

Anthropogenic noise affects female, not male house wren response to change in signaling network

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Abstract

Vocal signals mediate social relationships, and among networks of territorial animals, information is often shared via broadcast vocalizations. Anthropogenic noise may disrupt communication among individuals within networks, as animals change the way they vocalize in noise. Furthermore, constraints on signal transmission, including frequency masking and distance, may affect information exchange following a disruption in social networks. We tested the hypothesis that signaling interactions within networks of breeding male and female house wrens (*Troglodytes aedon*) depend on distance, ambient noise, and receiver nesting stage. We used playback experiments to simulate territorial intrusions with and without noise playbacks on the territories of established males and simultaneously recorded the vocal responses of neighbors. To examine whether intrusions impacted interactions between males, we used randomization tests to determine whether treatment, distance, noise, or nesting stage affected vocal coordination between challenged and neighboring males. We also quantified singing patterns to explore whether intrusions on territories of challenged males affected singing by males and females on neighboring territories. Males sang at the lowest rates and were less likely to overlap songs with the challenged male when their partner was laying, compared to males during early and late nesting stages. Noise and distance did not affect vocal coordination or male singing rates. Fewer females sang during the intruder-only treatment compared to the control and intrusions with noise. Added noise in the territories of challenged males may have masked signals, and as a result, females only changed their behavior during the intruder-only treatment. Our results suggest that the fertility of breeding partners may be more important to males than short-term changes on rival male territories. Elevated noise did little to alter male responses to threats within networks. Females appeared to eavesdrop on interactions involving neighboring males, but noise may have prevented detection of their interactions.

KEYWORDS

context-dependent signaling, eavesdropping, signal masking, signaling network, territory intrusion, vocal coordination

1 | INTRODUCTION

Animals give vocalizations structured for long-distance transmission to convey information regarding sender identity, quality, and motivation (Bradbury & Vehrencamp, 1998). Vocal signals mediate social relationships, linking signal senders and receivers in complex signaling networks (McGregor, 2005; McGregor & Dabelsteen, 1996; McGregor & Peake, 2000; Peake, McGregor, & Dabelsteen, 2005). Within signaling networks, territorial males actively gain information regarding other males through countersinging or passively through eavesdropping (McGregor, 2005; Peake et al., 2005), adjusting their own behavior according to information gained (Amy, Sprau, de Goede, & Naguib, 2010; Naguib, Amrhein, & Kunc, 2004; Peake, Terry, McGregor, & Dabelsteen, 2002; Schmidt, Amrhein, Kunc, & Naguib, 2007). Simultaneously, females eavesdrop on and alter their behavior in response to male counter-signaling interactions (Snijders, van Oers, & Naguib, 2017), using acquired information to guide mate choice decisions (Mennill, Ratcliffe, & Boag, 2002; Otter et al., 1999). Thus, variation in male signaling behavior is closely tuned to the specifics of their social environment. Accordingly, changes in the social environment will likely affect patterns of vocal interactions among the members of territorial signaling networks.

Constraints on signal transmission that affect the ability of receivers to detect, discriminate, and decode signals may weaken exchanges among individuals. Acoustic signals attenuate over space and become further degraded as they are absorbed by vegetation or scatter through the environment with increasing distance from the signaler (Marten & Marler, 1977; Morton, 1975; Wiley & Richards, 1978). Additionally, frequency masking by other sounds decreases the area over which signals can be detected (Klump, 1996), limiting the ability of receivers to hear and perceive signals. Human-generated noise pollution adds to these natural causes of signal degradation and further limits information sharing due to masking (Patricelli & Blickley, 2006). As a result, in noise-polluted areas, vocal interactions among neighboring territorial males and females may change. For example, individuals may move closer together to increase the likelihood of detecting signals (Owens, Stec, & O'Hatnick, 2012). Alternatively, neighbors may not interact at all if they miss information as a result of frequency masking, signal attenuation, or a combination of both. Therefore, the effects of anthropogenic noise masking, compounded by distance, may fundamentally alter the structure of social interactions within signaling networks.

