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Eastern Bluebirds Alter their Song in Response to Anthropogenic Changes in the Acoustic Environment

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Synopsis Vocal responses to anthropogenic noise have been documented in several species of songbird. However, only a few studies have investigated whether these adjustments are made in “real time” or are longer-term responses to particular soundscapes. Furthermore, increased ambient noise often is accompanied by structural changes to the habitat, including the introduction of noisy roadways and the removal of native vegetation. To date, no studies have simultaneously investigated the impact of both acoustic and structural disturbance on the same species. The relevance of each of these variables must be quantified if we wish to refine our understanding of the ways in which human activities influence avian communication. In this study, we quantified both among-male and within-male adjustments of song in response to ambient noise, and also investigated whether anthropogenic modifications of the habitat explained variations in songs’ parameters. Recordings of songs were collected from male, breeding eastern bluebirds (*Sialia sialis*) residing in a network of nestboxes distributed across a gradient of anthropogenic disturbance. Levels of ambient noise were associated both with the average song-parameters of each male and with the change in a male’s song-parameters between the loudest and quietest periods at his nest box. Males’ song parameters were also related to habitat structure, as assessed using geographic information systems techniques. Males in noisier sites produced both higher-pitched and louder songs than did birds in quieter areas. Likewise, individual males demonstrated immediate adjustments to disturbance by noise, increasing the amplitude of their song between periods of quiet and loud ambient noise. Both spectral and temporal aspects of a male’s song were related to whether his habitat was more “natural” or “anthropogenic.” Our results indicate that males’ adjustments of song may represent simultaneous responses to multiple modifications of the habitat by humans. However, we also conclude that biotic noise remains an important influence on avian signals even in anthropogenic areas. We suggest that human habitats provide an ideal setting in which to perform experiments on communication strategies, with resulting data poised to reveal underlying evolutionary processes while also informing conservation and management.

Introduction

Vocal responses to anthropogenic noise have been documented both in aquatic and terrestrial species (Rabin and Greene 2002; Patricelli and Blickley 2006; Warren et al. 2006; Slabbekoorn and Ripmeester 2008; Slabbekoorn et al. 2010). Among terrestrial animals, birds have been particularly well studied. Avian responses to noise-pollution by humans include altering the frequency (Slabbekoorn and Peet 2003; Fernández-Juricic et al. 2005; Slabbekoorn and den Boer-Visser

2006; Wood et al. 2006; Bermúdez-Cuamatzin et al. 2009; Nemeth and Brumm 2009; Francis et al. 2010; Hu and Cardoso 2010; Potvin et al. 2011; Goodwin and Podos 2013; Slabbekoorn 2013), amplitude (Brumm 2004b; Lowry et al. 2012), and composition (Slabbekoorn and Peet 2003; Fernández-Juricic et al. 2005; Slabbekoorn and den Boer-Visser 2006; Wood et al. 2006) of songs, as well as changing the time of day during which songs are performed (Fuller et al. 2007).

Birds in noisy areas may consistently produce vocalizations that differ from those of their counterparts in quieter habitats; however, several species show within-individual flexibility, making signal-adjustments in real time (Bermúdez-Cuamatzin et al. 2009; Halfwerk and Slabbekoorn 2009; Verzijden et al. 2010; Hanna et al. 2011; Montague et al. 2013). In both scenarios, the vocal alterations help birds avoid masking the signal, which occurs when high-amplitude sounds (e.g., car traffic) obscure lower-amplitude sounds (e.g., birds' vocalizations) that occur within the same frequency bandwidth (Klump 1996). By reducing acoustic overlap between their signals and ambient noise, signalers can improve, or at the very least maintain, the odds that receivers will be able to detect their vocalizations and respond accordingly (Wiley 1994).

Reception of the signal is also affected by the physical structure of the habitat through which sound waves travel (Morton 1975; Wiley and Richards 1978)—a relationship that has received some attention in natural habitats (e.g., Dabelsteen et al. 1993; Forrest 1994; Nemeth et al. 2001) but which has received less attention in human-altered areas (Warren et al. 2006; but see Kight et al. 2012a; Swaddle et al. 2012). Anthropogenic modifications of habitat may add new sources of reverberation (e.g., buildings), remove objects formerly responsible for attenuation (e.g., trees), and reduce the number of perches available for optimal height from which to deliver songs (Nemeth et al. 2001). Even if the total number, placement, and proximity of habitat structures remains approximately the same, humans often replace natural materials such as wood and foliage with metal, glass, and cement—all of which can alter the amount of reverberation and attenuation of ambient noises (Warren et al. 2006).

Because selection should favor the use of signals that can be most easily detected by the intended receivers, birds in closed and open habitats should produce songs with consistently different temporal and spectral properties—the acoustic adaptation hypothesis (Morton 1975; Marten and Marler 1977; Boncoraglio and Saino 2007). Likewise, it follows that signalers should produce vocalizations that receivers are capable of detecting against local ambient noise (Lohr et al. 2003; Brumm 2004b). Taken together, then, these two predictions suggest that the recent ecological modifications associated with urbanization and increased expansion by humans could have serious impacts on signals' efficacy, thereby acting as a selective force on avian vocalizations.

A few studies only, to our knowledge, have analyzed the presence of both noise and structural disturbance while investigating differences in the production and/or transmission of birds' song in humans' habitats (Fernández-Juricic et al. 2005; Leader et al. 2005; Slabbekoorn et al. 2007). All three studies focused mainly on the effects of noise, although noting that noise and habitat-structure often simultaneously vary, either within anthropogenic habitats (Fernández-Juricic et al. 2005; Leader et al. 2005) or between anthropogenic and natural areas (Slabbekoorn et al. 2007). Furthermore, this research did not take into consideration the fact that features of the habitat and level of ambient noise may be related (Habib et al. 2007; Bayne et al. 2008), which makes it difficult to assess the cause of modifications in avian song.

