SINGING SEASIDE: PACIFIC WRENS (*TROGLODYTES PACIFICUS*) CHANGE THEIR SONGS IN THE PRESENCE OF NATURAL AND ANTHROPOGENIC NOISE

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ABSTRACT.—Noise pollution poses a significant obstacle to vocal communication. Songbirds rely on acoustic signals for mate choice and territory defense, and masking of these signals can have negative fitness consequences. Prior investigations reveal that birds mitigate the negative effects of acoustic masking by increasing their signal amplitude or by singing with higher minimum frequencies. In this study, we evaluate the responses of male Pacific Wrens (*Troglodytes pacificus*) to natural ambient noise (ocean surf) and anthropogenic noise (highway traffic) in Pacific Rim National Park Reserve, B.C., Canada. Pacific Wrens, known for their complex songs, are specialists of old-growth forest. We hypothesized that Pacific Wrens would compensate for the effects of ambient noise in their environments through modifications to their songs that enhanced their transmission properties. Recognizing that longer, higher frequency, and more complex signals propagate better in noisy environments, we predicted that Pacific Wrens would increase the length of their songs, the length of the syllables within their songs, the number of syllables per song, and the minimum frequency of their songs. Recordings of 52 territorial Pacific Wrens showed that proximity to highway traffic noise had a significant effect on song duration but no significant effect on any of the other measured variables. Pacific Wrens that were recorded near the shoreline, however, sang songs with longer syllables, and higher intra-individual variation in song duration. Number of syllables, syllable minimum frequency, and song duration did not vary with distance from the shoreline. We conclude that natural and anthropogenic noise sources influence the singing behavior of Pacific Wrens. *Received 3 June 2013. Accepted 20 January 2014.*

Key words: acoustic masking, bird song, noise, Pacific Wren, signal transmission, *Troglodytes pacificus*.

Many animals use acoustic signals to communicate (Bradbury and Vehrencamp 2011). For songbirds, vocalizations play a central role in mate choice and territory defense (Catchpole and Slater 2008). The transmission properties of vocal signals are affected greatly by background noise (Lengagne et al. 1999, Brumm 2004, Brumm and Slabbekoorn 2005). Birds that emit acoustic signals face potential limitations by absorption of sound from the ground, the air, and forest vegetation along with masking from environmental noise, which occurs whenever the frequency of signals and noise overlap (Morton 1975, Wiley and Richards 1978, Lengagne et al. 1999, Brumm 2004).

Noise produced by abiotic sources such as ocean surf and wind, biotic sources such as the avian dawn chorus, or anthropogenic sources such as traffic, poses a barrier to efficient acoustic communication. Animals that live in the presence of noise may benefit by changing their vocalizations to compensate for the masking effects caused by noise. Many studies have shown that birds in urban areas sing at higher frequencies than those in non-urban habitats (Slabbekoorn and Peet 2003, Slabbekoorn and den Boer-Visser 2006, Nemeth and Brumm 2009, Hu and Cardoso 2010, Potvin et al. 2011); this may be an adaptive response, reducing spectral overlap with low-frequency noise. Common Nightingales (*Luscinia megarhynchos*) increase their signal amplitude in noisy conditions for improved signal transmission (Brumm and Todt 2002), and can adjust their vocal amplitude depending on the intensity of background noise (Brumm 2004). When Common Blackbirds (*Turdus merula*) encounter low-pitched traffic noise, they increase their song pitch because these songs can be produced at higher amplitudes (Nemeth et al. 2013).

The Acoustic Adaptation Hypothesis states that natural selection favors vocalizations fitted to a certain habitat for effective transmission between a signaler and a receiver (Morton 1975). There are costs to ensuring effective communication in a noisy environment, such as increased probability of detection by predators caused by increasing the duration and complexity of songs (Brumm 2004, Quinn et al. 2006). In addition, modifications to

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songs in noisy conditions might improve signal
transmission properties but simultaneously reduce
attractiveness to females if the modified songs
do not meet the preferred criteria of females
(Halfwerk et al. 2011). Consequently, increases in
anthropogenic noise that accompany expanding
urbanization can pose severe challenges to a wide
range of taxa, including birds (Reijnen and
Foppen 1994, Rheindt 2003, Parris et al. 2009).

