1 **Workflow for constructing social networks from automated telemetry systems**

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9 **Running headline:** Creating social networks from automated telemetry

Abstract:

1. Advances in datalogging technologies have provided a way to monitor the movement of individual animals at unprecedented spatial and temporal scales, both large and small. When used in conjunction with social network analyses, these data can provide insight into fine scale associative behaviors. The variety of technologies demand continuous progress in workflows to translate data streams from automated systems to social networks, based on biologically relevant metrics.

2. Here we present a workflow for generating flexible association matrices from automated radio-telemetry data that can be parsed into both spatial and temporal dimensions. These can then be used to generate and compare social networks across space and time.

3. We illustrate this workflow using data collected from an automated telemetry study of acorn woodpeckers (*Melanerpes formicivorus*), a cooperatively breeding bird. The data were collected continuously over two years at base stations placed within social group territories. We use this system to demonstrate how this flexible data structure can be used to answer a number of biological questions, specifically 1) how assortative are social associations at the population scale, 2) how do association patterns among territory visitors vary across territories, 3) and how does seasonality affect assortative affiliation within groups?

4. This flexible method allows one to generate social networks that can be used to ask a variety of biological questions pertinent to a wide range of animal systems, exploiting the investigative power that can be gained by using automated radio-telemetry in conjunction with social network analyses.

Introduction:

Social organization, the patterns of associations among individuals in a population, has important effects on individual fitness (Wolf, Brodie III, & Moore, 1999; Kappeler, 2019; Snyder-Mackler et al. 2020). A major challenge in the study of social organization has been the logistics of collecting data on social interactions and associations *in situ*. Rapid advances in automated datalogging technology, however, have recently ushered in an age of "reality mining" of animal sociality (Krause et al., 2013) with exponential decreases in the size of animal tracking devices. These 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.

Concomitant with technological advancements, the application of social network analyses to animal social behavior has progressed rapidly. Such approaches are now routinely used to quantify and analyze patterns and dynamics of social associations across space and time (Pinter-Wollman et al., 2014; Farine & Whitehead, 2015). The integration of automated datalogging with more advanced approaches to social network analyses has led to key discoveries 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 fine-scale dynamics in social contagion of cooperation (Dakin & Ryder, 2018). Critical to these advances in our understanding of social dynamics in nature is the ability to flexibly slice and combine data on social associations and interactions collected at different sites across time.

Because different technologies collect a variety of information, there is no one-size-fits-all method for converting empirical data into social networks (Smith & Pinter-Wollman *In*

58   *Press*). Types of automated datalogging systems that have been used to build social networks of

59   free-living animals include: (1) geographic positioning system tags (Sih et al., 2018), (2)

60   proximity loggers (St. Clair et al., 2015), (3) radio frequency identification (RFID) tags (Aplin et

61   al., 2015), and (4) automated telemetry systems (Dakin & Ryder 2018, 2020). Methodological

62   standards for inferring social networks from data have been established for some methods such

63   as RFID (Psorakis et al., 2015) but not others. Here, we focus on the methodological challenges

64   associated with automated telemetry systems and their use in social network analyses.

65   Automated telemetry systems typically use tags that emit coded identifiers in parallel

66   with receivers that record signals from multiple individuals simultaneously (Pegan et al., 2018).

67   These tags are lightweight and have relatively long battery life, particularly when they integrate

68   solar charging capacity. Such automated telemetry systems usually scan multiple individuals

69   within short temporal spans (e.g., seconds) from fixed receivers, often referred to as "base

70   stations", that monitor tags over the landscape using either directional or omni-directional

71   antennas. Automated telemetry typically generates large volumes of data based on proximity of

72   individuals to base stations, thus significantly expanding the number of individuals that can be

73   tracked, spatial extent of monitoring, and duration of data collection. Such automated telemetry

74   systems have wide applications for monitoring vagile organisms, particularly for environments

75   and contexts where direct observation is difficult (e.g., in marine environments [Finn et al.,

76   2014], migratory species [Lefevre & Smith, 2020; Baldwin, Leap, Finn, & Smetzer, 2018; Bird

77   Studies Canada, 2019], and for territorial organisms that live in spatially large and socially

78   complex systems with substantial intra-day movement (Aplin et al., 2015; Barve et al., 2020a).

79   Tags differ in their signal attenuation, and in some cases, strength of signal can be used to infer

80   spatial proximity to detection stations (Barve, Lahey, Brunner, Koenig, & Walters, 2020b).

81   While automated telemetry systems have great potential for the study of social networks

82   in free-living animals, the ability to infer social patterns depends on key factors such as spatial

83   proximity, tag detection distance (Mourier, Bass, Guttridge, Day, & Brown, 2017), and,

84   critically, the spatial arrangement of base stations with respect to ecologically relevant features in

85   the landscape. Moreover, an ideal workflow would facilitate flexible downstream analyses to

86   examine complex spatial and temporal social dynamics. Here, we develop and implement a

87   method for generating a flexible data structure from which one can construct and analyze social

88   network dynamics based on detections of individuals at group-defended home territories. We

89   describe how data on the duration of association at a particular territory can be converted to a

90   temporal association index to be used in social network analyses. We use data from a 2-year

91   automated telemetry study of social associations in a well-studied population of a cooperatively

92   breeding bird, the acorn woodpecker (*Melanerpes formicivorus*). While these birds live in stable

93   cooperatively breeding groups year-round, both breeders and helpers make multiple daily

94   prospecting forays to other territories (Barve et al. 2020a), and thus social associations occur

95   both at home territories and during forays. We demonstrate that this approach allows one to parse

96   out patterns of association across a variety of social (e.g., within a home territory vs. prospecting

97   for breeding vacancies), temporal (e.g., across days or seasons), and spatial (e.g., at different

98   territories spread over the study area) contexts. Using this approach, we provide proof-of-concept

99   analyses that consider these contexts in network structure.

