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Traffic noise alters individual social connectivity, but not space-use, of Red-backed Fairywrens

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ABSTRACT

The prevalence of human-generated noise is posing novel challenges to birds, by changing how they communicate or causing them to disperse away from the source of noise. We sought to understand how noise affected space-use and social connectivity in a small passerine bird, the Red-backed Fairywren (*Malurus melanocephalus*). As the displaced birds would likely be forced to occupy a smaller area that may already have resident individuals, we predicted that noise-affected birds would show increased social connectivity that may include new individuals. To test this, we introduced an experimental point-source of traffic noise to groups of fairywrens in an otherwise quiet habitat and compared the change in social connectivity of birds in groups exposed to noise to the changes in social connectivity in neighbouring groups unaffected by noise. Contrary to our prediction, noise-affected birds had reduced social connectivity during experimental noise treatments, as measured by weighted-degree, which was driven by a reduction of interactions with birds of neighbouring groups outside the noise zone. Additionally, we did not discern a change in space-use in response to our noise treatment. Therefore, we suggest that noise reduces the efficacy of signal transmission and detection in this species, resulting in the reduction of social connectivity between groups of this otherwise highly social songbird.

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Introduction


Anthropogenic noise is increasingly prevalent in previously unaffected areas of wildlife habitation (Buxton *et al.* 2017). Anthropogenic noise, henceforth referred to as 'noise', tends to occur at a lower frequency (pitch, mostly between 1–2 kHz) and at higher amplitudes (loudness) than many naturally occurring sounds (Slabbekoorn and Peet 2003; Slabbekoorn and Ripmeester 2008). Thus, noise changes the acoustic environment and creates novel challenges for wildlife in the transmission and accurate reception of acoustic signals and cues. Acoustic signals used for attracting and retaining mates are often masked by noise (Lengagne 2008; Schmidt *et al.* 2014). This noise-related degradation of mating signals can ultimately impact aspects of wildlife fitness such as hatching success (Kleist *et al.* 2018), egg production and nestling body condition (Injaian *et al.* 2018) in birds and ultimately reproductive success (Halfwerk *et al.* 2011). Many species of wildlife use auditory cues to warn against threats of depredation. Therefore, animals occupying noisy environments often increase vigilance, and subsequently reduce time spent foraging (Rabin *et al.* 2006; Meillere *et al.* 2015; Mahjoub *et al.* 2015; Ware *et al.* 2015; Kern and Radford 2016; Quinn *et al.* 2017). Beyond the degradation of acoustic signals and cues, noise might also be a generalised

stressor that imposes physiological costs. For example, chronic noise exposure is sometimes associated with changes in corticosterone stress hormones (Chloupek *et al.* 2009; Crino *et al.* 2011; Blickey *et al.* 2012; Kleist *et al.* 2018) and decrease body weight and food intake (Alario *et al.* 1987).

Birds are particularly susceptible to the costs associated with environmental noise because they are such vocal organisms. Responses of birds to noise include (i) adjusting their vocalisations, such as increasing number of vocalisations or altering amplitude (loudness) and frequency (pitch), presumably to reduce acoustic masking or degradation by environmental noise (Potvin *et al.* 2011; Slabbekoorn 2013; Derryberry *et al.* 2016); (ii) adjusting when they vocalise to avoid acoustic masking or degradation (Fuller *et al.* 2007; Cartwright *et al.* 2014); (iii) huddling, or reducing nearest-neighbour distance to increase vigilance efforts (Fernández-Juricic *et al.* 2005; Owens *et al.* 2012) and perhaps decrease acoustic masking or degradation as vocal amplitudes are louder when individuals are closer together and (iv) dispersing from a noise-affected area entirely (Francis *et al.* 2011; Mahjoub *et al.* 2015; Swaddle *et al.* 2016).

Disrupting or changing communication and altering group closeness or membership in response to noise could likely also influence social behaviour.

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 Supplemental data for this article can be accessed [here](#).

