Original Article

Photoperiod and rainfall are associated with seasonal shifts in social structure in a songbird

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Seasonally breeding animals often exhibit different social structures during non-breeding and breeding periods that coincide with seasonal environmental variation and resource abundance. However, we know little about the environmental factors associated with when seasonal shifts in social structure occur. This lack of knowledge contrasts with our well-defined knowledge of the environmental cues that trigger a shift to breeding physiology in seasonally breeding species. Here, we identified some of the main environmental factors associated with seasonal shifts in social structure and initiation of breeding in the red-backed fairywren (*Malurus melanocephalus*), an Australian songbird. Social network analyses revealed that social groups, which are highly territorial during the breeding season, interact in social "communities" on larger home ranges during the non-breeding season. Encounter rates among non-breeding groups were related to photoperiod and rainfall, with shifting photoperiod and increased rainfall associated with a shift toward territorial breeding social structure characterized by reductions in home range size and fewer encounters among non-breeding social groups. Similarly, onset of breeding was highly seasonal and was also associated with non-breeding season rainfall, with greater rainfall leading to earlier breeding. These findings reveal that for some species, the environmental factors associated with the timing of shifts in social structure across seasonal boundaries can be similar to those that determine timing of breeding. This study increases our understanding of the environmental factors associated with seasonal variation in social structure and how the timing of these shifts may respond to changing climates.

Key words: climate variation, fairywren, non-breeding season, seasonal social structure, social network analysis, timing of breeding.

INTRODUCTION

Animal societies vary widely in social structure and quantifying this variation has long been recognized as an important component of understanding evolution (Allee 1927; Wilson 1975; Hinde 1976). A species' social structure can play an important role in determining the strength of both natural and sexual selection by influencing competition for resources and mates (e.g., Kasumovic et al. 2008; Oh and Badyaev 2010; McDonald et al. 2013), predation risk (e.g., Fitzgibbon 1990; Kelley et al. 2011), foraging efficiency (e.g., Aplin et al. 2012; Allen et al. 2013), parasite load (e.g., Chiyo et al. 2014; Sih et al. 2017), and more. The consequences of variation in social structure are often compared across species

(Rubenstein and Abbot 2017), but variation in social structure also occurs within species across populations (Lott 1984), and within populations across time (Llusia et al. 2013; Firth and Sheldon 2016; Ryder and Sillett 2016). Seasonal shifts in social structure are among the most common forms of within-population variation in social structure and often track seasonal variation in resource abundance associated with non-breeding and breeding periods (Wittemyer et al. 2005; Schradin et al. 2010; Papageorgiou et al. 2019; Prehn et al. 2019). For example, the non-breeding season of many bird species is a period defined by large home ranges and reduced territoriality at least in part due to a lessening of resource availability (Crook 1965; Ekman 1989; Matthysen 1993), but as the non-breeding season progresses and resources become more abundant and defensible, many species switch from loose flocking social structures to territorial behavior prior to breeding (Hinde 1956; Sun et al. 2020).

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The timing of shifts from non-breeding to breeding social structure could have important consequences for evolutionary processes due to the strong connections between social structure and selection (Alberts 2019; Cantor et al. 2020). However, most previous research investigating variation in social structure across seasonal boundaries have employed categorical comparisons of non-breeding and breeding season social structure, often suggesting that abiotic environmental variables, such as rainfall, are strongly associated with seasonal variation in social structure (Wittemyer et al. 2005; Nandini et al. 2017; Papageorgiou et al. 2019; Prehn et al. 2019). While useful, this reliance on categorical comparisons means that our understanding of when seasonal shifts in social structure occur, and how this timing is influenced by environmental factors, remains limited. Importantly, this gap in knowledge comes at a time when ongoing climate change is expected to continue shifting environmental norms that could be associated with the timing of these events (Lawrence et al. 2022). Identifying the environmental factors associated with temporal shifts in social structure may help to reveal how evolutionary processes tied to social structure will be influenced by shifting climates (van de Pol and Cockburn 2011; Ridley et al. 2021).

In contrast to our poor understanding of the environmental variables associated with temporal shifts in social structure between non-breeding and breeding periods, decades of research have led to a well-developed understanding of the environmental cues that lead to the development of physiological breeding phenotypes and the initiation of breeding (Rani and Kumar 2012; Helm et al. 2013; Goymann and Helm 2014). For example, in species that breed in predictable environments, such as high latitude environments with distinct, ecologically divergent seasons, changes in photoperiod often lead to rapid changes in physiology associated with breeding, including gonadal growth and testosterone production (Rowan 1925; Dawson et al. 2001; Sharp 2005). Later, separate local cues, such as leaf-out and budburst, are then associated with fine-scale initiation of breeding in some species (Visser et al. 1998; Lany et al. 2016). In contrast, for species living in less predictable environments, physiological changes are often triggered by short-term climate variation, such as variation in rainfall or temperature (Wikelski and Wingfield 2000; Hau 2001) and these same factors are often associated with timing of breeding (Hidalgo Aranzamendi et al. 2019; Lv et al. 2019). The development of breeding phenotypes and initiation of breeding often coincide with changes in social behavior (Helm et al. 2006; Hirschenhauser and Oliveira 2006; Goymann et al. 2007), but it is unclear whether the environmental variables that lead to the initiation of breeding are also associated with the timing of shifts in social structure at seasonal boundaries. If these associations are similar, then our knowledge of the environmental factors associated with breeding onset can guide further work to identify the factors associated with shifts in social structure at seasonal boundaries. However, if these associations are different, this will warrant further investigation into the factors driving variation in social structure and whether variation in the timing of shifts in social structure in relation to breeding could have important implications for processes such as dispersal and identification of extra-pair mates that often take place prior to breeding (Mulder and Magrath 1994; Beck et al. 2020).

Here, we investigated the environmental factors associated with the transition from non-breeding to breeding social structure and those associated with timing of breeding in the red-backed fairywren, a small Australian passerine in the genus *Malurus*. The Fairywrens (genus *Malurus*) offer a unique opportunity to study the relationships between environmental variation and the timing of shifts in social structure and timing of breeding because they are non-migratory and often exist in seasonal habitats, facilitating the study of the same individuals across seasonal periods (Schodde 1982; Rowley and Russell 1997; Camerlenghi et al. 2022). The non-breeding social structure of one species, the superb fairywren (*Malurus cyaneus*) has been described in detail and has been observed to form a multilevel social structure during the non-breeding season in which individuals form social groups and super groups that interact in larger communities (Camerlenghi et al. 2022). The breeding social structure of multiple fairywren species has been described in detail, with many species forming territorial breeding groups composed of two parents that are sometimes joined by multiple helpers, typically offspring raised in prior breeding seasons that assist with raising offspring and nest defense (Rowley and Russell 1997). Timing of breeding initiation in fairywrens is known to be influenced by both temperature or rainfall: in the superb fairywren, variation in the timing of breeding initiation across years is strongly associated with variation in minimum temperatures just prior to the breeding season (Lv et al. 2019), and in the purple-crowned fairywren (*Malurus coronatus*), the likelihood of breeding initiation was strongly associated with the occurrence of rainfall in the preceding 3 weeks (Hidalgo Aranzamendi et al. 2019).