In addition to limitations imposed by environmental constraints, variation in signaling patterns among callers may be context-dependent (Snijders & Naguib, 2017). Between rival males, vocal coordination, or the probability of song alternation and overlap may depend on social conditions, such as group size and whether or not males have paired (Fernandez, Vignal, & Soula, 2017). In response to intruders on the territories of neighbors, males respond more strongly when intrusions are in close proximity to their own territory (Foote, Fitzsimmons, Mennill, & Ratcliffe, 2011) or reflect a greater risk (Fitzsimmons, Foote, Ratcliffe, & Mennill, 2008). Female responses to male signaling interactions may also vary by context, as social

interactions linked to reproductive success will vary across stages of breeding. Females may adjust their spatial behavior (Snijders et al., 2017) to facilitate eavesdropping for future mate decisions (Mennill et al., 2002; Otter et al., 1999) or may synchronize interactions at the nest with their social mate, as intruders on neighboring territories may pose a risk to reproductive investment. Therefore, measuring patterns of signaling interactions among multiple male and female callers may reveal otherwise hidden interactions between individuals within networks. By investigating context-dependent signaling in conjunction with measurement of anthropogenic noise, we can gain a better understanding of the primary drivers of social interactions among individuals (McGregor & Horn, 2015; Snijders & Naguib, 2017).

We tested the hypothesis that environmental constraints and social context affect patterns of singing among territorial male and female house wrens (*Troglodytes aedon*) within signaling networks. To test our hypothesis, we used playbacks to simulate territorial intrusions with and without anthropogenic noise on territories of established males (hereafter, "challenged males"), but focused on the vocal behavior of neighbors to explore whether environmental factors (noise and distance from challenged male) and social context (nesting stage) influenced singing. We measured vocal coordination, or patterns of signal overlap and alternation between challenged and neighboring males (Araya-Salas, Wojczulanis-Jakubas, Phillips, Mennill, & Wright, 2017; Fernandez et al., 2017; Masco, Allesina, Mennill, & Pruett-Jones, 2016), and total song output by neighbors in response to simulated intruders to understand factors that influence the vocal responses of neighbors. As the responses of neighboring males and females to challenged males may differ (Snijders et al., 2017), we evaluated female vocal responses by determining whether neighboring females sang during treatments. Our objective was to assess the change in song output and patterns of signaling interactions in response to simulated territorial intrusions, not information contained within the challenged males' signal itself (e.g., aggressive intent or male quality). We predicted that, if challenges are detected by neighbors, both male and female neighbors would change their singing behavior, by either signaling more to affirm territory ownership and partnership, or less to facilitate eavesdropping. However, anthropogenic noise masking and distance-related signal attenuation could decrease the probability of detection, resulting in less coordinated interactions between challenged males and their neighbors in noisier networks or between challenged males and more distant neighbors.

Both male and female house wrens sing throughout the breeding season (Krieg & Getty, 2016; Rendall & Kaluthota, 2013), but total song output varies across nesting (Grabarczyk, Pipkin, Vonhof, & Gill, 2018; Johnson & Kermott, 1990, 1991; Rendall & Kaluthota, 2013; Tove, 1988). Paired and unpaired males prior to clutch initiation sing long songs at high rates (Grabarczyk et al., 2018; Johnson & Kermott, 1991; Rendall & Kaluthota, 2013), whereas laying-stage males almost cease singing entirely (Johnson & Kermott, 1991). After egg-laying, singing behavior is variable, but generally males sing more during incubation and nesting stages

(Johnson & Kermott, 1991; Rendall & Kaluthota, 2013). At any stage, high levels of noise masking significantly decrease the distance over which male long-distance songs transmit, such that signals may not be detected beyond the boundary of a male's own territory (Grabarczyk & Gill, 2019b, 2020). Females produce a variety of signal types, but overall sing at lower rates than males (Johnson & Kermott, 1990). Female wrens sing to coordinate with breeding partners during early stages of breeding, including occasionally during incubation (Johnson & Kermott, 1990), and give high-frequency, low-amplitude signals in response to territorial intruders of both sexes (Krieg & Burnett, 2017; Krieg & Getty, 2016). Consequently, noise pollution on territories may affect both within-pair and among-neighbor signaling interactions.

2 | METHODS

2.1 | House wren signaling networks

From 2016 to 2017, we monitored a color-banded population of house wrens at three sites in Kalamazoo County, Michigan, USA (Supporting Information). We used mist nets to capture house wrens at their nest boxes and fitted each adult with three color bands and one numbered aluminum band to discriminate between individuals. We sexed adults in hand based on cloacal protuberance (male) and brood patch (female) and confirmed sex and territory ownership by observing sex-specific male and female songs at the nest box. Prior to house wren arrival on the breeding grounds, we arranged nest boxes ($N = 96$) into 16 networks, each containing six nest boxes in areas of open habitat near a forest edge. Within networks, boxes were arranged into hexagons, placing adjacent boxes at a 60° angle and separating them by 45–50 m. Networks were separated by at least 150 m to minimize detection of long-distance male songs between networks (Grabarczyk & Gill, 2019b). Networks varied in spatial proximity to anthropogenic noise sources such as local roads and highways (Grabarczyk & Gill, 2019b, 2020) and therefore differed in ambient noise levels (Supporting Information).