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Additionally, social interactions are often mediated by acoustic signalling. For example, acoustic signals can reinforce pair-bonds (Swaddle and Page 2007), influence extra-pair courtship (Otter *et al.* 1999), and aid in defence of territories (Amy *et al.* 2010). Thus, we suspect that the degradation of acoustic signals by anthropogenic noise might influence social interactions of groups of birds.

Habitat disturbance can alter social interactions in birds. For example, increasing forest fragmentation for mixed-species flocks of birds reduced social connectivity (weighted-degree; number of social partners and frequency of interactions with those partners) between species (Mokross *et al.* 2014), flock size and species richness (Maldonado-Coelho and Marini 2004). Experimentally presented white noise appeared to decrease pair bond strength in Zebra Finches (*Taeniopygia guttata*) (Swaddle and Page 2007). Additionally, in Red-backed Fairywrens (*Malurus melanocephalus*), fire-disturbed habitat decreased social connectivity in groups of birds compared to groups residing in undisturbed habitat, possibly due to loss of grassland cover (Lantz and Karubian 2017). Likewise, noise disturbance seems to increase male-male interactions in White-crowned Sparrows (*Zonotrichia leucophrys*) and could therefore lead to more social connectivity (Phillips and Derryberry 2018). Though not an avian species, anthropogenic noise (specifically noise from pile-driving) resulted in reduced group cohesion in European seabass (*Dicentrarchus labrax*) shoals, possibly due to the masking of sensory information (Herbert-Read *et al.* 2017).

In this study, we sought to understand how experimentally introduced traffic noise affects social ties in free-living and highly social songbirds, Red-backed Fairywrens (*Malurus melanocephalus*). While some species are susceptible to their calls being masked by anthropogenic noise due to overlapping frequencies, Red-backed Fairywren calls occur between 6–10 kHz which does not overlap with typical frequency ranges for traffic noise (1–2 kHz) (Slabbekoorn and Peet 2003; Dowling and Webster 2013; Lowry *et al.* 2019). However, high-frequency songs attenuate faster and travel shorter distances, so noise can degrade fairywren songs by decreasing the range of transmission through scattering and fluctuations in amplitude (Slabbekoorn and Ripmeester 2008; Brumm and Naguib 2009). Additionally, noise disrupts the ability for birds to process cross-sensory information such as visual stimuli by distracting them from other stimuli (Halfwerk and van Oers 2020). Based on the previous literature described, we hypothesised that anthropogenic noise would affect social connectivity by degrading acoustic signalling and possibly dispersing birds away from the source of noise. We therefore measured social connectivity using weighted-degree (Whitehead 2008; Farine *et al.* 2015) and measured changes in

space-use by interpreting utilisation distributions. We predicted that noise-affected individuals would have increased social connectivity as they would be displaced away from the experimental point-source of noise, which might bring focal groups into contact with other groups of conspecifics. Alternatively, we predicted that noise would degrade the calls of birds that remain in a noise-affected area, which would limit the range of transmission to surrounding birds and thus decrease their social connectivity.

Methods

Study system and site

The Red-backed Fairywrens are highly social birds 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). The species is sexually dimorphic and dichromatic. The dominant paired-male of the group often moults into their namesake red-black nuptial plumage, which consists of black feathers and beak with a reddish-orange back plumage, early in the non-breeding season. 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 that resembles females' plumage. During the non-breeding season, both 'bright' and 'dull' males will often foray to neighbouring females and partake in courtship displays. Non-breeding season behaviours impact the outcome of subsequent breeding seasons in other species of fairywrens (Mulder and Magrath 1994, Joseph Welklin unpublished data). Therefore, changes of social structure during the non-breeding periods could have longer-term implications for mating outcomes.

