Life history stage explains behavior in a social network before and during the early breeding season in a cooperatively breeding bird

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Abstract

19 In species with stage-structured populations selection pressures may vary between different life
20 history stages and result in stage-specific behaviors. We use life history stage to explain variation
21 in the pre and early breeding season social behavior of a cooperatively breeding bird, the Florida
22 scrub-jay (Aphelocoma coerulescens) using social network analysis. Life history stage explains
23 much of the variation we observed in social network position. These differences are consistent
24 with nearly 50 years of natural history observations and generally conform to a priori predictions
25 about how individuals in different stages should behave to maximize their individual fitness.
26 Where the results from the social network analysis differ from the a priori predictions suggest
27 that social interactions between members of different groups are more important for breeders
28 than previously thought. Our results emphasize the importance of accounting for life history
29 stage in studies of individual social behavior.

Introduction

32 The social environment can have far reaching consequences for individual survival and
33 reproduction, and the magnitude of these effects may vary with age and sex (Alberts, 2019). In
34 stage-structured populations, life history stages are not necessarily related to age and each is
35 described by its own set of demographic parameters. Because selection pressures in each stage
36 are different (Schluter, Price & Rowe, 1991; Pujolar et al., 2015), the stage-structure of a
37 population can have profound impacts on its demography (Tuljapurkar & Caswell, 2012;
38 Caswell & Vindenes, 2018), ecology (Miller & Rudolf, 2011; Wesner, 2019), conservation

39 (Crouse, Crowder & Caswell, 1987; Kindsvater et al., 2016; van Rees et al., 2018), and ability to
40 respond to environmental change (Cotto et al., 2019). Individuals in different life history stages
41 have different strategies to maximize their fitness, which can affect social behaviors within a
42 population (Rudolf, 2007; Blumstein, Wey & Tang, 2009; Fischhoff et al., 2009).
43
44 Cooperative breeders are highly social and tend to have stage-structured populations (Ekman et
45 al., 2004), making them excellent model systems in which to study the effects of life history
46 stage on social behavior. Here, we examine the influence of life history stage on the social
47 behavior of Florida scrub-jays (Aphelocoma coerulescens), a well-studied cooperative breeder,
48 with thoroughly described stage-specific behavioral differences (Woolfenden & Fitzpatrick,
49 1984, 1990), using social network analysis.
50
51 In social networks, individuals are considered connected when they interact or are detected
52 together (Whitehead & Dufault, 1999; Krause, Lusseau & James, 2009;Farine, 2015).Social
53 network analyses are powerful because they move beyond dyadic interactions to quantify the
54 social structure of groups or populations (Croft, James & Krause, 2008; Cantor et al., 2019).
55 From these networks, a variety of metrics can be calculated, characterizing an individual's
56 number and strength of connections as well as its position relative to others in the network
57 (Krause, Lusseau & James, 2009). The ability to quantify the social environment as it is
58 experienced by each individual has led to improvements in the description of social structures
59 (Wittemyer, Douglas-Hamilton & Getz, 2005; Lusseau et al., 2006; Wey et al., 2008;Webber &
60 Vander Wal, 2019), insights into individual variation and its consequences (Oh & Badyaev,
61 2010; Aplin et al., 2013), and a better understanding of interactions between the social and
62 physical environment (Firth & Sheldon, 2015; Pinter-Wollman, 2015; Leu et al., 2016). The
63 influence of individual traits, including stress physiology (Boogert, Farine & Spencer, 2014;
64 Moyers et al., 2018), genetic relatedness (Ilany & Akçay, 2016), and personality (Krause, James
65 & Croft, 2010; Wilson et al., 2013; Snijders et al., 2014; Sih et al., 2018) on social network
66 position has been widely studied. Although several studies have examined the effects of
67 reproductive status on social behavior (Fischhoff et al., 2009; Patriquin et al., 2010; Wey et al.,
68 2013; Menz et al., 2017), few have explicitly examined the effects of life history stage (but see
69 Wey et al., 2013).
70
71 Florida scrub-jays are territorial and non-migratory, living in family groups consisting of a
72 single, monogamous breeding pair that monopolizes all reproductive effort and 0-7 helpers
73 (Woolfenden & Fitzpatrick, 1984; Townsend et al., 2011). Helpers are most commonly the
74 offspring of the breeding pair on whose territory they reside, but occasionally (less than 15%) are
75 associated with unrelated or distantly-related breeders (Woolfenden & Fitzpatrick, 1990). Within
76 these family groups a strict dominance hierarchy exists; breeders are the most dominant, and
77 among helpers, males are dominant over females, and older birds are dominant to younger birds,
78 and hierarchies exist among brood mates (Woolfenden & Fitzpatrick, 1977, 1984; Tringali &

79   Bowman, 2012). Although this species is territorial, social relationships extend beyond territory
80   boundaries. Dispersal distances are short, on average individuals only breed one or two
81   territories away from their natal territory. This results in related jays tending to be clustered
82   together on the landscape and allows for social relationships among parents, offspring, and
83   siblings to persist after dispersal. Juveniles and helpers also make forays away from their natal
84   territories, sometimes forming large, temporary aggregations of non-breeders. Dominance
85   hierarchies also exist across cohorts, between jays from different family groups (Woolfenden &
86   Fitzpatrick, 1977).