Red-backed fairywrens defend territories during the breeding season (Rowley and Russell 1997), then are thought to form a multilevel social structure during the non-breeding season (Camerlenghi et al. 2022). Previous reports have suggested this non-breeding social structure is composed of groups of parents, their helpers, and the parent's offspring from the previous breeding season that interact to form larger foraging flocks (Lord 1956; Schodde 1982; Rowley and Russell 1997; Nakamura et al. 2010; Lantz and Karubian 2017), but these ideas have not been tested. We first quantified the structure and composition of these non-breeding social groups and the structure of larger non-breeding social communities composed of interacting social groups using social network analysis of field observations and analyses of genetic relatedness. Second, we confirmed that our study period included the transition from the non-breeding to the breeding season by analyzing changes in home range size over our study period, expecting home range sizes to decrease when breeding approached. Third, we combined our categorical identification of social groups with a continuous approach by measuring whether encounters rates between social groups were associated with variation in environmental factors. Finally, we identified the environmental factors associated with onset of breeding and compared these to the environmental factors associated with changes in encounter rates among groups. The findings generated by these analyses will advance our understanding of the abiotic environmental factors associated with transitions in social structure across seasonal boundaries and may help to reveal how temporal variation in social structure may be influenced by climate change.

METHODS

Study system

We studied a population of color-banded red-backed fairywrens in a grassland and forest habitat on the edge of Lake Samsonvale (27° 16'S, 152° 41'E), approximately 30 km north-west of Brisbane, Queensland, Australia. This species' breeding system has been described in previous work from northern Queensland (Webster et al. 2010; Varian-Ramos and Webster 2012; Potticary et al. 2016), the Kimberly region of Western Australia (Murphy et al. 2010),

and this location (Baldassarre and Webster 2013; Baldassarre et al. 2016). At Lake Samsonvale, red-backed fairywrens breed from approximately August through January, and breeding groups are typically composed of a breeding male and female pair (85% of breeding groups) or a breeding pair and a single helper son that is at least 1 year old (8% of breeding groups). Together breeding groups cooperatively defend nesting and foraging territories. Most young females disperse before or during the beginning of the breeding season; thus, groups with single helper daughters or multiple helpers are rare (2% and 5% of breeding groups, respectively; Webster, unpublished data). Here, we define individuals in their first non-breeding season as "young" and, to maintain consistency with previous studies, our study seasons are named for the year in which the breeding season ends (Karubian 2002; i.e., data collected in June 2018 is referred to as being part of the 2019 study season). All analyses were performed in R (version 3.5.2, R Core Team 2018) unless otherwise specified. All procedures involving animals were approved by the Cornell Institutional Animal Care and Use Committee (IACUC 2009–0105), Tulane University IACUC (2019–1715), and the James Cook University Animal Ethics Committee (A2100), and were performed under a Scientific Purposes Permit from the Queensland Government Department of Environment and Heritage Protection (WISP15212314).

Field methods

We conducted non-breeding season field work during the Australian winter, from approximately late May through August 2015–2018 (2016–2019 study seasons). Preliminary observations revealed that as previously described (Lord 1956; Schodde 1982; Rowley and Russell 1997; Nakamura et al. 2010; Lantz and Karubian 2017), Red-backed Fairywrens at our site formed foraging flocks during the non-breeding season that moved and vocalized in a coordinated manor, typically remaining within 20 m of one another. The number of individuals in a flock was typically low in number (8 or fewer), but at times these flocks included as many as 35 individuals. Only very rarely did we observe individuals on their own. Therefore, in our analyses, we focus on social groups identified through social network analysis rather than individuals as the most relevant social tier in terms of defining non-breeding social structure.

Over four non-breeding seasons, from approximately mid-June through late August (Supplementary Table S1), we conducted observations of non-breeding flocks by recording the number and identities of all individuals in a flock via resighting of color bands and recorded a GPS waypoint of the flock's location every 5 min. We recorded instances of courtship and aggression to the closest minute mark and observers attempted to remain at least 20 m away from flocks at all times to avoid influencing their movement or behavior. During the 2016–2018 study seasons, we followed flocks for 4–6 sampling points (15–25 min) for each observation unless the observer lost contact with the flock, and in 2019, we extended our target timeframe to an hour for each observation. We terminated observations when we lost sight of the birds and could not find them again, but if a flock was lost and re-found, we continued recording sampling points on the same 5-min interval track we had started on until we reached our sampling point goal. For flocks that were not re-found, we included observations in our analyses as long as the observer spent at least 5 min identifying the individuals in the flock. We attempted to sample each focal area of our field site equally but if we spent an hour searching an area for a flock

without finding one, we moved on to sample a different area. In over 40,000 sightings (a record of a single individual at a specific location and time) across four non-breeding seasons, 4.5% sightings were of unbanded individuals, and among banded birds, we were unable to identify 10% of those sighted. Most observations were completed between 0600 and 1400 h, but a few (less than 1% in the 2018 season) were completed between 1600 and 1700 h. We also conducted a limited number of nocturnal observations of roosting non-breeding groups just after dusk using a FLIR thermal monocular (FLIR Systems, Wilsonville, OR) and a flashlight. Nocturnal observations were not included in any social network analyses. We conducted breeding season fieldwork between August and January from 2011 to 2018 and determined breeding social group composition through observations of social and nesting behavior (Webster et al. 2010).

Non-breeding social structure

We analyzed Red-backed Fairywren non-breeding social structure by applying the "gambit of the group" method to our social observations (Whitehead and Dufault 1999). We considered individuals seen together in a flock during a sampling point to be associating and built social networks using the simple ratio index implemented in the R package "asnipe" (Farine 2013). We removed any sampling points prior to calculating association indices where the observer reported multiple individuals were present but only identified the color band combination of one individual to reduce the effect of individual location errors. We did retain sampling points that included unidentified individuals in our association index calculations if at least two color-banded individuals were identified. This means our association indices as calculated by the simple ratio index are likely lower than they should be because we did not account for individual identification error (Hoppitt and Farine 2017).

To confirm we had fully measured the social environment of all banded individuals in the dataset, we plotted the relationship between the number of times an individual was seen and the number of individuals it was seen with (degree) for each yearly network. We then removed individuals that were seen very few times until the relationship between times seen and degree was nonsignificant (Pearson's correlation P-value greater than 0.05; Farine and Whitehead 2015). Importantly, we removed individuals from the association matrix that were seen fewer times than the minimum value after we had calculated association indices. This way, individuals that we had seen few times were not included in our social group and social community identification steps in case we had not fully measured their social environment, but if these rarely seen individuals were recorded in sampling points with well-seen individuals, those encounters still counted toward calculating the association indices of the well-seen individuals.

To identify grouping levels of social structure, we took a multilayer network approach (e.g., Finn et al. 2019) and based our analyses on known within-group and across-group behaviors to improve our ability to define social structure. Previous results have suggested that red-backed fairywren non-breeding groups are likely continuations of breeding groups from the previous breeding season, composed of parents and their offspring (Schodde 1982; Rowley and Russell 1997). In the breeding season we rarely observe male Red-backed Fairywrens courting the female they are paired to but often observe adult males in red-and-black plumage courting neighboring females (Welklin and Lantz, personal observation). This observation matches findings from Superb Fairywrens

showing the same result during the breeding season (Mulder 1997). We also see very little aggression within groups during the breeding season but sometimes observe chases when groups interact.

Our preliminary observations of non-breeding season behavior revealed very similar behaviors. When foraging flocks were small (e.g., eight individuals or less), they typically included only one male in ornamented red-black plumage per flock, a phenotypic trait mostly restricted to older adult males at this point in the non-breeding season (Welklin et al. 2021). We rarely observed courtship or aggression when flock sizes were this small and only one red-black male was present. However, we often observed courtship when flock sizes were large and multiple ornamented males were present in non-breeding flocks. Thus, previous reports of non-breeding social structure being composed of family groups from the previous breeding season appeared to be true for our site as well, given the very similar social contexts in which we observed courtship and aggression occurring across both seasons. Therefore, to better identify social group membership during the non-breeding season, we first created a "foraging" network that included all sampling points where flock members were foraging or engaging in affiliative behaviors such as allopreening, but did not include any sampling points within 8 min of a courtship or aggressive event in the same social observation. We then created a second "full" network that included all sampling points and all behaviors. We used the foraging network to identify social group structure and used the full network to identify social community structure composed of interacting social groups.

