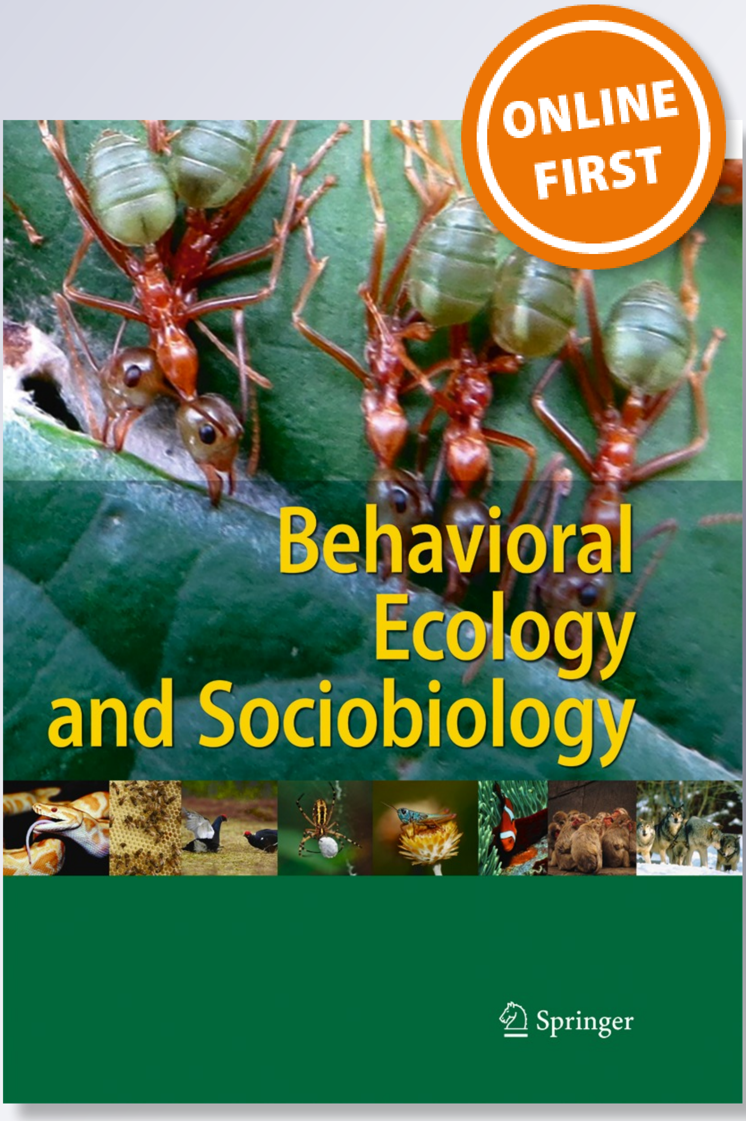
Anthropogenic noise is associated with changes in acoustic but not visual signals in red-winged blackbirds

Alejandro A. Ríos-Chelén, Gavin C. Lee & Gail L. Patricelli

Behavioral Ecology and Sociobiology

ISSN 0340-5443

Behav Ecol Sociobiol
DOI 10.1007/s00265-015-1928-7



Springer

Behav Ecol Sociobiol
DOI 10.1007/s00265-015-1928-7

ORIGINAL PAPER

Anthropogenic noise is associated with changes in acoustic but not visual signals in red-winged blackbirds

Alejandro A. Ríos-Chelén [1,2] **· Gavin C. Lee** [1] **· Gail L. Patricelli** [1]

Received: 23 November 2014 / Revised: 14 April 2015 / Accepted: 16 April 2015

Abstract Some birds in noisy areas produce songs with higher frequency and/or amplitude and altered timing compared to individuals in quiet areas. These changes may function to increase the efficacy of acoustic signals by reducing masking by noise. We collected audio recordings of red-winged blackbirds and measured noise levels. We found that males in noisier places produced songs with fewer syllables and slower repeat rate of elements in some components (rattles). Birds may also improve the efficacy of communication in noise by increasing usage of other signaling modalities. Red-winged blackbirds also perform a visual display in different intensities while singing. We also tested whether this species performs the visual display in different intensities according to current noise levels, and predicted that if the efficacy of songs is impaired in noisy places, males would compensate by performing a more intense visual display. For this, we also collected visual recordings from the same males from which we obtained acoustic recordings. We found no association between acoustic noise and the intensity of the visual display; thus, our results do not support the idea that males are using the visual display as a backup signal to communicate under acoustic noise. We discuss some possible explanations of this negative finding and for the observed noise-related changes in song length and rattle rate in the context of communication under noise.

Keywords Chronic noise · Anthropogenic noise · Red-winged blackbird · Multimodal signaling · Birdsong · Visual signal

Introduction

Urban noise can have negative effects on bird species. Several studies have found a reduced number of species or individuals with increasing noise (e.g., Rheindt 2003; Francis et al. 2009; Blickley et al. 2012; McClure et al. 2013), and some studies have suggested a link between noise and reduced breeding success (Halfwerk et al. 2011a; Kight et al. 2012; Schroeder et al. 2012). By masking the acoustic signals of birds, noise can impair communication and potentially interfere during social interactions (Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006; Warren et al. 2006; Ríos-Chelén 2009; Brumm and Zollinger 2013; Slabbekoorn 2013; Gil and Brumm 2014). Direct evidence that noisy environments can affect the outcome of female mate choice and male–male vocal interactions is now accumulating (Swaddle and Page 2007; des Aunay et al. 2014; McMullen et al. 2014); these effects may contribute to the observed reduction in avian richness, abundance, and poor reproductive success. Noise may also be beneficial in some cases; for example, Francis et al. (2009) found higher nest success for some species in areas with high noise levels compared to similar, quieter areas. This increase may be an indirect effect caused by reduced interspecific competition and/or reduced predator abundance in noisy areas.

In some bird species, individuals in areas with higher anthropogenic noise sing songs with higher frequency (i.e., pitch), than individuals in quiet areas (e.g., Slabbekoorn and

Communicated by H. Brumm

✉ Alejandro A. Ríos-Chelén
aarios@ecologia.unam.mx

[1] Department of Evolution and Ecology, University of California, Davis, CA, USA

[2] Centro Tlaxcala de Biología de la Conducta, Universidad Autónoma de Tlaxcala, Carretera Tlaxcala-Puebla Km 1.5 C.P., 90070 Tlaxcala, México

Peet 2003; Fernández-Juricic et al. 2005; Slabbekoorn and den Boer-Visser 2006; Wood and Yezerinac 2006; Bermúdez-Cuamatzin et al. 2009; Hu and Cardoso 2009; Nemeth and Brumm 2009; Potvin et al. 2011). These and other noise-related changes in acoustic signals may improve the efficacy of communication in noise (Lohr et al. 2003; Halfwerk et al. 2011b; Pohl et al. 2012, 2013). Because most energy of urban noise is found at low frequencies, an increase in song frequencies may reduce noise masking. These changes may arise during ontogeny due to selective learning of the songs most easily heard (Luther and Baptista 2009; Ríos-Chelén et al. 2012), and/or these changes may reflect behavioral plasticity, with birds changing their songs in "real-time" while experiencing different noise levels (Tumer and Brainard 2007; Halfwerk and Slabbekoorn 2009; Gross et al. 2010; Verzijden et al. 2010; Bermúdez-Cuamatzin et al. 2011). These changes in vocalizations may also arise through evolutionary divergence among populations, though there is little evidence of genetic differences between populations in noisy and quiet areas (Partecke et al. 2004, 2006; Potvin et al. 2013; but see Partecke and Gwinner 2007). Whether or not an increase in pitch represents an adaptation to deal with noise has been recently debated (Nemeth and Brumm 2010; Cardoso and Atwell 2011, 2012; Nemeth et al. 2012; Slabbekoorn et al. 2012; Zollinger et al. 2012; Nemeth et al. 2013; Potvin and Mulder 2013).

Animals can use a variety of other strategies to cope with noise, including singing at other times of the day when noise levels are lower (Fuller et al. 2007; Gil et al. 2015), increasing song redundancy (Brumm and Slater 2006) and amplitude (Brumm 2004), increasing vocal activity (Díaz et al. 2011), increasing sound tonality (Hanna et al. 2011), song length or number of elements (Francis et al. 2011; Ríos-Chelén et al. 2013), and syllable length (Brumm et al. 2004). All of these vocal modifications may result in a higher probability of being heard in a noisy environment.

In addition to changing properties of their vocalizations, it is possible that birds could also increase their emphasis on the visual channel of communication to cope with acoustic noise (Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006; Partan et al. 2010; Partan 2013). This may be expected if multimodal signals act as redundant or backup signals (Møller and Pomiankowski 1993; Hebets and Papaj 2005; Partan 2013), with birds shifting more toward the visual modality when the acoustic modality is less effective. It might also be expected if the visual components of the signal function to capture attention for the acoustic signal (Hebets and Papaj 2005; Partan and Marler 2005), with the need for such attention increasing in acoustic noise. For example, Amézquita and Hödl (2004) found that Amazonian tree frogs (*Hyla parviceps*) use a variety of acoustic and visual signals in male–male interactions (i.e., calling, and foot and arm movements), suggesting that the use of both acoustic and visual modalities may enhance the probability of being detected in an acoustically noisy background (see also Grafe and Wanger 2007). Similarly, many bird species are colorful and perform visual displays during social interactions (e.g., Smith 1967; Malacarne et al. 1991), and it is possible that these species will modify their vocalizations as well as their visual displays to improve the probability of being detected in an acoustically noisy background.