87

88   Florida scrub-jays' social system allows us to classify all adults into one of three life history
89   stages: (1) breeders, who own territories and have been associated with a nest with contents; (2)
90   dominants, who own territories, but have not yet bred; and (3) helpers, who neither own
91   territories nor breed (Woolfenden & Fitzpatrick, 1984, 1990). Typically, dominants have only
92   recently acquired a territory, and may or may not have paired with a mate. Individuals usually
93   remain classified as dominants for less than a year but in rare cases, dominant birds or their
94   mates are infertile, failing to produce eggs after multiple breeding seasons. Hereafter, we will use
95   dominant as it refers to life history stage, and not as a position within the social hierarchy.

96

97   Life history stage specific behaviors have been described. Breeders defend their territories,
98   engage in courtship behavior with their mate, and build and tend to their nest (Stallcup &
99   Woolfenden, 1978; Woolfenden & Fitzpatrick, 1984). Both parents provision young, but only the
100   female incubates eggs and broods young (Woolfenden & Fitzpatrick 1984). Non-breeding
101   helpers are seeking their first breeding opportunity. During this time, helpers reside at their natal
102   or home territory and assist with its defense and vigilance against predators while also making
103   repeated forays off-territory in search of potential breeding opportunities. Many routes to
104   becoming a breeder exist, including pairing with a recently widowed breeder or unpaired
105   dominant, establishing a territory in vacant habitat or, for males, inheriting all or a portion of
106   their natal territory (Woolfenden & Fitzpatrick, 1977, 1978, 1984, 1990; Breininger, 1999; Stith,
107   1999). Dominant birds are those that are defending a territory but have yet to breed (defined as
108   laying or siring an egg). They may be paired or unpaired. If unpaired, they may defend against
109   many more potential usurpers than do established pairs and they also may foray, attempting to
110   attract a mate.

111

112   If life history stage-specific tactics to maximize individual fitness influence social behavior, then
113   social behavior should vary with life history stage. We draw on 50 years of study to predict how
114   stage specific behaviors would be reflected in the metrics calculated from the social network
115   (Table 1). Breeders do not foray, which restricts the pool of individuals with which they can
116   associate to family-group members, neighbors, and helpers foraying nearby. Helpers may foray
117   frequently, and dominants may foray if unpaired, thus we predict that (1) breeders will have the
118   fewest associations and helpers the most, (2) breeders will rarely connect otherwise unconnected

119   individuals and helpers will do so frequently, (3) breeders will exhibit more "cliquish" behavior,
120   associating with individuals that are themselves associated, and helpers will not and (4) breeders
121   will be detected at the fewest unique locations and helpers at the most. Because there is one way
122   to defend a territory, but many ways to obtain one, we predict that (5) breeders will exhibit the
123   least within-stage variation and helpers the most.
124

Materials & Methods

125

126   **In the field**
127   We conducted this study on an individually-marked population of Florida scrub-jays at Archbold
128   Biological Station in Highlands County, Florida (21° 10'N, 81° 21'W). As part of a long term
129   and ongoing study, we band all scrub-jays with unique combinations of color bands and census
130   the population monthly (see Woolfenden and Fitzpatrick 1984 for a detailed description of our
131   demographic study methods). The nesting season can begin as early as February and continues
132   into June. Each year, we find all nests and map the boundaries of each territory.
133

134   From February through April of 2016 and 2017, we surveyed for jays at points placed at least
135   200 m apart and non-randomly stratified across all territories (Fig.1). Florida scrub-jays
136   vigorously defend their territories, which average about 9 ha (Woolfenden & Fitzpatrick, 1990).
137   While deep intrusion of one group's territory by another is relatively infrequent, mutual defense
138   along shared boundaries is routine. Prospecting forays by non-breeding helpers tend to occur
139   along these boundaries (Woolfenden & Fitzpatrick, 1990). Thus, we stratified sampling at the
140   intersections of territory boundaries to ensure that 1) we captured interactions of birds foraying
141   away from their home territory among themselves and with local birds and 2) all individual birds
142   had an opportunity to be sampled, even those that did not foray. Because sampling began just
143   prior to the onset of breeding and before we map territories, we based the placement of sampling
144   points on the territory boundaries mapped in April of the previous year. Territory boundaries are
145   relatively stable but do fluctuate annually and within a season (Woolfenden, 1975; Woolfenden
146   & Fitzpatrick, 1990).
147

148   We sampled these points twice a week in 2017 and 2018 using playback of territorial calls. Calls
149   were sourced from recordings made in the same metapopulation as our study population (Coulon
150   et al., 2008), but are several decades old. Thus, these calls are in the local dialect, but not from
151   individuals known to any jays in our study. We randomized the order in which we visited points
152   using a random number generator. We played territorial calls on a portable speaker for a total of
153   2 minutes, 30 seconds in each cardinal direction, with 30-second breaks after each. Then we
154   waited an additional minute for birds to respond, so that each visit lasted a minimum of 5
155   minutes. We recorded the identities of all birds present at survey points using Survey123 (ESRI,
156   2018).
157

