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## Effects of Anthropogenic Noise on Songbird Social Networks

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Effects of Anthropogenic Noise on Songbird Social Networks

Carly Elizabeth Hawkins

Springfield, Pennsylvania

B.S. in Biology, Penn State University, 2016

A Thesis presented to the Graduate Faculty  
of The College of William & Mary in Candidacy for the Degree of  
Master of Science

Department of Biology

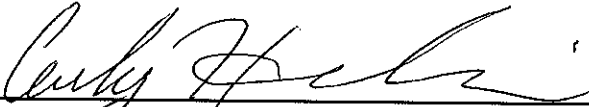
College of William & Mary  
August, 2018



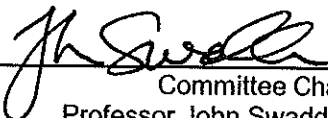
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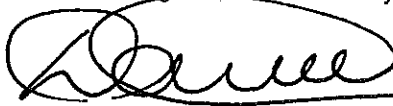
This Thesis is submitted in partial fulfillment of  
the requirements for the degree of


Master of Science

  
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Approved by the Committee, May, 2018

  
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## COMPLIANCE PAGE

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## ABSTRACT

Anthropogenic noise, which is increasing globally, affects birds from gene expression up through alteration of community composition. As urbanization pushes further into undisturbed habitat, noise often disperses birds away from the point source. The impacts of this dispersal on surrounding quieter areas is not well understood. Therefore, in the first chapter, we sought to understand how noise-related dispersal affected the sociality of groups of songbirds as they moved away from the source of noise. As the displaced birds would likely be forced to occupy a smaller area that may already have resident individuals, we predicted that displaced birds would show a tighter clustered social network that may include new individuals, and that individuals within the flock would have more social connections overall. In the second chapter, we were interested in chronic, inescapable noise, the kind that birds living in urbanized areas might experience, and how that affects sociality. We predicted that birds would distribute themselves along a noise gradient and prefer the quieter areas and that the resulting density of birds would increase both flock clustering and individual sociality. We tested these ideas in two songbird systems, free-living red-backed fairy wrens (*Malurus melanocephalus*) to study dispersal and captive domesticated zebra finches (*Taeniopygia guttata*) to study chronic noise exposure. Contrary to our prediction, the free-living red-backed fairywrens became less social when dispersing from noise, as measured by node strength, during experimental noise treatments. Additionally, these birds tended to shift their space use away from the sound source. In our captive system, our hypothesis was supported that both flock cluster and individual sociality increased with noise treatments. However, the birds did not alter their distribution in accordance to the noise gradient, thus we propose support for the Increased Threat Hypothesis and suggest that increased vigilance was responsible for flock clustering and sociality. If social networks are altered consistently, there may be implications for future breeding success, detection of communication signals, and even for pathways of disease transmission among individuals.

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# **Chapter 1: Effects of chronic anthropogenic noise on urban songbird social networks in captive zebra finches (*Taeniopygia guttata*)**

## **Introduction**

### *Background*

Humans change the global ecosystem by transforming landscapes through urban development, exploiting natural resources, and even altering biogeochemical cycles (Vitousek et al. 1997). In addition to our ever-increasing population, urbanization is expanding even faster than our numbers, a phenomenon known as “urban sprawl” (Meyer and Turner 1992; Marzluff 2001). As a result, wildlife are subjected to novel ecological pressures in increasingly urbanized habitat. In songbirds, prior studies have observed the effects of urbanization by comparing urban and rural populations and found that birds in urban areas are subject to an increased parasite load (Giraudeau et al. 2014), altered stress response (Partecke et al. 2006), and changed song behavior (Slabbekoorn and den Boer-Visser 2006). Our research attempts to isolate the behavioral effects of urbanization to just one of its many ecological novelties: noise pollution.

Though all habitats contain some element of background noise (e.g. wind, wave action, etc.), anthropogenic noise alters the soundscape entirely due to its lower frequency (pitch) and higher amplitudes (volume) (Slabbekoorn and Ripmeester 2008). Birds rely on the acoustic environment for communication, for purposes such as attracting mates or warning others of an approaching predator. The Acoustic Niche Hypothesis states that in addition to an ecological niche, wildlife have their own acoustic niche in which they communicate, a range of frequencies

that they can hear and vocalize (Krause 2007; Villanueva-Rivera 2014). Therefore, when anthropogenic noise, such as traffic noise, overlaps with a species' acoustic niche, they must adjust their behavior to cope with the new soundscape or reduce their realized niche to avoid the noise-altered area.

To cope with noise pollution, birds adjust their vocalizations to stand out over the noise (Cynx et al. 1998; McMullen et al. 2014; Kight and Swaddle 2015), and increase vigilance behavior and reduce time spent foraging to better locate approaching predators (Meillere et al. 2015; Quinn et al. 2017). Despite these behavioral adjustments, birds in noise conditions experience increased stress, decreased immune systems, and often a reduction of reproductive success (Chloupek et al. 2009; Halfwerk et al. 2011; Blickley et al. 2012). However, most of the work done on urbanized birds in noise have either compared rural-urban gradients or introduced novel noise to birds that would normally be in quieter areas. Our study looks at a relatively unexplored ecological phenomenon of “urban” birds that are always noise-associated.

Urban birds grew up in noise conditions, as did many generations, and are always exposed to some degree of noise. Therefore, we were interested in how changes in noise gradients across an urban area affects these urbanized birds. Many species, including birds, rely on acoustic signaling to interact with conspecifics, such as relaying spatial information of conspecific roosts in noctule bats (*Nycatalus noctula*) (Urban et al. 2011), relaying individual personality as a sexual signal in collared flycatchers (*Ficedula albicollis*) (Eens 2008), and defending territories (Nowicki et al. 1998). Since vocalizations play such a pivotal role in how organisms interact with one another, and noise from urban areas can mask these

vocalizations, we were ultimately interested in how noise could affect the sociality of urban songbirds.

Sociality is a behavioral process that modulates all of these aspects of avian life history, and has yet to be studied in the context of noise pollution for birds. To study sociality we use social network theory, and while it is commonly applied in human structures and economics, it only recently has been applied to ecological analyses (Wey et al. 2008). Social networks are represented by a graph consisting of nodes and edges. Nodes can represent individuals or groups, and edges represent the interactions between these individuals or groups. This graph allows for complex analysis of social organization and behavior, accounting for parameters such as intensity, directedness, and frequency of interactions between nodes (Krause et al. 2007).

While ecologists frequently look at “big-picture” measures of community structure, it is more apparent that this lower-level measure of social structure within a population affects processes on a population level. For example, the structure and properties of a social network can dictate the flow of information among individuals such as song-learning in juvenile males, the location of new resources, and reputational information about competitive individuals (Krause et al. 2007; Sih et al. 2009; Aplin et al. 2012; Farine and Sheldon 2015). Additionally, social networks influence reproductive success, by providing access to available mates (Formica et al. 2012), altering perception of ornamentation (Oh and Badyaev 2010), and influencing female choice (Sih et al. 2009). We hypothesize that the change in acoustic environment can affect acoustic signaling between conspecifics by masking acoustic information, and thus we are interested in the effect of chronic noise

pollution on avian sociality, specifically individual gregariousness (as measured by node strength) and flock-level social connections (as measured by global clustering coefficient). Node strength is the sum of all edges (calculated by SAI) connected to a node and is indicative of the level of sociality for an individual (Whitehead 2008). Global clustering coefficient (GCC) measures the degree in which individuals in a network cluster together by measuring how many triplets of individuals are connected divided by total number of possible connected triplets within the network (Proulx et al. 2005).

In an attempt to explore a potential mechanism through which noise could alter sociality, we are also interested in whether birds alter their spatial distribution and foraging behavior in an area with chronic noise pollution according to the volume (dB SPL) of the noise pollution present. Birds alter habitat use and spatial distribution along noise gradients, decreasing abundance as noise increases (McClure et al. 2013; Chen and Koprowski 2015), but the studies that have investigated this phenomenon established full gradients from loud noise (~80dB) to natural ambient noise conditions (~40dB), which is not reflective of birds that are in a chronically noise-polluted environment, like a city. Therefore, our study created a sound gradient in an experimental set-up in which the gradient goes from high noise (such as next to a road, ~80dB) to lower noise (~60dB) that would still commonly be present in an urban area. In accordance with this, we were also interested in whether urban birds alter their foraging behavior to reflect the sound pressure level of their environment, as European starlings (*Sturnus vulgaris*) preferentially forage in quiet locations over noise-ridden locations (Mahjoub et al. 2015).

## *Objectives*

The overarching goal of this study was to understand how anthropogenic noise pollution in urbanized areas affects songbird sociality and flocking behavior as well as foraging and habitat preference. We introduced a gradient of sound pressures across an outdoor aviary using traffic noise to captive zebra finches (*Taeniopygia guttata*) to mimic noise experienced in urbanized areas. We measured changes in their individual sociality and flock clustering before, during, and after the introduction of traffic noise. If sociality is affected by noise, we propose one mechanism could be by altering space use, and birds physically clustering in quieter spaces of the aviary. Therefore, we also recorded space use for individual birds throughout trials and measured food consumed in varying noise conditions to gauge how space use changed from before to during noise treatments. We predicted that flocks would become more clustered with the introduction of traffic noise, due to becoming more physically clustered to lower sound pressure areas. In turn, due to increased flock clustering we hypothesized that each bird would obtain more social partners as well as increase the frequency of interactions with conspecifics, and thus individual birds would have an increase in sociality. For habitat use, we predicted that birds would adjust their foraging behavior to minimize acoustic masking, and thus would be more likely to use the quieter side of the aviary and consume less food on the side that had the highest sound pressure during the noise treatment, compared to before the treatment, when sound pressure was more spatially uniform.