Here, we present the results of a study investigating whether, and how, a breeding songbird adjusts its song-parameters in response to both auditory and physical disturbance by humans. We examined adult male eastern bluebirds (*Sialia sialis*) breeding in nestboxes across a gradient of anthropogenic disturbance. We measured average ambient noise and variation in environmental noise within each breeding territory. Correspondingly, we collected recordings of songs from each resident male in order to assess both among-male and within-male variation in song-parameters in association with ambient noise. We also quantified habitat structure and composition so that we could relate the physical features of breeding territories both to ambient levels of noise and the song-parameters of males. Cumulatively, these analyses were designed to reveal potential adaptations of bluebirds to acoustic disturbance, thereby improving our ability to predict how similar species might fare in increasingly anthropogenic environments.

We hypothesized that males in noisier territories would display altered vocalizations. Specifically, we predicted that males in noisier sites would sing louder (greater amplitude) and at a higher pitch (frequency) (Brumm and Zollinger 2011). Because of the increased energetic demands of these louder songs, we also predicted that males at noisier sites would increase their internote intervals, decrease the number of their songs' elements, and decrease overall lengths of songs. Similarly, we hypothesized that each male would adjust his song dynamically to background noise (Brumm and Todt 2002; Verzijden et al. 2010). Specifically, a male in a noisier setting (compared with a quieter one at the same location) would show similar adjustments in vocalizations: a louder song at a higher pitch, with increased

internote intervals, decreased number of song-elements, and decreased overall length of song. We also hypothesized that habitat structure would influence males' song-parameters. We predicted that habitats with more vertical and acoustically hard surfaces, which would cause reverberation, would be associated with songs of higher frequency and longer internote intervals, as reverberation would affect these songs less than those that were lower in frequency with shorter internote intervals.

Materials and methods

Species studied and description of the site

We studied breeding eastern bluebirds occupying nest-boxes across a gradient of disturbance in Williamsburg, VA, USA. The 60 territories reported upon here are part of a 400-box network that has been studied since 2003 (LeClerc et al. 2005; Kight and Swaddle 2007; Cornell et al. 2011; Kight et al. 2012b). Previous work indicates that territories do not vary significantly in available food, and that there is little systematic variation in the relative size and body condition of breeding adults (LeClerc et al. 2005; Burdge 2009; Hubbard 2009; J. P. Swaddle, unpublished data). Results of previous studies examining differences in the proximity, amount, and type of anthropogenic disturbance at each site (Kight 2005; Kight and Swaddle 2007), as well as the propagation of sound within each site (Kight 2009; Kight et al. 2012a), indicate that the boxes sampled in this study are representative of nearly the entire available range of anthropogenic ambient noise.

Eastern bluebirds are particularly interesting to study in the context of ambient noise because they are known to nest in close proximity to humans (Gowaty and Plissner 1998) and to be rather tolerant of a variety of disturbances by humans (Kight 2005; Kight and Swaddle 2007). Perhaps more importantly, their vocalizations occur almost exclusively within the 2–5-kHz range, while anthropogenic noise occurs most prominently in the 1–3-kHz range (Huntsman and Ritchison 2002; Slabbekoorn and Peet 2003). In addition to this overlap in bandwidth, bluebirds tend to have rather low-amplitude songs in comparison to many other songbirds (Huntsman and Ritchison 2002; C. R. Kight, unpublished data), which is likely to make them particularly susceptible to masking by noise-pollution unless they communicate over very short distances.

Recording of males' songs and ambient noise

Recordings of singing, male eastern bluebirds were collected during the breeding seasons of 2007 ($n=28$) and 2008 ($n=32$). Because males were

given unique combinations of colored leg-bands we were able to identify repeat singers. In our area, male eastern bluebirds sing sporadically throughout the day, beginning as early as 0600 h and singing as late as 1800 h. Preliminary observations indicated no obvious quantitative differences in songs performed at different times of day (C. R. Kight, unpublished data); thus, samples for each male were collected throughout this vocally active period. All recordings were collected by C.R.K. during the nest-building phase of the breeding season. Once eggs were laid, all males stopped singing until their chicks were fledged.

Rather than record spontaneous songs for each male, we used playback to stimulate vocal performances, thus standardizing the techniques of data collection and minimizing the likelihood that among-male variations are a result of differences in motivation (Marler and Slabbekoorn 2004). We created a single stimulus-song for playback, constructed of samples of songs obtained from the Borror Acoustic Laboratory (Columbus, OH, USA). Each sample was originally recorded several decades prior to our study, from a single bird living more than 10,000 km away. Thus, the stimulus should have been equally unfamiliar to all males in our population. We broadcast the song using an Apple iPod (Cupertino, CA, USA) connected to a set of Sony SRS T70 personal travel speakers (Tokyo, Japan). The playback was approximately 4 min long, but was paused at whatever point the focal male began singing. If the male stopped singing before the recording quota was met (see below), C.R.K. resumed a broadcast of the stimulus. However, if the male refused to sing after two full repeats of the playback, the attempt to record his song was abandoned for that day.

The procedure for recording was as follows. We broadcasted the playback recording from the location of a male's nestbox. Once the focal male began singing, the playback was paused and we began recording the territorial male, using a Sennheiser ME65 directional microphone with windscreen (Wedemark, Germany), and a Marantz PMD660 solid-state recorder (Kanagawa, Japan) on the 44.1 kHz setting recording at 64 kbps. Recordings continued for as long as the male would sing, with 1 min set as a minimum recording-length. Many males changed perches as they sang, typically making a gradual circuit around the nestbox. As the males moved, we adjusted the direction of the microphone and recorded the new height and distance of each perch. These values were used to assess the actual distance to each male so that all values of amplitude

(see below) reflect the calculated volume at 1 m from the singing bird. We analyzed recordings only when the focal male was facing the microphone (approximately ± 45 degrees, to ensure that the directional microphone recorded sounds at peak amplitude from the male) (cf. Patricelli et al. 2008). Prior to recordings we calibrated the microphone and recorder using tones of known amplitude and frequency, recorded at known distances from the source of the sound, and that were broadcast in a soundproof room. This calibration allowed us to convert the levels of sound pressure that were recorded in the field to amplitudes at a 1 m distance from the source of the sound (e.g., a male that was singing).

For each male, we selected two songs for analysis. These were the vocal performances occurring when environmental noise was lowest and highest. Recordings were visualized both as spectrograms and as power spectra and analyzed by hand using RavenPro 1.3 acoustic software (Cornell Laboratory of Ornithology, Ithaca, NY, USA). All recordings were analyzed in a consistent manner. In preparation for these analyses we bandpass-filtered recordings of males' vocalizations to cut out extraneous noise that was either below or above the frequency of their songs. These limits were most common at 2 and 4 kHz, respectively, although some males were filtered at other frequencies if their songs were outside this range.