The focal population was resident and sedentary to a field site near Samsonvale, Queensland, Australia (S27° 16.689', E152° 51.268'). The field site was located between a stretch of road and a large reservoir (Lake Samsonvale) and predominantly comprised tall grassland with patches of eucalypt-dominated wooded areas with understory dominated by invasive lantana (*Lantana camara*). During June and July 2016, we assessed ambient noise throughout the field site using a calibrated sound pressure metre (Extech Instruments model 407,730, A-weighting on slow setting, reporting an average of 9 consecutive readings that were 1 min apart) using points on transect lines that ran directly west to east. We took recordings along transects every 200 m and ran transects across the field site 200 m apart from north to south (Figure 1). Most of the site did not experience human-audible amplitudes of traffic noise (< 40 dBA, as our sound metre cannot detect sound

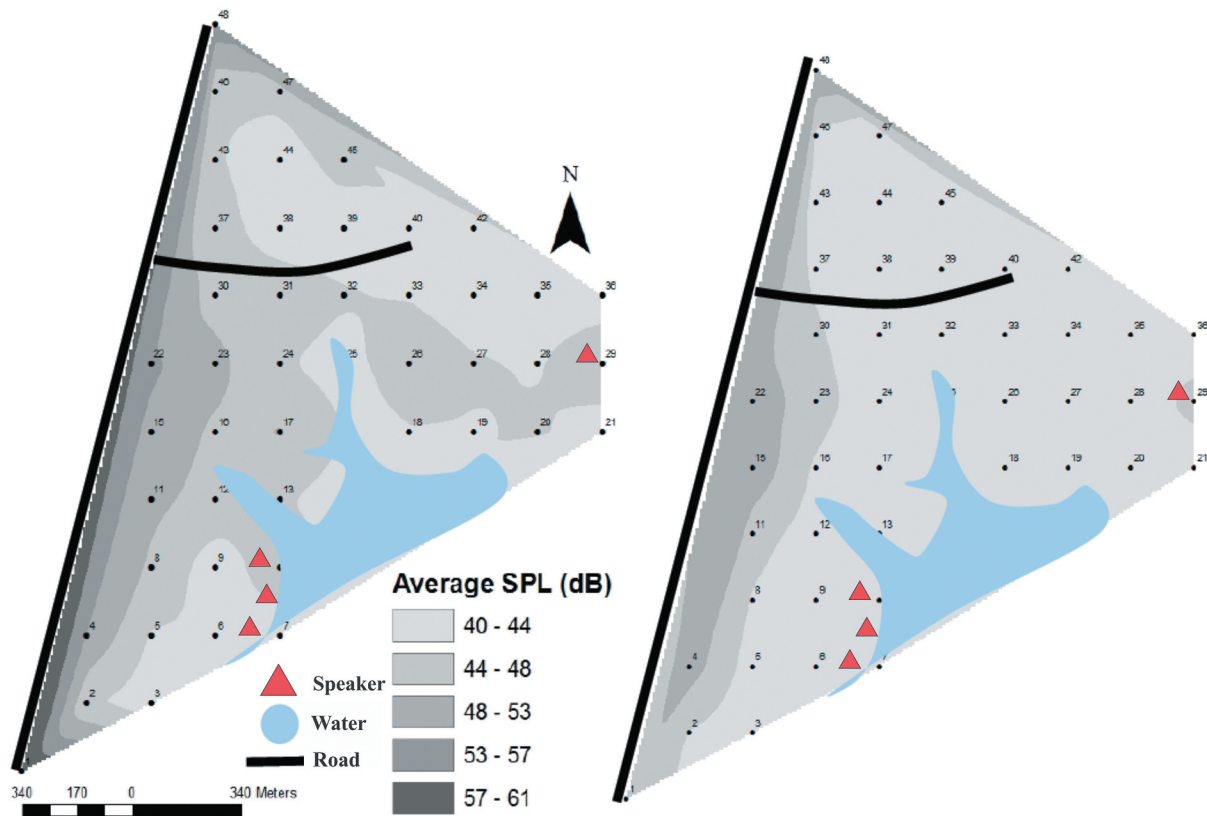


Figure 1. Maps for noise gradient across the field site on weekdays (left) and weekend days (right).

pressures below 40 dBA); although there was a thin strip of habitat that bordered a road where traffic noise rose above 53 dBA SPL (Figure 1). The groups we studied resided in areas where traffic noise was apparently inaudible, with the four trials located near transect points 7, 10, and 29 (Figure 1). Hence, we assumed that traffic noise was not an entirely novel stimulus to the focal birds, but none of the individuals in this study were chronically exposed to traffic noise before our observations began.