## **Methods**

### *Study System*

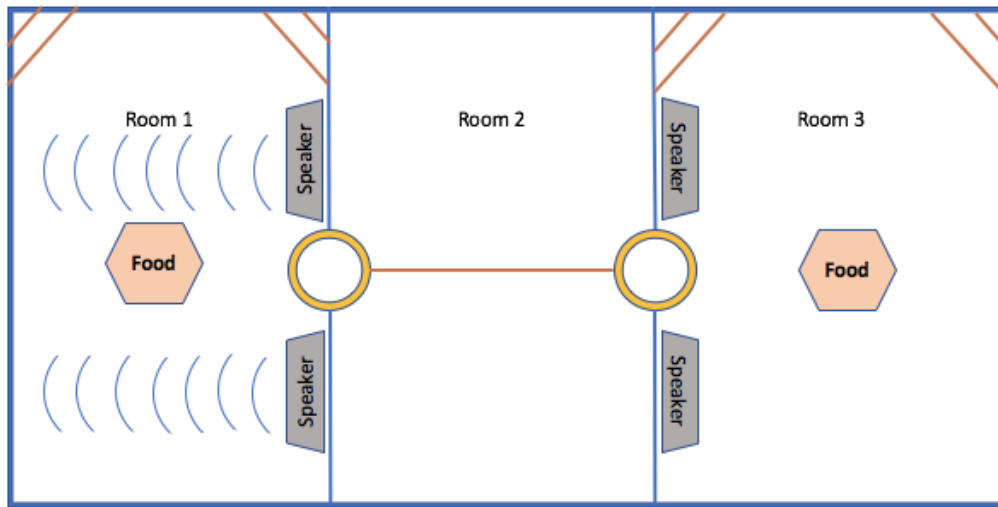
We used a colony of outbred, domesticated zebra finches in the outdoor aviaries at William & Mary (Williamsburg, Virginia, USA, 37.3 °N, 76.7° W). Though domesticated, zebra finches maintain their highly social flocking nature when housed in free-flight rooms. They quickly form pair bonds within the flock and are rarely without their social partner, and engage in flock-activities such as feeding, watering, and allopreening (Zann 1996). Additionally, these birds rely on auditory cues for individual recognition (Zann 1996), making them particularly vulnerable to changes in noise conditions. Birds used in this study were raised in relatively noisy conditions, as their parents had been for at least 8 generations, due to the incidental effects of having a captive breeding colony in indoor rooms with a relatively old HVAC system and highly reflective concrete walls and floors. Typical noise levels in breeding rooms range between 55 - 86 dBA SPL. Therefore, these zebra finches serve as a model for a sedentary urbanized species that spends their whole life in urban areas, (eg. house sparrows (*Passer domesticus*), European starlings, and Brewer's blackbirds (*Euphagus cyanocephalus*). All procedures used on animals were approved by Institutional Animal Care and Use Committee (IACUC2015111610733jpswad).

### *Experimental Design*

We conducted a total of 11 trials between May-October 2017 in two large outdoor aviaries. Each aviary consisted of three conjoined rooms (3 x 3 x 6 m) between which birds could freely move (see Figure 1). Birds had *ad libitum* access to food, a nutritionally balanced diet of millet mix (Volkman Super Finch Blend). Feeders were placed in Rooms 1 & 3 of the aviary (see Figure 1). For each trial, one



aviary served as “experimental” and the other was “reference.” The reference aviary did not directly receive experimental sound manipulation, but data were collected throughout the same timeframe as the experimental aviary in an attempt to disentangle the effects of time on sociality and the experimental noise treatment.



**Figure 1:** Aviary set-up for both experimental and reference aviaries. Only experimental aviaries had speakers in one room turned on. Each room is 3 x 3 x 6 m.

We released 12 birds (six male, six female) marked with individual color bands into each aviary (12 in the experimental aviary, and a separate 12 birds in the reference aviary) for each trial and gave them three days to acclimate and establish their social groups. Of the 12 birds in each flock, the females were not familiar with the males but birds could have been familiar with each other within the sexes, as individuals were previously housed with approximately 100 others in same-sex free-flight conditions. Each bird was used only once and did not appear in subsequent trials. Hence, we used 264 birds over the course of 11 trials. Each trial was divided

into three 3-day experimental phases, (i) “*before*” which was the phase before the experimental noise manipulation; (ii) “*noise*” when the experimental group received the noise manipulation; and (iii) “*after*,” which was the time period immediately following the termination of the *noise* phase (See Table 3). During the “*noise*” phase, speakers played a looped audio recording of highway traffic noise that varied in maximum dB SPA (~65 - 80 dBA) depending on the amount of cars and trucks passing on the highway throughout the recording (8 Hours of 2014), and played in either Room 1 or 3 of the aviary depending on trial (Figure 1). The experimental trial created a sound gradient across the three rooms, ~80 dBA SPL in the speaker room, ~70 dBA SPL in Room 2, and ~65 dBA SPL in the far room, compared to average ambient noise pressure of ~55 dBA SPL. This allowed the birds to reduce their noise exposure, but not entirely escape it, a situation that is ecologically relevant to urbanized areas. The reference aviary would not receive experimental noise during any time-period. We used a standardized blocking procedure to determine the aviary and room that would receive sound treatment, thus we used both aviaries for experimental groups equally and alternated which room had noise for each trial (Figure 1). This was to account for any innate preferences for rooms or aviaries that the birds may have independent of our experimental manipulation.

We collected social network data by conducting focal-follows of each bird and defining interactions using an ethogram (Table 2). A focal-follow is when one individual bird is observed for a pre-determined length of time, in our research 8 min, and all interactions it has with other birds are systematically recorded (Whitehead 2008). Each data collection period consisted of focal-follows of every bird in both treatments (experimental and reference) and data collection occurred

daily throughout a trial in a randomized order. We assigned each color-banded bird an individual number and then used a random numbers generator to randomize the order of the focal-follows for each day of data collection. Over the course of the study, 260 birds were observed for a total of 312 hours of data collection (total birds had been 264 but four birds died early in their trials and were thus excluded from the data).

We were interested in how introduced noise altered the space use of the birds within the experimental aviary. To test this, we noted all rooms each focal bird used during its focal follow throughout the trial, to figure out the proportion of observations it was found in each room in each phase. To estimate the overall distribution of birds across the three-room system, we summed the total percentages of individual bird-use for each room and divided by the number of birds in the trial, to generate overall percentages of flock space-use for each of the three rooms in the aviary. We then compared the proportion of flock use in the noise room before noise was playing to during noise manipulation. Additionally, we measured food consumed daily in the experimental aviary. Prior to the start of each morning observation, food was weighed and re-filled to 120g. When weighing food from the previous day, we would remove feces from feeders to remove the added of weight, and then subtracted the current weight from the 120g given the day before to determine how much was consumed. We quantified the percent change in food eaten in the noise room before and during the noise treatments to determine if the noise deterred the birds from using that room.

		Before	Noise	After
Experimental				
	Mean	59.146	78.545	59.543
	S.D.	3.894	4.263	7.484
Reference				
	Mean	60.121	62.290	58.797
	S.D.	4.745	2.347	5.585

**Table 1:** Average maximum dBA SPL in experimental and reference aviaries  $\pm$  standard deviation throughout phases of trials (n = 11). The reference aviary was slightly affected by the noise played in the experimental aviary, but at a less extreme level.

Abbreviation	Behavior	Definition
F	Feeding	The bird is eating
M	Migrating	The bird moves between rooms.
W	Water	The bird is drinking water
B	Cuttlebone	The bird is using the cuttlebone
P	Perched	The bird is perched (sitting on perch or wall)
G	Preening	The bird is grooming itself or another bird
N	Naptime	The bird is sleeping
CS	Courtship	Male performs directed song and waltz or attempts to mount female
S	Sex	The bird is mating
NS	Nesting	The bird is gathering supplies to add to nest or building nest
V	Out of View	The bird is somewhere out of view/observer lost sight of bird
O	Other	The bird is doing a behavior not listed

**Table 2:** Ethogram used for collecting behavioral and interaction data.

Interactions were defined using the ethogram (Table 2) and networks were constructed using only non-aggressive interactions, as aggressive interactions tended to be the displacement of another individual to keep them away from their social group. We then transformed these interactions into association matrices using

the simple association index (SAI):  $\frac{x}{x+y_a+y_b+y_{ab}}$  where  $x$  is the total number of observations,  $y_a$  is the number of times the focal individual was observed,  $y_b$  is the number of times the interacting individual was observed, and  $y_{ab}$  is the total observations where the focal individual and interacting individual were observed together (Whitehead 2008). These interactions are the edges between nodes in a social network system. Both of our metrics of interest, the individual metric of node strength and the group-level metric of clustering coefficient, are repeatable and consistent across time (Jacoby et al. 2014). For this reason, we felt these metrics would be appropriate to study the effects of noise disturbance, as any observed changes could be attributed to our noise treatment.