For each song, we measured the following characteristics: overall length of song, internote interval, total number of song-elements, internote distance, minimum frequency, maximum frequency, peak frequency (frequency with the greatest power, hereafter discussed as "emphasis"), range of frequency, and average amplitude of RMS. We isolated the RMS amplitude of song from that of overall song + noise (Bradbury and Vehrencamp 2011) and then standardized the amplitudes to the equivalent of transmission over a 1-m distance, following the methods of Brumm (2004b). These calculated values were converted to dB SPL for figures. These parameters were chosen because they were identified previously as traits likely to be adjusted in response to ambient noise (Slabbekoorn and Peet 2003; Fernández-Juricic et al. 2005; Wood et al. 2006; Slabbekoorn et al. 2007; Bermúdez-Cuatatzin et al. 2009; Francis et al. 2010; Potvin et al. 2011; Lowry et al. 2012).

We used principal components analysis (PCA) to reduce variables to a more manageable number and to account for the natural correlations among the metrics of our songs. The analysis returned four principal components (PCs) with $\lambda > 1$, explaining

Table 1 Loading factors for PCA of the song-parameters of male eastern bluebirds

| Variable | Song PC1 (32.3%) | Song PC2 (18.2%) | Song PC3 (15.2%) | Song PC4 (12.5%) |
|-------------------------|---------------------|---------------------|---------------------|---------------------|
| Song length | 0.560 | -0.707 | 0.063 | 0.017 |
| Number of song elements | 0.531 | -0.700 | -0.057 | 0.057 |
| Internote distance | 0.181 | -0.221 | 0.733 | -0.141 |
| Minimum kHz | -0.598 | -0.313 | -0.306 | 0.031 |
| Maximum kHz | 0.833 | 0.353 | -0.151 | -0.082 |
| Peak kHz | 0.164 | -0.197 | -0.714 | -0.400 |
| kHz range | 0.906 | 0.393 | -0.034 | -0.072 |
| Average RMS amplitude | -0.227 | -0.010 | 0.207 | -0.897 |

Note: Percentages indicate the amount of variance accounted for by each PC.

a total of 78.2% of the variance (Table 1). PC1 (32.3% of variance) predominantly comprised the characteristics of frequency, loading highly positively both for maximum frequency and for range in frequency. Hereafter, we will refer to this PC as higher-pitched. The second PC (18.2% of variance) loaded negatively both for length of song and for number of song-elements, but did not load strongly for any other parameters. We have named this PC shorter songs. PC3 (15.2% of variance) loaded positively for internote distance and negatively for peak frequency. This indicates songs with a slower pace/lower emphasis. Finally, the fourth PC (12.5% of variance) loaded negatively for amplitude. Hereafter, we will call this PC quieter. Component scores met assumptions of sphericity.

We evaluated the ambient noise from these same recordings. We measured amplitude of RMS (converted to dB SPL for figures) and peak frequency of environmental noise in samples occurring 0.05 s directly before each song began. This length of recording was chosen as it approximates the average amount of space between syllables of bluebirds' songs (see Results), and thus the length of time over which a male might detect, and respond to, variations in ambient noise. We compared these directional recordings of ambient noise with those we also obtained through 360-degree recordings (in 45-degree increments) at the same sites using the same recordings equipment and found strong accordance between the techniques. There was also strong accordance with sound pressure meter recordings, performed at select sites. Therefore, as we were interested in assessing males' rapid adjustments of song to current noise levels we analyzed the data obtained

from the single directional recordings as these rendered noise estimates that occurred immediately before and after the vocalizations. We also found these short samples of ambient noise to be representative of other recordings at the same site during the same recording session. As with the characteristics of males' songs, we used PCA to condense variables. The analysis yielded a single PC explaining 51.2% of the variance. This PC loaded negatively for amplitude of noise (-0.715) and positively for peak frequency (0.715), indicating that quieter noises tended to have a higher frequency emphasis, while louder noises tended to have a lower frequency emphasis. Hereafter, we will refer to this ambient noise PC as decreased noise, since increasingly high PC values indicate quieter, higher-pitched sounds.

We also compared power spectra both for male's song and for environmental noise in order to calculate a metric of signal-to-noise ratio (SNR). We extracted spectral data for environmental noise from a spectrogram-slice occurring halfway (in time) through the 0.05-s clip of ambient noise; spectral data for the songs of males were extracted from a spectrogram-slice positioned halfway through the second note of the focal song. The latter criterion was chosen to standardize our protocol across all males, as some males introduce their songs with an uncharacteristically loud call-note, and some songs were only two notes long. Prior to evaluating spectral curves of the songs, we isolated amplitude-values of the signal from the overall signal + noise spectra (Brumm 2004b). We then measured the total area under each curve and calculated SNR by subtracting the total area of the noise-curve from the total area of the signal-curve (Fig. 1). The range of frequency of this analysis was limited to the range that a male's song exhibited. This method generated a measure of difference in power between background noise and the vocalizations of males that likely relates to the detectability of the signal.

Because the characteristics of males' songs, particularly frequency, can be influenced by body size (Brumm 2004b; Marler and Slabbekoorn 2004), we also attempted to capture and measure as many males as possible in order to control for morphology (using wing length, mm) in all analyses. We did not use mass as a measure of body size because it can fluctuate substantially throughout the day, depending on how recently a bird has eaten. We employed trap doors (placed in nestboxes during the brood-care phase of the breeding season) and mist nets to catch males. Despite our efforts, 21 males evaded capture. Rather than exclude them from our analyses, we estimated their sizes using regressions of body

