AGGRESSION AND MULTI-MODAL SIGNALLING IN THE EUROPEAN ROBIN (*ERITHACUS RUBECULA*)

by

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STATEMENT OF AUTHORSHIP

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THESIS TITLE: AGGRESSION AND MULTI-MODAL SIGNALLING IN THE EUROPEAN ROBIN (*ERITHACUS RUBECULA*)

ABSTRACT

Urban habitats are polluted with acoustic noise, which may disrupt communication between urban-living wildlife. Urban birds rely heavily on acoustic signals in many contexts, such as mate attraction and territorial defense. Aggressive interactions may escalate more rapidly when communication between rivals is disrupted. One way to respond to this challenge is to shift signaling effort to a less noisy modality. A common inhabitant of wooded areas and urban parks, European robins (*Erithacus rubecula*) use acoustic and visual signals during territorial defense. The present study investigates how European robins holding territories in urban and rural areas respond to simulated intrusions with or without experimental noise playback. We predicted that under experimental noise, European robins would show an increase in aggressive behaviors and shift their signaling effort from the acoustic modality to the visual. Since urban robins may have adapted to increased acoustic noise conditions, we expected them to show a steeper increase in aggression and a more prominent shift to the visual modality than that exhibited by rural robins. While urban robins were generally more aggressive, noise playback increased aggression only in rural robins. In accordance with the multi-modal shift hypothesis, noise playback resulted in lowered song rates in only urban robins. However, we did not detect a significant effect of noise playback on visual signals. The results suggest that plastic responses to transient increases in noise may be shaped by longer-term processes in urban European robins.

Keywords: anthropogenic noise, multi-modal shift, territorial aggression, bird song, European robin

TEZ BAŞLIĞI: KIZILGERDANLARDA (ERITHACUS RUBECULA) SALDIRGANLIK VE MULTIMODAL KAYMA

ÖZET

Kentsel yaşam alanlarında bulunan akustik gürültü kirliliği, kentte yaşayan yaban hayatı arasındaki iletişimi bozabilmektedir. Kentte yaşayan kuşlar için kur davranışı ve bölge savunması gibi birçok bağlamda akustik sinyaller önemli bir rol taşır. Rakipler arasındaki iletişim sekteye uğradığında agresif etkileşimler daha hızlı kızışabilir. Bu soruna verilebilecek yanıtlardan biri sinyal aktarma çabasını gürültünün daha az olduğu bir modaliteye kaydırmaktır. Ormanlık alanlarda ve şehir parklarında sıkça rastlanan kızılgerdanlar (Erithacus rubecula), bölge savunmasında akustik ve görsel sinyaller kullanır. Bu çalışma kentsel ve kırsal alanlarda bölgeleri olan kızılgerdanların, kayıttan çalınan gürültü altında veya gürültü olmadığında bölgelerinin sınırlarının ihlal edilmesinin deneysel olarak canlandırılmasına nasıl tepki verdiklerini araştırmaktadır. Kayıttan çalınan gürültü altında, kızılgerdanların saldırgan davranışlarınd artış görüleceğini ve sinyal aktarma çabalarını akustik modaliteden görsel modaliteye kaydıracaklarını öngördük. Kentte yaşayan kızılgerdanlar yüksek akustik gürültü koşullarına adapte olmuş olabileceklerinden, bu kuşların saldırganlıklarında daha keskin bir artış görmeyi ve görsel modaliteye geçişin kırsalda yaşayan kızılgerdanlara göre daha belirgin olmasını bekledik. Sonuçlar kentte yaşayan kızılgerdanların genellikle daha saldırgan olduğunu gösterirken kayıttan çalınan gürültü yalnızca kırsal alanda yaşayan kızılgerdanlarda saldırganlığı arttırdı. Multimodal kayma hipotezine uygun olarak, kayıttan çalınan gürültü yalnızca kentte yaşayan kızılgerdanlarda şarkı sıklığının düşmesine yol açtı. Ancak kayıttan çalınan gürültünün görsel sinyaller üzerinde anlamlı bir etkisini tespit edemedik. Sonuçlar, gürültüdeki geçici artışlara verilen plastik tepkilerin, kentte yaşayan kızılgerdanlarda daha uzun vadeli süreçler tarafından şekillendirilmiş olabileceğini göstermektedir.

Anahtar sözcükler: insan kaynaklı gürültü, multimodal kayma, bölge savunması, kuş şarkısı, kızılgerdan

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CHAPTER 1 – INTRODUCTION

1.1 OVERVIEW

Animals living in urban habitats must cope with problems that may not have parallels in non-urbanized habitats and as a result may have adaptations that are unique to urban populations of a species, or individuals with certain characteristics may be more abundant in urban environments. Aggressiveness might be one such characteristic, as it has been extensively shown to increase in urban birds, especially in song sparrows (Evans et al., 2010; Scales et al, 2011; Davies and Sewall, 2016; Hardman and Dalesman, 2018; Phillips and Derryberry, 2018). Human disturbance may affect animal behavior in many ways. Anthropogenic noise in urban habitats has been shown to disrupt communication between urban animals (Brumm and Slabbekoorn, 2005). As animals often use signals to mediate aggressive interactions, this may lead to aggressive interactions escalating more rapidly in urban habitats. Heightened ambient noise levels have indeed been associated with more aggressive responses to simulated territorial intrusions (Phillips and Derryberry, 2018; Akçay et al., 2020; but see Kleist et al., 2016). According to the multimodal shift hypothesis, one way to cope with noise in the acoustic modality might be to favor the use of signals in other modalities and thus increase the chance of the signals being received (Partan et al., 2010; Partan, 2017). Below, we discuss the current literature on the effects of urbanization and anthropogenic noise on aggression and communicative signals of avian fauna which dominates research in this area. We conclude this section by describing the territorial defense behavior of the European robin.

1.2 AGGRESSION

Animals often have disputes over access to resources, mates and territories which they may resolve within an aggressive interaction. Disputes often consists of two opponents threatening each other with aggressive signals. When two male birds have a dispute over a territory, they rely heavily on acoustic signals instead of physical aggression, which would lead to significant energy expenditure and injury risk (Maynard Smith and Price, 1973). Using threat signals to handle disputes prevents resorting to physical aggression, and it has been shown that when these signals cannot be used, aggressive interactions become more costly to the parties involved (Logue et al., 2010). When aggressive signals are disrupted, for instance by anthropogenic acoustic noise, aggressive interactions may get physical more rapidly.

Studies investigating the anthropogenic effects on avian aggression consist mostly of playback experiments simulating territorial intrusions by conspecifics in urban and rural habitats. Intrusions are simulated by placing a speaker in the territory of a male bird and playing conspecific song, which elicits a territorial defense response from the resident bird. In this section, we discuss the findings of playback experiments that have measured territorial aggression levels in urban and rural songbirds.

Evans et al. (2010) used experimental conspecific song playback to assess the responses of 41 rural and 18 urban song sparrows in 2 rural and 1 urban sites in eastern US. Their response measure for aggression was the average distance to the speaker. They found that urban birds were more aggressive than their rural counterparts. The study also found that urban birds were bolder, and the authors suggest that heightened aggression is part of a behavioral syndrome in urban song sparrows. Scales et al (2011) carried out a similar playback experiment to replicate the results of the Evans et al. (2010) study, this time in 1 rural and 2 urban sites with an increased urban sample size (n=33). This study also found that urban song sparrows were bolder and more aggressive than rural song sparrows, which lead the authors to assert these traits are part of an urban behavioral syndrome.

In another playback experiment with 35 urban and 38 rural song sparrows, Davies and Sewall (2016) recorded the average distance from the speaker, number of songs, soft songs and wing waves and used principal component analysis to create a signal aggression score from these measures. Urban birds were more aggressive than rural birds. The authors argue that heightened aggression in urban habitats might be due to increased resource availability, which affords urban individuals more time and energy to spend in aggressive interactions. It should be noted that their aggression measures are flawed, since songs and wing waves are aggressive signals rather than aggressive behaviors.

Hardman and Dalesman (2018) carried out a conspecific song playback experiment with great tits (*Parus major*) in 9 urban and 8 rural sites. They expected a response consistent with the urban behavioral syndrome described above. Their response measures for aggression were latency to approach the speaker, latency to sing over the playback, closest approach distance, time spent within 5 meters of the speaker, and the number of flights across the speaker. They found that urban birds were generally showed heightened territorial aggression, but the repeatability was significant for only latency to approach the speaker and latency to sing over the playback. Phillips and Derryberry (2018) carried out a playback experiment with 18 white-crowned sparrows (*Zonotrichia leucophrys*) across an urban noise gradient. They found that males who held territories in noisier areas tended to have shorter approach latencies and closer approach distances and concluded that there is a correlation between urban noise and aggressiveness.

Foltz et al. (2015) simulated territorial intrusions with song sparrows in 3 urban and 3 rural territories over a period of nearly 3 years. Their response measures for aggression were the number of flights around the speaker, number of songs, closest approach distance, and time spent within 4 meters of the speaker. Using PCA, they created a single aggression score from these measures. They found that urban males were consistently more aggressive than rural males over the 3-year period. They hypothesized that the elevated aggression in urban habitats might be due to increased resource availability and carried out an experiment where they supplied additional food to half of the subjects and compared them to the control group. They found a significant effect of food supplementation on aggression in both urban and rural birds, but rural birds showed a more drastic increase in aggression.