### *Statistical Analyses*

We wrote a custom Python script to manipulate data, which converted raw interaction data to a matrix of association indices. To process social network metrics, we used the “igraph” package in R (Csárdi and Nepusz 2006; R Core Team 2016). We used linear mixed models (LMM) for both of our response variables, node strength and GCC. Our fixed predictor variables were *Treatment*, which had two levels (reference and experimental), and *Phase*, which had three levels (*before*, *noise*, *after*). Individual bird identity nested within trial was a random effect for both models. The model with fixed effects was therefore:

$$y = \alpha + \beta_1 Treatment + \beta_2 PhaseContrast_1 + \beta_3 PhaseContrast_2 + \beta_4 Treatment * PhaseContrast_1 + \beta_5 Treatment * PhaseContrast_2 + \varepsilon$$

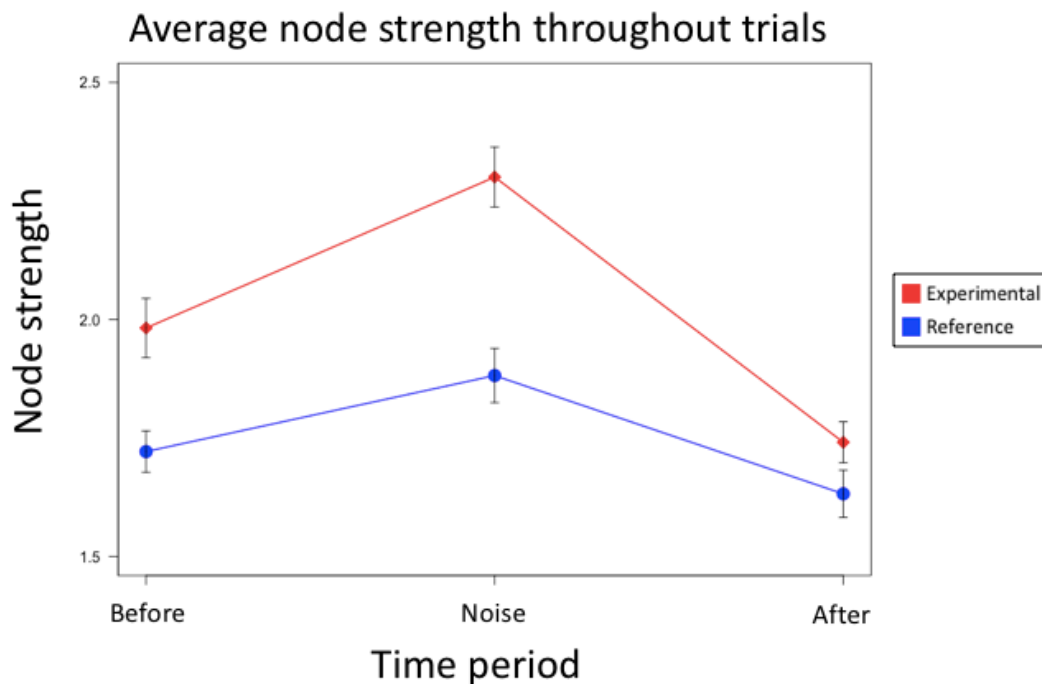
We used a sum-to-zero contrast, and in this contrast system, the mean of the dependent variable (*Treatment* or *Phase*) for the level coded as 1 is compared to the overall mean across all levels of the dependent variable (Wendorf 2017). The contrast *PhaseContrast<sub>1</sub>* thus compares the *before* phase to the mean of all three phases and the contrast *PhaseContrast<sub>2</sub>* compares the *noise* phase to the mean of all three phases. A -1 is assigned to the level that is never compared to the others (i.e. so that the number of regression predictors is one fewer than the total number of levels). The *Treatment* contrast sets reference as 1 and assigns -1 to experimental. By using this contrast coding, the intercept of the fit regression model is equal to the grand mean across all treatments and each regression coefficient is equal to the deviation from that grand mean associated with a particular level (i.e. the level specified by a value of 1). In order to fit clustering coefficient data to a normal distribution, we used a logit transformation. We generated our LMMs in R using the package “afex” (R Core Team 2016; Singmann et al. 2018).

Finally, to analyze spatial use of the aviary with the onset of noise, we compared both the proportion of birds in the experimental room and the food weight data from *before* to *during* to determine the effects of noise on bird distribution throughout the aviary. We ran paired t-tests comparing the proportion of bird use in the experimental room and the weight of food eaten in the experimental room from before to during noise manipulation.

## **Results**

### *Changes to individual sociality (node strength)*

Node strength was significantly influenced by Treatment ( $F_{1, 256.95} = 20.5847$ ,  $p < 0.001$ ), Phase ( $F_{2, 517.05} = 44.8093$ ,  $p < 0.001$ ), and their interaction ( $F_{2, 517.05} = 6.5034$ ,  $p = 0.002$ ). The effect of *Treatment* ( $\beta_1 = -0.131519 \pm \text{S.E.} = 0.028998$ ) indicates that on average, node strength increased in the experimental treatment. The effect of *PhaseContrast*<sub>1</sub> ( $\beta_2 = -0.024779 \pm 0.0248$ ) indicates that the effect of being in the *before* treatment was slight, but the effect of *PhaseContrast*<sub>2</sub> ( $\beta_3 = 0.189766 \pm 0.0248$ ) indicates that the *noise* treatment had a substantial positive effect on node strength. The *after* treatment declined in node strength (Table 3;  $\alpha + \beta_2(-1) + \beta_3(-1) = 1.686868$ ). These effects, as well as the interaction effects, are given in Table 3. These results reveal that experimental birds experienced change in sociality directly related to the *noise* phase of the experiment and sociality was also affected by the noise disturbance being turned off (Figure 2).



**Figure 2:** Average node strength, with corresponding standard error bars, of experimental birds ( $n = 131$ ) and reference birds ( $n = 129$ ) throughout eleven trials.

### Mean node strength (Gaussian)

	Estimate	Std. Error
(Intercept)	1.876664	0.028988
Treatment; Reference	-0.131519	0.028998
Treatment; Experimental	0.131519	0.028998
<i>Before</i> vs. all; PhaseContrast <sub>1</sub>	-0.024779	0.024800
<i>Noise</i> vs. all; PhaseContrast <sub>2</sub>	0.214575	0.024800
<i>Before</i> Treatment:PhaseContrast <sub>1</sub> vs. all	0.001009	0.024800
<i>Noise</i> Treatment:PhaseContrast <sub>2</sub> vs. all	-0.077958	0.024800

**Table 3:** Results of LMM for node strength. The Intercept term gives the grand mean across all factors, and *Treatment* and *PhaseContrast* can be interpreted using the sum-to-zero contrasts discussed in *Statistical Analysis* in the Methods.

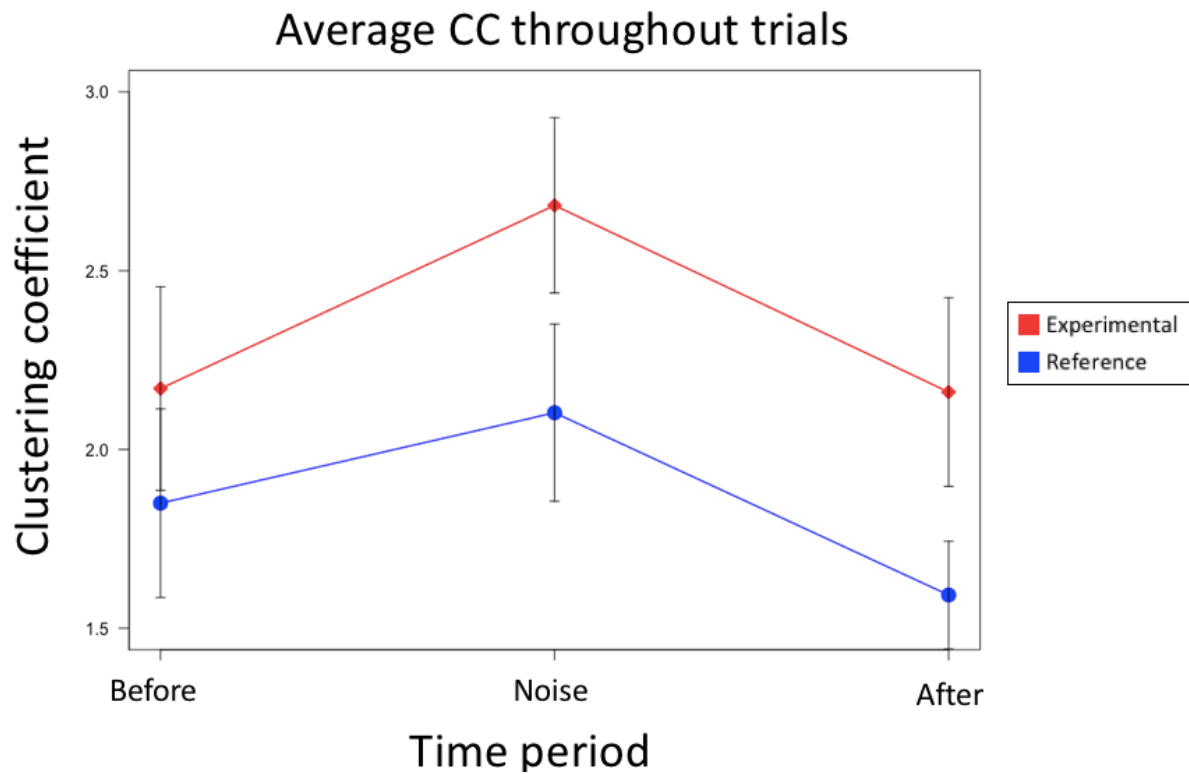
Estimates are the coefficients for the LMM and their standard error, which gives the deviation from the intercept associated with factor levels.

