Urban Ecosyst (2014) 17:561–572
DOI 10.1007/s11252-013-0318-z

Urban noise affects song structure and daily patterns of song production in Red-winged Blackbirds (*Agelaius phoeniceus*)

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Abstract Traffic noise is becoming a more prominent fixture in urban environments as cities and highways expand to accommodate the growing human population. Birds, in particular, rely heavily on vocal communication and have recently been shown to change the structure of their signals in response to environmental noise. Our objective was to determine the impact of traffic noise on Red-winged Blackbird (*Agelaius phoeniceus*) song structure and song timing. We recorded bird songs using a directional microphone and installed permanent recording devices to monitor daily song patterns at both high traffic noise sites and low traffic noise sites throughout southern Ontario, Canada. Our results indicate that at sites with high traffic noise, Red-winged Blackbirds sing songs with fewer introductory syllables, which are an important component of individual recognition and repertoire formation. In addition, the typical diurnal singing pattern of birds associated with noisy urban sites is more homogeneous than that of birds associated with quiet rural marshes. In the early morning and evening, singing effort was higher at rural sites than at urban sites, while in the midday singing effort at urban sites was higher than at rural sites. Birds at our noisy urban sites appear to be avoiding acoustic masking by increasing song production during the quiet part of the day and decreasing song production during the noisy rush hour periods. Based on our results, urban noise is impacting communication structure and the daily pattern of song production in a marsh-nesting species. These results have important implications for avian conservation and land use planning for urban development.

Keywords Urbanization · Birds · Song · Marshes · Traffic

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Introduction

Communication requires the effective transmission of sound between animals. In birds, acoustic communication is particularly important and has many functions including territory defence, mate selection and pair bond maintenance (Wiley 1994; Swaddle and Page 2007). Natural and anthropogenic noise, however, can mask avian signals and obscure the communication process, thereby decreasing the likelihood that acoustic signals are received properly by their intended receivers (Patricelli and Blickley 2006; Parris and Schneider 2009; Barber et al. 2010). With growing levels of urbanization throughout the world (Hofmann 2001; Marzluff 2001; Guindon et al. 2009), urban noise may be impeding the ability of birds to communicate and survive in natural areas located in or near urban centres.

Some bird species have been shown to change the structural characteristics of their vocalizations in response to urban noise, which is primarily low frequency (<2 kHz) (Slabbekoorn and Peet 2003; Hanna et al. 2011). In the presence of noise, there are five mechanisms of a signal that could be modified to change the signal-to-noise ratio and change the probability of masking: frequency, amplitude, type of signal, tonality and timing of the signal (Rheindt 2003; Patricelli and Blickley 2006; Hanna et al. 2011). For example, several bird species have been shown to increase their minimum song frequency when environmental noise masks the lower frequencies of their songs (e.g. *Parus major*; Slabbekoorn and Peet 2003; *Melospiza melodia*; Wood and Yezerinac 2006; *Colluricincla harmonica*; Parris and Schneider 2009). In Red-winged Blackbirds (*Agelaius phoeniceus*), Hanna et al. (2011) found that when the frequency of the noise and song did not overlap, there was no change in the minimum frequency of the species' song but instead, an increase in the tonality of songs.

In addition to changing the structural characteristics of individual signals, birds can also avoid masking by producing signals during periods of the day when masking noise is low. For example, many birds avoid the natural masking effect of wind by participating in an early morning chorus prior to an increase in wind-related noise (Brenowitz 1982; Brown and Handford 2003; Halfwerk et al. 2011). Brenowitz (1982) found that Red-winged Blackbird songs travelled up to 189 m in the early morning when wind speed was low, but only 118 m in the afternoon when wind speed was at its peak. Brown and Handford (2003) investigated how wind specifically affects the transmission of songs for both the White-throated Sparrow (*Zonotrichia albicollis*) and the Swamp Sparrow (*Melospiza georgiana*). For these species, it was not transmission distance per se that was affected by wind in midday, but rather the consistency of the transmitted signal. They noted that if a signal was not being transmitted consistently, it would be difficult for the receiver to recognize the signaller, thus leaving ambiguity in the intended message. Masking by anthropogenic noise could also significantly affect the timing of bird vocalizations. Unlike wind and other natural sources of noise, urban noise, such as traffic, is a relatively recent occurrence, and birds may not have had sufficient time to adapt. It is therefore important to understand if and how bird species adapt to these sudden changes in their environment (Hanna et al. 2011).

