Urban sparrows respond to a sexually selected trait with increased aggression in noise

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Animals modify acoustic communication signals in response to noise pollution, but consequences of these modifications are unknown. Vocalizations that transmit best in noise may not be those that best signal male quality, leading to potential conflict between selection pressures. For example, slow paced, narrow bandwidth songs transmit better in noise but are less effective in mate choice and competition than fast paced, wide bandwidth songs. We test the hypothesis that noise affects response to song pace and bandwidth in the context of competition using white-crowned sparrows (Zonotrichia leucophrys). We measure male response to song variation along a gradient of ambient noise levels in San Francisco, CA. We find that males discriminate between wide and narrow bandwidth songs but not between slow and fast paced songs. These findings are biologically relevant because songs in noisy areas tend to have narrow bandwidths. Therefore, this song phenotype potentially increases transmission distance in noise, but elicits weaker responses from competitors. Further, we find that males respond more strongly to stimuli in noisier conditions, supporting the ‘urban anger’ hypothesis. We suggest that noise affects male responsiveness to song, possibly leading to more territorial conflict in urban areas.

The acoustic adaptation hypothesis states that organisms will adapt their vocalizations to transmit best in their respective environments1,2. There are many studies supporting this hypothesis in natural soundscapes, with organisms changing the timing, amplitude, or frequency of vocalizations to maximize sound transmission to receivers3. More recently, research has shown that animals also adjust their signals to evolutionarily unprecedented anthropogenic soundscapes4, which can alter the acoustic window of optimal signal transmission5. This phenomena occurs across a variety of taxa, including mammals6, amphibians7, fish8,9, invertebrates10, and birds11. Bird song has the most accumulated evidence for an effect of anthropogenic noise on communication, with many species singing higher pitched songs in urban areas11.

Generated by machines – such as boats, cars, and industrial equipment – anthropogenic noise is typically loudest at low frequencies (<2 kHz), and often overlaps (i.e. masks) the lower frequency range of animal signals12. Masking can decrease the ability of receivers to detect or discriminate the information content of a signal13 and thus alter the behavioral response of the receiver. For example, masking noise decreases the ability of budgerigars (Melopsittacus undulatus) and zebra finches (Taeniopygia guttata) to discriminate between different calls13. Furthermore, great tits (Parus major) are less efficient at discriminating low frequency songs in urban noise14. Another study shows that female grey treefrogs (Hyla chrysoscelis) took longer to orient and approach male signals in masking noise, and their detection thresholds increased15. Therefore, masking noise can even lead to ‘evolutionarily inappropriate responses’ by receivers16, resulting in fitness costs to the signaler, the receiver, or both.

As songs in birds are often used for mate attraction and territory defense, environmentally induced modifications to signals may pose fitness costs and benefits17. In the context of mate choice, fertile females typically prefer low pitch songs when they can hear them, suggesting sexual selection on lower song frequencies via mate choice; however, in noisy conditions, females respond more to high pitch songs14,18. In the context of male-male competition, territorial males of several species respond less to urban associated increases in song minimum frequency11. These findings suggest that males that produce songs with higher minimum frequencies are less competitive, at least in areas with lower noise levels19. Therefore, noise can affect how signals are perceived, and acoustic adaptation may sometimes work in opposition to the preference or competitive function of the signal.
Birds adjust not only pitch but also many other features of song to urban noise levels, but the functional consequences of these changes remains poorly resolved. A loss of bandwidth due to changes in minimum but not maximum frequency in noisy areas has been reported in many species\(^{11,12}\). Northern cardinals (*Cardinalis cardinalis*) and gray catsbirds (*Dumetella carolinensis*) show a reduced bandwidth from changes in both minimum and maximum frequencies with increasing levels of noise\(^{19}\). City birds also change the rate or number of notes in noise, with some birds singing fewer notes\(^{11,21}\), or more of certain notes, like the twitter phrase of common blackbirds (*Turdus merula*)\(^{22}\). Acoustic adaptation theory posits that vocal signals are adapted to best travel in their given environment\(^{2,12}\). Thus, adjustments to bandwidth and trill rate in cities may be adaptations to transmit better in urban soundscapes, as slow trills and narrower bandwidths are less likely to degrade in ‘urban canyons’ (i.e., where buildings and other impervious structures become reverberating echo chambers)\(^{23–25}\), and narrow bandwidths require lower signal-to-noise ratios to be detectable\(^{33}\). However, variation in trill rate and bandwidth is also under sexual selection in the contexts of female mate choice and male-male competition\(^{36–39}\). Therefore, adjustments to trill rate and bandwidth via acoustic adaptation may interfere with a signaler’s ability to convey information to a receiver.

Broadband vocalizations of repeated notes (trills) are difficult to produce because many songbirds coordinate rapid vocal tract and beak movements to track dominant frequencies and filter out harmonics\(^{52–55}\). In birds with broadband trilled notes, there is a tradeoff between the rate of note production (trill rate) and note bandwidth. To sing slow trills, males can produce wide or narrow frequency bandwidths, because the timing between notes allows for mechanical movements of the bill, laryngeal muscles, and syrinx\(^{31–36}\). As a male increases his trill rate, timing between notes is decreased, and bandwidth is limited by mechanical constraints. A review across families of songbirds (Emberizidae, Cardinalidae, Fringillidae, and Passerellidae) found that this performance tradeoff forms a triangular distribution\(^{37}\), which has since been described in many other taxonomic groups\(^{26,29,38}\). How well a male can perform this tradeoff is called vocal deviation, and can be measured as the orthogonal deviation from an upper bound regression on this triangular distribution; a larger deviation score indicates lower performance, and a small deviation indicates higher performance\(^{39}\).