To test the possibility that birds change their acoustic and visual signals to deal with acoustic noise, we collected audio and video recordings of red-winged blackbirds (*Agelaius phoeniceus*) singing under different levels of anthropogenic noise. The red-winged blackbird is a sexually dimorphic species, with males having a slightly larger body size than females and black plumage with red epaulets on their wings. This is an ideal species on which to examine visual and acoustic signaling in noise because singing males perform a visual display (i.e., the song-spread display) in which the wings are spread and the red epaulet is erected (Peek 1972; Searcy and Yasukawa 1995; Beletsky and Orians 1996). Peek (1972) showed that both males who were unable to sing and males whose red patches were dyed black, or cut off with scissors, had more difficulty defending their territories than unmanipulated males. This suggests that both acoustic and visual signals play a role in territorial defense in this species (see also Yasukawa 1981a; Roskaft and Rohwer 1987; Metz and Weatherhead 1991, 1992). Males can perform the visual display with different intensities, ranging from high-intensity displays involving wings spread broadly and epaulets fully erected, to incipient displays involving little to no visual display (Peek 1972). Yasukawa (1978) found that the intensity of the visual display reflects the level of aggressive motivation toward other males, with higher intensity displays used more often during close confrontations and before attacks (see also Peek 1972). Peek (1972) also found an association between higher-intensity visual displays and the presence of females.

In the present study, we tested whether red-winged blackbirds show differences in their songs and intensities of the visual display with different noise levels. We predicted that males should perform the visual display at higher intensity in noisy areas. This could be the case if a high intensity display is more conspicuous than a low intensity one and thus increases the chances of being detected under acoustic noise.

Material and methods

Study site and recordings

From May 18 to June 8, 2012, and from around 6:20 AM to 10 AM, we recorded red-winged blackbirds near Davis, CA, USA. Because males were not color banded, we minimized the probability of recording each male more than once by recording them as observers followed a single direction from one point to another and not recording males that were left behind and that were <100 m away from each other. We recorded from multiple males closer than 100 m apart only when more than one male could be observed simultaneously in a single area to assure that they were different individuals. We audio-recorded a total of 74 males (Sennheiser K6/ME66 shotgun microphone connected to a Marantz solid state recorder PMD670; 16 bit, 44.1 KHz linear PCM), but 5 of them were not included in song measures and analyses because the background noise was too high to allow song measures. Of these 69 remaining males, 32 were recorded in Conaway Ranch, a private ranch north of Davis (38°38′ N, 121°42′ W); 15 were recorded in the Wetlands, a waste water treatment plant (38°35′ N, 121°39′ W); 14 were recorded in the Yolo Bypass Wildlife Area, a natural reserve (38°33′ N, 211°37′ W); and 8 were recorded in the intersection of highway E6 with road 104, hereafter referred to as Covell Corner (38°33′ N, 121°41′ W). All four of these locations shared a similar type of habitat where red-winged blackbirds are commonly found: a mix of wetlands (Conaway Ranch, Yolo Bypass Wildlife Area, and the Wetlands), grasslands, and/or cattails (Conaway Ranch, Yolo Bypass Wildlife Area, the Wetlands, and Covell Corner).

Males were also video recorded with a Sony Handycam HDR-CX260 placed on a tripod. While one observer was recording the visual displays, another one was recording the songs of the same individual. Observers' comments about the behavior of the focal male (e.g., which songs were produced by the focal male, whether he flew, etc.) were recorded both in the visual and audio files, allowing us to synchronize audio and video recordings of events. For each recording session, we also counted the number of males (singing or not) that were <50 m from our focal male.

Most noise in this study came from motor vehicles and airplanes. While recording each male, we occasionally measured the noise levels during silent intervals when the bird was not singing (mean=2.2 times per male). After we stopped recording the focal male, we also obtained six additional noise level measures pointing the microphone of a Larson Davis System 824 sound level meter (slow response; with wind screen) toward the sky and taking a measure every 10 s for 1 min. These measures (from when the bird was singing and afterwards) were averaged for each individual and used in further analyses. All amplitude measures are presented as A-weighted dB SPL (re 20 μPa). Because higher pitched sounds can attenuate more rapidly with distance than low frequencies in environments with objects (trees, bushes, and leaves; Bradbury and Vehrencamp 2011), we also obtained a measure of distance between the observer and the focal male whenever the bird was perching or changed to another perch. We used a Leupold RX-750 True Ballistic Laser Rangefinder for these readings.

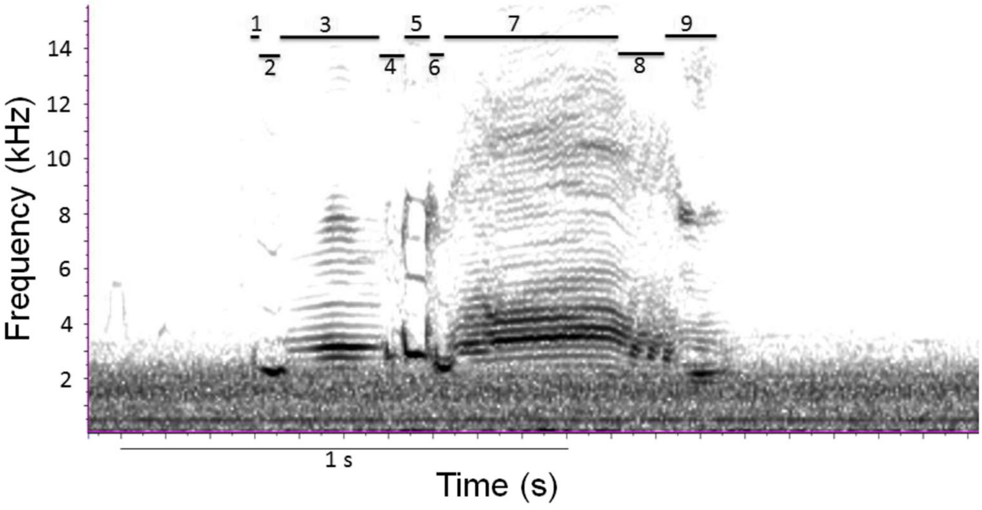
Song measures

With our total sample of 74 males, we calculated the proportion of males that sang songs with rattles (see discussion of rattles below). However, for further and more detailed song measures and analyses, we used a subset of 69 males where the recording quality was good enough for more detailed acoustic measures. For each of these males, song types were categorized by visual inspection of spectrograms, based on similarity of the content and order of syllables (Searcy and Yasukawa 1983; Patricelli et al. 2008). When we had more than two examples of a song type from a single male, we chose the two songs of each song type with the highest recording quality for measurements.

To measure the songs, we generated spectrograms and power spectra in Raven Pro v.1.4 (windows, Hann; FFT, 512; overlap, 50; frequency resolution, 86.1 Hz). For the entire song, we measured the following song parameters: song minimum and maximum frequencies (Hz) with power spectra (see below), song length (s) with spectrograms (see below), and song frequency range (song maximum frequency–song minimum frequency, Hz). We also counted the number of song syllables (visually distinctive traces in a song in the spectrogram) (Fig. 1) and obtained the syllable rate in the song (number of syllables/s). Temporal measures were done using spectrograms rather than waveforms, and syllables were also selected with spectrograms (see below). Obtaining durations of acoustic signals from spectrograms can potentially bias results due to background noise (Zollinger et al. 2012). To check whether our duration measures taken from spectrogram did not differ from temporal measures taken from waveforms, we randomly selected a subsample of 25 songs with rattles (each song from a different male) encompassing a noise range of 39–67 dB. We remeasured the length of the song, the length of a randomly taken syllable in the song, and the length of the rattle, using spectrograms and waveforms. We found that song length, syllable length, and rattle length did not differ between methods (paired *t* test: song length, $t=-1.07$, $df=24$, $P=0.292$; syllable length, $t=0.51$, $df=24$, $P=0.615$; rattle length, $t=1.09$, $df=24$, $P=0.284$).

To assess more detailed variation in the distribution of energy across the frequency range, we also obtained other frequency measures for each song syllable: peak frequency (the frequency with highest energy, Hz), first quartile frequency (the frequency that divides the sound in two parts containing 25 and 75 % of the energy, Hz), third quartile frequency (the frequency that divides the sound in two parts containing 75 and 25 % of the energy, Hz), frequency 5 % (the frequency that divides the sound into two intervals containing 5 and 95 % of the energy), and frequency 95 % (the frequency at which the energy is divided in two intervals containing 95 and 5 % of the energy). To obtain these acoustic attributes, syllables were selected using spectrograms; Raven automatically

Fig. 1 Red-winged blackbird song. A red-winged blackbird song recorded in Covell Corner. This song has nine different syllables (distinctive concentrations of energy). *Black lines with numbers* were added above each syllable to aid interpretation. Syllable 8 is a rattle



measured the acoustic attributes of the selections. All these song syllable attributes were averaged among syllables for each song. We also measured song tonality (Hanna et al. 2011). However, in preliminary analyses, we found a decrease in song tonality with higher noise levels (data not shown); this was probably a noise artifact, whereby higher background noise levels from our treatments increased entropy. Therefore, song tonality was not included in the final analyses.