2.2 | Playback experiment

We ran playback experiments between June 6–July 21, 2016, and April 28–July 2, 2017, on 18 challenged male territories ($n = 7$ territories in 2016 and $n = 11$ territories in 2017), while simultaneously recording all house wrens breeding in each network ($n = 43$ neighboring males and $n = 33$ neighboring females). Challenged males were tested either prior to clutch initiation or during incubation. Each network was tested only once per year; five networks tested in 2016 were tested again in 2017. Three color-banded males were tested and included in analysis for both years. In total, 37 out of 43 males (86%) and 18 out of 33 females (55%) were color-banded.

In networks occupied by two or more males, we placed Wildlife Acoustics Song Meter 2 units (SM2; Maynard, MA, 44.1 kHz sample

rate, 16-bit, .wav format) at each active nest box. House wrens were recorded at their nest boxes by attaching a microphone (Wildlife Acoustics, SMX-II model) to the nest box pole and connecting the microphone to an SM2 unit with a 3, 10, or 50 m cord (some units recorded two nest boxes on separate channels; Supporting Information). Units were pre-programmed to begin recording 1 hr before to 4 hr after sunrise (Eastern Standard Time, EST) in 30-min recording increments. Playbacks took place between sunrise and 1100 (EST) on days with minimal wind speed and no precipitation and followed the same procedure used by Grabarczyk and Gill (2019a). Briefly, we created 28 playbacks from recordings of male house wrens breeding in southwest Michigan during 2015–2016. Males sing with eventual variety, repeating the same terminal section several times before gradually transitioning to a new song type (Kroodsma, 1977; Rendall & Kaluthota, 2013). Therefore, to mimic natural singing patterns, a single song type was repeated every 15 s for 10 min, similar to typical rates of singing (Grabarczyk & Gill, 2019a). From the collection of 28 exemplars used in Grabarczyk & Gill, 2019a, 16 were randomly selected for use in the present study (two playbacks were used twice, one in 2016 and one in 2017). For noise playbacks, we created a pink noise signal in Avisoft SASLab Pro v5.2 (R. Specht, Glienicke/Nordbahn, Germany). Pink noise is a continuous noise signal, comparable to white noise, except that it has more energy concentrated at low frequencies (0–2 kHz), similar to anthropogenic noise (44.1 kHz sample frequency, lowpass 1/f, frequency cut off at 0.20 Hz).

Each challenged male received three treatments: intruder playback only, intruder plus noise, and noise only. We randomly selected the order of treatments. Each stimulus consisted a 10-min control period, a 10-min playback, followed by a 20-min break before start the next playback. To simulate a territorial intruder, an amplified SME-AFS speaker (Saul Mineroff Electronics) was placed 5–10 m from the challenged male's nest box. We broadcast noise from a second speaker that was placed 10 m in the opposite direction. Both pink noise and simulated intruder playback were broadcast at 76 dBA measured with a SPL meter at 1 m, fast averaging mode (American Recorder Technology SPL-8810; Supporting Information). We selected 76 dBA for playbacks because paired male house wrens sing at this amplitude (Grabarczyk & Gill, 2019b) and noise playbacks broadcast >80 dBA completely mask the songs of males singing nearby, preventing analysis of song traits (Grabarczyk et al., 2018).

2.3 | Acoustic analysis

Because network recordings during trials were made on two to six SM2 units with time manually set, we needed to account for the relative time difference between units before extracting the timing of male songs relative to one another. Therefore, after playback experiments, units were synchronized by setting all units side-by-side, programming them to start at the same time and recording for 5 min during which we played pre-recorded house wren song through an iPhone. From recordings, we determined the time offset

between units and aligned the recordings such that start of playback experiments occurred within 0.01 ms across recorders. In Avisoft, we inserted point labels indicating the start and end of each 10-min experimental period on all recordings (i.e., before, during, and after each of the three treatments). We defined the control as the first 10-min period of the trial, prior to any treatments.