We lack an understanding of the communication function of vocal performance as measured by vocal deviation (hereafter, vocal performance) for sexual selection in the context of urban soundscapes. It is unknown whether this measure of vocal performance is a salient signal in areas of high anthropogenic noise, such as cities. Female birds and mammals prefer higher performance songs\(^{26,40–42}\). Males of various songbird species are able to discriminate between high and low performance\(^{27,31}\). However, no studies have considered selective pressures on vocal performance for signal transmission in conjunction with selective pressure for signals that inform receivers of signaler quality.

The Nuttall’s white-crowned sparrow (*Zonotrichia leucophrys nuttalli*; NWCS) is a good system in which to address this question because of previous work both on the function of vocal performance in male-male competition\(^{29,43}\), and on correlations between anthropogenic noise levels and variation in trill rate, bandwidth and vocal performance of their songs\(^{36,44,45}\). In previous studies, we found that male NWCS in both urban and rural areas respond more strongly to high performance than to much lower performance songs\(^{27}\). Further, males in rural areas respond equally to songs of similar vocal deviation, whether that vocal deviation is close to population average performance through increasing bandwidth or through increasing trill rate\(^{41}\). We do not know if this pattern of response holds in anthropogenic noise. In urban areas, NWCS adjust both trill rate and bandwidth in response to anthropogenic noise levels; males defending territories with higher than average noise levels (hereafter, noisier territories) produce songs with faster trill rates but narrower bandwidths than males on quieter territories and have lower performance songs\(^{29,45}\). Urban males also respond less to songs with narrower bandwidths\(^{27}\), yielding the hypothesis that noise-dependent adjustments of bandwidth and trill rate might have functional consequences, and that these consequences could vary with ambient noise levels.

Here, we test this hypothesis by measuring male response to variation in vocal performance as measured by vocal deviation across an urban gradient of noise, using NWCS breeding in San Francisco, CA U.S.A. We measure response to three stimulus treatments: 1) a high performance song with fast trill, wide bandwidth, 2) a lower performance song with fast trill, narrow bandwidth (typically found in noisier territories), and 3) a lower performance song with slow trill, wide bandwidth (typically found in quieter territories). We make several predictions about the importance and directional responses of males to vocal performance across noise conditions. First, we predict that males in noisier areas will not respond differently to wide bandwidth (high performance) and narrow bandwidth (low performance) songs, because noise masks low frequencies in the song, potentially making it difficult for males to detect differences in bandwidth. We predict that even in noisy conditions males will respond more to fast trill (high performance) than to slow trill (low performance) songs, as our urban birds are not found in ‘urban canyons’ which can mask fast trills. Based on studies finding stronger response to playback in cities\(^{36–38}\), we also predict that males will respond more strongly to song playback in noisier areas. Finally, we predict that as noise increases, discrimination between song types will be reduced, consistent with studies on other avian species\(^{31}\).

**Methods**

**Song recordings and stimuli.** We recorded songs in San Francisco using a Marantz PMD 661 digital recorder, Sennheiser omnidirectional microphone, and Saul Mineroff SME-1000 parabola from colorbanded males 2–3 years prior to conducting playbacks. The songs were recorded at 44.1 kHz sampling rate and stored as.wav files. To measure trill rate and bandwidth, we first resampled songs at 25 kHz and high pass filtered songs at 1500 Hz to remove noise below the range of NWCS songs. We then took trill minimum and maximum frequencies at –36 dB relative to the peak amplitude frequency from spectrograms (256 pt transform, frequency resolution: 97.7 Hz, 10.2 ms time resolution); this method captured variation in frequency bandwidth while excluding background noise\(^{47}\). We calculated frequency bandwidth as the difference between the maximum and minimum
frequencies, and trill rate as the average number of trill notes produced per second. We collected all song data in Signal 552. To calculate vocal performance, we used the published equation for the upper bound regression on a set of 1572 Emberizidae songs, $y = -0.124 \times + 7.5537$. We calculated vocal performance as the orthogonal deviation of each song from this upper bound regression, hereafter referred to as vocal deviation. Vocal deviation is one of many ways to calculate performance\(^53\–55\), and has been shown to be robust in Emberizids\(^56\).

From the measured recordings described above, we created San Francisco dialect stimuli for song playback experiments\(^57\). Songs selected for stimuli had high signal to noise ratios. From the recordings, we drew pairs of songs that differed naturally by at least 500 Hz in trill bandwidth and then manipulated each song to create a slow and a fast trill version. To create specific trill rates, we repeated the first trill note eight times with the desired spacing between notes. We made stimulus sets that consisted of three song treatments: (A) wide bandwidth, fast trill rate, (B) narrow bandwidth, fast trill rate, and (C) wide bandwidth, slow trill rate (Fig. 1). We calculated the necessary slow and fast trill rate for each stimulus set such that stimuli ‘wide bandwidth, slow trill rate’ and ‘narrow bandwidth, fast trill rate’ would have roughly the same vocal performance value (t-test, $t = 1.3$, d.f. = 32, $p = 0.2$; Table 1). Amplitude is known to affect male response to playback in this species\(^58\), thus we normalized stimuli amplitude in SIGNAL 5 52 and calibrated amplitude from the speaker at 1 meter to 81 dB with a Larson Davis 831 Sound Level Meter (PCB Piezotronics). All features of manipulated songs were within the normal range of songs for the San Francisco dialect\(^27\) (Table 1). We created 17 stimulus sets for trials based on the availability of high quality recordings with 500 Hz differences in bandwidth.

