

RESEARCH ARTICLE

Constructing social networks from automated telemetry data: A worked example using within- and across-group associations in cooperatively breeding birds

Daizaburo Shizuka¹  | Sahas Barve^{2,3}  | Allison E. Johnson¹  | Eric L. Walters³ ¹School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE, USA²Division of Birds, Smithsonian National Museum of Natural History, Washington, DC, USA³Department of Biological Sciences, Old Dominion University, Norfolk, VA, USA**Correspondence**Daizaburo Shizuka
Email: dshizuka2@unl.edu**Funding information**

National Science Foundation, Grant/Award Number: IOS-1455900 and IOS-1750606

Handling Editor: Nicolas Lecomte**Abstract**

1. Advances in data-logging technologies have provided a way to monitor the movement of individual animals at unprecedented spatial and temporal scales. When used in conjunction with social network analyses, these data can provide deep insight into the structure and dynamics of animal social systems. Emergence of these new technologies demands concomitant progress in workflows to translate data streams from automated systems to social networks, based on biologically relevant metrics.
2. Here we outline key considerations for constructing social networks from automated telemetry data. We highlight the need for paying particular attention to the spatial arrangement of receiver stations with respect to the ecology of study system and developing appropriate criteria for quantifying associations.
3. We provide a case study for constructing social networks from automated telemetry data collected over 1 month during a study of acorn woodpeckers *Melanerpes formicivorus*, a cooperatively breeding bird. The data consisted of detections of known birds near receiver stations placed within core areas of group territories. We use this system to demonstrate how to build social networks to investigate biological questions about patterns of associations between group members and territory visitors across the landscape.

KEYWORDS

acorn woodpeckers, automated radiotelemetry, movement ecology, reality mining, social associations, social behaviour, social network analysis

1 | INTRODUCTION

A major challenge in the study of social organization is the logistics of collecting data on social interactions and associations in situ. Rapid advances in automated data-logging technology, however, have recently ushered in an age of 'reality mining' of animal sociality (Krause et al., 2013). Automated data-logging systems for tracking the social associations of free-living animals include: global positioning system (GPS) tags (e.g. Spiegel et al., 2018), proximity loggers (e.g. St Clair et al., 2015), radio frequency identification tags (e.g. Aplin et al., 2015)

and automated telemetry systems (e.g. Dakin & Ryder, 2018, 2020; Jacoby et al., 2016). These technological advances have enabled pioneering studies measuring movement and associative patterns in increasingly smaller organisms at finer spatial and temporal scales over extended periods of time. With such fine-scale data-logging of individual organisms, automated systems provide a unique opportunity to address the feedback between individual behaviour, spatial variation, space use and social associations (Cantor et al., 2021).

Concomitant with technological advancements, the application of social network analyses to animal social behaviour has progressed

rapidly. Such approaches are now routinely used to quantify and analyse patterns and the spatiotemporal dynamics of social associations. The integration of automated data-logging with social network analyses has led to a fine-scaled understanding of processes such as the rapid spread of experimentally introduced information through wild populations (Aplin et al., 2015), the reorganization of social networks in response to a resource pulse (St Clair et al., 2015) and the dynamics of social contagion of cooperation (Dakin & Ryder, 2018). This list will continue to grow as more high-throughput tracking technologies emerge (Ripperger et al., 2020; Toledo et al., 2020). A key to leveraging the power of social network analysis and data-logging is the development of workflows that allow researchers to convert data into ecologically relevant inferences about social behaviour (Psorakis et al., 2012; Smith & Pinter-Wollman, 2021).

Here, we focus on the methodological challenges associated with automated telemetry systems and their use in social network analyses. Automated telemetry systems have wide applications for monitoring vagile organisms, particularly in environments and contexts where direct observation is difficult. Automated telemetry systems come in different forms, including automated acoustic telemetry, often used in aquatic environments, and automated radiotelemetry, typically used in terrestrial environments with either directional or omni-directional antennas. Receiver arrays with omni-directional antennas can be used to detect the time, frequency and duration of presence of a tag within the detection range of receiver stations (Barve et al., 2019; Dakin & Ryder, 2018; Ryder et al., 2012; Taylor et al., 2017). Receiver arrays with overlapping detection ranges can further be used to track fine-scale movement of individuals using triangulation, direction-of-arrival information (Kays et al., 2011) or timing-of-arrival information (Armansin et al., 2016). In this paper, we focus primarily on automated telemetry systems that rely on detection of the presence of a tag within range of receiver stations.

Automated telemetry systems have great potential for the study of social networks in free-living animals, however, the ability to infer social patterns depends on the design of the telemetry system as well as the underlying ecology of the study organism. Here, we review key considerations for designing studies of social networks using automated telemetry data. We then use data from an ongoing study on acorn woodpeckers, *Melanerpes formicivorus*, to demonstrate a workflow for extracting and analysing social networks from an automated telemetry array.

2 | KEY CONSIDERATIONS FOR CONSTRUCTING SOCIAL NETWORKS WITH AUTOMATED TELEMETRY DATA

2.1 | Detecting associations using automated telemetry

A critical challenge in constructing animal social networks is developing methods for detecting biologically meaningful social associations. Prior knowledge about the natural history of the study

organism and clear, pre-defined biological questions are critically important for developing appropriate criteria for detecting social associations from empirical data (Farine & Whitehead, 2015; Ferreira et al., 2020; Haddadi et al., 2011; Smith & Pinter-Wollman, 2021). Automated telemetry data, when coupled with knowledge of underlying natural history, can provide a powerful tool for inferring social behaviour. Careful consideration of the placement of receiver stations across the landscape is of primary importance because it can provide valuable contextual information about the type of social behaviour being detected. For example, placing receiver stations at known display sites of wire-tailed manakins *Pipra filicauda* allowed Dakin and Ryder (2018) to study the social dynamics of cooperative displays among males. Conversely, sparsely distributed receiver arrays in a uniform matrix may only provide coarse information on locations and contexts of social associations (Jacoby et al., 2016; Mourier et al., 2017).

In addition to the ecological importance of the receiver sites, detecting social associations also requires matching spatial and temporal scales of the automated telemetry data with those of the social behaviour within the study system. For example, different models of tags have varying transmission ranges, and inferring associations based on data with large spatial error can lead to uninformative social networks (Mourier et al., 2017). However, with ground truthing, signal strength can be used to estimate distance of tags from receivers, allowing researchers to define associations based on co-presence within a relatively specific radius around the receiver. This approach was used in studies of wire-tailed manakins, where associations were defined as two individuals being present within a 25-m radius from the centre of a known display site, estimated by signal strength (Dakin & Ryder, 2018; Ryder et al., 2012). Using a different approach, Armansin et al. (2016) used acoustic receiver arrays with overlapping detection ranges to triangulate positions of wobbegong sharks *Orectolobus maculatus* and defined associations based on interindividual distance relative to body length (i.e. individuals were associated if detected within two body lengths of each other, accounting for estimated positional error).