Akçay et al. (2019) carried out a playback experiment with 42 rural and 36 urban song sparrows. Their aggression measures were flight rate, closest approach distance and proportion of time spent within 1 meter of the speaker. The latter two measures correlated significantly with increased ambient noise. They also observed more attacks in urban rather than rural birds. Akçay et al. (2020) carried out playback experiments in great tit territories across a traffic noise gradient. They used PCA to calculate an aggression score from the response measures flight rate, closest approach distance and proportion of time spent within 1 meter of the model. They found a significant correlation between noise levels and aggression. Birds that lived closer to a highway responded more aggressively to the simulated territorial intrusion.

In contrast to the studies above, Kleist et al. (2016) found that spotted towhees (*Pipilo maculatus*) and chipping sparrows (*Spizella passerina*) in sites with heightened ambient noise levels were later to orient themselves toward the speaker, to approach the speaker, and to respond with song during simulated territorial intrusions. The authors argue that this might be due to signals taking longer to be received under ambient noise. It is worth noting that the ambient noise in this study came from industrial machines, which overlaps with the frequency range of the songs of both species as the authors indicate. Road traffic, which is usually the type of ambient noise in the studies comparing urban and rural aggression, is usually very low frequency and does not overlap with most of the song elements.

Anthropogenic factors other than acoustic noise might be contributing to the observed urban aggression. In a playback experiment with northern mockingbirds (*Mimus polyglottos*) on a gradient of lead pollution, McClelland et al. (2019) found that increased lead in soil was associated with increased aggression in territorial defense. Davis et al. (2013) set out to observe tree hollow usage by birds in forest remnants in urban sites and undisturbed forests by setting up cameras near the hollows. The recordings showed that there were significantly more inter- and intraspecific aggressive encounters in forest remnants. The authors suggest that the heightened aggression might be due to the shortage of high-quality nesting holes in urban habitats.

Together, these studies point to increased aggression in urban compared to rural songbirds, which may be due to increased resource availability, decreased availability of nesting spaces, bolder and more aggressive individuals being selected by urban habitats, or due to the disruption of threat signals. One issue that emerges upon reviewing the literature is the inconsistent measures of aggression. While most studies do share one or more measures, there are cases where aggressive signals rather than physical behaviors have been included in PCAs, which makes it difficult to explore a possible causal link between signal disruption and aggression. The field could benefit from a more standardized approach.

1.3 MULTIMODAL SHIFT

Many animals have signals in more than one modality, which may afford them with flexibility in communication (Bro-Jørgensen, 2010). Animals may use redundant signals in multiple modalities simultaneously to increase the change of getting the message across. (Partan and Marler, 1999). According to the multi-modal shift hypothesis, when communication is disrupted by noise in one modality, animals may shift their signals to a less noisy modality (Partan, 2017). For instance, whales have been observed to switch from songs to tail slaps on the water surface in response to increased wind noise (Dunlop et al., 2015). Human activity creates noise in many modalities and as a result may inhibit the signals of urban-living wildlife (Halfwerk and Slabbekoorn, 2015).

Partan et al. (2010) set out to understand how urban and rural gray squirrels (*Sciurus carolinensis*) use visual and auditory alarm signals. They first observed gray squirrels for 21 days to identify alarm signals. Then, they created a robotic squirrel model with which they conducted playback experiments with grey squirrels. They found that urban squirrels responded more to the visual alarm signal (tail flagging) than did rural gray squirrels, possibly because there was less noise in the visual modality in urban habitats. Urban squirrels also used vocal alarm signals significantly more often and thus increased the serial redundancy of their signals. This may be a strategy to ensure signal reception under heightened ambient noise levels.

Studies on multi-modal shift in avian models are limited. Ríos-Chelén et al. (2015) sampled the acoustic and visual signals of 74 male red-winged blackbirds (*Agelaius phoeniceus*) within a 20-day period. Focal males were recorded on a video camera as well as a recorder in order to capture all signals. After each sampling period, the researchers took ambient noise measurements. The analysis did not reveal any significant correlation between increased noise the use of visual signals, which goes against the multi-modal shift hypothesis. Instead, the authors found that urban birds sang shorter songs with fewer syllables.

As mentioned above, Akçay et al. (2019) carried out a playback experiment contrasting aggressive signals and behaviors in urban and rural song sparrows. The authors found that urban song sparrows used more wing waves as well as soft songs (a type of song associated with aggressive intent in song sparrows). A later study by Akçay and Beecher (2019) aimed to assess whether the shift to the visual modality was a plastic response to increased noise by simulating territorial intrusions. In the experimental treatment, song playback was accompanied by experimental noise playback. In the control treatment, the subjects were presented only with conspecific song. The results did not reveal a significant effect of experimental noise on wing waves. This suggests that heightened levels of visual signaling in urban song sparrows might not be a plastic response, but might be due to selective processes.

1.4 TERRITORIAL DEFENSE IN THE EUROPEAN ROBIN

The territorial defense behavior of the European robin has been described extensively by Lack (1943). Lack indicates that during the spring, males hold territories where they sing to attract mates, and at times male will quarrel over a territory by using various threat signals. An intruding male will enter an owned territory and start singing, to which the resident will respond again by song. As the conflict continues, the males may approach each other and use visual threat signals once they are within each other's range of vision. The most common visual signal is the neck display, where a robin raises his head to expose the red patch on his neck. Other visual signals include wing flutters, perking the tail up, and swaying from side-to-side. Robins have been shown to respond to both visual and acoustic signals during territorial intrusions (Chantrey and Workman, 1984).

Few studies have investigated the effects of experimental noise playback on the territorial defense behavior of the robin. McLaughlin and Kunc (2012) used conspecific song playback to attract robins and switched to noise playback once the robin was within 4 meters of the speaker. They gradually increased the noise level and found that robins moved away from the noise playback and sang shorter songs with increasing noise levels. Zwart et al. (2016) carried out an experiment with three trials —one with only wind turbine noise playback, one with only conspecific song playback, and one with both noise and song playback. They found that noise playback during simulated territorial intrusions was associated with higher flight rates, which is often used as a measure of aggression. They did not detect any significant change in song rates or visual signals in response to noise playback.

1.5 HYPOTHESES

The European robin is a suitable candidate for a test of the multi-modal shift hypothesis since they use both visual and acoustic signals in territorial disputes. We propose a conspecific song playback experiment paired with experimental acoustic noise in urban and rural European robins. In congruence with the playback experiments described above, we expected urban European robins to be generally more aggressive than their rural counterparts, and to increase their level of aggression more visibly in response to noise playback. In response to noise playback, we expect the robins to decrease their song rate and rely more heavily on visual threat signals. We expect this shift to be more pronounced in urban habitats.

CHAPTER 2 – METHODS

2.1 OVERVIEW

We carried out playback experiments with European robins holding territories in urban parks and wooded areas in Sarıyer, İstanbul (Sarıyer, Istanbul, 41° 9' 50.73971"N, 29° 0' 32.25243"E). The experiment consisted of one trial with conspecific song and experimental noise playback, and one that only contained song playback.

2.2 STUDY SITES AND SUBJECTS

The study was carried out in urban parks and wooded areas in Sarıyer, İstanbul. A month prior to the study, we recorded songs in some of these areas to generate playback stimuli. We estimated the center of the territory during these recording and observation periods and gave the birds numbers. We revisited some of the territories and attracted the territory holders by playing the song of an unrelated robin. If only one male responded to the playback, we selected it as a subject for the experiment. We also visited areas that we hadn't before and listened for robin song. If a male was singing alone in a territory for about 5 minutes, we selected it for the experiment.

There were a total of 9 urban birds and 12 rural birds. Seven of the nine urban birds held territories in Hacıosman Park. The park is located next to a highway and has frequent human activity around the robin territories. One urban subject was located in the edge of Emirgan Park next to a road with loud traffic. Emirgan park also has many visitors. The other one was in a green area in a neighborhood of Sarıyer, again next to a road with loud traffic. The rural birds were in Belgrad forest and in the wooded areas around the Koç University campuses and faculty housing.

2.3 STIMULI

We used a song playback and a noise playback as auditory stimuli, and a decoy as a visual stimulus. The decoy was was a 3-D printed bird model that we had painted in the colors of a robin (dimensions: height, 8 cm; length, 12 cm; width, 4.5 cm).

We created song stimuli that lasted for 3 minutes at 9 songs per minute. As mentioned above, we had recorded robin songs in the areas where the experiment was held a month prior to the study. Songs were recorded if the robin was singing alone in a territory. To avoid recording the same bird twice, we only recorded birds that were over 200m apart. The recordings were then scanned on the software Syrinx for clear, viable songs with limited background noise. We removed frequencies under 1000 Hz, since no robin song elements are in that frequency range but low-frequency anthropogenic noise was sometimes present in the recordings under that frequency limit. We did this because we wanted to avoid introducing noise within the song playback.

We used the songs of only one robin to generate 1 playback stimulus. We clipped the viable songs and pasted them into an empty sound file. The songs lasted for seven seconds on average. We introduced 3 second silent breaks between the songs. We generated 1-minute-long song sequences and repeated them twice to create a 3-minute stimulus since collecting enough clean songs for 3 minutes was not possible for each recording, and we wanted to standardize the contents of the playback so that each of them had the same repetition rates. Ultimately, we had 17 such 3-minute stimuli. During each experiment, we chose a song stimulus recorded from a robin that held a territory at least a kilometer away from the subject. The same stimulus was used in both the noise and no noise trials that the subject received.