**Table 1.** A comparison of San Francisco songs and experimental stimuli for vocal deviation, trill rate, and bandwidth (range; mean ± SD). Ranges for San Francisco (SF) dialect are from Phillips & Derryberry (2017a).

| Song Type                                    | No. of songs | Vocal deviation (range) | Trill rate (Hz) | Bandwidth (Hz) |
|----------------------------------------------|--------------|-------------------------|-----------------|---------------|
| SF dialect                                   | 780          | 5.3–37.4; 22.2 ± 5.2    | 6.1–13.3; 9.2 ± 1.2 | 1690.4–5735.4; 2753.2 ± 648.8 |
| SF narrow bandwidth, fast trill stimuli       | 17           | 12.2–33; 23.9 ± 4.2     | 9.3–12.5; 11.4 ± 0.9 | 1975.7–4699.8; 3194.1 ± 563.8 |
| SF wide bandwidth, slow trill stimuli         | 17           | 10.9–32.3; 22 ± 4.2     | 6.1–6.67; 6.3 ± 0.2  | 2768.7–5424.1; 4034.6 ± 515.8 |
| SF wide bandwidth, fast trill stimuli         | 17           | 6.4–28.6; 16.7 ± 4.2    | 9.3–12.5; 11.4 ± 0.9 | 2768.7–5424.1; 4034.6 ± 515.8 |

**Playback experiment design.** We used repeated measures territorial playback experiments to test whether free-living adult males ($n = 22$) in urban environments responded differently to songs that varied in vocal performance and its component parts, trill rate and bandwidth. Territorial playback is a standard experimental design that simulates territorial intrusion by playing songs on subjects’ territories and measuring their behavioral response\(^57\). Subjects held territories in the Presidio of San Francisco (Golden Gate National Recreation Area) in the May 2016 breeding season (Fig. 2). Most males were colorbanded ($n = 18$), and all male territories were observed prior to playback to establish song perches and boundaries. Playbacks were conducted between sunrise and noon during the breeding season. We tested each male three times, once for each stimulus treatment; trials were conducted with at least 48 hours between trials to minimize habituation. Order of presentation was randomized across males. Neighbors were never tested on the same day, and we did not use songs from neighboring males as stimuli.
For each focal male, we observed song perches and determined the approximate location of the territory center. Before each trial, an inMotion iMT320 speaker (Altec Lansing) with an Apple iPod Nano (6th generation) was placed near the territory center on a platform 0.5 m above the ground. The same location was used each time the male was tested. We started the playback when the focal male was in view within 24 m of the speaker to ensure he was on his territory. Once a trial began, songs were broadcast at a typical song bout speed (6 songs/min).

During each trial, we recorded the male’s movement behaviors at 10-sec intervals. We recorded responses during a three-minute playback period and a six-minute post-playback period. Post-playback was examined because responses tend to vary most between stimuli during the post-playback period in white-crowned sparrows.60 The response variables therefore are latency to approach and approach distance to the speaker (m) during both playback and post-playback. We examine these two responses because approach distance is interpretable as likelihood to attack59,61,62 and latency to approach may serve as a proxy for an animal’s ability to detect a signal (following Kleist et al. 2016). To approximate distance measures, we placed a string radiating out from the speaker with distance categories marked with flagging tape. The distance categories used were 0–2 m, 2–4 m, 4–8 m, 8–16 m, and greater than 16 m. We used the median distance of each category and 24 m for the ‘greater than 16 m’ category to calculate the male’s average distance from the speaker during the playback and post-playback periods62.

Playback procedures were carried out in accordance with approved guidelines set by Tulane University Institutional Animal Care and Use Committee (protocol 0427-R), Bird Banding Laboratory Permit (23900), California State Collecting Permit (6799), Golden Gate National Recreation Area (GGNRA) Scientific Research and Collecting Permit (GOGA-00079), and San Francisco Parks and Recreation Permit (032014).

Ambient noise level measurements. We measured ambient noise levels within five minutes of playback experiments using a Larson Davis 831 Class 1 Sound level meter (PCB Piezotronics). We took readings for one minute in each cardinal direction for a total of 4 minutes, following published methods.63 Our values were recorded in LAeq, which accounts for noise fluctuations over time and adjusts for the range of audible noise for humans, which overlaps with that of songbirds.64

Statistical analyses. To assess the effects of noise, stimulus treatment, and potential interactions between noise and stimulus treatment on approach distance during playback and post-playback, we explored all combinations of the fixed effects of stimulus and noise using linear mixed-effect models implemented in lme465 and Akaike’s Information Criterion for small sample sizes, AIC.66 To examine directionality of response to fixed effects, we used post hoc Tukey t-tests for stimulus treatment and linear regression for territory noise. We examined the interaction between noise and stimulus because of our prediction that discrimination strength between stimuli would change with noise levels, which would result in different slopes for the relationship between noise and response for each stimulus treatment. We re-used 5 stimulus sets (stimulus sets: n = 17, total songs used as stimuli: n = 51; focal males: n = 22); thus, we included stimulus exemplar as a random effect in all models. Because males were tested with multiple stimuli in a repeated measures design, bird identity was also included as a random effect in all models. To examine relative variable importance, we averaged models within the 95% cumulative weight using MuMIn67–69. Response variables were log-transformed to meet model assumptions. To

Figure 2. Map of focal male territories in the Presidio, San Francisco, California, USA. Circles denote an individual male and the average territory noise across three measurements. Map created in ArcMap 10 (ESRI, Redlands, CA, USA) with ESRI world imagery (Sources: ESRI, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community).
account for multiple comparisons in post-hoc tests, we use Bonferroni correction, with $\alpha = 0.017$. We performed all statistical analyses in R.

Data availability. The datasets analyzed during the current study are available in the Supplemental Material.