158   Use of playback is appropriate for this species for two reasons: 1) it mimics what occurs when
159   there is a disturbance in the existing social structure, such as the death of a breeder, which are the
160   types of opportunities foraying helpers are searching for and 2) breeders, dominants, and helpers
161   all defend their territorial boundaries. In order for individuals to hear and respond to the
162   playbacks, they must already be in the vicinity of the sampling point. Territories are large and
163   scrub habitat is generally low and open, and we do not observe jays flying in from far away in
164   response to the playbacks, which supports the idea that the individuals responding to playback
165   are nearby. Florida scrub-jays are vigilant, territorial, and social, making them likely to detect
166   jays along or within their territory boundary and interact with them. Therefore, we assume that
167   individuals detected at a sampling point at the same time are associated. We have no reason to
168   suspect that the associations we observe during sampling would not exist in the absence of the
169   playbacks.
170
171   To maximize the number of edges recorded (Davis, Crofoot & Farine, 2018) between jays from
172   non-adjacent territories, we also recorded opportunistic observations of aggregations of jays
173   when they contained individuals from non-adjacent territories. These aggregations are
174   ephemeral, and it is difficult to predict when or where they will occur. We did not record
175   opportunistic observations of members of the same territory or neighboring territories because
176   these edges are easily captured by the point sampling, which occurs along relatively static and
177   vigorously defended territory boundaries. Because ignoring opportunistic observations of
178   individuals from the same or neighboring territories interacting underestimates the strength of
179   connections between family members and neighbors, we used binary, and not weighted, degree.
180
181   All research was conducted under the required permits from the United States Geological Survey
182   Bird Banding Lab (07732) and the United States Fish and Wildlife Service (TE824723-9) issued
183   to RB.
184
185   **Constructing the social networks**
186   We included all individuals detected three or more times in group-by-individual matrices for
187   each year. We chose this cutoff because it reduced the proportion of dyads below the
188   recommended threshold simple ratio index denominator of 20 (Farine & Strandburg-Peshkin,
189   2015; Davis, Crofoot & Farine, 2018) without excluding too large a portion of the female
190   breeders. We used R package asnipe to build a network for each year, using the simple ratio
191   index to correct for detection probabilities (Whitehead, 2008; Farine & Whitehead, 2015;
192   Hoppitt & Farine, 2018). We chose three metrics that we thought would best capture the
193   differences in behavior between helpers, who make frequent off-territory forays, and breeders,
194   who do not (Table 2): (1) binary degree, the number of individuals an individual was associated
195   with; (2) vertex betweenness centrality (hereafter betweenness), the importance of a focal
196   individual in connecting other birds or connected groups, i.e., the number of times a focal
197   individual lies on shortest paths between two other individuals; and (3) local clustering

198   coefficient, the proportion of the focal individual's associates which are themselves associated
199   (Croft, James & Krause, 2008; Beveridge & Shan, 2016). We calculated these metrics using R
200   package igraph (Csardi & Nepusz, 2006). We also counted the number of unique sampling points
201   at which each individual was detected.
202
203   **Statistical analyses**
204   We adopted spatial criteria for inclusion in our statistical analyses because yearly changes to
205   territory boundaries could result in uneven sampling coverage and because territories along the
206   periphery have fewer neighboring territories and tended not to have helpers. We calculated the
207   distance between the territory edge and the nearest sampling point and number of immediately
208   adjacent territories for all territories as they were mapped in the year they were sampled using
209   the Generate Near Table and Polygon Neighbors tools in ArcMap (ESRI, 2015).
210   Individuals from territories that did not have a sampling point within 100 m of their territory
211   boundary and those from territories with one or fewer immediately adjacent neighboring
212   territories were excluded from the statistical analyses. Then we used ANOVA to confirm that
213   that individuals in different life history stages did not differ in the distance between the territory
214   on which they reside and the nearest sampling point (2017: $F_{2,\,164} = 1.04$, p = 0.36; 2018: $F_{2,\,169}$
215   $= 2.46$, p = 0.09) nor the number of adjacent territories (2017: $F_{2,\,164} = 1.71$, p = 0.18; 2018: $F_{2,}$
216   $_{169} = 3.23$, p = 0.04). In 2018, dominant birds resided on territories significantly farther from the
217   nearest sampling point than helpers (p = 0.01) and breeders (p = 0.05), but the observed
218   differences were less than 15 meters. In 2018, helpers resided on territories with nearly 1 more
219   adjacent territory than breeders (p = 0.05) and dominants (p = 0.05), likely an artifact of
220   territories in the center of our study area tending to be more productive.
221
222   We also estimated the robustness of our social networks for each year. For each dyad in each
223   year, we calculated the denominator of the simple ratio index (the number of observations in
224   which either individual was detected). The proportion of dyads at or above the minimum simple
225   ratio index threshold of 20 (Farine & Strandburg-Peshkin, 2015; Davis, Crofoot & Farine, 2018),
226   increased from 2017 to 2018 (Table 2).
227
228   We constructed a set of linear models to explain each social network metric in each year by sex,
229   life history stage, their interaction, the number of territories adjacent to their territory, and the
230   distance between their territory and the nearest sampling point. We calculated the proportion of
231   variance explained by each parameter, η2, as the sum of squares divided by the residual sum of
232   squares.
233
234   To determine if the social network metrics differed between life history stages, we used the same
235   set of models and calculated between group differences using the TukeyHSD() command in R (R
236   Core Team, 2017). To determine if variances differed among life history stages we used Brown-
237   Forsythe tests. We compared the observed differences and F statistics to those calculated from

238   one thousand data-stream permutations. We computed the data-stream permutations using the
239   network_permutation() command in R package asnipe, which allowed us to control for the
240   number of times an individual was observed as well as the location of those observations (Farine
241   & Whitehead, 2015; Farine, 2017). Then we calculated one-tailed p-values to test for significant
242   differences.