We created a visual representation of non-breeding social structure by building dendrograms for each yearly foraging network using the UPGMA method (Sneath and Sokal 1973). The UPGMA method calculates the average association distance (inverse of the association index) between a closely associated pair and the next most closely associated individual (Sneath and Sokal 1973). We then assigned individuals to non-breeding groups by cutting each dendrogram at the bifurcation point with the highest average silhouette width (Rousseeuw 1987). Silhouette width is a clustering quality score based on a comparison of the distance between nodes (individuals) within a cluster (social group) to the distance to the next-closest cluster. This score is calculated for each node based on its social group assignment then averaged across all nodes to obtain a network-wide score. An average silhouette width close to 1 indicates a well-clustered network, while a silhouette width close to 0 indicates no clustering (Rousseeuw 1987). In following analyses, we excluded groups with single individuals because we rarely ever saw fairywrens on their own while conducting observations, meaning for groups with one individual, it was more likely they were on the periphery of our study site and we failed to see the rest of their group often enough to include them in the network.

We visualized social communities of interacting social groups by applying a network size reduction method to the full network that included sampling points associated with courtship and aggression (Arenas et al. 2007). In our implementation of this method, each social group became a node and the association rate between any two social groups was the sum of the association indices between every possible pair of individuals across the two groups. We then used the modularity-optimizing "fast.greedy" algorithm in the R package "igraph" to detect social community structure within this reduced network (Csárdi and Nepusz 2006).

For both social groups and social communities, we compared the clustering metrics of our observed networks to those of 1000 randomized networks created using a data stream permutation to test whether the observed social structure was more structured than expected by chance (Bejder et al. 1998; Farine and Whitehead 2015). We measured the robustness of our social groups and social communities to potential sampling error for each yearly network following Shizuka and Farine (2016). To measure how non-breeding social structure was related to breeding social structure, we calculated the average weighted assortment coefficients of both previous and upcoming breeding group members during the non-breeding season for each yearly network using the R package "assortnet" (Farine 2014). Then, we compared the observed assortment coefficients to those of 1000 randomized networks created using data stream permutations to determine whether social classes (male previous breeder, female previous breeder, helper, young male, young female) were assorted more or less than expected by chance. To measure how within-group association rates differed from across-group association rates, we measured the difference between the mean association index of within-group associations and across-group associations by calculating the association indices of all observed within-group and across-group associations in each season's full network. We then calculated a single within and across-group mean association index for all four seasons by combining data from each season and calculating the mean value for each association type. We tested whether the observed difference between within and across-group association indices was greater than expected by chance by comparing the mean observed difference to 1000 mean difference values calculated using the same method using 1000 datastream-permuted networks for each season.

Genetic relatedness estimates

We calculated genetic relatedness estimates from blood samples of all individuals in our non-breeding networks to understand how relatedness was associated with social network structure. We obtained relatedness data by performing double-digest RAD sequencing and aligned sequences to a de novo assembly of loci using STACKS v2.53 (Rochette et al. 2019) to identify single-nucleotide polymorphisms following Thrasher et al. (2018). We used the program COANCESTRY (Wang 2011; version 1.0.1.9) to estimate the pairwise relatedness among all pairs of individuals in our dataset using the Wang (2002) estimator. We identified each individual's sex through breeding season observations at nest sites or through PCR, following Fridolfsson and Ellegren (1999).

Changes in home range size

We measured how home range size changed over the course of the non-breeding season by calculating auto-correlated kernel density estimates (aKDE) using the "ctmm" package in R (Calabrese et al. 2016). We split each non-breeding season into three non-overlapping periods using date ranges that maximized the number of individuals that were sighted in at least five observations within a period. We required that individuals occur in at least five observations to be included within a given period, but they did not need to occur in every period. We used a linear mixed model with period as a fixed effect and individual identity, social class, and social group identity (see below) as random effects and compared the estimated marginal means of differences in aKDE area across periods within a season using the "emmeans" package in R (Lenth 2020). Between one to five individuals each year had an unknown social class due to a lack of clarity about its breeding position in the previous breeding season. We used a permutation test to determine whether the observed differences between periods within seasons were greater than expected by chance (Supplementary Methods).

Social group encounters and climate

We employed sliding window analyses to measure how short-term climate variation influenced encounters among social groups in the non-breeding season. This method searches for a climate window that best improves upon a baseline model when the data from the climate window is added to the baseline model as a fixed effect (van de Pol et al. 2016). For our response variable, we used the number of social groups encountered by the focal social group of each observation. We used a generalized linear mixed model with a Poisson distribution and log link function for our baseline model. Fixed effects included the number of sampling points the focal social group occurred in during the observation (length of observation), the day of year of the observation (to represent photoperiod), and study season. We included the identity of the focal social group nested within the identity of the focal social group's social community as separate random effects.

We ran sliding window analyses independently for seven climate variables: total rainfall, mean minimum temperature (and anomaly), mean maximum temperature (and anomaly), mean windspeed, and mean normalized difference vegetation index (NDVI). Tests of mean maximum and minimum temperature anomalies measured the importance of daily temperature variation, whereas non-anomaly temperature measured seasonal trends. For total rainfall, we considered all windows from 250 to 1 days before the observation date, and for all temperature variables, we used a range of 100 to 1 days. Date ranges were based on preliminary analyses that showed windows including dates beyond these ranges were nonsignificant. For both rainfall and temperature, we required windows to be more than 5 days long, as extremely short climate windows are often biologically implausible (Bailey and van de Pol 2016). For mean windspeed, we used a range of 10 to 0 days prior to the observation date. For NDVI, we used a range of 63 to 0 days before the observation date due to the availability of satellite data in our first year. We assessed the importance of these climate variables using a relative window, meaning the start and stop dates of the window shift with the response variable's collection date while the length of the window remains the same. The sliding window analysis then compares the ability of all possible lengths of windows to improve upon the baseline model using change in Akaike information criterion (AIC) from the baseline model (ΔAIC).

Because we were interested in within-season variation in social organization, we centered each climate window on each study season to remove across-season variation (van de Pol and Wright 2009). We did the same for the number of sampling points the focal group was observed in and then tested for a linear and quadratic effect of each climate variable on the number of social groups encountered by the focal group. We tested whether our climate windows were false positives by comparing the ΔAIC value of our observed best window to the ΔAIC values of 100 randomized versions of the same dataset run through the same analysis (Bailey and van de Pol 2016). We considered any climate window a potential fixed effect in our final model if its ΔAIC value was less than 95% of the randomizations and if its ΔAIC value was within 2 AIC units of the climate variable's top window. See Supplementary Materials for details on randomizations. We removed any climate windows that correlated with photoperiod (Pearson's correlation coefficient > 0.4) because many climate variables exhibited seasonal trends that correlated with photoperiod and photoperiod was always the stronger predictor. We checked our model for overdispersion by calculating a point estimate for overdispersion following Harrison (2014) and checked model assumptions using the R package

"DHARMa" (Hartig 2018). We calculated a marginal R^2 value for our final model using the trigamma method following Nakagawa et al. (2017) and calculated ΔR^2 values for each fixed effect in the final model by subtracting the marginal R^2 value of the full model from the marginal R^2 value of a model lacking the fixed effect, following Lv et al. (2019).