100

101   *Study System*

102   Social behavior of acorn woodpeckers has been studied at Hastings Reservation (36.387° N,

103   121.551° W) in central coastal California, USA since 1968 (MacRoberts & MacRoberts, 1976;

104   Koenig & Mumme, 1987). Based on previous genetic work (Dickinson et al. 1995; Barve et al.

105   2019), adults on their natal territory with their social / genetic parents are considered

106   nonbreeding helpers, whereas group members living outside their natal territories, or living with

107   non-related birds of the opposite sex, are considered putative breeders (Koenig, Haydock &

108   Stanback, 1998). Since 1973, the majority of the woodpecker population has been color-banded

109   ($N = 6,404$) and censused bimonthly to determine group composition (Koenig, Walters, &

110   Haydock, 2016).

111   Acorn woodpeckers live in polygynandrous social groups with nonbreeding helpers of

112   both sexes (Koenig et al., 2016). Cobreeding males and females are closely related within sex,

113   and mating outside the group or between breeders and helpers is exceptionally rare (Dickinson,

114   Haydock, Koenig, Stanback, & Pitelka, 1995; Barve et al., 2019b). Helpers can become breeders

115   by inheriting their natal territories after the death or disappearance of all opposite sex social

116   parents, by dispersing to a territory with a breeding vacancy, or by dispersing and founding a

117   new territory (Koenig, Hooge, Stanback, & Haydock, 2000). Females are the dispersive sex,

118   dispersing farther than males (Koenig, Van Vuren, & Hooge, 1996); males are more likely to

119   inherit natal territories than are females, and they remain philopatric for longer than females

120   (Koenig, Haydock, & Stanback, 1998).

121   Acorn woodpeckers are highly reliant on stored acorns for overwinter survival, and thus

122   territory quality is typically quantified by the size of the "granary", a specialized acorn-storage

123   structure that may consist of thousands of individual holes in which acorns are placed (Koenig,

124   Walters, Stacey, Stanback, & Mumme, 2020). Acorns are stored in the autumn, mostly harvested

125   from trees within a 150-m radius around the granary (Koenig, McEntee, & Walters, 2008).

126   Because granaries provide survival and reproductive benefits to group members (Koenig,

127   Walters, & Haydock, 2011), they are zealously guarded and fought over (Barve et al., 2020b).

128   Granaries thus represent an ecologically important resource within defended territories where

129   group members often spend a significant portion of time and where social interactions are most

130   likely to occur (Mumme & de Queiroz 1985). The acorn woodpecker breeding season for the

131   Hastings population is primarily from April to July but may extend into early November in years

132   with warm summers and large acorn crops (Koenig et al., 2020).

133   Acorn woodpeckers track associations between individuals outside their social groups

134   (Pardo et al., 2018; Pardo, Hayes, Walters, & Koenig, 2020), and both breeders and helpers make

135   multiple extra-territorial forays almost daily. Foray distance can be over 4 km and individuals

136   may spend several hours, or even days, on forays (Barve et al., 2020a). This suggests that the

137   motives behind foray behavior may go beyond merely finding dispersal opportunities but may

138   also include information-gathering and maintaining social associations with other birds in the

139   extended social "neighborhood" (Barve et al., 2020a).

140

141   **Materials and Methods:**

142   *Automated radio-telemetry system*

143   A total of 132 acorn woodpeckers were caught opportunistically and fitted with dorsally

144   mounted solar-powered nanotags (Fig. 1a; Pegan et al., 2018) with leg loop harnesses adjusted

145   for body size (Fig. 1b; Rappole & Tipton, 1991). All tags weighed less than 1% of body mass

146   and all birds tagged were of known sex and status within each social group. Thirty nine base

147   stations (Fig. 1c, d) were placed at the center of active territories, generally near the granary.

148   While four were placed within the centroid of a cluster of territories where territories were < 100

149   m apart. Thus, we tracked woodpeckers at 51 territories using 43 base stations. Tags were

150 programmed to produce an encoded 64-bit radio ping every 1.5 sec when exposed to sunlight,

151 even in cloudy weather. Here, we use data collected at base stations between July 1, 2017 and

152 March 19, 2019.

153
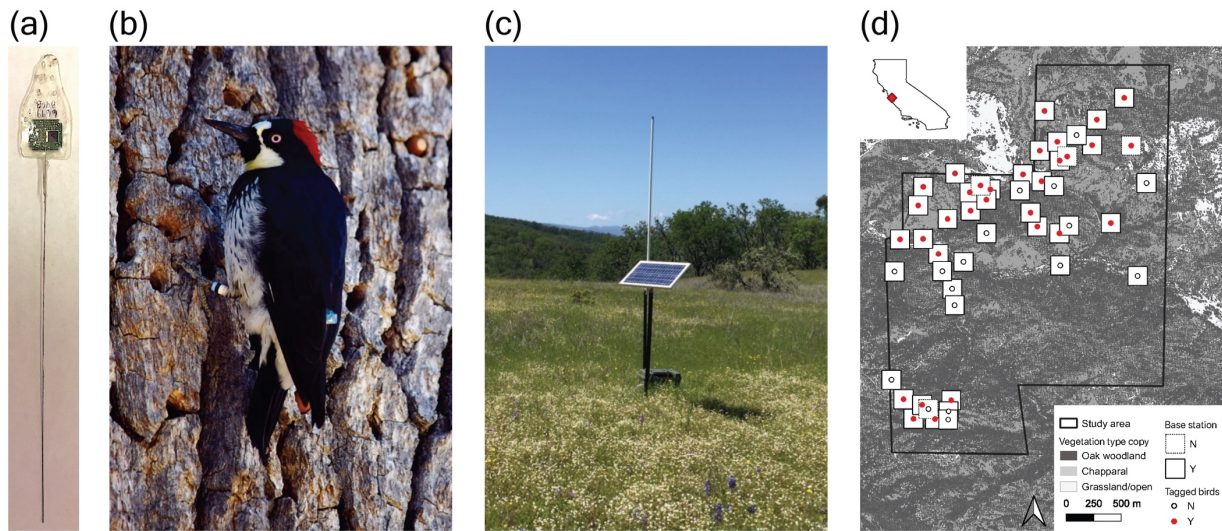
Figure 1: Automated radio-telemetry was used to study acorn woodpecker behavior. Individuals were fitted with solar-powered radio tags (a) mounted dorsally (b). Autonomous base stations, usually placed near woodpecker granaries, detected all radio-tagged woodpeckers in the vicinity (c). Base stations 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 area in California.