#### *Changes to flock (global clustering coefficient)*

Global clustering coefficient (GCC), or overall connectedness of the network, was significantly influenced by *Phase* ( $F_{2,40}$ ,  $p = 0.03$ ), but not by *Treatment* ( $F_{1,20}$ ,  $p = 0.08$ ) or by their interaction ( $F_{2,40}$ ,  $p = 0.74$ ). The effect of *PhaseContrast*<sub>1</sub> ( $\beta_2 = -0.08476 \pm \text{S.E.} = 0.11096$ ) indicates that the effect of being in the *before* treatment was negligible, but the effect of *PhaseContrast*<sub>2</sub> ( $\beta_3 = 0.21809 \pm \text{S.E.} = 0.11096$ ) indicates that the *noise* treatment had a substantial positive effect on GCC in both treatment groups. The *after* treatment declined in GCC (Table 4;  $\alpha + \beta_2(-1) + \beta_3(-1) = 1.9614$ ). All of these effects are given in Table 4. The lack of statistical significance within the treatment effects and the interaction effects indicates that the treatment groups (reference and experimental) were not independent, as the



reference group was being affected by the noise given to the nearby experimental group (Table 1) and instead served as a low-level experimental group rather than a reference. Mirroring the results of node strength, the noise treatment resulted in a more clustered social network during noise, and a decreased cluster following noise disturbance (Figure 3).



**Figure 3:** Average global clustering coefficient (logit transformed), with corresponding standard error bars, of experimental flocks (n = 11) and reference flocks (n = 11) throughout trials.

Mean global clustering coefficient (logit transformed to Gaussian)

	Estimate	Std. Error
(Intercept)	2.09473	0.13427
Treatment; Reference	-0.24630	0.13427
Treatment; Experimental	0.24630	0.13427
<i>Before</i> vs. all; PhaseContrast <sub>1</sub>	-0.08476	0.11096
<i>Noise</i> vs all; PhaseContrast <sub>2</sub>	0.21809	0.11096

<i>Before Treatment:PhaseContrast</i> <sub>1</sub> vs. all	0.08599	0.11096
<i>Noise Treatment:PhaseContrast</i> <sub>2</sub> vs. all	-0.03746	0.11096

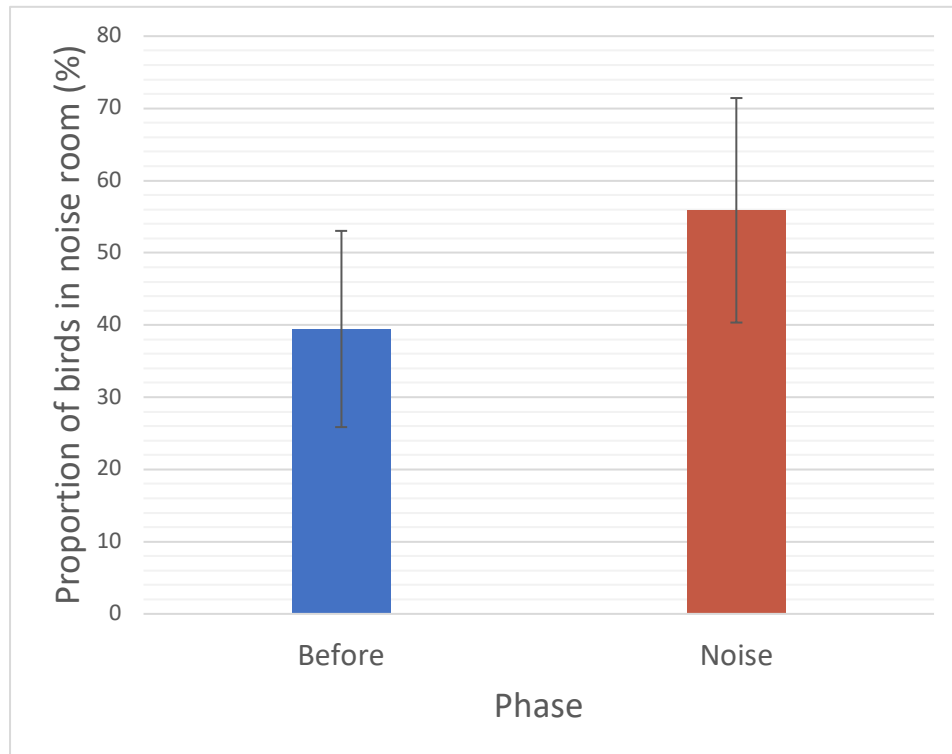
**Table 4:** Results of LMM for GCC. The Intercept term gives the grand mean across all factors, and *Treatment* and *PhaseContrast* can be interpreted using the sum-to-zero contrasts discussed in *Statistical Analysis* in the Methods. Estimates are the coefficients for the LMM and their standard error, which gives the deviation from the intercept associated with factor levels.

We were unable to demonstrate that birds altered their spatial distribution in response to the noise gradient established during the *noise* phase of the trial. Though, contrary to what we expected, there was an apparent trend of birds increasing their use of the noise room (all but 2 trials, see Table 5), though this trend was not statistically significant ( $n = 11, p = 0.07$ ; Figure 4). Throughout trials, there was no consistent change in feeder use in the noise room (Table 6), indicating that birds did not alter their spatial use of the experimental aviary in relation to introduced traffic noise ( $n = 7, p = 0.1223$ ).

	Before	Noise	Change
Trial 1	70.67%	35.64%	-35.03%
Trial 2	54.52%	60.17%	5.65%
Trial 3	18.09%	46.58%	28.49%
Trial 4	16.50%	61.42%	44.92%
Trial 5	86.84%	100%	13.16%
Trial 6	27.25%	65.67%	38.42%
Trial 7	24.92%	0%	-24.92%
Trial 8	20.11%	41.91%	21.80%
Trial 9	40.15%	81.50%	41.35%
Trial 10	44.96%	48.56%	3.60%
Trial 11	29.94%	73.30%	43.36%

Average Change: 16.44%

**Table 5:** Proportion of birds in experimental noise room before and during sound manipulation.



**Figure 4:** Proportion of birds in experimental noise room before and during sound manipulation (n = 11, p = 0.07). Bars indicate average with 95% confidence intervals.

	Before	Noise	Change
Trial 3	8.4	5.5	-2.9
Trial 5	35.75	39.5	-6.35
Trial 6	5.3	21.4	16.1
Trial 7	11.3	0.025	-11.275
Trial 9	25.3	69.65	44.35
Trial 10	57.6	69.6	12
Trial 11	22.1	49.9	27.8

**Table 6:** Food eaten (g) in experimental noise rooms before and during sound manipulation.

## Discussion

These results supported our prediction that individual sociality (node strength) and flock cluster (GCC) would both increase with the onset of introduced noise pollution. Unexpectedly, we also found that removing the noise source led to the birds not just “recovering” from their increased social state, but becoming less social than in their pre-disturbance state. Unintentionally, our reference group instead became a “low-level” treatment group, and revealed that even at low levels of introduced traffic noise, birds adjusted their sociality in both GCC and node strength. However, the “low-level” birds experienced a less extreme response compared to their high-level treatment counterparts.

Increased sociality in urban-dwelling birds can have a variety of ecological implications for similar urban sedentary species. Social network size and individual sociality both can affect disease transmission, as individuals with high node strength have a disproportionate effect on the disease transmission throughout a population (Hamede et al. 2009; Rushmore et al. 2013), thus denser flocks of birds with more social constituents could alter the rate and prevalence of pathogen transmission. This could possibly contribute to increased parasite loads found in urban-dwelling birds compared to their rural counterparts (Giraudeau et al. 2014). However, the same process of increased sociality can alter the transmission of symbiotic microbes and change the gut microflora biodiversity in birds, increasing resistance

to disease (Archie and Tung 2015; Levin et al. 2016). Additionally, increased sociality and flock clustering can increase familiarity between conspecifics, which can decrease individual aggressiveness (Geffroy et al. 2014), and corresponds to previous findings of decreased aggressiveness in urban house finches (*Haemorhous mexicanus*) compared to their rural counterparts (Hasegawa et al. 2014).

The reduction in sociality following disturbance in the *after* phase indicates a level of resistance to disturbance in these zebra finches. While the resulting decreased levels of both GCC and node strength surpassed their baseline levels in the *before* period, it would be interesting to see if this would return to baseline with a more prolonged observation period following the noise disturbance. This recovery from a disturbed social network implies that remediation strategies for noise pollution could return birds to their natural social state, a phenomenon that has been observed in dolphin social networks following the implementation of legislation limiting commercial fisheries in their habitat (Ansmann et al. 2012).