Breeding start and climate

We employed sliding window analyses to measure how short-term climate variation influenced timing of breeding across eight seasons (2012–2019). For this analysis, we searched for an absolute window, or a fixed range of dates during which the sum or mean of a climate variable best predicted when breeding was initiated across years. Our baseline model was a linear mixed model with the day of year of each female's first egg date as the response variable, the number of helpers and whether the breeding pair had been paired previously as fixed effects, and female identity as a random effect. We only used females that were 2 years old or older for these analyses, established territory holders, as 1-year old females must disperse and find a mate before breeding and thus may be expected to breed later than established territory holders.

We ran sliding window analyses predicting breeding initiation for the seven climate variables listed above. For rainfall and all temperature variables, we explored climate windows within a range of 200 to 1 days before August 1st. This date was chosen because most first egg dates occurred in or after August. Preliminary analyses indicated that no dates past 200 days were meaningful. For NDVI, we used a range of 100 to 1 days before August 1st because we were limited by the availability of satellite imagery. We used k-fold cross-validation implemented by the "climwin" package in R to improve the accuracy of our model statistics that could be influenced by our low sample size (Bailey and van de Pol 2016). We only tested for the presence of linear effects of climate on first egg dates since our sample size was small and we measured differences among our models using change in AICc from the baseline model (ΔAICc). We tested whether our climate windows were false positives using randomizations as above. In the final model, we included year as a random effect to account for any other potential differences among years not explained by our fixed effects or female identity and checked model assumptions using the R package "DHARMa" (Hartig 2018). We calculated a marginal R^2 value for our final model and calculated ΔR^2 values for each fixed effect in the final model as above.

RESULTS
Non-breeding season social structure

Red-backed fairywrens formed distinct social groups during the non-breeding season that were robust to potential sampling error and were more structured than expected by chance (Table 1, Figure 1, Supplementary Figures S3–S6). Social group sizes ranged from two to eight individuals (Table 1, Supplementary Table S7), and fairywrens spent the majority of their daytime hours interacting with members of their own social group rather than interacting across social groups (mean within-group association index: 0.62; range: 0.14–1.00 versus mean across-group association index: 0.05; range: 0.01–0.41, permutation P-value = 0.02, Supplementary Figure S8). At night, individuals remained with their social groups, roosting clumped together on a branch usually within a dense bush (six social groups seen at nighttime roosts, one to six nighttime visits

Table 1

Summary statistics for the four non-breeding social networks

(a) Social groups

Season	No.	Average silhouette width	Individuals per group	P-rand	r_{com}
2016	25	0.46	3.36 (2–5)	<0.001	0.97
2017	11	0.55	3.90 (2–6)	0.001	0.94
2018	21	0.66	3.14 (2–6)	<0.001	0.97
2019	20	0.66	3.70 (2–8)	<0.001	0.98

(b) Social communities

Season	No.	Modularity	Social groups per community	Individuals per community	P-rand	r_{com}
2016	5	0.63	5.00 (3–7)	16.8 (11–24)	0.001	0.83
2017	3	0.29	3.66 (3–5)	14.3 (14–15)	0.018	0.81
2018	8	0.71	2.63 (2–4)	8.25 (4–16)	<0.001	0.90
2019	6	0.64	3.34 (2–5)	12.3 (5–18)	0.001	0.87

Mean and (range) are reported for counts. Average silhouette width is the average silhouette width score for all social groups in each year. P-rand is the P-value of the comparison between the observed group or community structure to the group or community structure of randomized networks. r_{com} is an assortivity index calculated to compare the robustness of the observed group and community structure to potential sampling error. Modularity is the modularity of social communities within a reduced network using social groups as nodes.
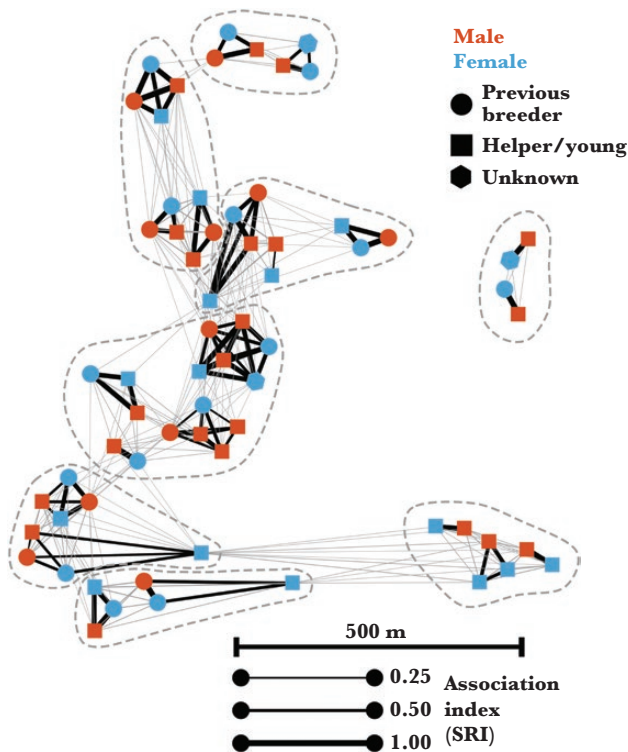

Figure 1

Social network from the 2018 non-breeding season. Edges connecting nodes are weighted by association index, with thicker lines representing more closely associated individuals. Black edges show within-social group connections and gray edges show across-social group connections. Dashed gray lines surround social communities. The network is plotted spatially, with each node plotted to the centroid of its home range then adjusted slightly to prevent node overlap for visual clarity. See Supplementary Figures for networks from other seasons.

per group; see Supplementary Materials for details). Neighboring social groups interacted often during the non-breeding season (Figure 1, Supplementary Figure S5), forming larger social

communities that were robust to potential sampling error and were more structured than expected by chance (Table 1, Supplementary Figure S9).

Membership of non-breeding social groups was similar to that of breeding groups in the previous and subsequent breeding seasons. Breeding group members from the previous breeding season had higher association scores during the non-breeding season than expected by chance (mean assortment: 0.84, permutation P-value < 0.001; Supplementary Table S10, Supplementary Figure S11) and a large percentage of individuals that were in a breeding group together occurred in the same social group during the subsequent non-breeding season (Supplementary Figure S12). Genetic relatedness among most non-breeding social group members was high and typically greater than expected by chance (mean ± SE: 0.18 ± 0.01; Supplementary Figures S12 and S13). Connections to the upcoming breeding season were also clear during the non-breeding season. Upcoming breeding group members associated more strongly during the non-breeding season than expected by chance (mean assortment: 0.73, permutation P-value < 0.001; Supplementary Table S10; Supplementary Figure S11) and 100% of upcoming helper males ($N = 26$) were in the same non-breeding group as the breeders they ended up helping. Further, 100% of upcoming breeding pairs composed of experienced breeders ($N = 36$) were in the same non-breeding social group (Supplementary Figure S12). This included some breeding pairs that were not paired in the previous breeding season ($N = 8$).

In contrast to social groups, mean relatedness among social community members in different social groups was typically low (mean ± SE: −0.01 ± 0.01; Supplementary Figures S14–S16). However, the mean relatedness of many male–male and male–female dyads within social communities was greater than expected by chance (Supplementary Figure S15), suggesting some kin structuring. Female–female dyads within social communities, though, were not more related than expected by chance (Supplementary Figure S15).