Experimental design

We collected social data from familial groups of Red-backed Fairywrens during the non-breeding season in two consecutive years (23rd June–3 August 2017, $n = 3$ groups studied; 28th June–15 July 2018, $n = 1$ group studied) for a total of four trials. We define a unit of sample as a pairing of an experimental group and a reference group. To collect social data from a familial group, we visually followed the focal group for 25 min and systematically recorded all interactions within the group as well as between members of the focal group and those of neighbouring conspecific groups (Whitehead 2008). Each experimental group of birds comprised four individuals except for one group in 2017 that had five. Based on pilot data (Samantha Lantz, personal observation), we defined

an interaction as coordinated group movement within a 20-m radius of each other, where they would maintain a maximum of 20-m distance from each other as they moved throughout the site. During the 25-min observation session, we noted the approximate centre (estimated by eye) of the group every 5 min based on the location of the individuals and later returned to the habitat to obtain GPS coordinates (Garmin GPS) of those noted locations. During all observations we remained ~20 m away from the birds and made all observations through binoculars to minimise the effects of the observer's presence on individual and group behaviour. The same observer recorded all social data.

Noise manipulation

We divided our observations of each group of birds into two 5-day experimental phases: (i) 'before', before the noise introduction and (ii) 'noise', during noise introduction. Each trial (hence, each group of focal birds) was 10 days and experienced both of these experimental phases. The start of this before-noise sequence was staggered by 5 days across groups, so that as the first group experienced their noise phase the second group started their before phase. While the first group experienced noise, the other groups did

not. Hence, we used these observations of non-noise groups over the same 10-day time period as our noise groups (i.e. before and noise) as reference observations to account for the progression of time throughout the field season independent of noise manipulations and to demonstrate that natural background noise does not affect social connectivity.

To introduce traffic noise, we placed a multidirectional playback system (Audio Experience AES0003 full-range 200 W speaker) connected to a marine-grade BOSS Audio MR 1002 amplifier, powered by a 12 V deep-cycle battery that was recharged by an AllPowers 60 W SunPower solar panel) in the approximate centre of the focal group's home range and transmitted, in a 24-h cycle a continuous loop, an 8-h recording of variable highway sounds that varied in maximum amplitude (Table 1) (<https://youtu.be/AVIDr14ZNJ4>). The speaker emitted an amplitude of ~85 dBA SPL 1 m from the source, and about 58 dBA SPL at 10 m from the source (Table 1). This amplitude dropped off to ~50 dBA SPL at about 22 m from the source and was considered relatively indistinguishable from background sounds at this latter distance (Table 1). In this way, we introduced loud traffic noise at the centre of a group's home range, but this noise dissipated quickly enough that there were areas of the original home range that did not experience the noise directly. We broadcasted this noise in a 24-hr cycle across the noise phase of the experiment. We determined the centre of the groups' home ranges by estimating the centre of Minimum Convex Polygons (MCP) derived from plotting GPS points (see above) collected during the *before* phase, in Google Earth. We realise the limitations of approximating the centre of a home range, but the inaccuracies of this methodology should not bias our data towards supporting or rejecting hypotheses.

Social network metrics

We used weighted social networks rather than binary networks, to account for frequency of interactions between individuals. We constructed association

Table 1. Average sound pressure readings (dBA SPL) surrounding the placed speaker while speaker is 'on' (experimental traffic noise) and 'off' (ambient noise).

Distance (m)	Speaker on (dBA SPL)	Speaker off (dBA SPL)
0–3	85.3	45.5
4–6	72.5	45.8
7–9	62.9	45.6
10–12	58.8	45.7
13–15	55.1	46.4
16–18	52.5	45.6
19–21	50.7	46.0
22–24	48.8	46.4