We did not find a statistically significant change in habitat use across the cage with the onset of sound (See Tables 10 & 11). Birds rarely used the aviary space evenly, and many trials did experience strong room biases, but these were not affected by the onset of noise regardless of preferred room. The observed trend of moving towards the noise could be related to natal environment, as these birds were raised in indoor rooms with highly reflective concrete walls and floors and cooled by a relatively old and noisy HVAC system, and sometimes natal environment can influence habitat preference later in life (Davis and Stamps 2004). We propose that since the observed increased flock clustering and individual

sociality is not spatial, it could instead be a symptom of perceived predation risk. In accordance with the Increased Threat Hypothesis, the noise the birds experienced could increase perceived threat by lowering the ability to vocally communicate predation risk (Kern and Radford 2016) and thus heighten vigilance within the flock, and physically clumping together more and increasing sociality could potentially lower the risk of missing a predatory cue (Owens et al. 2012). Other studies have noted the change in conspecific density with increased predation risk (Peacor and Lansing 2003), and across avian species there is a negative correlation with sociality and relaxed predation risk, which implies that species with higher predation risk have higher sociality (Beauchamp 2010).

We suggest future studies investigate if increased predation risk can alter sociality, which could explain the mechanism by which noise pollution is increasing flock cluster and individual sociality. Additionally, we recommend follow-up studies on how increased sociality in noise conditions can affect pathogen or gut microbe transmission, and aggressiveness and dominance. It is important to note that despite these findings, many birds that are not urban-dwellers will not be able to cope with increased noise disturbance and those that can possess certain life history traits that allow the phenotypic plasticity to adjust to a new soundscape (Møller 2009; Francis et al. 2011). In conclusion, this study has demonstrated that urban-dwelling sedentary songbirds do not distribute themselves in accordance with sound pressure level, but do increase individual sociality and overall flock clustering in response to chronic traffic noise disturbance, and we propose future studies work to identify the mechanism behind these social changes.

## **Chapter 2: Experimentally introduced traffic noise decreases sociality and affects space use in red-backed fairy-wrens (*Malurus melanocephalus*)**

### **Introduction**

#### *Background*

Urban expansion has introduced a variety of stressors on natural ecosystems, including pervasive noise pollution. Due to its ability to permeate forests and rural locations, noise is a particularly widespread pollutant (Forman and Alexander 1998). Although all habitats contain some element of noise, anthropogenic noise is evolutionarily novel compared to its natural counterpart, as anthropogenic noise tends to occur at a lower frequency (pitch) and at higher amplitudes (Slabbekoorn and Ripmeester 2008). Anthropogenic noise, hereby referred to as “noise,” therefore fundamentally changes the acoustic environment and creates novel challenges for wildlife in both sending and receiving acoustic information.

Many taxa, including birds, rely on acoustic information to moderate important aspects of their daily routines, such as assessing predation risk (e.g. alarm calls) or attracting and retaining mates (e.g. courtship songs). Additionally, acoustic signaling is heavily involved in the maintenance of social systems, such as reinforcing pair-bonds (Baldassarre et al. 2016), eavesdropping to acquire resource or reputational information of neighboring conspecifics (McGregor and Peake 2000; Snijders and Naguib 2017), defending territories (Amy et al. 2010), and influencing female choice in extra-pair courtship (Otter et al. 1999). Change in the acoustic environment instigates behavioral adjustments to cope with new auditory conditions,

or causes dispersal entirely, thus we are interested in how response to noise conditions and the masking of acoustic signaling can affect sociality in birds.

Birds that remain in noisy conditions face a range of challenges, behaviorally and physiologically. When acoustic signals are masked and less effectively transmitted, such as alarm calls or the sounds of approaching predators, it results in increased vigilance behavior and less time available for foraging (Halfwerk et al. 2011; Schmidt et al. 2014; Meillere et al. 2015). Additionally, masking of mating calls by noise can affect reproductive success, which has been documented in great tits (*Parus major*) (Halfwerk et al. 2011). To stand out over the noise, birds must adjust their vocalizations to be higher pitched and louder, as has been demonstrated in eastern bluebirds (*Sialia sialis*) and zebra finches (*Taeniopygia guttata*) (Cynx et al. 1998; Kight and Swaddle 2015). In addition to signal masking, organisms that remain in noisy areas experience increased stress and decreased immunity (Chloupek et al. 2009; Blickley et al. 2012). Rather than coping with these challenges presented by noise conditions, many birds will disperse from noise-degraded habitats to quieter areas (Francis et al. 2011).

Avian dispersal from noise has been widely documented, but the impacts from this dispersal are not as well understood (Francis et al. 2009; Mahjoub et al. 2015; Swaddle et al. 2016). Dispersal from noise alters community composition at noise-polluted sites based on vocal frequency, and this can sometimes prove beneficial for species who remain in noise if nest predators were excluded from the area (Francis et al. 2009; Francis et al. 2011). By degrading habitat and filtering out species, noise directly impacts habitat use, and alters occupancy and distribution as species avoid noisy areas (Goodwin and Shriver 2011; McClure et al. 2013; Chen



and Koprowski 2015; Ware et al. 2015). While many studies focus on the effects of noise on birds that remain in noise-polluted areas, we were interested in what happens to the individuals that disperse away from the source of noise. Specifically, we were interested if the dispersal away from noise could influence sociality in birds.

Sociality plays a large role in the ecology and life-history of many species, especially in birds. Sociality can modulate reproductive success (Formica et al. 2012), mate choice and availability (Oh and Badyaev 2010), information flow (Aplin et al. 2015; Farine and Sheldon 2015), disease transmission (Hamede et al. 2009; Rushmore et al. 2013), and ultimately evolutionary processes (Bromham and Leys 2005). An organism's social group has a considerable effect on mating success, through mechanisms such as female choice (Sih et al. 2009), perceived ornamentation (Oh and Badyaev 2010), and connections to available mates (Formica et al. 2012). Information transfer facilitated through a network can provide reputational information about competitive individuals, the allocation of resources, and song-learning in juvenile males (Krause et al. 2007; Sih et al. 2009; Aplin et al. 2015; Farine and Sheldon 2015). Additionally, social groups can be predictive of pathogen transmission among individuals, with highly connected individuals often having a disproportionate effect on disease risks for entire populations (Hamede et al. 2009; Rushmore et al. 2013). Therefore, alteration of a social system could have considerable effects on organismal and population processes.

Application of social network theory to observe the effects of disturbance on organisms is in its infancy, but a few studies have successfully established associations between social change and disturbance. In mixed-species flocks of birds, species-level sociality (as measured by node strength) declined with

increasing forest fragmentation (Mokross et al. 2014) and interactions between species and mean flock size declined with increased habitat fragmentation (Maldonado-Coelho and Marini 2004). In relation to anthropogenic noise, pile-driving noise reduced group cohesion in European seabass (*Dicentrarchus labrax*) shoals, possibly due to the masking of sensory information (Herbert-Read et al. 2017). We therefore hypothesized that anthropogenic noise would affect songbird sociality by degrading functional habitat and dispersing birds from the source and by masking acoustic signaling within noise areas. Specifically, we sought to understand how noise affects node strength, which is a measure of individual sociality or “gregariousness” quantified by number and frequency of interactions per individual (Whitehead 2008). Additionally, we were interested in adjustment of space use around a noise source to determine if dispersal from noise could serve as a mechanism underlying change in sociality.

### *Objectives*

The overall intention of this study is to determine if experimentally introduced traffic noise alters the sociality of a free-living, sedentary songbird population that had not previously been exposed to chronic of traffic noise, to further ascertain how increasingly prevalent noise pollution affects the behavior of wildlife. We introduced traffic noise to a population of red-backed fairywrens (*Malurus melanocephalus*) that occupied wooded habitat at a relatively secluded park and documented how their individual sociality (node strength) changed before, during, and after introduction of traffic noise. We predicted that birds would be displaced from the experimental point-source of traffic noise (i.e. our speaker) and adjust their space use to include locations where the traffic noise was quantifiably indistinguishable from background

sounds in the environment. Concomitantly, we predicted that this noise-related displacement would result in birds occupying smaller home ranges that would overlap those of their conspecific neighboring groups. Finally, we predicted that the sociality of individuals, as measured by node strength which is calculated by the number and frequency of interactions with other individuals, would increase as a result of this noise-mediated dispersal, due to occupying a smaller area more closely adjacent to neighboring groups.

## **Methods**

### *Study System*

The red-backed fairywren is a highly social bird species that can also serve as an indicator of ecosystem health (Rowley and Russell 1997; Skroblin and Murphy 2013). In the non-breeding season, they form familial groups consisting of one social pair and the offspring from the previous breeding season (often 4-6 birds per group). They are sexually dimorphic, and the dominant paired male of the group often molts into their namesake red-black nuptial plumage early in the non-breeding season, which consists of black feathers and beak with a reddish-orange back. Other males in the group, likely offspring from that year or 1-year-old offspring from a previous breeding season, maintain dull, light brown plumage indistinguishable from females (at least to the human eye). They are resident to our field site in QLD, Australia, and are fairly sedentary. They are exposed to some degree of traffic noise, from a nearby highway, but only if they venture close to the road. Hence, traffic noise is not an entirely novel acoustic stimulus but the birds are also not chronically exposed to traffic noise.

