

Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization

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Abstract

More humans reside in urban areas than at any other time in history. Protected urban green spaces and transportation greenbelts support many species, but diversity in these areas is generally lower than in undeveloped landscapes. Habitat degradation and fragmentation contribute to lowered diversity and urban homogenization, but less is known about the role of anthropogenic noise. Songbirds are especially vulnerable to anthropogenic noise because they rely on acoustic signals for communication. Recent studies suggest that anthropogenic noise reduces the density and reproductive success of some bird species, but that species which vocalize at frequencies above those of anthropogenic noise are more likely to inhabit noisy areas. We hypothesize that anthropogenic noise is contributing to declines in urban diversity by reducing the abundance of select species in noisy areas, and that species with low-frequency songs are those most likely to be affected. To examine this relationship, we calculated the noise-associated change in overall species richness and in abundance for seven common songbird species. After accounting for variance due to vegetative differences, species richness and the abundance of three of seven species were reduced in noisier locations. Acoustic analysis revealed that minimum song frequency was highly predictive of a species' response to noise, with lower minimum song frequencies incurring greater noise-associated reduction in abundance. These results suggest that anthropogenic noise affects some species independently of vegetative conditions, exacerbating the exclusion of some songbird species in otherwise suitable habitat. Minimum song frequency may provide a useful metric to predict how particular species will be affected by noise. In sum, mitigation of noise may enhance habitat suitability for many songbird species, especially for species with songs that include low-frequency elements.

Keywords: anthropogenic noise, bird song, diversity, frequency, urban abundance

Received 2 November 2012; revised version received 2 November 2012 and accepted 7 November 2012

The human population is increasingly concentrated in urban areas (Cohen, 2003). One of the most significant effects of urbanization may be loss of ecological diversity, eliminating species whose habitats are altered or removed (McKinney, 2006). Loss of mature vegetation and habitat fragmentation contributes to urban homogenization by favoring those species that flourish in patchy, early successional habitats (Marzluff & Ewing, 2001; Fontana *et al.*, 2011). Urban parks that preserve large tracts of mature habitat may, therefore, be vital for the preservation of urban biodiversity (Fernandez-Juricic & Jokimaki, 2001). However, it is possible that otherwise suitable habitats may remain unused by many species due to other factors such as anthropogenic noise.

Human development is characterized by high levels of low-frequency noise (Katti & Warren, 2004). The consequences of anthropogenic noise may be substantial for animals: potentially reducing species richness and abundance, altering age structure, and decreasing

reproductive success (Habib *et al.*, 2007; Gross *et al.*, 2010; Halfwerk *et al.*, 2011). Songbirds may be particularly susceptible to noise because they rely heavily on acoustic signals for communication (Rabin *et al.*, 2003; Slabbekoorn & Ripmeester, 2008). Several studies have documented declines in songbird density and abundance in noisy habitats (Reijnen *et al.*, 1995; Reijnen & Foppen, 2006; Bayne *et al.*, 2008; Francis *et al.*, 2009).

A likely mechanism by which anthropogenic noise affects songbirds is through masking of the frequencies used for acoustic communication (Patricelli & Blickley, 2006). The low frequencies of anthropogenic noise overlap the frequencies used by many, but not all, songbirds (<4 kHz; Skiba, 2000). Species that sing at frequencies which are not overlapped by anthropogenic noise may be more likely to inhabit noisy areas (Rheindt, 2003; Hu & Cardoso, 2009; Goodwin & Shriver, 2011). These findings have led some to suggest that birds with higher song frequencies are preadapted to live in noisy environments (Slabbekoorn & Ripmeester, 2008; Hu & Cardoso, 2009).

If noise affects the persistence of certain avian species, perhaps anthropogenic noise contributes to the

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generally low avian diversity in urban areas (Marzluff, 2001; Huste & Bouludier, 2007). In many cases, common urban species are those that cope well with altered vegetative patterns (Fernandez-Juricic, 2000). However, anthropogenic noise may exacerbate this loss of diversity by excluding species which could otherwise utilize urban parks and green spaces. We tested this hypothesis by surveying species richness and the abundance of seven songbird species across a range of noise levels and determining whether richness and each species' abundance were associated with noise. Second, we examined whether anthropogenic noise favors species with particular acoustic traits. Specifically, we tested whether noise-associated changes in abundance across seven songbird species were related to the lowest, highest, and loudest frequencies of their songs. We predicted that several species would become less abundant as noise levels increased, and that the species with the lowest frequency songs would be those most negatively affected by noise.