    There are many studies that have focused on
the responses of songbirds to traffic noise (e.g.,
Rheindt 2003, Slabbekoorn and Ripmeester 2008,
Parris and Schneider 2009, Hanna et al. 2011). To
our knowledge, no study has investigated the
influence of ocean noise on the singing behavior
of songbirds. However, one study has compared
the structure of the songs of coastal breeding
Eastern Willets (*Tringa semipalmata semipal-
mata*) with those of inland breeding Western
Willets (*Tringa semipalmata inornata*; Douglas
and Conner 1999); the masking and pulsing nature
of ocean waves appeared to select for shorter, and
higher frequency calls, delivered at an increased
tempo, in the eastern sub-species. White-throated
Dippers (*Cinclus cinclus*) vocalize at high fre-
quencies to mitigate the acoustic masking in their
noisy stream habitats (Brumm and Slabbekoorn
2005), and King Penguins (*Aptenodytes patago-
nicus*) increase their call output in windy envi-
ronments (Lengagne et al. 1999). Thus, noise
from ocean surf may play a significant role in
shaping the vocal behavior of coastal birds.
Studying the effects of natural noise on territorial
songbirds is important for understanding the
conditions under which birds can or will adapt
their singing behavior or song structure.

    In this study, our objective is to explore the
behavior of songbirds in response to ambient
noise from both natural sources of noise (ocean
surf) and anthropogenic noise (traffic). We
studied Pacific Wrens (*Troglodytes pacificus*),
territorial songbirds well known for their complex
song and large repertoire (Toews and Irwin 2008),
that live in coastal forests of western Canada
where they experience significant noise from both
ocean surf and traffic sources. We hypothesized
that Pacific Wrens would compensate for the
effects of ambient noise in their environments by
adapting their songs and singing behavior.
Specifically, we predicted that wrens holding
territories near the shoreline or a busy road would:
(1) increase the duration of their songs and the
syllables that comprise their songs. We base this

prediction on the idea that longer songs and
syllables are more detectable as they increase the
opportunity to be heard above periodic noise
sources (Lengagne et al. 1999), although we note
that some studies have found shorter songs in
noisy conditions (e.g., Douglas and Conner 1999,
Slabbekoorn and Peet 2003, Slabbekoorn and den
Boer-Visser 2006). We also predicted that: (2)
wrens would increase the number of syllables in
each song (increasing syllables improves the
opportunity for information transmission; Len-
gagne et al. 1999, Brumm and Slater 2006); and
(3) increase their minimum singing frequency
(pitch) to counteract masking effects of low-
pitched environmental noise (Slabbekoorn and
Peet 2003, Wood and Yezerinac 2006). Finally,
we predicted that there would be more intra-
individual song variation for individuals singing
in habitats near the highway or the ocean because
song variability may be favorable in environments
that experience varying levels of noise, and
because highly variable sound environments may
lead to intense sexual selection, which would
favor complex songs (Medina and Francis 2012).

METHODS

Study Species and Site.—Pacific Wrens are
small territorial songbirds that have only recently
been separated from Winter Wrens (*Troglodytes
hiemalis*), a species with a much wider circum-
boreal geographic distribution (Toews and Irwin
2008, Chesser et al. 2010). The geographic range
of the Pacific Wren extends from west of the
Rocky Mountains as far south as California and
Utah and north to the southern coast of Alaska and
the Aleutian Islands (Toews and Irwin 2012).
Thus, the habitat of this species features both
noise from increasing traffic in much of its range
as well as noise from the Pacific Ocean.

    We carried out this study in the Long Beach
Unit of Pacific Rim National Park Reserve on
the west coast of Vancouver Island in British
Columbia, Canada. This unit is one of three
geographically separated divisions of Pacific
Rim National Park Reserve (hereafter 'the park')
and is located between the communities of
Tofino (49° 9.2′ N, 125° 54.1′ W) and Ucluelet
(48° 55.5′ N, 125° 32′ W), British Columbia.
The park is a protected area of land and sea within
the Clayoquot Sound Biosphere Reserve. Our study
area included a 16-km sandy beach adjacent to two
types of forest: pristine ancient temperate rainforest
and 40-year-old second-growth forests in areas that

were logged before the park was established in 1970. The forests are dominated by western redcedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and Pacific silver fir (*Abies amabilis*). The shrub layer is composed of salmonberry (*Rubus spectabilis*), red huckleberry (*Vaccinium parvifolium*), and salal (*Gaultheria shallon*).