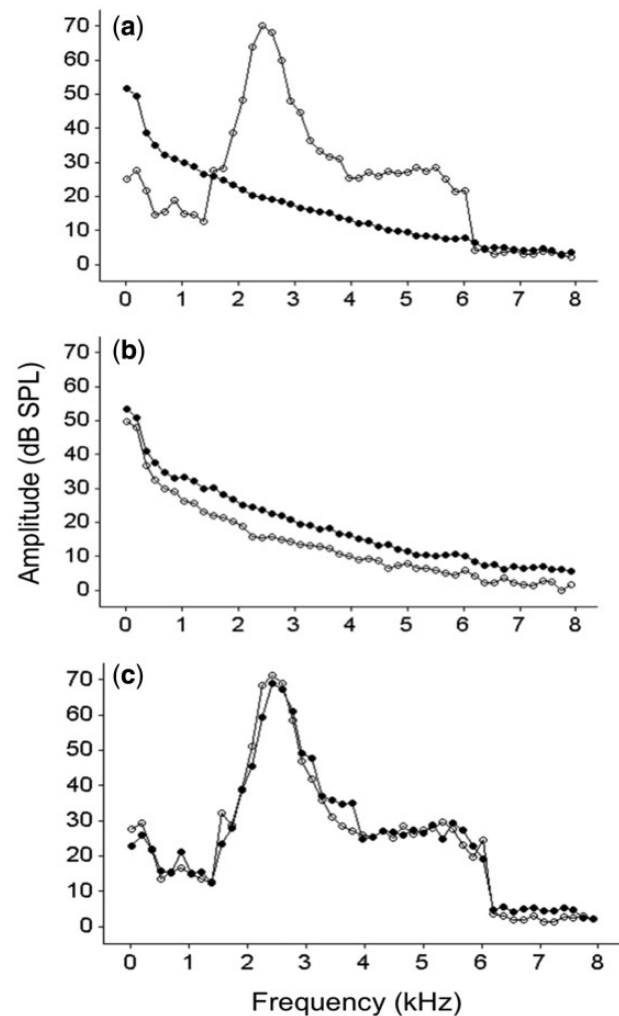


Fig. 1 Power spectra of environmental noise and eastern bluebirds' songs. (a) Power spectra of environmental noise in territories of eastern bluebirds (closed circles) and the corresponding songs of males (open circles). These spectra were created by averaging across all measurements of environmental noise and of males' songs, respectively. (b) Comparison of the spectra of environmental noise during the lowest and highest levels of noise recorded at territories where birds were active. These spectra were created by averaging spectral values across the highest and lowest recordings taken at all sites. (c) Comparison of males' song spectra in response to high levels of ambient noise (closed circles) and low levels of ambient noise (open circles). These spectra were created by averaging spectral values for all songs collected from males under each site's highest and lowest levels of ambient noise, respectively.

size against the characteristics of song measured from the 39 other males who were both recorded and measured. We generated multiple estimates of size by regressing wing length against parameters of frequency (minimum frequency, maximum frequency, peak frequency, and range in frequency), then used the resulting regression equation to extrapolate

Table 2 Loading scores for PCA of all habitat within a 100-m radius of the nestboxes of active eastern bluebirds

| Variable | Habitat PC1 (48.2%) | Habitat PC2 (35.2%) |
|----------------------------------|------------------------|------------------------|
| Short impervious surface (<3 m) | 0.491 | -0.727 |
| Short vegetation (grass, shrubs) | -0.943 | -0.223 |
| Tall impervious surface (>3 m) | 0.567 | -0.588 |
| Trees (forest and ornamental) | 0.691 | 0.695 |

Note: Percentages indicate the amount of variance accounted for by each PC.

independent measures of each unmeasured male's size. We used the average of the extrapolated predictions from these regression analyses to estimate the wing length of unmeasured males.

Evaluation of habitat

We quantified the habitat of breeding male bluebirds using ArcGIS v. 9.3.1 (ESRI, Redlands, CA, USA), employing methods that have been described elsewhere in more detail (Kight et al. 2012a). Since breeding bluebirds show defensive behaviors within 50 m of their nestboxes (Gowaty and Plissner 1998), we defined a territory as the circular area 100 m in diameter and centered on each nestbox. We classified habitat as belonging to one of four categories: short, impervious surface (<3 m; sidewalks and roads); short vegetation (grass and shrubs <1 m); tall, impervious surface (>3 m; buildings and walls); or trees (shrubs and trees >1 m). We measured the total area of each of these categories for each territory, and then condensed our dataset using PCA. The analysis produced two PCs explaining a total of 83.4% of the variance (Table 2). Habitat PC1 (48.2% of variance) loaded negatively for short vegetation but positively for the other three variables. This is consistent with more human-disturbed habitats (e.g., suburban neighborhoods, campuses, sports facilities), which incorporate impervious surface in the form of sidewalks, roads, and buildings, and which include many relatively small ornamental trees. We will, therefore, refer to this PC as anthropogenic habitat. The second habitat PC (35.2% of variance) loaded negatively both for short and for tall impervious surfaces, but positively for trees. As these relationships are consistent with unmanaged woodland habitats (e.g., parks, cemeteries), we called this PC woodland.

Statistical analyses

We utilized a model-selection approach (Anderson and Burnham 2004) to answer three main questions. First, do levels of ambient noise explain among-male

variations in song? To investigate the relationships between males' song and environmental noise, we calculated a single value per male by averaging across his high and his low recordings of ambient noise, which we used in comparison among males. Second, do changes in levels of ambient noise explain within-male variations in song? We measured change by subtracting values of high ambient noise from those of a combination of males' song and environmental noise. Thus, negative values represent instances when acoustic parameters were higher in lower noise settings than in higher noise settings. Third, do habitat features predict males' song-parameters? For a subset of 22 of our 60 sites, we examined relationships between habitat structure and males' song parameters (averaged across the two focal recordings), as we collected detailed information on habitat for a smaller number of sites. This smaller set of sites represented the range of habitats observed across all sites.

All analyses included the (random) variable "year" in order to control for potential annual variations in song and environmental noise. Analyses with song-parameters included the variable "male-size" to control for potential morphological impacts on song.

Prior to statistical analyses, distributions of all variables were checked for normalcy and transformed when necessary. We used SPSS v. 15 (LEAD Technologies, Inc, Chicago, IL, USA) to create generalized, linear, mixed models to calculate Akaike's Information Criterion (AIC) for each model. These were then used to calculate AIC_c , which adjusts AIC for small sample sizes, and ΔAIC_c , the difference between the model with the lowest AIC_c and each subsequent model. Models with ΔAIC_c scores within 4.0 of the best model were considered to have strong support and were assigned Akaike weights (w_i) to quantify the degree of support for each model (Anderson and Burnham 2004). We used all candidate models with Akaike weights to calculate model-averaged variable coefficients. We also calculated the standard error of the mean (SEM) associated with each model parameter, which allowed us to visualize the likely range of values that our estimated parameters could take. When this range (coefficient value \pm SEM) overlapped with 0, we concluded there was little evidence for the effect of a predictor variable.