Birds can adjust the timing of signal production in response to natural sound sources such as wind; however, there is very little evidence that bird species also adjust the timing of song production in response to daily patterns of anthropogenic noise. European Robins (*Erithacus rubecula*) provide a notable exception. In well lit and loud urban settings, European Robins were found to have adjusted their normal diurnal singing patterns to a nocturnal pattern, when urban noise is much lower (Fuller et al. 2007). This leads us to question whether or not other birds exhibit similar masking behaviour in response to traffic noise.

Generalist species, such as the Red-winged Blackbird, are ideal for studying the impacts of traffic noise on bird songs because they can be found in both noisy and quiet sites and breed in both wetlands and upland vegetation allowing for large sample sizes and broad conservation applicability. Building on previous observations by Hanna et al. (2011), who found that the trill portion of the Red-winged Blackbird song becomes more tonal in noisy environments, we want to investigate effects of noise on the number of introductory syllables and daily patterns of song production. The specific objectives of this research are to examine 1) song structure and 2) diurnal singing patterns of Red-winged Blackbirds breeding in marshes affected by varying levels of urbanization and traffic noise.

Materials and methods

We used two complementary approaches to compare singing behavior to ambient noise. First, we used high-quality focal recording equipment to accurately quantify song structure from certain individuals. Second, we used long-term recorders called SongMeters (Wildlife Acoustics Inc., Concorde, MA, USA) to quantify patterns of daily song production.

Song structure

We selected 11 marshes throughout southern Ontario that are impacted by varying degrees of traffic noise (Fig. 1, Tables 1 and 2). Bronte Creek, Mercer's Glen, Rattray Marsh and Van Wagner's Pond were surveyed between 19 May 2011 and 27 May 2011, and Brant Marsh, Cootes Paradise Marsh, Credit River, Fifteen Mile Creek, Jordan Harbour Marsh, Oakville Marsh and Wye Marsh were surveyed between 8 May 2012 and 30 May 2012. We used an Audio-Technica AT8015 directional microphone (Stow, OH, USA, frequency response 40–20,000 Hz) and a Marantz Portable Digital Recorder PMD 660 (WAVE format, 44.1 kHz sampling rate, 16 bits, Mahwah, JH, USA) to record vocalizations of individual birds. All songs were recorded without solicitation by playback, with an un-obstructed path between the microphone and the bird. The distance between the bird and the microphone was 17±5.1 m (mean ± SD).

We obtained recordings by walking along the edge of the marsh or walking through emergent marsh vegetation; all sampling was carried out only in fair weather conditions (no rain, light wind) between the hours of 0600 and 1000 on weekdays. We recorded an average of 17.4 songs (range 3–49) for each individual and excluded individuals that sang fewer than three songs. We excluded these individuals because one or two songs would likely not address the within-individual variation as well as three songs, although we did not analyze this directly (seven individuals were excluded). To ensure that we did not inadvertently record more than one individual twice within a wetland, we visually tracked the movement of each bird closely (keeping our eye on one bird while we transitioned to another). This was necessitated because our birds had not been colour-banded for individual identification. Immediately after recording each bird, we measured the ambient noise level (traffic noise) in decibels using a Checkmate Digital Sound Pressure Level Meter (Galaxy Audio, Wichita, KS, USA, A-weighting, fast response). The sound pressure level meter was held vertically at 1.3 m above the ground at the location where the directional microphone was taking recordings. We took six measurements at 10 s intervals and then calculated the mean.

Song timing

We used automated recording devices called SongMeters (Wildlife Acoustics Inc., Concorde, MA, USA) to record daily patterns of Red-winged Blackbird song production.