Materials and methods

Site selection

The City of Edmonton, Alberta, Canada (53°30'N, 113°30'W), has preserved one of the largest urban green spaces in North America, with over 7400 hectares of park area (Hobson *et al.*, 2008). Much of this parkland is comprised of mature deciduous and coniferous forests similar to nearby rural locations (Mandryk & Wein, 2006). Our work shows that the ambient noise levels range from 30 to 60 dB SPL(A), with higher noise levels most often originating from nearby roadways. Point counts were conducted at 113 locations in natural areas throughout the North Saskatchewan River valley in the City of Edmonton. All points were separated by >300 m and were located along a multiuse trail system which is exposed to a gradient of anthropogenic noise. The use of trails for all point counts minimized the difference in edge habitat between roadside and interior locations, and regular foot and animal traffic reduced the possibility that differences in abundance were due to visual disturbance. Points were distributed over a 7500 hectare area and encompassed at least 20 unique road noise sources.

Species selection

To compare noise-associated changes in abundance with acoustic traits, we assessed abundance for seven passerine species that were as follows: (1) regularly found within the study area (20+ individuals), (2) generally associated with the forest and forest-edge habitat that comprised our study area, (3) vocally conspicuous and easily identifiable by sight and sound (to promote consistency in our ability to locate individuals within various noise levels and to reduce potential errors in aural identification), and (4) species whose vocalizations

contained frequencies that fall below 4 kHz, and are potentially masked by the dominant frequencies of road noise (Skiiba, 2000). Focal species included black-capped chickadees (*Poecile atricapillus*) and white-throated sparrows (*Zonotrichia albicollis*), who possess tonal songs produced between 2.8 and 4.5 kHz (Ficken *et al.*, 1978; Waas, 1988). The single song of the black-capped chickadee is highly stereotyped, whereas the white-throated sparrow sings two distinct song types which can be classified by whether they ascend or descend following the introductory note (Weary & Weisman, 1992). For this study, sparrow songs were classified into these two categories. Red-eyed vireo (*Vireo olivaceus*) and western tanager (*Piranga ludoviciana*) songs consist of several warbling notes. Tanager songs are slightly lower than red-eyed vireo songs (2–5 kHz; Shy, 1984), and vireo songs are more variable, often consisting of multiple different phrases ranging from 2 to 8 kHz (Borror, 1981). The least flycatcher (*Epidomax minimus*) possesses a single two-note song with broadband notes that typically span 1.5–7 kHz (Kasumovic *et al.*, 2003). The song of the red-breasted nuthatch (*Sitta canadensis*) consists of a broadband combination of harmonic-like bands of sound ranging from 2–9 kHz (Ghalambor & Martin, 1999). Yellow warblers (*Dendroica petechia*) possess two songs types, classified based on presentation (Spector, 1991). Type I songs consist of repeated presentation of the same song phrases, whereas Type II songs consisted of multiple unique phrases presented with very little repetition. Phrases from both song types generally range from 3 to 10 kHz. However, we classified all yellow warbler songs as Type I or Type II for analysis. We did not use calls or any abnormal song output from any species. Two of our focal species, the least flycatcher and western tanager, are declining within the City of Edmonton (Hobson *et al.*, 2008). However, these species could still be found with regularity within the large, intact forests within the City of Edmonton.

Study 1: Species richness and abundance

Ambient noise. At each point, a stationary observer recorded the ambient noise level for 11 min with a Marantz digital recorder (PMD 670; 44 100 Hz sampling rate, gain 2.5/10, PCM, 16 bit format) with an omni-directional microphone (Sennheiser ME62; Wedemark, Germany) placed vertically at 1.5 m above the ground. To eliminate sounds due to nonanthropogenic sources (i.e., wind, bird song), we measured average power (dB) in the 0.3–10 kHz bandwidth in six, 1-s sound windows that were free of bird song or other atypical ambient sound sources in SIGNAL 5.0 (Berkeley, CA, USA). We randomly selected 1-s sound windows by dividing each recording into 30-s time bins, and utilizing the first available song free, 1-s sample in each of the first six bins. Three biologically relevant measures of ambient noise were collected: (1) highest mean sound level recorded at any particular visit, (2) lowest mean sound level recorded at any particular visit, and (3) the mean of all sound recordings from all four visits. To avoid pseudoreplication, a principle component analysis was employed to reduce the three measures of ambient noise to a single variable (PC1) for analysis.

Point counts. Following the first minute of noise measurement, the observer noted all passerine species located by sight or sound for 10 min within one of two distance bands; 0–50 or 50–100 m (Hutto *et al.*, 1986; Bibby *et al.*, 1992). Each point was visited four times between 30 min prior to sunrise and 11:00 hours from May 2 to June 27, 2008. To increase the likelihood of detections at noisy locations and minimize singing differences due to time of day, all points were visited twice in the early morning and twice later in the morning. Point counts were not conducted in precipitation or winds >2 on the Beaufort scale (Bibby *et al.*, 1992). To acknowledge the potential effect of distance from the road separate from road noise (Summers *et al.*, 2011), we calculated the Euclidian distance to the closest high use road (>10 000 cars day; 2007 City of Edmonton Traffic Flow Map) for each count location.