Some songs had rattles, which are repetitions of the same element type (Fig. 1). An element was considered as a trace in the spectrogram within the rattle. Songs from other red-winged blackbird populations also show a sequence of syllable repetitions at the end of the song, typically called a "trill," which plays an important role in species recognition (Beletsky et al. 1980; Brenowitz 1982). However, the rattles we found in this population are slower and shorter than the trills found in other populations (compare Fig. 1 this study, with Figs. 1 and 2 in Kroodsma 1994), and are usually not the last syllable of the song. For this reason, we refer to the element sequences found in our study as rattles rather than as trills. A rattle was considered as a single syllable. For the rattles, we measured the same attributes as for the entire song as described above. We also counted the number of elements in each rattle and calculated their rate (rattle rate, elements/s). For descriptive purposes, and because the rattles are not always placed at the end of the song as is usually the case with the trills of other red-winged blackbird populations (see above), we also described the relative position of the rattles within the songs. We classified the rattles as being at the beginning, middle, or end of the song if it was located somewhere in the first part of the song (i.e., with more song syllables after than before the rattle), exactly in the middle of the song (i.e., with the same number of song syllables after and before the rattle), or in the second part of the song (i.e., with more syllables before than after the rattle), respectively.

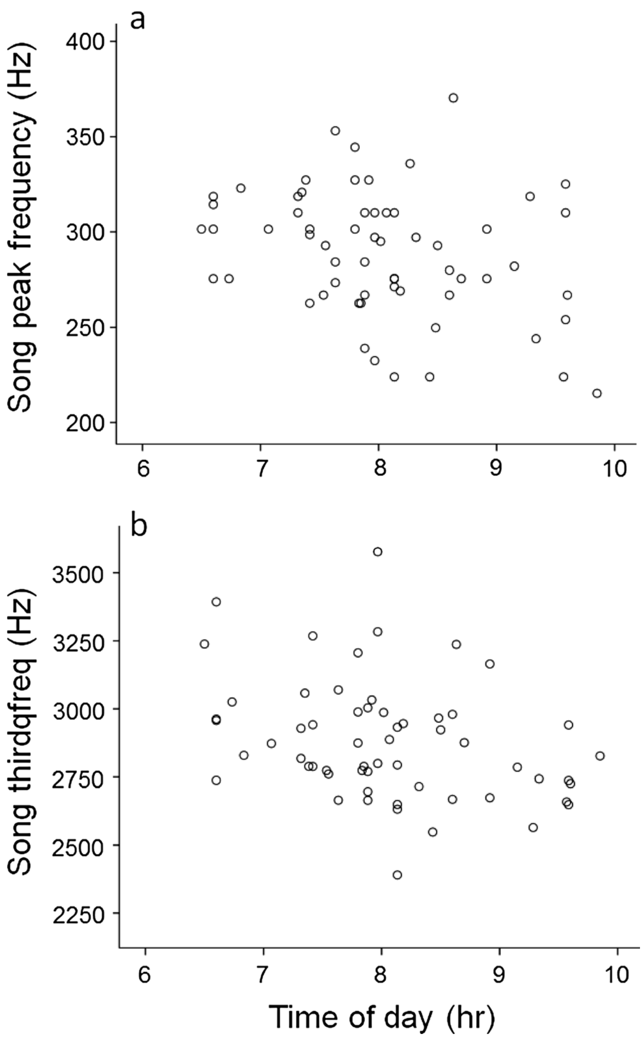


Fig. 2 Song peak frequency, song thirdqfreq (third quartile frequency), and time of the day. Birds apparently sang songs with a lower peak frequency (**a**) (P=0.022), and song thirdqfreq (**b**) (P=0.028) later in the morning. Time of the day is given in hours (i.e., 6.5 h=6:30AM)

To measure the minimum and maximum frequencies of each complete song and rattles, we used a power spectrum to determine the frequency that corresponded to a drop in energy of 10 dB from the amplitude of the peak frequency; we took as the song minimum and maximum frequencies those that corresponded to this drop in the lower and higher part of the frequency axis, respectively. The advantage of this technique is that it is not prone to observer bias, and the resulting measure is not affected by the level of background noise (Podos 1997).

Measuring the minimum and maximum frequency of songs with a 20-dB threshold did not change the direction of our results (data not shown), but considerably reduced the sample size (from 69 to 59 males).

Scoring visual displays

We scored the visual display following Peek (1972). We used his scale, and terminology, ranging from 1 to 4, with one being an incipient visual display and four representing a high intensity visual display. An incipient display (1) corresponds to a condition where the singing bird keeps its wings folded and the tail is slightly fanned; a low intensity display (2) occurs when the wings are moved away from the body and the tail is lowered and fanned; a moderate display (3) refers to a display where the wings are well extended from the body, the tail lowered and fanned, and the epaulets raised and exposed; and a high intensity song spread (4) occurs when the individual fully extends its wings from the body, the tail is extremely lowered and the bird has a disc-like shape (Peek 1972). For photographs of different intensities, see Nero (1956). For each measured song, we scored its associated visual display.

Statistical analyses

We examined the relationships between each of our noncorrelated song attributes (see below) and several independent variables: noise level, locality, date, time of day, distance from the observer to the focal bird, and number of males within 50 m. Most acoustic and visual measures were normally distributed (Kolmogorov–Smirnov, $P>0.05$), except song maximum frequency, and number of song types sang by each male.

Some song attributes were intercorrelated (Table 1). We checked song maximum frequency separately as it was not normally distributed. This song attribute was also correlated with other song parameters: Song maximum frequency was correlated with song frequency range ($r=0.951$, $P<0.001$, $n=68$), and with song frequency 95 % ($r=0.417$, $P=0.001$, $n=67$). For further analyses, we used only those song parameters that were not intercorrelated, that is, song minimum frequency, song peak frequency, song third quartile frequency, song frequency 95 %, and number of song syllables. Some rattle attributes were also intercorrelated (Table 2). As with song variables, for further analyses, we used only those rattle attributes that were not correlated, that is, rattle minimum frequency, rattle frequency range, and rattle rate. The noncorrelated attributes were entered into stepwise regression analyses (where measures were entered stepwise) as dependent variables to investigate a possible relation with any of our independent variables (noise level, site, date, time of day, number of males within 50 m, and distance from the observer to the bird). We averaged song measures for each individual so that each data point represents a single individual in the analyses. The intensity of the visual display was also analyzed with a stepwise regression, taking into account all the independent variables. The scored visual displays were averaged for each male, and these values entered into the stepwise regression model, so each data point represents a single bird. Number of different song types sang by each male was not normally distributed and was analyzed with Spearman correlation (to check for a correlation with noise, date, distance, number of males, and time of day) and Kruskal–Wallis test (to check for differences among localities). We used SPSS Statistics v.17.0 for all statistical analyses.

Results

General

Individuals were recorded a mean (±SE) of 174.7±28.9 s (range, 7–1158 s). We recorded 540 songs from the total sample of 74 males (mean±SD=7.3±5.6 songs per male). Within this sample, we found that some males sang only one song type during the recording bout, while others produced up to three song types (mean±SD=1.3±0.60 song types per male). From the total sample of 74 males, 43 (58.10 %) produced songs without rattles, 23 (31.08 %) produced songs with rattles, and 8 (10.81 %) produced a combination of songs with and without rattles. The 31 males that produced songs with rattles sang 38 different song types with rattles. The rattle of the majority of these song types (26 song types, 68.42 %) was placed somewhere at the end of the song; 7 song types (18.42 %) had their rattle somewhere at the beginning of the song; 4 song types (10.52 %) had two rattles, one at the beginning and one at the end of the song; we found only one song type (2.63 %) with its rattle at the middle of the song. For definitions of "at the end of the song," "at the beginning of the song," and "at the middle of the song," see above ("Song measures"). Only five song types had their rattle at

Table 1 Pearson correlation coefficients for song attributes that conformed to a normal distribution

	SongLenght	FreqRange	PeakFreq	FirstqFreq	ThirdqFreq	Freq5	Freq95	#Syllables	SyllableRate
MinFreq	-0.414**	0.446**	-0.048	0.552**	0.117	0.591**	-0.041	-0.349**	0.001
SongLenght	–	0.188	-0.101	-0.324**	-0.222	-0.319**	-0.179	0.578**	0.347**
FreqRange	–	–	0.053	-0.214	0.142	-0.237	0.453**	0.273*	0.112
PeakFreq	–	–	–	0.183	0.080	0.001	-0.084	-0.024	0.086
FirstqFreq	–	–	–	–	0.530**	0.903**	0.23	-0.127	0.153
ThirdqFreq	–	–	–	–	–	0.425**	0.574**	0.037	0.244*
Freq5	–	–	–	–	–	–	0.154	0.131	0.162
Freq95	–	–	–	–	–	–	–	0.019	0.184
#Syllables	–	–	–	–	–	–	–	–	0.548**

Some song attributes were intercorrelated. Because Bonferroni correction can entail some problems (e.g., inflating type II error, Moran 2003; Nakagawa 2004), *P* values were not subjected to Bonferroni correction

SongLenght song length, *FreqRange* frequency range, *PeakFreq* peak frequency, *FirstqFreq* first quartile frequency, *ThirdqFreq* third quartile frequency, *Freq5* frequency 5 %, *Freq95* frequency 5 %, *#Syllables* number of syllables, *SyllableRate* syllable rate

*Correlation is significant at the 0.05 level, ** correlation is significant at the 0.01 level

the very end of the song (i.e., the rattle being the last syllable in the song).