To create the noise stimulus, we first recorded traffic noise in Sarıyer, İstanbul. We analyzed the recording to calculate the average amplitude spectrum using the R package seewave (Sueur et al. 2008). We then created a white noise file in Audacity and filtered it to fit into the the amplitude spectrum of the traffic noise recording.

2.4 EXPERIMENT DESIGN

The robin decoy was placed on a speaker (Anker Soundcore Bluetooth Speaker, Anker, Inc.) and set on a natural perch such as a tree branch or a bush in the estimated center of a male robin’s territory. Another speaker was placed on the ground directly under the first speaker. In the noise trial, we played the song stimulus from the speaker attached to the bird model. Noise was played from the speaker on the ground.

Each trial lasted 3 minutes. Noise and song playback were also 3 minutes long and stated and ended with the trial. We counterbalanced the order of the trials so that half of the subjects received the noise trial first, and half received the no-noise trial first. After the first trial with a subject, we waited for an hour before carrying out the next trial to avoid carryover effects.

We could not record data blind because the hypothesis included the habitat which could not have been blinded, and the noise stimulus was audible to all. Video recordings were not possible because the robins were often flying between in tree branches and it was only possible to spot them with two sets of human eyes.

2.5 PROCEDURE

After selecting a subject as we mentioned above, we placed the speakers in the estimated center of the territory. In eleven of the trials where the robin was not already singing, we started song playback until it responded with song or approached the model. This period of attracting the robin lasted on average 64.9 s (SD = 40.8). We aborted the trial if another male robin came within 10m of the speaker.

The trial period started after the first response of the resident robin. Two observers standing about 10 meters away from the experimental set up used a Marantz PMD660 with a Sennheiser ME66/K6 microphone, or on a Zoom H5 handheld recorder with a Zoom SGH6 shotgun microphone to record the songs and calls of the resident robin. The observers also commented on the behaviors of the robin. Since song stimulus was present, we commented on the songs of the resident to be able to tell them apart. We also commented on the flights, the distance from the speaker after each flight, any visual signals, and any other behaviors of the robin. After the trial ended, we collected the experimental setup and took ambient noise measurements in four directions twice. In three of the territories, we were only able to collect noise measurements once.

2.6 RESPONSE MEASURES

Table 1. Visual displays of European robins during territorial interactions (Lack (1943); see S7)

Behavior	**Description**
Neck display	The robin raises his head, displaying his neck.
Wing flutter	The robin flutters his wings.
Swaying	The robin rhythmically sways his body from one side to the other.
Tail up	The robin perks his tail up.

Ambient noise levels were averaged in order to determine whether the ambient noise level was indeed higher in urban habitats.

We analyzed the experiment recordings using the software Syrinx. We annotated the spectrograms, marking the beginning and end of each trial, the beginning of the stimulus and the first response time. We selected the songs of the resident robin relying on the comments made by the observers. We also marked each visual signal and flight noted by the observers while making the recording.

From this data, we extracted for each subject the song rate, song length, flight rate, the presence or absence of visual displays, closest approach distance to the model, and the proportion of time spent within 5 meters of the speaker.

CHAPTER 3 – RESULTS

3.1 OVERVIEW

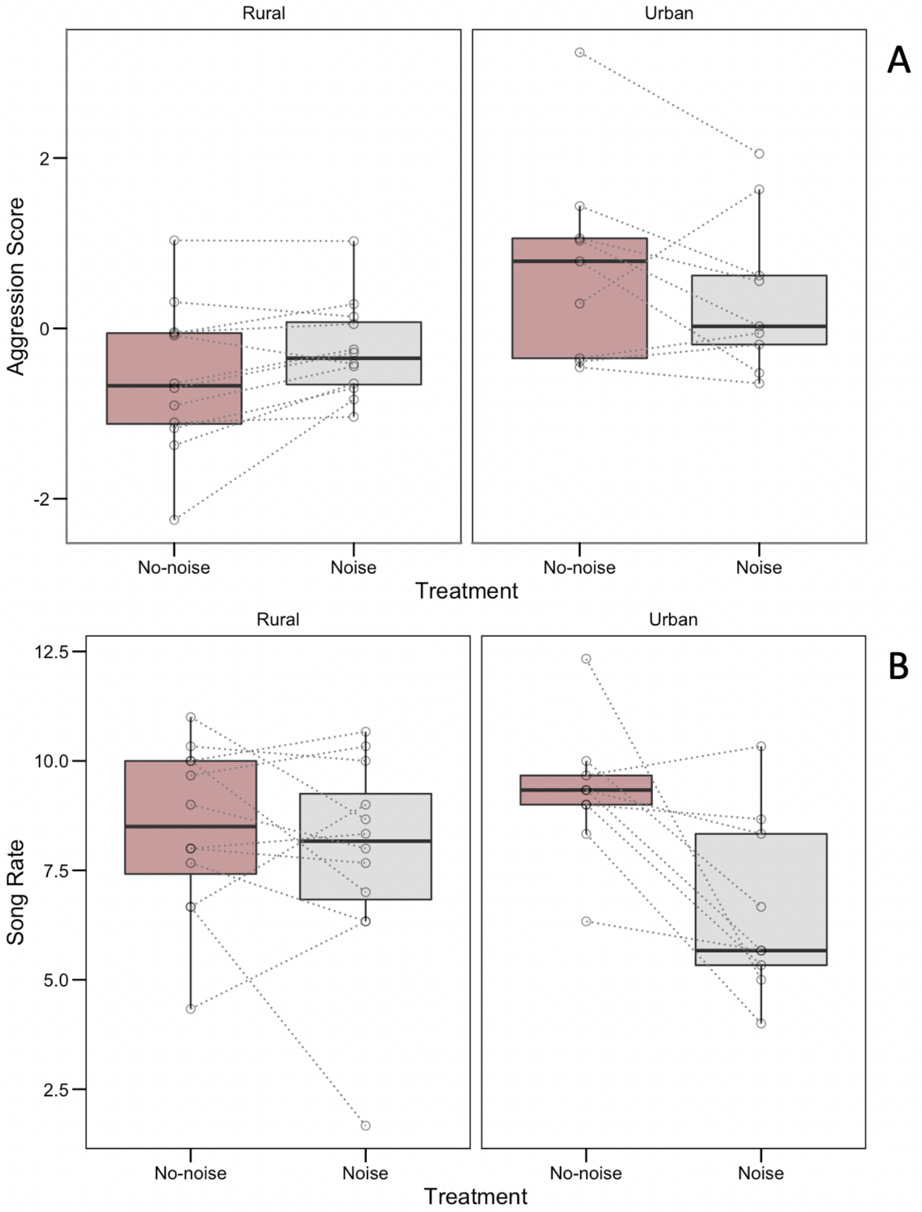

Figure 1. The relationship of aggression scores (A) and song rate (B) with habitat and noise treatment. The boxes indicate interquartile ranges, the middle line indicates median, and whiskers indicate 95% confidence intervals. Dots connected by dotted lines represent data from individual subjects

Our a priori hypotheses predicted that urban birds would be more aggressive, sing at lower rates and use more visual signals than their rural counterparts, and this difference would be increased by experimental noise playback. We carried out linear mixed models with the main effects of habitat type and experimental treatment as well as the interaction effect of habitat and treatment on song rate, the use of visual signals, and aggressive behaviors. We also predicted that song duration would decrease under noise conditions. We extracted the relevant data form trial recordings and field notes. Trial recordings were loaded onto the software Syrinx to create sonograms (John Burt, Portland, OR). From the recordings, we extracted the number and duration of songs, calls, any visual signals (see Table 1), flights and distance to the speaker after each landing. After data extraction, all analyses were performed in R version 4.1.0 (R Core Team 2021).

To confirm our assumption that urban habitats would be noisier than rural habitats, we contrasted the ambient noise levels in each habitat type. To operationalize ambient noise, we averaged the noise measurements taken after each trial and performed a linear mixed model (LMM) with these values as the dependent variable (DV). In this model, habitat type (urban or rural) was the independent variable, and territory ID was the random variable (RV). To perform this and all following LMMs, we used the *lme* function in the R package *nlme* (Pinheiro et al. 2022). The main effect of habitat type on average noise measurements was significant, with urban robin territories showing higher levels of ambient noise than their rural counterparts. (urban: M = 49.0, SD = 7.1; rural: M = 39.9, SD = 3.6; LMM, coefficient = 8.97, SE = 2.37, p = 0.0012).

In order to assess whether or not ambient noise measurements were repeatable across trials in the same territory, we used the rpt function in package rptR (Stoffel et al. 2017). Our analysis showed that noise measurements were highly repeatable across trials (intra-class correlation coefficient; r=0.96, standard error: 0.02; p < 0.0001).

Since the robins in this study were subjected to two trials separated by an hour-long break, we wanted to rule out a possible order effect on aggression scores, song rate and visual displays. We carried out 3 LMMs taking each of these variables as the DV, with the order of the trial (first or second) as the IV and territory ID as the RV. The main effect of trial order was not significant on aggression score (LMM, coefficient = -0.22, SE = 0.15, p = 0.16) or song rate (LMM, coefficient = -0.68, SE = 0.60, p = 0.28). However, there was a significant order effect on the presence or absence of visual signals (GLMM, estimate = -15.32, SE = 6.22, p = 0.01). All of the eight subjects that used visual signals used them in the first trial, while only two out of the eight also used visual signals in the second trial. Since we detected an order effect, all analyses on visual signals were carried out on a subset of first trials only.

