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

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In species with stage-structured populations selection pressures may vary between different life history stages and result in stage-specific behaviors. We use life history stage to explain variation in the pre and early breeding season social behavior of a cooperatively breeding bird, the Florida scrub-jay (*Aphelocoma coerulescens*) using social network analysis. Whether an individual is a breeder or helper explains much of the variation we observed in social network metrics. These differences are consistent with nearly 50 years of natural history observations and conform to *a priori* predictions about how individuals in different stages should behave to maximize their individual fitness. Our results emphasize the importance of accounting for life history stage in studies of individual social behavior and validate our sampling methodology.

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17

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. Whether an individual is a
23 breeder or helper explains much of the variation we observed in social network metrics. These
24 differences are consistent with nearly 50 years of natural history observations and conform to a
25 priori predictions about how individuals in different stages should behave to maximize their
26 individual fitness. Our results emphasize the importance of accounting for life history stage in
27 studies of individual social behavior and validate our sampling methodology.

28

Introduction

30 A powerful way of quantifying social behaviors is social network analysis (Croft, James &
31 Krause, 2008). In these networks, individuals are considered connected when they interact or are
32 detected together (Whitehead & Dufault, 1999; Krause, Lusseau & James, 2009). From these
33 networks, a variety of metrics can be calculated, characterizing an individual's number and
34 strength of connections as well as its position relative to others in the network (Krause, Lusseau
35 & James, 2009). The ability to quantify the social environment as it is experienced by each
36 individual has led to improvements in the description of social structures (Wittemyer,
37 Douglas-Hamilton & Getz, 2005; Lusseau et al., 2006; Wey et al., 2008), insights into individual
38 variation and its consequences (Oh & Badyaev, 2010; Aplin et al., 2013), and a better

39 understanding of interactions between the social and physical environment (Firth & Sheldon,
40 2015; Pinter-Wollman, 2015; Leu et al., 2016). The influence of individual traits, including stress
41 physiology (Boogert, Farine & Spencer, 2014; Moyers et al., 2018), genetic relatedness (Ilany &
42 Akçay, 2016), and personality (Krause, James & Croft, 2010; Wilson et al., 2013; Snijders et al.,
43 2014; Sih et al., 2018) on social network position has been widely studied. Although several
44 studies have examined the effects of reproductive status on social behavior (Fischhoff et al.,
45 2009; Patriquin et al., 2010; Wey et al., 2013), few have explicitly examined the effects of life
46 history stage (but see Wey et al., 2013).
47
48 In stage-structured populations, life history stages are not necessarily related to age and each is
49 described by its own set of demographic parameters. Because selection pressures in each stage
50 are different (Schluter, Price & Rowe, 1991), the stage-structure of a population can have
51 profound impacts on its demography (Tuljapurkar & Caswell, 2012), ecology (Miller & Rudolf,
52 2011), and conservation (Crouse, Crowder & Caswell, 1987). Individuals in different life-history
53 stages have different strategies to maximize their fitness, which can affect social behaviors
54 within a population (Rudolf, 2007; Blumstein, Wey & Tang, 2009; Fischhoff et al., 2009).
55
56 In species and during times during the annual cycle when life history strategies differ among
57 stages, we can make robust predictions about how social behavior might vary and thus, the social
58 network position of individuals in different stages. These predictions can provide a suitable
59 model against which we can evaluate whether the social network, and the data from which it is
60 derived, are accurate representations of real-world behavior.
61
62 Cooperative breeders are highly social and tend to have stage-structured populations (Ekman et
63 al., 2004), making them excellent model systems in which to evaluate social networks. Florida
64 scrub-jays (Aphelocoma coerulescens) are a well-studied cooperative breeder, and stage-specific
65 behavioral differences are thoroughly described (Woolfenden & Fitzpatrick, 1984, 1990). Florida
66 scrub-jays are territorial and non-migratory, living in family groups consisting of a single,
67 monogamous breeding pair that monopolizes all reproductive effort and 0-7 helpers
68 (Woolfenden & Fitzpatrick, 1984; Townsend et al., 2011). Helpers are most commonly the
69 offspring of the breeding pair on whose territory they reside, but occasionally (less than 15%) are
70 associated with unrelated or distantly related breeders (Woolfenden & Fitzpatrick, 1990). Within
71 these groups a strict dominance hierarchy exists; breeders are the most dominant, and among
72 helpers, males are dominant over females, and older birds are dominant to younger birds
73 (Woolfenden & Fitzpatrick, 1977, 1984). Hierarchies also exist within stages, cohorts, and
74 broods (Woolfenden & Fitzpatrick, 1977; Tringali & Bowman, 2012).
75
76 Florida scrub-jays' rigid breeding system allows us to classify all adults into one of three stages:
77 (1) breeders, who own territories and have been associated with a nest with contents; (2)
78 dominants, who own territories, but have not yet bred; and (3) helpers, who neither own