243

244   **Results**
245   In April of 2017, 209 individuals were in the population (Table 2). In 2017, we made 1104
246   sampling observations of 215 individuals. Of these individuals, 191 were detected three or more
247   times and included in the 2017 network. We analyzed data for 167 of the 191 included in the
248   network (Table 2). We excluded six individuals that did not survive to the end of the sampling
249   period, nine breeders and one helper from territories that did not meet the maximum distance
250   criterion and six breeders and two helpers from territories that did not meet the number of
251   adjacent territories criterion. In April of 2018, 194 individuals were in the population. The
252   network was based on 1324 observations of 206 individuals. From our analysis we excluded 12
253   individuals who did not survive the sampling period, three who were moving on and off our
254   study tract, and 17 breeders and 2 helpers from territories that did not meet the spatial inclusion
255   criteria.

256

257   The results conformed to some, but not all of our predictions (Table 1). Life history stage
258   explained a high proportion of the variance observed in all metrics in all years (Table 3).
259   Breeders tended to have fewer connections, lower betweenness, higher clustering coefficients,
260   and visited fewer unique points than helpers, and dominants were intermediate (Fig. 2, Table 4).
261   However, breeders did not have consistently less variation in their social network metrics than
262   helpers (Fig. 2, Table 5).

263

264   Dominants behaved as predicted, typically having metric scores between those of breeders and
265   helpers (Fig. 2). However, these differences were not consistent across metrics or years (Table
266   4). Dominants were detected at more unique points than breeders in all years and had higher
267   degree than breeders in 2017. Dominants had lower betweenness than helpers in both 2017 and
268   2018 and higher clustering coefficient in 2017.

269

270   Helpers differed significantly from breeders in all metrics in 2017 (Table 4). Helpers had higher
271   degree and betweenness, lower clustering coefficients, and were detected at more unique points
272   than breeders (Fig. 2). Although this pattern was also true in 2018, only the differences in
273   betweenness and the number of unique points detected were statistically significant. Female
274   helpers tended to have higher degree and betweenness, lower clustering coefficients, and to be
275   detected at more unique points than males (Fig.2). However, the magnitude of the sex
276   differences in degree, betweenness, and clustering coefficient only reached statistical

277   significance in 2017 (Table 4). The difference in the number of unique points female and male
278   helpers were detected was not significant in any year.
279
280
281   **Discussion**
282   We examined how social network position is shaped by life history stage in a cooperatively
283   breeding bird. Our results show that life history stage explains much of the observed variation in
284   social network position during the pre and early breeding season. The social network metrics we
285   calculated were generally consistent with our predictions based on nearly 50 years of
286   observations of Florida scrub-jay natural history (Woolfenden, 1975; Stallcup & Woolfenden,
287   1978; Woolfenden & Fitzpatrick, 1984, 1990; Stith, 1999). However, breeder behavior was
288   more variable than expected.
289
290   Our sampling period began approximately one month before the onset of nesting and ended
291   shortly after most pairs had active nests with eggs or young (Woolfenden & Fitzpatrick, 1984).
292   During the breeding season, breeders must defend their territory and tend their nest (Stallcup &
293   Woolfenden, 1978). Thus, breeders interacted primarily with their neighbors and group
294   members, which is reflected in all of the variables we measured. Breeders were detected at
295   relatively few unique points because they remained on or near their territory. This restricted the
296   pool of individuals with which they associated to primarily group-members and neighbors, and
297   occasionally helpers foraying nearby, leading to a paucity of connections. Group members and
298   neighbors are already directly connected to one another, thus breeders have little opportunity to
299   connect otherwise unconnected individuals, resulting in their low betweenness and high
300   clustering coefficient.
301
302   During our sampling period, helpers frequently forayed off their natal territory, occasionally
303   forming aggregations of unrelated helpers (Woolfenden & Fitzpatrick, 1990). Forays provide an
304   opportunity to interact with individuals from non-adjacent territories. These forays explain why
305   helpers are detected at more unique points, as well as their higher degree and betweenness, and
306   lower clustering coefficient. By interacting with jays from non-adjacent territories, helpers
307   indirectly connected their group members and neighbors to the families and neighbors of
308   individuals with which they associated on forays. Female Florida scrub-jays disperse earlier and
309   farther than males (Woolfenden & Fitzpatrick, 1978, 1984, 1990), thus we expected that female
310   helpers would have higher degree and betweenness, lower clustering coefficients, and visit more
311   unique points. However, we only detected significant differences between male and female
312   helpers in 2017 and only in degree, betweenness, and clustering coefficient. Despite females
313   being the dispersing sex, they were not detected at more unique points than males in either year.
314
315   Like breeders, dominants must defend their territory and, like helpers, they may be searching for
316   a mate, either by foraying or waiting for foraying helpers to visit their territories. Dominants'