154 *Raw telemetry data collection, collation, and cleaning*

155 Raw data from each base station were stored in removable memory drives as data files (.txt

156 format). Base stations were programmed to create a data file at every 15-min interval irrespective

157 of detection of tagged birds. Each data file included all detections of tagged birds within the

158 interval, along with the signal strength of each detection. Thus, for each day, the number of data

159 files created by each base station varied relative to day length. Data from each base station were

160 retrieved approximately every 7 days. Date-time synchrony among the entire array was checked

161   and maintained to within 30 sec each week. This system, thus, allowed for the simultaneous and

162   continuous tracking of all tagged birds during daylight hours.

163   *Collating raw data files for analysis*

164   We used the R (R Core Team, 2020) package *tidyverse* (Wickham, 2017) to collate all detections

165   from all base stations into a single large dataset (.csv). Each row in the dataset represented a

166   single detection of a bird at a particular base station with its associated date, time, and high

167   signal-strength stamp. This dataset was then manipulated to retain only those detections where

168   the bird was detected with sufficient signal strength (equivalent to a distance $\leq$ 100 m from the

169   base station, N=3116947 detections). This signal strength threshold determined with high

170   certainty that an individual was closer to that particular base station than any other in the array

171   (Barve et al., 2020b). Other demographic attributes such as sex and social status of each

172   individual were also coded within the dataset for each detection. We provide an annotated R

173   script (Supplementary Material S2) for the code associated with collating, cleaning, and

174   manipulating the dataset.

175

176   *Converting point detections to time windows of presence*

177   The first hurdle to converting raw detection data to social association networks is to establish a

178   criterion for inferring when any given individual is present within an ecologically relevant space

179   where associations may occur. If tag detections were perfect, this would entail finding start and

180   end times of each temporal window during which tags were detected, based on signal interval

181   (i.e. the tag ping interval). Field conditions, however, introduce several sources of error in tag

182   detection, such as signal obstructions, signal interference, or changes in ping rates because of

183   inconsistent power issues (especially for solar powered tags that may not be exposed to the sun).

184   Thus, the challenge is to define a threshold such that: (a) detection intervals (i.e., time interval

185   between pings) below this threshold are considered false negatives (i.e., the individual was

186   present in the territory but not detected) and (b) detection intervals above this threshold are

187   considered true negatives (i.e., the individual was not in the territory). This threshold should be

188   set based on the specification of the tags, known sources of detection error, the biology of the

189   species being tracked, and the study question at hand.

190   To determine the threshold criterion for our study, we first manually examined subsets of

191   the raw detection data using accumulation curves of detection intervals (see Supplemental

192   Methods). When tags were operating normally, most detection intervals occurred within a few

193   seconds, indicating no or few detections were missed. However, some tags exhibited periods

194   during which pings were detected at regular intervals longer than 1.5 sec, suggesting power

195   issues, perhaps due to insufficient charging and / or low light levels that affected solar gathering

196   ability. These delays in detection intervals never exceeded 40 sec. We conservatively set the

197   detection interval threshold to 60 sec and considered lags longer than this to be evidence that an

198   individual left the territory (see Supplemental Methods). In other words, we inferred presence

199   whenever a tag was detected within 60 sec at a signal strength indicating the bird was within the

200   100 m detection range. Conversely, if a detection interval was > 60 sec, we concluded that the

201   bird was outside of the 100-m detection range during that time. With this criterion, there is a

202   possibility that some short-distance movements away from the territory that lasted under 60 sec,

203   such as a short foraging bout, were missed. Thus, while these detection criteria may not be

204   appropriate for assessing such brief movements, we feel it is appropriate for estimating

205   association between individuals at territories within the acorn woodpecker system. For other

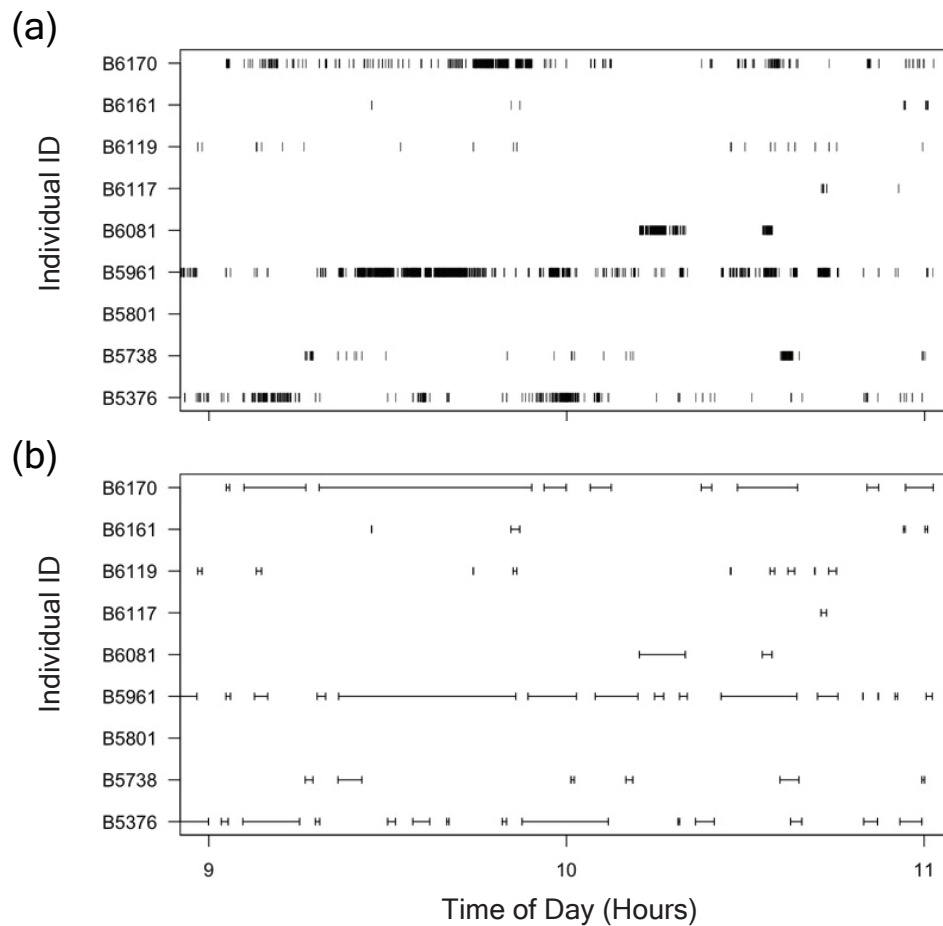206   study systems, the appropriate threshold for inter-detection interval and spatial detection