In order to visualize the relationships between sound-propagation variables and interaction terms, we categorized values of one variable in the term as "high" or "low" with respect to median values. This allowed us to plot separate trend lines (e.g., song PC1 in woodlands with low anthropogenic

disturbance, versus song PC1 in woodlands with high anthropogenic disturbance) in order to compare the direction and strength of each relationship. These categories were not used in any statistical analyses, but are useful for visualizing the effects of the interaction terms.

Results

On average, we found that song-parameters of our focal birds ($n=60$) were similar to those reported previously for eastern bluebirds (Huntsman and Ritchison 2002). Songs lasted for approximately 0.710 ± 0.178 s (range = 0.280–1.178 s) and comprised an average of 3.37 ± 0.932 elements (range = 2–6) that were 0.062 ± 0.043 s apart (range = 0–0.426 s). The average minimum frequency for songs was 1574.1 ± 213.5 Hz (range = 996.6–2055.6 Hz), while the average maximum frequency was 4045.6 ± 598.4 Hz (range = 3052.1–5889.1 Hz). Male bluebirds were capable of some modulation of frequency during their songs, with an average change in frequency of 2471.5 ± 694.3 Hz (range = 1322–4360.2 Hz). The peak frequency of their songs, 2488.6 ± 317.1 Hz (range = 1378.1–3445.3 Hz) fell very near the midpoint of their frequency range. The average amplitude of a male bluebird's song, extrapolated to 1 m from the singing bird, was 51.99 ± 21.74 dB SPL (range = 40.33–87.93 dB SPL). Males' spectral curves, on average, encompassed a larger area on the graph of amplitude versus frequency than those for environmental noise (mean area under curve of amplitude versus frequency = 574.1 ± 315.5), but there was considerable variation in whether the RMS amplitude of the songs exceeded that of noise, and, if so, by how much (range = –387.05 to 1409.63).

Does ambient noise explain among-male variations in song?

There was a negative relationship between decreased noise PC and males' song PC1 higher-pitched ($B = -0.199$, $SEM = 0.134$), such that males sang at a higher frequency where ambient noise was loudest. This pattern has been reported in several other species (Slabbekoorn and Peet 2003; Fernández-Juricic et al. 2005; Wood et al. 2006; Francis et al. 2011b). Models for PC2 shorter songs and PC3 slower pace/lower emphasis did not find any strong relationships between males' song and environmental noise (PC2: $B = 0.0079$, $SEM = 0.129$; PC3: $B = -0.042$, $SEM = 0.133$). However, song PC4 quieter was positively related to environmental noise, indicating that males in noisier environments sang, on average,

louder songs ($B = 0.260$, $SEM = 0.125$). This apparent match between the amplitudes of song and environmental noise was further confirmed by the absence of a relationship between environmental noise and SNR ($B = -28.9$, $SEM = 42.1$). In summary, at sites where ambient noise was loudest, males sang louder and at higher frequencies.

Do changes in ambient noise explain within-male variations in song?

Changes in environmental noise were related to within-individual changes in two of the song PCs. Male bluebirds delivered songs that were higher-pitched (PC1: $B = 0.170$, $SEM = 0.143$) and quieter (PC4: $B = 0.253$, $SEM = 0.140$) as ambient noise levels became higher in frequency and lower in amplitude. In other words, as ambient noise became louder and lower-pitched, males altered their songs to be louder and also lower-pitched.

Changes in environmental noise also were strongly related to variation in SNR ($B = -149.9$, $SEM = 49.8$). The SNR of bluebirds' songs increased as the amplitude of ambient noise became louder and lower-pitched. Although this result at first seems counterintuitive, it probably reflects the fact that song-masking is less likely when noise is dominated by low frequency sounds; even though the sounds are loud, they often occur beneath the lowest pitches that bluebirds tend to use, and therefore do not overlap in bandwidth. There were no other strong associations between changes in ambient noise levels and either of the other two metrics of song (PC2: $B = -0.045$, $SEM = 0.147$; PC3: $B = 0.034$, $SEM = 0.155$).

Cumulatively, these results suggest that males adjust both the amplitude and frequency of their vocalizations in real time, as has been reported for house finches (*Haemorhous mexicanus*) (Bermúdez-Cuamatzin et al. 2009), chiffchaffs (*Phylloscopus collybita*) (Verzijden et al. 2010), and great tits (*Parus major*) (Halfwerk and Slabbekoorn 2009). Yet the change in song-frequency is opposite to that which is often reported and does not match our among-male analysis.

Do features of the habitat predict song-parameters?

In model sets for song PCs 1–4, all candidate models were within 4 AIC_c units of the best model and were therefore included in the final, averaged model (Table 3). Habitat type was a predictor of each of the song's parameters; habitat PC1 anthropogenic habitat and the interaction variable habitat PC1*PC2 each appeared in three of the four

Table 3 Values used in generalized linear regression models to explore effects of habitat on male bluebirds' song PCs 1–4 (a–d) and SNR (e)