Results

**Stimulus treatment and territory noise level affect playback approach distance.** AICc model selection supports that stimulus treatment + territory noise predicts approach distance during the playback period ($\text{AIC}_c = 164.4$, weight $= 0.46$, ER $= 39.56$, Table 2). The next supported model within 2 AICc includes only stimulus treatment (Table 2). A model average of the three models within the 95% cumulative weight shows stimulus treatment with a relative weight of 100%, territory noise level with a relative weight of 65%, and the interaction between the two has a relative weight of 16%. Post-hoc tests show playback approach distance is significantly closer to fast trill, wide bandwidth songs than to fast trill, narrow bandwidth songs ($t = 3.47$, $p < 0.001$) but not to slow trill, wide bandwidth songs ($t = 1.78$, $p = 0.17$; Fig. 3a). Males did not differ in their response to songs of similar vocal performance (i.e., fast trill, narrow bandwidth and slow trill, wide bandwidth songs; Tukey's t-test: $z = -1.67$, $p = 0.17$; Fig. 3a). Post-hoc tests show playback approach distance is significantly closer to fast trill, wide bandwidth songs than to fast trill, narrow bandwidth songs (Tukey's t-test: $z = 3.47$, $p < 0.001$) but not to slow trill, wide bandwidth songs (Tukey's t-test: $z = 1.78$, $p = 0.17$; Fig. 3a). Males did not differ in their response to songs of similar vocal performance (i.e., fast trill, narrow bandwidth and slow trill, wide bandwidth songs; Tukey's t-test: $z = -1.67$, $p = 0.21$; Fig. 3a). Post-hoc analysis also showed that males approached the playback speaker more closely as territory noise level increased across treatments ($\beta = -0.05$, $R^2 = 0.09$, $F_{1,44} = 6.24$, $p = 0.015$; Fig. 3b), but discrimination strength between high and low performance songs did not change with average territory noise ($\beta = 0.2$, $R^2 = 0.03$, $F_{1,42} = 1.6$, $p = 0.2$).

**Noise affects post-playback approach distance.** AICc model selection supports that territory noise predicts approach distance during the post-playback period ($\text{AIC}_c = 165.49$, weight $= 0.71$, ER $= 6.45$, Table 3).
Model averaging within the 95% cumulative weight shows the relative weight of territory noise across models was 88% and for stimulus treatment was 15%. Tukey’s post-hoc comparison of stimulus treatments showed no significant differences between all three treatments (Fig. 4a; all \( p > 0.05 \)). A post-hoc linear regression shows territory noise to be a significant predictor of male response, with males approaching more closely as noise increases (\( \beta = -0.05, R^2 = 0.095, F_{1, 64} = 6.17, p = 0.012 \); Fig. 4b).

Males tend to approach more quickly in noise. The top model for latency to approach had a fixed effect of territory noise (\( AIC_c = 176.98, \text{weight} = 0.65, \text{ER} = 2.9 \)), followed by the null model (\( AIC_c = 179.11, \text{weight} = 0.22 \)). A Type II ANOVA of the top model was significant (\( x^2 = 7.9, \text{d.f.} = 1, p = 0.03 \)). Tukey’s post-hoc comparison of stimulus treatments showed no significant differences between all three treatments in latency to approach (all \( p > 0.05 \)). A post-hoc linear regression shows territory noise weakly predicts latency to approach, with males tending to approach more quickly as noise increases (\( \beta = -0.3, R^2 = 0.095, F_{1, 64} = 6.17, p = 0.012 \); Fig. 4b).

**Discussion**

Overall, we find that urban male NWCS approach more closely to wide bandwidth than to narrow bandwidth songs, but they do not respond differently to fast and slow trills. These results are opposite of our predictions. Consistent with our predictions of a more aggressive response in noise, we found that territory noise level may affect response distance, especially during post-playback. As noise increases, males tend to approach more closely to stimulus songs during playback, and remain close or move closer after playback no matter which stimulus was played. We found weak support for a predicted interaction between stimulus treatment and territory noise levels during the playback period, and no support for an interaction during the post-playback period. These results suggest no decrease in discrimination strength between stimulus types in noisy conditions. Together, our findings indicate that urban males assess variation in bandwidth but not in trill rate, and that males defending noisier

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**Table 3. AIC\(_c\) model selection for post-playback approach distance.**

| Model                               | K   | \( AIC_c \) | \( \Delta AIC_c \) | \( w_i \) | Cumulative \( w_i \) |
|-------------------------------------|-----|-------------|---------------------|---------|----------------------|
| Noise                              | 5   | 165.49      | 0                   | 0.71    | 0.71                 |
| Stimulus + Noise                   | 7   | 168.74      | 3.24                | 0.14    | 0.85                 |
| Null                               | 4   | 169.19      | 3.69                | 0.11    | 0.96                 |
| Stimulus                           | 6   | 172.08      | 6.58                | 0.03    | 0.99                 |
| Stimulus + Noise + Stimulus*Noise  | 9   | 173.60      | 8.11                | 0.01    | 1                    |

**Figure 4.** Post-playback approach distance results. (a) Boxplot of approach distance for post-playback for three stimulus treatments: (A) fast trill, wide bandwidth (7.11 ± 0.96 m), (B) fast trill, narrow bandwidth (7.54 ± 1.41 m), and (C) slow trill, wide bandwidth (8.54 ± 1.19 m). All post-hoc comparisons between treatments \( p > 0.05 \). (b) Linear regression of male approach distance during post-playback and territory noise (\( \beta = -0.05, p = 0.012 \)).
Territories may be more likely to face costly fights, because a closer approach to an intruding male increases the probability of attack.