79 territories nor breed (Woolfenden & Fitzpatrick, 1984, 1990). Typically, dominants have only
80 recently acquired a territory, and may or may not have paired with a mate. Individuals usually
81 remain classified as dominants for less than a year but in rare cases, dominant birds or their
82 mates are infertile, failing to produce eggs after multiple breeding seasons. Hereafter, we will use
83 dominant as it refers to life history stage, and not as a position within the social hierarchy.
84
85 Prior to and during the early breeding season, behavioral strategies vary with life history stage.
86 Breeders already have a territory and must maintain it and breed. They defend their territories,
87 engage in courtship behavior with their mate, and build and tend to their nest and its contents
88 (Stallcup & Woolfenden, 1978; Woolfenden & Fitzpatrick, 1984). Non-breeding helpers are
89 seeking their first breeding opportunity. During this time, helpers reside at their natal or home
90 territory and assist with its defense and vigilance against predators while also making repeated
91 forays off-territory in search of potential breeding opportunities. Many routes to becoming a
92 breeder exist, including pairing with a recently widowed breeder or unpaired dominant,
93 establishing a territory in vacant habitat or, for males, inheriting all or a portion of their natal
94 territory (Woolfenden & Fitzpatrick, 1977, 1978, 1984, 1990; Breininger, 1999; Stith, 1999).
95 Dominant birds are those that are defending a territory, but have yet to breed (defined as laying
96 or siring an egg). They may be paired or unpaired. If unpaired, they may defend against many
97 more potential usurpers than do established pairs and they also may foray, attempting to attract a
98 mate.
99
100 In this paper, we test the hypothesis that Florida scrub-jay social behavior during the pre and
101 early breeding season reflects stage-specific differences in life-history strategy. We draw on 50
102 years of study to make several predictions (Table 1). Because there is one way to defend a
103 territory, but many ways to obtain one, we predict that (1) breeders will exhibit the least within-
104 stage variation and helpers the most. Breeders do not foray, which restricts the pool of
105 individuals they can associate with to family-group members, neighbors, and helpers foraying
106 nearby. Helpers may foray frequently, and dominants may foray if unpaired, thus we predict that
107 (2) breeders will have the fewest associations and helpers the most, (3) breeders will rarely
108 connect otherwise unconnected individuals and helpers will do so frequently, (4) breeders will
109 exhibit more "cliquish" behavior, associating with individuals that are themselves associated,
110 and helpers will not and (5) breeders will be detected at the fewest unique locations and helpers
111 at the most. We also predict that individuals will change their social behavior when they
112 transition from one stage to another. Additionally, we argue that confirmation to these a priori
113 predictions validates the use of our point-count methodology to collect the aggregation data with
114 which we construct social networks and the usefulness of social network position to describe
115 variation in social behavior in this species.
116
117
118
119 **Materials & Methods**

120 **In the field**
121 We conducted this study on an individually marked population of Florida scrub-jays at Archbold
122 Biological Station in Highlands County, Florida (21° 10'N, 81° 21'W). As part of a long term
123 and ongoing study, we band all scrub-jays with unique combinations of color bands and census
124 the population monthly (see Woolfenden and Fitzpatrick 1984 for a detailed description of our
125 demographic study methods). The nesting season can begin as early as February and continues
126 into June. Each year, we find all nests and map the boundaries of each territory.
127 From February through April of 2016 and 2017, we surveyed for jays at points placed at least
128 200 m apart and non-randomly stratified across all territories (Fig.1). Florida scrub-jays
129 vigorously defend their territories, which average about 9 ha (Woolfenden & Fitzpatrick, 1990).
130 While deep intrusion of one group's territory by another is relatively infrequent, mutual defense
131 along shared boundaries is routine. Prospecting forays by non-breeding helpers tend to occur
132 along these boundaries (Woolfenden & Fitzpatrick, 1990). Thus, we stratified sampling at the
133 intersections of territory boundaries is to ensure that 1) we capture interactions of birds foraying
134 away from their home territory among themselves and with local birds and 2) all individual birds
135 had an opportunity to be sampled, even those that did not foray. Because sampling begins just
136 prior to the onset of breeding and before we can accurately map territories, we based the
137 placement of sampling points on the territory boundaries mapped the previous year. Territory
138 boundaries are relatively stable each year, but do fluctuate annually and within a season
139 (Woolfenden, 1975; Woolfenden & Fitzpatrick, 1990).
140
141 We sampled these points once a week in 2016 and twice a week in 2017 using playback of
142 territorial calls. Use of playback is appropriate for this species for two reasons: 1) it mimics what
143 occurs when there is a disturbance in the existing social structure, such as the death of a breeder,
144 which are the types of opportunities foraying helpers are searching for and 2) breeders,
145 dominants, and helpers all defend their territorial boundaries. Therefore, this sampling scheme
146 will detect individuals foraying off-territory without creating artificial associations. Calls were
147 sourced from recordings made in the same metapopulation as our study population (Coulon et
148 al., 2008), but are several decades old. Thus, these calls are in the local dialect, but not from
149 individuals known to any jays in our study. We randomized the order in which we visited points
150 using a random number generator. We played territorial calls on a portable speaker for a total of
151 2 minutes, 30 seconds in each cardinal direction, with 30-second breaks after each. Then we
152 waited an additional minute for birds to respond, so that each visit lasted a minimum of 5
153 minutes. We recorded the identities of all birds present at survey points using Survey123 (ESRI,
154 2018). We assumed that all birds detected together at a point were associated. We also recorded
155 opportunistic observations of aggregations of jays from non-adjacent territories.
156
157 All research was conducted under the required permits from the United States Geological Survey
158 Bird Banding Lab (07732) and the United States Fish and Wildlife Service (TE824723-9).
159