317   metrics were intermediate between those of helpers and breeders, as predicted by the natural
318   history observations. Dominants were detected at more points than breeders in all years and had
319   higher degree in 2017. Dominants had significantly lower betweenness than helpers in 2017 and
320   2018, and higher clustering coefficient in 2017, but did not differ in the number of unique points
321   at which they were detected in any year. For helpers, we inferred that their high betweenness and
322   low clustering coefficients were driven by their foraging, which is reflected in the high number
323   of unique points at which they were detected. However, dominants and helpers did not differ in
324   the number of unique points at which they were detected but tended to differ in betweenness and
325   clustering coefficient. This suggests that the identity of the points at which an individual was
326   detected, and not only the number of unique points, may drive some of the variation in
327   betweenness and clustering coefficient. Dominants' low betweenness and high clustering
328   coefficients relative to the number of unique points they were detected could also be explained
329   by increased territorial intrusion from neighboring family groups. Territorial intrusions will
330   mainly be from groups with which the dominant bird shares a territorial border. These intrusions
331   may draw individuals residing on opposite sides of a dominant's territory together which could
332   increase dominants' clustering coefficients and decrease betweenness.
333
334   The quantitative social network metrics we calculated were generally consistent with the
335   qualitative observations previously published. However, the differences we predicted were not
336   statistically significant in all years and we observed more variation among breeders than
337   predicted. Yearly differences in demography, breeding opportunities, or both, driven by
338   environmental variation, may explain why we failed to detect significant differences between
339   breeders and helpers in 2018 that were evident in 2017. Between 2017 and 2018, the number of
340   scrub-jay family groups declined by 10, resulting in fewer breeders in our population. Yearly
341   changes in social behavior could be a passive reflection of, rather than an active response to,
342   changes in the social landscape. When individuals are removed or added to the network the
343   existence and arrangement of relationships in the network change (Shizuka & Johnson, 2019)
344   and changes to group composition can reduce the repeatability of social network metrics (Plaza
345   et al., 2019). Additionally, individual personality affects behavior (Aplin et al., 2013) and the
346   sets of individuals in any given life history stage are different every year. Therefore, some
347   amount of annual variation may be attributable to demographic changes rather than behavioral
348   plasticity.
349
350   Alternatively, the yearly variation we observed may be due to behavioral responses to
351   environmental conditions or the probability of breeding successfully. During 2018, the scrub-
352   jays experienced unusually low reproductive success. Nest success was much lower (32% versus
353   55% in 2017) and many pairs did not attempt to breed at all; only 56 of the 75 groups produced
354   nests with contents. Once a breeding pair lays their first egg, their behavior changes
355   dramatically: the breeding female incubates or broods, the breeding male provisions both female
356   and nestlings. Prior to laying, the behavior of breeding birds may be much more like dominants.

357 Thus, we reran the analysis for 2018 with the breeders that did not lay eggs categorized as
358 dominants, but as in the previous analysis we failed to detect significant differences in degree or
359 clustering coefficient between breeders that laid eggs and helpers. However, in 2018 the onset of
360 breeding also was delayed. On average, pairs began laying 20 days later in 2018 than in 2017.
361 Because our observational sampling period ends near the end of the first third of the breeding
362 season, we had many fewer sampling days where even breeders that eventually laid eggs, had
363 nests with contents, and thus may have been behaving more like dominants. It does suggest that
364 not only life-history stage, but individual life-histories and the environment can influence social
365 behavior.
366
367 Alternatively, the similarities we observed between breeders and helpers in 2018 could be
368 explained by helpers reducing their foray behavior. If helpers perceived that their chances of
369 breeding in 2018 were low, they may have reduced foraying behavior, choosing to further delay
370 dispersal until a year with better prospects. However, we see no evidence of reduced helper foray
371 behavior in 2018 and their social metrics were similar between 2017 and 2018. Therefore, we
372 conclude that extra-territory socialization is important regardless of life history stage, but may be
373 influenced by a variety of factors that might alter the costs and benefits of conducting off-
374 territory forays. When not actively tending nests with eggs or young, breeders may allocate more
375 time to interacting with individuals from other groups.
376
377 Current thinking frames the social behavior of Florida scrub-jay helpers as part of a strategy to
378 maximize their probability of obtaining a breeder position. However when breeders do not have
379 an active nest they socialize with a similar number of individuals, exhibit similar amounts of
380 cliquishness, and visit a similar number of unique points as individuals who are seeking a
381 territory and mate. This suggests that extra-territorial social behavior during the pre and early
382 breeding season has adaptive value beyond establishing a territory and finding a mate. Social
383 interactions between neighbors may reduce the overall costs of territory defense, either by
384 establishing boundaries prior to the increased energetic demands associated with breeding, or by
385 establishing coalitions to repel potential usurpers (Temeles 1994, Christensen and Radford
386 2018). Increased sociality also may serve to reduce predation risk or time spent in vigilance
387 (Groenewoud et al. 2016, Mady and Blumstein 2017, Waterman et al. 2019).
388
389 The physical environment and spatial distribution and availability of resources influence social
390 behavior, network structure and the transmission of information (Slobodchikoff, 1988; Foster et
391 al., 2012; Webster et al., 2013; Leu et al., 2016). Each year, we observe aggregation hotspots,
392 where helpers tend to aggregate frequently and in large numbers. These spots change yearly, but
393 little is known about what drives this variation. Helpers may be cueing in on habitat quality, the
394 availability of undefended habitat, or potential mates. Alternatively, they may be relying on
395 information transmitted through the social network about the location of these aggregations.
396 Regardless of what determines hotspot locations, helpers' attraction to them has the potential to