Male house wren song consists of two parts, a low-amplitude introduction section that is structured for short-distance transmission, followed by the high-amplitude terminal section capable of transmitting beyond the typical boundaries of a male's territory under low-noise conditions (Figure 1, Video S1; Grabarczyk & Gill, 2019a). On recordings, we used Avisoft to mark the terminal section of all songs recorded for each male with section labels on the spectrogram window (Flat top window, 512 FFT length, 93.75% overlap, 0.725 ms time resolution). All recordings were processed by E. Grabarczyk. To ensure that songs were assigned to the correct male, we generated spectrograms of all simultaneous recordings (i.e., trials) within networks and confirmed that each song was credited to one male (i.e., had the highest SNR in the spectrogram and followed typical male eventual variety singing patterns). In addition to the terminal section of male songs, we labeled all female-specific songs during each treatment and the control. This excluded chatter vocalizations that are uttered by both sexes. Across treatments and the control period, we included 4,076 songs from 43 males and 384 songs from 34 females in our analysis (male $\bar{x} \pm SD$: 23.2 ± 21.9 , range: 0–98 songs per treatment; female $\bar{x} \pm SD$: 2.8 ± 6.2 , range: 0–40 songs per treatment).

2.4 | Male–male vocal coordination

To explore vocal coordination between challenged males and each of their neighbors, we approximated the probability of song overlap and alternation between pairs of males. From Avisoft, we exported section label metadata, including the start and end time of each male song for calculation of coordination estimates. We used the `coord.test` function in `warbleR` (Araya-Salas & Smith-Vidaurre, 2017) in R program software v.3.3.3 (R Core Development Team). This function uses Monte Carlo randomization tests to determine whether males overlap or alternate songs more than what is expected by chance. The function estimates a coordination score, in which negative values indicate that males alternate their songs, whereas positive

values suggest overlap (Araya-Salas & Smith-Vidaurre, 2017). Pairs of males breeding in the same network were included in analysis if males each sang more than 20 songs during each 10-min treatment ($n = 35$ neighboring males included in coordinated singing analysis). Males prior to clutch initiation typically sing 3.4 ± 2.0 songs per minute (Grabarczyk & Gill, 2019a). Therefore, we reasoned that if males sang less than two songs per min, we could not be sure whether they were countersinging with focal males, eavesdropping on them, or simply not present on their territories during treatments.

2.5 | Quantifying environmental factors

Noise varies over space and time; therefore, males breeding in the same network may experience different levels of noise on their territories at any given moment (Gill, Job, Myers, Naghshineh, & Vonhof, 2015; Gill, Grabarczyk, Baker, Naghshineh, & Vonhof, 2017). We assessed the influence of noise on signaling interactions and assumed that noise levels on territories of neighbors contribute to variation in their singing behavior. We quantified from recordings full spectrum sound pressure levels (rms, dB) on each neighbor's territory during treatment and control periods. We used a Larson Davis CAL 200 sound level calibrator to calibrate SM2 unit and microphone pairs by recording a 1-kHz 94 dB tone. Using the Calibration function in Avisoft, we set the recording amplitude to 0 dB (re 20 μ Pa) based on the recorded calibration tone. To determine average ambient noise levels, we randomly selected five 1-s samples from each 10-min experimental period and the control. We used the automated parameter tool in Avisoft to extract amplitudes (rms, dB) for each 1-s noise sample and calculated a log-average for each treatment and the control. To account for signal attenuation due to distance, we measured the distance between neighbors and challenged male nest boxes. We used a Garmin handheld unit (GPSmap 60CSx) to generate GPS locations and measured the distance between challenged and neighboring male territories with ArcGIS 10.5 software (distance tool; ESRI Redlands).

2.6 | Nesting stage

Nest boxes were checked every three days and from this record, we defined social context as nesting stage, during which house wrens