160 **Constructing the social networks**
161 We included all individuals detected three or more times in group-by-individual matrices for
162 each year. We used R package asnipe to build a network for each year, using the simple ratio
163 index to correct for detection probabilities (Whitehead, 2008; Farine & Whitehead, 2015;
164 Hoppitt & Farine, 2018). We calculated three metrics to describe individuals' behavior in the
165 network using R package igraph (Csardi & Nepusz, 2006): (1) degree, the number of individuals
166 an individual was associated with; (2) vertex betweenness centrality (hereafter betweenness), the
167 importance of a focal individual in connecting other birds or connected groups, i.e., the number
168 of times a focal individual lies on shortest paths between two other individuals; and (3) local
169 clustering coefficient, the proportion of the focal individual's associates which are themselves
170 associated (Croft, James & Krause, 2008; Beveridge & Shan, 2016). We also counted the
171 number of unique sampling points at which each individual was detected.
172
173 **Statistical analyses**
174 We adopted spatial criteria for inclusion in our statistical analyses because yearly changes to
175 territory boundaries could result in uneven sampling coverage and because territories along the
176 periphery have fewer neighboring territories and tended not to have helpers. We calculated the
177 distance between the territory edge and the nearest sampling point and number of immediately
178 adjacent territories for all territories as they were mapped in the year they were sampled using
179 the Generate Near Table and Polygon Neighbors tools in ArcMap (ESRI, 2015).
180 Individuals from territories that did not have a sampling point within 100 m of their territory
181 boundary and those from territories with one or fewer immediately adjacent neighboring
182 territories were excluded from the statistical analyses. Then we used ANOVA to confirm that the
183 life history stages did not differ in the distance to nearest sampling point (2016: $F_{2, 177} = 0.04$, p
184 = 0.96; 2017: $F_{2, 164} = 1.04$, p = 0.36) nor number of adjacent territories (2016: $F_{2, 177} = 0.06$,
185 p = 0.94; 2017: $F_{2, 164} = 1.71$, p = 0.18).
186
187 We constructed two sets of linear models. The first set explained each social network variable in
188 each year by sex, life history stage, their interaction, the number of territories adjacent to their
189 territory, and the distance to the nearest sampling point. We used this set of models to calculate
190 the proportion of variance explained by each parameter and whether the amount of variation
191 differed among life history stages. We calculated the proportion of explained variance, η^2, as the
192 sum of squares divided by the residual sum of squares. We used Brown-Forsythe tests to
193 determine if variances differed among life history stages for each of our four metrics.
194
195 To determine if the social network metrics differed between life history stages, we constructed a
196 second set of linear models which explained each metric in each year as a response of life history
197 stage, sex, and their interaction. Degree was square root transformed prior to analyses. We used
198 the TukeyHSD() command in R (R Core Team, 2017) to calculate between group differences. To
199 test for significance, we used one thousand node-based permutations, where the social network is

200   left constant, but attributes (sex, life history stage, or both) of the individuals, or nodes, are
201   randomized in each permutation (Farine & Whitehead, 2015; Farine, 2017). Using these
202   permutations we estimated one-tailed p-values.

203

204   To test the prediction that individuals would change their behavior when their life history stage
205   changed we used paired t-tests. For these analyses we used birds that were helpers in 2016 and
206   analyzed them in two separate groups: those that remained helpers in 2017 and those that
207   transitioned to breeders. To test for significance we used node-based permutations, where the
208   metrics were randomized with respect to the year they were measured (Farine & Whitehead,
209   2015).

210

211   Results

212   In April of 2016, 227 scrub-jays were present in our study population (Table 2). During the 2016
213   sampling period we made 307 observations of 221 individuals. Of these individuals, 189 were
214   detected three or more times, and thus included in the 2016 network (Table 2). We analyzed data
215   for 180 of the 189 individuals included in the network. We excluded three individuals that did
216   not survive to the end of the sampling period, one that dispersed outside of our study area during
217   sampling, and breeders from four territories that did not meet the maximum distance criterion
218   and one that did not meet the number of adjacent territories criterion (Table 2). In April of 2017,
219   209 individuals were in the population (Table 2). In 2017, we made 618 sampling observations
220   of 215 individuals. Of these individuals, 191 were detected three or more times and included in
221   the 2017 network. We analyzed data for 166 of the 191 included in the network (Table 2). We
222   excluded six individuals that did not survive to the end of the sampling period, nine breeders and
223   one helper from territories that did not meet the maximum distance criterion and six breeders and
224   two helpers from territories that did not meet the number of adjacent territories criterion. We
225   applied the same criteria to our analysis of whether behavior changed with life history stage and
226   analyzed data for seven individuals that helped in 2016 and bred in 2017 and ten that helped in
227   both years.

228

229   Overall, the results conformed to our predictions (Table 1). Life history stage explained a high
230   proportion of the variance observed in all metrics in all years (Table 3). Breeders had less
231   variation than helpers in the number of connections, betweenness, and number of unique points
232   visited than helpers (Fig. 2, Table 4). Breeders had fewer connections, lower betweenness, higher
233   clustering coefficients, and visited fewer unique points than helpers, and dominants were
234   intermediate (Fig. 2, Table 5).

235

236   Dominants behaved as predicted, typically having metric scores between those of breeders and
237   helpers (Fig. 2). However, these differences were not consistent across metrics or years (Table
238   5). In 2016, dominants differed significantly from breeders in clustering coefficient and number
239   of unique points detected, and from helpers in number of connections, betweenness, and

240   clustering coefficient. In 2017, dominants differed significantly from breeders in degree,
241   clustering coefficient, and number of unique points detected, but not from helpers.
242
243   Helpers differed significantly from breeders in all metrics in all years (Table 5). As expected,
244   helpers had higher degree and betweenness, lower clustering coefficients, and were detected at
245   more unique points (Fig. 2). Female helpers tended to have higher degree and betweenness,
246   lower clustering coefficients, and to be detected at more unique points than males (Fig.2).
247   However, the magnitude of these sex differences only reached statistical significance for degree
248   in 2017 and clustering coefficient in 2016 (Table 5).
249
250   Individuals that helped in both 2016 and 2017 did not differ in their number of connections,
251   betweenness, or number of unique points detected from one year to the next (Fig. 3, Table 5).
252   However, their clustering coefficient did increase significantly from 2016 to 2017. Individuals
253   that helped in 2016 and bred in 2017 significantly reduced their number of connections and
254   increased their clustering coefficients as breeders (Fig. 3, Table 5). Those that transitioned also
255   tended to have lower betweenness and fewer number of unique points detected as breeders than
256   as helpers, but these trends were not statistically significant (Fig. 3).
257