3.2 AGGRESSION

Table 2. Loading coefficients of the Principal Component Analysis

Factor	**Loading coefficient to PC1**
Flight rate	0.65
Proportion of time spent within 5 meters	0.83
Closest approach distance	-0.85
SS loadings	1.83
%Variance	61%

Our aggression measures (flight rate, closest approach distance and the proportion of time spent by the subject within 1m of the decoy and speaker) were significantly correlated with each other (all $p<0.05$). Therefore, we used a principal component analysis (PCA) to create a single aggression score for each trial (Akçay et al. 2013). The first component of the PCA (PCA1) explained 61% of the variance and was therefore used as the aggression score (see Table 2).

We carried out a linear mixed models exploring the interaction between habitat type and experimental noise treatment on aggression. In this model, habitat type and experimental treatment were the independent variables (IVs), aggression was the dependent variable (DV), and territory ID was the random variable. We looked for the main effects and interaction effects of habitat and treatment.

Our analysis showed that the main effect of habitat on aggression was significant, while that of the noise treatment was not significant (see Table 3). There was a significant interaction effect between habitat type and experimental treatment. We carried out separate paired t-tests for urban and rural birds to explore the interaction effect with noise treatment as the IV. The effect of the noise treatment was not significant for urban birds ($t(8)=-1.23$, $p= 0.25$). Rural birds, however, were more aggressive under the noise treatment compared to the no-noise treatment, but they did not reach the aggression levels of the urban birds.

We also carried out separate LMMs to understand the effects of each one of the variables included in the PCA (see Appendix).

Table 3. Coefficients (SE) from the linear mixed models and the p-values from Wald t tests, examining the effect of habitat and experimental noise treatment. Statistically significant values are shown in bold type

	Aggression Score		**Song Rate**		**Song Duration**	
Predictors	*Estimates (SE)*	*p*	*Estimates (SE)*	*p*	*Estimates (SE)*	*p*
(Intercept)	-0.58 (0.26)	**0.035**	8.44 (0.59)	**<0.001**	1.86(0.14)	**<0.001**
Treatment	1.32 (0.39)	**0.003**	0.61 (0.65)	0.36	0.04(0.21)	0.8454
Habitat	0.32 (0.19)	0.105	0.81 (0.90)	**0.38**	0.03(0.11)	0.7890
Treatment*Habitat	-0.68 (0.29)	**0.031**	-2.02 (1.00)	0.059	0.11(0.17)	0.5376

3.3 ACOUSTIC SIGNALS

We used sonograms created on the software Syrinx to manually select the beginning and end points of songs. We divided the number of songs recorded during the trial period by the duration of the trial (180 seconds) to get the song rate. We used the beginning and end time of the song selections to calculate durations, which we then averaged to use in the analysis.

3.3.1 SONG RATE

We carried out a linear mixed model with habitat type and experimental treatment as the IVs, territory ID as the RV, and song rate as the DV. We looked for main effects of the IVs as well as the interaction effect. The main effect of habitat and treatment were not significant, but we detected an almost-significant interaction effect. We carried out further t-tests in urban and rural subsets with experimental treatment as IV and song rate as DV. The results showed that urban birds sang at significantly lower rates under experimental noise (t(9)=3.15, p= 0.014). Experimental noise playback had no significant effect on the song rates of rural birds (paired t-test; t(11)=1.01, p= 0.33).

3.3.2 SONG DURATION

We performed an LMM with song duration as the DV and habitat and treatment as the IVs. There was no significant main effect of either IV and the interaction effect was also not significant (see Table 3).

3.4 VISUAL SIGNALS

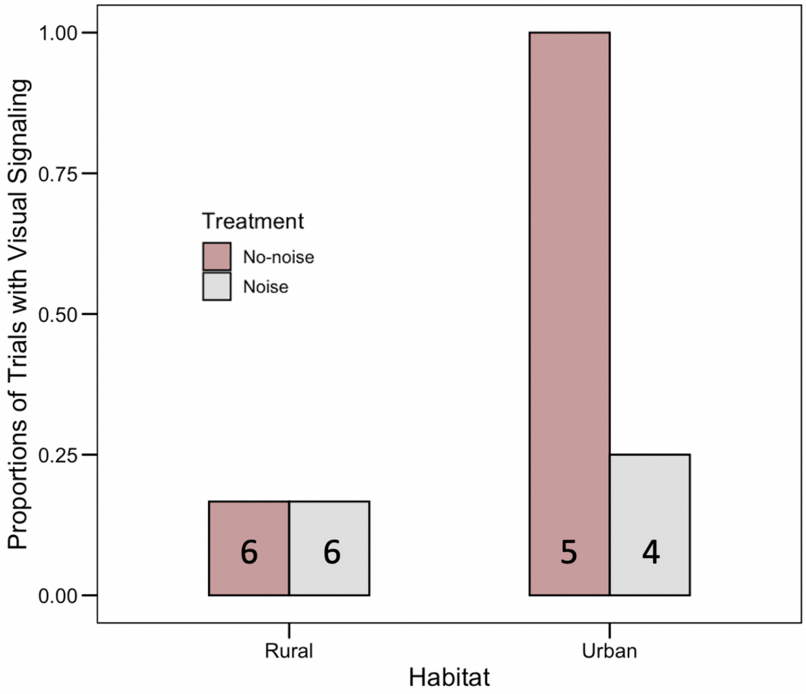

Figure 2. Proportion of first trials where the resident male used visual signals, grouped by habitat and noise treatment. The numbers at the bottom of each bar indicates the total number of subjects for each combination

Out of the 21 subjects, only eight used visual signals. Therefore, we coded this variable as a binomal. We gave each trial a score of 0 or 1 representing absence or presence of visual signals by the subject. Since we coded visual signals as a binomial, we used generalized linear models (GLM) in our analyses including visual signals using the base R function glm.

We carried out a GLM with the presence or absence of visual signals as the DV, habitat type and experimental treatment as the IVs, and territory ID as the random variable. The main effect of habitat type was significant, with urban birds using visual signals at higher rates than did rural birds (χ^2= 9.75, p=0.0018). The main effect of the experimental noise treatment was not significant (χ^2= 0.00, p=1.0). The interaction effect of habitat and treatment was almost significant (χ^2= 3.72, p=0.053). To explore the interaction effect, we carried out GLMs in urban and rural subsets and found that urban birds used visual singals more in the no noise treatment, albeit the difference was not significant (χ^2= 3.22, p=0.07).

Since the use of visual signals is associated with escalating aggression, we wanted to explore the connection between aggression scores and the use of visual signals. We performed a GLMM with aggression score as the IV, the presence or absence of visual signals as the DV and territory ID as the random variable. The main effect of aggression on the use of visual signals was significant (estimate +- SD = 3.33 +- 1.5, p=0.0266).

CHAPTER 4 – DISCUSSION

4.1 MAIN FINDINGS

Using simulated territorial intrusions, we investigated the effects of habitat type and experimentally recreated acute increases in noise on the multimodal signals and aggressive behaviors of the European robin. Based on earlier studies on territorial defense behavior, we expected both noise and habitat to have a significant effect on signal modality and aggression level. We also expected to see an interaction effect, such that urban robins would be more aggressive and use visual signals more than rural robins overall, and that noise playback would exacerbate this difference.

As we predicted, we found that urban robins were more aggressive, used visual signals more often overall, and decreased song rates in response to noise playback. However, the effect of experimental noise was not entirely in line with our hypotheses. We did find an interaction effect between habitat and noise playback, but the direction of the effect was the opposite of what we expected. Contrary to our predictions, noise playback significantly increased aggression scores only in rural birds. We did not find evidence for a change in song duration under any of the conditions.

4.2 CONTRIBUTIONS

Our findings on aggression levels between urban and rural birds are in line with those of previous studies showing that urban birds are more aggressive (Evans et al., 2010; Davies and

Sewall, 2016; Hardman and Dalesman, 2018; Phillips and Derryberry, 2018). However, our findings about the effect of experimental noise playback did not confirm our a priori hypotheses. Earlier studies have suggested that urban birds would be more flexible in their response to acute increases in noise (LaZerte et al., 2016; Gentry, et al. 2017). We found an effect in the opposite direction, that is, rural birds increased their aggression in noise while urban birds did not show a significant increase.

The lack of a plastic response to increased noise in urban birds is interesting since they are exposed to such increases and would be expected to have developed a strategy to cope with this hinderance. It is important to note that even under noise, rural birds did not reach the aggression levels of the urban birds, so it is possible that urban birds had reached the ceiling in terms of aggression and therefore we could not detect a significant effect of noise playback. This may also be the explanation for rural birds showing a more steep increase in aggression compared to urban birds in response to the food supplementation experiment in Foltz et al. (2015) described above. It is also possible that experimental noise playback did not create a significant difference in the already-noisy urban territories. This interpretation, taken together with the finding that rural robins were more aggressive under noise, supports the notion that anthropogenic noise leads to the increased aggression observed in urban birds.

Our findings support the multimodal shift hypotheses in that urban birds used visual signals significantly more often than rural birds. We also found an interaction effect between habitat and condition on song rates. Urban robins sang at lower under experimental noise, whereas no change was observed for rural robins. However, we did not detect a significant change in visual signaling under experimental noise. In fact, the subjects tended to use visual signals in the no-noise trial instead of the noise trial. This is consistent with the findings of Zwart et al. (2016), who also detected visual signals more often in the experimental condition with only conspecific song playback.