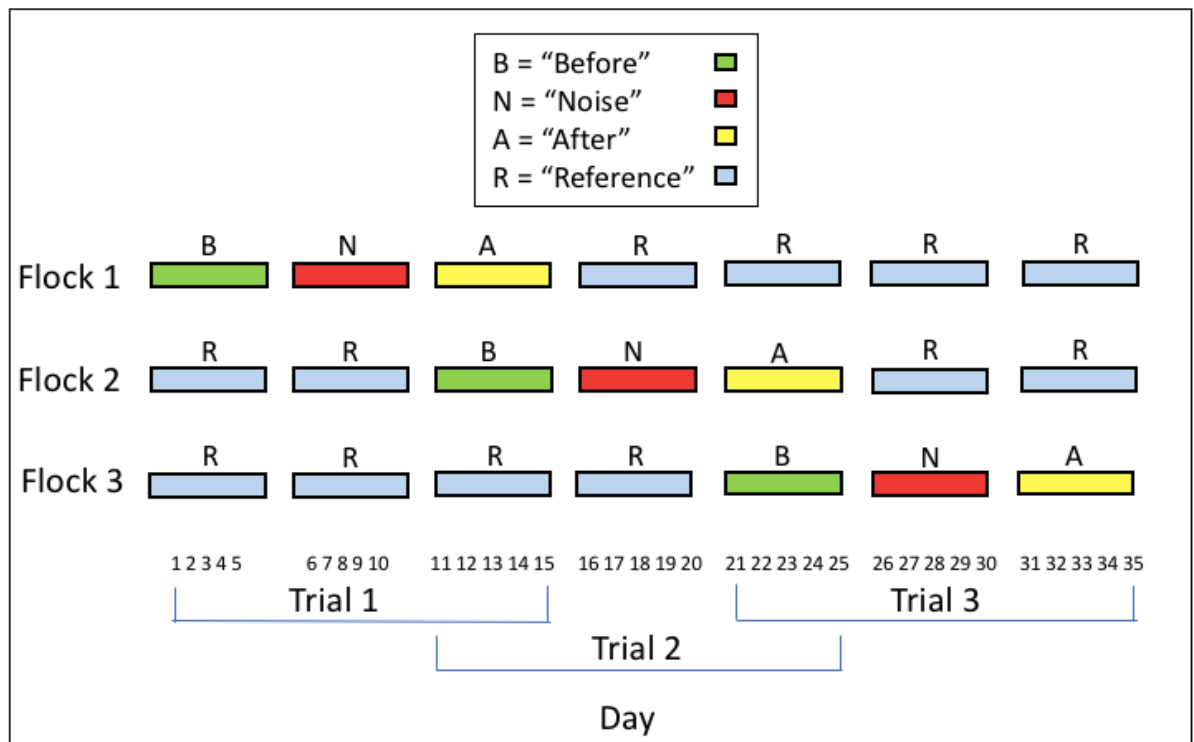
During the non-breeding season, males will often foray to neighboring females and partake in courtship displays. Non-breeding season behaviors impact the outcome of subsequent breeding seasons in other species of fairywrens (Mulder and Magrath 1994). Therefore changes of social structure during the non-breeding periods could have longer-term implications for mating outcomes.

### *Data Collection*

We conducted fieldwork during a portion of the 2018 non-breeding season (June 23rd-August 3rd) at an established field site located on Lake Samsonvale near Samford, Queensland, Australia (S27° 16.689' E152° 51.268') on a color-banded population of red-backed fairywrens. To collect social data, we conducted 25 min focal-follows of each of the three familial groups daily. A focal-follow consists of following one flock of birds for a pre-determined length of time and systematically recording all interactions of birds within that flock and with outside conspecific birds visiting that flock (Whitehead 2008). During a 25 min focal-follow we would identify and record all individuals within a 20-m radius every 5 min to generate a proximity network, defining an interaction as coordinated flock movement within a 20-m radius of each other. We based these methods on previous (unpublished) social network work with the red-backed system that 20-m tended to be the greatest distance in which birds would interact. Following the focal-follow session, we georeferenced (Garmin GPS) the approximate center of where the group of birds were observed at every 5-min interval. We focally-followed three familial flocks daily throughout three full trials, for a total of 53 hours of social observations.

### *Experimental Design*

We divided the observations of each group of birds into three 5-day experimental phases: (i) “before”, before noise introduction; (ii) “noise”, during noise introduction; and (iii) “after”, the period immediately after we stopped introducing the noise to the experimental flock of birds. A full trial consisted of the three 5-day experimental phases (15 days total) during which we recorded social data for three separate flocks of birds. Each trial had one experimental group, that would receive the noise treatment in the “noise” phase, and two reference groups, that would not receive noise over the same time period (Figure 5). We conducted three trials throughout the field season. Each flock was experimentally manipulated for one trial and served as reference groups for the other two trials.



**Figure 5:** Schematic for field experiment, demonstrating each trial and flock through time. Note that Flocks 2 & 3 “Before” period also served as a final reference for the

previous trial. Therefore, the first trial was days 1-15, the second trial was days 11-25, and the third trial was days 21-35.

During the *noise* phase, we introduced traffic noise to the experimental group by placing a speaker (Audio Experience AES0003 full-range 200W), connected to a marine-grade amplifier (BOSS Audio MR 1002) that was powered by a 12V car battery recharged by a solar panel (ALLPOWERS 60W Foldable SunPower Solar Panel), in the approximate center of the focal group's home range. We roughly estimated the center of the focal group's home range by creating Minimum Convex Polygons (MCP) generated from 30 GPS points collected during the *before* phase and roughly estimating the center by eye by overlaying the MCP onto satellite imagery. Noise treatments consisted of a looped 8-hour recording of highway sounds that varied in maximum dB SPA (~65 - 80 dBA) depending on the amount of cars and trucks passing on the highway throughout the recording (8 Hours of, 2014). While we did not do any formal surveys of vegetation cover, all speakers were located in similar grassland habitat with 0% canopy cover, and we trampled down tall grass surrounding the speaker. Thus, we are confident that vegetation did not differ greatly between any of our speaker locations and would have minimal influence on the introduction of noise for each trial. To confirm this, we also took sound pressure readings at 1m increments for all three trials and found no outstanding differences between speaker locations.

Noise was turned on following the final data collection of the *before* phase and turned off following the final data collection of the *noise* phase for a total of five days of noise manipulation per experimental group. The speaker emitted an

amplitude of approximately 80 dBA SPL 1m from the source, and about 51 dBA SPL at 10m from the source (see Table 7). This amplitude dropped off to approximately 47 dBA SPL at about 22m from the source and was considered indistinguishable from background sounds (see Table 7). In this way, we introduced loud traffic noise at the center of a group’s home range but that noise dissipated quickly enough that there were areas of the original home range that were relatively unaffected by the noise.

Distance	Speaker on	Speaker off
0-3m	86.144	45.419
4-6m	71.833	45.685
7-9m	63.437	45.637
10-12m	59.011	45.793
13-15m	55.467	46.652
16-18m	53.233	45.593
19-21m	51.522	46.215
22-29m	47.638	46.315

**Table 7:** Sound pressure readings (dBA SPL) surrounding the placed speaker while speaker is on playing traffic noise and is off and the area is just ambient noise.

### *Social Network Metrics*

We used weighted social networks rather than binary networks, to account for strength and frequency of interactions. Social networks consist of “nodes” and “edges,” where a node represents an individual or group (in this case, individual birds) and the edges represents interactions between nodes. We defined interactions by proximity, birds within 20 m of each other were considered to be interacting with each other. We constructed association matrices using the simple

association index (SAI):  $\frac{x}{x+ya+yb+yab}$  (Whitehead 2008). This generated “edge weights” from 0 to 1 which is the proportion of observations where the two subjects were observed together out of all of the observations for the focal birds, this value then served as the edge between nodes in the network. A high value indicates that those two individuals are often interacting (i.e. birds that were observed together for every observation have a value of 1), whereas a low value indicates that those two individuals were seen together for a smaller proportion of observations and interact less frequently. Our social metric of interest, node strength, is calculated as the sum of all weighted edges connected to an individual node, and therefore indicates the “gregariousness” or “sociality” of the birds (Whitehead 2008). We used a custom Python script to convert raw interaction data to a matrix of association indices. We processed these matrices using the “igraph” package in R (Csárdi and Nepusz 2006; R Core Team 2016), generating node strength for each individual bird throughout all phases within experimental and reference trials. Since there is natural individual variation for sociality, we calculated the change in node strength between phases for each bird ( $\Delta$ NS: “*noise*” minus “*before*”, and “*after*” minus “*noise*”) rather than using the raw values.

In addition to how sociality is changing generally, we were interested in what aspects of sociality in these birds were driving observed individual changes. Therefore, in addition to our overall experiment we examined subsets of the data to determine whether it was changes within-familial group interactions or between-group interactions that influenced individual bird node strength. To determine within-group sociality, we excluded any between-group interactions from our dataset. To determine exclusively between-group interactions, nodes represented entire family



groups rather than individual birds, thus only between-group interactions were included in these analyses.

### *Estimates of space use*

We uploaded GPS points from focal follows into ArcMap, with approximately 30 points (average of 28.4) for each familial group for each phase (*before*, *noise*, *after*) throughout the three trials. Due to two instances of losing birds after 3-4 GPS points during data collection, not all trials had 30 points. We generated kernel densities (KDs) using Geospatial Modeling Environment, and then generated utilization distributions (UDs) based on KDs in ArcMap GIS. UD's estimate the proportion of space used by the birds across an area (Worton 1989), which allowed us to quantify space use of each familial group at each phase during the study. To quantify the change in space use with the onset of sound, we summed cell-level UD values within the "noise zone", (i.e. the 20-m diameter circle surrounding the speaker) before and during sound playback. Since UD's estimate the probability of space use, the sum of overlap of UD's in the noise area tells us the probability of birds spending time in space affected by our speaker out of their total observed space use.