For further analyses, we used a subset of 69 males from whom we obtained higher-quality recordings; this encompassed a wide range of noise levels (see below, "Noise levels"). Most males (67 out of 69, 97 %) did not share song types in our sample. Even though we recorded a total of 540 songs, when we had more than two songs of the same type per male, we chose to measure only two of them; this was done for a subset of 69 males (see "Song measures"). Thus, we measured a total of 154 songs (mean±SD=2.2±0.95; range, 1–5 songs/male) for detailed acoustic analyses. Table 3 shows descriptive statistics for each of the measured song and visual attributes.

Noise levels

Noise levels differed between some localities (ANOVA: $F_{3, 65}=22.68$, $P<0.001$). However, some localities did not significantly differ from each other: Conaway Ranch did not differ from Covell Corner ($P=0.167$), and Covell Corner showed a nonsignificant tendency to have lower noise levels than the Yolo Bypass Wildlife Area ($P=0.061$). Although we covered a wide range of noise level among localities [range=39–67 dB(A)], overall noise levels overlapped among them: the Wetlands [mean±SD=44±3 dB(A), range=39–49 dB(A)], Conaway Ranch [mean±SD=48±4 dB(A), range=39–59 dB(A)], Covell Corner [mean±SD=52±4 dB(A), range=

Table 2 Pearson correlation coefficients for rattle attributes

	MaxFreq	RattleLenght	FreqRange	PeakFreq	FirstqFreq	ThirdqFreq	Freq5	Freq95	#Elem	ElemRate
MinFreq	0 .552**	−0.097	−0.346	0.757**	0.907**	0.701**	0.931**	0.698**	0.073	0.002
MaxFreq	–	0.211	0.591**	0.727**	0.750**	0.861**	0.703**	0.921**	0.279	−0.087
RattleLenght	–	–	0.331	−0.141	−0.113	0.050	−0.100	0.051	0.140	−0.595**
FreqRange	–	–	–	0.085	−0.034	0.292	−0.109	0.362	0.243	−0.100
PeakFreq	–	–	–	–	0.929**	0.758**	0.837**	0.760**	0.472*	0.341
FirstqFreq	–	–	–	–	–	0.842**	0.968**	0.825**	0.293	0.185
ThirdqFreq	–	–	–	–	–	–	0.802**	0.946**	0.236	0.018
Freq5	–	–	–	–	–	–	–	0.771**	0.147	0.077
Freq95	–	–	–	–	–	–	–		0.267	0.014
#Elem	–	–	–	–	–	–	–	–	–	0.641**

Some rattle attributes were intercorrelated. Because Bonferroni correction can entail some problems (e.g., inflating type II error, Moran 2003; Nakagawa 2004), *P* values were not subjected to Bonferroni correction

Abbreviations as in Table 1, except *RattleLength* rattle length, *#Elem* number of elements, *ElemRate* element rate

*Correlation is significant at the 0.05 level, ** correlation is significant at the 0.01 level

Table 3 Descriptive statistics of measured song and rattle parameters, and visual display

	n	Minimum	Maximum	Mean	SD
Song minimum frequency (Hz)	59	793	2150	1550	301
Song maximum frequency (Hz)	68	3346	9567	6379	1493
Song frequency range (Hz)	69	1309	8054	4824	1626
Song peak frequency (Hz)	69	2067	3703	2895	353
Song first quartile frequency (Hz)	67	1991	2863	2405	186
Song third quartile frequency ((Hz)	67	2390	3576	2873	218
Song frequency 5 % (Hz)	67	1754	2616	2082	189
Song frequency 95 % (Hz)	67	2947	5455	3714	501
Song length (s)	69	0.52	1.26	0.97	0.17
Number of song syllables	69	4	11.5	7	1.52
Song syllable rate (syllables/s)	69	4.86	12.12	7.3	1.4
Rattle minimum frequency (Hz)	27	1327	3053	2327	353
Rattle maximum frequency (Hz)	27	2535	4541	3499	413
Rattle frequency range (Hz)	27	270	1956	1172	366
Rattle peak frequency (Hz)	27	1808	3466	2729	335
Rattle first quartile frequency (Hz)	27	1808	3186	2650	303
Rattle third quartile frequency (Hz)	27	2088	3876	3062	363
Rattle frequency 5 % (Hz)	27	1615	3100	2489	326
Rattle frequency 95 % (Hz)	27	2347	4263	3328	416
Rattle length (s)	27	0.05	0.29	0.125	0.04
Number of rattle elements	27	3	10.75	5.32	1.99
Rattle rate (elements/s)	27	19.28	83.33	47.11	20.17
Visual display (score)	67	1	4	2.13	0.90

Visual display (score)=intensity in visual display. See song measures for a description of each variable. N size varies across song attributes and visual display score because for some males we could not obtain a reliable measure

Mean mean values obtained among males, *SD* standard deviation of the mean, *Minimum* mean minimum value, *Maximum* mean maximum value, *N* number of males

47-57 dB(A)], and Yolo Bypass Wildlife Area [mean±SD= 57±7 dB(A), range=50–67 dB(A)].

Song attributes

When we considered our song attributes, we found that song minimum frequency was not related to any of our independent variables and, thus, did not enter the model.

We recorded songs with lower peak frequency and lower third quartile frequency during later times of the day (stepwise regression: $R^2=0.111$, song peak frequency, $\beta=-124.68$, SE=52.68, $P=0.022$, Fig. 2a; $R^2=0.105$, song third quartile frequency, $\beta=-72.35$, SE=31.87, $P=0.028$, Fig. 2b). Song frequency 95 % was not associated with any of our independent variables, and these were not entered into the model. Birds in noisier places sang songs with less syllables than their counterparts in quieter areas (stepwise regression: $R^2=0.195$; noise, $\beta=-0.107$, SE=0.032, $P=0.002$, Fig. 3). Shorter songs may be associated with a higher song rate; however, we found no significant association between number of song syllables and song rate (Pearson's correlation: $r=0.11$, $P=0.398$, $n=55$) or between song rate and noise level (Pearson's correlation: $r=-0.04$, $P=0.779$, $n=55$).

When the stepwise regressions were performed on rattle attributes, we found no association between rattle minimum frequency, rattle length, and rattle frequency range, and our independent variables; thus, these independent variables were not entered into the model. We found that, in noisier places, birds sang slower rattles (stepwise regression: $R^2=0.248$; rattle rate, $\beta=-1.232$, SE=0.52, $P=0.030$, Fig. 4). Slower rattles were a product of singing rattles with fewer elements (Pearson's correlation, rattle rate vs. number of elements in the rattles: $r=0.641$, $P<0.001$, $n=27$, Table 2, Fig. 5a) and of increasing rattle length (Pearson's correlation, rattle rate vs. rattle length: $r=-0.599$, $P=0.001$, $n=27$, Fig. 5b). When an outlier was removed from this last correlation, the association between rattle length and rattle rate was still significant ($r=-0.606$, $P=0.001$, $n=26$, Fig. 5b). The number of elements in rattles was not significantly correlated to noise level ($r=-0.304$, $P=0.124$, $n=27$, Fig. 6a). Rattles were longer in noisy places ($r=0.485$, $P=0.010$, $n=27$, Fig. 6b). However, this correlation was dependent upon an outlier; after removing

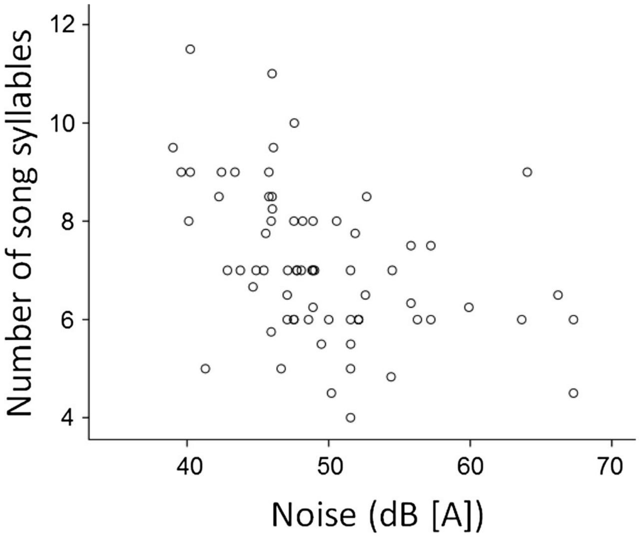


Fig. 3 Number of song syllables and noise level. Birds sang songs with fewer syllables in noisier places (P=0.002)

this data point, the association became nonsignificant (r=0.28, P=0.165, n=26, Fig. 6b). Number of song types sung by each male was not related to noise level, distance, number of males, date, time of day (Spearman's correlation, P>0.3 in all) or to locality (Kruskal–Wallis, P>0.7).