4.3 LIMITATIONS

The main limitation in our study was the small sample size, which made it especially difficult to make conclusions about the use of visual signals. Only 8 of the subjects used visual signals during the trials, which might be due to our visual stimulus not being convincing enough, although robins have been reported to display their necks even at balls of red feathers (Lack 1943). Because of the small number of birds who used visual signals, we needed to code visual displays as a binomial variable and thus were not able to assess how the frequency of visual signal use differed with habitat type or noise playback. In addition, there was a significant order effect on the presence of visual displays, which meant that we had to restrict our analysis to the first trials where the subjects were significantly more likely to use visual signals. There was also a non-significant tendency of urban birds to use visual signals in the no-noise condition. A total of five urban birds received the no-noise treatment first, and they all used visual signals. In contrast, out of the 4 urban robins that received the noise trial first, only one used visual signals. The effect of noise playback on the use of visual signals should be explored in future studies with either a between-subject design or a longer break period between noise and no-noise trials.

4.4 CONCLUSION

Our results reveal a complex interaction between habitat type and response to acute increases in noise during territorial disputes. Further research is needed to elucidate the role of long-term adaptation on plastic responses to disturbances in urban-living wildlife.

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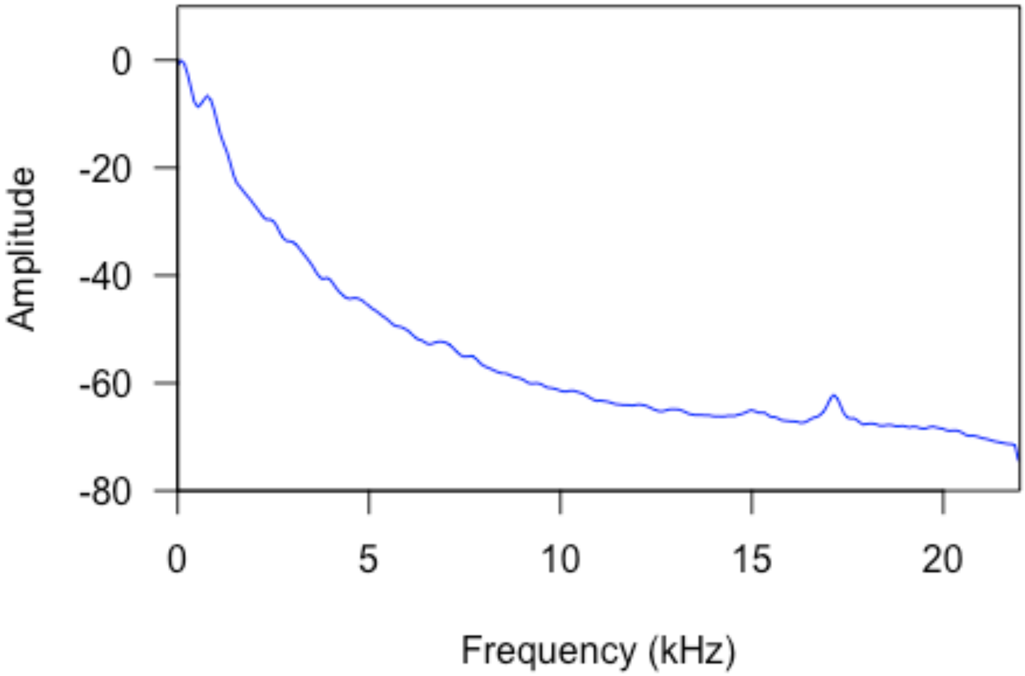
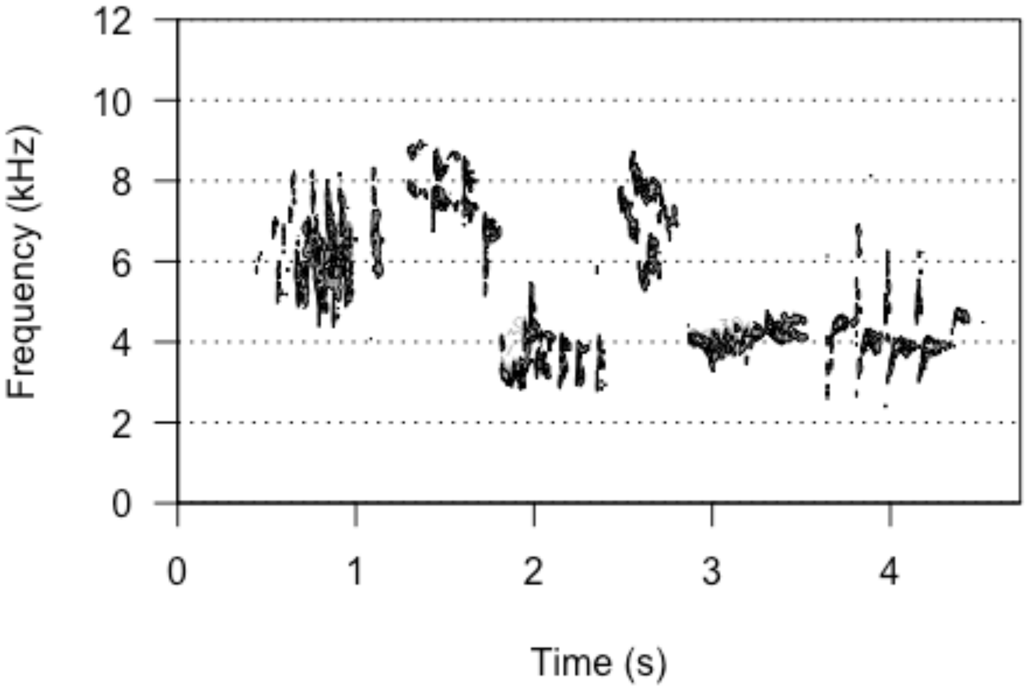
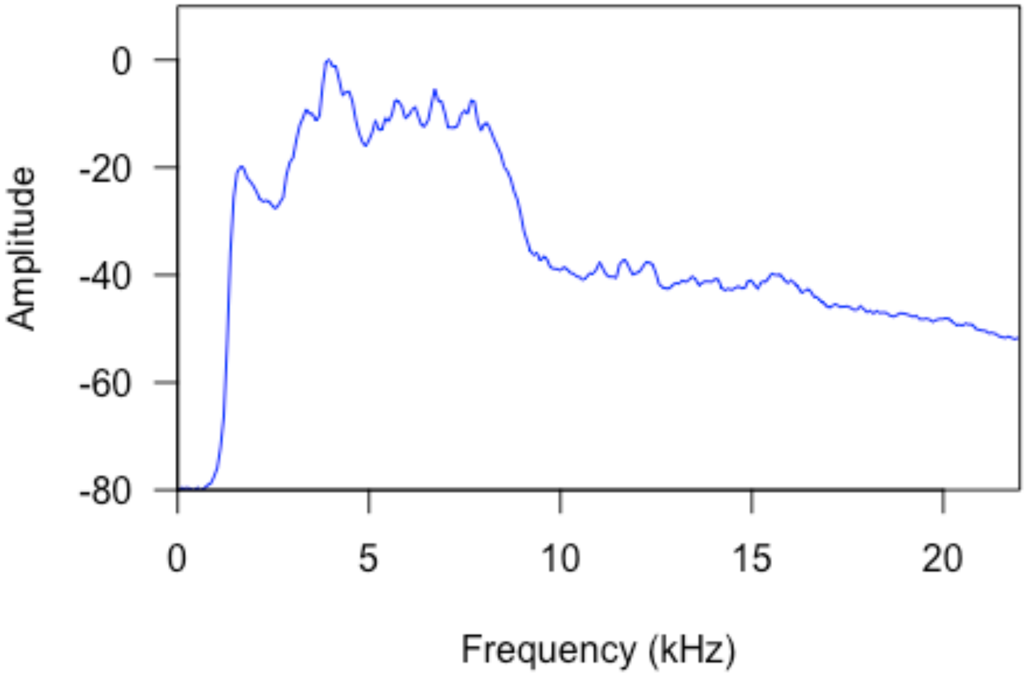
APPENDIX

Noise Playback Power Spectrum (Figure S1)



Song Spectrogram & Power spectrum (Figure S2 and S3)


12
10
8
6
4
2
0
Frequency (kHz)
0
1
2
3
4
Time (s)



Principal Component Analyses on spatial variables

Correlations

Flight rate and proportion of time spent within 1m

```
##
##  Pearson's product-moment correlation
##
## data:  Robin2021$FlightRate and Robin2021$prop1m
## t = 2.2194, df = 40, p-value = 0.03219
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
##  0.03023823 0.57698971
## sample estimates:
##       cor
## 0.3311264
```

Flight rate and closest approach(m)

```
##
##  Pearson's product-moment correlation
##
## data:  Robin2021$FlightRate and Robin2021$ClosestApproachM
## t = -2.3596, df = 40, p-value = 0.02326
## alternative hypothesis: true correlation is not equal to 0
```