Vegetative structure. To account for differences in bird abundance due to habitat and edge effects, vegetative structure was assessed at each point count location in July and August, 2008 (methods modified from Habib *et al.*, 2007; Hannon *et al.*, 2002). Using a random initial azimuth, four 100 m transect lines radiated from the center of each point at 90° angles. All trees >5 m tall within 1 m of the transect line were counted, identified to species (see Table 1), and classified based on their diameter at breast height (dbh; <8, 8–15, 16–23, 24–28,

>28 cm). The number of trees along each transect was used to calculate density and relative dominance for each species. In addition, we calculated the percentage of each transect characterized as forest (dominant canopy >5 m in height), shrub (2–5 m), open (<2 m), and water.

At 20, 40, 60, 80, and 100 m along each transect we counted all snags (dead but not downed trees >8 cm dbh) within 5 m, classified dominant canopy height (5–10, 10–15, 15–20, 20–25, >25 m), and estimated canopy cover (tree canopies separated by: 0, 1–2, 3–5, 5–10, >10 m). Visual estimation of distances was calibrated during training sessions with a range finder (Bushnell Yardage Pro X500; Ontario, Canada), and cross-checked regularly throughout the season. To quantify ground cover, a 1 m² quadrant was placed at each sampling point, and the percentage of cover belonging to lawn (manicured), grass (natural), bare ground, herbaceous plants, and leaf litter was estimated. The stems of large (>2 m) and small (0.5–2 m) shrubs were also counted within each quadrant. Data were averaged for all four transect lines resulting in one measurement for each vegetative variable per site (Table 1).

Statistical analysis. Species richness was calculated as the total number of passerine species observed at each site over all four visits. Abundance of each focal species was calculated as the highest count at any one visit, as this represents the maximum utilization for a species at each point count location (Forrest & St. Clair, 2006). To account for the declining ability to audibly detect species at increased distances in noisier locations, we determined the detection probability (P_a) using half-normal binomial distance methods (DISTANCE 6.0; Thomas *et al.*, 2010) in four separate noise categories (quartiles), classified by the average noise level at each site. We divided the raw abundance (n) for each species by the detection probability (P_a) derived for the corresponding noise category to minimize the confounding effects of noise on detectability (Buckland *et al.*, 2008). We used the formula: $N = A*(n/a*P_a)$ Where N = corrected abundance, A = total area, n = observed abundance, a = survey area, and P_a = detection probability. Because abundance was calculated for each point count, $A = a$, and this formula simplifies to: $N = n/P_a$. This correction reduced the inherent bias toward lower abundance in noisy sites that is due to detectability.

We assessed the effects of noise, distance, and vegetation on detectability-corrected species richness and abundance for our seven focal species with general linear models (GLM; Stata 10; Statacorp., TX, USA). To account for the high numbers of zeros and potential overdispersion in our abundance data, we used the negative binomial distribution (Hardin & Hilbe, 2007). We obtained best fit models for each species through a hierarchical model building procedure (Tremblay & St. Clair, 2009), which retains the best measures of a given type of variable. In the first tier, variables were grouped by ecological similarity. We established seven categories: (1) ground cover, (2) habitat type, (3) forest stand qualities, (4) shrubs, (5) tree species, (6) ambient noise, and (7) distance from the road (Table 1). In each category we retained the univariate model with the lowest AICc value (Burnham & Anderson, 2002), and then added additional variables from the same category until they no longer reduced the model AICc (i.e., forward step-

Table 1 Categories and variables for abundance models

(1) Ground cover	Lawn
	Grass
	Bare ground
	Herb
	Leaf litter
(2) Habitat characterization	Forest
	Shrub
	Open
	Water
(3) Forest stand qualities	Snags
	Tree density
	Tree height
	Tree diameter (DBH)
	Canopy cover
(4) Shrub stems	High shrubs
	Low shrubs
(5) Tree species	Relative dominance
	Aspen poplar
	Balsam poplar
	White birch
	White spruce
	Other species
	Species density
	Aspen poplar
	Balsam poplar
	White birch
White spruce	
Other species	
(6) Ambient noise	
(7) Distance to road	

wise). Correlated variables (>0.6) were not included in the same model. In the second tier, we compared the top model from each of the six categories (termed category model) via AICc. We retained the most parsimonious category model, and then employed forward stepwise addition of other category models to derive the most parsimonious final model. To examine the fit of the final model we compared its explanatory power with that of the null model. Each dependent variable in the final regression model was standardized ($\bar{X} = 0 \pm 1$ SD) so coefficients could be used to compare the relative effects of modeled parameters.

