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Workflow For Constructing Social Networks From Automated Telemetry Systems

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

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8

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

10 **Abstract:**

- 11 1. Advances in datalogging technologies have provided a way to monitor the movement of
12 individual animals at unprecedented spatial and temporal scales, both large and small.
13 When used in conjunction with social network analyses, these data can provide insight
14 into fine scale associative behaviors. The variety of technologies demand continuous
15 progress in workflows to translate data streams from automated systems to social
16 networks, based on biologically relevant metrics.
- 17 2. Here we present a workflow for generating flexible association matrices from automated
18 radio-telemetry data that can be parsed into both spatial and temporal dimensions. These
19 can then be used to generate and compare social networks across space and time.
- 20 3. We illustrate this workflow using data collected from an automated telemetry study of
21 acorn woodpeckers (*Melanerpes formicivorus*), a cooperatively breeding bird. The data
22 were collected continuously over two years at base stations placed within social group
23 territories. We use this system to demonstrate how this flexible data structure can be used
24 to answer a number of biological questions, specifically 1) how assortative are social
25 associations at the population scale, 2) how do association patterns among territory
26 visitors vary across territories, 3) and how does seasonality affect assortative affiliation
27 within groups?
- 28 4. This flexible method allows one to generate social networks that can be used to ask a
29 variety of biological questions pertinent to a wide range of animal systems, exploiting the
30 investigative power that can be gained by using automated radio-telemetry in conjunction
31 with social network analyses.

32

33 **Keywords:** acorn woodpeckers, automated radio-telemetry, cooperative breeding, social
34 network analyses, social network dynamics,

35 **Introduction:**

36 Social organization, the patterns of associations among individuals in a population, has
37 important effects on individual fitness (Wolf, Brodie III, & Moore, 1999; Kappeler, 2019;
38 Snyder-Mackler et al. 2020). A major challenge in the study of social organization has been the
39 logistics of collecting data on social interactions and associations *in situ*. Rapid advances in
40 automated datalogging technology, however, have recently ushered in an age of “reality mining”
41 of animal sociality (Krause et al., 2013) with exponential decreases in the size of animal tracking
42 devices. These advances have enabled pioneering studies measuring movement and associative
43 patterns in increasingly smaller organisms at finer spatial and temporal scales over extended
44 periods of time.

45 Concomitant with technological advancements, the application of social network analyses
46 to animal social behavior has progressed rapidly. Such approaches are now routinely used to
47 quantify and analyze patterns and dynamics of social associations across space and time (Pinter-
48 Wollman et al., 2014; Farine & Whitehead, 2015). The integration of automated datalogging
49 with more advanced approaches to social network analyses has led to key discoveries such as the
50 rapid spread of experimentally introduced information through wild populations (Aplin et al.,
51 2015), the reorganization of social networks in response to a resource pulse (St Clair et al.,
52 2015), and fine-scale dynamics in social contagion of cooperation (Dakin & Ryder, 2018).
53 Critical to these advances in our understanding of social dynamics in nature is the ability to
54 flexibly slice and combine data on social associations and interactions collected at different sites
55 across time.

56 Because different technologies collect a variety of information, there is no one-size-fits-
57 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