Automated telemetry systems can be used to calculate the frequency or duration of association between pairs of individuals that are detected in proximity of each other, and this information can be used to quantify the relative strength of social relationships. For studies triangulating the location of individuals, one can measure the duration of time spent in proximity to other individuals (e.g. Armansin et al., 2016). If the data consist only of detections of individuals within range of receiver stations, there are several options for quantifying associations. One could calculate the frequency or duration of bouts of simultaneous presence of two individuals near a receiver station (hereafter 'co-presence': Dakin & Ryder, 2018; Section 3 case study). Alternatively, some studies have measured the number of times two individuals that were detected within predefined (often arbitrary) temporal windows (e.g. 10 s: Ryder et al., 2012; 10 min: Mourier et al., 2017). Finally, machine-learning methods such as Gaussian mixture modelling (Psorakis et al., 2012) can also be used to detect 'gathering events', with pairs of individuals associating when they

co-occur in the same event (Jacoby et al., 2016). This last approach has the advantage of avoiding arbitrarily defined temporal thresholds (Psorakis et al., 2012). However, Gaussian mixture modelling is only useful when receivers are placed in sites where individuals visit (alone or in groups) in pulses, such as foraging sites, but not sites where individuals reside for extended periods, such as territories. Thus, having prior ecological knowledge about the behaviour of animals at receiver station sites is a prerequisite for making decisions about how to detect association patterns (Figure 1).

2.2 | Accounting for sampling error in calculating association indices

In many animal social networks, the connections, or edges, are weighted using an association index. Such association indices convert the frequency of observed associations between a pair of individuals into an association rate that takes into account, in various ways, the frequency with which either bird was observed in total (e.g. simple ratio index, half-weight index: Cairns & Schwager, 1987; Farine & Whitehead, 2015). With continuous data-logging systems, the association rates can be quantified as the frequency of discrete bouts of association between each pair of individuals (Dakin & Ryder, 2018), or the total duration (e.g. in seconds) of association between each pair (Section 3: case study). Automated systems allow for the potential for much denser sampling than is possible with direct observations, and it may be possible to quantify all instances of associations within range of receiver stations for certain periods of time depending on receiver and tag operation. However, in practice, sampling errors will often become a factor because of inevitable lack of coverage or receiver and tag failure.

Different association indices may generate biased estimates of association rates depending upon the sources of sampling error that could exist in the data. Hoppitt and Farine (2018), for example, provide a useful guide for how to account for two forms of sampling error: group location error (i.e. unsampled groups) and individual identification error (i.e. missing individuals), which can be adapted to particular sources of error in automated telemetry systems (Figure 2). For example, group location error occurs when receiver stations fail to detect locations where social associations occur, or when receiver stations fail because of technical malfunction. Individual

identification error arises when there are untagged individuals and/or when individuals are undetected because of tag failure or signal interference. Hoppitt and Farine (2018) introduce several new association indices that better account for these sources of sampling error, including the very simple ratio index (vSRI), group location error corrected index (GLECI) and the combined errors corrected index (CECI). We illustrate the conditions under which each association index may be best employed (Figure 2). If receiver stations cover all sites of social associations among tagged individuals, it is possible to calculate unbiased measures of association strength (SRI or vSRI). When certain validation data are available, unbiased estimates of association strength (GLECI and CECI) may be calculated even when the coverage of receiver stations is imperfect. If both tag failure and receiver failure occur at relatively low but unknown rates, it may be safer to use the more traditional simple ratio index (SRI), while considering the potential effects of biases (Hoppitt & Farine, 2018). We provide an example of how different association indices may be used in our case study in Section 3.

2.3 | Temporal and spatial dynamics of social networks

Social network structure may change across time because of changes in patterns of social associations (Hobson et al., 2013), or because of loss and gain of new individuals as a result of demographic processes (Shizuka & Johnson, 2020). Static social network approaches that fail to account for such temporal changes may obscure important patterns in social behaviour (Blonder et al., 2012; Pinter-Wollman et al., 2014). Similarly, social networks are also dynamic across space (Cantor et al., 2012; Pinter-Wollman et al., 2014). Sources of spatial dynamics may include individual differences in space-use patterns (Spiegel et al., 2017), spatial constraints to social interactions (Pinter-Wollman et al., 2017), spatial heterogeneity in resource distribution (He et al., 2019) and territoriality.

Automated telemetry systems are ideal for exploring fine-scale temporal dynamics of social networks because data can be collected continuously over long time periods. Because temporal data are encoded in all detection data, automated telemetry data may be particularly well-suited for dynamic network analyses. The resolution of these dynamic networks can span anywhere from the

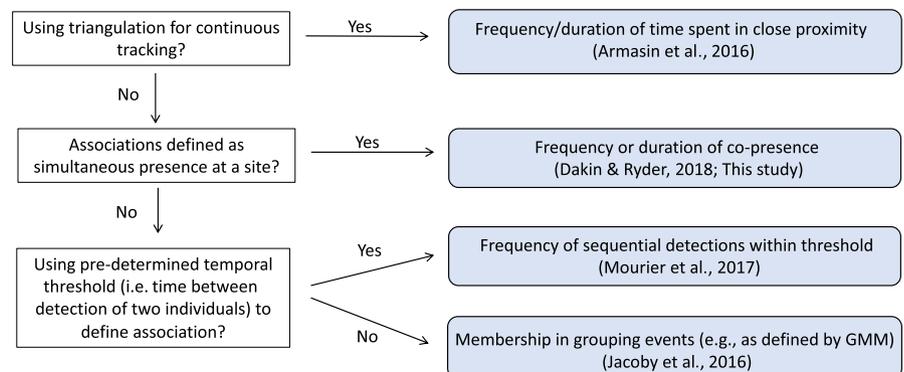


FIGURE 1 Decision tree using currently available methods for quantifying associations from automated telemetry data. GMM, Gaussian mixture modelling

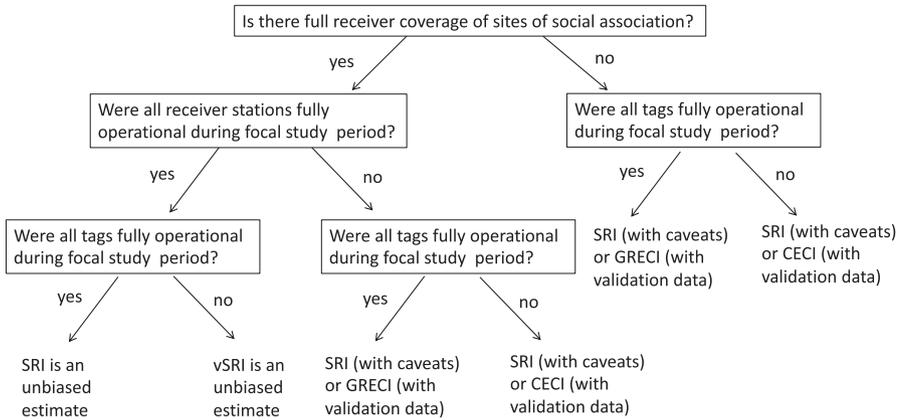


FIGURE 2 Decision tree for selecting association indices when automated telemetry systems are used to detect social associations at sites with receiver stations. The calculation of simple ratio index (SRI: Cairns & Schwager, 1987) is explained in Section 3 case study. The calculation of vSRI, GLECI and CECI is explained in Hoppitt and Farine (2018)

burst rate of individual tags to the duration of the study. Comparing network structure across time can allow researchers to investigate how changes or stability in social partnerships influence the overall dynamics of a social system (Farine, 2018; Hobson et al., 2013). For example, Dakin and Ryder (2018) generated daily time-aggregated networks from automated telemetry data to measure the stability of social partnerships across days. We suggest that automated telemetry systems hold great promise as a method for generating data that can be used to investigate network dynamics. We present how to generate daily social network data from automated telemetry data in our workflow document (Appendix S1; also archived at <https://osf.io/gwb6d/>), and these approaches can be adapted to produce time-aggregated dynamic networks.