matrices between every combination of two birds using the simple association index (SAI): $\frac{x}{x+y_a+y_b+y_{ab}}$ (Cairns and Schwager 1987; Whitehead 2008), in which x is the number of observations individuals A and B were observed together, y_a is when only individual A was observed, y_b is when only individual B was observed, and y_{ab} is when individuals A and B were observed separately. This generated a weighted value from 0 to 1 which is the proportion of observations where the two subjects were observed together out of the total observations in which either bird was observed, this value then served as the edge between nodes (focal birds) in the network. We calculated weighted-degree as the sum of the edge weights connected to an individual node to determine social connectivity. Node-level metrics, such as weighted-degree, are more robust than network-level metrics when studying a limited number of discrete groups (Farine *et al.* 2015). Using a custom Python script, we converted raw interaction data to a matrix of association indices (Python Core Team 2015). We processed these matrices using the 'igraph' package in R (Csárdi and Nepusz 2006), generating weighted-degree for each individual bird throughout the two phases of the study (i.e. before and noise). As individuals vary in their social connectivity, we calculated the within-individual change in weighted-degree between phases for each bird (Δ WD: *noise* minus *before*) so that each bird served as its own reference point.

Estimates of space-use

We uploaded the GPS locations of the approximate centre of each focal group, at each observation time in each phase of the experiment and used ArcMap to generate utilisation distributions (UDs). UD values are a kernel-based method that create a three-dimensional relative frequency distribution of the locations used by the birds over time (Worton 1989), in order 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 UD values within the 'noise zone', which we defined as a 20-m diameter circle surrounding the speaker, before and during noise playback. As total distribution of UD sums to 1, summing the UD's in a particular area estimate the probability of space-use in that area. Therefore, the sum of overlap of UD's in the noise area tells us the probability of birds spending time in the space most affected by our speaker.

Statistical analyses

To examine how the introduction of traffic noise influenced social ties in individual birds, we calculated the change in weighted-degree from *before* to *noise*. We used a linear model using the afex package in

R (Singmann *et al.* 2020) to determine the average change in weighted-degree between experimental focal birds and reference birds (reference birds belonged to the groups that were not presented with experimental noise in that trial). The linear model included change in weighted-degree as the response variable (Δ WD: *noise minus before*) with treatment (*experimental* or *reference*) and Trial (1, 2, 3 or 4) as predictor variables and group ID as a random factor. We included Trial as a predictor variable in case the time period in which a trial took place influenced weighted-degree of birds, as there was a chance that social connectivity could change as the field season progressed. For our space-use data, we ran a paired t-test to compare the probability of finding the experimental group of birds in the noise-affected area (UD) before and during noise introduction for each of the four trials.

Results

Weighted-degree, which is a metric of individual social connectivity, decreased notably during noise treatments in all four groups of experimental birds ($n = 17$ birds) compared with average change in weighted-degree of reference birds ($n = 20$ birds), which remained stable during the

same experimental phase (Table 2; Figure 2). The sample size for experimental and reference birds differed as two birds dispersed prior to their group being experimentally manipulated and one reference group was not manipulated due to equipment failure. It is possible that the decrease in individual social connectivity (weighted-degree) was driven by between-group interactions, interactions between birds of different familial groups, as well as within-group interactions, interactions between only members of the same familial group (Supplemental Material Figure S1). Hence, we reran the same analyses using weighted-degree data that were generated solely from within-group interactions (Table 2; Figure 2) and found the noise-associated decrease in weighted-degree did not occur when analysing within-group interactions alone, despite an apparent downward trend ($n = 37$, $P = 0.086$). However, when including only between-group interactions, weighted-degree decreased in association with the noise treatment ($n = 4$, $P < 0.01$, Table 2). Therefore, the presentation of traffic noise decreases between-group social connectivity by limiting the extent of interactions among groups of fairywrens but does not strongly affect within-group cohesion. Overall, individual birds have fewer social ties, as measured by weighted-degree, during the noise treatment.

For three of the experimental groups, the birds generally occupied space further from the noise source (20-m radius from the speaker) while the traffic sounds were being broadcast compared with the period before the traffic sounds were broadcast. However, we observed the opposite shift in space-use in a fourth group, in which birds moved closer to the speaker while the traffic noise was being broadcast. Overall, we did not discern a consistent pattern in shifts of space-use in association with traffic noise ($P = 0.940$, Table 3).