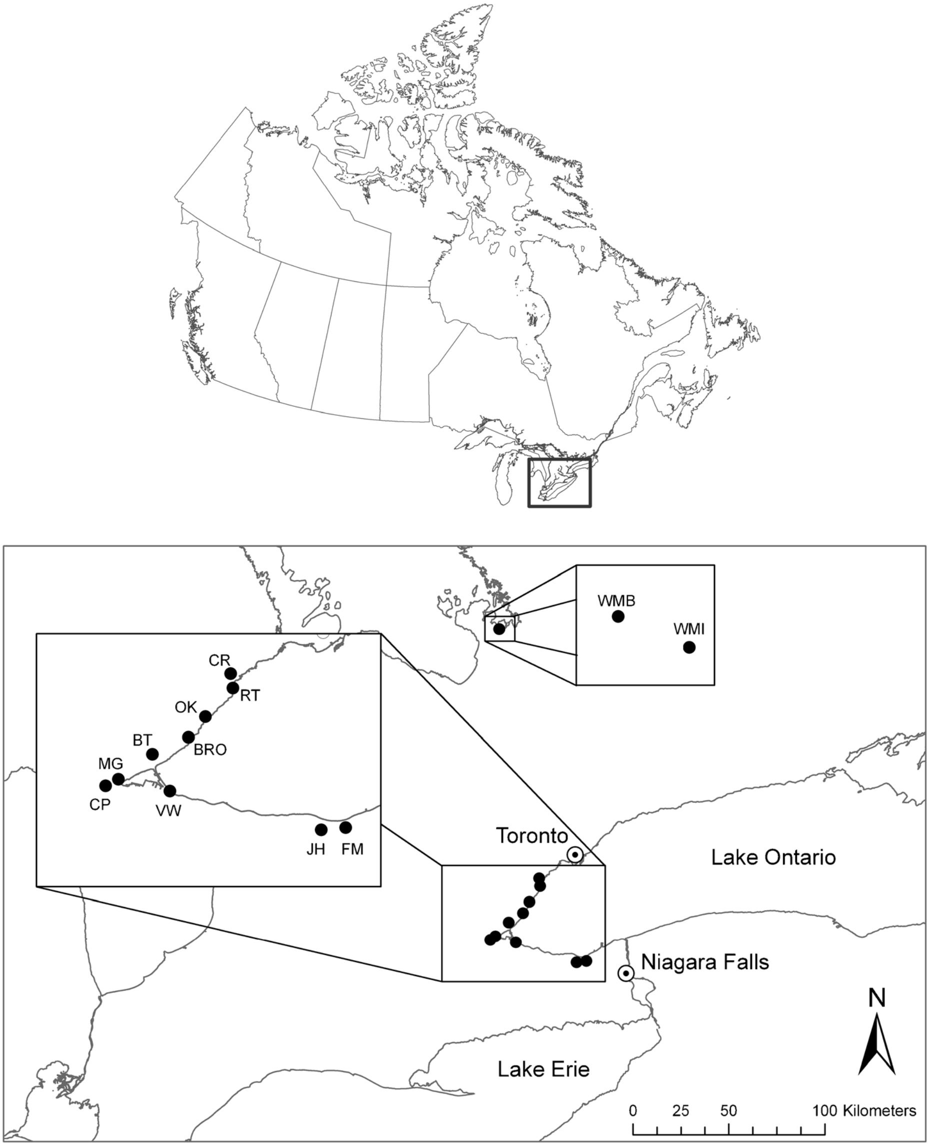

Fig. 1 Distribution of study sites in southern Ontario (Canada) surveyed between 2011 and 2012 including Brant Marsh (BT), Bronte Creek (BRO), Cootes Paradise Marsh (CP), Credit River Marsh (CR), Fifteen Mile Creek (FM), Jordan Harbour Marsh (JH), Mercer's Glen (MG), Oakville Marsh (OK), Rattray Marsh (RT), Van Wagner's Pond (VW) and Wye Marsh (WY) including Wye Marsh Island (WMI) and Wye Marsh Boardwalk (WMB)

This was more practical than having a researcher in the field enumerating songs throughout the day, and it also reduced unintended potential impacts of researcher presence on singing activity (Acevedo and Villanueva-Rivera 2006; Swiston and Mennill 2009).

The recorders were set-up near major highways in three urban marshes from 4 May 2011 to 17 June 2011 in the Golden Horseshoe region of Southern Ontario, Canada (Fig. 1); one each in West Hamilton (Mercer's Glen), East Hamilton (Van Wagner's Pond), and Southern

Table 1 Study site specifics for directional recordings of Red-winged Blackbird (RWBL) song structure. Sites that had a songmeter set-up are also indicated

