, the sensitivity of network metrics to sampling coverage, frequency, and duration underscores the need for careful consideration of these factors in study design. Our study also highlighted the potential of agent-based modeling as a powerful tool for hypothesis testing and exploration of various scenarios in animal social network analysis. By simulating complex social interactions and integrating environmental constraints, ABM offers a flexible framework for investigating the dynamics of animal behavior and network structure.

Overall, our study contributed to advancing our understanding of how to design studies to collect data with sampling configurations that can maximise the contribution of research effort (time and costs) in terms of producing accurate and reliable animal social networks. Our work underscored the importance of informed sampling strategies and computational modeling approaches in understanding the complexities of animal behavior and network dynamics.

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Author contributions PK and DF conceived the ideas, designed the methodology and implemented model code with the help of MS-T. PK analysed the data and wrote the manuscript, edited by DF, MS-T and SC. All authors contributed critically to the drafts and gave final approval for publication.

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Code availability The code used for the agent-based simulations is available on GitHub at the following repository: https://github.com/PrabhleenKaur19/Agent-Based-Model.git. Please refer to this repository for the R scripts for parameter settings and model implementation.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Alarcón-Nieto G, Graving JM, Klarevas-Irby JA, Maldonado-Chaparro AA, Mueller I, Farine DR (2018) An automated bar- code tracking system for behavioural studies in birds. Methods Ecol Evol 9:1536–1547. https://doi.org/10.1111/2041-210x.13005

Anderson JH, Downs JA, Loraamm R, Reader S (2017) Agent-based simulation of muscovy duck movements using observed habitat transition and distance frequencies. Comput Environ Urban 61:49–55. https://doi.org/10.1016/j.compenvurbsys.2016.09.002

Aplin LM, Firth JA, Farine DR et al (2015) Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. Anim Behav 108:117–127. https://doi.org/10.1016/j.anbehav.2015.07.016

Aureli F, Schaffner CM, Boesch C et al (2008) Fission-fusion dynamics. Curr Anthropol 49:627–654. https://doi.org/10.1086/586708

Bernardi S, Scianna M (2020) An agent-based approach for modelling collective dynamics in animal groups distinguishing individual speed and orientation. Phil Trans R Soc B 375:20190383. https://doi.org/10.1098/rstb.2019.0383

Costenbader E, Valente TW (2003) The stability of centrality measures when networks are sampled. Soc Netw 25:283–307. https://doi.org/10.1016/S03788733(03)00012-1

Cristiani E, Frasca P, Piccoli B (2010) Effects of anisotropic interactions on the structure of animal groups. J Math Biol 62:569–588. https://doi.org/10.1007/s00285-010-0347-7

Croft DP, James R, Krause J (2008) Exploring Animal Social Networks. Princeton University Press, Princeton

Cross PC, Creech TG, Ebinger MR, Heisey DM, Irvine KM, Creel S (2012) Wildlife contact analysis: Emerging methods, questions, and challenges. Behav Ecol Sociobiol 66:1437–1447. https://doi.org/10.1007/s00265-012-1376-6

Davis GH, Crofoot MC, Farine DR (2018) Estimating the robustness and uncertainty of animal social networks using different observational methods. Anim Behav 141:29–44. https://doi.org/10.1016/j.anbehav.2018.04.012

de Almeida SJ, Ferreira RPM, Eiras ÁE, Obermayr RP, Geier M (2010) Multi-agent modeling and simulation of an *Aedes aegypti* mosquito population. Environ Modell Softw 25:1490–1503. https://doi.org/10.1016/j.envsoft.2010.04.021

Diaz SG, DeAngelis DL, Gaines MS, Purdon A, Mole MA, Aarde RJv, (2021) Development and validation of a spatially-explicit agent-based model for space utilization by African savanna elephants (*Loxodonta africana*) based on determinants of movement. Ecol Model 447:109499. https://doi.org/10.1016/j.ecolmodel.2021.109499

Ellers J, Hoogendoorn M, Wendt D (2010) An agent-based modeling approach to investigate emergent patterns in ecological systems. In: Hoeber O, Li Y, Huang XJ (eds) IEEE/WIC/ACM International Conference on Web Intelligence and Intelligent Agent Technology, Toronto, pp 6–13. https://doi.org/10.1109/WI-IAT.2010.200. https://ieeexplore.ieee.org/document/5615858