Reliable inference about spatial dynamics of social networks from automated telemetry systems fundamentally depends on understanding how receiver stations are placed with respect to the ecology of the study system. For example, Spiegel et al. (2018) used GPS tags to show that male sleepy lizards *Tiliqua rugosa* interact primarily at peripheries of their territories. Thus, whether automated telemetry systems would detect such social dynamics depends on whether territory peripheries are encompassed by the range of receiver stations. The placement of receiver stations needs to also account for the spatial scale of movement of individuals. For example, social networks constructed from data collected at two distant receivers will likely detect different social structures than those constructed from data at two receivers in close proximity because of the variation in movement patterns among individuals. Social dynamics between the same individuals may also differ depending on the spatial context of associations, for example, based on relative distance from territories or among resource patches. Comparisons between social networks generated by automated telemetry at different study sites or with different organisms will be challenging because they must take into account all factors affecting spatial movements between receiver stations in addition to social dynamics. Because the spatial arrangement of the receiver array is so critical to the interpretation of the social networks created from automated telemetry, we suggest that researchers carefully and explicitly document and include the rationale for the placement of receivers in publications.

3 | CASE STUDY: SOCIAL NETWORK OF WITHIN- AND ACROSS-GROUP ASSOCIATIONS IN ACORN WOODPECKERS

Here, we illustrate a workflow for constructing and analysing social networks based on detections of individuals at group-defended territories. We use a subset of data from an ongoing automated telemetry study of social behaviour in a well-studied population of a cooperatively breeding bird, the acorn woodpecker. While these birds live in stable social groups year-round, automated telemetry data have revealed that both breeders and helpers make multiple daily prospecting forays to other territories (Barve, Hagemeyer, et al., 2020). Thus, social associations occur both at home territories and at other territories during forays. We describe how the duration of association at each territory can be converted to a temporal association index to be used in social network analyses. We demonstrate that this approach allows one to parse patterns of association across a variety of social (e.g. within a home territory vs. during extraterritorial forays), and spatial (e.g. at different territories spread over the study area) contexts. A guided workflow with full R codes and the raw data files are archived at <https://osf.io/gwb6d/>.

3.1 | Study species

Social behaviour of acorn woodpeckers has been studied at Hastings Reservation (36.387°N, 121.551°W) in central coastal California, USA since 1968 (Koenig & Mumme, 1987; MacRoberts & MacRoberts, 1976), and social group composition has been tracked since 1974 (Koenig et al., 2016). Acorn woodpeckers live in polygynandrous social groups (mean group size = 4.98: (Barve et al., 2019) with nonbreeding helpers of both sexes (Koenig et al., 2016). Cobreeding males and females are closely related within sex, and mating outside the group or between breeders and helpers is exceptionally rare (Barve et al., 2019; Dickinson et al., 1995).

Acorn woodpeckers are highly reliant on stored acorns for overwinter survival. Thus, territory quality is typically quantified by the size of the 'granary', a specialized storage structure that may consist of thousands of stored acorns (MacRoberts & MacRoberts, 1976).

Because granaries provide survival and reproductive benefits to group members (Koenig et al., 2011), they are zealously guarded and fought over (Barve, Lahey, et al., 2020). Thus, granaries represent an ecologically important resource within defended territories where group members spend a significant portion of time and where social interactions occur frequently (Mumme & de Queiroz, 1985).

Acorn woodpeckers track associations among individuals outside their social groups (Pardo et al., 2018, 2020), and both breeders and helpers make multiple extra-territorial forays almost daily. Foray distance can be over 4 km and individuals may spend several hours, or even days, on forays (Barve, Hagemeyer, et al., 2020). This suggests that the motives behind foray behaviour may go beyond merely finding dispersal opportunities but may also include information-gathering and maintaining social associations with other birds in the extended social 'neighbourhood' (Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020).

3.2 | Automated radiotelemetry system

Individual woodpeckers were caught opportunistically and fitted with dorsally mounted solar-powered nanotags (Figure 3a; Cellular Tracking Technologies) with leg loop harnesses adjusted for body size (Figure 3b). All tags weighed <1% of body mass and all birds tagged were of known sex and status within each social group. Thirty-nine base stations were placed at the centre of active territories, generally near the granary (Figure 3c,d), and four were placed within the centroid of a cluster of territories where territories were <100 m apart. Thus, we tracked woodpeckers at 51 territories using 43 receiver stations. Tags were programmed to produce an encoded 64-bit radio ping every 1.5 s when exposed to

sunlight, even in cloudy weather. Date-time synchrony among the entire array was checked and maintained to within 30 s each week. Here, we use data collected from 58 individuals over a single month, October 2018, as an example for how we can convert these data into social networks.

We collated all detections from all base stations into a single large dataset. Each row in the dataset represented a single detection of a bird at a particular receiver station with its associated date, time and signal strength. An annotated R script for the code associated with collating, cleaning, and manipulating the dataset is provided as a Supplementary File (Appendix S2, also archived at <https://osf.io/gwb6d/>). From the raw data, we retained only those detections where the bird was detected with signal strength equivalent to a distance approximately ≤ 100 m from the receiver station (signal strength criterion based on field trials; Barve, Lahey, et al., 2020), which roughly corresponds to the typical core activity area of a territory (MacRoberts & MacRoberts, 1976). When individuals were detected from multiple receiver stations during the same 'time window' (see Section 3.4, below), we assigned the location to the receiver station that had the strongest signal strength. For individuals from territories that share a receiver station, we assumed that they were on their home territory when they were detected at that receiver.