Visual display

No independent variable (noise, site, date, time of day, number of neighbors, and distance) explained variation in the intensity of the visual display, and thus, none were entered into the stepwise regression model.

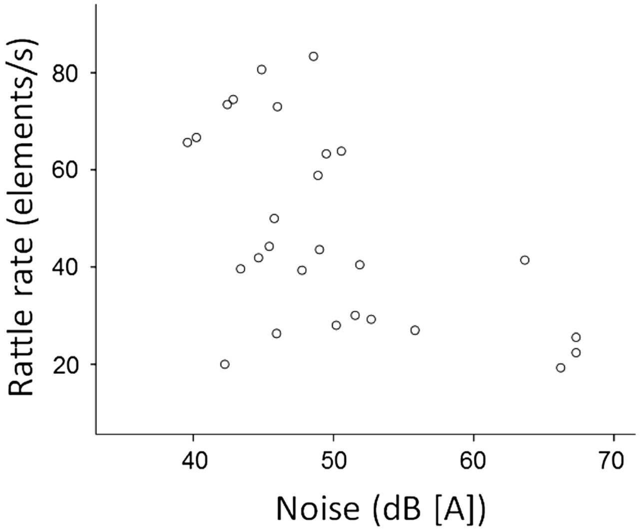


Fig. 4 Rattle rate and noise level. Rattles within songs were produced at a slower rate in noisy places (P=0.030)

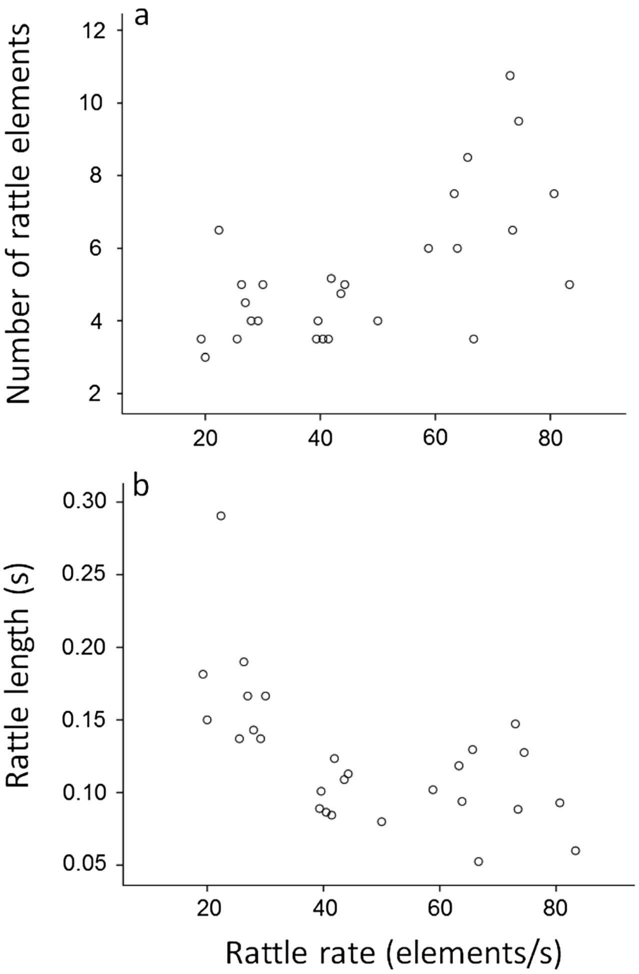


Fig. 5 Rattle rate, number of rattle elements, and rattle length. Slower rattle rates were achieved by decreasing the number of rattle elements (**a**) (P<0.001) and by increasing rattle length (**b**) (P=0.001). When the outlier (higher point in the Y-axis in **b** was removed, this last correlation was still significant (P=0.001).

Discussion

Acoustic communication in noise

We found that male red-winged blackbirds produced songs with fewer syllables in areas where noise levels were higher. This decrease in number of syllables was not related to increased song repetition rate, suggesting that males are not producing shorter songs to increase song rate and improve the chances of signal detection under intermittent noisy conditions. Previous studies in different animal taxa have found an increase in syllable length (e.g., Brumm et al. 2004; Foote et al. 2004; Love and Bee 2010; Bermúdez-Cuamatzin et al. 2011) and evidence for increased song length or number of song elements (Francis et al. 2011; Ríos-Chelén et al. 2013) with increased noise. These changes are consistent with signal detection theory, which predicts that longer signals are easier to detect and discriminate under noisy conditions (Brumm and

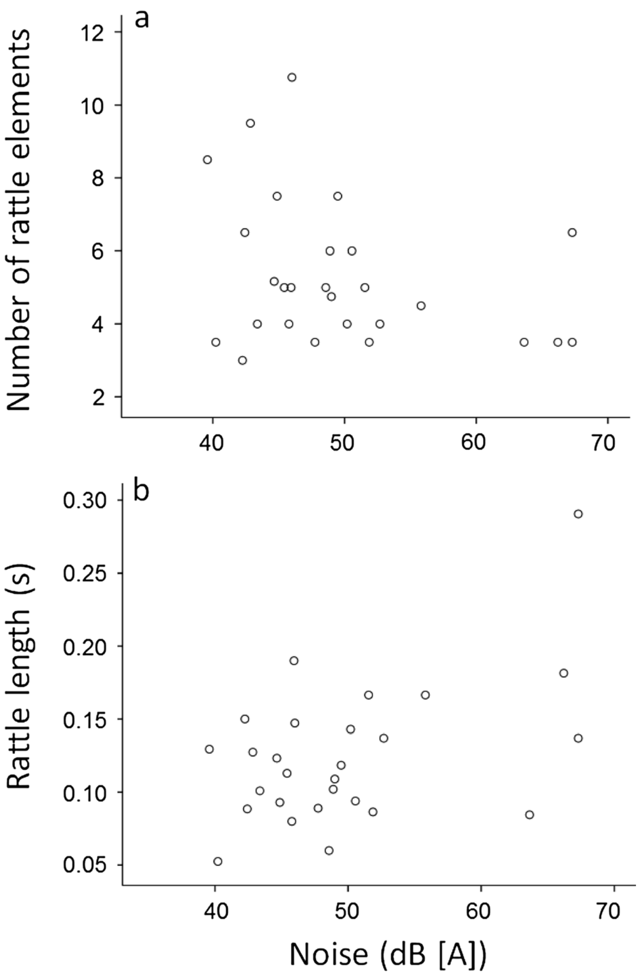


Fig. 6 Noise, number of rattle elements, and rattle length. Noise level was not significantly correlated with the number of rattle elements (**a**) (P=0.124). As noise level was higher rattles were longer (**b**) (P=0.010). However, this correlation should be taken causiously because, after removing the outlier (upper data point), this correlation became nonsignificant (P=0.165)

Slabbekoorn 2005; Wiley 2006). Thus, we find it difficult to explain our finding of songs with fewer syllables in noisier places as a possible adaptation to noise. However, our result is consistent with that from other studies that have found shorter songs in noisier areas (e.g., Fernández-Juricic et al. 2005; Slabbekoorn and den Boer-Visser 2006; Verzijden et al. 2010; Francis et al. 2011; Proppe et al. 2011; McLaughlin and Kunc 2013). Verzijden et al. (2010) speculated on the possibility that shorter songs come about by removing the syllable(s) with lowest frequency, which could increase the overall signal/noise ratio of the song. The fact that we did not find a significant association between noise and song minimum frequency casts doubts on this possibility for our study. This negative result cannot be explained by differences in noise levels between this and other studies since we included similar or even bigger ranges in noise levels than other previous studies that found an association between noise and vocal attributes (e.g., Slabbekoorn and Peet 2003; Brumm et al. 2004; Love and Bee 2010; Bermúdez-Cuamatzin et al. 2011). Similar to our study, another study with red-winged blackbirds also found songs with fewer syllables in noisier places (Cartwright et al. 2014). It is possible that the number of syllables is correlated with another unmeasured song parameter such as song amplitude and that birds face a trade-off between singing loud and long songs in noisy areas. It would be interesting in future studies to investigate whether red-winged blackbirds produce louder vocalizations in noisy places as has been found for several bird species and other animals (review in Brumm and Zollinger 2011), and whether different song types are associated with different amplitudes.