Change in home range size over the non-breeding season

Red-backed fairywrens spent most of their time during the non-breeding season within a home range that included, but extended

beyond, their breeding season territory. Home range size decreased over the non-breeding season, but the magnitude of this change varied across years (Figure 2). In 3 out of 4 years, the decrease in home range size from the first period of data collection to the third period was statistically significant (permutation tests: 2016: P = 0.002; 2017: P = 0.006; 2019: P = 0.037; Figure 2, Supplementary Tables S17–S19, Supplementary Figures S20 and S21), and the fourth showed the same trend but was marginally nonsignificant (2018: P = 0.068; Figure 2, Supplementary Tables S17–S19, Supplementary Figures S20 and S21).

Encounters among social groups and climate

Photoperiod (represented by day of year) and short-term climate variation correlated with encounters among non-breeding social groups (Table 2, Figures 3 and 4, Supplementary Table S22, Supplementary Figures S23–S25). Photoperiod was the best predictor of the number of social groups encountered by the focal social group during an observation, followed by a quadratic effect of within-season variation in the amount of rainfall 56–43 days before the observation. Photoperiod and total rainfall exhibited negative linear terms in relation to the number of social groups encountered, with later dates and more rainfall leading to focal groups interacting with fewer neighboring social groups (Figure 4). We also found a quadratic effect of within-season variation in the mean maximum temperature anomaly 85–60 days before the observation (Table 2). The quadratic term for mean maximum temperature anomaly was negative, meaning both warmer and cooler than average temperatures during this distant window led to fewer encounters among social groups (Figure 4). The effect of the quadratic term for the rainfall climate window was minimal and nonsignificant (P = 0.117). The sliding window analyses revealed multiple other rainfall, temperature, and NDVI windows that improved upon the baseline model and were not false positives, but these were correlated with photoperiod (Supplementary Table S22). Mean windspeed improved upon the baseline model but was found to be a false positive when compared to randomizations (Supplementary Table S22; Supplementary Figures S23 and S24).

Breeding start date and climate

Mean first egg dates ranged from August 16 to October 12 across eight non-breeding seasons. Variation in breeding start dates across years was most strongly associated with the amount of rainfall between February 27 and June 15, with more rainfall during this 3.5-month period leading to earlier breeding initiation (Table 3, Figures 3 and 5, Supplementary Table S26; Supplementary Figures S27–S29). All other climate windows revealed by this sliding window analysis were false positives (Supplementary Table S26; Supplementary Figures S27 and S28). Neither the number of helpers in the breeding group nor whether the breeding male and female had been paired in the previous breeding season were statistically significant predictors of breeding start date (Table 3).

DISCUSSION

Many species exhibit seasonal variation in social structure associated with non-breeding and breeding periods, but we have little understanding of whether the environmental variables that differ seasonally across these periods are associated with the timing of seasonal shifts in social structure. This lack of knowledge contrasts with our well-developed understanding of the environmental cues associated with the development of breeding physiological phenotypes. Here, we show that the environmental variables associated with the timing of transitions from non-breeding to breeding social structure can be similar to those associated with onset of breeding within a species. In red-backed fairywrens, the transition from non-breeding to breeding social structure and the onset of breeding were both strongly associated with photoperiod, which likely serves as a broad seasonal cue, whereas non-breeding rainfall was associated with more fine-scale variation in the timing of these events. Within a season, social structure shifted from non-breeding flocks toward territoriality following rainfall, and across seasons, more rainfall during the non-breeding season led to earlier initiation of breeding. These results suggest that in some animal systems we might be able to predict how social structure will respond to climate change by considering the environmental factors associated with the development of breeding physiological phenotypes and initiation of breeding.

Environmental predictors of shifts in social structure

We found that red-backed fairywren social groups interacted frequently early in the non-breeding season, sometimes forming flocks containing up to eight social groups and >30 individuals. However, as the non-breeding season advanced toward the beginning of breeding, home range size and the number of social groups encountered by a focal social group decreased (Figure 6). Of the environmental factors that we evaluated, photoperiod was the environmental predictor most strongly associated with this transition from non-breeding social structure to territorial breeding social structure. This finding likely suggests that lengthening photoperiod
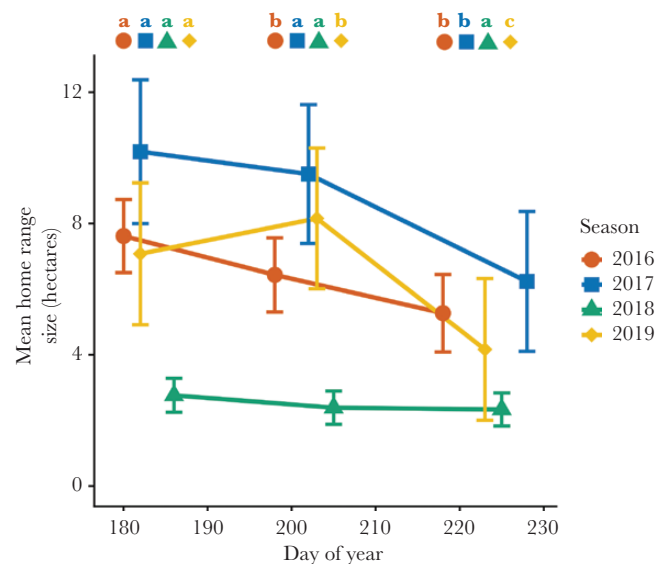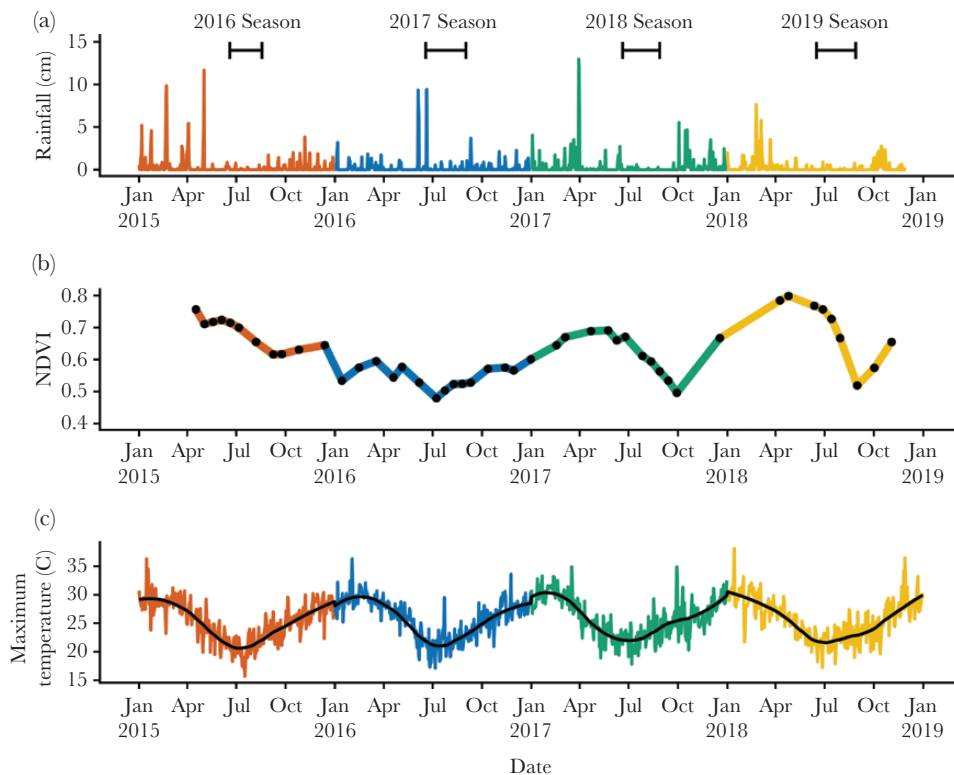

Figure 2

Change in red-backed fairywren home range size across the non-breeding season. Points show the estimated marginal means of autocorrelated 85% kernel density estimates for three periods in each season and are aligned to the middle date of each period on the x-axis. Error bars show standard errors and letters show significance categories determined by permutation tests.