We find partial support for our hypothesis that noise-dependent adjustments of bandwidth and trill rate in urban populations have functional consequences. Specifically, males approached more closely to wide bandwidth songs than to narrow bandwidth songs during playback. A closer approach to a speaker in a male's territory is interpreted as a stronger response to that stimulus; thus, males respond more strongly to wide bandwidth songs. This finding is consistent with previous studies testing response to variation in song bandwidth in both urban and rural males, and supports the hypothesis that males producing narrower bandwidth songs have less potent signals in the context of male-male competition. Male white-crowned sparrows that defend noisier territories produce songs with significantly narrower bandwidth than males that defend quieter territories (Luther et al. 2016b). This trend is found in many urban species, such as song sparrows (Melospiza melodia), dark-eyed juncos (Junco hyemalis), great tits (Parus major), European robins (Erithacus rubecula), chipping sparrows (Spizella passerina), cardinals (Cardinalis cardinalis), and catbirds (Dumetella carolinensis). Thus, noise-dependent shifts in bandwidth have consequences for NWCS and potentially for other songbird species, at least in the context of territory acquisition and maintenance.

We found no support for our hypothesis that noise-dependent adjustments of trill rate affect transmission in city noise in this species. Work indicates that songs with higher minimum frequency and narrower bandwidth transmit over greater communication distances. It may be that males on noisy territories have a decreased response to simulated territory intrusions, and so this finding suggests that territory noise levels may also be a factor in song transmission.

The inability to detect songs during noisy times of day because low frequency songs do not transmit as well (Luther et al. 2016b) suggests no functional difference among the songs produced by males holding territories with different ambient noise levels. However, it is important to note that despite the increase in trill rate on noisier territories, urban males still produce songs of lower performance. Males do tend to approach more closely to wide bandwidth, slow trill songs than narrow bandwidth, fast trill songs (Fig. 2). Our playback experiment indicates that male receivers respond less to songs of lower performance, supporting that songs more typical of NWCS defending noisier territories are less potent than those of males defending quieter territories, on average.

Our hypothesis that the functional consequences of noise-dependent song adjustments vary with ambient noise levels was partially supported. We predicted that the strength of response to variation in vocal performance would decrease with increasing levels of ambient noise and that overall level of response to stimulus playback would increase. This can also be described as a ceiling effect such that as response increases to all stimuli, the difference in response to different stimuli will decrease. Although we did find a significant increase in the level of response to all stimuli with increasing levels of noise, we did not find a ceiling effect. There was no interaction between song treatment and ambient noise levels, indicating that response slopes did not vary among the song treatments. In other words, males are responding less to narrow bandwidth songs on both quiet and noisier territories, not just less on noisier territories.

We found that males on noisier territories come closer to all stimulus song types than do males on quieter territories. One interpretation of this result is that the urban environment, with particularly high levels of noise, may lead to overall higher aggression levels in cities, or so-called 'urban anger'. Increased aggression has been observed in urban birds, typically as measured by approach distance. However, the cause of urban anger has been elusive – studies have not found support for higher population density, available nesting habitat, or testosterone levels as predictors of aggression levels in urban males, although one study finds some support for food availability as a driver of urban aggression. We find that males on noisier territories approach more closely to simulated territory intrusions, and so this finding suggests that territory noise levels may also be a factor in increased levels of aggression in urban areas. It may be that males on noisy territories have a decreased response threshold caused by acoustic masking, which leads to unnecessary or inappropriately strong responses. Future experimental studies could test the effects of chronic noise on aggression levels, and if detection threshold patterns are similar in NWCS as in species previously tested.

Another interpretation of the finding that males approach songs more closely in noise is that males on noisier territories cannot detect song playbacks as readily as males on quieter territories. Detection is the ability of a bird to hear a sound at a certain distance whereas discrimination is the ability of a bird to tell the difference between sounds, or identify their characteristics. However, if males on noisier territories could not detect song playbacks as quickly as males on quieter territories, then we would expect a longer latency to approach in noise (e.g. Luther & Magnotti 2014; Kleist et al. 2016). Instead, we find that males on noisier territories tend to have a shorter latency to approach. In other words, males approach playbacks more quickly in noise. Thus, our findings suggest that males on noisier territories can detect song playbacks as readily as males on quiet territories but may not be
able to discriminate fine features of the song without approaching more closely. Thus, our results suggest that to assess song performance, males may have to approach more closely to enter the active space or listening distance (of the signal bandwidth). If a male cannot assess an intruding male without getting closer, both are more likely to incur a physical cost.

Lower performance songs have a greater communication distance in noise but are less salient in territorial intrusions. Some animals may be able to use tactical allocation to minimize this apparent cost of signaling in noise. Selection should favor males to be flexible within their performance range, such that they sing at their performance limit only when a female or intruder is nearby (thus reducing the communication distance and associated effects of sensory drive). When territorial males are not contending with nearby intruders or potential mates, producing a song with a lower performance value that transmits further may be beneficial, as increasing communication distance may outweigh any performance costs. This type of tactical allocation falls under the 'Maximizing Received Signal Hypothesis.' For example, house finches (Haemorhous mexicanus) display some syllable plasticity in pitch (Bermudez-Cuamatzin et al. 2008) and white-crowned sparrows show immediate flexibility in song production by varying number of trill notes based on motivation levels. However, a recent study shows male white-crowned sparrows do not change song pitch in real time in response to changing levels of noise, suggesting that they may not be able to adjust song bandwidth. However, if males in this species exhibit immediate flexibility in trill rate, then tactical allocation might be a solution to conflicting selection pressures from urban noise and male-male competition.