Figure 2: Visualization of the tag detection data at a given territory as point detections (a) to time 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-hour period.

207   threshold will depend on the hardware, behavior of the organism, as well as the question of

208   interest.

209   Using the 60-sec threshold, we converted the raw point detections (Fig. 2a) to temporal

210   windows of presence at a given territory (Fig. 2b). Thus, this dataset consisted of information on

211   individual, territory location, date, and start time and end time (in seconds) for each temporal

212   window. By using this approach, we were able to reduce the data from > 10 million raw

213   detections to approximately 2.5 million lines of data.

214

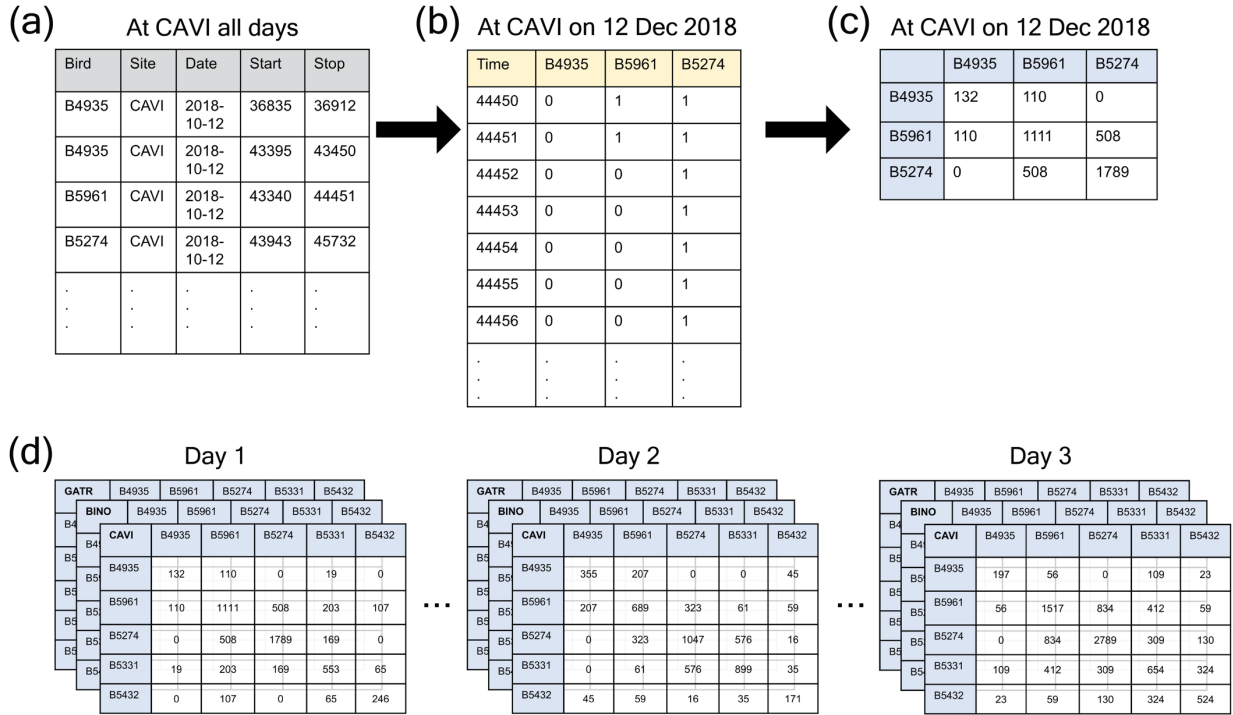215   *Creating a four-dimensional array of co-presence for the entire dataset*

Figure 3: Visualization of the workflow. The time window data (a) shows the start and end times (in seconds in the day) of the periods when an individual was present near a given base station. We then converted this data for a given station on a given day into a fine-grained presence matrix where each row was a second in the day and each column an individual (b). Each cell was given a value of 1 if the individual was present at the station in that second, and 0 if not. We then converted this information into a co-presence matrix for a given station on a given day (c). Finally, we conducted the same routine for all stations on all days and arranged them to form a 4-dimensional array of co-presence of individuals across all stations and all days (d). The final array had the dimensions N x N x S x T, where N = number of individuals, S = number of sites, and T = number of days.

216   Using the temporal presence windows (Fig. 2b, Fig. 3a), we calculated the timing and duration of

217   overlap between every bird dyad at each territory on a given date. To do this, we created a time

218   (sec)-by-individual matrix of presence/absence of N individual for every second of each

219   observation day at each territory (Fig. 3b). We then multiplied this matrix with its transpose to

220   create an N x N *co-presence matrix* (Fig. 3c). The diagonal of this matrix was the total number of

221   seconds each individual was present at the territory on that day, and the off-diagonal elements

222   tabulated the number of seconds that each pair of individuals in the population was present at a

223   given territory / station together on a particular day.