Site name	Year surveyed (SM – songmeter, DR – directional recordings)	Number of RWBL's recorded	Average number of songs recorded per RWBL (range)	Total number of songs analyzed	Average ambient sound pressure level (dB) determined from directional recordings (range)
Brant Marsh	2012 – DR	8	17.3 (9–27)	138	56 (52.2–58.1)
Bronte Creek	2011 – DR	7	15.4 (4–23)	109	46.8 (45.6–48.2)
Cootes Paradise Marsh	2012 – DR	7	24.6 (8–40)	172	43.8 (42–45.3)
Credit River Marsh	2011 – SM 2012 – DR	6	23 (19–28)	115	49.3 (44.3–56.3)
Fifteen Mile Creek	2012 – DR	6	12.5 (4–22)	50	46.4 (42.6–50.1)
Jordan Harbour Marsh	2012 – DR	7	18 (4–41)	108	41.1 (37.6–42.7)
Mercer's Glen	2011 – DR, SM	8	10.9 (3–40)	86	62.9 (61–63.9)
Oakville Marsh	2012 – DR	8	17.6 (3–38)	141	46.5 (44.3–50)
Rattray Marsh	2011 – DR	6	21.2 (9–36)	127	43.6 (42.7–45.9)
Van Wagner's Pond	2011 – DR, SM	7	13.3 (4–21)	94	62.2 (59.5–65.1)
Wye Marsh	2011 – SM 2012 – DR	12	17.9 (4–49)	161	41 (39.3–42.9)

Mississauga (on the Credit River). We also used SongMeters to record at sites with no major traffic in order to compare urban sites (high traffic noise) to rural sites (low traffic noise). Two rural sites were used and were located in Wye Marsh, near Midland, Ontario (Fig. 1). Rural recordings were made from 20 June 2011 to 25 July 2011 with the same recording parameters. This temporal difference was because we only had three SongMeters available for our use. SongMeters were set up against a tree facing away from traffic noise and

Table 2 Study site characteristics. Distance measured was from the centroid of the sample points used to collect information on song structure to the edge of the marsh or the edge of the nearest road

Site name	Distance from sample points to marsh edge (m)	Distance from sample points to nearest road (m)
Brant Marsh	18	73
Bronte Creek	45	90
Cootes Paradise Marsh	0	415
Credit River Marsh	37	119
Fifteen Mile Creek	0	65
Jordan Harbour Marsh	139	150
Mercer's Glen	10	36
Oakville Marsh	36	117
Rattray Marsh	28	252
Van Wagner's Pond	53	53
Wye Marsh	175	982

towards marsh vegetation. The SongMeter recorders were programmed to record every half hour for fifteen-minute intervals, 24 h per day.

Our urban sites were characterized as those with a combination of high sound pressure levels (>51 dB), located directly adjacent to a busy highway (<119 m), and with a surrounding land cover consisting of >39 % impervious and pervious urban cover and roads within a 5,000 m radius buffer. Our rural sites were characterized as those with a combination of low sound pressure levels (<40 dB), located far from a busy highway (>982 m), and with a surrounding land cover consisting of <15 % impervious and pervious urban cover and roads within a 5,000 m radius buffer. All sites contained similar habitat with the primary emergent vegetation being cattails for Red-winged Blackbird nesting.

Since it was not practical to analyze all of the recordings collected during the study period (2,030 h), we used data that had been collected in the early part of the season at Mercer's Glen to determine variation in daily song patterns during three randomly selected days of the week (Monday, Tuesday and Wednesday) and three randomly selected days of the weekend (one Saturday and two Sundays). We noted the timing of general peaks and troughs over the course of a day to identify critical times that reveal the diurnal pattern during weekdays and weekends. We used Mercers Glen only to determine the time points for comparing urban and rural sites because Mercers Glen was an urban site and the song meters were set up in the urban sites early in the year (due to the equipment limitations mentioned above). We had to determine the time points while the urban SongMeters were still set up to visit them to determine the corresponding sound pressure levels at each urban site at each of our selected time points. Sound pressure level data were collected separately from the SongMeters using a SPL meter.

Based on this preliminary analysis, we determined that 6:30 (peak), 8:30 (trough), 10:00 (peak), 11:00 (trough), 14:00 (peak), 17:00 (neither a peak nor trough but an intermediate time) and 20:00 (peak) were critical times when songs should be monitored to determine the effect of traffic noise. These times were also chosen because they were evenly distributed throughout the day when the birds were singing, and included the full range of traffic conditions based on general knowledge of traffic patterns.

We measured the average ambient sound pressure level (dB) at each urban site at seven times throughout the day (6:30, 8:30, 10:00, 11:00, 14:00, 17:00, 20:00). Each urban site was visited in early June 2011 on one randomly chosen day during the week (Monday–Friday) and during the weekend (Saturday–Sunday), to capture a representative range of traffic noise during the daylight hours. All ambient sound pressure data were collected under fair-weather conditions. At each of the seven times during the day a total of 30 readings of sound pressure level were taken at each urban site; these consisted of ten readings at each of three randomly chosen locations along a transect in each marsh. The inclusion of three transect points was to account for spatial variability in noise attenuation from the highways. The rural sites were visited in late June 2011 during the week and readings of ambient sound pressure level were taken at each of the time points; however, readings were consistently below detection limit of our meter (i.e. <40 dB). We were unable to visit the sites during the weekend to measure the sound pressure level, but after listening to recordings from the weekend, we had no reason to believe the levels were any different than during the week. Therefore we considered rural ambient sound pressure levels to be 40 dB or lower at each of the seven times on weekdays and weekends.