Study 2: Song frequency

Vocal recording. From April 25 to June 26, 2008, observers collected audio recordings of song bouts from the seven focal species. These recordings coincided with point counts, although observers remained >500 m from the active point count location. Each area was intentionally visited at different times of the morning across multiple visits to reduce the likelihood that time of day confounded our results (similar to Summers *et al.*, 2011). Once a focal bird was located, the observer moved as close to the bird as possible while minimizing disturbance (generally <25 m). All audio recordings were made with a Marantz digital recorder (PMD 670; 44 100 Hz sampling rate, gain 2.5/10, PCM, 16 bit format) and a directional microphone (Sennheiser ME67; Wedemark, Germany). Recording ceased when the focal individual moved out of view, or a sufficient number of songs (>30) was recorded. Recording generally lasted <5 min, and rarely exceeded 10 min.

Statistical analysis. Songs were randomly selected for analysis from 20 individuals of each species. To avoid recording the same individual twice, all recorded individuals were separated by >300 m (Bibby *et al.*, 1992). We analyzed 10 songs per individual (similar to Ripmeester *et al.*, 2010), except in a few cases where only 4–9 songs were available from an individual and a satisfactory replacement could not be found. As it is known that several bird species sing at different song frequencies as noise increases (e.g., Slabbekoorn & Peet, 2003), we selected individuals from a similar set of distance and noise ranges across species to minimize the effect of these variables on the interspecies variance in vocal frequencies (Wiley & Richards, 1982; Patricelli & Blickley, 2006).

We measured three song frequency characteristics. Peak frequency (PF), or frequency at the maximum amplitude, signifies which frequencies were emphasized in each vocalization, and was measured on a frequency spectrum in SIGNAL 5.0 (FFT; ≥ 65 536 points, ≥ 0.7 Hz resolution). Minimum frequency (F_{\min}) shows to what extent the lower song elements overlap with anthropogenic noise, and maximum frequency (F_{\max}) reveals how much spectral separation existed between the upper end of the signal and anthropogenic noise. F_{\min} and F_{\max} were calculated as the highest and lowest frequencies where the song amplitude was within 35 dB of the peak amplitude (Charrier *et al.*, 2004; Proppe & Sturdy, 2009). To increase the accuracy of our frequency measurements, we removed background noise from the audio files before

measuring F_{\min} and F_{\max} (1500–10 000 Hz band pass filter, and the noise reduction procedure in Goldwave 5.55; St John's, NL, Canada; Baker & Logue, 2007). All song exemplars used in the analysis exceeded background noise by at least 35 dB. Upon completion, all measurements were compiled to calculate one mean for each species for each frequency measure.

To examine whether each frequency measure predicted a species willingness to inhabit noisy locations, we developed a single dependent variable, termed noise susceptibility, which represented a species change in abundance as anthropogenic noise increased. This variable was derived by: (1) calculating the residuals from the top habitat abundance model for each species (noise excluded), (2) standardizing the residuals so that they could be compared across species ($\bar{X} = 0 \pm 1$ SD), and (3) performing a general linear model with the standardized residuals and ambient noise measures (PC1). The beta coefficient for ambient noise from this regression represented noise susceptibility. The more negative the coefficient the more abundance decreased as noise increased and *vice versa*. To determine whether any of the frequency measures correlated with noise susceptibility we performed separate general linear models for each frequency measure. Because the final regression contained only one dependent variable, we used the P value <0.05 to determine significance.

Results

Study 1: Species richness and abundance

The top three models for species richness all included anthropogenic noise (AICc weight = 100%; Table S1). In the top model, species richness declined significantly with increasing noise ($\beta = -1.22 \pm 0.30$, $z = -4.10$, $P < 0.001$; Fig. 1). Noise was also retained in the top abundance model for three species (Table S1). In each case, noise was included in at least two of the top three explanatory models, and models that included noise accounted for $>98\%$ of the AICc weight (Table S1). For all three species, abundance declined significantly with increasing levels of ambient noise (Fig. 2): western tanager ($\beta = -0.56 \pm 0.27$, $z = -2.05$, $P = 0.041$); least flycatcher ($\beta = -1.24 \pm 0.28$, $z = -4.45$, $P < 0.001$); and red-breasted nuthatch ($\beta = -0.69 \pm 0.19$, $z = -3.63$, $P < 0.001$). Distance from the road was retained in the top abundance model for western tanagers ($\beta = 0.92 \pm 0.95$, $z = 3.70$, $P < 0.001$), but not for any other species. Abundance for each of these species was also associated with vegetative characteristics (Table 2). In the final model for the western tanager, noise ranked below distance and three vegetative variables, but above four other predictive variables. For the least flycatcher, noise ranked below two, and above six, vegetative predictors. Noise was the second strongest predictor of abundance in the red-breasted nuthatch.