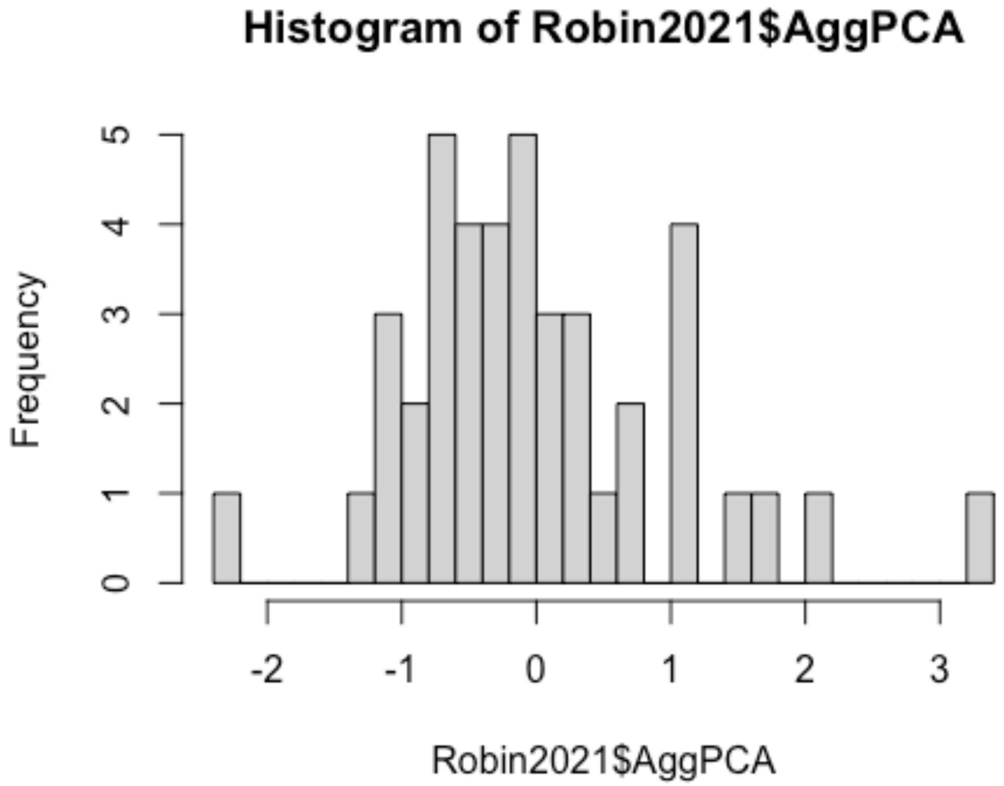
```
## 95 percent confidence interval:
##  -0.59072113 -0.05103777
## sample estimates:
##       cor
## -0.349547
```

Closest approach(m) and proportion of time spent within 1m

```
##
##  Pearson's product-moment correlation
##
## data:  Robin2021$ClosestApproachM and Robin2021$prop5m
## t = -4.5283, df = 40, p-value = 5.25e-05
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
##  -0.7528763 -0.3380341
## sample estimates:
##        cor
## -0.5821553
```

Aggression scores (PCA1) distribution (Figure S4)

```
## Principal Components Analysis
## Call: principal(r = PhysicalMeasures, nfactors = 1, residuals = FALSE,
##     rotate = "none", covar = FALSE)
## Standardized loadings (pattern matrix) based upon correlation matrix
##                              PC1   h2   u2 com
## Robin2021$FlightRate        0.65 0.42 0.58   1
## Robin2021$ClosestApproachM -0.85 0.73 0.27   1
## Robin2021$prop5m            0.83 0.68 0.32   1
##
##                 PC1
## SS loadings    1.83
## Proportion Var 0.61
##
## Mean item complexity =  1
## Test of the hypothesis that 1 component is sufficient.
##
## The root mean square of the residuals (RMSR) is  0.2
##  with the empirical chi square  9.75  with prob <  NA
##
## Fit based upon off diagonal values = 0.79
```



Ambient Noise

Ambient Noise and Habitat, LMM

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##        AIC      BIC    logLik
##   204.1462 210.5899 -98.07312
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept) Residual
## StdDev:     5.27673 1.324208
##
## Fixed effects:  Average ~ Habitat
##                  Value Std.Error DF   t-value p-value
## (Intercept)  39.69781  1.550891 19 25.596782  0.0000
## HabitatUrban  8.96880  2.367907 19  3.787648  0.0012
##  Correlation:
##              (Intr)
## HabitatUrban -0.655
##
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max
```

```
## -1.31435938 -0.58807449 -0.05934325  0.59745834  1.62135675
##
## Number of Observations: 39
## Number of Groups: 21
```

```
##             numDF denDF   F-value p-value
## (Intercept)     1    19 1380.5883  <.0001
## Habitat         1    19   14.3463  0.0012
```

Repeatability of noise measurements

```
## Bootstrap Progress:
```

```
##
##
## Repeatability estimation using the lmm method
##
## Repeatability for MaleID
## R  = 0.964
## SE = 0.021
## CI = [0.912, 0.985]
## P  = 2.56e-12 [LRT]
##      NA [Permutation]
```

Ambient noise by habitat, Mean and SD

Urban

```
## [1] 48.98088
```

```
## [1] 7.071437
```

Rural

```
## [1] 39.94472
```

```
## [1] 3.570615
```

Order effect

Order Effect on song rates

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##        AIC      BIC    logLik
##   188.9021 195.6576 -90.45104
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept) Residual
## StdDev:    0.898853 1.972697
##
## Fixed effects:  SongRateTrial ~ Order
##                 Value Std.Error DF   t-value p-value
## (Intercept)  8.396825 0.4730585 20 17.750079  0.0000
## Ordersecond -0.682540 0.6087876 20 -1.121146  0.2755
##  Correlation:
```

```
##             (Intr)
## Ordersecond -0.643
##
## Standardized Within-Group Residuals:
##        Min         Q1        Med         Q3        Max
## -2.4872641 -0.4720833  0.2082500  0.6657558  2.2505976
##
## Number of Observations: 42
## Number of Groups: 21
```

```
## Analysis of Deviance Table (Type III tests)
##
## Response: SongRateTrial
##               Chisq Df Pr(>Chisq)
## (Intercept) 315.065  1     <2e-16 ***
## Order         1.257  1     0.2622
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Order effect on aggression scores (PCA1)

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##        AIC      BIC    logLik
##   110.5753 117.3308 -51.28765
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept)  Residual
## StdDev:   0.8792328 0.4889573
##
## Fixed effects:  AggPCA ~ Order
##                  Value Std.Error DF    t-value p-value
## (Intercept)  0.1107159 0.2195373 20  0.5043147  0.6196
## Ordersecond -0.2214318 0.1508955 20 -1.4674515  0.1578
##  Correlation:
##             (Intr)
## Ordersecond -0.344
##
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max
## -1.64117543 -0.40591283  0.01055451  0.46065047  1.71283940
##
## Number of Observations: 42
## Number of Groups: 21
```

```
## Analysis of Deviance Table (Type III tests)
##
## Response: AggPCA
##              Chisq Df Pr(>Chisq)
## (Intercept) 0.2543  1     0.6140
## Order       2.1534  1     0.1423
```

Order effect on visual displays

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
##   Approximation) [glmerMod]
##  Family: binomial  ( logit )
## Formula: VisualDisplay ~ Order + (1 | MaleID)
##    Data: Robin2021
##
##      AIC      BIC   logLik deviance df.resid
##     31.9     37.1    -12.9     25.9       39
##
## Scaled residuals:
##       Min        1Q    Median        3Q       Max
## -0.006653 -0.003376 -0.000002 -0.000002  0.096861
##
## Random effects:
##  Groups Name        Variance Std.Dev.
##  MaleID (Intercept) 3371     58.06
## Number of obs: 42, groups:  MaleID, 21
##
## Fixed effects:
##             Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -11.344      3.358  -3.379 0.000729 ***
## Ordersecond  -15.323      6.221  -2.463 0.013778 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Correlation of Fixed Effects:
##             (Intr)
## Ordersecond 0.474

## Analysis of Deviance Table (Type III Wald chisquare tests)
##
## Response: VisualDisplay
##               Chisq Df Pr(>Chisq)
## (Intercept) 11.4147  1  0.0007286 ***
## Order        6.0664  1  0.0137778 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Aggression score analyses

Linear mixed models on Aggression scores, with habitat and treatment as predictors (Table 3)

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##        AIC      BIC    logLik
##   105.9003 115.7259 -46.95017
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept)  Residual
```

```
## StdDev:   0.7549836 0.4650489
##
## Fixed effects:  AggPCA ~ Habitat * Condition
##                                  Value Std.Error DF   t-value p-value
## (Intercept)                 -0.5826742 0.2559737 19 -2.276304  0.0346
## HabitatUrban                 1.3208684 0.3910064 19  3.378125  0.0032
## Conditionnoise               0.3229697 0.1898554 19  1.701135  0.1052
## HabitatUrban:Conditionnoise -0.6761866 0.2900089 19 -2.331606  0.0309
##  Correlation:
##                             (Intr) HbttUr Cndtnn
## HabitatUrban                -0.655
## Conditionnoise              -0.371  0.243
## HabitatUrban:Conditionnoise  0.243 -0.371 -0.655
##
## Standardized Within-Group Residuals:
##        Min         Q1        Med         Q3        Max
## -1.6836177 -0.3376003  0.0175153  0.3696283  1.9579139
##
## Number of Observations: 42
## Number of Groups: 21