224   We calculated co-presence matrices for each base station and for each day and stacked

225   these N x N matrices of co-presence for each of S stations into a three-dimensional array (N x N x

226   S). These daily co-presence arrays were stacked for all T days of the study to create a four-

227   dimensional array (N x N x S x T; Fig. 3d). This array contained the number of seconds that

228   every pair of individuals were together across the entire study period, organized by stations and

229   days.

230   Once the 4-dimensional array of co-presence was created, we sliced the data based on

231   base station and day, allowing us to constrain the data to certain base stations or certain days.

232   Thus, this data structure preserved flexibility for downstream analyses such that analyses could

233   be conducted on data from any set of days and any set of base stations.

234

235   *Calculating a temporal association index to generate association networks*

236   From a given set of co-presence matrices across sites and days, we generated a *temporal*

237   *association index* for each dyad. Based on a Simple Ratio Index (SRI: Cairns & Schwager,

238   1987):

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

240   where x is the number of sampling periods in which the dyad A and B were associated, y_A is the

241   number of sampling periods where A was observed but not B, y_B is the number of sampling

242   periods where B was observed but not A, and y_{AB} is the number of sampling periods where both

243   A and B were observed but not associated. We adapted this metric to an index of temporal

244   duration of association at a given location, which we term *temporal SRI*:

245     $Temporal\ SRI = \frac{T_x}{T_x + T_{yA} + T_{yB}}$,

246   where T_x is the duration (sec) that the dyad (A and B) were both present at the same site, and T_{yA}

247   was the duration that A was present but not B, and T_{yB} was the duration that B was present but

248   not A. Thus, this temporal SRI represents the number of seconds two individuals co-occurred

249   within the same territory, divided by the number of seconds that each individual was detected at

250   any territory. This measure duly serves as edge weights in a social network.

251

252   *Generating separate social networks based on spatial context or seasons*

253   To make networks based on particular locations or dates, one can simply restrict the 4-

254   dimensional array to slices that correspond to locations or dates of interest. One can then sum the

255   N x N co-presence matrices for the different stations (S) and times (T) to generate a co-presence

256   matrix of interest. From this co-presence matrix, for each set of locations and time, one can

257   calculate temporal-SRI indices to generate an adjacency matrix, which defines the nodes and

258   edges of each social network.

259   We tested three proof-of-concept questions to show how one can flexibly generate social

260   networks at particular sets of locations or dates and demonstrate how these results can provide

261   novel insights into context-specific social dynamics. We investigated 1) whether group members

262   associated more strongly than non-group members overall, 2) whether patterns of associations

263   among visitors varied by territory, and 3) whether patterns of association between breeders and

264   helpers within groups changed across the annual cycle.

265   To ask whether patterns of associations are dependent on group membership (Question

266   1), we first compared the mean association index among members of the same group *versus*

267   members of different groups. We then measured the assortment coefficient (Newman, 2002;

268   Farine, 2014), using group membership as the node attribute and edge weights. The assortment

269   coefficient, r, can range from -1 in which associations occur only between nodes that were

270   different, such as members of different groups, to 1 in which associations occur only between

271   nodes that were the same, such as members of the same group. The assortment coefficient is 0

272   when associations occur randomly with respect to the trait of interest. Because acorn

273   woodpeckers live in stable, cooperatively breeding groups, we expected that association indices

274   would be greater among members of the same social group, and that the assortment coefficient

275   would be >0.

276   To ask whether patterns of associations between visitors depended on the territory being

277   visited (Question 2), we restricted the data to detections of birds outside their own home territory

278   (i.e., during forays). We then calculated associations between visitors at particular territories. We

279   use spatially explicit network visualizations to illustrate variations in the patterns of connection

280   between visitors from different home groups at each territory. We expected factors such as

281   territory quality, home group size, or number of adjacent territories would cause social network

282   structure to vary by focal territory location; however testing specific hypotheses about the cause

283   of spatial variation was beyond the scope of this study and not pursued.

284   To ask whether patterns of associations between breeders and helpers within groups

285   changed across time over the annual cycle (Question 3), we restricted the data to associations

286   that occurred between individuals only at their own home territories and partitioned the data into

287   temporal windows that corresponded roughly with changes in breeding phenology of acorn

288   woodpeckers in our study population. The breakdown of seasons were: January – March (early

289   non-breeding season), April – July (main breeding season), August – September (secondary
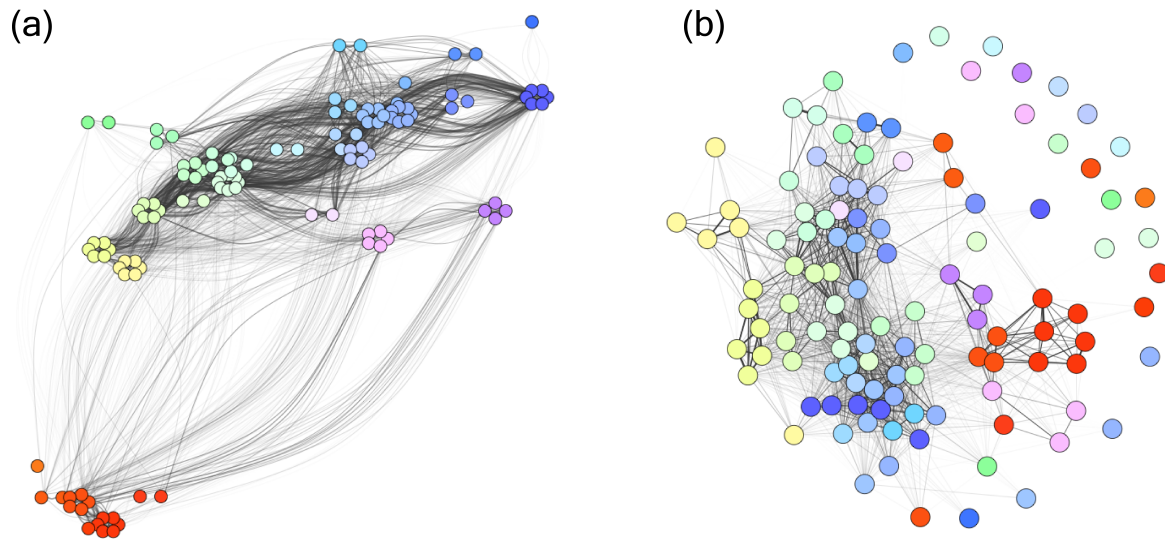
Figure 4: The total aggregated social network, displayed using a spatial layout (a) and a force-directed network layout (b). In each figure, each node represents a tagged bird, and the edges connect individuals that were detected at the same territory at the same time. The edge widths are proportional to the association index, which represents the number of seconds that two birds were detected at a territory, divided by the number of seconds that either or both birds were detected at any territory. The nodes are colored to reflect distinct social groups, and groups that are spatially adjacent have similar colors. 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 using the algorithm by Fruchterman and Reingold (1991). 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 (same color) or adjacent groups (similar colors) are often linked tightly, though it is clear that there are many connections between members of different groups. Individuals at the periphery of the network are connected by very weak edges.