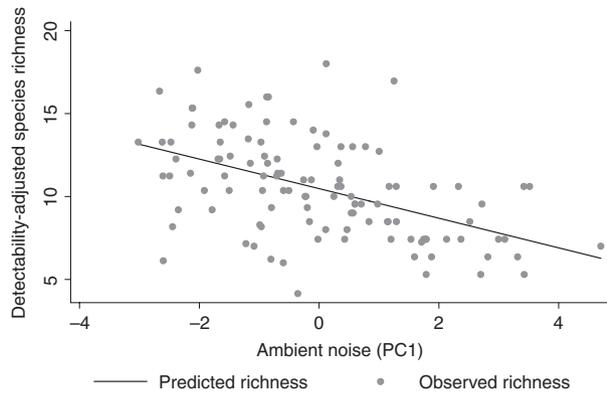


Fig. 1 Species richness adjusted for noise-based detectability differences, and plotted against the result of a principle component analysis of ambient noise level. Solid black lines represent the predicted richness values from a general linear model after accounting for covariates. Gray circles represent observed richness levels, after adjustment to account for detectability.

Abundance was not significantly related to noise for four species. All but one species, however, did retain vegetative predictors. Black-capped chickadee abundance increased with relative dominance of aspen ($\beta = 0.27 \pm 0.11$) and spruce ($\beta = 0.22 \pm 0.11$). Red-eyed vireo abundance increased with leaf litter ($\beta = .23 \pm 0.14$) and density of 'other' tree species ($\beta = 0.16 \pm 0.11$). White-throated sparrow abundance increased with forest ($\beta = 0.54 \pm 0.14$) and shrub cover ($\beta = 0.23 \pm 0.14$). The abundance of the yellow warbler was not significantly affected by noise or any other variable collected in this study (Table S1). However, AICc weight of the null model was only slightly higher (0.24) than the next best model which including high shrubs (0.16), suggesting that this variable may have some effect on yellow warbler abundance ($\beta = 0.11 \pm 0.10$).

Study 2: Song frequency

Frequency characteristics were analyzed for 1382 total songs (183–203 per species). For white-throated sparrows 84 songs were classified as ascending and 119 were descending. Type 1 songs accounted for 119 of the analyzed yellow warblers songs, and 82 additional songs were Type 2. As the two song types in these two species are distinctly different, they were treated as separate data points in the analysis. For all songs analyzed, minimum frequencies ranged from 1.7 to 3.6 kHz. Peak frequency ranged from 2.6 to 5.5 kHz and maximum song frequencies ranged from 3.9 to 9.0 kHz. The minimum song frequency (F_{\min}) of a species' song was predictive ($r^2 = 0.57$) of a species' noise

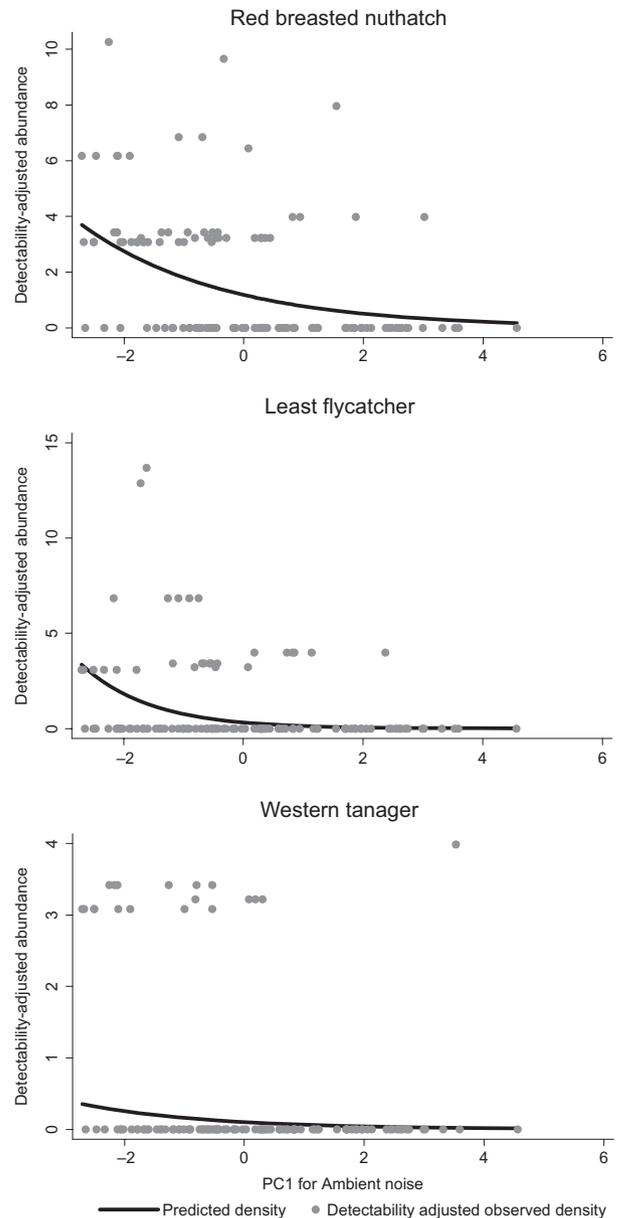


Fig. 2 Maximum point count abundance adjusted for noise-based detectability differences, and plotted against the result of a principle component analysis of ambient noise level for the three species whose abundance was associated with ambient noise levels. Solid black lines represent the predicted density values from negative binomial regression models after accounting for covariates. Gray circles represent observed abundance levels, after adjustment to account for detectability. Note that y axes are not on the same scale for different species. To improve visual acuity, one outlier (at 6.44) was removed from the observed western tanager abundance.

susceptibility ($\beta = 5.63E-05 \pm 1.86E-05$, $t = 3.02$, $P = 0.003$; Fig. 3). PF and F_{\max} however, had no effect on noise susceptibility ($P \geq 0.193$; Table 3).