Although several studies have found a positive correlation between song frequency measures and noise levels (reviews in Brumm and Slabbekoorn 2005; Patricelli and Blickley 2006; Ríos-Chelén 2009; Brumm and Zollinger 2013; Gil and Brumm 2014), most oscine passerines studied so far do not increase the minimum frequency of their vocalizations in response to noise. Of 48 investigated oscine species in studies that looked at vocal parameters in relation to noise (Table 7.3 in Brumm and Zollinger 2013), 29 species (60.4 %) were reported to show some change in frequency measure (including the minimum frequency), but only 20 species (41.6 %) were reported to show changes in minimum frequency (review in Brumm and Zollinger 2013). Ríos-Chelén et al. (2012) found that the minimum frequency of learnt vocalizations (i.e., oscine songs) show a tighter adjustment (i.e., bigger effect size) with noise levels than the minimum frequency of nonlearnt vocalizations (i.e., sub-oscine songs), presumably because the scope for song variation is related to the process of song learning (Kroodsma 1982). Studies on vocal pitch adjustment to noise for one type of presumably nonlearnt vocalization, bird call, have reported different results: While there are studies showing an association between noise and call minimum frequency (Leonard and Horn 2008; Potvin et al. 2011; Potvin and Mulder 2013), a recent study by Grace and Anderson (2015) found no association between the minimum frequency of Carolina chickadees (*Poecile carolinensis*)'s calls and noise levels. Grace and Anderson (2015) also remarked the importance of measuring minimum frequencies using power spectra (as we did in the present study), rather than from spectrograms, to avoid the possibility of measuring bias resulting from masking noise. A study in a different red-winged blackbird population in Canada found no association between noise and the minimum frequency of trills (Hanna et al. 2011). Thus, the evidence supports the idea that red-winged blackbirds do not change the minimum frequency of the trill (Hanna et al. 2011) or the song (this study) to deal with noise. Nemeth and Brumm (2010) showed that an increase in song amplitude has a larger effect on communication distance than an increase in song pitch. However, a shift in frequency may be a valuable mechanism by which some birds respond to noise (see also Potvin and Mulder 2013).

We also found that song peak frequency and song third quartile frequency were negatively related to time of day, a variable that has not been included in many previous studies. On average, we recorded lower pitched songs later in the morning. The fact that some other correlative studies have not included time of day rises the possibility that some of the reported results in the literature have been confounded with this variable. It is known that higher frequency sounds are more attenuated than lower pitched ones in hot and dry air conditions (Wiley and Richards 1982; Slabbekoorn 2004; Catchpole and Slater 2008). If temperature rises and humidity decreases later in the morning, this could explain our negative association between song pitch and time of day. Alternatively, red-winged blackbirds may indeed be singing lower pitched song types later in the morning as a way to enhance sound transmission. These two nonmutually exclusive possibilities await further research.

We also found that birds produced slower rattle rates as noise levels were higher. Slower rattle rates result from a decrease in the number of rattle elements and an increase in the length of the rattle. Longer rattles are consistent with the idea that longer sounds are easier to detect (Brumm and Slabbekoorn 2005), and our results parallel previous studies that have found increased vocalization length with noise (e.g., Brumm et al. 2004; Foote et al. 2004; Love and Bee 2010; Bermúdez-Cuamatzin et al. 2011; Francis et al. 2011; Ríos-Chelén et al. 2013). Indeed, sounds of the order of a few hundred milliseconds, like rattles (mean, 125 ms, Table 3), are more easily detected (i.e., at a lowered amplitude) if they are longer (e.g., Dooling 1979; Dooling and Searcy 1985; Brown and Maloney 1986), and a recent study on great tits (*Parus major*) showed the benefits of increased detectability of longer sounds under natural and urban noisy conditions (Pohl et al. 2013). However, the interpretation that red-winged blackbirds are singing longer rattles in noisy places as a way to aid signal detection should be taken cautiously because the positive association between noise and rattle length was dependent upon one outlier. The association between noise and rattle rate was more robust. Some studies have found different repetition rates of acoustic elements (e.g., songs, elements, pulses) associated with different noise levels: in birds (e.g., Slabbekoorn and Smith 2002; Slabbekoorn and den Boer-Visser 2006), fishes (Picciulin et al. 2012), whales (Lesage et al. 1999), and frogs (Kaiser and Hammers 2009). It remains to be investigated whether different rattle rates convey a detection advantage in noisy conditions. In any case, noise-related modifications in rattles could have consequences if rattles convey important information to receivers. Previous studies have found evidence that trills convey species identity in other red-winged blackbird populations (Beletsky et al. 1980; Brenowitz 1982, 1983). However, this possibility is unlikely in our study population because, unlike many other red-winged blackbird populations where trills are present in all or nearly all songs, the majority of our males (58 %) did not include rattles in their songs during the sample period. Additionally, the rattles that we found were quite different from other rattle-like components (i.e., trills) reported for other populations (Beletsky et al. 1980; Brenowitz 1983; Searcy 1990; Patricelli et al. 2008): Our rattles are shorter, slower, and often present somewhere else in the song, rather than exclusively at the end (Fig. 1): From 38 song types with rattles, we found that the rattle of only five of them was the last syllable of the song. Further, Beletsky et al. (1980) found that in order for the trill to function in species recognition, it must be longer than 180 ms; this is longer than the mean rattle length in our population (Table 3). These results suggest that the rattles may not have the same species identification function as trills. Kroodsma (1994) similarly found songs without trills in other California red-winged blackbird populations. One possible explanation for a lack of trills in our sample (and lack of rattles in the majority of males) is that they were lost or altered through a process of character displacement, facilitating easier discrimination of songs from sympatric icterid species (Smith and Reid 1979; Yasukawa et al. 1980; Yasukawa 1981b; Brenowitz 1983). A study on red-winged blackbird songs by Hanna et al. (2011) found no differences in trill length when males were exposed to experimental noise, further suggesting that the rattle and trill have different functions.

Differences in great tit songs from noisy and quieter places seem to come about by singing different song types (Slabbekoorn and den Boer-Visser 2006). Because the majority of male red-winged blackbirds (97 %) in our sample did not share song types, our observed differences in songs (shorter songs and slower rattle rates in noisy places) can also be attributed to the production of different song types. Cartwright et al. (2014) also found that male red-winged blackbirds sing less in the morning and evening and show a less marked drop in song activity during midday in urban (noisy) habitats than in rural (more quiet) ones. Thus, it appears that birds in noisy places shift their song timing towards quieter times of the day. Hanna et al. (2011) found that tonality of red-winged songs was higher as noise increased. Thus, our study adds to the evidence of noise-related changes in red-winged blackbirds songs.

Visual communication in noise

We did not find support for our prediction that birds would perform the visual display in a more intense way in noisy conditions. One possible explanation for this finding is that males do not use the visual display as a backup signal to compensate for decreased efficacy of acoustic signals. There is evidence that visual and acoustic displays may function in different social contexts, suggesting that these traits convey different information. Peek (1972) proposed that red-winged blackbird songs function as a first line of territorial defense for long distances, while the visual display may function for shorter distance interactions. Peek (1972) found that males produced more visual displays of high intensity (levels 3 and 4) when a conspecific (male or female) was close to the focal male. Yasukawa (1978) found that the intensity of the visual display may be a signal of aggressive intent. Therefore, the intensity of the visual display in red-winged blackbirds depends at least in part on the social context in which they are produced (see also Yasukawa 1981a; Roskaft and Rohwer 1987; Metz and Weatherhead 1992). If visual and acoustic signals are varied in part in response to different social stimuli, this may preclude their use as redundant backup signals. In addition, this social influence complicates any predicted association between noise and the intensity of the visual display in an observational study such as this, where the social circumstances are not controlled. Similarly, a study with tree swallows (*Tachycineta bicolor*) found no association between the intensity of the posture when chicks were begging for food and noise levels (Leonard and Horn 2005). Finally, while we did not find evidence of an increased reliance on visual signals in areas where acoustic communication may be impaired by noise, it would be interesting to address this possibility in other species. This type of compensation may be more likely when visual and acoustic signals have similar functions and may serve as redundant signals (e.g., in the gray squirrel *Sciurus carolinensis*, Partan et al. 2010; review in Partan and Marler 2005).

In future studies, it would be important to further address the possible effects of noise-related changes in signals during social interactions. This is a subject that has started to be studied in a few bird species (Mockford and Marshall 2009; Ripmeester et al. 2010; Halfwerk et al. 2011b), but much more research is necessary to establish whether or not noise induced shifts in vocalization (and in other channels of communication) confer benefits and costs (Read et al. 2014) to animals in terms of, for example, communication efficacy, sexual selection, and reproduction.

Acknowledgments Ríos-Chelén was supported by a UC MEXUS-CONACYT fellowship. Support for the data collection was provided by UC MEXUS-CONACYT to AAR-CH, and by UC Davis and NSF grants (IOS-0925038 and IOS-1258217) to GLP. This project was approved by the U.C. Davis Institutional Animal Care and Use Committee (Protocol #16927). For advice and help in data collection and analysis, we thank Tom Hahn, Jessica Blickley, Alan Krakauer, Rene Beamonte, and members of the Patricelli Lab. We thank Mike Hall for allowing us to work in Conaway ranch, the Wetlands reserve, for allowing us to work in the Wetlands, and Jeff Stoddard for allowing us to work in the Yolo Bypass Wildlife Area. We are very thankful to Steve Funderburk who kindly read throughout the manuscript and detected typos and writing errors. We thank two anonymous reviewers who helped improving a previous version of this article. The authors declare that they have no conflict of interest.