Table 2

Summary of a generalized linear mixed model testing which environmental variables influenced the number of red-backed fairywren social groups encountered by the focal social group on a given date during the non-breeding season

Fixed effects	β	SE	z-statistic	*P*-value	ΔR^2 (%)
Intercept	−0.80	0.18	−4.53	<0.001	
Number of sampling points in observation	0.26	0.04	6.58	<0.001	−0.88
Photoperiod (day of year)	−0.32	0.05	−6.22	<0.001	−1.47
Total rainfall (cm) 56–43 days before observation	−0.19	0.07	−2.93	0.003	−0.25
Total rainfall^2	0.05	0.03	1.57	0.117	
Mean maximum temperature anomaly (C) 85–60 days before observation	−0.15	0.05	−2.79	0.005	−0.51
Mean maximum temperature anomaly^2	−0.11	0.04	−2.90	0.004	
Season (relative to 2016)					−0.47
2017	0.01	0.29	0.04	0.967	
2018	−0.35	0.24	−1.47	0.142	
2019	0.18	0.25	0.73	0.468	
Random effects	Variance	Standard deviation			
Focal social community identity	0.12	0.34			
Focal social group identity	0.09	0.30			

Model dataset includes 1181 observations of 75 social groups in 22 social communities across 4 non-breeding seasons. All continuous fixed effects in this table are centered and standardized to allow for comparisons of variable importance. The marginal R^2 of the model is 6.46%.

Figure 3
Climate variables over the 4 years of this study. (a) Daily rainfall in centimeters. Black horizontal lines show range of dates when social data were collected during each non-breeding season. (b) Mean normalized difference vegetation index (NDVI) measured using Landsat 8 (USGS) satellite images. Points represent dates when satellite images were cloud-free and NDVI could be calculated. (c) Daily maximum temperature (colored lines) and maximum temperature loess trendline (black) calculated separately for each year. Non-breeding seasons were named for the year the subsequent breeding season ended.

led to physiological changes that resulted in gradual changes in social behavior. The hypothalamo-pituitary-gonad (HPG) axis is a key candidate for mediating the effect of photoperiod on social behavior as production of gonadotropin-releasing hormone (GnRH) is known to increase with lengthening photoperiod (Dawson et al. 2001), leading to the development of breeding physiology (Sharp

2005). GnRH is also a precursor to testosterone production and increased testosterone is often associated with increased territoriality at the beginning of breeding (Wingfield and Hahn 1994), as well as with variation in social environment in many birds (Goymann et al. 2007), including fairywrens (Boersma et al. 2022). Thus, lengthening photoperiod may lead to GnRH production, followed by
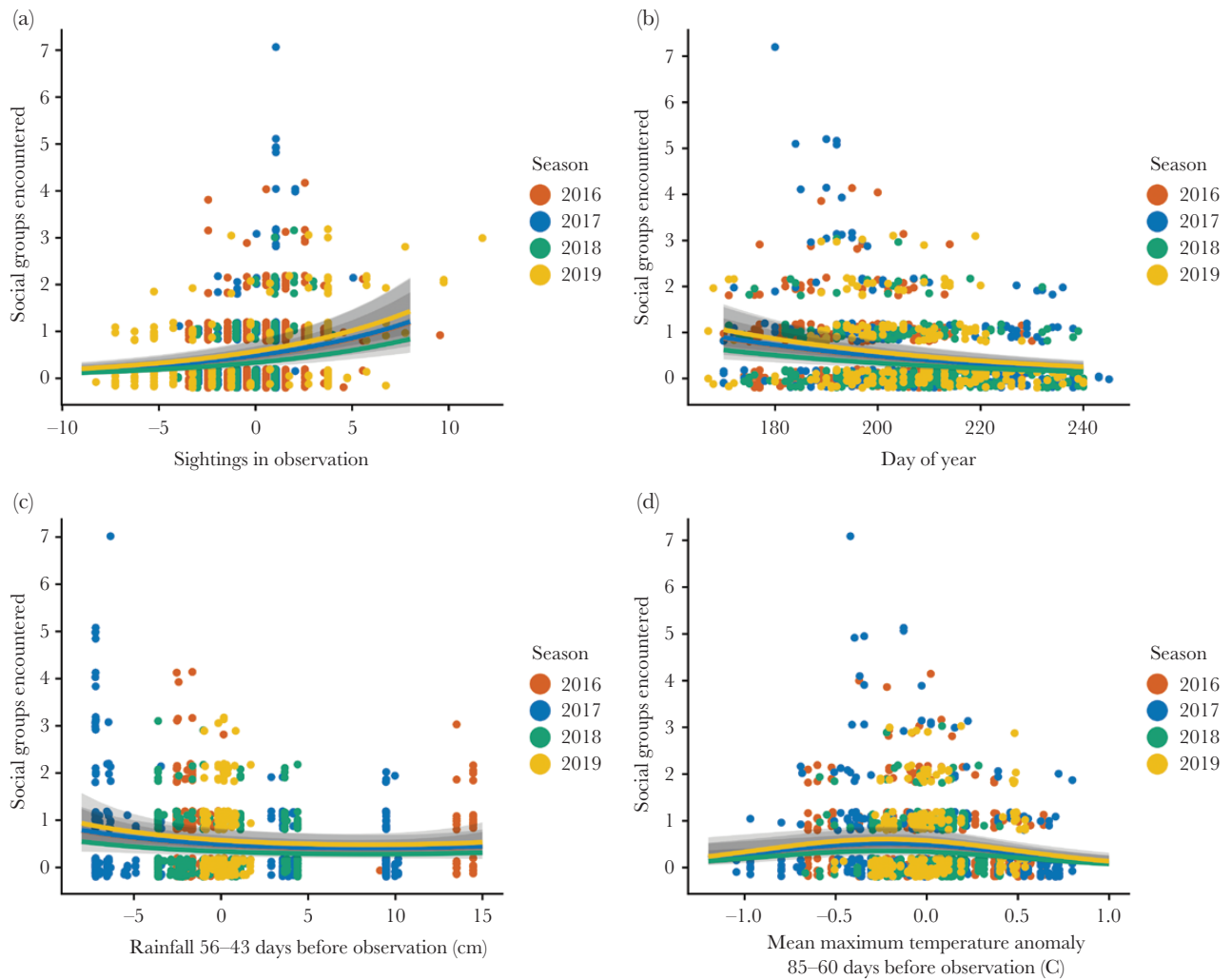
Figure 4

Model predictions of relationships between fixed effects and the number of social groups encountered by the focal social group on a given date. In all graphs, points are raw data jittered slightly in respect to the y-axis to facilitate assessments of sample size and colored lines are the model predictions for each season from the model described in Table 2. All other variables in the model were set to their mean, and in A, C, and D, day-of-year is set at 200 (July 19th) which is near the middle of our field season. Gray shaded areas represent the 95% confidence intervals of the season lines. Panels show the relationships between the number of social groups encountered by a focal group and: (A) the number of sampling points in an observation; (B) day-of-year; (C) the sum of rainfall 56–43 days before the observation date; and (D) mean maximum temperature anomaly 85–60 days before the observation date.

increased testosterone levels, leading to increased territoriality and expression of behaviors associated with breeding such as courtship (Boersma et al. 2022).