## Analysis of Deviance Table (Type III tests)
##
## Response: AggPCA
##                     Chisq Df Pr(>Chisq)
## (Intercept)        5.1816  1  0.0228278 *
## Habitat           11.4117  1  0.0007298 ***
## Condition          2.8939  1  0.0889176 .
## Habitat:Condition  5.4364  1  0.0197214 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

LMM on aggression scores with noise treatment as predictor, Rural Subset

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##   Subset: Habitat == "Rural"
##        AIC      BIC    logLik
##   50.36621 54.73038 -21.18311
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept)  Residual
## StdDev:   0.6600083 0.3242974
##
## Fixed effects:  AggPCA ~ Condition
##                     Value Std.Error DF   t-value p-value
## (Intercept)    -0.5826742 0.2122851 11 -2.744772  0.0191
## Conditionnoise  0.3229697 0.1323939 11  2.439462  0.0329
##  Correlation:
##                (Intr)
## Conditionnoise -0.312
```

```
##
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max
## -2.05344186 -0.32001375  0.08331217  0.26491375  1.30934217
##
## Number of Observations: 24
## Number of Groups: 12
```

LMM on aggression scores with noise treatment as predictor, Urban Subset

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##   Subset: Habitat == "Urban"
##        AIC      BIC    logLik
##   54.86982 57.96017 -23.43491
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept)  Residual
## StdDev:   0.8687837 0.6074828
##
## Fixed effects:  AggPCA ~ Condition
##                     Value Std.Error DF   t-value p-value
## (Intercept)     0.7381942 0.3533680  8  2.089024  0.0701
## Conditionnoise -0.3532169 0.2863701  8 -1.233428  0.2524
##  Correlation:
##                (Intr)
## Conditionnoise -0.405
##
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max
## -1.26451755 -0.53660150 -0.02836087  0.46799618  1.52319947
##
## Number of Observations: 18
## Number of Groups: 9
```

T test, aggression scores in urban and rural birds in noise treatment

```
##
##  Welch Two Sample t-test
##
## data:  AggPCA by Habitat
## t = -1.8348, df = 12.361, p-value = 0.04536
## alternative hypothesis: true difference in means between group Rural and group Urban is less than 0
## 95 percent confidence interval:
##         -Inf -0.01995465
## sample estimates:
## mean in group Rural mean in group Urban
##          -0.2597045           0.3849773
```

Models with Individual Spatial Measures

Closest Approach Distance (m)

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##       AIC      BIC    logLik
##   230.135 239.9605 -109.0675
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept) Residual
## StdDev:    3.392613 2.607776
##
## Fixed effects:  ClosestApproachM ~ Habitat * Condition
##                                 Value Std.Error DF   t-value p-value
## (Intercept)                 10.750000  1.235257 19  8.702642  0.0000
## HabitatUrban                -6.616667  1.886886 19 -3.506659  0.0024
## Conditionnoise              -3.583333  1.064620 19 -3.365833  0.0032
## HabitatUrban:Conditionnoise  3.827778  1.626234 19  2.353768  0.0295
##  Correlation:
##                             (Intr) HbttUr Cndtnn
## HabitatUrban                -0.655
## Conditionnoise              -0.431  0.282
## HabitatUrban:Conditionnoise  0.282 -0.431 -0.655
##
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max
## -1.44199595 -0.38285212 -0.03918232  0.39303293  2.93593593
##
## Number of Observations: 42
## Number of Groups: 21
```

```
## Analysis of Deviance Table (Type III tests)
##
## Response: ClosestApproachM
##                     Chisq Df Pr(>Chisq)
## (Intercept)       75.7360  1  < 2.2e-16 ***
## Habitat           12.2967  1  0.0004538 ***
## Condition         11.3288  1  0.0007631 ***
## Habitat:Condition  5.5402  1  0.0185842 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Proportion of time spent within 5m of the model

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##        AIC      BIC    logLik
##   38.72572 48.55123 -13.36286
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept)  Residual
```

```
## StdDev:   0.2194376 0.2368401
## 
## Fixed effects:  prop5m ~ Habitat * Condition 
##                                  Value  Std.Error DF    t-value p-value
## (Intercept)                  0.1129630 0.09320501 19  1.2119838  0.2404
## HabitatUrban                 0.3660494 0.14237301 19  2.5710588  0.0187
## Conditionnoise              -0.0509259 0.09668957 19 -0.5266951  0.6045
## HabitatUrban:Conditionnoise -0.0854938 0.14769576 19 -0.5788509  0.5695
##  Correlation: 
##                             (Intr) HbttUr Cndtnn
## HabitatUrban                -0.655              
## Conditionnoise              -0.519  0.340       
## HabitatUrban:Conditionnoise  0.340 -0.519 -0.655
## 
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max 
## -1.48439572 -0.29341059 -0.08769457  0.12624752  2.14809796 
## 
## Number of Observations: 42
## Number of Groups: 21

## Analysis of Deviance Table (Type III tests)
## 
## Response: prop5m
##                    Chisq Df Pr(>Chisq)  
## (Intercept)       1.4689  1    0.22552  
## Habitat           6.6103  1    0.01014 *
## Condition         0.2774  1    0.59841  
## Habitat:Condition 0.3351  1    0.56269  
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Flight Rate

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021 
##        AIC      BIC    logLik
##   168.7912 178.6168 -78.39562
## 
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept) Residual
## StdDev:      1.1967 1.320389
## 
## Fixed effects:  FlightRate ~ Habitat * Condition 
##                                 Value Std.Error DF   t-value p-value
## (Intercept)                  1.222222 0.5144184 19  2.375930  0.0282
## HabitatUrban                 1.148148 0.7857871 19  1.461144  0.1603
## Conditionnoise               0.250000 0.5390464 19  0.463782  0.6481
## HabitatUrban:Conditionnoise -1.027778 0.8234070 19 -1.248201  0.2271
##  Correlation: 
##                             (Intr) HbttUr Cndtnn
```

```
## HabitatUrban                -0.655
## Conditionnoise              -0.524  0.343
## HabitatUrban:Conditionnoise  0.343 -0.524 -0.655
##
## Standardized Within-Group Residuals:
##        Min         Q1        Med         Q3        Max
## -0.9975790 -0.4532515 -0.1859754  0.3122705  3.2416885
##
## Number of Observations: 42
## Number of Groups: 21
```

```
## Analysis of Deviance Table (Type III tests)
##
## Response: FlightRate
##                   Chisq Df Pr(>Chisq)
## (Intercept)      5.6450  1     0.0175 *
## Habitat          2.1349  1     0.1440
## Condition        0.2151  1     0.6428
## Habitat:Condition 1.5580  1     0.2120
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Song rate

LMM on song rates, with habitat and treatment as predictor variables (Table 3)

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##        AIC      BIC    logLik
##   180.6677 190.4932 -84.33385
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept) Residual
## StdDev:    1.260692 1.611867
##
## Fixed effects:  SongRateTrial ~ Habitat * Condition
##                                  Value Std.Error DF   t-value p-value
## (Intercept)                   8.444444 0.5907241 19 14.295074  0.0000
## HabitatUrban                  0.814815 0.9023460 19  0.902996  0.3778
## Conditionnoise               -0.611111 0.6580420 19 -0.928681  0.3647
## HabitatUrban:Conditionnoise -2.018519 1.0051757 19 -2.008125  0.0591
##  Correlation:
##                             (Intr) HbttUr Cndtnn
## HabitatUrban                -0.655
## Conditionnoise              -0.557  0.365
## HabitatUrban:Conditionnoise  0.365 -0.557 -0.655
##
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max
## -2.46977565 -0.44814419  0.02979613  0.44142364  1.66060285
##
```

```
## Number of Observations: 42
## Number of Groups: 21
```

```
## Analysis of Deviance Table (Type III tests)
##
## Response: SongRateTrial
##                     Chisq Df Pr(>Chisq)
## (Intercept)      204.3491  1    < 2e-16 ***
## Habitat            0.8154  1    0.36653
## Condition          0.8624  1    0.35305
## Habitat:Condition   4.0326  1    0.04463 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

LMM on song rates, with noise treatment as predictor variable, Urban subset

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##   Subset: Habitat == "Urban"
##        AIC     BIC    logLik
##   77.11524 80.2056 -34.55762
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept) Residual
## StdDev:   0.4530418 1.773432
##
## Fixed effects:  SongRateTrial ~ Condition
##                     Value Std.Error DF   t-value p-value
## (Intercept)     9.259259 0.6101283  8 15.175922  0.0000
## Conditionnoise -2.629630 0.8360040  8 -3.145475  0.0137
##  Correlation:
##                (Intr)
## Conditionnoise -0.685
##
## Standardized Within-Group Residuals:
##         Min          Q1         Med          Q3         Max
## -1.52328188 -0.48964768 -0.05582765  0.31825570  1.95462053
##
## Number of Observations: 18
## Number of Groups: 9
```

```
## Analysis of Deviance Table (Type III tests)
##
## Response: SongRateTrial
##               Chisq Df Pr(>Chisq)
## (Intercept) 230.309  1  < 2.2e-16 ***
## Condition     9.894  1   0.001658 **
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