Sources of Ambient Noise.—The Trans-Canada Highway (Highway 4) runs through the study site. The highway is a 2-lane road with a posted speed limit of 80 km/h. The traffic is largely made up by visitors to the park, locals, and delivery trucks to the two communities. Over one million people visit the site annually (Edwards 2005). Car traffic has increased steadily at the site, and is busiest in July and August (Edwards 2005). The number of cars entering the park per day has increased by 7%, 14%, and 8% for the months of May, June, and July, respectively from 2002–2011 (unpubl. road count data, Pacific Rim National Park Reserve, 2011). During the months of May, June, and July 2011, there was an average of 1,226, 1,541, and 2,000 vehicles (respectively) entering the park per day (unpubl. road count data, Pacific Rim National Park Reserve, 2011). Previous work has characterized the acoustic properties of traffic noise at other sites; it is known to be loud and low pitched (Slabbekoorn and Ripmeester 2008). Sound pressure level (SPL) measurements of morning traffic noise from two sites along the Trans-Canada Highway at our study site ranged between 80–90 dB (A-weighted decibels) SPL (collected 5 m away from the edge of the highway and averaged over a 10-min period in August 2012 using a Pyle PSPL25 sound level meter, Brooklyn, New York, USA; frequency range: 31.5 Hz to 8 kHz). Throughout, we refer to sound pressure level measurements as A-weighted decibel SPL (i.e., dBA).

A second major source of ambient noise is ocean surf. Our study site borders the Pacific Ocean, and crashing waves can be fairly strong, depending on wind direction and speed as well as water levels and tidal height. Like traffic noise, ocean noise is considered to be periodic noise, because noise levels decrease at low tide and between crashing waves. During August 2012, the average SPL measurement collected during the morning from four sites 5 m from the shore in Pacific Rim National Park Reserve was 73 dBA.

Experimental Design.—We recorded the songs produced by male Pacific Wrens at different distances away from the sources of ambient noise (ocean and traffic) within the Park during the breeding season from 0530–1300 Pacific Daylight Time (PDT) from 3 May to 12 July 2011. To minimize the influence of other noise sources, we only recorded individuals when there was little wind and no precipitation. We collected weather data (i.e., humidity, temperature, wind speed, and pressure) with a Kestrel weather tracker (4500 NV Pocket Weather Tracker). We used a handheld loudspeaker (Edge by Expedite; Hudson, WI, USA) to play back a conspecific Pacific Wren's song and stimulate the singing of individuals. All individuals received the same playback at the same volume level, which approximated the amplitude of a live singing Pacific Wren based on our assessment in the field. The playback was used for as long as necessary to stimulate singing of an individual (from 1 song to 10 min of playback at a rate of 5 songs/min).

We used a directional microphone (model: Audio-Technica AT8015; Stow, OH, USA) and a digital recorder (model: Marantz PMD670; recording settings: WAVE format, 44.1 kHz sampling rate, 16-bit accuracy) to record a total of 93 individuals for $\geq$30 min. The birds in this study were not individually marked. Instead, we distinguished between birds based on the location of their territories. We presumed that the birds we recorded were different individuals based on their geographic separation (i.e., individuals $\leq$200 m apart were not recorded). We entered each individual's location at the time of recording into a global positioning system (GPS; model: Garmin GPS 76CSX). We used the GPS coordinates of each recording location to determine the distance from each male to the nearest shore and to the nearest highway.