3.3 | Defining associations

In the context of this study system, we defined social associations as instances where pairs of individuals were simultaneously present within the core area of a group territory. Using long-term data on membership of these cooperative breeding groups, we could further infer different types of associations. Co-presence of 'home group'

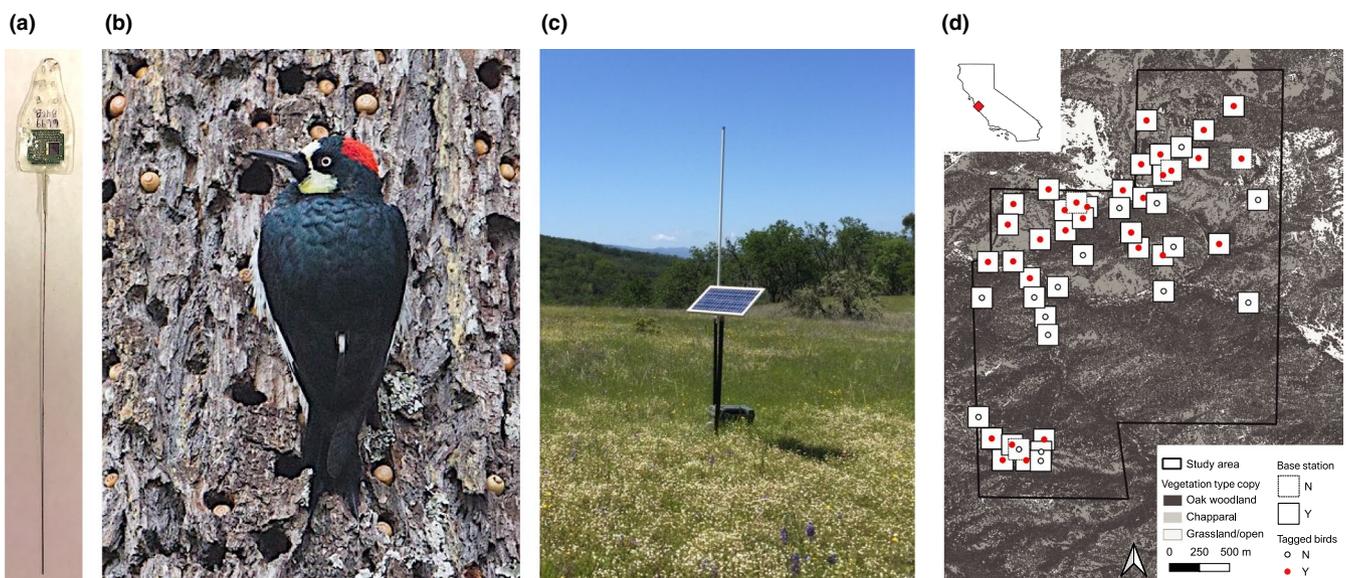


FIGURE 3 Automated radiotelemetry was used to study acorn woodpecker behaviour. Individuals were fitted with solar-powered radio tags (a) mounted dorsally. (b) Autonomous base stations, usually placed near woodpecker granaries, detected all radio-tagged woodpeckers in the vicinity. (c) Base stations were stratified across appropriate habitat within the study area at Hastings Natural History Reservation in Carmel Valley, California. (d) Inset map shows approximate location of the study

members at a base station represented the time group members spent together at their home territory. Co-presence of 'home group' members and 'visitors' may represent opportunities for information exchange about the state of social groups across the landscape (Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020). Co-presence of visitors at a territory may represent shared interest in a territory, or it could potentially represent coalitions of individuals during forays. While the biological significance of patterns of associations during forays has yet to be established, we use these data to demonstrate the potential for partitioning social connections based on their ecological context.

3.4 | Estimating time windows of presence from imperfect detection data

Automated telemetry data represent point detections of the presence of an individual within the predefined detection range. Our goal was to use these point detections to infer 'time windows' of the presence of an individual (Figure 4). In so doing, we needed to account for sources of error in tag detection, such as signal obstructions, signal interference or inconsistent power. Thus, the challenge was to define a threshold such that: (a) detection intervals below this threshold would be considered false negatives (i.e. the individual was present in the territory but not detected) and (b) detection intervals above this threshold would be considered true negatives (i.e. the individual was not in the territory).

To determine a threshold criterion for determining time windows of presence for an individual, we first manually examined subsets of the raw detection data (all individuals over the month of data used here) using accumulation curves of detection intervals. When tags were operating normally, most detection intervals occurred within a few seconds, indicating no or few detections were missed. However, some tags exhibited sustained detection intervals longer than 1.5 s (up to approximately 40 s in the current sample), perhaps due to individual differences in tag responsiveness, insufficient charging and/or low light levels that affected solar gathering ability. We conservatively set the detection interval threshold to 60 s, a threshold which minimizes tag-based variation in this system, and considered lags longer than this to be evidence that an individual had left the territory. Using the 60-s threshold, we converted the raw point detections (Figure 4a) to temporal windows of presence at a given territory (Figure 4b). While these detection criteria may not be appropriate for assessing brief movements such as very short foraging bouts or birds moving around at the boundary of the detection range, we feel it was appropriate for estimating associations between individuals at territories in this system. Other, more statistically rigorous methods for estimating 'residence times' from automated telemetry data exist (e.g. Capello et al., 2015), and these could be adapted to further explore the appropriate thresholds for determining time windows where individuals are continuously present on a territory.

3.5 | Calculating association indices to generate association networks

Using the temporal presence windows (Figure 4b), we first calculated the cumulative duration of overlap, in number of seconds, between every bird dyad at each territory on a given date, resulting in a 'co-presence matrix'. These daily co-presence matrices were stacked for all S receiver stations and all T days of the study to create a four-dimensional array ($N \times N \times S \times T$).

We also calculated the number of seconds during which each pair of individuals were both detected anywhere (i.e. at any receiver station) for each day. The difference between the co-presence matrix and this 'simultaneous detection matrix' was used to calculate the number of seconds during which two individuals were known to be in separate locations (included in the denominator for calculating association indices below). The simultaneous detection matrix was stacked across all T days to generate a three-dimensional array ($N \times N \times T$).

Because we did not have comprehensive coverage of potential sites of social association nor appropriate validation data, we calculated the SRI (Cairns & Schwager, 1987), while acknowledging that there are potential biases in this metric if individuals and groups have different detection probabilities (Figure 2; Hoppitt & Farine, 2018). The index is:

$$\text{SRI} = \frac{x}{x + y_{AB} + y_A + y_B},$$

where x is the number of sampling periods in which the dyad A and B were associated, y_A is the number of sampling periods where A was observed but not B, y_B is the number of sampling periods where B was observed but not A, and y_{AB} is the number of sampling periods where both A and B were observed but not associated. In our case, we use each second as the sampling period, such that x represents the number of seconds that A and B were associated. In our implementation, we calculate SRI using only the set of individuals that were observed at least once per day on average (i.e. 31 times over the month of October 2018). We extracted values of x , y_{AB} , y_A and y_B using the co-presence matrix (summed across territories of interest) and the simultaneous detection matrix. In our workflow document (Appendix S1, also archived at <https://osf.io/gwb6d/>), we also show how one can calculate an alternative index, vSRI (Figure 2; Hoppitt & Farine, 2018), which may be a good estimator of association rate in cases where group detection error is likely to be low. We calculated the association index between every pair of individuals in the population to generate an *adjacency matrix* of the social network.