| Model | Parameters | AIC _c | Δ -AIC _c | Weight | Likelihood |
|--------------|--|------------------|----------------------------|--------|------------|
| (a) Song PC1 | | | | | |
| 1 | Year, male size, habitat PC2 | 69.73 | 0 | 0.340 | 1 |
| 2 | Year, male size, habitat PC1 | 69.83 | 0.098 | 0.326 | 0.952 |
| 3 | Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2 | 71.03 | 1.30 | 0.178 | 0.521 |
| 4 | Year, male size, habitat PC1, habitat PC2 | 71.33 | 1.60 | 0.154 | 0.450 |
| (b) Song PC2 | | | | | |
| 1 | Year, male size, habitat PC1 | 66.56 | 0 | 0.361 | 1 |
| 2 | Year, male size, habitat PC2 | 66.58 | 0.023 | 0.357 | 0.989 |
| 3 | Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2 | 68.40 | 0.184 | 0.144 | 0.398 |
| 4 | Year, male size, habitat PC1, habitat PC2 | 68.46 | 0.190 | 0.139 | 0.387 |
| (c) Song PC3 | | | | | |
| 1 | Year, male size, habitat PC1 | 54.37 | 0 | 0.416 | 1 |
| 2 | Year, male size, habitat PC2 | 55.62 | 1.25 | 0.223 | 0.536 |
| 3 | Year, male size, habitat PC1, habitat PC2 | 55.90 | 1.48 | 0.198 | 0.477 |
| 4 | Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2 | 56.24 | 1.87 | 0.164 | 0.394 |
| (d) Song PC4 | | | | | |
| 1 | Year, male size, habitat PC1 | 63.00 | 0 | 0.454 | 1 |
| 2 | Year, male size, habitat PC2 | 64.04 | 1.04 | 0.270 | 0.594 |
| 3 | Year, male size, habitat PC1, habitat PC2 | 65.05 | 2.05 | 0.163 | 0.358 |
| 4 | Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2 | 65.77 | 2.77 | 0.114 | 0.250 |
| (e) SNR | | | | | |
| 1 | Year, male size, habitat PC1, habitat PC2, habitat PC1*PC2 | 302.72 | 0 | 0.997 | 1 |
| 2 | Year, male size, habitat PC1, habitat PC2 | 314.52 | 11.8 | 0.003 | 0.003 |
| 3 | Year, male size, habitat PC1 | 325.16 | 22.44 | <0.001 | <0.001 |
| 4 | Year, male size, habitat PC2 | 328.91 | 26.18 | <0.001 | <0.001 |

models explaining song PCs, while habitat PC2 woodland appeared in two models (Table 4).

Song PC1 higher-pitched was negatively related to habitat PC1 anthropogenic habitat but positively related to habitat PC2 woodland. Interestingly, this implies that bluebirds are delivering lower-pitched songs in the environments typically associated with lower-frequency ambient noise. However, song PC1 also loaded positively for frequency range, which means that songs in anthropogenic areas tend to have a narrower bandwidth, while those in more natural areas have a wider bandwidth. This is a pattern previously reported for red-winged blackbirds (*Agelaius phoeniceus*) (Hanna et al. 2011).

Variations in song PC1 were also explained by the habitat-interaction term (habitat PC1*PC2). A visualization of this relationship revealed that song PC1 was positively related to habitat PC2 (woodland) at both low and high levels of habitat PC1; however, songs in forested areas increased in frequency more

quickly when there were also high levels of anthropogenic features in the habitat.

Song PC2 shorter songs was related only to the habitat PC1*PC2 interaction term (Table 4). In forested habitats with few anthropogenic features, there was a negative relationship between amount of tree cover and the length of song; conversely, in forested areas with more anthropogenic features, there was a positive association between tree cover and the length of song (Fig. 2a).

Song PC3 slower pace/lower emphasis was positively related to total amount of anthropogenic habitat (PC1), but negatively related to woodland tree cover (PC2; Table 4). The relationship between song PC3 and the habitat-interaction term is shown in Fig. 2b. In environments with lower levels of anthropogenic habitat features, an increasing amount of tree cover is associated with slower songs that have a lower frequency emphasis (greater power at lower frequencies). However, in areas with more

Table 4 Parameters included in final models explaining the relationship between habitat and male bluebirds' song PCs 1–4 (a–d) and SNR (e)

| Parameter | B | SEM | B ± SEM | |
|-------------------|--------|-------|---------|--------|
| | | | Lower | Upper |
| (a) Song PC1 | | | | |
| Year (2007) | −0.553 | 0.099 | −0.652 | −0.454 |
| Male size | −0.098 | 0.025 | −0.124 | −0.073 |
| Habitat PC2 | 0.077 | 0.040 | 0.037 | 0.117 |
| Habitat PC1 * PC2 | −0.050 | 0.035 | −0.085 | −0.015 |
| Habitat PC1 | −0.039 | 0.022 | −0.061 | −0.017 |
| Year (2008) | 0 | 0 | 0 | 0 |
| (b) Song PC2 | | | | |
| Year (2007) | −0.556 | 0.092 | −0.648 | −0.464 |
| Male size | −0.139 | 0.023 | −0.162 | −0.116 |
| Habitat PC1 * PC2 | 0.035 | 0.028 | 0.007 | 0.064 |
| Habitat PC1 | 0.013 | 0.032 | −0.018 | 0.045 |
| Habitat PC2 | −0.002 | 0.020 | −0.022 | 0.017 |
| Year (2008) | 0 | 0 | 0 | 0 |
| (c) Song PC3 | | | | |
| Year (2007) | −0.377 | 0.061 | −0.439 | −0.316 |
| Habitat PC1 | 0.132 | 0.033 | 0.100 | 0.165 |
| Male size | 0.058 | 0.014 | 0.044 | 0.072 |
| Habitat PC1 * PC2 | −0.054 | 0.029 | −0.083 | −0.025 |
| Habitat PC2 | −0.032 | 0.018 | −0.050 | −0.014 |
| Year (2008) | 0 | 0 | 0 | 0 |
| (d) Song PC4 | | | | |
| Year (2007) | 0.203 | 0.067 | 0.136 | 0.270 |
| Male size | −0.143 | 0.037 | −0.180 | −0.105 |
| Habitat PC1 | 0.079 | 0.022 | 0.057 | 0.100 |
| Habitat PC2 | −0.016 | 0.026 | −0.043 | 0.010 |
| Habitat PC1 * PC2 | 0.011 | 0.019 | −0.009 | 0.030 |
| Year (2008) | 0 | 0 | 0 | 0 |
| (e) SNR | | | | |
| Habitat PC1 | −114 | 13.3 | −128 | −101 |
| Habitat PC1 * PC2 | −83.0 | 24.1 | −107 | −58.9 |
| Male size | 79.4 | 9.61 | 69.8 | 89.0 |
| Habitat PC2 | −19.8 | 15.4 | −35.2 | −4.40 |
| Year (2007) | 0.644 | 32.5 | −31.8 | 33.1 |
| Year (2008) | 0 | 0 | 0 | 0 |

anthropogenic features, greater amounts of tree cover are associated with faster songs that have a higher frequency emphasis (greater power at higher frequencies).