Discussion

259   We examined how social network position is shaped by life history stage in a cooperatively
260   breeding bird. Our results show that life history stage explains much of the observed variation in
261   social network position during the early breeding season. The social network metrics we
262   calculated are consistent with predictions from nearly 50 years of observations of Florida scrub-
263   jay natural history (Woolfenden, 1975; Stallcup & Woolfenden, 1978; Woolfenden &
264   Fitzpatrick, 1984, 1990; Stith, 1999). The concordance of our quantitative measures of Florida
265   scrub-jay social behavior with previously published qualitative natural history descriptions also
266   validates the suitability of our sampling methodology.
267
268   Our sampling period begins approximately one month before the onset of nesting and ends about
269   the time most pairs have active nests with eggs or young (Woolfenden & Fitzpatrick, 1984).
270   During the breeding season, breeders must defend their territory and tend their nest (Stallcup &
271   Woolfenden, 1978). Thus, they are interacting primarily with their neighbors and group
272   members, which is reflected in all of the variables we measured. Breeders are detected at fewer
273   unique points because they are remaining on or near their territory. This restricts the pool of
274   individuals with which they associate to primarily group-members and neighbors, and
275   occasionally helpers foraging nearby, leading to a paucity of connections. Group members and
276   neighbors are already directly connected to one another, thus breeders have little opportunity to
277   connect otherwise unconnected individuals, resulting in their low betweenness and high
278   clustering coefficient.
279

280 During our sampling period, helpers frequently foray off their natal territory, occasionally
281 forming aggregations of unrelated helpers (Woolfenden & Fitzpatrick, 1990). Forays provide an
282 opportunity to interact with individuals from non-adjacent territories. These forays explain why
283 helpers are detected at more unique points, as well as their higher degree and betweenness, and
284 lower clustering coefficient. By interacting with jays from non-adjacent territories, helpers
285 indirectly connect their group members and neighbors to the families and neighbors of
286 individuals with which they associated on forays. Female Florida scrub-jays disperse earlier and
287 farther than males (Woolfenden & Fitzpatrick, 1978, 1984, 1990), thus we expected that female
288 helpers would have higher betweenness and lower clustering coefficients. However, the only
289 significant difference we detected between male and female helpers was in clustering coefficient
290 in 2016.
291
292 Like breeders, dominants must defend their territory and, like helpers, they may be searching for
293 a mate, either by foraying or waiting for foraying helpers to visit their territories. Dominants
294 tended to have higher degree and were detected at more unique points in 2017, thus it appears
295 that dominants forayed more in 2017 than in 2016, which explains why their metrics were
296 similar to helpers in 2017 and breeders in 2016. Although dominants behaved more similarly to
297 breeders in one year and helpers in another, their metrics were intermediate between the two in
298 both years, as predicted by the existing natural history observations.
299
300 The quantitative social network metrics we calculated are consistent with the qualitative
301 observations previously published. Because of the robust nature of these natural history
302 observations, we believe the concordance observed indicates that our sampling methodology is
303 suitable to construct a social network for Florida scrub-jays. However breeders, especially
304 females, are less likely to meet the detection criteria for inclusion in the network. This is driven
305 in part by biology; our sampling period overlaps the onset of nesting and breeding females may
306 be reluctant to leave the vicinity of their nest during laying and incubation. While this means that
307 the differences we observe between life history stages are conservative, we would need to
308 sample more intensively to detect differences among breeders.
309
310 We hypothesized that if life history stage is an important driver of social behavior individuals
311 should change their behavior when they transition from one stage to another. Helpers that
312 became breeders showed a significant reduction in their number of connections and tended to be
313 detected at fewer points as breeders. Although we did not detect significant changes in all
314 metrics after life history stage transition, the high proportion of variance explained by life history
315 stage, combined with the changes we did observe, demonstrate that it is an important driver of
316 individual variation in social behavior.
317
318 The tendency to change behavior with stage suggests that social behaviors are plastic. If this is
319 true, individuals that help in multiple years may change their behavior yearly, exploiting