3.6 | Constructing context-specific social networks

We first constructed a time- and space-aggregated social network using only tagged individuals whose home territory contained a receiver station (Figure 5). Restricting the data to these individuals allowed us to compare the relative rates of associations within

FIGURE 4 Visualization of tag detection data from a given territory as point detections (a) converted to temporal windows of presence (b) at a single territory. The data are illustrated for all individuals (indicated along the y-axis) detected in a single 2-hr period

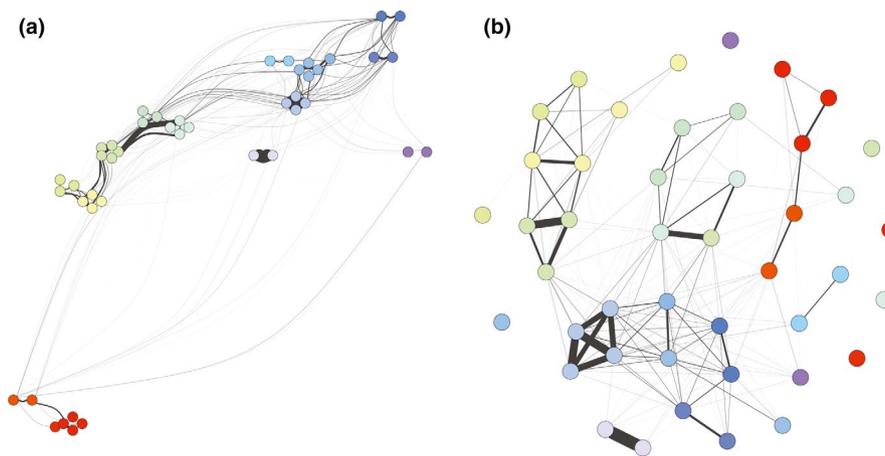
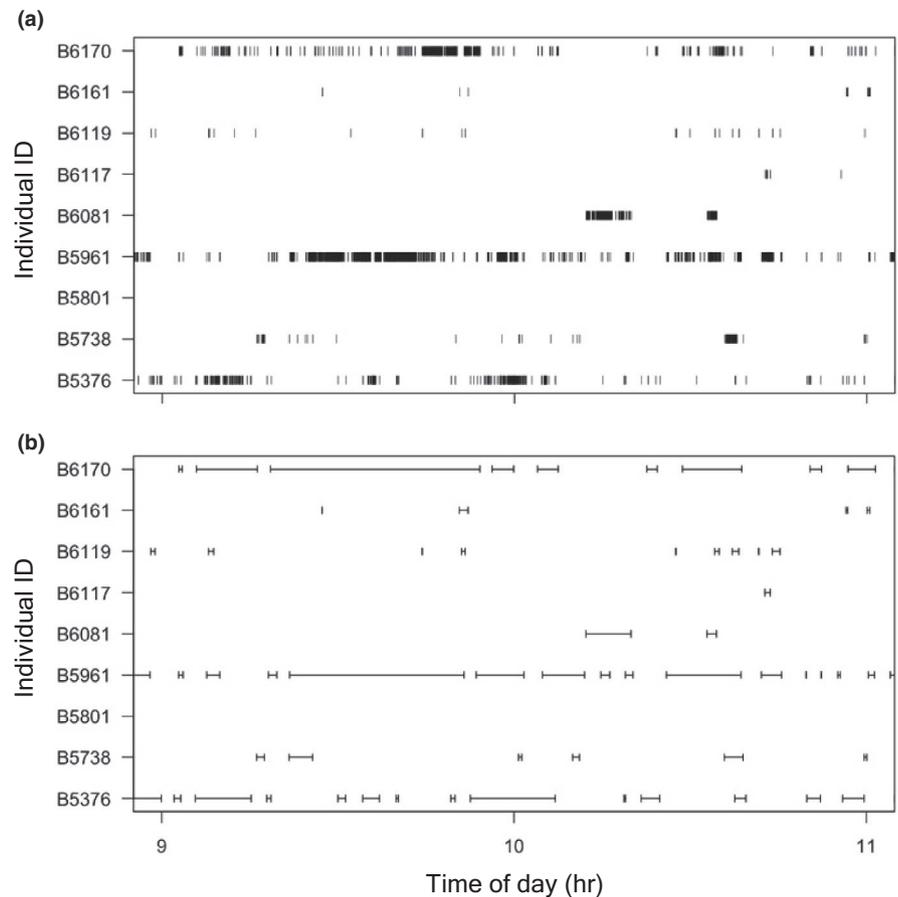


FIGURE 5 An aggregated social network of acorn woodpecker associations in October 2018, displayed using a spatial layout (a) and a force-directed network layout (b). In each figure, each node represents a tagged bird, and the edges connect individuals that were detected at the same territory at the same time. We included only individuals from social groups whose territory contained a receiver station ($N = 44$). Edge widths are proportional to the SRI association index. The node colours reflect distinct social groups, and groups that are spatially adjacent have similar colours. In the spatial layout (a), nodes (individuals) are arranged at their home territory. In the force-directed layout (b), nodes that are more tightly linked together are placed closer together. In this layout, we discarded the lowest 10% of edges based on edge weights for illustration purposes. This layout shows that individuals from the same group or adjacent groups are often linked tightly

and between social groups. This network thus captures both social associations that occur among group members at their territory as well as between members of different social groups during extraterritorial forays. Individuals associated most with members of their social group, a finding consistent with the known behaviour

of acorn woodpeckers which maintain year-round cooperative social groups (Koenig et al., 2016). This was illustrated in two ways, first, mean (\pm SD) edge weight among members of the same social group (0.065 ± 0.15) was greater than mean edge weight among members of different social groups (0.003 ± 0.001). Second, using group

membership as the node attribute and edge weights, we confirmed that there was high assortment by home group (assortment coefficient: $r = 0.574 \pm 0.061$; Farine, 2014), meaning individuals associated more with members of the same group.

We also found many associations occur between groups when individuals engaged in forays to other group territories (Barve, Hagemeyer, et al., 2020). To demonstrate how we can specifically explore the patterns of associations during extra-territorial forays, we constructed a 'co-visitation social network'. We first restricted the data to detections of birds outside their own home territory (i.e. only during forays), then calculated SRI for every pair of individuals. Figure 6a shows the social network of foraging woodpeckers using a spatial layout. Breaking down this network by the receiver station at which social associations are detected reveals that patterns of associations between visiting birds can differ across spatial contexts (here focal territories: Figure 6b–d). This heterogeneity in association patterns at small spatial scales shows that automated telemetry systems may be useful for revealing complex interplay between spatial and social processes in ways that would be obscured in an aggregated network (Mourier et al., 2019). In this example, we have chosen to display the patterns of associations at three adjacent territories, showing that some sites tend to be visited by multiple individuals at the same time (Figure 6b,c), others are rarely visited by multiple individuals at the same time (Figure 6d), despite all three sites being within close proximity of each other. These patterns may be related

to various ecological factors that affect the patterns of extraterritorial forays by woodpeckers (Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020).