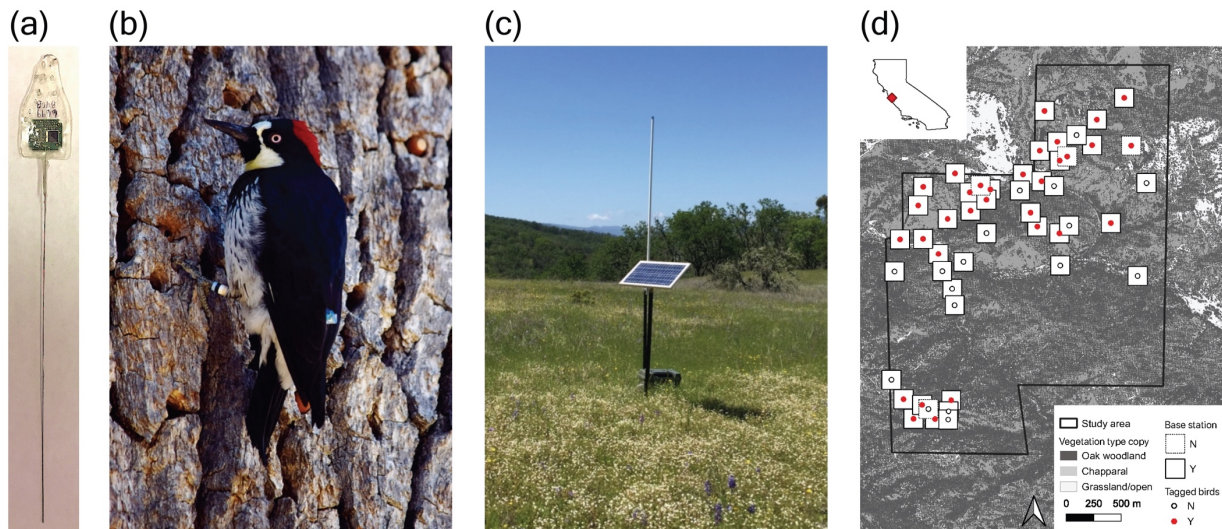


Figure 1: Automated radio-telemetry was used to study acorn woodpecker behavior. Individuals were fitted with solar-powered radio tags (a) mounted dorsally (b). Autonomous base stations, usually placed near woodpecker granaries, detected all radio-tagged woodpeckers in the vicinity (c). Base stations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

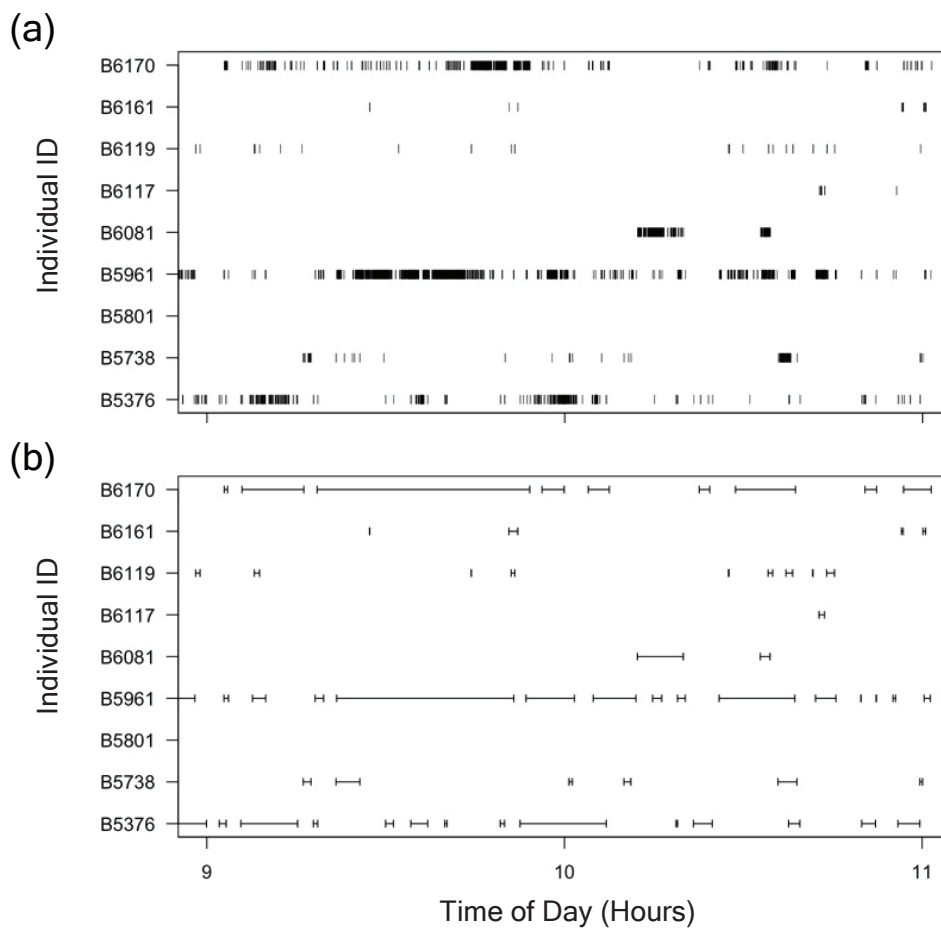


Figure 2: Visualization of the tag detection data at a given territory as point detections (a) to time windows of presence (b) at a single territory. The data are illustrated for all individuals (indicated along the y-axis) detected in a single 2-hour period.