320 different socialization and exploration tactics depending on the type, number, and spatial
321 distribution of breeding opportunities available.
322
323 Yearly changes in behavior also could be a reflection of, rather than a response to changes in the
324 social landscape. Individual personality affects behavior (Aplin et al., 2013) and the sets of
325 individuals in any given life history stage are different every year. Therefore, some amount of
326 annual variation may be attributable to individual identity rather than behavioral plasticity.
327 Our data suggest that an individual's social behavior as a helper may affect its probability of
328 transitioning to a breeding position. For example, helpers that transitioned to breeders in 2017
329 tended to have lower degree and betweenness, and higher clustering coefficient as helpers than
330 helpers who remained helpers (Fig. 3). Although our investigation into this possibility is
331 ongoing, similarly adaptive socialization strategies have been documented in other species. Great
332 tits (Parus major) increase their chance of acquiring a breeding territory by associating with late-
333 arrivers to the breeding grounds, who are less likely to breed (Farine & Sheldon, 2015). In
334 Florida scrub-jays, larger natal territory size and nestling mass are associated with increased
335 probability of breeding (Mumme et al., 2015). Scrub-jays could manipulate their pool of
336 associates similarly in order to maximize their competitive advantage.
337
338 Various paths to obtaining a breeding position exist, but the probability of success for these
339 routes likely varies with individual attributes. We would expect a male high in the social
340 hierarchy with a high probability of inheriting all or some of his natal territory to make fewer
341 forays than his lower ranking sibling, whose best chance at obtaining a breeding position might
342 be pairing with a widow or establishing a new territory. For a given individual, the most likely
343 path to becoming a breeder will vary by individual attributes (i.e. mass, social dominance rank)
344 and population-wide factors (i.e. breeder mortality or amount of available habitat) and thus may
345 explain both the high variance in within-year helper behavior and some of the interannual
346 variation we observed (Fig. 2).
347
348 The physical environment and spatial distribution and availability of resources influence social
349 behavior, network structure and the transmission of information (Slobodchikoff, 1988; Foster et
350 al., 2012; Webster et al., 2013; Leu et al., 2016). Each year, we observe aggregation hotspots,
351 where helpers tend to aggregate frequently and in large numbers. These spots change yearly, but
352 little is known about what drives this variation. Helpers may be cueing in on habitat quality, the
353 availability of undefended habitat, or potential mates. Alternatively, they may be relying on
354 information transmitted through the social network about the location of these aggregations.
355 Regardless of what determines hotspot locations, helpers' attraction to them has the potential to
356 affect the network metrics of individuals in the vicinity. Thus, the ecological needs of individuals
357 in one life history stage may influence the network position of individuals in other stages, even if
358 they are not exploiting the same resource.
359

360 Ecological needs and selection pressures change with life history stage. Therefore, life history
361 stage can have profound impacts on an individual's behavior and social network position. Social
362 behavior is adaptive (Alexander, 1974; Silk, Alberts & Altmann, 2003), and current social
363 behavior can affect future reproduction (McDonald, 2007). We demonstrate that life history
364 stage can explain much of the observed variation in individual social network position and that
365 some metrics of social behavior change with life history stage. These findings indicate that social
366 network analysis will be a useful tool for evaluating how variation in social behavior influences
367 recruitment to breeding and subsequent variation in fitness. Because many social species have
368 stage-structured populations, it is important to consider the effect of life history stage on
369 individual position within the social network.
370

Conclusions

372 We hypothesized that behavior within a social network would reflect life-history stage in the
373 cooperatively breeding Florida scrub-jay. We found that social behavior varies with life history
374 stage and is plastic. Research into whether individuals employ different socialization strategies
375 depending on the types and location of breeding opportunities is ongoing. Social network
376 analysis is becoming an increasingly widely used tool and our results demonstrate the power of
377 life history stage to explain variation in these metrics.
378

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383

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522

Table 1(on next page)

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

1

Metric	Breeders	Dominants	Helpers	Justification 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.
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.
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.
Local Clustering Coefficient, proportion of an individual's associates which are themselves associated	high	intermediate	low	• Same rational as betweenness
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

2

Table 2(on next page)

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.

1

Year	2016						2017					
Stage	Breeder		Dominant		Helper		Breeder		Dominant		Helper	
Sex	F	M	F	M	F	M	F	M	F	M	F	M
Study Population	80	79	7	7	30	24	69	73	10	7	22	28
Included in Network	58	65	8	7	28	23	57	65	9	7	25	28
Survived to End of Sampling	58	65	7	6	28	21	56	64	9	7	22	27
Analyzed	56	62	7	6	28	21	49	55	9	7	20	26
n			180						166			

2

Table 3(on next page)

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

1

Metric	Factor	2016				2017			
		SS	df	F	η^2	SS	df	F	η^2
Degree	Distance to Nearest Point	7.68	1	5.30	0.03	2.26	1	0.94	0.01
	Number of Adjacent Territories	48.37	1	33.33	0.19	116.98	1	48.68	0.31
	Life History Stage	116.86	2	40.23	0.47	138.45	2	28.81	0.36
	Sex	0.21	1	0.15	0.00	0.07	1	0.03	0.00
	Life History Stage *Sex	2.08	2	0.72	0.01	5.95	2	1.24	0.02
	Residuals	249.57	172			379.66	158		
Betweenness	Distance to Nearest Point	0.000	1	0.38	0.00	0.000	1	0.00	0.00
	Number of Adjacent Territories	0.002	1	0.49	0.04	0.001	1	2.04	0.01
	Life History Stage	0.016	2	25.53	0.29	0.010	2	6.47	0.08
	Sex	0.001	1	2.20	0.02	0.000	1	0.57	0.00
	Life History Stage *Sex	0.001	2	2.01	0.02	0.003	2	1.85	0.02
	Residuals	0.055	172			0.121	158		
Clustering Coefficient	Distance to Nearest Point	0.24	1	10.16	0.06	0.00	1	0.01	0.00
	Number of Adjacent Territories	0.27	1	11.66	0.07	0.54	1	26.70	0.17
	Life History Stage	2.04	2	43.40	0.51	1.47	2	36.62	0.48
	Sex	0.01	1	0.30	0.00	0.01	1	0.32	0.00
	Life History Stage *Sex	0.24	2	5.05	0.06	0.02	2	0.61	0.01
	Residuals	4.00	170			3.10	154		
Unique Points Detected	Distance to Nearest Point	0.86	1	0.71	0.00	23.94	1	4.80	0.03
	Number of Adjacent Territories	5.23	1	4.29	0.03	174.23	1	34.93	0.23
	Life History Stage	85.74	2	35.17	0.41	357.80	2	35.86	0.47
	Sex	0.01	1	0.01	0.00	1.17	1	0.23	0.00
	Life History Stage *Sex	5.38	2	2.21	0.03	19.37	2	1.94	0.03
	Residuals	208.42	171			758.24	152		