Surprisingly, we found a positive association between song PC4 quieter and habitat PC1 anthropogenic habitat, suggesting that males in more

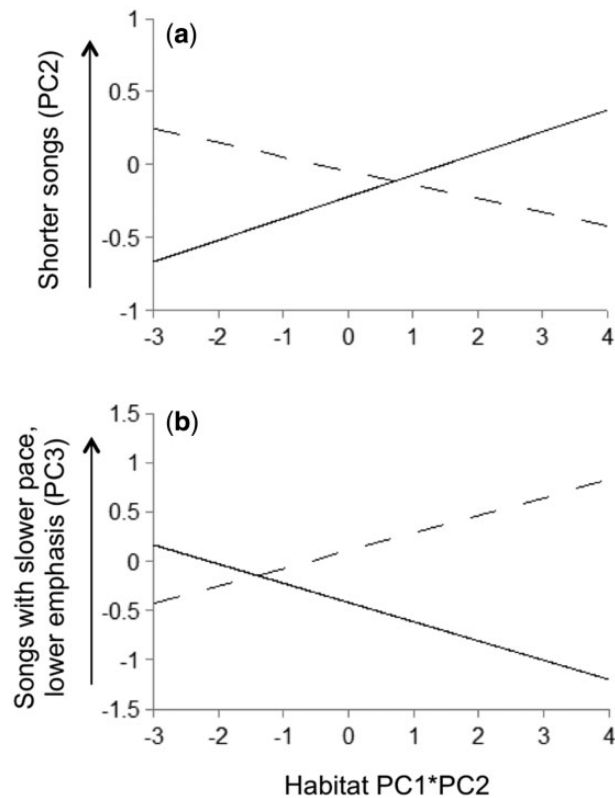


Fig. 2 Visualization of the interactions between males' songs and the habitat interaction term (PC1*PC2): (a) Male song PC2 (shorter songs) regressed against habitat PC1 (anthropogenic habitat) at low (solid line) and high (dashed line) levels of habitat PC2 (woodland). (b) Male song PC3 (slower pace/lower emphasis) regressed against habitat PC1 at low (solid line) and high (dashed line) levels of habitat PC2.

anthropogenic sites sing quieter songs. However, when we repeated the analysis after including decreased noise PC as a covariate, this relationship disappeared ($B=0.122$, $SEM=0.132$).

Only one model met the criteria for inclusion in the model-set investigating the relationship between habitat and SNR (Table 4). Both anthropogenic habitat (PC1) and woodland (PC2) were strongly negatively associated with SNR. This indicates that males had the poorest SNR in sites with either high levels of impervious surface cover or high amounts of tree cover. Interestingly, when we repeated the analysis after including decreased noise PC as a control variable, only the relationship with habitat PC1 (anthropogenic habitat) remained strong (habitat PC1: $B=-121.8$, $SEM=57.6$; habitat PC2: $B=-44.9$, $SEM=63.7$). Thus, it appears that ambient noise could explain the association between SNR and habitat in woodland areas, but that the habitat-features themselves explained variation in SNR in more anthropogenic areas.

SNR was also strongly related to the habitat-interaction term. Visualizations of this relationship revealed that SNR decreased as the amount of tree cover increased in areas with both low and high levels of anthropogenic modifications; however, SNR decreased more rapidly as tree cover increased in less anthropogenic sites.

Discussion

Here, we present evidence that the songs of male eastern bluebirds are impacted by two anthropogenic disturbances: noise-pollution and modification of the habitat. However, the presence of both among-male and within-male variations in song suggests that this species could cope with at least some anthropogenic factors by displaying behavioral flexibility in the form both of modulations of frequency and amplitude that could reduce masking and help maintain a higher SNR under noisier conditions. This latter observation helps explain why these birds readily nest along this gradient of disturbance (Gowaty and Plissner 1998; Kight 2005; Kight and Swaddle 2007).

Several other species are known to employ similar vocal modifications to those reported here. Arguably the easiest way to maintain SNR in the face of fluctuating environmental conditions is adjustment of amplitude, which has been reported both for songs (Brumm 2004b; Brumm and Slater 2006; Francis et al. 2010; Lowry et al. 2012) and calls (Pytte et al. 2003; Brumm et al. 2009). Because this vocal modification, also known as the Lombard effect, appears to be rather common among animals (Brumm and Todt 2002; Brumm 2004a; Brumm and Zollinger 2011), we were not surprised to observe it in our focal birds.

We also found that songs in noisy environments have a higher peak frequency than those performed in quieter areas. This was another anticipated result, since shifts in frequency appear to be a relatively common, and potentially adaptive, mechanism for escaping masking by ambient noises (Slabbekoorn and Peet 2003; Fernández-Juricic et al. 2005; Leonard and Horn 2005, 2008; Slabbekoorn and den Boer-Visser 2006; Wood et al. 2006; Bermúdez-Cuamatzin et al. 2009; Francis et al. 2010). There has been some debate over whether such changes in frequency arise merely as a byproduct of the Lombard effect (Cardoso and Atwell 2011; Zollinger et al. 2012). Unfortunately, our current methodology does not allow us to determine whether the co-occurrence of shifts in amplitude and frequency are separate responses to ambient noise or whether they result from the morphological

constraints of song production—a useful and important distinction to make in order to understand the potential limits, and evolutionary implications, of vocal responses to environmental noise. However, we did find that males can both increase amplitude and lower frequency of their songs, supporting the notion that modulation of amplitude and frequency are under somewhat separate control.