### *Statistical Analyses*

To examine how sociality changed in association with the introduction of traffic noise, we calculated the change in node strength from *before* to during *noise*, and also from *before* to *after* noise had been removed. By calculating the difference in node strength between experimental phases for each bird, rather than the raw value for birds in each phase, we account for the lack of independence among observations for individual birds throughout the entirety of the experiment. We used

linear models to determine the change in node strength between experimental birds and reference birds in our overall experiment and the subsets of our dataset (between-group and within-group). The linear model included change in node strength as the response variable ( $\Delta NS$ : either “*noise*” minus “*before*”, or “*after*” minus “*noise*”), with treatment (*experimental* or *reference*) and Trial (1, 2, or 3) as predictor variables. We included Trial as a blocking variable to account for variation between groups tested at different time periods in the field season (refer to Figure 5 for time period), as there was a chance that sociality could change as the field season progressed. For these models, we used sum-to-one contrasts. Therefore, for the treatment variable, zero was assigned to the *experimental* treatment and 1 was assigned to the *reference* treatment. For Trial, slope estimates in our model related to Trial 1, and we had two contrasts to compare Trials 2 and 3 to Trial 1. *Contrast 1* compared the mean of Trial 2 to Trial 1, and *Contrast 2* compared the mean of Trial 3 to Trial 1. The linear model with fixed effects was therefore:

$$y = \alpha + \beta_1 Treatment + \beta_2 Contrast_1 + \beta_3 Contrast_2 + \beta_4 Treatment * Contrast_1 + \beta_5 Treatment * Contrast_2 + \varepsilon$$

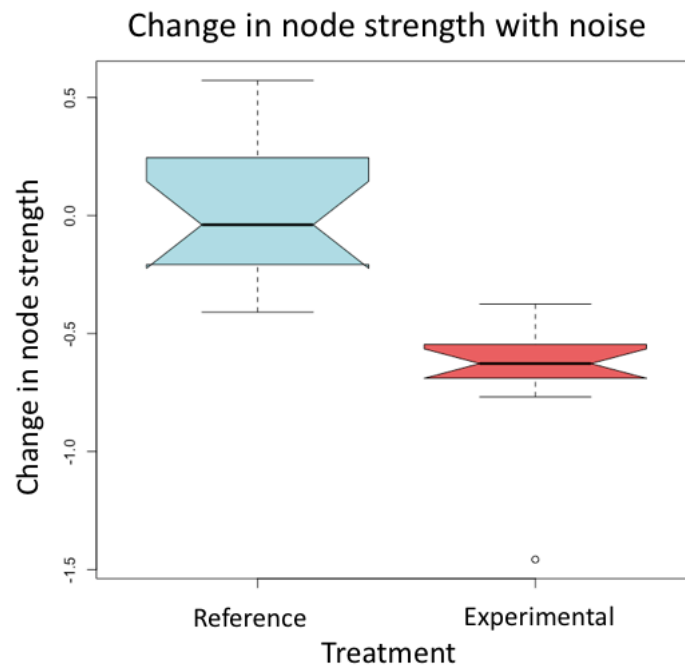
For our space use data, which will be analyzed after our second field season, we intend to calculate the difference in UD overlap with speaker before and during noise, and analyze with a t-test.

## Results

For our overall experiment, node strength decreased during noise treatments in experimental flocks of birds ( $n = 13$ ) compared with reference birds ( $n = 15$ ) ( $F_{46.20}$ ,  $p < 0.001$ ). Note that two birds present during reference trials had dispersed prior to that flock being experimentally manipulated, thus the difference in sample size for the experimental and reference birds. Our subset that included only between-group interactions revealed that node strength still decreased in association with the noise treatment ( $F_{548.62}$ ,  $p < 0.01$ ). Finally, when analyzing the data subset of exclusively within-group interactions, the node strength still decreased ( $F_{14.74}$ ,  $p < 0.001$ ). Therefore, the presentation of traffic noise within home ranges decreases both within-flock sociality, which we infer relates to within-family cohesion, and also the extent of interactions among flocks of fairywrens. This demonstrates that the birds are becoming less social, as measured by node strength, in response to noise treatments.

	Sum Sq	df	Mean Sq	F	P
<b>Overall</b>					
Treatment	4.3143	1	4.3143	46.2034	9.42E-08
Trial	0.6669	2	0.3334	3.5709	0.03946
Treatment: Trial	0.2548	2	0.1274	1.3646	0.26953
Residuals	3.0814	33	0.0934		
<b>Between Group</b>					
Treatment	0.89882	1	0.89882	548.619	0.001818
Trial	0.10505	2	0.05253	32.061	0.030247
Treatment: Trial	0.09931	2	0.04966	30.308	0.031940
Residuals	0.00328	2	0.00164		
<b>Within Group</b>					
Treatment	1.5573	1	1.55730	14.7388	0.000593
Trial	0.0187	2	0.00937	0.08870	0.915370
Treatment: Trial	0.0940	2	0.04701	0.44490	0.645031
Residuals	3.1698	30	0.10566		

**Table 8:** ANOVA output of linear models for analysis of change in node strength from before to during noise treatments. We determined significance with a p-value ( $\alpha = 0.05$ ). We ran these models for overall experiment ( $n = 28$ ), between-groups only ( $n = 3$ ), and within-groups only ( $n = 28$ ).



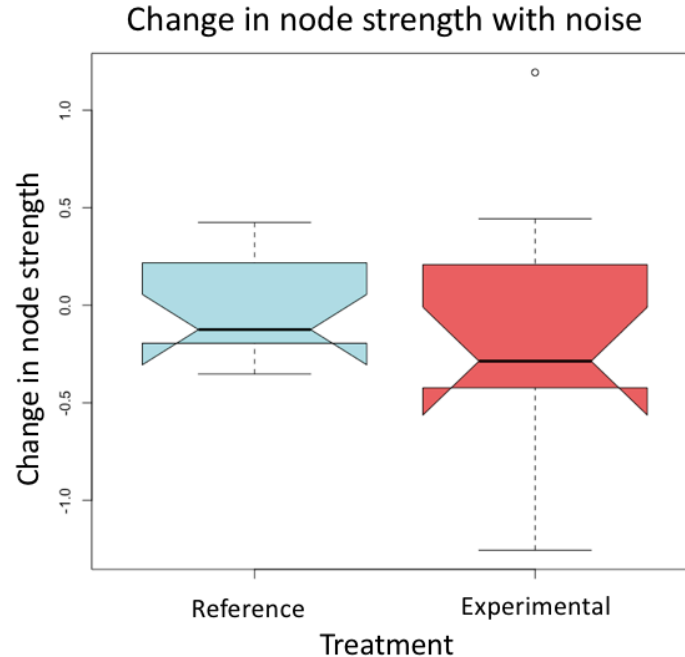
**Figure 6:** Box-and-whisker plot of change in node strength of reference birds ( $n = 15$ ) and experimental birds ( $n = 13$ ) calculated by the difference of *noise* – *before*. Reference birds are in blue, with a median line at -0.039, and experimental birds are in red, with a median line at -0.657. The whiskers indicate the range of the data and one outlier.

We were also interested in whether birds were able to recover following the termination of noise disturbance, and thus our second model looked at the change in node strength from the noise period to the time period after noise manipulation.

This model found no statistically significant effect of treatment (Table 9;Figure 7), indicating that birds remained less social following the noise manipulation.

	Sum Sq	df	Mean Sq	F	P
<b>Overall</b>					
Treatment	0.1092	1	0.10916	0.7441	0.3954337
Trial	1.5473	2	0.77367	5.2737	0.0111315
Treatment: Trial	2.7193	2	1.35967	9.2682	0.0007725
Residuals	4.2544	29	0.14670		

**Table 9:** ANOVA output of linear model for analysis of change in node strength from during noise to after noise treatments. We determined significance with a p-value ( $\alpha = 0.05$ ). This model was used for overall treatment (n = 28).