2

3

Table 4(on next page)

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

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

1

Metric	Year	Observed F Statistic for Homogeneity	Mean Randomized F ± 95% Confidence Level, 1000 permutations	p
Degree	2016	7.45	0.97 ± 0.06	**0.001**
	2017	10.38	1.00 ± 0.06	**< 0.001**
Betweenness	2016	26.25	1.02 ± 0.08	**< 0.001**
	2017	6.39	1.05 ± 0.07	**0.007**
Clustering Coefficient	2016	0.70	0.96 ± 0.06	0.46
	2017	0.59	0.97 ± 0.06	0.55
Unique Points Detected	2016	10.92		**< 0.001**
	2017	10.89		**< 0.001**

2

Table 5 (on next page)

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 differences and p-values for metrics calculated from the social network were estimated using 1000 node-based permutations. P-values smaller than 0.05 are in bold.

Comparison	Metric	Year	Observed Difference ± 95% Confidence Level	Mean Randomized Difference ± 95% Confidence Level, 1000 permutations	p
Breeders vs. Dominants	Degree	2016	-0.515 ± 0.918	-0.002 ± 0.028	0.12
		2017	-1.429 ± 1.117	0.002 ± 0.033	**0.005**
	Betweenness	2016	-0.005 ± 0.012	0 ± 0.0004	0.18
		2017	-0.007 ± 0.017	0.0003 ± 0.0005	0.19
	Clustering Coefficient	2016	0.123 ± 0.112	-0.002 ± 0.004	**0.02**
		2017	0.146 ± 0.098	0 ± 0.003	**0.001**
	Unique Points	2016	-0.812 ± 0.765		**0.03**
		2017	-2.086 ± 1.572		**0.006**
Dominants vs. Helpers	Degree	2016	-1.301 ± 0.981	-0.003 ± 0.031	**0.003**
		2017	-0.601 ± 1.208	0.004 ± 0.037	0.16
	Betweenness	2016	-0.017 ± 0.013	0 ± 0.0004	**0.01**
		2017	-0.011 ± 0.019	0 ± 0.001	0.07
	Clustering Coefficient	2016	0.114 ± 0.120	0.002 ± 0.004	**0.04**
		2017	0.065 ± 0.105	0 ± 0.003	0.12
	Unique Points	2016	-0.760 ± 0.821		0.08
		2017	-1.259 ± 1.711		0.19
Breeders vs. Helpers	Degree	2016	-1.816 ± 0.534	-0.006 ± 0.016	**< 0.001**
		2017	-2.029 ± 0.736	-0.013 ± 0.022	**< 0.001**
	Betweenness	2016	-0.022 ± 0.007	0 ± 0.0002	**< 0.001**
		2017	-0.018 ± 0.012	0 ± 0.0003	**< 0.001**
	Clustering Coefficient	2016	0.237 ± 0.065	0 ± 0.002	**< 0.001**
		2017	0.211 ± 0.064	0 ± 0.002	**< 0.001**
	Unique Points	2016	-1.572 ± 0.448		**< 0.001**
		2017	-3.345 ± 1.063		**< 0.001**
♀ vs. ♂ Helpers	Degree	2016	0.175 ± 1.106	-0.025 ± 0.025	0.33
		2017	0.994 ± 1.509	0.008 ± 0.035	**0.04**
	Betweenness	2016	0.012 ± 0.015	0 ± 0.0006	0.11
		2017	0.012 ± 0.024	0 ± 0.001	0.16
	Clustering Coefficient	2016	-0.114 ± 0.135	0.002 ± 0.003	**0.002**
		2017	-0.065 ± 0.131	0 ± 0.003	0.07
	Unique Points	2016	0.548 ± 0.926		0.56
		2017	-1.623 ± 2.188		0.27
Yearly differences: helped in both years	Degree		2.600 ± 19.72	0.052 ± 0.528	0.39
	Betweenness		0 ± 0.038	0 ± 0.001	0.52
	Clustering Coefficient		-0.147 ± 0.120	0 ± 0.004	**< 0.001**
	Unique Points		-2.375 ± 2.525		0.06