Table 2 Standardized effect sizes, significance level, and confidence intervals for variables in the top model for richness and for individual species

Species	Variable	β	SEM	z	$P > z $	95% CI	
Species richness	Noise	-1.22	0.30	-4.10	0.000	-1.80	-0.64
	Open habitat	1.19	0.47	2.55	0.011	0.27	2.11
	Lawn habitat	-1.16	0.38	-3.07	0.002	-1.90	-0.42
	Distance	0.49	0.29	1.73	0.084	-0.07	1.05
	den. other	-0.37	0.24	-1.56	0.119	-0.84	0.10
	Forest habitat	-0.33	0.65	-0.51	0.608	-1.60	0.94
	den. birch	0.29	0.25	1.16	0.246	-0.20	0.79
	Herb cover	0.26	0.36	0.73	0.467	-0.44	0.97
	Shrub habitat	-0.20	0.44	-0.45	0.651	-1.07	0.67
	Water	0.17	0.33	0.51	0.613	-0.48	0.81
Western tanager	Leaf litter	0.89	0.32	2.74	0.006	0.25	1.52
	High shrub stems	-0.88	0.36	-2.45	0.014	-1.59	-0.18
	Distance	0.88	0.24	3.65	0.000	0.41	1.35
	rel. spruce	0.69	0.23	2.97	0.003	0.24	1.15
	Noise	-0.56	0.27	-2.05	0.041	-1.09	-0.02
	dbh	0.50	0.22	2.32	0.020	0.08	0.93
	Low shrub stems	0.36	0.26	1.43	0.154	-0.14	0.86
	Tree height	0.14	0.26	0.53	0.597	-0.38	0.65
	Lawn habitat	0.12	0.33	0.36	0.718	-0.53	0.78
	Least flycatcher	den. spruce	-1.24	0.28	-4.45	0.000	-1.79
Herb cover		1.24	0.29	4.28	0.000	0.67	1.80
Noise		-1.11	0.28	-3.90	0.000	-1.67	-0.55
Leaf litter		1.04	0.22	4.62	0.000	0.60	1.48
High shrub stems		-0.84	0.22	-3.85	0.000	-1.27	-0.41
den. aspen		-0.81	0.21	-3.93	0.000	-1.22	-0.41
Low shrub stems		-0.39	0.27	-1.43	0.154	-0.92	0.14
den. birch		-0.20	0.17	-1.17	0.241	-0.52	0.13
den. poplar		-0.14	0.19	-0.73	0.463	-0.51	0.23
Red-breasted nuthatch		Canopy cover	-0.78	0.27	-2.90	0.004	-1.30
	Noise	-0.55	0.17	-3.21	0.001	-0.89	-0.22
	Open habitat	0.45	0.18	2.57	0.010	0.11	0.80
	Low shrub stems	0.36	0.18	2.03	0.042	0.01	0.71
	Forest habitat	-0.19	0.40	-0.47	0.638	-0.97	0.59
	Snag	0.18	0.18	1.04	0.298	-0.16	0.53
Black-capped chickadee	Shrub habitat	-0.04	0.24	-0.18	0.860	-0.51	0.42
	rel. aspen	0.27	0.11	2.51	0.012	0.06	0.49
Red-eyed vireo	rel. spruce	0.22	0.11	2.03	0.042	0.01	0.44
	Leaf litter	0.23	1.14	2.06	0.040	0.01	0.46
White-throated sparrow	den. other	0.16	0.11	1.43	0.152	-0.06	0.37
	Forest habitat	0.54	0.14	3.81	<0.001	0.26	0.82
Yellow warbler*	Shrub habitat	0.23	0.14	1.63	0.103	-0.05	0.51
	High shrub stems	0.11	0.10	1.09	0.276	-0.09	0.31

*The null model was the top model for the yellow warbler, but the second candidate model is shown because of the small difference in AIC weights ($\Delta AIC_w = 0.09$).

Discussion

After accounting for differences in vegetative structure, species richness declined significantly with increasing noise. In addition, the abundance of three of seven focal species – the red-breasted nuthatch, least flycatcher, and western tanager – was lower at higher levels of

anthropogenic noise. Furthermore, our results show that a species' minimum song frequency was highly predictive of whether its abundance would be reduced with increasing anthropogenic noise.