Variation in rainfall and mean maximum temperature anomaly within a year were also associated with the timing of shifts from non-breeding to breeding social structure. Specifically, encounters among groups decreased approximately a month and a half after a major rainfall event and approximately 2 months after warmer or cooler than average temperatures. For both climate windows, the long stretch of time between the event and its effect on social behavior suggests that fairywrens were likely responding to the effects of these events rather than the events themselves. For rainfall, a change in vegetation greenness (NDVI) is a well-known consequence of rainfall (Nightingale and Phinn 2003; Chamaille-Jammes et al. 2006), and a sliding window analysis confirmed that rainfall led to increased NDVI at our field site as well (Supplementary Results; Supplementary Figures S30 and

S31). An increase in NDVI is often associated with increased insect abundance (Lassau and Hochuli 2008; Pettorelli et al. 2011), and research from similar habitats in Australia has shown that insect abundance varies in response to rainfall (Recher et al. 1996; Hidalgo Aranzamendi et al. 2019). Thus, non-breeding rainfall may have led to increased vegetation growth, followed by increased insect abundance that may have reduced the need for social groups to forage beyond their breeding season territory boundaries, as home range size is often related to resource abundance (Hixon 1980). We did not find any direct impacts of NDVI on encounters among social groups, but this may have been due to the low resolution of the NDVI data available. The Landsat 8 images of our field site are collected every sixteen days, but these images were often occluded by clouds, meaning we could only measure NDVI once a month in some months.

The importance of the mean maximum temperature anomaly approximately 2 months prior to an observation is less clear, but

Table 3

Summary of a linear mixed model testing which social and abiotic environmental variables determined when female red-backed fairywrens laid their first egg

Fixed effects	β	SE	t-statistic	P-value	ΔR^2 (%)
Intercept	337.42	10.75	31.38	<0.001	
Number of helpers	−1.87	1.95	−0.96	0.349	−0.05
Breeding pair paired previously	0.04	2.07	0.02	0.985	0
Total rainfall (cm) between February 27 and June 15 (days-of-year 58-166)	−1.82	0.26	−7.05	<0.001	−46.78
Random effects	Variance	Standard deviation			
Female identity	61.31	7.83			
Season	24.32	4.93			
Residual	140.06	11.84			

Model dataset includes 186 female-seasons: 123 females across 8 breeding seasons. The marginal R^2 of the model is 47.20%.
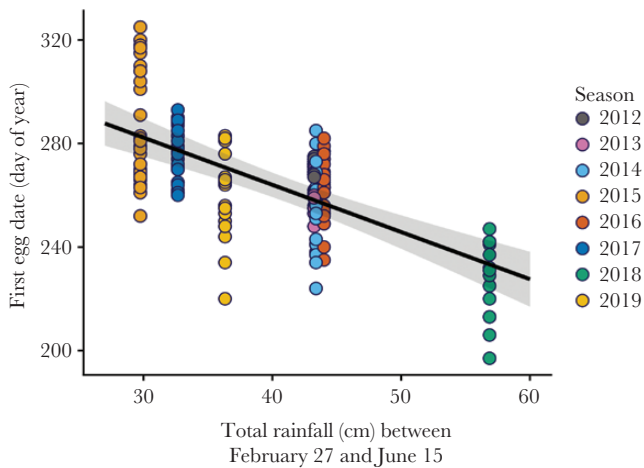
Figure 5

Relationship between non-breeding season rainfall and first egg date. Points are raw data and the trendline shows the prediction from the model described in Table 3, with all other variables set to their mean value. Shading around the line shows the 95% confidence intervals of the model prediction.

this temperature window did strongly correlate with the rainfall climate window. This correlation revealed that in 2 of the 4 years of our study, rainfall events were associated with above-average temperatures in the weeks preceding the rainfall event, suggesting above average maximum temperatures may only be important when they lead to rainfall (Supplementary Figure S25). The rainfall window was one of the few climate windows that did not strongly correlate with photoperiod, which may suggest that variation in sociality across years could be associated with yearly variation in rainfall. Further research conducted over more years may offer valuable contributions to our understanding of how environmental change can influence variation in social behavior across years. The low R-squared values of each predictor in the social group encounters model (Table 2) indicate there are many more factors influencing the day-to-day encounter rates among groups than just these environmental variables, such as male courtship of neighboring females and dispersal, but our similar results across 4 years of data indicate that these climate variables are associated with the broad timing of shifts from non-breeding to breeding social structure.

Environmental predictors of breeding

Initiation of breeding was highly seasonal across years in red-backed fairywrens, with breeding consistently beginning at the end of winter and the beginning of spring (i.e., late August/September). This repeatable seasonality of breeding suggests that, like many other avian species, timing of breeding in red-backed fairywrens likely is determined in part by photoperiodic cues that govern broad-scale variation in phenology through its effects on physiology (Rowan 1925; Dawson et al. 2001; Sharp 2005). Although we did not observe any effect of temperature on variation in the timing of breeding across years, the general seasonality of breeding could also be influenced by temperature, as the coldest temperatures of the year typically occur in July, just before breeding begins (Figure 3). These cold temperatures coincide with short day lengths, thus these combined cues could be associated with broad-scale timing of breeding. As with shifts in social structure, fine-scale variation in the initiation of breeding across years was primarily associated with variation in rainfall during the non-breeding season. In years that received high rainfall between February 27 and June 15, breeding began as early as mid-August, whereas in dry years, breeding did not begin until late September or October. These findings compliment previous results from this system indicating that rainfall is also an important predictor of nest initiation once breeding has begun (Webster et al. 2010).

Our results are also supported by many other previous studies of species living in tropical or unpredictable environments, which have revealed rainfall is an important cue for initiation of breeding and the development of breeding physiological phenotypes (Wikelski and Wingfield 2000; Hau 2001). However, our discovery of a rainfall window conflicts with a similar study on superb fairywrens which revealed temperature as the main predictor of variation in timing of breeding across years (Lv et al. 2019). The seasonality of breeding in both red-backed and superb fairywrens differs from observations of purple-crowned fairywrens showing that breeding can take place year-round (Hidalgo Aranzamendi et al. 2019). Differences across these closely related species are likely due to the major environmental variation across the geographical regions where these species reside. In cool climates, like Canberra, Australia, where the superb fairywren study was conducted, temperature may outweigh rainfall in terms of importance in determining when breeding begins (Dunn and Winkler 2010; Lv et al. 2019). However, in extremely tropical climates, such as northwest Australia where the purple-crowned fairywren study was conducted, rainfall is extremely unpredictable, such that fairywrens living in these areas may be adapted to breed whenever conditions allow (Hidalgo Aranzamendi et al. 2019). Comparisons of the cues associated with timing of breeding in locations where these species overlap may help to reveal whether the environmental factors that trigger
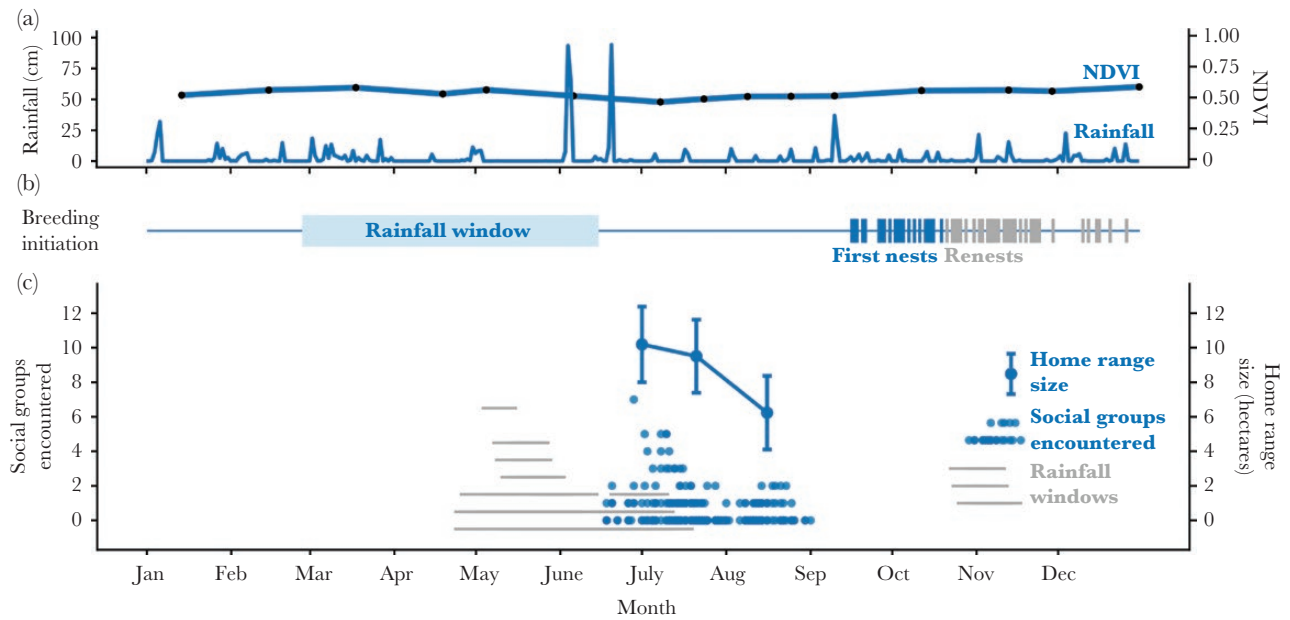
Figure 6