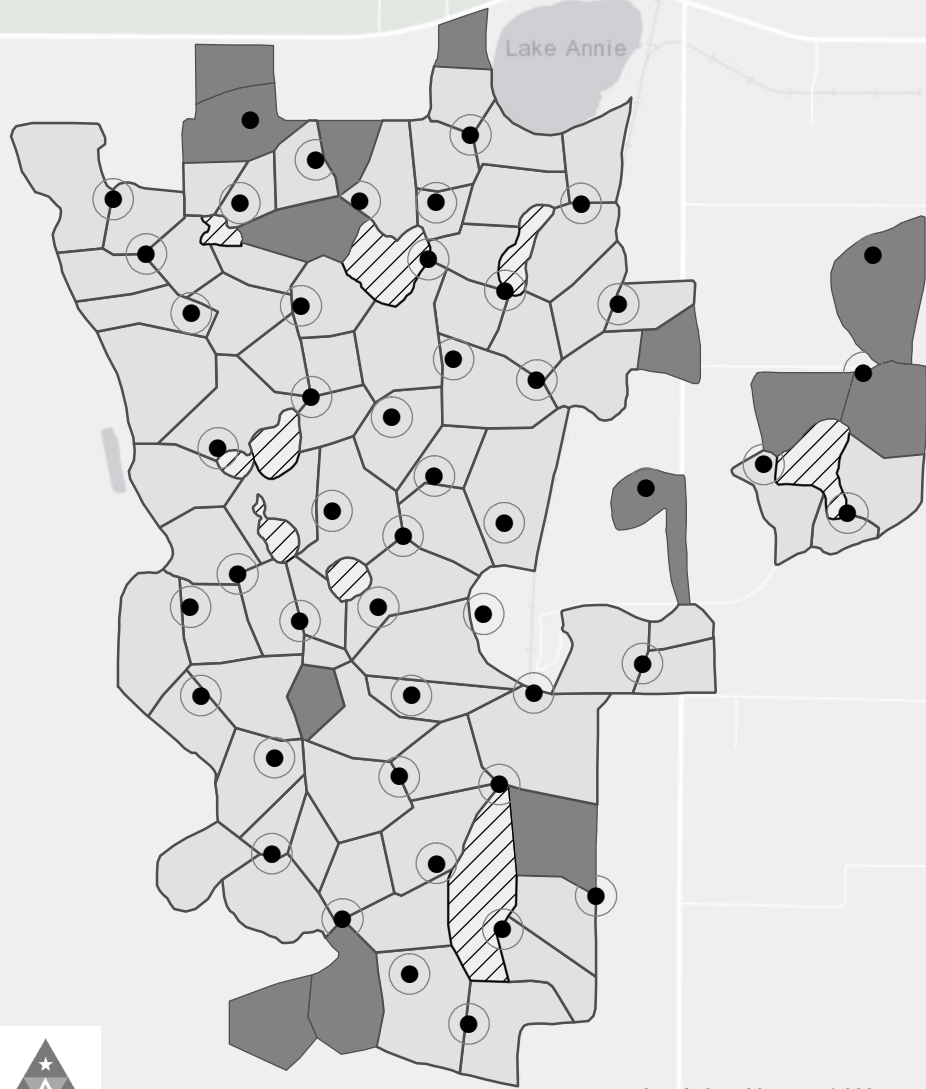| Yearly differences: helped in 2016, bred in 2017 | Degree | 11.750 ± 10.506 | -0.010 ± 0.365 | **0.03** |
	Betweenness	0.005 ± 0.017	0 ± 0.0004	0.255
	Clustering Coefficient	-0.199 ± 0.146	0 ± 0.006	**0.007**
	Unique Points	0.125± 2.584		0.91

2

Figure 1(on next page)

Location of Florida scrub-jay (Aphelocoma coerulescens) territories and aggregation sampling points at Archbold Biological Station in 2016 and 2017.

Boundaries shown here are as they were mapped in April of the sampling year. Sampling points were non-randomly stratified with respect to territory boundaries as mapped the previous year. 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.
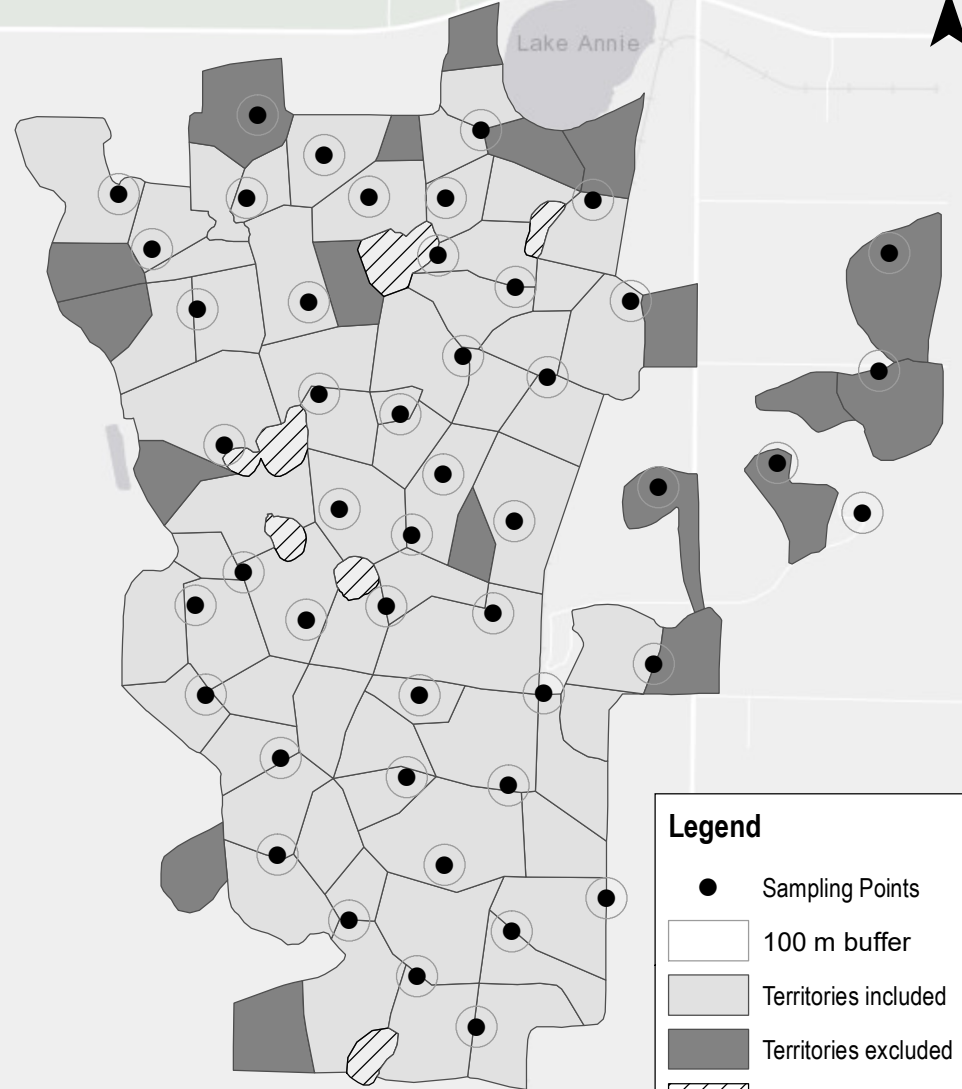
2016