Song structure analysis

We analyzed the trill component of the Red-winged Blackbird songs collected in 2011 to look for changes in duration, minimum frequency, maximum frequency, bandwidth (frequency range), quartiles (25, 50, 75) and entropy. Songs were analyzed with Avisoft SASLab Pro (version 4.38; R. Specht, Berlin, Germany) based on the same parameters as Hanna et al. (2011). We counted the number of introductory syllables prior to the trill for Red-winged Blackbird songs recorded both in 2011 and 2012 using Raven Pro (version 1.3; Cornell Lab of Ornithology, Ithaca, NY, USA). These syllables were counted by a "blind" researcher that was not made aware of the context of the study.

Song timing analysis

In addition to only counting songs at the seven specific times throughout the day, we excluded days with >1 mm of rain according to Environment Canada's archival weather data or when rain was detected during recordings, to avoid confounding effects of weather on singing activity (Bird Studies Canada 2012). This left us with an average of 12 days for each of the urban sites and 7 days for each of the rural sites. We listened to the 15-minutes of recording corresponding to the seven critical times of the day and counted the number of male Red-winged Blackbird territorial songs during these periods. A total of 126 h were analyzed. To enable comparisons across sites, we calculated the proportion of daily songs that occurred during each time interval by dividing the number of songs during a particular interval by the total number of songs recorded for that day.

Statistical analyses

We used simple linear regression to determine the impact of ambient sound pressure level (dB) on song structure parameters (trill duration, minimum frequency, maximum frequency, bandwidth, quartiles (25, 50, 75) and entropy) and on the number of introductory syllables. We first calculated an average per individual and then calculated an average for each marsh, and we used marsh as our statistical unit for these analyses. To determine the difference in song timing between weekdays versus weekends and urban versus rural, we conducted a repeated measures analysis of variance for each of the seven times after ArcSin Sqrt transformations (6:30, 8:30, 10:00, 11:00, 14:00, 17:00 and 20:00). Weekday vs. weekend was the repeated measure, urban vs. rural was the categorical predictor and singing effort was the dependent variable.

We were unable to conduct a similar analysis on the SPL data because our SPL readings were consistently below 40 dB at both of our rural sites (Wye Marsh Island and Wye Marsh Boardwalk). Therefore, we conducted a one-sample t-test comparing the mean SPL at the urban sites to 40 dB. We then did a dependent t-test comparing SPL between weekday and weekend at the urban sites at each of the seven times.

Results

Song structure

In 2011, we recorded 28 males and analyzed the song structure of 416 individual songs at four marshes. We found no significant relationship between ambient noise level and trill duration (R^2=0.055, $F_{1,2}$=0.116, p=0.766), minimum frequency (R^2=0.0003, $F_{1,2}$=0.0005, p=0.984), maximum frequency (R^2=0.150, $F_{1,2}$=0.354, p=0.612), bandwidth (R^2=0.322, $F_{1,2}$=0.948, p=0.433), 25th quartile (R^2=0.007, $F_{1,2}$=0.013, p=0.919), 50th quartile (R^2= 0.082, $F_{1,2}$=0.178, p=0.714), 75th quartile (R^2=0.028, $F_{1,2}$=0.057, p=0.833) or entropy

(R^2=0.074, $F_{1,2}$=0.159, p=0.728) using site average as our independent statistical unit. Between 2011 and 2012 we recorded a total of 82 males and 1,301 songs at 11 sites and found a significant negative relationship between ambient sound pressure level and the number of introductory syllables sung by Red-winged Blackbirds (R^2=0.769, $F_{1,9}$=29.9, p=0.0004; Fig. 2).

Song timing

When all data were considered, ambient sound pressure level was significantly higher at the urban sites (60.1 dB) compared to the rural sites (40 dB; t_2=9.11, p=0.011). There were significant differences in ambient sound pressure level between weekdays and weekends at the urban sites at 6:30 (t_2=7.27, p=0.018) and 20:00 (t_2=5.693, p=0.030). Ambient sound pressure level was higher on weekdays (62.1 dB) at 6:30 than weekends (57.0 dB), and lower on weekdays (58.1 dB) than weekends (60.3 dB) at 20:00.