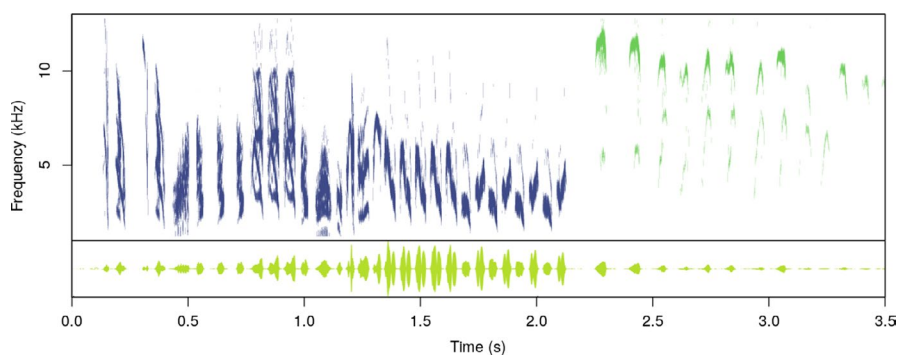
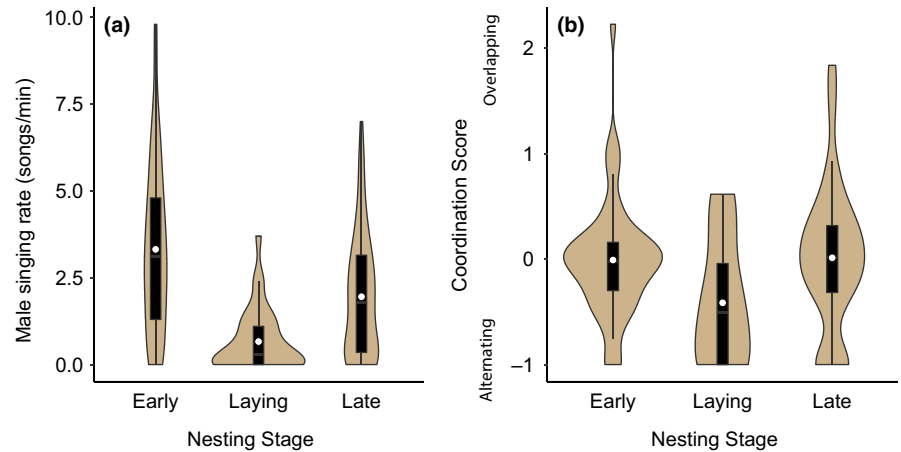


FIGURE 1 Spectrogram image of male and female house wren songs. Male house wrens (blue) sing frequency modulated, high-amplitude songs that transmit beyond a male's own territory under quiet conditions. Female house wrens (green) produce a variety of songs that tend to be low amplitude and span a broad range of frequencies

FIGURE 2 Male house wrens sang at lower rates (a) and were less likely to overlap songs with challenged males (b) if their breeding partner was laying on the day of recording. Violin plots show mean responses (white circle) and the width of the plot indicates the distribution of male responses



vary predictably in singing behavior. We grouped stages into three main categories (early, laying, and late stages). Early stage included unpaired males as well as paired males and females prior to clutch initiation. Pairs were considered laying if the female breeding partner had laid an egg on the day of recording. Neighbors were considered late stage if the female was incubating a clutch or if the pair were provisioning nestlings inside the nest box. In total, 29 neighboring house wrens were tested during early nesting stages ($n = 19$ males and 10 females), 18 during laying stages ($n = 9$ males and nine females), and 30 during late nesting stages ($n = 15$ males and 15 females). Of the 18 challenged males, nine were tested prior to clutch initiation (early nesting) and nine were tested during incubation (late nesting).

2.7 | Statistical analysis

2.7.1 | Do neighboring males adjust their singing behavior?

We used general linear mixed effect models to test the a priori hypothesis that neighbor responses (singing rate [songs/min] and vocal coordination scores, respectively) are affected by treatment, the environment, and nesting stage. We tested whether an interaction term between environmental factors (distance by noise) or an interaction between nesting stage and treatment improved model fit using the Akaike information criteria corrected for small sample sizes (AICc) values and found that the interaction terms did not significantly improve fit for either model (Burnham & Anderson, 2004; Supporting Information). Therefore, we included treatment (four levels; three treatments plus the control), environmental factors (distance from challenged male [m] and ambient noise levels [rms, dB]), and nesting stage (three levels; early, laying, and late) as fixed effects, and male identity nested within network as a random effect. We centered and scaled continuous predictor variables (distance and noise) prior to analysis. We used the R package lme4 (Bates, Maechler, Bolker, & Walker, 2015) for model testing and report fixed effect coefficients as well as a bootstrapped 95% confidence intervals ($N = 2,000$ simulations). We assessed model adequacy with residual plots and used a

square root transformation on coordination scores as residual plots indicated heteroscedasticity (Zuur, Ieno, & Elphick, 2010). We used box plots to confirm that presentation of consecutive treatments did not result in a carryover effect. We plotted model residuals against date and year, but found no patterns, therefore did not include either in our model.