Espín-Noboa L, Wagner C, Karimi F, Lerman K (2018) Towards quantifying sampling bias in network inference. In: WWW '18: Companion Proceedings of The Web Conference, Lyon. ACM, New York, pp 1277–1285. https://doi.org/10.1145/3184558.3191567

Farine DR (2014) Measuring phenotypic assortment in animal social networks: Weighted associations are more robust than binary edges. Anim Behav 89:141–153. https://doi.org/10.1016/j.anbehav.2014.01.001

Farine DR, Whitehead H (2015) Constructing, conducting and interpreting animal social network analysis. J Anim Ecol 84:1144–1163. https://doi.org/10.1111/1365-2656.12418

Farine D (2016) assortnet: Calculate the Assortativity Coefficient of Weighted and Binary Networks. R package version 0.20, https://CRAN.R-project.org/package=assortnet

Fragaszy DM, Boinski S, Whipple J (1992) Behavioral sampling in the field: Comparison of individual and group sampling methods. Am J Primatol 26:259–275. https://doi.org/10.1002/ajp.1350260404

Fründ J, McCann KS, Williams NM (2015) Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. Oikos 125:502–513. https://doi.org/10.1111/oik.02256

Gilbertson ML, White LA, Craft ME (2021) Trade-offs with telemetry-derived contact networks for infectious disease studies in wildlife. Methods Ecol Evol 12:76–87. https://doi.org/10.1111/2041-210X.13355

Gochanour B, Fernández-López J, Contina A (2023) abmr: An R package for agent-based model analysis of large-scale movements across taxa. Methods Ecol Evol 14:218–230. https://doi.org/10.1111/2041-210X.14014

Grimm V, Railsback SF, Vincenot CE et al (2020) The ODD protocol for describing agent-based and other simulation models: a second update to improve clarity, replication, and structural realism. JASSS-J Artif Soc S 23:7. https://doi.org/10.18564/jasss.4259

He P, Maldonado-Chaparro AA, Farine DR (2019) The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. Behav Ecol Sociobiol 73:9. https://doi.org/10.1007/s00265-018-2602-7

He P, Klarevas-Irby JA, Papageorgiou D, Christensen C, Strauss ED, Faine DR (2022) A guide to sampling design for gps -based studies of animal societies. Methods Ecol Evol 14:1887–1905. https://doi.org/10.1111/2041-210X.13999

Hebblewhite M, Haydon DT (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Phil Trans R Soc B 365:2303–2312. https://doi.org/10.1098/rstb.2010.0087

Hoegh A, van Manen FT, Haroldson M (2021) Agent-based models for collective animal movement: Proximity-induced state switching. J Agric Biol Envir S 26:560–579. https://doi.org/10.1007/s13253-021-00456-0

Hoppitt WJ, Farine DR (2018) Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. Anim Behav 136:227–238. https://doi.org/10.1016/j.anbehav.2017.08.029

James R, Croft DP, Krause J (2009) Potential banana skins in animal social network analysis. Behav Ecol Sociobiol 63:989–997. https://doi.org/10.1007/s00265-009-0742-5

Jonker CM, Treur J (2004) Agent-based simulations of animal behavior. Appl Intell 15:83–115. https://doi.org/10.1023/a:1011246304650

Jung TS, Hegel T, Bentzen TW et al (2018) Accuracy and performance of low-feature GPS collars deployed on bison *Bison bison* and caribou *Rangifer tarandus*. Wildlife Biol 2018:1–11. https://doi.org/10.2981/wlb.00404

Kaur P, Ciuti S, Ossi F et al (2024) A protocol for assessing bias and robustness of social network metrics using gps based radio-telemetry data. Mov Ecol 12:55. https://doi.org/10.1186/s40462-024-00494-6

Kaur P (2024) aniSNA: Statistical Network Analysis of Animal Soc. Netw. R package version 1.1.1, https://CRAN.R-project.org/package=aniSNA

Khazaii J (2016) Agent-based modeling. In: Advanced Decision Making for HVAC Engineers: Creating Energy Efficient Smart Buildings. Springer, Cham, pp 137–144. https://doi.org/10.1007/978-3-319-33328-1_13