Ethical standards This study complies with the current laws of the country in which it was performed.

References

Amézquita A, Hödl W (2004) How, when, and where to perform visual displays: the case of the Amazonian frog *Hyla parviceps*. Herpetologica 60:420–429

Beletsky LD, Chao S, Smith DG (1980) An investigation of song-based species recognition in the red-winged blackbird (*Agelaius phoeniceus*). Behaviour 73:189–203

Beletsky LD, Orians GH (1996) Red-winged blackbirds. Decision-making and reproductive success. The University of Chicago Press, Chicago

Bermúdez-Cuamatzin E, Ríos-Chelén AA, Gil D, Macías Garcia C (2009) Strategies of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use? Behaviour 146:1269–1286

Bermúdez-Cuamatzin E, Ríos-Chelén AA, Gil D, Macías Garcia C (2011) Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. Biol Lett 7:36–38

Blickley JL, Blackwood D, Patricelli GL (2012) Experimental evidence for the effects of chronic anthropogenic noise on abundance of greater sage-grouse at leks. Conserv Biol 26:461–471

Bradbury JW, Vehrencamp SL (2011) Principles of animal communication, 2nd edn. Sinauer, Sunderland, MA

Brenowitz EA (1982) Long-range communication of species identity by song in the red-winged blackbird. Behav Ecol Sociobiol 10:29–38

Brenowitz EA (1983) The contribution of temporal song cues to species recognition in the red-winged blackbird. Anim Behav 31:1116–1127

Brown CH, Maloney CG (1986) Temporal integration in two species of Old World monkeys: blue monkeys (*Cercopithecus mitis*) and grey-cheeked mangabeys (*Cercocebus albigena*). J Acoust Soc Am 79:1058–1064

Brumm H (2004) The impact of environmental noise on song amplitude in a territorial bird. Anim Ecol 73:434–440

Brumm H, Slabbekoorn H (2005) Acoustic communication in noise. Adv Stud Behav 35:151–209

Brumm H, Slater PJB (2006) Ambient noise, motor fatigue, and serial redundancy in chaffinch song. Behav Ecol Sociobiol 60:475–48

Brumm H, Voss K, Köllmer I, Todt D (2004) Acoustic communication in noise: regulation of call characteristics in a New World monkey. J Exp Biol 207:443–448

Brumm H, Zollinger SA (2011) The evolution of the Lombard effect: 100 years of psychoacoustic research. Behaviour 148:1173–1198

Brumm H, Zollinger SA (2013) Avian vocal production in noise. In: Brumm H (ed) Animal communication and noise, animal signals and communication 2. Springer-Verlag, Berlin, pp 187–227

Cardoso GC, Atwell JW (2011) On the relation between loudness and the increased song frequency of urban birds. Anim Behav 82:831–836

Cardoso GC, Atwell JW (2012) On amplitude and frequency in birdsong: a reply to Zollinger et al. Anim Behav 84:e10–e15

Cartwright LA, Taylor DR, Wilson DR, Chow-Fraser P (2014) Urban noise affects song structure and daily patterns of song production in Red-winged Blackbirds (*Agelaius phoeniceus*). Urban Ecosyst 17:561–572

Catchpole CK, Slater PJB (2008) Bird song. Biological themes and variations. Cambridge University Press, Cambridge

des Aunay GH, Slabbekoorn H, Nagle L, Passas F, Nicolas P, Draganoiu TI, Aunay GH, Slabbekoorn H, Nagle L, Passas F, Nicolas P, Draganoiu TI (2014) Urban noise undermines female sexual preferences for low-frequency songs in domestic canaries. Anim Behav 87:67–75

Díaz M, Parra A, Gallardo C (2011) Serins respond to anthropogenic noise by increasing vocal activity. Behav Ecol 22:332–336

Dooling RJ (1979) Temporal summation of pure tones in birds. J Acoust Soc Am 65:1058–1060

Dooling RJ, Searcy MH (1985) Temporal integration of acoustic signals by the budgerigar (*Melopsittacus undulatus*). J Acoust Soc Am 77: 1917–1920

Fernández-Juricic E, Poston R, De Collibus K, Morgan T, Bastain B, Martin C, Jones K, Treminio T (2005) Microhabitat selection and singing behavior patterns of male house finches (*Carpodacus mexicanus*) in urban parks in a heavily urbanized landscape in the western U.S. Urban Habitats 3:49–69

Foote AD, Osborne RW, Rus Hoelzel A (2004) Whale-call response to masking boat noise. Nature 428:910

Francis CD, Ortega CP, Cruz A (2009) Noise pollution changes avian communities and species interactions. Curr Biol 19:1415–1419

Francis CD, Ortega CP, Cruz A (2011) Different behavioural responses to anthropogenic noise by two closely related passerine birds. Biol Lett 7:850–852

Fuller RA, Warren PH, Gaston KJ (2007) Daytime noise predicts nocturnal singing in urban robins. Biol Lett 3:368–370

Gil D, Brumm H (2014) Acoustic communication in the urban environment: patterns, mechanisms, and potential consequences of avian song adjustments. In: Gil D, Brumm H (eds) Avian urban ecology. Oxford University Press, Oxford, pp 69–83

Gil D, Honarmand M, Pascual J, Pérez-Mena P, Macias-Garcia C (2015) Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. Behav Ecol 26:435–443

Grace MK, Anderson RC (2015) No frequency shift in the "D" notes of Carolina chickadee calls in response to traffic noise. Behav Ecol Sociobiol. doi:10.1007/s00265-014-1838-0

Grafe TU, Wanger TC (2007) Multimodal signaling in male and female foot-flagging frogs *Staurois guttatus* (Ranidae): an alerting function of calling. Ethology 113:772–781

Gross K, Pasinelli G, Kunc HP (2010) Behavioral plasticity allows short-term adjustment to a novel environment. Am Nat 176:456–464

Halfwerk W, Bot S, Buikx J, van der Velde M, Komdeur J, ten Cate C, Slabbekoorn H (2011a) Low-frequency songs lose their potency in noisy urban conditions. Proc Natl Acad Sci U S A 108:14549–14554

Halfwerk W, Holleman LJM, Lessells CM, Slabbekoorn H (2011b) Negative impact of traffic noise on avian reproductive success. J Appl Ecol 48:210–219

Halfwerk W, Slabbekoorn H (2009) A behavioural mechanism explaining noise-dependent frequency use in urban birdsong. Anim Behav 78:1301–1307

Hanna D, Blouin-Demers G, Wilson DR, Mennill DJ (2011) Anthropogenic noise affects song structure in redwinged blackbirds (*Agelaius phoeniceus*). J Exp Biol 214:3549–3556

Hebets EA, Papaj DR (2005) Complex signal function: developing a framework of testable hypotheses. Behav Ecol Sociobiol 57:197–214

Hu Y, Cardoso GC (2009) Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas? Behav Ecol 20: 1268–1273

Kaiser K, Hammers JL (2009) The effect of anthropogenic noise on male advertisement call rate in the neotropical treefrog, *Dendropsophus triangulum*. Behaviour 146:1053–1069

Kight CR, Saha MS, Swaddle J (2012) Anthropogenic noise is associated with reductions in the productivity of breeding eastern bluebirds (*Sialia sialis*). Ecol Appl 22:1989–1996

Kroodsma DE (1982) Learning and the ontogeny of sound signals in birds. In: Kroodsma DE, Miller EH, Ouellet H (eds) Acoustic communication in birds, vol 2. Academic Press, New York, pp 1–23

Kroodsma DE (1994) Song variation within and among populations of red-winged blackbirds. Wilson Bull 106:156–162

Leonard ML, Horn AG (2005) Ambient noise and the design of begging signals. Proc R Soc Lond B 272:651–656

Leonard ML, Horn AG (2008) Does ambient noise affect growth and begging call structure in nestling birds? Behav Ecol 19:502–507

Lesage V, Barrette C, Kingsley MCS, Sjare B (1999) The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River estuary, Canada. Mar Mammal Sci 15:65–84

Lohr B, Wright TF, Dooling RJ (2003) Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. Anim Behav 65:763–777

Love EK, Bee MA (2010) An experimental test of noise-dependent voice amplitude regulation in Cope's grey treefrog, *Hyla chrysoscelis*. Anim Behav 80:509–515

Luther D, Baptista L (2009) Urban noise and the cultural evolution of bird songs. Proc R Soc Lond B 277:469–473

Malacarne G, Cucco M, Camanni S (1991) Coordinated visual displays and vocal duetting in different ecological situations among Western Palearctic non-passerine birds. Ethol Ecol Evol 3:207–219

McClure CJW, Ware HE, Carlisle J, Kaltenecker G, Barber JR (2013) An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. Proc R Soc B 280: 20132290

McLaughlin KE, Kunc HP (2013) Experimentally increased noise levels change spatial and singing behaviour. Biol Lett 9:20120771