2.7.2 | Vocal responses of neighboring females

Initial data exploration of female responses showed that neighboring females sang during 48% of the 10-min treatment and control periods (71 out of 136 trials). Females typically sing at a low rate and the data showed over-dispersion. Therefore, we used generalized linear mixed effects models (family = binomial, link = logit) to test whether treatment, the environment, or nesting stage predict whether or not a female sang. We included treatment (four levels), distance to challenged male (m), ambient noise levels (rms, dB), and nesting stage (three levels) as fixed effects and female identity nested within network as a random effect. We centered and scaled continuous predictor variables (distance and noise) prior to testing. We explored whether adding an interaction between environment variables (distance by noise) or between nesting stage and treatment improved model fit, but found that it did not (Supporting Information). Box plots confirmed that presentation of consecutive treatments did not result in a carryover effect. We plotted model residuals against date and year, but found no patterns, therefore did not include either in our model. We report fixed effect test coefficients and 95% bootstrapped confidence intervals.

3 | RESULTS

3.1 | Nesting stage, not noise, predicts signaling behavior by neighboring males

During experiments, challenged males ($n = 18$) sang between 0 and 123 songs per treatment, whereas neighboring males ($n = 43$) sang between 0 and 98 songs per treatment. Variation in singing rate of

neighboring males and vocal coordination between neighboring and challenged males were predicted by nesting stage. Males that were recorded on a day in which their social mate was laying sang at lower rates (Figure 2a; Table 1) and were more likely to alternate songs or show no patterns of coordination with challenged males (Figure 2b; Table 1). Males recorded during early and late nesting stages sang at higher rates, but showed no predictable patterns of overlap or alternation with challenged males, which indicates no evidence for local coordination at these stages (Figure 2b). Male responses were not predicted by distance to challenged male, ambient noise levels on their territories, or playback treatment, regardless of nesting stage (Table 1).

3.2 | Fewer females sang during intruder-only treatments

A smaller proportion of neighboring females sang during the intruder-only treatment than during the control, noise-only, and intruder plus noise treatments (Figure 3, Table 1). Noise levels, distance to challenged male, and nesting stage did not predict the proportion of females that sang during treatments (Table 1).

4 | DISCUSSION

We tested whether distance, anthropogenic noise, or nesting stage affected the vocal behavior of male and female house wrens in response to a simulated intruder on their neighbor's territory. For males, neither the distance to challenged males, ambient noise levels, nor treatment affected patterns of singing. Instead, the vocal behavior of males was predicted by nesting stage; males recorded on a day that their partner was laying sang at lower rates and were less likely to overlap songs with the challenged male. During early and late stages of breeding, males sang at high rates and showed no

predictable patterns of alternation or overlap with challenged males. Fewer females sang during the intruder-only treatment compared to control, noise-only, and intruder with noise treatments. Females may have been more likely to sing during the latter treatments if added noise in the territories of challenged males masked reception of signals. Our results suggest that singing patterns of neighboring male house wrens are synchronized with the fertility of their breeding partner, whereas females were less likely to sing when territorial challenges occurred within networks.

Between territories, reception of vocal signals by neighbors may be limited by distance and further constrained by noise masking (LaZerte, Slabbekoorn, & Otter, 2017; Pohl, Leadbeater, Slabbekoorn, Klump, & Langemann, 2012; Pohl, Slabbekoorn, Klump, & Langemann, 2009). The effects of noise masking will likely be greatest near the sound source, thus noise in close proximity to signalers may further limit detection and discrimination of acoustic signals by territorial neighbors within signaling networks. Indeed, noise appears to mask intrusions on challenged male territories and thereby affect detection by neighbors, as fewer female house wrens sang during the intruder-only treatment. By contrast, during the intruder treatment with added noise, females may not have altered their responses if they were unable to detect the songs of the challenged male. In response to noise, territorial males may reduce masking and increase the active space of their signals by adjusting signal amplitude or the frequency of songs (Halfwerk, Lohr, & Slabbekoorn, 2018). Such adjustments may only have a small impact on transmission distances (Nemeth & Brumm, 2010; Parris & McCarthy, 2013) and, as a result, may not improve signal detectability outside of their own territory. Therefore, in habitats that experience high levels of noise, the ability to detect and discriminate the signals of neighbors may decrease, resulting in social networks that are less connected by acoustic signaling interactions.

Vocal signals may convey similar information to both male and female conspecifics, but depending on the context, selection might favor sex-specific responses (Bradbury & Vehrencamp, 1998).