We found that eastern bluebirds were able to improve their SNR in response to rising levels of ambient noise by increasing the amplitude and but, surprisingly, decreasing the frequency of their own songs. We believe they decreased the frequency of their songs as the increase in amplitude of ambient noise was also associated with a decrease in frequency of this noise. Hence, noisier situations were also situations of lower-frequency, background sounds, allowing males to sing at lower frequencies while still maintaining high SNR. Immediate behavioral flexibility in song has been documented for several species (Bermúdez-Cuamatzin et al. 2010; Gross et al. 2010; Verzijden et al. 2010; Hanna et al. 2011; Montague et al. 2013), suggesting that such flexibility may be common among songbirds inhabiting humans' habitats. However, it is not clear whether anthropogenic conditions select for this flexibility, or whether behaviorally flexible birds are particularly common in anthropogenic environments—perhaps because they are preadapted for life in noisy areas (Hu and Cardoso 2009). Given that increased amplitude of song may reflect the quality or attractiveness of the male (Brumm 2004a; Ritschard et al. 2010), it is intriguing that at least some males choose not to consistently sing at the elevated SNRs of which they are capable of achieving, when required. This may reflect higher energetic costs of higher-amplitude song, the potential danger of being exposed to predators that can cue in on sound, and/or the lack of importance of high amplitude as a vocal characteristic in these species.

One common critique of research on anthropogenic noise is that most studies do not address the many correlates that may be responsible for driving the observed vocal trends (Habib et al. 2007; Bayne et al. 2008). This is an important issue to consider, as species could have experienced some degree of selection that optimized the transmission of signals in particular environments (Morton 1975; Brumm and Naguib 2009; Kirschel et al. 2009). We found that several aspects of song (pitch, pace, amplitude, SNR) correlated with features of the habitat. In general, males sang at higher frequency in woodland habitats and at lower frequency in more anthropogenic habitats. These patterns are consistent with

habitat-dependent divergence in song (Ripmeester et al. 2010; Luther and Derryberry 2012). However, much additional work (e.g., on song-learning, dispersal, and song-copying) needs to be conducted in order to explore this possibility sufficiently.

Some of the relationships we found between song and habitat are surprising, given other known associations between both song and noise, and habitat and noise. For instance, although males at noisy sites sang at higher frequencies and amplitudes, those in sites that were structurally consistent with anthropogenic habitats sang quieter, lower-frequency songs. In other words, “human-modified” and “noisy” may not always be synonymous, and may not always provoke the same behavioral adjustments in wildlife. Indeed, when we examined propagation of sound in a separate study in these same areas, we found that territories with fewer anthropogenic structures had higher levels of ambient noise than did those with more anthropogenic objects (Kight et al. 2012a). This could explain why SNR was negatively related to both of our current habitat PCs: High levels of tree cover are associated with several biotic sources of noise (e.g., wind rustling through leaves, calling by treefrogs and insects, heterospecific and conspecific birdsong) which, cumulatively, have the potential to generate noise-levels comparable to those recorded near sites with human activities. These possible explanations are an important reminder that biotic noise is a significant influence that should not be discounted or overlooked in developed habitats. What is less clear is why males at sites with anthropogenic features should sing more quietly and at a lower frequency. This may reflect deliberate modifications of the song (e.g., that promote propagation of sound, or that makes the bird less obvious to predators), or may simply be a by-product of differential use of the habitat by males with different morphologies and/or condition, or males with different characteristics of song.

Altogether, the current study indicates that adult male bluebirds have the vocal flexibility to communicate effectively despite multiple manipulations of their acoustic space by humans. This result, similar to those from our previous studies on eastern bluebirds, emphasizes that some species are quite capable of coexisting with humans across a variety of anthropogenic habitats (Kight 2005; Kight and Swaddle 2007; Cornell et al. 2011; Kight et al. 2012b). Like other species studied within the context of anthropogenic noise, eastern bluebirds consistently live in disturbed territories even when there are vacancies (i.e., empty nestboxes) in nearby areas that are less disturbed (C. R. Kight and J. P. Swaddle,

unpublished data). This species has been living in the proximity of humans for hundreds of years and, prior to this, evolved adaptations to early successional areas created by unpredictable natural events (Gowaty and Plissner 1998). Thus, adult eastern bluebirds’ behavioral flexibility in anthropogenic environments may stem from a preadaptation to disturbed habitats, a longer-term response to unpredictable disturbances by humans (e.g., acoustic adaptation), substantial phenotypic plasticity, or a combination of all three. On the other hand, species that have different life-history traits and requirements are likely to have a more constrained norm of reaction (Blumstein 2006) and show less behavioral flexibility—particularly when they have evolved a preference for less variable habitats and have had little historical experience with disturbances from humans. Future work on non-typical species such as these will facilitate comparative analyses that may reveal the origins of tolerance to humans and improve our ability to predict which birds will be most impacted by human-mediated deterioration of the soundscape (Francis et al. 2011a; Pijanowski et al. 2011).

We also encourage researchers to turn their attention to the other end of the communication process and examine the impacts of modifications of the soundscape on receivers. These efforts should attempt to quantify the ways in which ambient noise and the structure of the habitat alter detection and discrimination of signals; further, they should examine whether, and to what extent, vocal modifications compensate for disturbances by humans. Additional work on within-species and among-species interactions (e.g., mate choice, territorial displays, alarm calls) will help elucidate whether signal-adjustment alters information-content; this, in turn, should shed light on the potential fitness costs of vocal plasticity (Dall et al. 2005; Halfwerk et al. 2011). Interestingly, in a separate study of the same population of eastern bluebirds, we found that increased ambient noise was associated with a decrease in fitness (Kight et al. 2012b). That pattern appeared to be driven by brood-reduction and, hence, not likely related to the known functions of the songs of adult males. Rather, we hypothesize that parent–offspring communication is disrupted, thereby reducing nestlings’ survival (Swaddle et al. 2012).

Species that occupy habitats subjected to disturbance by humans provide opportunities to conduct “natural experiments” investigating the relative strengths of environmental pressures at different life-history stages. The song a male produces is a product of many factors, including his condition

(past and present), his morphology, his original song-tutor, his audience, and his current environmental setting (Marler and Slabbekoorn 2004). Longitudinal studies documenting all of these variables (and more) in ever-changing anthropogenic environments can be used to understand which parameters are most sensitive to change, and therefore are most likely to cause permanent alterations to vocal performance if they are manipulated (Nottebohm and Nottebohm 1978; Derryberry 2007; Baker and Gammon 2008). Such approaches will allow us to understand how environmental constraints (caused by habitat structure and ambient noise, and mediated by behaviors such as mate choice and immigration) can underlie the evolution of communication within a species. Furthermore, these data offer insights into the potential long-term influences of anthropogenic pressures on animals' communication and cognition, thereby improving our ability to develop plans for effective mitigation and conservation where necessary.

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