Summary of all data from the 2017 study season to show relationships between rainfall and NDVI to egg dates, home range size, and encounters among social groups. (A) Mean normalized difference vegetation index (NDVI; upper line) and daily rainfall in centimeters (lower line). Points on the NDVI line show dates when NDVI was measured. (B) Egg dates and the rainfall window (February 27 to June 15) that best predicted when first egg dates occurred across years. Blue tick marks show egg dates from first nests, and gray tick marks show egg dates of renests. (C) Change in home range size over the non-breeding season (upper blue line) and social groups encountered by date (lower blue points). Gray lines show the range of rainfall dates that correspond to each value of the social groups encountered variable based on the 56–43-day relative rainfall window.

breeding are species-specific or can vary across a species range. Indeed, in the tropics, red-backed fairywrens have been reported to breed year-round, suggesting timing of breeding may be plastic in response to environmental conditions (Rowley and Russell 1997).

As with shifts in social structure, the long stretch of time between the rainfall window and the initiation of breeding suggests that red-backed fairywrens likely respond to the effects of rainfall rather than rainfall itself. Rainfall early in the non-breeding season could have led to increased insect abundance that remained throughout the non-breeding season allowing birds to begin breeding early, or alternatively, increased insect abundance may have allowed fairywrens to achieve and maintain better body condition throughout the non-breeding season (Welklin et al. 2021), also leading to earlier breeding. Current climate projections indicate that eastern Australia, where we conducted this study, is likely to receive more extreme rainfall as well as an increased likelihood of drought in the future (Lawrence et al. 2022). If these projections hold true, these intensified climate conditions may lead to greater variation in timing of breeding across years. Increased rainfall may lead to earlier shifts toward breeding social structure and earlier breeding in this system, which could have implications for the number of nesting attempts a pair can complete, whereas drought years may lead to late breeding and therefore shorter breeding seasons. Both scenarios may have important implications for individual reproductive success and population growth.

Non-breeding social structure

Previous studies have reported that red-backed fairywrens form loose foraging flocks during the non-breeding season (Lord 1956; Nakamura et al. 2010; Lantz and Karubian 2017), and then transition to territoriality prior to breeding (Schodde 1982). Our analysis of non-breeding social structure and changes in home range size over the non-breeding season support these previous reports. We found red-backed fairywrens formed tight social groups during the non-breeding season, which were continuations of breeding groups from the previous breeding season. That is, most breeding pairs, their offspring, and some helper males from the previous season remained together during the non-breeding season, a result reflected by high relatedness scores among most dyads within social groups. The few low relatedness scores we observed within non-breeding groups can be explained by unrelated male–female breeding pairs and the extremely high rates of extra-pair paternity observed in this species, which would cause males to be unrelated to some of their social offspring (Baldassarre et al. 2016).

We also found that some pairs preparing to breed together for the first time formed during the non-breeding season. Many young females in our social networks appeared to have dispersed into our study site between the end of the previous breeding season (January/February) and the start of our non-breeding season data collection (June), as most of these were unbanded and of unknown origin prior to our data collection. This observation is consistent with previous research on superb fairywrens showing two phases of young female dispersal, one early in the non-breeding season, followed by another just prior to the beginning of breeding (Mulder 1995).

Individuals spent most of their time interacting within their non-breeding social groups and social groups generally occupied the same region where they had bred in the previous season, but with a home range size that extended well beyond the previous

breeding territory. As a result, social groups interacted frequently with other social groups in the same area to form "social communities," which likely correspond to the "large foraging flocks" reported previously (Lord, 1956; Nakamura et al. 2010; Lantz and Karubian 2017). The make-up of a social community appeared to be determined by geographic boundaries and male philopatry. Social communities were often separated by dense forest and open stretches of water that red-backed fairywrens infrequently cross (Welklin and Lantz, personal observation), suggesting an importance of habitat structure in influencing encounters among social groups and therefore social community connections, a relationship described previously in this species in response to fire (Nakamura et al. 2010; Lantz and Karubian 2017), as well as in other species of birds (He et al. 2019) and other taxa (Webster et al. 2013; Leu et al. 2016). Relatedness measurements within social communities pointed to evidence of male philopatry and female-biased dispersal as previously shown in multiple species of fairywrens (Mulder 1995; Rowley and Russell 1997). Relatedness among males was high within social communities but low among females, suggesting young males disperse short distances from their natal territory but females disperse long distances (see Varian-Ramos and Webster 2012).

The nested social structure of non-breeding groups within larger social communities likely represents a multilevel social structure as has recently been described in superb fairywrens (Camerlenghi et al. 2022) and vulturine guineafowl (Papageorgiou et al. 2019), as well as many species of mammals (Grueter et al. 2020), and has been hypothesized for this species (Camerlenghi et al. 2022). Indeed, our observation of social groups that interact within larger social communities closely matches findings from Superb Fairywrens showing similar social relationships. However, while we expect these groups and communities are stable across years based on the stability of breeding pairs across breeding seasons, we did not follow the same non-breeding groups across years, thus we cannot confirm whether red-backed fairywren non-breeding social structure is multilevel or not (Grueter et al. 2020).

CONCLUSION

Here, we have shown that the environmental factors associated with the timing of shifts from non-breeding to breeding social structure and those associated with initiation of breeding are similar in red-backed Fairywrens. Photoperiod and rainfall were the strongest predictors with photoperiod likely acting on social behavior through physiological changes that may match those leading to initiation of breeding, such as an increase in HPG axis activity, whereas rainfall may act through its effect on vegetation greenness and insect abundance that could lead to a decline in home range size and better physiological condition, allowing breeding to begin earlier. The non-breeding season is a dynamic social setting for many species and can have far-reaching consequences that extend into the breeding season (Beck et al. 2021, Mulder and Magrath 1994, Reudink et al. 2009). However, the vast majority of research on non-human animal systems has focused on breeding periods because breeding is directly associated with variation in reproductive success (Marra et al. 2015). Further study of non-breeding season social dynamics and how they are influenced by shifting climate norms may help us better predict how both non-breeding and breeding season processes will be influenced by ongoing climate change.

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