4 | CONCLUSION AND FUTURE PROSPECTS

We expect that automated telemetry systems will be increasingly used in combination with social network analyses to study social dynamics in animal systems. There will certainly be further advances in approaches for constructing social networks that harness the breadth and depth of information that can be mined from automated telemetry data. However, we suggest that several features of automated telemetry systems will be universally important to consider whenever the data are used for social network analysis.

First, no amount of data can be substituted for natural history knowledge, and better understanding of the ecology of the study system will always lead to clearer inference from the patterns gleaned from automated radiotelemetry. Receivers should be placed with the ecology of the species and its habitat use in mind, as it will be central to making correct interpretations about the nature of social behaviour of focal individuals. For example, in the acorn woodpecker study, our long-term data on cooperatively breeding groups allowed us to (i) position receiver stations to detect associations at

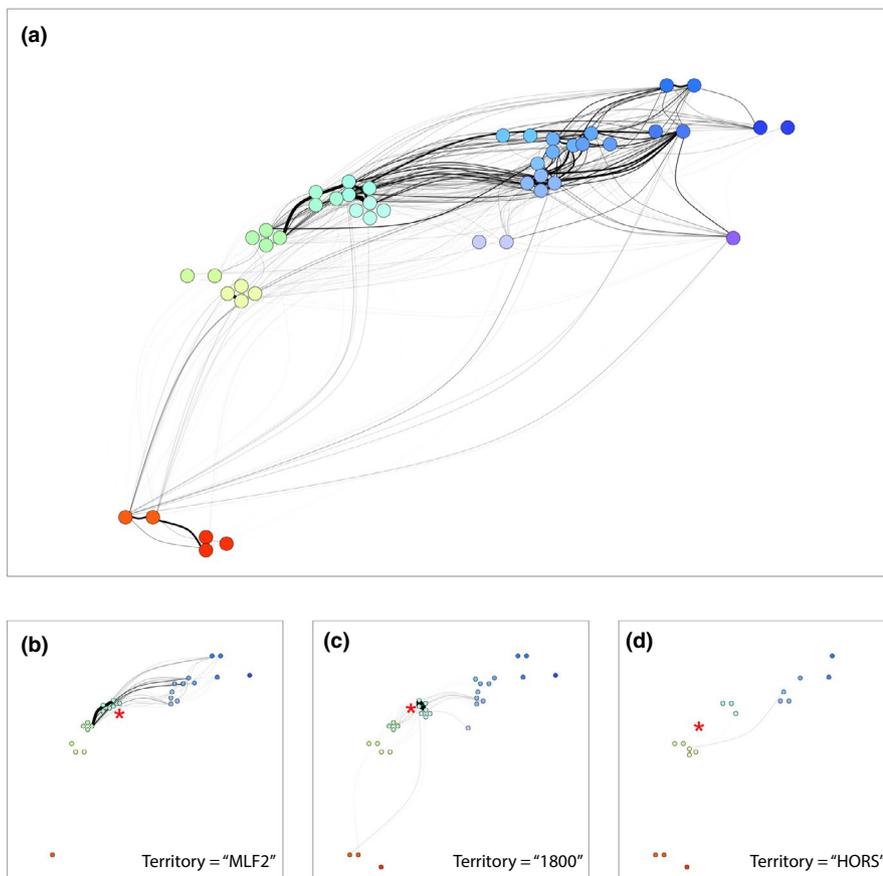


FIGURE 6 The 'co-visitation social network' shows patterns of associations between individuals during extraterritorial forays. The node colours reflect home social groups, and groups that are spatially adjacent have similar colours. The total aggregated network for October 2018 (a). Three different site-specific networks (i.e. associations between visitors at a particular territory) at three different territories reveal that these connections arise heterogeneously across the landscape (b–d). In (b–d), each network includes all individuals that visited a particular territory (indicated in red asterisk)

core areas within territories associated with high-value resources (i.e. granaries), and (ii) understand patterns of associations in the context of 'home group members' and 'visitors'.

Second, researchers should consider the unique features of automated telemetry systems to evaluate which association indices may be most appropriate for their questions of interest. For example, automated receiver arrays have the potential to locate all groups (e.g. if the array has complete coverage of sites of association and all receivers are fully functional), which may allow one to use vSRI as an unbiased estimator of association rate, even when individual tags are incompletely sampled (Hoppitt & Farine, 2018). Further considerations for the design of automated systems may help improve how capture patterns of association of free-living animals are determined.

Finally, we currently lack a formal statistical procedure to account for stochastic and spatial processes that could influence inferences related to network patterns. There are now well-established null model approaches for accounting for such spurious effects in group observations (Farine, 2017; Farine & Whitehead, 2015) and GPS tracking data (Spiegel et al., 2016). Automated detection of individuals at receiver stations present a different data structure that will require further innovations in statistical methods for social network analyses. Moreover, the appropriate statistical methods will depend on the particular question at hand as well as the ecology of the study system and prior information. For example, detecting non-random patterns in associations during extraterritorial visits will need to account for spatial movement patterns during forays, while patterns of associations at home territories may require accounting for differences in foraging behaviour or territorial behaviour among individuals. Formalizing methods for construction of social networks from these data is only the first step to understanding the processes that may generate non-random patterns in sociality using these data.

There are myriad opportunities for additional application of automated telemetry systems for studying animal social networks. The case study presented here is only the first step towards a general workflow that could be applied to multiple biological systems. Further development of such workflows will allow researchers to harness the data-logging revolution that is occurring within the field of animal behaviour and continue to uncover hidden aspects of animal sociality at unprecedented scale and resolution.

ACKNOWLEDGEMENTS

We thank all of our colleagues and 162 field assistants who have assisted with the acorn woodpecker project since its inception, and Hastings Natural History Reservation for logistical support. We especially thank Natasha Hagemeyer, Russell Winter, and the many field assistants who participated in data collection over the 2 years spanning the data shown here (2017–2019). We also thank Rich Gabrielson, Vince Voegeli, and David Winkler for help with development of the radiotelemetry system, and Walt Koenig for logistical support (NSF IOS-1455881) and comments on the manuscript. This study was conducted under the auspices of the Animal Care and Use Committees of the University of California, Berkeley

(protocol R010–0412), Cornell University (protocol 2008–0185) and Old Dominion University (protocol 12–001). D.S. and A.E.J. were supported by National Science Foundation IOS-1750606, S.B. and E.L.W. by NSF IOS-1455900.

CONFLICTS OF INTEREST

None of the authors have any conflict of interest to declare.

AUTHOR'S CONTRIBUTIONS

S.B. and E.L.W. obtained funding, managed data collection, including setup of the automated radiotelemetry system; D.S., S.B. and A.E.J. developed the workflow, and performed the network analyses; D.S. wrote the first draft and D.S., S.B., A.E.J. and E.L.W. edited the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/2041-210X.13737>.

DATA AVAILABILITY STATEMENT

The raw data, R script for collating the raw data and a workflow document with complete R scripts and additional analyses are archived at OSF (<https://osf.io/gwb6d/>).