Although we have demonstrated that males holding territories with high ambient noise levels may bear a cost in singing lower performance songs in the context of male-male competition, we do not know what costs they may face in the context of female mate choice. Females in other songbirds prefer high performance songs, so urbanization of song may also affect female mate choice. It remains to be seen if female choice is affected by noise in NWCS. One study suggests that great tit females may respond less to high-pitched songs that have narrower bandwidth (i.e., lower performance songs; Halfwerk et al. 2011). Masking of songs has also been shown to alter female preference for a pair-bonded mate. Males may be able to negate a loss of female preference in noise by singing louder, moving closer to females, or by enhancing their performance via bandwidth when females are most fertile. Future studies examining whether preferences for song change in noisy anthropogenic conditions are essential.

Conclusions
Our study highlights a functional consequence of song modification in urban landscapes, particularly for birds with trilled vocalizations. Additionally, our study is the first to show that assessment of vocal performance, a known sexually selected trait, is at least partially affected by ambient noise levels. We found that males approach simulated intruders more closely in noisier conditions, suggesting an increase in the chance for territorial disputes as males assess sexual signals. Closer approach in noise may indicate increased aggression or the need for receivers to enter the active space of the signal to discriminate song characteristics—disentangling these two interpretations is an open field of inquiry. Future research is needed to examine these consequences in the context of other performance measures of song (song rate, repertoire size, amplitude) in additional species and across a wider range of soundscapes. As anthropogenic soundscapes become more the norm than the exception, understanding the impacts humans have on animal communication is critical.