There were no significant interaction effects for each time (all p>0.18) except for data collected at 8:30 ($F_{1,3}$=18.74, p=0.023) when examining song output. Therefore, we were able to interpret the main effects for most of our analyses. Differences between urban and rural sites were seen throughout the day, with both exhibiting parabolic patterns (Fig. 3). There were significant differences between the proportion of songs produced between urban and rural sites at 10:00 ($F_{1,3}$=15.9, p=0.028), 11:00 ($F_{1,3}$=17.8, p=0.024), 14:00 ($F_{1,3}$=114.5, p=0.002), and 20:00 ($F_{1,3}$=47.3, p=0.006; Fig. 3a, b).

The proportion of songs was higher at the rural sites than at urban sites at 20:00, and higher at the urban sites than at rural sites at 10:00, 11:00 and 14:00 (Fig. 3a, b). The proportion of songs was higher at the beginning and end of the day at the rural sites, with a drop in midday, whereas there was a more consistent proportion of songs throughout the day

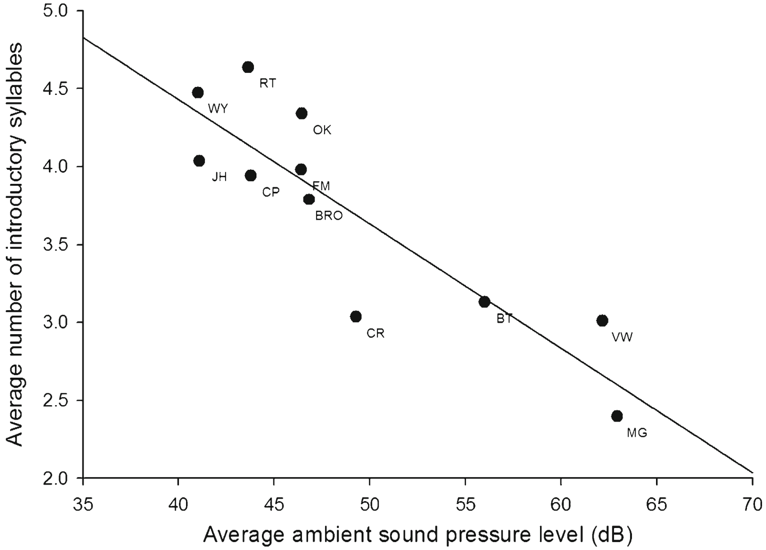

Fig. 2 Ambient sound pressure level impacts on the average number of introductory syllables sung by Red-winged Blackbirds at 11 marshes including Brant Marsh (BT), Bronte Creek (BRO), Cootes Paradise Marsh (CP), Credit River Marsh (CR), Fifteen Mile Creek (FM), Jordan Harbour Marsh (JH), Mercer's Glen (MG), Oakville Marsh (OK), Rattray Marsh (RT), Van Wagner's Pond (VW) and Wye Marsh (WY)