397 affect the network metrics of individuals in the vicinity. Additionally, helpers contribute to nest
398 and territory defense and vigilance against predators and their presence may allow breeders with
399 helpers to engage in more social behavior, especially with non-group members, than breeders
400 without helpers. Thus, individuals in one life history stage may influence the network position of
401 individuals in other stages, even if they are not exploiting the same resource.
402
403 Ecological needs and selection pressures change with life history stage. Therefore, life history
404 stage can have profound impacts on an individual's behavior and social network position. Social
405 behavior is adaptive (Alexander, 1974; Silk, Alberts & Altmann, 2003), and current social
406 behavior can affect future reproduction (McDonald, 2007). We demonstrate that life history
407 stage can explain much of the observed variation in individual social network position and that
408 breeding may constrain social behavior. Because many social species have stage-structured
409 populations, it is important to consider both the effect of life history stage and breeding status on
410 individual position within the social network.
411

Conclusions

412
413 We hypothesized that behavior within a social network would reflect life-history stage in the
414 cooperatively breeding Florida scrub-jay. We found that social behavior varies with life history
415 stage and between years. Research into whether individuals employ different socialization
416 strategies depending on the types and location of breeding opportunities is ongoing. Our results
417 demonstrate the power of life history stage to explain variation in social behavior and suggest
418 that social relationships between members of different groups may be more important than
419 previously realized.
420

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421
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A priori predictions about Florida scrub-jay social behavior based on life history stage.

Metric	Breeders	Dominants	Helpers	Justification for Predictions	Support for predictions
Within Stage Variance	low	high	high	• Little variation in how to maintain a territory and tend to young • Dominants foray if unpaired, remain on territory if paired • Helpers seek breeding opportunities and diverse routes to breeding increase variance in foray strategies.	Mixed • Differences in the amount of variation between life history stages was not consistent across years or metrics. • The variation in the number of unique points detected varied with life history stage in both years.
Degree, number of individuals an individual was associated with	low	intermediate	high	• Breeders typically defend only against neighbors • Dominant birds defend against usurpers and neighbors, may foray • Helpers foray, increasing the pool of individuals with which they can interact.	Mixed • Breeders differed from dominants and helpers in 2017, but not 2018. • Dominants and helpers did not differ in either year
Betweenness, the importance of a focal individual in connecting others	low	intermediate	high	• Breeders interact with group members and neighbors, all directly connected. • Dominants interact with more foraying non-breeders during territory defense • Helpers and unpaired dominants interact with individuals from non-adjacent territories during forays, connecting their group and neighboring groups to individuals from farther away.	Yes • Breeders and helpers differed significantly in both years • Dominants and helpers differed significantly in both years • Breeders and dominants did not differ in either year
Local Clustering Coefficient, proportion of an individual's	high	intermediate	low	• Same rational as betweenness	Mixed • Breeders differed from helpers in 2017, but not 2018. • Dominants differed from helpers in 2017, but not 2018.

associates which are themselves associated					
Number of Unique Points Detected	low	intermediate	high	• Breeders seen only at or near territory • Dominant birds seen at or near territory and on occasional forays • Helpers foray frequently and at longer distances	Yes • Breeders significantly differed from dominants and helpers in both years

Individuals in the population (counted April of the study year), network, and analyses.

Individuals that were included in the network and survived through the sampling period, but were not included in the analyses were from territories that failed to meet the spatial criteria for inclusion.

Year	2017						2018					
Stage	Breeder		Dominant		Helper		Breeder		Dominant		Helper	
Sex	F	M	F	M	F	M	F	M	F	M	F	M
Study Population	69	73	10	7	22	28	57	58	11	11	28	29
Included in Network	56	64	9	7	24	27	62	60	9	10	32	28
Analyzed	49	56	9	7	20	26	48	50	9	10	29	26
n	167						172					
% dyads SRI denominator < 20 (Denominator mean ± SE)	30% (30.16 ± 0.12)						6% (42.14 ± 0.11)					

Life history stage explains the highest proportion of explained variance, η^2, for all measured variables in both years.