TABLE 1 Fixed effect coefficients and bootstrapped 95% confidence intervals from general and generalized linear mixed effects models testing the vocal responses of male and female house wrens to simulated territorial intrusions on their neighbor's territory

	Male song rate ^a			Vocal coordination ^a			Females that sing ^b		
	Est	Lower 95% CI	Upper 95%	Est	Lower 95% CI	Upper 95% CI	Est	Lower 95% CI	Upper 95% CI
Intercept	3.18	2.21	4.15	1.35	1.25	1.46	0.50	-0.94	2.07
Treatment: noise-only	0.29	-0.28	0.86	0.03	-0.10	0.16	-0.28	-1.56	0.97
Treatment: intruder + noise	0.18	-0.39	0.76	0.10	-0.08	0.16	-0.30	-1.63	0.83
Treatment: intruder-only	0.50	-0.07	1.11	0.03	-0.03	0.23	-1.22	-2.75	-0.15
Distance (m)	0.30	-0.15	0.72	-0.02	-0.06	0.03	0.46	-0.14	1.14
Ambient SPLs (dB)	-0.07	-0.41	0.28	-0.003	-0.05	0.04	-0.25	-0.93	0.30
Stage: Late	-1.42	-2.54	-0.33	0.002	-0.09	0.10	-0.04	-1.67	1.52
Stage: Laying	-2.77	-4.23	-1.33	-0.16	-0.30	-0.01	-0.16	-2.11	1.75

^aGeneral linear mixed effects models testing whether male singing rate (songs/min) or vocal coordination scores.

^bGeneralized linear mixed effect model (family = binomial, link = logit) testing whether females sang (yes = 1, no = 0) during treatments and the control.

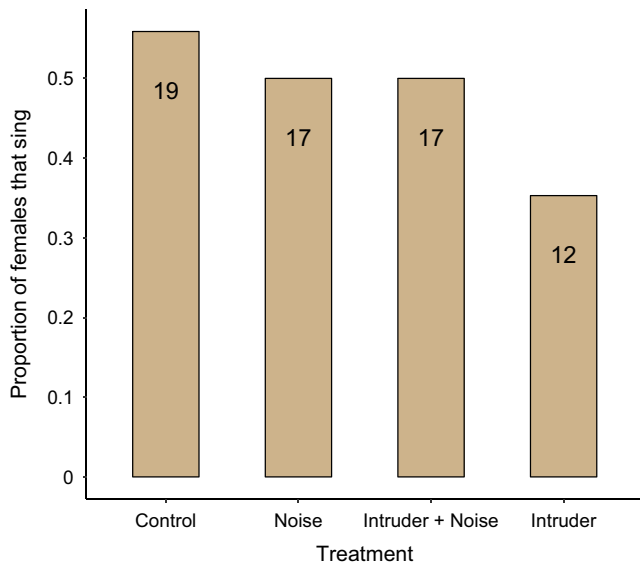


FIGURE 3 Fewer females sang during the intruder-only treatment compared to the control, noise-only, and intruder plus noise treatments. Bar height shows the proportion of females that sang during each treatment ($n = 34$) and values inside each bar indicate the number of females that sang during experiments

Female house wrens that ceased singing during intruder-only treatments may have been eavesdropping on the challenged male's response to the simulated intruder to guide either future reproductive or defense decisions. In a population of radio-tagged great tits (*Parus major*), neighboring females were attracted to interactions between simulated intruders and challenged males, moving closer to neighbors that responded aggressively, whereas males were repelled, moving farther away (Snijders et al., 2017). Female rock sparrows (*Petronia petronia*) responded to simulated courtship interactions on neighboring territories by spending more time at their nest box, but males did not change their behavior (Dabelsteen, Peake, Matessi, & McGregor, 2007). Females may perceive interactions between a neighboring male and fertile female as a threat to her own nest site and reproductive investment (Dabelsteen et al., 2007). In house wrens, intraspecific competition among males and females for mates and nest sites is common (Belles-Isles & Picman, 1986; Krieg & Getty, 2020). Following a successful territorial takeover, new males often destroy the eggs of the previous territory holder (Johnson & Kermott, 1989). Fewer females sang during intrusions, and while we did not observe them during these times, it is possible the females may have detected the interaction, ceased singing, and moved closer to their nest boxes to protect their reproductive investment.