ORCID

Daizaburo Shizuka  <https://orcid.org/0000-0002-0478-6309>

Sahas Barve  <https://orcid.org/0000-0001-5840-8023>

Allison E. Johnson  <https://orcid.org/0000-0002-6447-3179>

Eric L. Walters  <https://orcid.org/0000-0002-9414-5758>

REFERENCES

- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, *518*(7540), 538–541. <https://doi.org/10.1038/nature13998>
- Armansin, N. C., Lee, K. A., Huvneers, C., & Harcourt, R. G. (2016). Integrating social network analysis and fine-scale positioning to characterize the associations of a benthic shark. *Animal Behaviour*, *115*, 245–258. <https://doi.org/10.1016/j.anbehav.2016.02.014>
- Barve, S., Hagemeyer, N. D. G., Winter, R. E., Chamberlain, S. D., Koenig, W. D., Winkler, D. W., & Walters, E. L. (2020). Wandering woodpeckers: Foray behavior in a social bird. *Ecology*, *101*(2), e02943. <https://doi.org/10.1002/ecs.2943>
- Barve, S., Koenig, W. D., Haydock, J., & Walters, E. L. (2019). Habitat saturation results in joint-nesting female coalitions in a social bird. *The American Naturalist*, *193*(6), 830–840. <https://doi.org/10.1086/703188>
- Barve, S., Lahey, A. S., Brunner, R. M., Koenig, W. D., & Walters, E. L. (2020). Tracking the warriors and spectators of acorn woodpecker wars. *Current Biology*, *30*(17), R982–R983. <https://doi.org/10.1016/j.cub.2020.07.073>
- Blonder, B., Wey, T. W., Dornhaus, A., James, R., & Sih, A. (2012). Temporal dynamics and network analysis. *Methods in Ecology and Evolution*, *3*(6), 958–972. <https://doi.org/10.1111/j.2041-210X.2012.00236.x>
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, *35*(5), 1454–1469. [https://doi.org/10.1016/S0003-3472\(87\)80018-0](https://doi.org/10.1016/S0003-3472(87)80018-0)

- Cantor, M., Maldonado-Chaparro, A. A., Beck, K. B., Brandl, H. B., Carter, G. G., He, P., Hillemann, F., Klarevas-Irby, J. A., Ogino, M., Papageorgiou, D., Prox, L., & Farine, D. R. (2021). The importance of individual-to-society feedbacks in animal ecology and evolution. *Journal of Animal Ecology*, 90(1), 27–44. <https://doi.org/10.1111/1365-2656.13336>
- Cantor, M., Wedekin, L. L., Guimarães, P. R., Daura-Jorge, F. G., Rossi-Santos, M. R., & Simões-Lopes, P. C. (2012). Disentangling social networks from spatiotemporal dynamics: The temporal structure of a dolphin society. *Animal Behaviour*, 84(3), 641–651. <https://doi.org/10.1016/j.anbehav.2012.06.019>
- Capello, M., Robert, M., Soria, M., Potin, G., Itano, D., Holland, K., Deneubourg, J. L., & Dagorn, L. (2015). A methodological framework to estimate the site fidelity of tagged animals using passive acoustic telemetry. *PLoS One*, 10(8), e0134002. <https://doi.org/10.1371/journal.pone.0134002>
- Dakin, R., & Ryder, T. B. (2018). Dynamic network partnerships and social contagion drive cooperation. *Proceedings of the Royal Society B: Biological Sciences*, 285, 8.
- Dakin, R., & Ryder, T. B. (2020). Reciprocity and behavioral heterogeneity govern the stability of social networks. *Proceedings of the National Academy of Sciences of the United States of America*, 117(6), 2993–2999. <https://doi.org/10.1073/pnas.1913284117>
- Dickinson, J., Haydock, J., Koenig, W., Stanback, M., & Pitelka, F. (1995). Genetic monogamy in single-male groups of acorn woodpeckers, *Melanerpes formicivorus*. *Molecular Ecology*, 4(6), 765–770. <https://doi.org/10.1111/j.1365-294X.1995.tb00277.x>
- Farine, D. R. (2014). Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. *Animal Behaviour*, 89, 141–153. <https://doi.org/10.1016/j.anbehav.2014.01.001>
- Farine, D. R. (2017). A guide to null models for animal social network analysis. *Methods in Ecology and Evolution*, 8(10), 1309–1320. <https://doi.org/10.1111/2041-210X.12772>
- Farine, D. R. (2018). When to choose dynamic vs. Static social network analysis. *Journal of Animal Ecology*, 87(1), 128–138. <https://doi.org/10.1111/1365-2656.12764>
- Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology*, 84(5), 1144–1163. <https://doi.org/10.1111/1365-2656.12418>
- Ferreira, A. C., Covas, R., Silva, L. R., Esteves, S. C., Duarte, I. F., Fortuna, R., Theron, F., Doutrelant, C., & Farine, D. R. (2020). How to make methodological decisions when inferring social networks. *Ecology and Evolution*, 10(17), 9132–9143. <https://doi.org/10.1002/ece3.6568>
- Haddadi, H., King, A. J., Wills, A. P., Fay, D., Lowe, J., Morton, A. J., Hailes, S., & Wilson, A. M. (2011). Determining association networks in social animals: Choosing spatial-temporal criteria and sampling rates. *Behavioral Ecology and Sociobiology*, 65(8), 1659–1668. <https://doi.org/10.1007/s00265-011-1193-3>
- He, P., Maldonado-Chaparro, A. A., & Farine, D. R. (2019). The role of habitat configuration in shaping social structure: A gap in studies of animal social complexity. *Behavioral Ecology and Sociobiology*, 73(1), 9. <https://doi.org/10.1007/s00265-018-2602-7>
- Hobson, E. A., Avery, M. L., & Wright, T. F. (2013). An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. *Animal Behaviour*, 85(1), 83–96. <https://doi.org/10.1016/j.anbehav.2012.10.010>
- Hoppitt, W. J. E., & Farine, D. R. (2018). Association indices for quantifying social relationships: How to deal with missing observations of individuals or groups. *Animal Behaviour*, 136, 227–238. <https://doi.org/10.1016/j.anbehav.2017.08.029>
- Jacoby, D. M. P., Papastamatiou, Y. P., & Freeman, R. (2016). Inferring animal social networks and leadership: Applications for passive monitoring arrays. *Journal of The Royal Society Interface*, 13(124), 20160676. <https://doi.org/10.1098/rsif.2016.0676>
- Kays, R., Tilak, S., Crofoot, M., Fountain, T., Obando, D., Ortega, A., Kuemmeth, F., Mandel, J., Swenson, G., Lambert, T., Hirsch, B., & Wikelski, M. (2011). Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. *The Computer Journal*, 54(12), 1931–1948. <https://doi.org/10.1093/comjnl/bxr072>
- Koenig, W. D., & Mumme, R. L. (1987). *Population ecology of the cooperatively breeding acorn woodpecker*. Princeton University Press.
- Koenig, W. D., Walters, E. L., & Haydock, J. (2011). Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the acorn woodpecker. *The American Naturalist*, 178(2), 145–158. <https://doi.org/10.1086/660832>
- Koenig, W. D., Walters, E. L., & Haydock, J. (2016). Acorn woodpeckers: Helping at the nest, polygynyandry, and dependence on a variable acorn crop. In W. D. Koenig & J. L. Dickinson (Eds.), *Cooperative breeding in vertebrates* (pp. 217–236). Cambridge University Press. <https://doi.org/10.1017/CBO9781107338357.014>
- Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S., & Rutz, C. (2013). Reality mining of animal social systems. *Trends in Ecology & Evolution*, 28(9), 541–551. <https://doi.org/10.1016/j.tree.2013.06.002>
- MacRoberts, M. H., & MacRoberts, B. R. (1976). Social organization and behavior of the acorn woodpecker in Central Coastal California. *Ornithological Monographs*, 21, iii–115. <https://doi.org/10.2307/40166738>
- Mourier, J., Bass, N. C., Guttridge, T. L., Day, J., & Brown, C. (2017). Does detection range matter for inferring social networks in a benthic shark using acoustic telemetry? *Royal Society Open Science*, 4(9). <https://doi.org/10.1098/rsos.170485>
- Mourier, J., Lédée, E. J. I., & Jacoby, D. M. P. (2019). A multilayer perspective for inferring spatial and social functioning in animal movement networks [Preprint]. *Animal Behavior and Cognition*. <https://doi.org/10.1101/749085>
- Mumme, R. L., & De Queiroz, A. (1985). Individual contributions to cooperative behaviour in the acorn woodpecker: Effects of reproductive status, sex, and group size. *Behaviour*, 95(3–4), 290–312. <https://doi.org/10.1163/156853985X00163>
- Pardo, M. A., Hayes, C. E., Walters, E. L., & Koenig, W. D. (2020). Acorn woodpeckers vocally discriminate current and former group members from nongroup members. *Behavioral Ecology*, 31(5), 1120–1128. <https://doi.org/10.1093/beheco/araa059>
- Pardo, M. A., Sparks, E. A., Kuray, T. S., Hagemeyer, N. D., Walters, E. L., & Koenig, W. D. (2018). Wild acorn woodpeckers recognize associations between individuals in other groups. *Proceedings of the Royal Society B: Biological Sciences*, 285(1882), 20181017. <https://doi.org/10.1098/rspb.2018.1017>
- Pinter-Wollman, N., Fiore, S. M., & Theraulaz, G. (2017). The impact of architecture on collective behaviour. *Nature Ecology & Evolution*, 1(5), 1–2. <https://doi.org/10.1038/s41559-017-0111>
- Pinter-Wollman, N., Hobson, E. A., Smith, J. E., Edelman, A. J., Shizuka, D., de Silva, S., Waters, J. S., Prager, S. D., Sasaki, T., Wittemyer, G., Fewell, J., & McDonald, D. B. (2014). The dynamics of animal social networks: Analytical, conceptual, and theoretical advances. *Behavioral Ecology*, 25(2), 242–255. <https://doi.org/10.1093/beheco/art047>
- Psorakis, I., Roberts, S. J., Rezek, I., & Sheldon, B. C. (2012). Inferring social network structure in ecological systems from spatio-temporal data streams. *Journal of the Royal Society Interface*, 9(76), 3055–3066. <https://doi.org/10.1098/rsif.2012.0223>
- Ripperger, S. P., Carter, G. G., Page, R. A., Duda, N., Koelpin, A., Weigel, R., Hartmann, M., Nowak, T., Thielecke, J., Schadhauer, M., Robert, J., Herbst, S., Meyer-Wegener, K., Wägemann, P., Schröder-Preikschat, W., Cassens, B., Kapitza, R., Dressler, F., & Mayer, F. (2020). Thinking small: Next-generation sensor networks close the size gap in vertebrate biologging. *PLOS Biology*, 18(4), e3000655. <https://doi.org/10.1371/journal.pbio.3000655>