Recent studies have suggested that anthropogenic noise contributes to observed declines in songbird abundance, and may partially account for lower biodi-

Table 3 Results from linear regression of noise susceptibility and the species means for multiple frequency measures. Absolute measures include minimum (F_{\min}), peak (PF), and maximum (F_{\max}) song frequencies. Noise susceptibility is a standardized coefficient representing each species change in abundance in response to increasing noise levels. It is calculated by standardizing the residuals after linear regression with all variables from the top abundance model (except noise), and recording the beta coefficient for noise from a subsequent regression of the residuals and ambient noise. A species whose abundance decreases with increasing noise levels will have a negative noise susceptibility coefficient, and *vice versa*

Variable	β	SEM	t	$P > t $	95% CI		r^2
F_{\min}	5.63E-05	1.86E-05	3.020	0.003	1.22E-05	1.03E-04	0.565
PF	2.54E-05	1.76E-05	1.440	0.150	-1.63E-05	6.70E-05	0.229
F_{\max}	8.67E-06	9.58E-06	0.900	0.366	-1.40E-05	3.13E-05	0.105

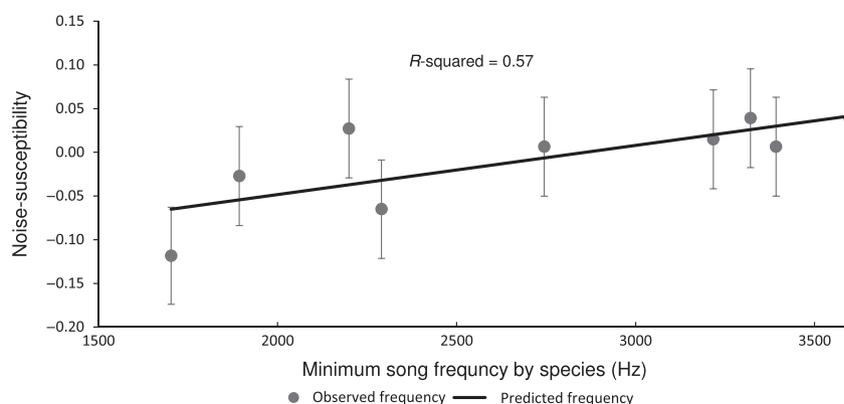


Fig. 3 Mean minimum song frequency for each bird species (including two song types for the white-throated sparrow and the yellow warbler) regressed against a coefficient representing each species change in abundance with increasing noise (termed noise susceptibility). A species whose abundance decreased with increasing noise levels will have a negative noise susceptibility coefficient, and *vice versa*. Error bars represent standard deviation.

versity in urban areas (Slabbekoorn & Ripmeester, 2008; Laiolo, 2010). Our results provide empirical support for this hypothesis. The contiguous, mature forests in our study area provided suitable vegetative habitat for many bird species, including all seven of our focal species. However, overall richness declined significantly in areas with high levels of ambient noise, and the abundance for three of our seven focus species (43%) declined. Moreover, of the three species whose abundance was significantly associated with noise, two have been identified as declining in the study area (least flycatcher and western tanager; Hobson *et al.*, 2008). The causes of low urban biodiversity (Clergeau *et al.*, 2006; Puppim de Oliveira *et al.* 2011) are varied, but our results suggest that anthropogenic noise is exacerbating the situation.

Our results also support the notion that the effects of anthropogenic noise are frequency dependent (Slabbekoorn & Ripmeester, 2008). Specifically, bird species with lower minimum song frequencies are more likely to be less abundant in noisy areas. In the current study, road noise was the primary source of

anthropogenic noise; a relatively ubiquitous feature of developed areas (Coffin, 2007; Kociolek *et al.*, 2011). In addition to its widespread prevalence, the low-frequency distribution of noise produced by road noise is remarkably consistent across different surface types (e.g., Sandberg, 1987). Furthermore, other industrial activities such as air traffic and industrial machinery have sound signatures similar to that of roads (Beglund *et al.*, 1996). The selective pressure on acoustic frequencies exhibited by noise in our study is strikingly similar to other noise-affected areas regardless of geographic proximity (Hu & Cardoso, 2010; Francis *et al.*, 2011; Goodwin & Shriver, 2011). If this is the case, we can expect that anthropogenic noise is selecting for and against a similar subset of species in noise-affected areas, contributing to the loss of diversity within these areas, and potentially to homogenization between them.