290   breeding season), and October – December (early non-breeding season). We then measured the

291   assortment coefficient of the network (see above) with breeder status (breeder versus helper) as

292   the node attribute. We expected that there would be stronger assortment by breeding status

293   during the breeding seasons.

294

295   **RESULTS**

296   *1. Patterns of associations based on group affiliation and breeding status*

297   Our results show that the acorn woodpecker social network was highly structured based on social

298   group membership (Fig. 4), a finding consistent with their maintenance of year-round

299   cooperative social groups (Koenig et al., 2016). We also found substantial associations between

300   groups when individuals engaged in forays (Barve et al., 2020a) to other group territories (as

301   evidenced by edges crossing territories in the network in the spatial layout (Fig. 4a), and by

302   clustering of nodes of different colors when using a layout based on patterns of social

303   connections (Fig. 4b). In the total aggregated network (i.e., including all associations at home

304   and during forays), mean (± SD) edge weight among members of a social group (0.097 ± 0.105)

305   was greater than mean edge weight among members of different social groups (0.007 ± 0.020).

306   Accordingly, there was high assortment by home group ($r = 0.321 ± 0.029$), meaning individuals

307   associated more with members of the same group.

308   *2. Patterns of associations during extra-territorial forays varies by territory*

309   Acorn woodpeckers of both sexes and breeding status make multiple forays to other

310   territories each day (Barve et al., 2020a). Fig. 5a-c shows the patterns of associations between

311   woodpeckers during such forays, where individuals from up to two different home territories

312   may associate at a third territory they were visiting. Moreover, these patterns of associations

313   between visiting birds differ among territories, exemplifying how the spatial and ecological

314   contexts associated with each territory can affect social network structure. In this example, we

315   have chosen to display the patterns of associations at three adjacent territories (Fig. 5d). All three

316   territories received visitors from both near and far territories (shown by colors of nodes, with

317   spatial locations of the bird's home territory shown in Fig. 5d). Some visitors formed tight

318   clusters based on their group identity at some territories, as in Fig. 5a where members of the

319   same group made forays to the focal territory together, while other dyads did not (Fig. 5b,c).

320   Visitors seemed to attend some territories alone (i.e., many visitors were not associated with

321   other visitors as in Fig. 5b), while some territories hosted clusters of visitors (i.e., visitors formed
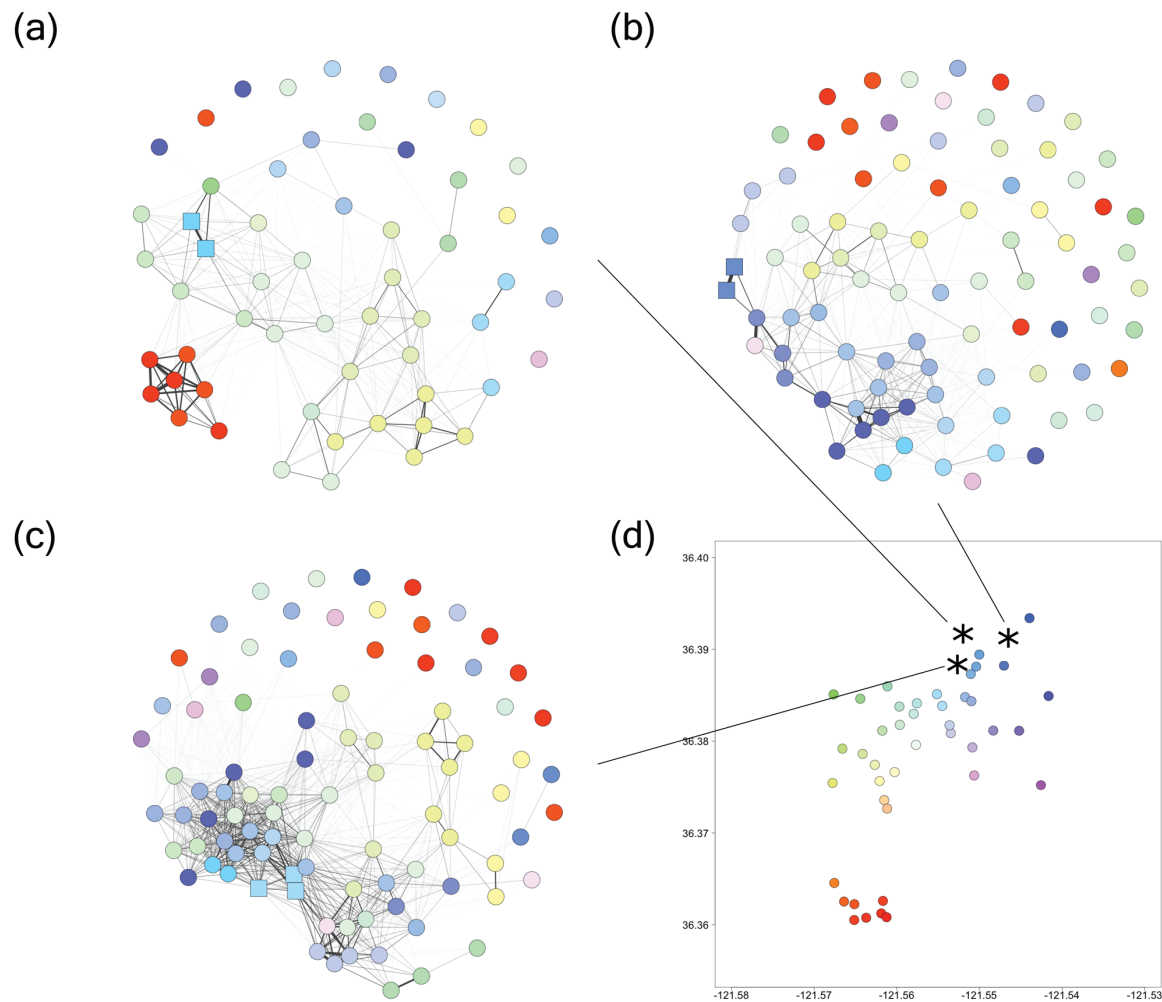
Figure 5: The social network of visitors differed dramatically by spatial context—i.e., the territory being visited. In each social network (a–c), each node represents a bird, with the color representing their social group membership. The color of each home group is represented on the spatial map of base stations (d) where the territories being considered are shown as asterisks (?). Individuals that belong to the home group of the territory being visited are represented as squares.