Metric	Factor	2017				2018			
		SS	df	F	η^2	SS	df	F	η^2
Degree	Distance to Nearest Point	280.00	1.00	1.19	0.01	643.00	1.00	3.53	0.02
	Number of Adjacent Territories	9019.00	1.00	38.21	0.24	11695.50	1.00	64.17	0.39
	Life History Stage	14190.00	2.00	30.06	0.38	13759.90	2.00	37.75	0.46
	Sex	15.00	1.00	0.06	0.00	166.40	1.00	0.91	0.01
	Life History Stage *Sex	868.00	2.00	1.84	0.02	203.50	2.00	0.56	0.01
	Residuals	37534.00	159.00			29890.20	164.00		
Betweenness	Distance to Nearest Point	0.0000	1.00	0.00	0.00	0.0002	1.00	0.43	0.00
	Number of Adjacent Territories	0.0016	1.00	2.06	0.01	0.0002	1.00	0.49	0.00
	Life History Stage	0.0100	2.00	6.58	0.08	0.0110	2.00	12.60	0.15
	Sex	0.0004	1.00	0.54	0.00	0.0002	1.00	0.54	0.00
	Life History Stage *Sex	0.0028	2.00	1.83	0.02	0.0001	2.00	0.16	0.00
	Residuals	0.1207	159.00			0.0714	164.00		
Clustering Coefficient	Distance to Nearest Point	0.000	1.00	0.00	0.00	0.026	1.00	1.46	0.01
	Number of Adjacent Territories	0.541	1.00	26.75	0.17	0.207	1.00	11.79	0.07
	Life History Stage	1.507	2.00	37.24	0.48	0.485	2.00	13.80	0.17
	Sex	0.004	1.00	0.22	0.00	0.003	1.00	0.15	0.00
	Life History Stage *Sex	0.021	2.00	0.52	0.01	0.007	2.00	0.19	0.00
	Residuals	3.137	155.00			2.880	164.00		
Unique Points Detected	Distance to Nearest Point	23.29	1.00	4.68	0.03	8.31	1.00	1.75	0.01
	Number of Adjacent Territories	174.86	1.00	35.16	0.23	194.03	1.00	40.90	0.25
	Life History Stage	362.22	2.00	36.42	0.48	373.13	2.00	39.32	0.48
	Sex	1.41	1.00	0.28	0.00	8.46	1.00	1.78	0.01
	Life History Stage *Sex	18.61	2.00	1.87	0.02	13.37	2.00	1.41	0.02

Residuals 760.94 153.00 778.13 164.00

Observed and randomized differences in social network metrics ± 95% CI between life history stages in Florida scrub-jay (*Aphelocoma coerulescens*).

Observed differences were calculated using Tukey's honestly significant differences.Randomized difference and p-values for metrics calculated from the social network were estimated using 1000 data stream permutations. P-values < 0.05 are in bold.

Comparison	Metric	Prediction	Year	Observed Difference ± 95% Confidence Level	Mean Randomized Difference ± 95% Confidence Level, 1000 permutations	p
Breeders vs. Dominants	Degree	lower	2017	-17.12 ± 9.76	-16.18 ± 0.04	**< 0.001**
			2018	-14.19 ± 8.00	-13.76 ± 0.04	0.23
	Betweenness	lower	2017	-0.008 ± 0.017	-0.008 ± 0.0001	0.51
			2018	-0.001 ± 0.012	0.002 ± 0.0001	0.50
	Clustering Coefficient	higher	2017	0.173 ± 0.091	0.161 ± 0.0006	0.10
			2018	0.068 ± 0.079	0.081 ± 0.0002	0.99
	Unique Points	fewer	2017	-2.66 ± 1.42		**< 0.001**
			2018	-2.43 ± 1.29		**< 0.001**
Dominants vs. Helpers	Degree	lower	2017	-2.56 ± 10.55	-2.10 ± 0.03	0.14
			2018	-4.70 ± 8.50	-5.44 ± 0.04	0.79
	Betweenness	lower	2017	-0.009 ± 0.019	-0.003 ± 0.0001	**0.01**
			2018	-0.016 ± 0.013	-0.013 ± 0.0001	**< 0.001**
	Clustering Coefficient	higher	2017	0.032 ± 0.098	0.018 ± 0.0003	**< 0.001**
			2018	0.046 ± 0.083	0.039 ± 0.0003	0.12
	Unique Points	fewer	2017	-0.60 ± 1.55		0.63
			2018	-0.66 ± 1.37		0.49
Breeders vs. Helpers	Degree	lower	2017	-19.68 ± 6.43	-18.28 ± 0.02	**< 0.001**
			2018	-18.90 ± 5.38	-19.20 ± 0.03	0.80
	Betweenness	lower	2017	-0.018 ± 0.012	-0.012 ± 0.0001	**< 0.001**
			2018	-0.017 ± 0.008	-0.014 ± 0.0000	**< 0.001**
	Clustering Coefficient	higher	2017	0.206 ± 0.060	0.179 ± 0.0004	**< 0.001**
			2018	0.115 ± 0.053	0.121 ± 0.0002	0.98
	Unique Points	fewer	2017	-3.26 ± 0.96		**< 0.001**
			2018	-3.09 ± 0.87		**< 0.001**
♀ vs. ♂ Helpers	Degree	higher	2017	6.54 ± 13.18	1.87 ± 0.03	**< 0.001**
			2018	4.26 ± 10.51	5.90 ± 0.03	0.99
	Betweenness	higher	2017	0.009 ± 0.024	-0.002 ± 0.0002	**< 0.001**
			2018	0.000 ± 0.016	-0.001 ± 0.0002	0.41
	Clustering Coefficient	lower	2017	-0.025 ± 0.122	0.026 ± 0.0002	**< 0.001**
			2018	-0.024 ± 0.103	0.018 ± 0.00054	0.20
	Unique Points	more	2017	0.89 ± 1.98		0.79
			2018	1.08 ± 1.70		0.45

Brown-Forsythe tests for homogeneity of variance across life history stages.

The variance of degree, betweenness, clustering coefficient, and the number of unique points at which an individual was detected are not equal among life history stages in some years.