References
1. Morton, E. S. Ecological sources of selection on avian sounds. Am. Nat. 109, 17–34 (1975).
2. Endler, J. A. Signals, signal conditions, and the direction of evolution. Am. Nat. 139, S125–S153 (1992).
3. Luther, D. & Gentry, K. Sources of background noise and their influence on vertebrate acoustic communication. Behaviour 150, 1–24 (2013).
4. Swaddle, J. P. et al. A framework to assess evolutionary responses to anthropogenic light and sound. Trends Ecol. Evol. 30, 550–560 (2015).
5. Wilkins, M. R., Seddon, N. & Safran, R. J. Evolutionary divergence in acoustic signals: causes and consequences. Trends Ecol. Evol. 28, 156–66 (2013).
6. Rabin, L. A., McCowan, B., Hooper, S. L. & Owings, D. H. Anthropogenic noise and its effect on animal communication: an interface between comparative psychology and conservation biology. Int. J. Comp. Psychol. 16, 172–192 (2003).
7. Parrish, K. M., Velik-Lord, M. & North, J. M. Frogs call at a higher pitch in traffic noise. Ecol. Soc. 14, 25 (2009).
8. Radford, A. N., Kerridge, E. & Simpson, S. D. Acoustic communication in a noisy world: can fish compete with anthropogenic noise? Behav. Ecol. 25, 1022–1030 (2014).
9. Slabbekoorn, H. et al. A noisy spring: the impact of globally rising underwater sound levels on fish. Trends Ecol. Evol. 25, 419–427 (2010).
10. Morley, E. L., Jones, G. & Radford, A. N. The importance of invertebrates when considering the impacts of anthropogenic noise. Proc. R. Soc. B 281 (2014).
11. Slabbekoorn, H. Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Anim. Behav. 85, 1089–1099 (2013).
12. Shannon, G. et al. A synthesis of two decades of research documenting the effects of noise on wildlife. Biol. Rev. 91, 982–1005 (2016).
13. Lohr, B., Wright, T. F. & Dooling, R. J. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. Anim. Behav. 65, 763–777 (2003).
14. Pohl, N. U., Leadbeater, E., Slabbekoorn, H., Klump, G. M. & Langemann, U. Great tits in urban noise benefit from high frequencies in song detection and discrimination. Anim. Behav. 83, 711–721 (2012).
15. Bee, M. A. & Swanson, E. M. Auditory masking of anuran advertisement calls by road traffic noise. Anim. Behav. 74, 1765–1776 (2007).
16. Wiley, R. H. In Behavioral Mechanisms in Ecology (ed. Real, L.) 157–189 (University of Chicago Press, 1994).
17. Catchpole, C. K. & Slater, P. J. B. Bird song: biological themes and variations. https://doi.org/10.1007/s13398-014-0173-7.2 (Cambridge University Press, 2008).
18. Halfwerk, W. et al. Low-frequency songs lose their potency in noisy urban conditions. Proc. Natl. Acad. Sci. 108, 14549–14554 (2011).
19. Dowling, J. L., Luther, D. A. & Marra, P. P. Comparative effects of urban development and anthropogenic noise on bird songs. Behav. Ecol. 23, 201–209 (2011).
20. Job, J. R., Kohler, S. L. & Gill, S. A. Song adjustments by an open habitat bird to anthropogenic noise, urban structure, and vegetation. Behav. Ecol. 27, 1734–1744 (2016).
21. Cartwright, L. A., Taylor, D. R., Wilson, D. R. & Chow-Fraser, P. Urban noise affects song structure and daily patterns of song production in Red-winged Blackbirds (Agelaius phoeniceus). Urban Ecosyst. 17, 561–572 (2014).
22. Slabbekoorn, H. & den Boer-Vosser, A. Cities change the songs of birds. Curr. Biol. 16, 2326–2331 (2006).
23. Warren, P. S., Katti, M., Ermann, M. & Brael, A. Urban bioacoustics: it’s not just noise. Anim. Behav. 71, 491–502 (2006).
24. Wiley, R. H. & Richards, D. G. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav. Ecol. Sociobiol. 3, 69–94 (1978).
25. Gall, M. D., Ronald, K. L., Bestrom, E. S. & Lucas, J. R. Effects of habitat and urbanization on the active space of brown-headed cowbird song. J. Acoust. Soc. Am. 132, 4053–62 (2012).
26. Paasch, B., George, A. S., Campbell, P. & Phelps, S. M. Androgen-dependent male vocal performance influences female preference in Neotropical singing mice. Anim. Behav. 82, 177–183 (2011).
27. Phillips, J. N. & Derryberry, E. P. Vocal performance is a salient signal for male-to-male competition in white-crowned sparrows. Auk 134, 1–11 (2017).
28. Luther, D. A., Phillips, J. & Derryberry, E. P. Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. Behav. Ecol. 27, 332–340 (2016).
29. Moseley, D. L., Lahti, D. C. & Podos, J. Responses to song playback vary with the vocal performance of both signal senders and receivers. Proc. R. Soc. B 280 (2013).
30. Dubois, A. L., Nowicki, S. & Searcy, W. A. Discrimination of vocal performance by male swamp sparrows. Behav. Ecol. Sociobiol. 65, 717–726 (2011).
31. Podos, J., Lahti, D. C. & Moseley, D. L. In Advances in the Study of Behavior (ed.Behavioral, M. N. K. Z. N. S. C. V. M. J. B. T.-A. in the S. of Volume 40, 159–195 (Academic Press, 2009).
32. Westneat, M. W., Long, J. H. Jr., Hose, W. & Nowicki, S. Kinematics of birdsong: functional correlation of cranial movements and acoustic features in sparrows. J. Exp. Biol. 182, 147–171 (1993).
33. Podos, J. Motor constraints on vocal development in a songbird. Anim. Behav. 51, 1061–1070 (1996).
34. Hoeve, W., Podos, J., NC, B. & Nowicki, S. Vocal tract function in birdsong production: experimental manipulation of beak movements. J. Exp. Biol. 203, 1845–1855 (2000).
35. Riede, T., Suthers, R. A., Fletcher, N. H. & Blevins, W. E. Songbirds tune their vocal tract to the fundamental frequency of their song. JNABS 103, 5543–5548 (2006).
36. Nowicki, S., Searcy, W. A. & Peters, S. Brain development, song learning and mate choice in birds: A review and experimental test of the ‘nutritional stress hypothesis’. J. Comp. Physiol. A Neuroethol. Sensory, Neural, Behav. Physiol. 188, 1003–1014 (2002).
37. Podos, J. A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). Evolution (N. Y.) 51, 537–551 (1997).
38. Derryberry, E. P. Ecology shapes birdsong evolution: variation in morphology and habitat explains variation in white-crowned sparrow song. Am. Nat. 174, 24–33 (2009).
39. Podos, J. Correlated evolution of morphology and vocal signal structure in Darwin’s finches. Nature 409, 185–188 (2001).
40. Dragoonio, T. I., Nagle, L. & Kreutzer, M. Directional female preference for an exaggerated male trait in canary (Serinus canaria) song. Proc. R. Soc. B 269, 2525–2531 (2002).
41. Ballentine, B., Hyman, J. & Nowicki, S. Vocal performance influences female response to male bird song: an experimental test. Behav. Ecol. 15, 163–168 (2004).
42. Caro, S. P., Sewall, K. B., Salvanite, K. G. & Sockman, K. W. Female Lincoln’s sparrows modulate their behavior in response to variation in male song quality. Behav. Ecol. 21, 562–569 (2010).
43. Phillips, J. N. & Derryberry, E. P. Equivalent effects of bandwidth and trill rate: support for a performance constraint as a competitive signal. Anim. Behav. 132, 209–215 (2017).
44. Davidson, B. M., Antonova, G., Dlott, H., Barber, J. R. & Francis, C. D. Natural and anthropogenic sounds reduce song performance: insights from two emberizid species. Behav. Ecol. 0, 1–9 (2017).
45. Luther, D. A. & Derryberry, E. P. Birdsongkeep pace with city life: changes in song over time in an urban songbird affects communication. Anim. Behav. 83, 1059–1066 (2012).
46. Scales, J., Hyman, J. & Hughes, M. Behavioral Syndromes Break Down in Urban Song Sparrow Populations. Ethology 117, 887–895 (2011).
47. Evans, J., Boudreau, K. & Hyman, J. Behavioural Syndromes in Urban and Rural Populations of Song Sparrows. Ethology 116, 588–595 (2010).
48. Scales, J., Hyman, J. & Hughes, M. Fortune favours the aggressive: territory quality and behavioural syndromes in song sparrows, Melospiza melodia. Anim. Behav. 85, 441–451 (2013).
49. Foltz, S. L. et al. Behavioral Get off my lawn: increased aggression in urban song sparrows is related to resource availability. Behav. Ecol. 26, 1548–1557 (2015).
50. Davies, S. & Sewall, K. B. Agonistic urban birds: elevated territorial aggression of urban song sparrows is individually consistent within a breeding period. Biol. Lett. 12, 133–143 (2016).
51. Luther, D. A. & Magnotti, J. Can animals detect differences in vocalizations adjusted for anthropogenic noise? Anim. Behav. 92, 111–116 (2014).
52. Beevan, K. In Animal Acoustic Communication: Sound Analysis and Research Methods (eds Hopp, S. L., Owren, M. J. & Evans, C. S.) (Springer-Verlag, 1998).
53. Cardoso, G. C., Atwell, J. W., Ketterson, E. D. & Price, T. D. Song types, song performance, and the use of repertoire in dark-eyed junco (Junco hyemalis). Behav. Ecol. 20, 901–907 (2009).
54. Forstmeier, W., Kempenaers, B., Meyer, A. & Leisler, B. A Novel song parameter correlates with extra-pair paternity and reflects male longevity. Proc. R. Soc. B 269, 1479–1485 (2002).
55. Podos, J. et al. A fine-scale, broadly applicable index of vocal performance: Frequency excursions. Anim. Behav. 116, 203–212 (2016).
56. Wilson, D. R., Bitton, P., Podos, J. & Mennill, D. J. Uneven sampling and the analysis of vocal performance constraints. Am. Nat. 183, 214–28 (2014).
57. Baptista, L. E. Song dialects and demes in sedentary populations of the white-crowned sparrow (Zonotrichia leucophrys natalii). Univ. Calif. Publ. Zool. 105 (1975).
58. Luther, D. A., Danner, R., Danner, J., Gentry, K. & Derryberry, E. P. The relative response of songbirds to shifts in song amplitude and song minimum frequency. Behav. Ecol. 28, 391–397 (2016).
59. McGregor, P. K. et al. In Playback and Studies of Animal Communication (ed. McGregor, P.) 1–9 (Penum Press, 1992).
60. Nelson, D. A. & Solha, J.A. Perception of geographical variation in song by male Puget Sound white-crowned sparrows, Zonotrichia leucophrys pugetensis. Anim. Behav. 68, 395–405 (2004).
61. Searcy, W. A., Anderson, R. C. & Nowicki, S. Bird song as a signal of aggressive intent. Behav. Ecol. Sociobiol. 60, 234–241 (2006).
62. Peters, S. S., Searcy, W. A. & Marler, P. Species song discrimination in choice experiments with territorial male swamp and song sparrows. Anim. Behav. 28, 393–404 (1980).