The frequency-dependent relationship between noise and a species susceptibility to noise may also enhance our ability to predict which species are most likely to decline as anthropogenic noise increases. Noise mitiga-

tion may be especially important for the maintenance of species with low minimum song frequencies. In the current study, the minimum frequencies of some species fell well below 4 kHz, into the frequencies where road noise is typically concentrated (Skiba, 2000). However, peak and maximum song frequencies were well above these frequencies. For example, least flycatcher songs contain low-frequency elements, but maximum frequencies often exceeded 7 kHz. The reason minimum song frequency appears to be more vital in noise-affected habitats than other measured frequencies is yet unknown. Low-frequency elements may be especially important for signal transmission because they generally propagate better than high-frequency elements (Wiley & Richards, 1982). Potentially, female songbirds that do not hear the low-frequency elements of a vocal signal fail to adequately perceive and assess the singing male, or deem him to be an ill-suited mate (Halfwerk *et al.*, 2011). Alternatively, vocal signals may be perceived as altered or abnormal if the lowest frequency elements cannot be heard. This may elicit weakened behavioral responses from the receiver, even if much of the signal remains intact (Nowicki *et al.*, 2001; Derryberry, 2007). Additional research across a wide range of taxa and in multiple geographic regions is needed to determine the extent to which minimum song frequency determines noise susceptibility.

Some bird species that vocalize at low song frequencies possess adaptations which may reduce the deleterious effect of anthropogenic noise on acoustic communication. For example, some species are known to increase the amplitude and frequency of their songs in the presence of noise (Slabbekoorn & Peet, 2003; Brumm, 2004). We speculate that two additional mechanisms warrant further examination. First, in the current study, the red-breasted nuthatch possessed the lowest minimum song frequency of all focal species, and was less common in noisy locations. However, red-breasted nuthatches often inhabit suburban areas, and utilize backyard feeders (Blewett & Marzluff, 2005). These areas are generally quieter than urban parks (Nilsson & Berglund, 2006), and may provide a valuable, but limited, escape from anthropogenic noise for species that can tolerate more isolated trees and a relative lack of understory. Second, despite its relatively low-frequency song, red-eyed vireos remained abundant in sites with high levels of anthropogenic noise. We speculate that the persistence of red-eyed vireos at noisy sites may be related to their unusual tendency to sing throughout the day (Hartshorne, 1956; Williams, 1971). Since noise from traffic and other bird species waxes and wanes throughout the day (Warren *et al.*, 2006), red-eyed vireos may be able to communicate effectively during periods of low traffic intensity. When

exposed to continuous noise near well pads, red-eyed vireo density was lower than that at quiet sites (Bayne *et al.*, 2008). Although this hypothesis has not been explicitly tested in vireos, the European robin (*Erithacus rubecula*) sings before dawn in locations that are exposed to daytime anthropogenic noise (Fuller *et al.*, 2007). Singing during predictably quiet time periods may increase the viability of bird species with low-frequency songs.

In sum, we show that anthropogenic noise may be contributing to loss of urban diversity by preventing some species from utilizing otherwise suitable habitat in urban parks and green spaces. In addition, minimum song frequency was a significant predictor of a species' response to elevated anthropogenic noise, suggesting that areas with similar noise patterns may favor a homogenized set of avian species. While some species with low-frequency songs may possess alternative spatial and temporal mechanisms for avoiding conflict with noise, species that lack these abilities may be expected to decline in urban areas, as appears to be the case for least flycatchers and western tanager in our study area. Increasingly, cities are tasked with creating and preserving green spaces for the protection of wildlife (Florgard, 2007; Zhou & Wang, 2011). Our results have several implications for city planners and wildlife managers. First, minimum song frequency may be a useful metric for predicting how birds will react to anthropogenic noise in diverse locations. Second, if residential neighborhoods provide a refuge for noise-sensitive species, their value might be increased for avian diversity by increasing habitat quality (e.g., understory plants, fruit and seed-bearing plants). Finally, mitigation aimed to conserve songbirds should identify methods for reducing the masking caused by anthropogenic noise, particularly road noise.

Acknowledgements

Funding supplied by Alberta Sport, Recreation, Parks, and Wildlife Foundation (D. S. P.), Natural Sciences and Engineering Research Council of Canada (NSERC), Discovery Grants (C. B. S. and C. C. S. C.), NSERC Discovery Accelerator Supplement (C. B. S.), Canada Foundation for Innovation (CFI), New Opportunities (C. B. S.) Fund and Infrastructure Operating Fund (C. B. S.), along with start-up funding and CFI partner funding from the University of Alberta (C. B. S.) and an Alberta Ingenuity Fund (AIF) New Faculty Grant (C. B. S.). All animal studies were conducted in accordance with the Canadian Council on Animal Care Guidelines and Policies with approval from the Animal Care and Use Committee for Biosciences for the University of Alberta. Research was carried out under an Environment Canada Canadian Wildlife Service Scientific permit, an Alberta Fish and Wildlife Capture and Research permits, and a City of Edmonton Parks Permit. Thanks to E. Bayne, H. P. Kunc, and two anonymous reviewers for helpful suggestions that improved the quality of the manuscript. Additional thanks to K.

Byers, E. Droessler, H. Lee, F. Gainer, A. McCartney, B. McCartney for their assistance with data collection and analysis.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Top three most parsimonious AICc selected general linear models for species richness and for each focal species.