McMullen H, Schmidt R, Kunc HP (2014) Anthropogenic noise affects vocal interactions. Behav Process 103:125–128

Metz KJ, Weatherhead PJ (1991) Color bands function as secondary sexual traits in male red-winged blackbirds. Behav Ecol Sociobiol 28:23–27

Metz KJ, Weatherhead PJ (1992) Uncovering coverable badges in red-winged blackbirds. Anim Behav 43:223–229

Mockford EJ, Marshall RC (2009) Effects of urban noise on song and response behaviour in great tits. Proc R Soc Lond B 276:2979–2985

Moran MD (2003) Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos 100:403–405

Møller AP, Pomiankowski AN (1993) Why have birds got multiple sexual ornaments? Behav Ecol Sociobiol 32:167–176

Nakagawa S (2004) A farewell to Bonferroni: the problems of low statistical power and publication bias. Behav Ecol 15:1044–1045

Nemeth E, Brumm H (2009) Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? Anim Behav 78:637–641

Nemeth E, Brumm H (2010) Birds and anthropogenic noise: are urban songs adaptive? Am Nat 176:465–475

Nemeth E, Pieretti N, Zollinger SA, Geberzahn N, Partecke J, Miranda AC, Brumm H (2013) Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. Proc R Soc B 280:20122798

Nemeth E, Zollinger SA, Brumm H (2012) Effect sizes and the integrative understanding of urban bird song. Am Nat 180:146–152

Nero RW (1956) A behavior study of the red-winged blackbird. I. Mating and nesting activities. Wilson Bull 68:5–37

Partan SR (2013) Ten unanswered questions in multimodal communication. Behav Ecol Sociobiol 67:1523–1539

Partan SR, Fulmer AG, Gounard MAM, Redmond JE (2010) Multimodal alarm behavior in urban and rural gray squirrels studied by means of observation and a mechanical robot. Curr Zool 56:313–326

Partan SR, Marler P (2005) Issues in the classification of multimodal communication signals. Am Nat 166:231–245

Partecke J, Gwinner E (2007) Increased sedentariness in European blackbirds following urbanization: a consequence of local adaptation? Ecology 88:882–890

Partecke J, Gwinner E, Bensch S (2006) Is urbanisation of European blackbirds (*Turdus merula*) associated with genetic differentiation? J Ornithol 147:549–552

Partecke J, Van't Hof T, Gwinner E (2004) Differences in the timing of reproduction between urban and forest European blackbirds (*Turdus merula*): result of phenotypic flexibility or genetic differences? Proc R Soc Lond B 271:1995–2001

Patricelli GL, Blickley JL (2006) Avian communication in urban noise: causes and consequences of vocal adjustment. Auk 123:639–649

Patricelli GL, Dantzker MS, Bradbury JW (2008) Acoustic directionality of red-winged blackbird (*Agelaius phoeniceus*) song relates to amplitude and singing behaviours. Anim Behav 76:1389–1401

Peek FW (1972) An experimental study of the territorial function of vocal and visual display in the male red-winged blackbird (*Agelaius phoenicues*). Anim Behav 20:112–118

Picciulin M, Sebastianutto L, Codarin A, Calcagno G, Ferrero EA (2012) Brown meagre vocalization rate increases during repetitive boat noise exposures: a possible case of vocal compensation. J Acoust Soc Am 132:3118–3124

Podos J (1997) A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: emberizidae). Evolution 51:537–551

Pohl NU, Leadbeater E, Slabbekoorn H, Klump GM, Langemann U (2012) Great tits in urban noise benefit from high frequencies in song detection and discrimination. Anim Behav 83:711–721

Pohl NU, Slabbekoorn H, Neubauer H, Heil P, Klump GM, Langemann U (2013) Why longer song elements are easier to detect: threshold level-duration functions in the great tit and comparison with human data. J Comp Physiol A 199:239–252

Potvin DA, Mulder RA (2013) Immediate, independent adjustment of call pitch and amplitude in response to varying background noise by silvereyes (*Zosterops lateralis*). Behav Ecol 24:1363–1368

Potvin DA, Parris KM, Mulder RA (2011) Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (*Zosterops lateralis*). Proc R Soc Lond B 278: 2464–2469

Potvin DA, Parris KM, Mulder RA (2013) Limited genetic differentiation between acoustically divergent populations of urban and rural silvereyes (*Zosterops lateralis*). Evol Ecol 27:381–391

Proppe DS, Sturdy CB, St Clair CC (2011) Flexibility in animal signals facilitates adaptation to rapidly changing environments. PLoS One 6:e25413

Read J, Jones G, Radford AN (2014) Fitness costs as well as benefits are important when considering responses to anthropogenic noise. Behav Ecol 25:4–7

Rheindt FE (2003) The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? J Ornithol 114:295–306

Ripmeester EAP, Mulder M, Slabbekoorn H (2010) Habitat-dependent acoustic divergence affects playback response in urban and forest populations of the European blackbird. Behav Ecol 21:876–883

Ríos-Chelén AA (2009) Bird song: the interplay between urban noise and sexual selection. Oecol Brasil 13:153–164

Ríos-Chelén AA, Quirós-Guerrero E, Gil D, Macías Garcia C (2013) Dealing with urban noise: vermilion flycatchers sing longer songs in noisier territories. Behav Ecol Sociobiol 67:145–152

Ríos-Chelén AA, Salaberria C, Barbosa I, Macías GC, Gil D (2012) The learning advantage: bird species that learn their song show a tighter adjustment of song to noisy environments than those that do not learn. J Evol Biol 25:2171–2180

Roskaft E, Rohwer S (1987) An experimental study of the function of red epaulettes and the black body colour of male red-winged blackbirds. Anim Behav 35:1070–1077

Schroeder J, Nakagawa S, Cleasby I, Burke T (2012) Passerine birds breeding under chronic noise experience reduced fitness. PLoS One 7:e39200

Searcy WA (1990) Species recognition of song by female red-winged blackbirds. Anim Behav 40:1119–127

Searcy WA, Yasukawa K (1983) Sexual Selection and red-winged blackbirds: variation among individuals in mating success has played an important role in the evolution of sexual dimorphism. Am Sci 71: 166–174

Searcy WA, Yasukawa K (1995) Polygyny and sexual selection in red-winged blackbirds. Princeton University Press, Princeton, NJ

Slabbekoorn H (2004) Singing in the wild: the ecology of birdsong. In: Marler P, Slabbekoorn H (eds) Nature's music: the science of birdsong. Elsevier, San Diego, pp 178–205

Slabbekoorn H (2013) Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Anim Behav 85: 1089–1099

Slabbekoorn H, den Boer-Visser A (2006) Cities change the songs of birds. Curr Biol 16:2326–2331

Slabbekoorn H, Peet M (2003) Birds sing at higher pitch in urban noise. Nature 426:267–267

Slabbekoorn H, Smith TB (2002) Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. Evolution 56:1849–1858

Slabbekoorn H, Yang X-J, Halfwerk W (2012) Birds and anthropogenic noise: singing higher may matter. Am Nat 180:142–145

Smith WJ (1967) Displays of the vermilion flycatcher (*Pyrocephalus rubinus*). Condor 69:601–605

Smith DG, Reid FA (1979) Roles of the song repertoire in red-winged blackbirds. Behav Ecol Sociobiol 5:279–290

Swaddle JP, Page LC (2007) High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. Anim Behav 74:363–368

Tumer EC, Brainard MS (2007) Performance variability enables adaptive plasticity of 'crystallized' adult birdsong. Nature 450:1240–1244

Verzijden MN, Ripmeester EAP, Ohms VR, Snelderwaard P, Slabbekoorn H (2010) Immediate spectral flexibility in singing chiffchaffs during experimental exposure to highway noise. J Exp Biol 213:2575–2581

Warren PS, Katti M, Ermann M, Brazel A (2006) Urban bioacoustics: it's not just noise. Anim Behav 71:491–502

Wiley RH (2006) Signal detection and animal communication. Adv Study Behav 36:217–247

Wiley RH, Richards DG (1982) Adaptations for acoustic communication in birds. Sound transmission and signal detection. In: Kroodsma DE, Miller EH, Ouellet H (eds) Acoustic communication in birds, vol 1. Academic Press, New York, pp 132–181

Wood WE, Yezerinac SM (2006) Song sparrow (*Melospiza melodia*) song varies with urban noise. Auk 123:650–659

Yasukawa K (1978) Aggressive tendencies and levels of a graded display: factor analysis of response to song playback in the redwinged blackbird (*Agelaius phoeniceus*). Behav Biol 23:446–459

Yasukawa K (1981a) Song and territory defense in the red-winged blackbird. Auk 98:185–187

Yasukawa K (1981b) Song repertoire in the red-winged blackbird (*Agelaius phoeniceus*): a test of the beau geste hypothesis. Anim Behav 29:114–125

Yasukawa K, Blank JL, Patterson CB (1980) Song repertoires and sexual selection in the red-winged blackbird. Behav Ecol Sociobiol 7:233–238

Zollinger SA, Podos J, Nemeth E, Goller F, Brumm H (2012) On the relationship between, and measurement of, amplitude and frequency in bird song. Anim Behav 84:e1–e9