- Ryder, T. B., Horton, B. M., van den Tillaart, M., Morales, J. D. D., & Moore, I. T. (2012). Proximity data-loggers increase the quantity and quality of social network data. *Biology Letters*, 8(6), 917–920. <https://doi.org/10.1098/rsbl.2012.0536>
- Shizuka, D., & Johnson, A. E. (2020). How demographic processes shape animal social networks. *Behavioral Ecology*, 31(1), 1–11. <https://doi.org/10.1093/beheco/arz083>
- Smith, J. E., & Pinter-Wollman, N. (2021). Observing the unwatchable: Integrating automated sensing, naturalistic observations and animal social network analysis in the age of big data. *Journal of Animal Ecology*, 90(1), 62–75. <https://doi.org/10.1111/1365-2656.13362>
- Spiegel, O., Leu, S. T., Bull, C. M., & Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, 20(1), 3–18. <https://doi.org/10.1111/ele.12708>
- Spiegel, O., Leu, S. T., Sih, A., & Bull, C. M. (2016). Socially interacting or in-different neighbours? Randomization of movement paths to tease apart social preference and spatial constraints. *Methods in Ecology and Evolution*, 7(8), 971–979. <https://doi.org/10.1111/2041-210X.12553>
- Spiegel, O., Sih, A., Leu, S. T., & Bull, C. M. (2018). Where should we meet? Mapping social network interactions of sleepy lizards shows sex-dependent social network structure. *Animal Behaviour*, 136, 207–215. <https://doi.org/10.1016/j.anbehav.2017.11.001>
- St Clair, J. J. H., Burns, Z. T., Bettaney, E. M., Morrissey, M. B., Otis, B., Ryder, T. B., Fleischer, R. C., James, R., & Rutz, C. (2015). Experimental resource pulses influence social-network dynamics and the potential for information flow in tool-using crows. *Nature Communications*, 6(1), 7197. <https://doi.org/10.1038/ncomms8197>
- Taylor, P. D., Crewe, T. L., Mackenzie, S. A., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C. M., Guglielmo, C. G., Hamilton, D. J., Holberton, R. L., Loring, P. H., Mitchell, G. W., Norris, D. R., Paquet, J., Ronconi, R. A., Smetzer, J. R., Smith, P. A., Welch, L. J., & Woodworth, B. K. (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology*, 12(1), art8. <https://doi.org/10.5751/ACE-00953-120108>
- Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y., & Nathan, R. (2020). Cognitive map-based navigation in wild bats revealed by a new high-throughput tracking system. *Science*, 369(6500), 188–193. <https://doi.org/10.1126/science.aax6904>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Shizuka, D., Barve, S., Johnson, A. E., & Walters, E. L. (2022). Constructing social networks from automated telemetry data: A worked example using within- and across-group associations in cooperatively breeding birds. *Methods in Ecology and Evolution*, 13, 133–143. <https://doi.org/10.1111/2041-210X.13737>