Table 2. Output of linear models for analysis of change in weighted-degree from *before* to *noise* treatments.

	Sum Sq	df	Mean Sq	F	P
Overall					
Treatment	2.10	1	2.10	21.3	< 0.001
Trial	1.91	3	0.638	6.47	0.001
Treatment:Trial	3.07	3	1.02	10.4	< 0.001
Residuals	4.14	42	0.099		
Between Group					
Treatment	0.573	1	0.573	349.7	0.003
Trial	0.265	3	0.088	53.9	0.018
Treatment:Trial	0.379	3	0.126	77.1	0.013
Residuals	0.003	2	0.002		
Within Group					
Treatment	0.293	1	0.293	3.10	0.086
Trial	0.027	3	0.009	0.097	0.961
Treatment:Trial	2.86	3	0.952	10.1	< 0.001
Residuals	3.49	37	0.094		

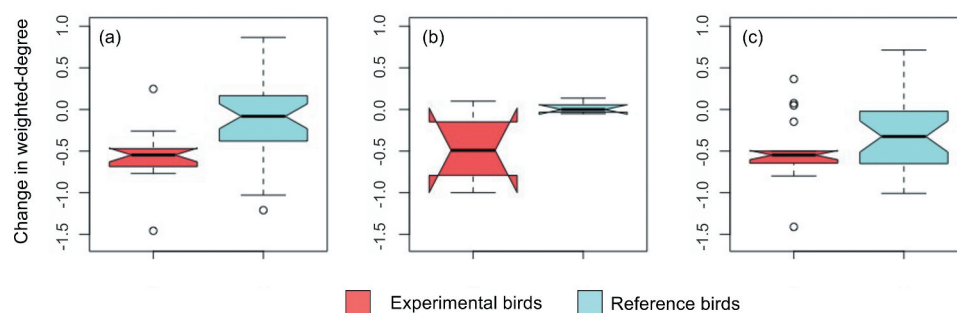


Figure 2. (a) Overall change in weighted-degree relative to traffic noise ($n = 51$, $P < 0.001$), (b) between-group change in weighted-degree relative to traffic noise ($n = 10$, $P < 0.01$), (c) within-group change in weighted-degree relative to traffic noise ($n = 45$, $P = 0.08$). The boxplots indicate the median of the data and \pm quartiles. The whiskers denote the range of the data and open circles indicate outliers.

Table 3. Percent overlap (represented as a decimal) of utilisation distribution within the 20 m radius noise zone for experimental groups, *before* and during *noise* introduction. Paired t-test revealed no statistically significant change in space-use due to noise treatment ($t = 0.081$, $df = 3$, $P = 0.940$).

	Before	Noise
Trial 1	0.16	0.13
Trial 2	0.19	0.45
Trial 3	0.23	0.11
Trial 4	0.22	0.08

Discussion

Contrary to our prediction that individual social connectivity (weighted-degree) would increase with noise due to more confined space-use, we observed an appreciable decrease in individual social connectivity for birds exposed to traffic noise (Table 2; Figure 2). In comparison, our reference groups (groups that did not receive additional noise at the same time as the focal groups) did not demonstrate a comparable change in their social connectivity, indicating that our observed effects were related to our experimental noise introduction and not to other social changes over the course of the field season. The reduction in social connectivity appeared to be driven by reduced between-group interactions (Table 2; Figure 2). We recognise that this sample size is small (i.e. we studied a relatively small number of groups of birds), but it is logistically difficult to have large sample sizes for many social network studies in field populations (Lantz and Karubian 2017). Despite our small sample of groups, we feel we have reasonable statistical evidence to support our hypotheses from our four experimental trials in which we track the within-individual change in social behaviour in association with noise. We collected data using the same methods across groups of birds, both reference and experimental, and therefore limited the influence of confounding changes in the birds and their environment with experimental presentations of traffic noise.