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

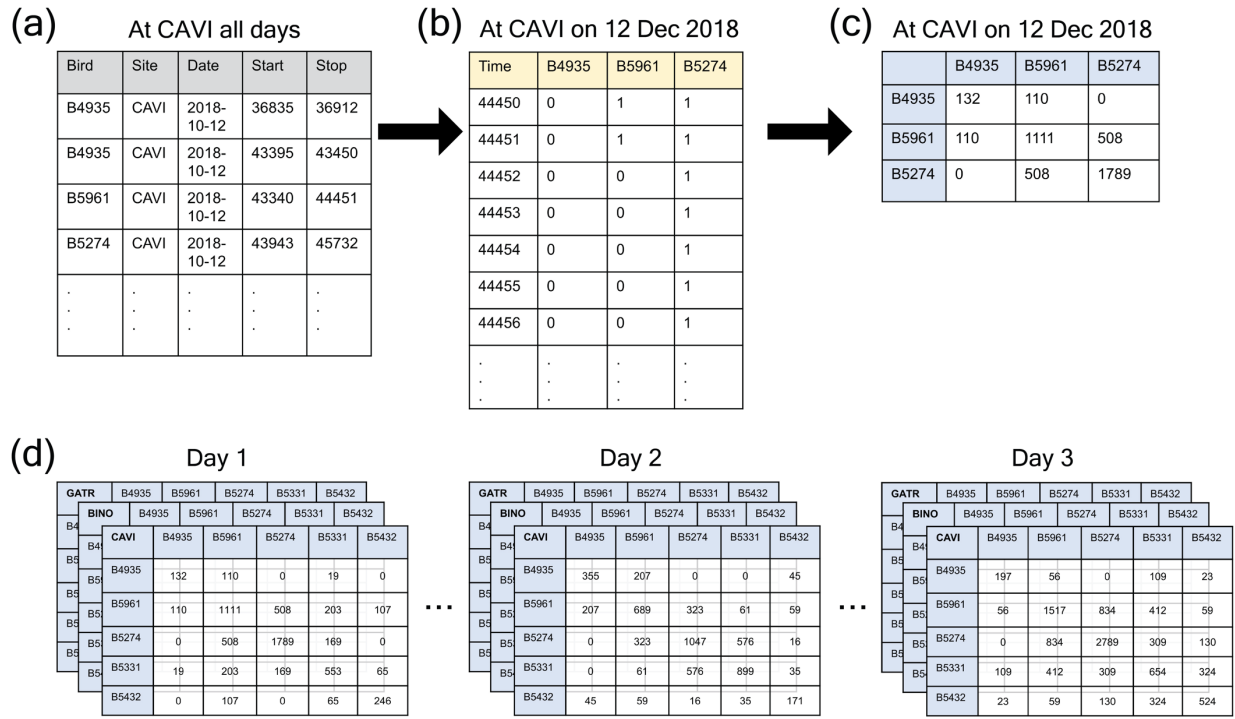


Figure 3: Visualization of the workflow. The time window data (a) shows the start and end times (in seconds in the day) of the periods when an individual was present near a given base station. We then converted this data for a given station on a given day into a fine-grained presence matrix where each 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 $N \times N \times S \times T$, 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 $N \times N$ 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 $N \times N$ matrices of co-presence for each of S stations into a three-dimensional array ($N \times N \times$
226 S). These daily co-presence arrays were stacked for all T days of the study to create a four-
227 dimensional array ($N \times N \times S \times T$; 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):

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

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

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 $N \times N$ 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