Lake Annie

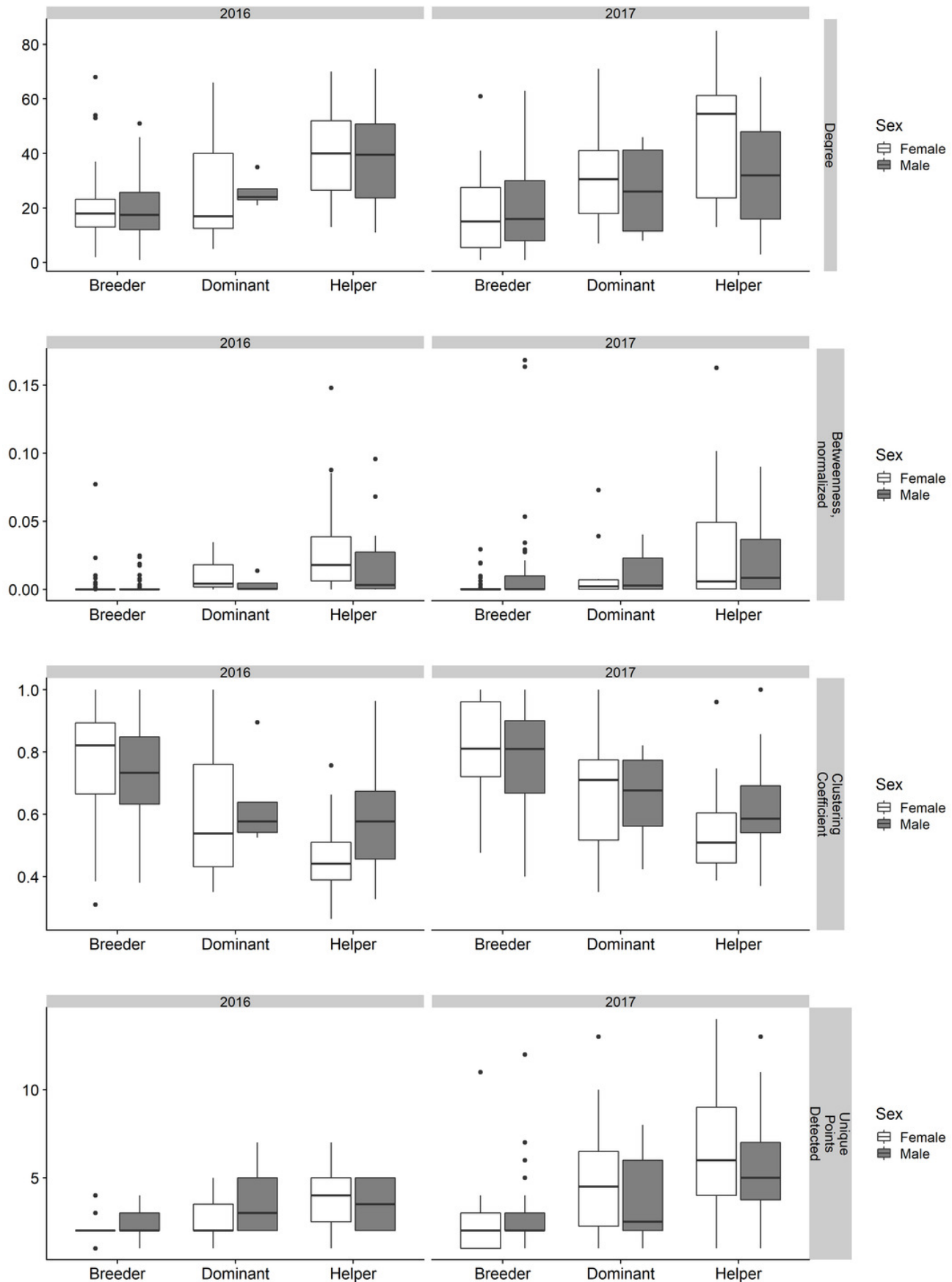**2017**

N

Lake Annie

A

0 250 500 1,000 Meters

Legend

● Sampling Points

☐ 100 m buffer

☐ Territories included

■ Territories excluded

▨ Undefended areas

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.

Breeders had less variation than helpers in degree, betweenness, and the number of unique points detected in both years. Compared to helpers, breeders also had fewer connections (lower degree), rarely connected otherwise unconnected individuals (lower betweenness), exhibited more "cliquish" behavior (higher clustering coefficient), and were detected at fewer unique points.

Figure 3

Changes in social behavior for individuals who remained in the same life history stage compared to those that transitioned from helpers to breeders.

Florida scrub-jays (Aphelocoma coerulescens) that helped in both 2016 and 2017 did not significantly change their number of connections (degree), propensity to connect otherwise unconnected individuals (betweenness), or number of unique points at which they were detected. Individuals who helped in 2016 and bred in 2017 significantly decreased their number of connections (degree) as breeders.