322   dense connections as in Fig. 5c). There are many other patterns that can be explored with such

323   territory-specific social networks, but an exhaustive examination of all patterns is beyond the

324   scope of this study.

325   *3. Patterns of associations within groups change across the annual cycle*

326   As an illustration of how one can use automated radio-telemetry data to explore temporal

327   dynamics of social networks, we examined how patterns of associations between breeders and

328   helpers within social groups changed between seasons. Restricting the data to only associations

329   between individuals while they were at their home group, we found substantial association by

330   social status, and further, that this pattern fluctuated across the annual cycle, with lower

331   assortment among breeders in the non-breeding season (Oct–Dec and Jan–Mar: Fig. 6). Again,

332   there are many specific hypotheses we could pursue here (e.g., sex differences in assortment

333   patterns), but testing of specific hypotheses were beyond the scope of this study.
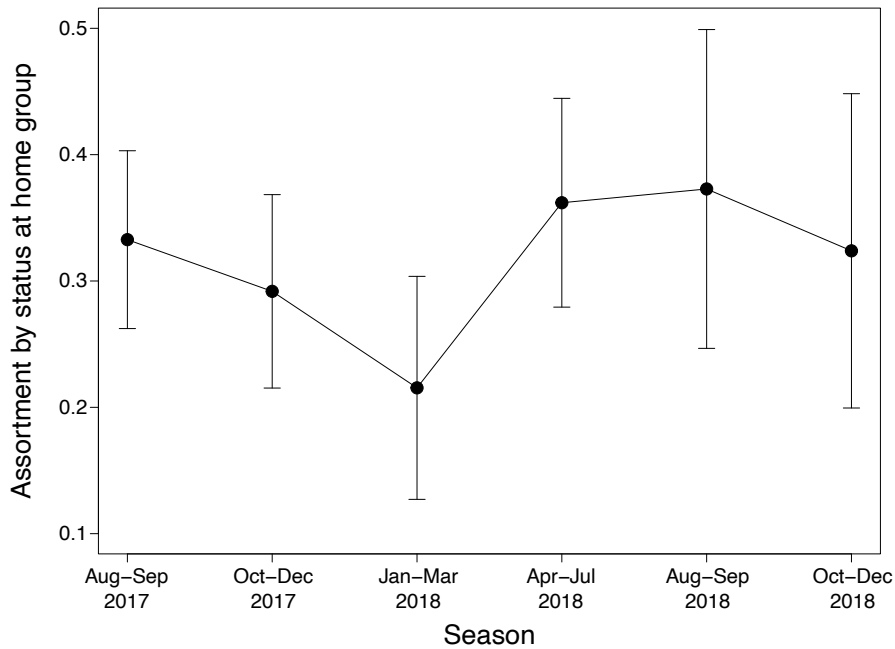
334

*Figure 6: Assortment of associations at home territory by breeding status across seasons.
The y-axis shows the coefficient of assortment by breeder status, which can vary from -1
(associations occur exclusively between individuals of different status) to 1 (associations
occur exclusively between individuals of the same status). Assortment of 0 indicates
associations are random with respect to breeder status. One can see that assortment patterns
are always positive, and the degree of assortment fluctuates across the year, peaking during
the breeding season (April–July and August–September) and dropping during the non-
breeding season (October–December, January–March). Error bars indicate standard error
estimated using the jackknife method.*

Discussion:

Here we present a method for collating data from automated telemetry systems into a flexible format for generating spatially and temporally explicit social networks using an association index that measures the number of seconds that two individuals spent together at a location, while accounting for the total time either individual was detected anywhere within the base station array. Our approach assumes that base stations are placed within ecologically relevant locations such as within defended territories, at display or lekking sites, or other locations where individuals will frequently encounter one another, such as feeders, watering holes, or foraging patches.