Despite the increased weighted-degree response to fire in this same species, which is thought to be a result of reduced habitat availability from burned grasslands (Lantz and Karubian 2017), our results suggest that traffic noise does not fragment available habitat, but instead might degrade vocalisations of birds within noise-affected areas. In fairywrens, vocalisations can serve for territory defence (Dowling and Webster 2013) and possible mate-guarding (Baldassarre *et al.* 2016). The impact of noise on reduced signal detection is well established (Pohl *et al.* 2009; Kleist *et al.* 2016) and therefore, we speculate that social connectivity decreased, rather than increased, due to this

degradation of vocal signals of the noise-affected groups. Degradation of vocal signals would limit both the transmission of signals to neighbouring groups and the reception and accurate decoding of vocal signals from neighbouring groups to our targeted group.

A reduction of social connectivity can ultimately affect vital processes in many organisms. For example, in eels (*Anguilla anguilla*) increased familiarity with conspecifics decreases aggressive interactions (Geffroy *et al.* 2014). Of course, there is a large phylogenetic gap between eels and fairywrens, so we interpret that previous study with suitable caution. Nevertheless, it is possible that the decline in between-group interactions that we observed in fairywrens exposed to traffic noise influenced the perception of familiarity among groups. Familiarity of neighbours in great tits (*Parus major*) was positively correlated with reproductive output, measured by both clutch size and likelihood of successfully fledging offspring (Grabowska-Zhang *et al.* 2012). Therefore, reduced familiarity with neighbouring groups of fairywrens could possibly have implications for reproductive success in the subsequent breeding season. Furthermore, between-group interactions among fairywrens often are in the context of seeking extra-pair copulations (Rowley and Russell 1990). Extra-pair paternity in fairywrens could be a mechanism for inbreeding avoidance (Tarvin *et al.* 2005; Varian-Ramos and Webster 2012). Thus, we speculate that limiting these between-group interactions through noise could have implications for extra-pair paternity rates and genetic structure of fairywren populations, if the noise was applied chronically to the habitat occupied by these groups.

Reduced social connectivity could also decrease the likelihood of obtaining new resources. Great tits that are less social tend to be less bold explorers, and are less likely to find and acquire new resources (Snijders *et al.* 2014). Additionally, in three species of tits (family *Paridae*), closely associating individuals are more likely to transfer information about new food or habitat resources (Aplin *et al.* 2012), so those with higher weighted-degree will have more access to new resources. In our Red-backed Fairywren system, helper fairywrens tend to disperse their 2nd or 3rd year to form their own breeding groups, so this decrease in weighted-degree could affect their ability to establish their own home range later in life.

Our results also revealed no consistent change in space-use with the introduction of noise. Three groups decreased their space-use in the noise treatment, while one group increased their space-use, indicating that these birds are not consistently displaced by noise (Table 3). Therefore, we tentatively rule out altered space-use as a mechanism for the observed social changes, and instead suggest follow-up studies to

investigate alternative mechanisms, such as how degradation of vocal signals by noise affects between-group communication. For example, the role of duetting in Red-backed Fairywrens affects likelihood of extra-pair paternity (Baldassarre *et al.* 2016), and while the function of duetting remains up for debate, several hypotheses argue its role is involved in mate-guarding to prevent females from attracting neighbouring males (Sonnenschein and Reyer 1983) and in broadcasting territory (Osmun and Mennill 2011). Therefore, it is possible that the traffic noise masked the presence and location of experimental groups from neighbouring groups of birds by degrading their vocal signals, thus the observed decrease in between-group interactions.

With noise pollution, specifically traffic noise, becoming more widespread and intense with expanding urbanisation, this study details the possible social consequences for Red-backed Fairywrens. Fairywrens are useful models in identifying potential vulnerabilities of anthropogenic pressures on passerines (Skroblin and Murphy 2013) and, therefore, these results inform how noise could affect sociality in similar songbirds. Reduction in social connectivity could affect many processes in a songbird population, from accessing resources to reproductive success. Traffic noise is the leading source of anthropogenic noise (Ouis 1999) and is continuing to expand its influence on natural ecosystems, it is therefore important to understand avian communities will be affected to anticipate conservation needs.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Ethics Statement

Research was approved by the College of William & Mary Institution for Animal Care and Use Committee (IACUC-

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