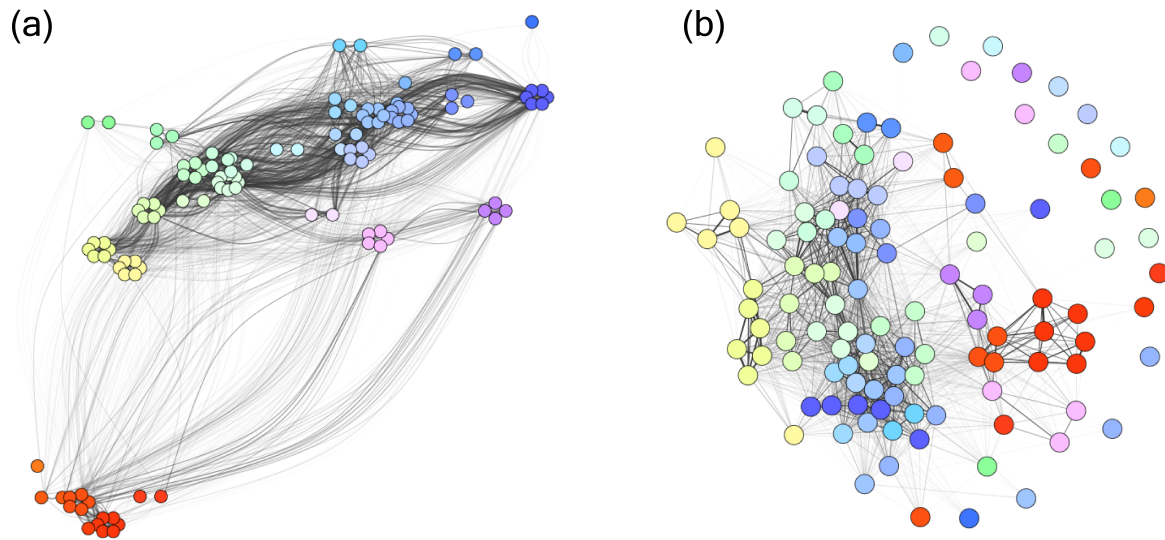


Figure 4: The total aggregated social network, displayed using a spatial layout (a) and a force-directed network layout (b). In each figure, each node represents a tagged bird, and the edges connect individuals that were detected at the same territory at the same time. The edge widths are proportional 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 (\pm 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 ($r = 0.321 \pm 0.029$), 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