SCIENTIFIC REPORTS | (2018) 8:7509 | DOI:10.1038/s41598-018-25834-6
63. Brumm, H. The impact of environmental noise on song amplitude in a territorial bird. J. Anim. Ecol. 73, 434–440 (2004).
64. Rossing, T. D. Springer Handbook of Acoustics. (Springer, 2007).
65. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48 (2015).
66. Mazerolle, M. J. AICmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0–4. 1–158 (2016).
67. Barton, K. MuMIn: Multi-model inference. R package version 1.0. 0. (2011).
68. Burnham, K. P. & Anderson, D. R. Model selection and multimodal inference. (Springer, 2002).
69. Arnold, T. W. Uninformative parameters and model selection using Aikake's Information Criterion. J. Wildl. Manage. 74, 1175–1178 (2010).
70. R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing 1, 409 (2011).
71. Wood, W. E. & Yezierinc, S. M. Song sparrow (Melospiza melodia) song varies with urban noise. Auk 123, 650–659 (2006).
72. Slabbekoorn, H., Yeh, P. & Hunt, K. Sound transmission and song divergence: a comparison of urban and forest acoustics. Condor 109, 67–78 (2007).
73. Hamao, S., Watanabe, M. & Mori, Y. Urban noise and male density affect songs in the great tit Parus major. Ethol. Ecol. Evol. 23, 111–119 (2011).
74. Montague, M. J., Danek-Gontard, M. & Kunc, H. P. Phenotypic plasticity affects the response of a sexually selected trait to anthropogenic noise. Behav. Ecol. 24, 343–348 (2012).
75. Botero, C. A. et al. Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. Anim. Behav. 77, 701–706 (2009).
76. DuBois, A. L., Nowicki, S. & Searcy, W. A. Swamp sparrows modulate vocal performance in an aggressive context. Biol. Lett. 5, 163–5 (2009).
77. Illes, A. E., Hall, M. L. & Vehrencamp, S. L. Vocal performance influences male receiver response in the banded wren. Proc. R. Soc. B 273, 1907–12 (2006).
78. Derryberry, E. P. et al. Patterns of song across natural and anthropogenic soundscapes suggest that white-crowned sparrows minimize acoustic masking and maximize signal content. PLoS One 1–17 https://doi.org/10.1371/journal.pone.0154456 (2016).
79. Wiley, R. H. Signal detection and animal communication. Adv. Study Behav. 36, 217–247 (2006).
80. Leonard, M. L., Orn, A. G. & Mukhid, A. False alarms and begging in nestling birds. Anim. Behav. 69, 701–708 (2005).
81. Pohl, N. U., Slabbekoorn, H., Klump, G. M. & Langemann, U. Effects of signal features and environmental noise on signal detection in the great tit, Parus major. Anim. Behav. 78, 1293–1300 (2009).
82. Kleist, N. J., Guralnick, R. P., Cruz, A. & Francis, C. D. Anthropogenic noise weakens territorial response to intruder's songs. Ecosphere 7, 1–11 (2016).
83. Nemeth, E. et al. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. Proc. R. Soc. B 280, 20122798 (2013).
84. Patricelli, G. L., Krakauer, A. H. & Taff, C. C. Variable signals in a complex world: Shifting views of within-individual variability in sexual display traits. Adv. Study Behav. 48, 319–386 (2016).
85. Nelson, D. A. & Poesel, A. Responses to variation in song length by male white-crowned sparrows. Ethology 118, 24–32 (2012).
86. Derryberry, E. P. et al. White-crowned sparrow males show immediate flexibility in song amplitude but not in song minimum frequency in response to changes in noise levels in the field. Ecol. Evol. 7, 4991–5001 (2017).
87. Swaddle, J. P. & Page, L. C. High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. Anim. Behav. 74, 363–368 (2007).

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Author Contributions
J.N.P. and E.P.D. both contributed to the concept and design of experiments. J.N.P. conducted all experiments, analyzed data, and wrote the manuscript. E.P.D. helped with manuscript revision and both authors gave final approval.

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