Krause J, Croft DP, James R (2007) Social network theory in the behavioural sciences: Potential applications. Behav Ecol Sociobiol 62:15–27. https://doi.org/10.1007/s00265-007-0445-8

Krause J, Krause S, Arlinghaus R, Psorakis I, Roberts S, Rutz C (2013) Reality mining of animal social systems. Trends Ecol Evol 28:541–551. https://doi.org/10.1016/j.tree.2013.06.002

Lusseau D, Whitehead H, Gero S (2008) Incorporating uncertainty into the study of animal social networks. Anim Behav 75:1809–1815. https://doi.org/10.1016/j.anbehav.2007.10.029

McLane AJ, Semeniuk C, McDermid GJ, Marceau DJ (2011) The role of agent-based models in wildlife ecology and management. Ecol Model 222:1544–1556. https://doi.org/10.1016/j.ecolmodel.2011.01.020

Perez AZ, Bone C, Stenhouse G (2021) Simulating multi-scale movement decision- making and learning in a large carnivore using agent-based modelling. Ecol Model 452:109568. https://doi.org/10.1016/j.ecolmodel.2021.109568

Perreault C (2010) A note on reconstructing animal social networks from independent small-group observations. Anim Behav 80:551–562. https://doi.org/10.1016/j.anbehav.2010.06.020

R Core Team (2022) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org

Salgado M, Gilbert N (2013) Agent based modelling. In: Teo T (ed) Handbook of quantitative methods for educational research. SensePublishers, Rotterdam. https://doi.org/10.1007/978-94-6209-404-8_12

Shizuka D, Barve S, Johnson AE, Walters EL (2021) Constructing social networks from automated telemetry data: A worked

example using within- and across-group asso- ciations in cooperatively breeding birds. Methods Ecol Evol 13:133–143. https://doi.org/10.1111/2041-210x.13737

Silk MJ (2018) The next steps in the study of missing individuals in networks: a comment on Smith et al. (2017). Soc Netw 52:37–41. https://doi.org/10.1016/j.socnet.2017.05.002

Silk MJ, Jackson AL, Croft DP, Colhoun K, Bearhop S (2015) The consequences of unidentifiable individuals for the analysis of an animal social network. Anim Behav 104:1–11. https://doi.org/10.1016/j.anbehav.2015.03.005

Smith JA, Moody J (2013) Structural effects of network sampling coverage i: Nodes missing at random. Soc Netw 35:652–668. https://doi.org/10.1016/j.socnet.2013.09.003

Smith JA, Moody J, Morgan JH (2017) Network sampling coverage II: The effect of non-random missing data on network measurement. Soc Netw 48:78–99. https://doi.org/10.1016/j.socnet.2016.04.005

Smith JA, Morgan JH, Moody J (2022) Network sampling coverage III: Imputation of missing network data under different network and missing data conditions. Soc Netw 68:148–178. https://doi.org/10.1016/j.socnet.2021.05.002

Sosa S, Jacoby DM, Lihoreau M, Sueur C (2021) Animal social networks: Towards an integrative framework embedding social interactions, space and time. Methods Ecol Evol 12:4–9. https://doi.org/10.1111/2041-210X.13539

Strandburg-Peshkin A, Farine D, Couzin ID, Crofoot MC (2015) Shared decision-making drives collective movement in wild baboons. Science 348:1358–1361. https://doi.org/10.1126/science.aaa5099

Tan RK, Bora S (2019) Adaptive parameter tuning for agent-based modeling and simulation. Simulation 95:771–796. https://doi.org/10.1177/0037549719846366

Tang W, Bennett DA (2010) Agent-based modeling of animal movement: a review. Geogr Comp 4:682–700. https://doi.org/10.1111/j.1749-8198.2010.00337.x

Thiele JC, Kurth W, Grimm V (2012) Agent-based modelling: Tools for linking NetLogo and R. Artif Soc S 15:8. https://doi.org/10.18564/jasss.2018

Voelkl B, Kasper C, Schwäb C (2011) Network measures for dyadic interactions: stability and reliability. Am J Primatol 73:731–740. https://doi.org/10.1002/ajp.20945

Wey T, Blumstein DT, Shen W, Jordán F (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim Behav 75:333–344. https://doi.org/10.1016/j.anbehav.2007.06.020