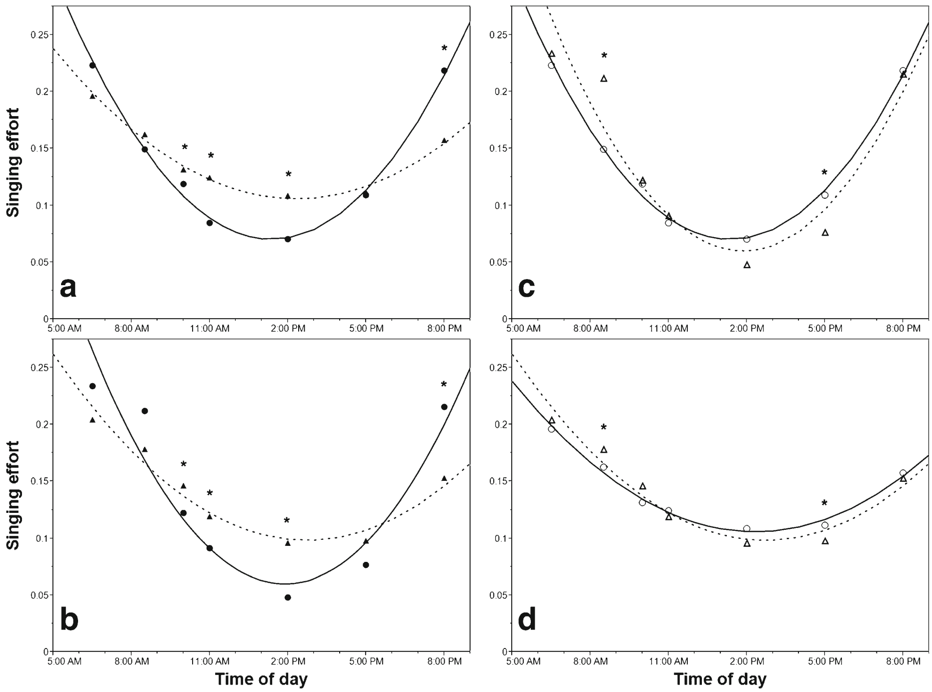

Fig. 3 Effects of time of day, urbanization and day of week on diurnal song pattern. Singing effort is shown as a proportion (number of songs at each time divided by the daily total number of songs). **a** Weekdays only, urban (*closed triangle*, *dashed line*), rural (*closed circle*, *solid line*); **b** weekends only, urban (*closed triangle*, *dashed line*), rural (*closed circle*, *solid line*); **c** Rural only, weekdays (*open circle*, *solid line*), weekends (*open triangle*, *dashed line*); **d** urban only, weekdays (*open circle*, *solid line*), weekends (*open triangle*, *dashed line*). Significant differences ($p<0.05$) are marked with an *

at the urban sites. Generally, the pattern at the urban sites was more homogeneous, with less pronounced peaks in the morning and evening and a smaller drop in midday. There was no significant difference between the proportion of songs produced between urban and rural sites at 17:00 ($F_{1,3}=2.13$, $p=0.240$) and there was a trend towards a greater singing effort at the rural sites compared with urban sites at 6:30 ($F_{1,3}=5.90$, $p=0.093$).

Our interaction effect at 8:30 indicated that singing effort was greater at urban sites on weekdays, but was greater at rural sites on weekends. Significant differences were also seen between weekdays and weekends at 17:00 ($F_{1,3}=15.8$, $p=0.028$; Fig. 3c, d), with greater singing efforts on weekdays. There was also a trend towards a decrease in singing at 14:00 on the weekends ($F_{1,3}=9.43$, $p=0.055$).

Discussion

Our study has shown that Red-winged Blackbirds are changing both their song structure and song timing in response to urbanization and traffic noise. Although we did not find any significant changes in song frequency, bandwidth, duration or entropy in the trill portion of the song, we did find a significant decrease in the number of introductory syllables sung before the trill. There were significantly fewer introductory notes sung by Red-winged Blackbirds breeding in noisy marshes than in quiet marshes.

With respect to song timing, Red-winged Blackbirds had a more homogeneous singing effort throughout the day in urban marshes compared to rural marshes. Birds in urban marshes sang more throughout the middle of the day (10:00, 11:00, 14:00) than did their rural counterparts. Despite our hypothesis that singing effort would be different between weekdays and weekends, we found little evidence to support this with differences between weekdays and weekends only significant at 17:00, with higher singing effort during the week.

The trill component of the song contains the species-specific information and acts primarily in territory defence (Brenowitz 1982). This portion of the song is intended for communication over relatively long distances and therefore we expected there to be a modification in trill structure with increasing urban noise. Contrary to our expectations, the trill component of the song did not show any changes in response to urban noise when we examined trill duration, amplitude, minimum and maximum frequency, frequency of quartiles, bandwidth and entropy. This could be due to the high background noise in our recordings that obscured the ability of our software to distinguish between changes in entropy or frequency of quartiles as found by Hanna et al. (2011), and we feel that this would have been a problem irrespective of the type of field-recording equipment. Hanna et al. (2011) sampled bird populations affected by 0.3–4 cars/min whereas our study examined bird populations affected by 8.3–86.7 cars/min and this caused higher background noise (Ontario Ministry of Transportation 2011, unpublished data). Therefore, our results can neither support nor refute the widely held belief that birds are changing the frequency characteristics of their songs in response to urban noise (Slabbekoorn and Peet 2003; Brumm 2004; Slabbekoorn and den Boer-Visser 2006; Wood and Yezerinac 2006; Leonard and Horn 2008; Hu and Cardoso 2010; Verzijden et al. 2010).