Using an array of base stations that are embedded in ecologically important locations for a focal species is critical for understanding the behavioral context of the social network. By placing base stations at relevant locations within the landscape, hypotheses for when, why, and with whom animals associate can be formulated and tested. Without this meaningful link between co-occurrence and location, the ecological contexts of social networks cannot be established, and the benefits gained from high resolution data are lost. In this study, we used the example of a social system of cooperatively breeding acorn woodpeckers, with base stations placed within defended group territories. Because this work was part of an ongoing long-term study of this population, we also had independent longitudinal data on social group composition, including breeder / helper status. This framework allowed us to use the automated telemetry data to separate associations between group members of different social status and sex at their home territory from associations that occurred during frequent forays where individuals visited other territories (Barve et al. 2020a). Thus, we could show that the social network of acorn woodpeckers was characterized by both strong associations within social groups, but also an

358   extensive set of associations between members of different groups that co-occur during forays to

359   visit other territories. Our approach also allowed us to examine the structure of associations

360   between visitors across different territories, and the temporal changes in social dynamics within

361   social groups across the annual cycle. Other researchers could adapt this same approach to ask

362   questions specific to a particular system. For example, Dakin & Ryder (2018, 2020) used a

363   similar automated telemetry system to study the social network dynamics of cooperatively

364   displaying wire-tailed manakins (*Pipra filicauda*). In those studies, the base stations were placed

365   within display sites, and signal strength was calibrated to a much smaller spatial scale than used

366   in our study, allowing them to infer instances of cooperative displays that occurred on a single

367   branch.

368   We were able to collate >10 million rows of data, collected continuously over nearly 2

369   years, to construct a dataset that allowed us to incorporate flexible and dynamic analyses of

370   social networks across both space and time. Despite the size of this dataset, the workflow for

371   network construction we describe was conducted on a laptop computer (Macbook Pro 3.1GHz,

372   8GB RAM; see Supplemental Material for code scripts). The key features of our data structuring

373   approach included: (1) the reduction of raw detection data into temporal windows of presence of

374   an individual at a location, (2) the use of a simple 4-dimensional array of association (in seconds)

375   between individuals for a given date and location, and (3) the use of the temporal SRI association

376   index, which described the cumulative strength of association between individuals, while

377   accounting for the amount of time each individual was detected. Each of these key features has

378   both pros and cons, and the details of these features can and should be customized for each

379   study.

380   The first feature of our data structuring approach, the reduction of detection data into

381   temporal windows relies on a threshold method for inferring when an individual is present or

382   absent from within a given detection region. This method is simple to implement and has the

383   major benefit of dramatically reducing the size of the dataset to make downstream analyses more

384   manageable—an important consideration with automated telemetry systems that generate very

385   large datasets. Such an approach, however, is also prone to both false negatives (e.g., classifying

386   an individual as absent from the detection region when inter-detection interval is increased due to

387   obstruction of signal or tag error) and false positives (e.g., inferring an individual was present in

388   the detection region when it had briefly left the area). While more sophisticated methods that

389   avoid arbitrary thresholds to infer social behavior are available for some automated datalogging

390   approaches, such as Gaussian mixture models available for RFID studies (Psoriakis et al. 2015),

391   the volume of data generated by long-term automated telemetry makes such approaches

392   challenging to implement without incurring large investments of time. Careful selection of

393   appropriate threshold values to manage potential false negative or false positive rates need to be

394   balanced, given the animal system, the distribution of base stations, and the research questions

395   being addressed, factors which will alter the relevant duration of the threshold.

396   Our method for collating data on the presence of individuals at territories into a 4-

397   dimensional array of co-presence across space and time provides flexibility for examining

398   temporal and spatial dynamics of social network structure. Maintaining this flexibility is

399   important because (i) social associations occur in space, and thus the spatial context of

400   associations (i.e., *where* the associations occur) is critical to understanding the ecological

401   underpinning of social networks (Wolf & Trillmich, 2018; Spiegel, Sih, Leu, & Bull, 2018), (ii)

402   social networks are inherently dynamic, with ever-changing patterns of social connections across

403   time (Blonder, Wey, Dornhaus, James, & Sih, 2012; Pinter-Wollman et al., 2014; Shizuka &

404   Johnson, 2020). Combined with a long-term dataset on ecological and social attributes of group

405   territories such as territory quality, group size, and group membership, there is great scope for

406   exploring the ecological underpinnings of how social interactions are distributed in space.

407   Likewise, our study demonstrates how temporally explicit data structure facilitates the study of

408   temporal dynamics of associations, fine-tuned to the biology of the study system. Depending on

409   the system and question at hand, the information can be parsed into different spatial and temporal

410   scales using the same basic data structure.

411   In this study, our association index described the probability that two individuals were

412   detected at the same territory while accounting for each individual's tendency to spend time

413   within detectable range of base stations. However, one could use alternative metrics to measure

414   strengths of associations appropriate to particular research questions. For example, one could

415   simply measure the absolute number of seconds that two birds spent at the same territory.

416   Alternatively, one could count the number of time windows during which two birds were

417   detected together (the number of association "bouts"; Dakin & Ryder, 2018, 2020). There are

418   many other ways that one can infer strengths of associations, and we encourage researchers to

419   explore these possibilities. For example, it may be possible to calculate association indices that

420   account for concordance in associations across time and space, which may help separate social

421   associations between individuals that are attracted to the same ecological resource from social

422   relationships that transcend particular ecological contexts (Spiegel et al., 2018).

423

424   **Conclusions:**

425   We expect that automated telemetry systems will be increasingly used in combination

426   with social network analyses to study social dynamics in a wide variety of animal systems.

427   However, there are many factors that must be considered to generate biologically relevant social

428   networks from these powerful data collection systems, including tag design, detection range, and

429   spatial arrangement of base stations (Mourier et al., 2017), as well as data structures that

430   facilitate analysis of fine-scaled spatial and temporal dynamics. Here, we presented a worked

431   example of a relatively simple and computationally tractable approach to constructing social

432   networks in flexible ways that we hope will be used by other researchers to facilitate rapid and

433   widespread advancements in our understanding of the ecology and evolution of complex social

434   structures within natural systems.

435

448

Author's contributions:

S.B. and E.L.W. obtained funding, managed data collection, including setup of the automated

radio-telemetry 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.

454

Data availablility:

Workflow for generating association matrices from automated radio-telemetry data (using

sample data of from one month of data collection), along with code, can be found in the

Supplementary Material.

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