Metric	Year	Observed F Statistic for Homogeneity	Mean Randomized F ± 95% Confidence Level, 1000 permutations	p
Degree	2017	10.38	9.67 ± 0.05	0.19
	2018	1.47	0.61 ± 0.01	**< 0.001**
Betweenness	2017	6.39	4.29 ± 0.07	0.09
	2018	10.95	10.31 ± 0.10	0.32
Clustering Coefficient	2017	0.59	0.12 ± 0.01	**< 0.001**
	2018	0.82	2.24 ± 0.03	0.99
Unique Points Detected	2017	10.89		**< 0.001**
	2018	3.50		**0.03**

Figure 1

Location of Florida scrub-jay (*Aphelocoma coerulescens*) territories and aggregation sampling points at Archbold Biological Station in 2017 and 2018.

Boundaries shown here are as they were mapped in April of (A) 2017 and (B) 2018. Sampling points were non-randomly stratified with respect to territory boundaries as mapped the previous year and placed at least 200 m apart. Darkly shaded territories indicate that no individual from that territory was included in the statistical analyses, either because the individuals were detected too few times to be included in the network, or because the territory failed to meet the spatial criteria for inclusion in the analyses.
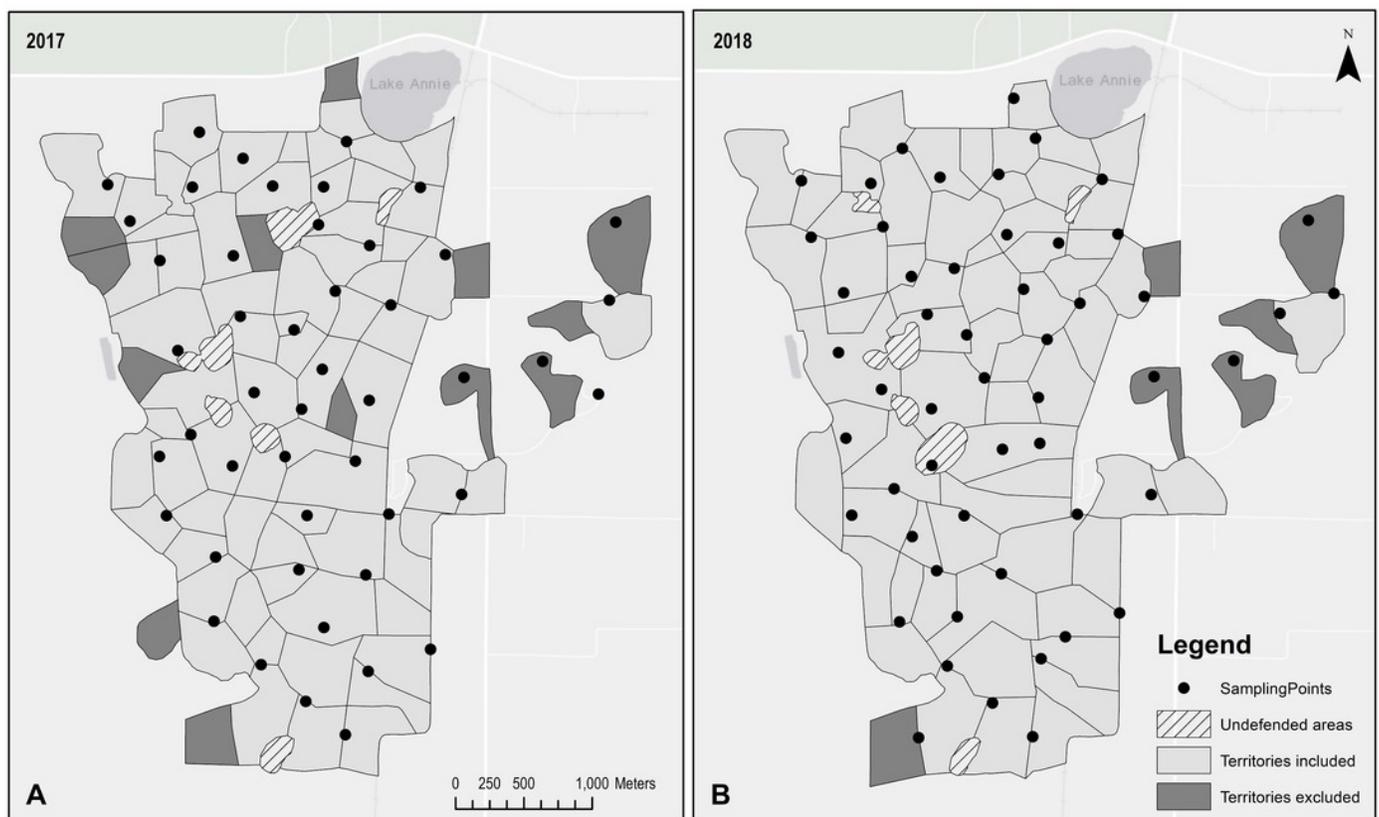
Figure 2

Boxplots showing degree, betweenness, clustering coefficient, and number of unique points visited for female and male Florida scrub-jays (*Aphelocoma coerulescens*) by life history stage.

(A) Breeders had significantly fewer connections (lower degree) than helpers in 2017. (B) Breeders connected otherwise unconnected individuals (lower betweenness) significantly less than helpers in both years. (C) Breeders exhibited significantly more "cliquish" behavior (higher clustering coefficient) than helpers in 2017. (D) Breeders were detected at significantly fewer unique points than helpers in 2017 and 2018.