In our study, Red-winged Blackbirds sang fewer introductory syllables in noisy urban sites and these results are consistent with other studies (Verzijden et al. 2010; Potvin et al. 2011). We did not examine if the decrease in number of syllables caused the entire song to shorten as has been predicted by other studies (Slabbekoorn and den Boer-Visser 2006). Contrary to the trill component, the introductory syllables are not thought to function in species-specific recognition or be particularly important by themselves in territory defence (Brenowitz 1981; Brenowitz 1982); instead, they are thought to be responsible for individual recognition (Brenowitz 1982). Introductory syllables also form the basis for much of the variation in song repertoire (Yasukawa 1981). Based on the Beau Geste Hypothesis, song repertoires have evolved in birds to mimic sites with high density and therefore fool new males searching for territories into thinking the site is occupied by more males than are actually there (Howard 1974; Krebs 1977; Slater 1978). Based on this hypothesis, if the number of syllables in a song is reduced, the possibility of forming large repertoires should be limited in populations exposed to higher levels of traffic noise and this could potentially lead to increased competition, smaller territories and more males in general at a marsh.

Singing patterns between urban and rural sites were significantly different at many times throughout the day. Singing effort was more evenly distributed throughout the day for birds in urban sites compared to rural sites, with the rural sites maintaining the more characteristic morning and evening choruses of songbirds. The more even distribution of singing effort at urban sites may be a result of masking by traffic noise early in the morning and in the evening, making it more conducive for birds to sing more often in the middle of the day. The lack of significant differences at 8:30 and 17:00 may not have any ecological explanation as these times fall at the intersection points between the urban and rural curves, but it may be worth investigating in a future study. These results are consistent with the predictions and findings of other studies that have shown a change in diurnal song pattern in response to traffic patterns in urban areas (Warren et al. 2006; Fuller et al. 2007).

There were higher singing efforts on weekdays compared to weekends at 14:00 and 17:00. Unfortunately it is difficult to interpret these results because there were no significant differences in ambient sound pressure level between weekdays and weekends at these times. On weekdays in urban sites, the influence of rush hour may truncate the length of the morning chorus by making the birds reduce their singing to try and avoid wasting energy during times of increased masking. With a truncated morning chorus on weekdays, the males may feel a need to start the evening chorus early to ensure their messages are conveyed effectively, and this may have led to associated increases on weekdays compared to weekends at 14:00 and 17:00.

Future studies should be conducted to determine if adjusting the structure and timing of songs could have any fitness consequences. These could be increased intrusion pressure and trespassing rates by floater males if the Beau Geste hypothesis holds, and thus an increase in expended energy if direct competition ensues. There is also the potential for a reduction in mate acquisition if singing males are not being perceived by females during the normal early morning and evening song periods. The differences in song timing between urban and rural sites could also eventually lead to speciation and reproductive isolation of populations (Slabbekoorn and Peet 2003; Patricelli and Blickley 2006). Future studies may use this and other knowledge of Red-winged Blackbird ecology to determine actual fitness costs of living in noisy urban areas, including mating success, nest success, nest predation rates and energy costs.

Our experimental design took advantage of natural differences in acoustic environments that have resulted from urbanization. However, as is typical for urbanization, multiple factors varied together, such as ambient noise, the presence or absence of a highway, and the addition of urban cover. Although our focus was on ambient noise, and although we made precise measurements of ambient noise and showed that it explained much of the variation in vocal behaviour, we cannot exclude the possibility that these other factors also influenced vocal behaviour.

Residential building projects in Ontario alone are expected to eliminate at least 1,000 km^2 of rural lands between 2001 and 2021 (Hofmann 2001), and it is essential to understand the influence this will have on wildlife living in natural areas near urban centres. Overall, this study has shown that Red-winged Blackbirds breeding in urban marshes have changed both their song structure and song timing compared to Red-winged Blackbirds using rural marshes. We hope that this study will put additional pressure on city planners and wildlife managers to consider and advocate for the implementation of noise control measures near urban natural areas (Slabbekoorn and Ripmeester 2007).

Acknowledgments We gratefully acknowledge the significant contributions of the Royal Bank of Canada Blue Water Fund and the continued support from McMaster University over the years. Thank you to the landowners of the marshes including the Credit River Conservation Authority, Hamilton Conservation Authority, Royal Botanical Gardens and Wye Marsh Wildlife Centre. We would also like to thank two anonymous reviewers for providing valuable comments and suggestions to improve the manuscript. We are most grateful for assistance in the field and support from M. Cvetkovic, G. Fraser, J. Gilbert, C. Markle, L. Meng, C. Sommer, Y. Yee and all of the members of the Chow-Fraser lab for your support.

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