LMM on song rates, with noise treatment as predictor variable, Rural Subset

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##   Subset: Habitat == "Rural"
##        AIC      BIC    logLik
##   106.0826 110.4468 -49.04129
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept) Residual
## StdDev:    1.611198 1.483353
##
## Fixed effects:  SongRateTrial ~ Condition
##                    Value Std.Error DF  t-value p-value
## (Intercept)     8.444444 0.6322115 11 13.35699  0.0000
## Conditionnoise -0.611111 0.6055764 11 -1.00914  0.3346
##  Correlation:
##                (Intr)
## Conditionnoise -0.479
##
## Standardized Within-Group Residuals:
##        Min         Q1        Med         Q3        Max
## -2.2764595 -0.2585715  0.0236137  0.5459746  0.9311823
##
## Number of Observations: 24
## Number of Groups: 12
```

```
## Analysis of Deviance Table (Type III tests)
##
## Response: SongRateTrial
##                Chisq Df Pr(>Chisq)
## (Intercept) 178.4093  1     <2e-16 ***
## Condition     1.0184  1     0.3129
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

Visual Signals

GLM on Visual Signals in the first trials, habitat and treatment as predictor variables

```
##
## Call:
## glm(formula = VisualDisplay ~ Habitat * Condition, family = binomial,
##     data = Robin2021, subset = Order == "first")
##
## Deviance Residuals:
##      Min        1Q    Median        3Q       Max
## -0.75853  -0.60386  -0.60386   0.00013   1.89302
##
## Coefficients:
##                            Estimate Std. Error z value Pr(>|z|)
## (Intercept)              -1.609e+00  1.095e+00  -1.469    0.142
```

```
## HabitatUrban                 2.018e+01  2.917e+03   0.007    0.994
## Conditionnoise               1.435e-15  1.549e+00   0.000    1.000
## HabitatUrban:Conditionnoise -1.966e+01  2.917e+03  -0.007    0.995
## 
## (Dispersion parameter for binomial family taken to be 1)
## 
##     Null deviance: 27.910  on 20  degrees of freedom
## Residual deviance: 15.312  on 17  degrees of freedom
## AIC: 23.312
## 
## Number of Fisher Scoring iterations: 17
```

```
## Analysis of Deviance Table (Type III tests)
## 
## Response: VisualDisplay
##                  LR Chisq Df Pr(>Chisq)   
## Habitat            9.7515  1   0.001792 **
## Condition          0.0000  1   1.000000   
## Habitat:Condition  3.7288  1   0.053480 . 
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

GLM on Visual Signals in the first trials, treatment as predictor variable, Urban Subset

```
## 
## Call:
## glm(formula = VisualDisplay ~ Condition, family = binomial, data = Robin2021, 
##     subset = Order == "first" & Habitat == "Urban")
## 
## Deviance Residuals: 
##      Min        1Q    Median        3Q       Max  
## -0.75853  -0.75853   0.00005   0.00005   1.66511  
## 
## Coefficients:
##                Estimate Std. Error z value Pr(>|z|)
## (Intercept)       20.57    7929.26   0.003    0.998
## Conditionnoise   -21.66    7929.26  -0.003    0.998
## 
## (Dispersion parameter for binomial family taken to be 1)
## 
##     Null deviance: 11.4573  on 8  degrees of freedom
## Residual deviance:  4.4987  on 7  degrees of freedom
## AIC: 8.4987
## 
## Number of Fisher Scoring iterations: 19
```

```
## Analysis of Deviance Table
## 
## Model: binomial, link: logit
## 
## Response: VisualDisplay
## 
```

```
## Terms added sequentially (first to last)
##
##
##           Df Deviance Resid. Df Resid. Dev
## NULL                          8    11.4573
## Condition  1   6.9586         7     4.4987
```

GLM on whether aggression scores predict visual displays (binomial response variable)

```
##
## Call:
## glm(formula = VisualDisplay ~ AggPCA, family = binomial, data = Robin2021,
##     subset = Order == "first")
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -1.1975  -0.4202  -0.1430   0.2025   2.1478
##
## Coefficients:
##             Estimate Std. Error z value Pr(>|z|)
## (Intercept)  -0.9017     0.7532  -1.197   0.2313
## AggPCA        3.3270     1.5002   2.218   0.0266 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##     Null deviance: 27.910  on 20  degrees of freedom
## Residual deviance: 11.821  on 19  degrees of freedom
## AIC: 15.821
##
## Number of Fisher Scoring iterations: 6

## Analysis of Deviance Table
##
## Model: binomial, link: logit
##
## Response: VisualDisplay
##
## Terms added sequentially (first to last)
##
##
##        Df Deviance Resid. Df Resid. Dev
## NULL                      20     27.910
## AggPCA  1   16.089        19     11.821
```

Song Duration

Song duration, habitat and treatment

```
## Linear mixed-effects model fit by REML
##   Data: Robin2021
##        AIC      BIC   logLik
```

```
##   62.00559 71.83111 -25.0028
##
## Random effects:
##  Formula: ~1 | MaleID
##         (Intercept)  Residual
## StdDev:   0.4053826 0.2693497
##
## Fixed effects:  SongLengthAvg ~ Habitat * Condition
##                              Value Std.Error DF   t-value p-value
## (Intercept)                1.8611417 0.1405004 19 13.246524  0.0000
## HabitatUrban               0.0424111 0.2146179 19  0.197612  0.8454
## Conditionnoise             0.0298425 0.1099616 19  0.271390  0.7890
## HabitatUrban:Conditionnoise 0.1054574 0.1679690 19  0.627839  0.5376
##  Correlation:
##                            (Intr) HbttUr Cndtnn
## HabitatUrban               -0.655
## Conditionnoise             -0.391  0.256
## HabitatUrban:Conditionnoise  0.256 -0.391 -0.655
##
## Standardized Within-Group Residuals:
##        Min         Q1        Med         Q3        Max
## -1.8093423 -0.5218645 -0.1315417  0.5450639  2.2035506
##
## Number of Observations: 42
## Number of Groups: 21

##                   numDF denDF  F-value p-value
## (Intercept)           1    19 384.6253  <.0001
## Habitat               1    19   0.2320  0.6355
## Condition             1    19   0.8149  0.3780
## Habitat:Condition     1    19   0.3942  0.5376
```

Figure S5- Visual displays in the first trials are correlated with aggression scores

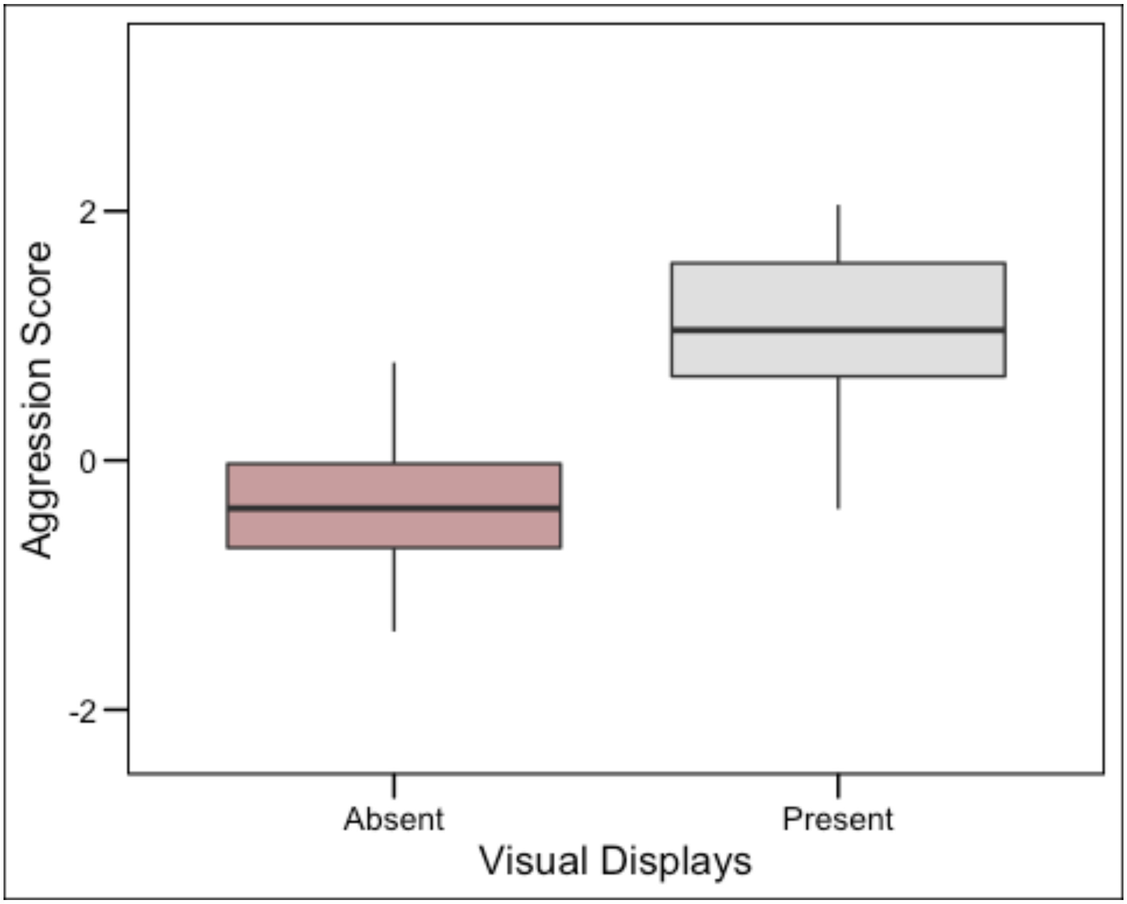


Figure S6 - Visual Stimulus

S7 - A video collage of visual displays used by robins: https://youtu.be/CBuSxSc24Io