Many male songbirds sing at high rates prior to mating, but adjust patterns of singing once they have attracted a breeding partner (Bradbury & Vehrencamp, 1998), giving fewer songs (Catchpole, 1973; Liu & Kroodsma, 2007) at lower amplitudes (Johnson & Kermott, 1991; Reichard, Rice, Schultz, & Schrock, 2013; Ritchison, 1995). In some species, males specifically adjust the structure and timing of songs according to the fertility of their breeding partner (Ballentine, Badyaev, & Hill, 2003; Bruni & Foote, 2014; Mace, 1987; Zhang, Celis-Murillo, & Ward, 2016). Male house wrens

with laying females sang fewer songs during experiments and were less likely to overlap or alternate songs with the challenged male. This pattern suggests that the fertility of female breeding partners, or mate guarding, may be more important to males than noise or intruders on neighboring territories. Behavioral adjustments that coincide the fertility of females may increase male fitness (Araya-Ajoy, Dingemanse, & Kempenaers, 2016), but whether males increase or decrease song rate, bout duration, or the structure of songs may be species specific (Gil, Graves, & Slater, 1999).

Evidence of vocal coordination among groups of birds is limited to species in which inter-individual spacing is small and all individuals have been recorded at the same stage of breeding. Lekking male long-billed hermits (*Phaethornis longirostris*) alternate songs during bouts of coordinated singing with other males that are advertising in close proximity, but the probability of overlap increases with increasing distance between males (Araya-Salas et al., 2017). Despite patterns of alternation, not all song bouts between pairs of hermits were coordinated; males actively adjusted the timing of songs during less than 50% of recorded bouts (Araya-Salas et al., 2017). Social factors may also play a key role in patterns of vocal coordination. Captive non-breeding zebra finches (*Taeniopygia guttata*) coordinated bouts of singing depending on group size and pairing status (Fernandez et al., 2017). In wild populations of birds, vocal coordination may only occur during early stages of breeding. For example, males may attend to the temporal singing patterns of other males and adjust their own singing patterns while they are advertising for mates. But additional energy expenditure to maintain coordinated song patterns with neighbors may not benefit males once paired. Moreover, the temporal window that we considered in this study (blocks of 10-min periods of singing) may be too short to detect vocal coordination, as evidence of coordination patterns have been found among groups of birds recorded over several hours and days (Araya-Salas et al., 2017; Fernandez et al., 2017; Taff, Patricelli, & Freeman-Gallant, 2014).

Although neighbor males during early and late nesting stages did not adjust the timing of their songs in response to treatments, they may instead alter their movements and use of their territories during intrusions on neighboring territories (Amy et al., 2010; Naguib et al., 2004; Snijders et al., 2017) or may adjust the composition or structure of their songs (Naguib, 2005). Depending on the strength of focal male responses, neighboring males may move away from shared territory boundary, avoiding costly physical interactions with a male that has recently protected his territory. Neighboring male great tits respond to intrusions on focal male territories by moving away from the simulated intrusion, and stronger responses from focal males resulted in stronger repulsion behaviors by neighbors (Snijders et al., 2017). Spatial responses may also depend on personality type, as male great tits with high exploration scores respond more quickly to simulated intruders, and the responses of neighbors depends on the personality type of the territorial male experiencing an intrusion (Amy et al., 2010). Alternatively, males with complex repertoires, such as house wrens, may alter the type of song or the frequency of song sung, matching that of a rival male. Such

responses may be regarded as aggressive (Searcy & Beecher, 2009) and may enable females to cross evaluate males signaling within networks (Logue & Forstmeier, 2008).

Anthropogenic noise masks long-distance vocal signals that birds use for mate attraction and territory defense. Abundant evidence exists that males adjust their signaling behavior in response to noise (Brumm & Zollinger, 2013), yet much less is known regarding perception of signals in noise and whether masking affects singing behavior of among groups of territorial callers. In this study, we considered both environmental and social conditions and found that added noise in the territories of challenged males affected the responses of female, but not male, neighbors. Fewer females sang during intruder-only treatments, suggesting that noise in the territories of challenged males may limit reception of signals. In contrast, nesting stage predicted singing patterns in males. Males did not immediately alter singing in response to intrusions on neighboring territories, but they may act later, adjusting their behavior instead in the days following an intrusion (Foote et al., 2011; Schmidt et al., 2007). Thus, environmental constraints on signal detection may affect male neighbor responses, but changes may only be detected over longer periods of time. Alternatively, males may be more in tune to within-pair interactions, adjusting their signaling behavior in accordance with their mate's breeding stage, rather than in response to changes in singing of established neighbors. Ultimately, monitoring both short and long-term interactions among male and female neighbors by measuring spatial and vocal behavior is important to fully understand the effects of anthropogenic noise pollution on signaling interactions in a social context.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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