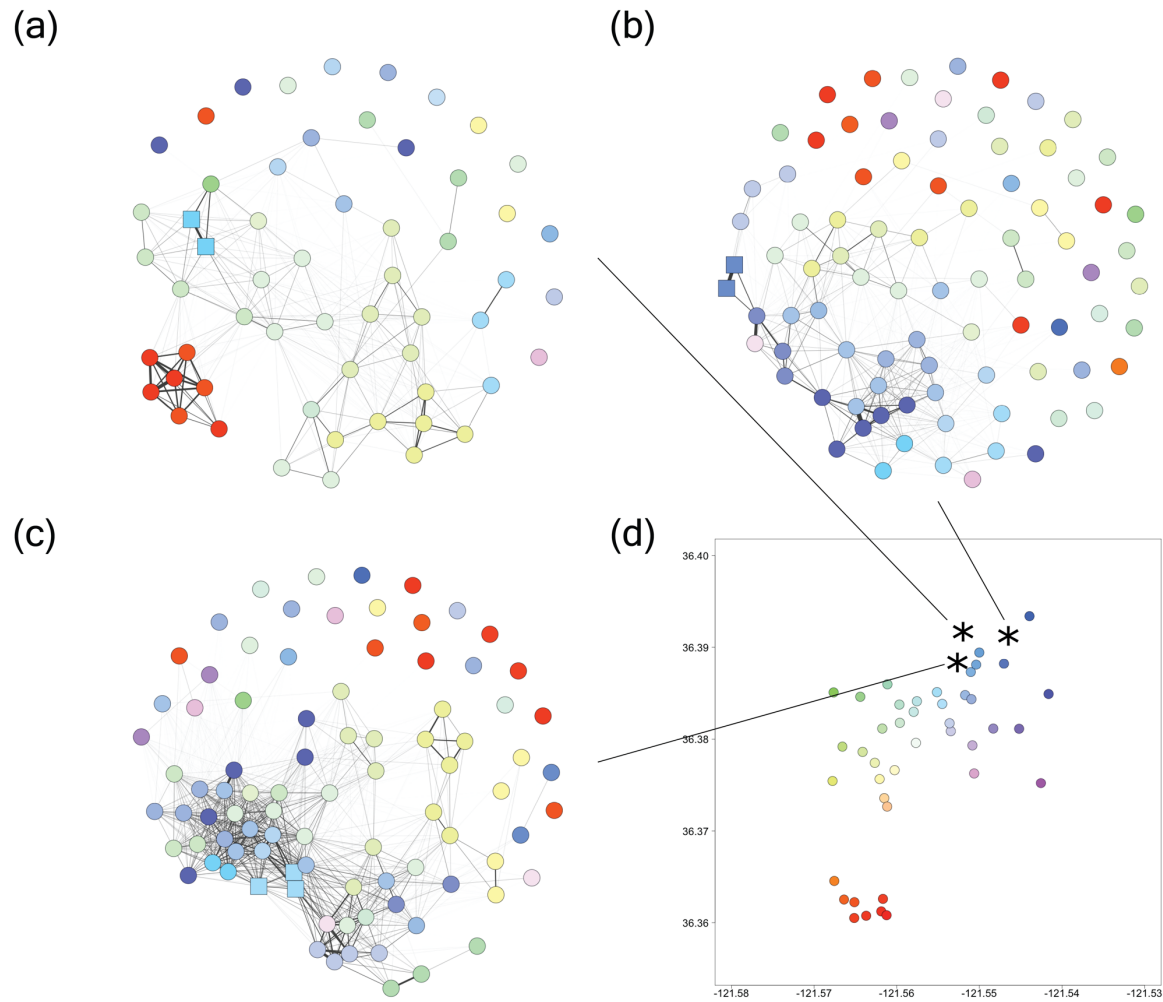


Figure 5: The social network of visitors differed dramatically by spatial context—i.e., the territory being visited. In each social network (a–c), each node represents a bird, with the color representing their social group membership. The color of each home group is represented on the spatial map of 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

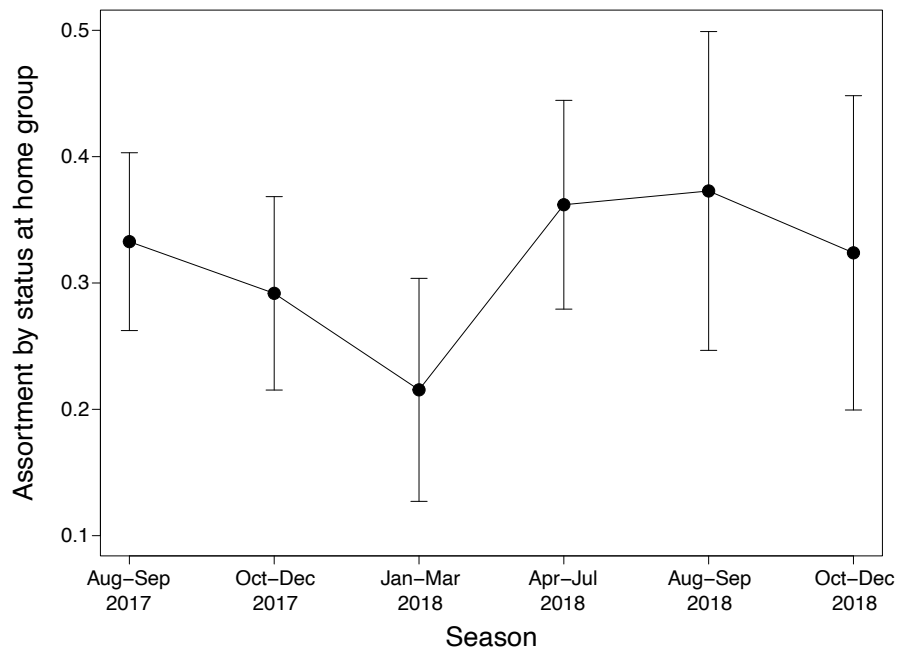


Figure 6: Assortment of associations at home territory by breeding status across seasons. The y-axis shows the coefficient of assortment by breeder status, which can vary from -1 (associations occur exclusively between individuals of different status) to 1 (associations occur exclusively between individuals 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.

335 **Discussion:**

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

344 Using an array of base stations that are embedded in ecologically important locations for
345 a focal species is critical for understanding the behavioral context of the social network. By
346 placing base stations at relevant locations within the landscape, hypotheses for when, why, and
347 with whom animals associate can be formulated and tested. Without this meaningful link
348 between co-occurrence and location, the ecological contexts of social networks cannot be
349 established, and the benefits gained from high resolution data are lost. In this study, we used the
350 example of a social system of cooperatively breeding acorn woodpeckers, with base stations
351 placed within defended group territories. Because this work was part of an ongoing long-term
352 study of this population, we also had independent longitudinal data on social group composition,
353 including breeder / helper status. This framework allowed us to use the automated telemetry data
354 to separate associations between group members of different social status and sex at their home
355 territory from associations that occurred during frequent forays where individuals visited other
356 territories (Barve et al. 2020a). Thus, we could show that the social network of acorn
357 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

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448

449 **Author's contributions:**

450 S.B. and E.L.W. obtained funding, managed data collection, including setup of the automated
451 radio-telemetry system. D.S., S.B, and A.E.J. developed the workflow, and performed the
452 network analyses. D.S. wrote the first draft and D.S., S.B., A.E.J. and E.L.W. edited the
453 manuscript.

454

455 **Data availability:**

456 Workflow for generating association matrices from automated radio-telemetry data (using
457 sample data of from one month of data collection), along with code, can be found in the
458 Supplementary Material.

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