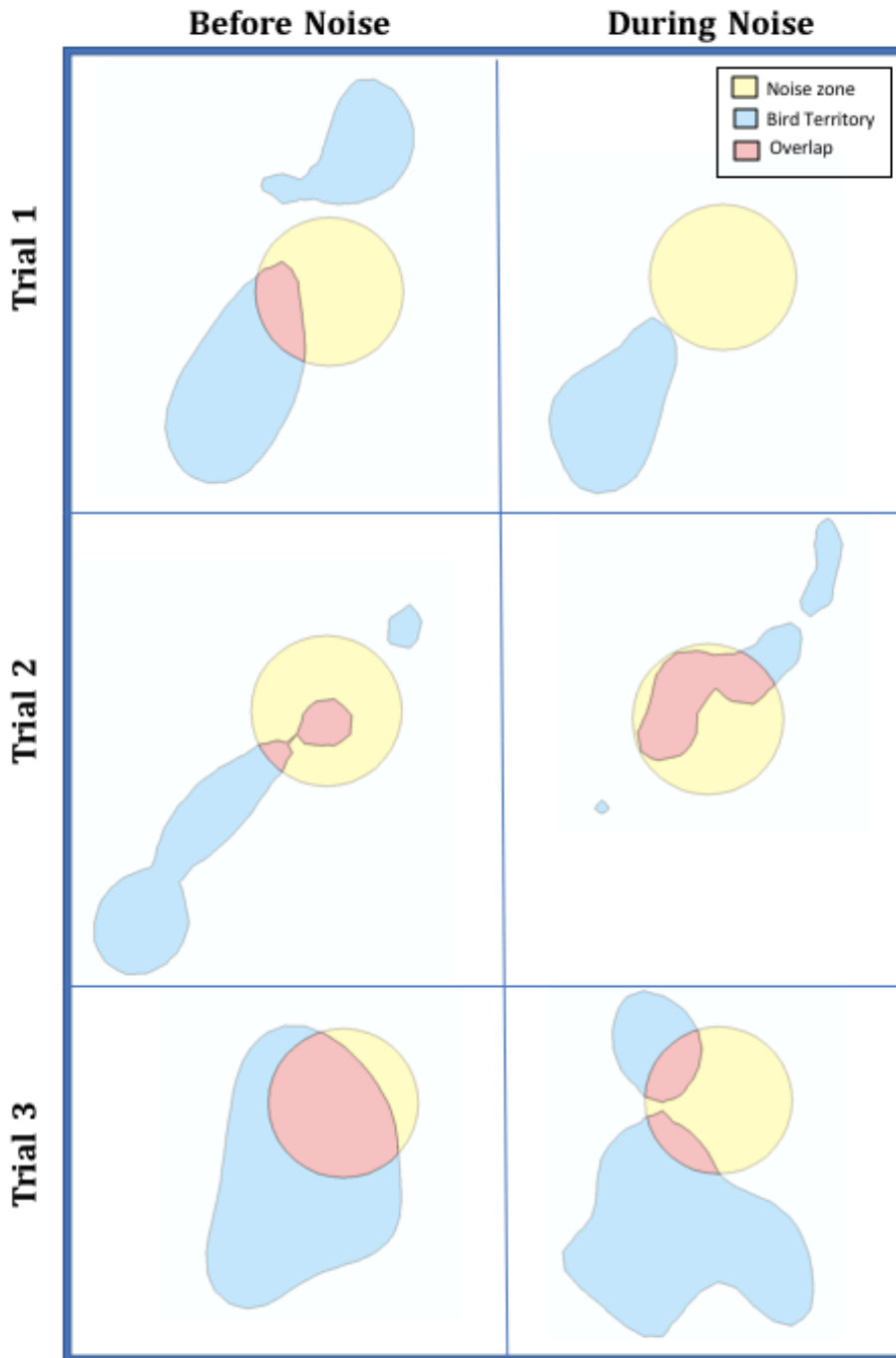


**Figure 7:** Box-and-whisker plot of change in node strength of reference birds (n = 13) and experimental birds (n = 13) calculated by the difference of *after – noise*.

Reference birds are in blue, with a median line at -0.125, and experimental birds are

in red, with a median line at -0.287. The whiskers indicate the range of the data and one outlier.

For two of the experimental groups, the birds generally occupied space further from the noise source while the traffic sounds were being broadcast compared with the period before the traffic sounds were broadcast (Figure 8). However, we observed the opposite shift in space use in a third group, in which birds moved closer to the speaker while the traffic noise was being broadcast (Figure 8). These patterns were evident in the proportional space-use by birds that overlapped with a 20-m radius around the experimental speaker. This metric decreased in association with traffic noise in two groups, but increased in one group (Table 10). Overall, we cannot yet discern a consistent pattern in shifts of space use, or change in area of space used, in association with traffic noise.



**Figure 8:** Space use by each experimental group before and during noise. The yellow circle indicates the 20 m radius of noise influence, but the noise is only playing in the “During Noise” column.

	Before	Noise	After
Trial 1	0.16	0.13	0.25
Trial 2	0.19	0.45	0.47
Trial 3	0.23	0.11	0.13

**Table 10:** Space use by birds, as estimated by utilization distribution, that overlaps with the 20-m radius circle surrounding the speaker throughout each trial phase.

## Discussion

Contrary to our prediction that individual sociality (node strength) would increase with noise due to more confined space, we have observed an appreciable decrease in individual sociality for birds exposed to noise (Table 8; Figure 6). In comparison, our reference groups that did not receive noise did not demonstrate a comparable change in their sociality, indicating that our observed effects were related to our experimental noise introduction and not to natural social changes over the course of the field season. The reduction in sociality was driven both by reduced between-flock interactions and an apparent reduction of within-flock cohesion (Table 8). Additionally, the flocks did not recover to their previous social state following the termination of noise disturbance (Table 9; Figure 7).

A reduction of sociality can ultimately affect many vital processes in these birds, as previous studies have detailed the extent in which individual personality can influence survival. For example, in eels (*Anguilla anguilla*) increased familiarity with conspecifics decreases aggressive interactions (Geffroy et al. 2014). The decline in between-group interactions that we observed could lead to less familiarity between family groups, and familiarity of neighbors in great tits (*Parus major*) was positively correlated with reproductive output, with females laying larger clutches



and with a higher percentage of offspring fledged (Grabowska-Zhang et al. 2012). Therefore, reduced familiarity in neighboring groups of fairywrens could possibly have implications for reproductive success in the subsequent breeding season.

The breakdown of within-group interactions and subsequent individual sociality can also lead to less familiarity and cohesion within a cooperatively breeding group. In fish, greater familiarity increased inclusive fitness (Ward and Hart 2003), and so a decrease in familiarity could negatively affect inclusive fitness. This could be problematic for helper fairywrens, they rely solely on inclusive fitness since they themselves do not reproduce but instead care for full- or half-siblings. Additionally, great tits that were less social tended to be less bold explorers, and missed out on finding new access to resources (Snijders et al. 2014). When new food or habitat resources were found, closely associating individuals were more likely to transfer the information about these resources (Aplin et al. 2012), so those with higher node strength will have more access to new resources. Therefore, with the observed decrease in individual node strength, it is possible that groups of fairywrens being affected by noise pollution will have less opportunity to find and access new habitat compared to unaffected neighboring groups. In our red-backed fairywren system, helper fairywrens tend to disperse their 2<sup>nd</sup> or 3<sup>rd</sup> year to form their own familial groups and breed themselves, so this decrease in node strength could affect their ability to establish their own home range later in life.

The lack of recovery following the termination of noise disturbance indicates that the effects of the short-term noise exposure were not corrected in at least 5 days. However, we are hesitant to make the claim that this effect carries in the long-term due to each trial ceasing after 5-days post-noise manipulation and instead

suggest longer-term studies investigate this further. If birds are unable to recover from noise disturbance, this result emphasizes the need to prevent further noise disturbance in current quiet areas.

Our results also revealed a slight trend indicating that birds are being displaced by noise and altering their space use in response to it (see Table 10). This apparent trend might become more evident as we add additional trials with our impending second field season. This shift in space-use indicates that sound can be a source for degrading available, functional habitat.

We suggest that the decrease in between-flock interactions was driven by the noise-induced change in spatial distribution. These changes in space-use may have led to less bordering habitat with neighboring groups, which in turn could have reduced the incidence of inter-flock interactions. As for the apparent breakdown of within-family cohesion, this may also have been related to the degradation of functional habitat that occurred as noise permeated the locations that had high space-use by the birds. Noise degradation of habitat is well-documented (Ware et al. 2015), and frequently alters species distributions across a landscape (Bayne et al. 2008). Their altered distribution could possibly exclude otherwise suitable foraging habitat, which could have contributed to the observed breakdown of flock cohesion and stability (Maldonado-Coelho and Marini 2000). Degradation of habitat can influence mixed-species flock composition (Sridhar and Sankar 2008), so it is possible that it is also influencing within-species flock dynamics. Additionally, when the birds remained within the noise zone, the increased masking of their vocalizations could explain this apparent weakening of within-group cohesion, which is consistent with previous findings that flocks of birds (specifically, green wood

hoopoes (*Pheonculus purpureus*) rely on vocalization to coordinate group movement (Radford 2004). One supported mechanism for reduced fitness in noise-disturbed habitat is the masking of parent-offspring vocalizations (Schroeder et al. 2012; Lucass et al. 2016), and while our study took place in the non-breeding season, our flocks consisted of a social-bonded pair and ~1-year-old offspring as helpers, thus we hypothesize that communication could play a role in preventing the dispersal of helper birds for the subsequent breeding season.

With noise pollution, specifically traffic noise, becoming more widespread and intense with expanding urbanization, this study details the possible social consequences for red-backed fairywrens that disperse from noise. These findings could be extrapolated to similar sedentary species (eg. chickadees and sparrows in North America). To our knowledge, this is the first study that has demonstrated that noise pollution affects individual sociality in a free-living population of songbirds. This observed reduction in sociality has the potential to affect many processes in a songbird population, from accessing resources to reproductive success. Urbanization continues to expand into undisturbed habitat, and traffic noise is the main source of anthropogenic noise (Ouis 1999), so it is important to understand how this will affect avian communities. We hope that this research can contribute to policy decisions when planning urban development, and suggest the use of less noise-conductive materials when constructing roads coupled with lower speed limits to lessen this unintended social effect on birds.

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