Estimation of Traffic and Ocean Noise as a Function of Distance.—We recorded the average noise level measurement during a 1-min period using the sound level meter at each of six positions moving away from noise sources (5 m, 25 m, 50 m, 75 m, 100 m, and 200 m) along 2–3 transects leading from each source. Both ocean surf and highway traffic are periodic noises; by calculating averages over a 1-min period, we generated a typical profile for what a nearby animal faces in terms of the amplitude of background noise. Distances from the shoreline or roadside were recorded using a hand-held GPS unit. Noise measurements were made in August 2012; we make the assumption that the noise

measurements from August are similar to noise measurements at the same sites in May through July when our bird recordings took place.

Analysis of Songs.—We used Avisoft SASLab Pro (version 5.1.20; R. Specht, Berlin, Germany) to generate spectrograms of songs from each of the recorded Pacific Wrens. From our 93 recordings, only 63 were of sufficiently high quality for detailed analysis. For each of the 63 males, we selected the first five songs that were not overlapped by the sounds of heterospecific animals and we used the 'automated parameter measurement' feature in Avisoft to extract detailed bioacoustic measurements (threshold setting: -15 dB relative to maximum; hold time: 5 ms). The use of automated parameter measurements minimized any subjectivity in collecting bioacoustic measurements. In all cases, we visually assessed the spectrograms to ensure that the automated parameter measurements were reasonable. We measured the song duration (ms), length of each syllable (ms), number of syllables (per song), and the syllable minimum frequency (Hz).

Data Analysis.—The response variables in this study were song duration, syllable length, number of syllables, and syllable minimum frequency. The independent variable was distance to noise source, whether to shoreline or edge of the highway. We verified that all response variables met the assumption of normality by inspecting histograms. Given that time of day can influence song characteristics (e.g., Dabelsteen and Mathevon 2002), and given that we recorded songs over an 8-hr period, we first tested for the effect of time of day on each response variable. When these regressions were not significant (for response variables syllable length, song duration, syllable minimum frequency), we proceeded with linear regressions of the song characteristics on distance to the noise sources. For one response variable, average number of syllables, we found a significant increase with time of day (regression equation: number of syllables $= 118.6230 + 4.6630$ decimal hour, $r^2 = 0.08$, $P = 0.023$); for this response variable we tested the effect of distance from source and time of day using multiple linear regression.

The path of the highway and the edge of the shoreline wind through our study site. At most locations, it was not possible for us to hear both the ocean surf and the traffic noise simultaneously. For wrens found within earshot range of both ocean and highway noise, we excluded birds that were within 100 m from one source, while testing the impacts of the second source (e.g., birds recorded within 100 m of ocean were excluded from regressions examining the impact of road noise). Five of the 63 birds recorded were excluded while testing the impacts of the ocean noise and 11 birds were excluded while testing the impacts of the highway noise.

To examine the effects of distance to the ocean or highway on the amount of variation within five songs of each individual, we performed a mixed model ANOVA for each of the response variables with distance to ocean and distance to the highway (near or far) as a fixed variable and the individual bird identity as a random factor. Near was considered to be 100 m or less from the source of noise and far was over a 100 m. These values were based on personal observation; after 100 m, our ability to detect the noise had decreased significantly. A variance-ratio test was performed subsequently given that the two sampled populations were normally distributed (Zar 2009).

We considered results to be statistically significant at $P < 0.05$. We plotted linear regressions for the song characteristics that varied significantly to determine whether the change in song characteristics matched the pattern of change in noise amplitude as a function of distance. Linear regressions were carried out in R version 2.13.1 (R Development Core Team 2011). Mixed model ANOVAs and verification of assumptions were performed using Statistica Version 7.0 for Windows (StatSoft, Inc. 2004).

RESULTS

Our recordings and noise level measurements demonstrated that both highway traffic noise and noise from ocean surf contribute substantial sources of noise (Fig. 1). Average traffic noise was measured at 85 dBA beside the highway, and dropped to 51 dBA 100 m away from the highway edge, while average ocean surf noise was measured at 73 dBA at the shore and 54 dBA 100 m from the ocean (Fig. 2). Songs of Pacific Wrens are long with a large number of syllables per song (Table 1). Minimum frequency varied minimally, whereas number of syllables and song duration varied moderately among individuals (Table 1).

Influence of Ocean Noise.—We found a significant negative relationship between average syllable
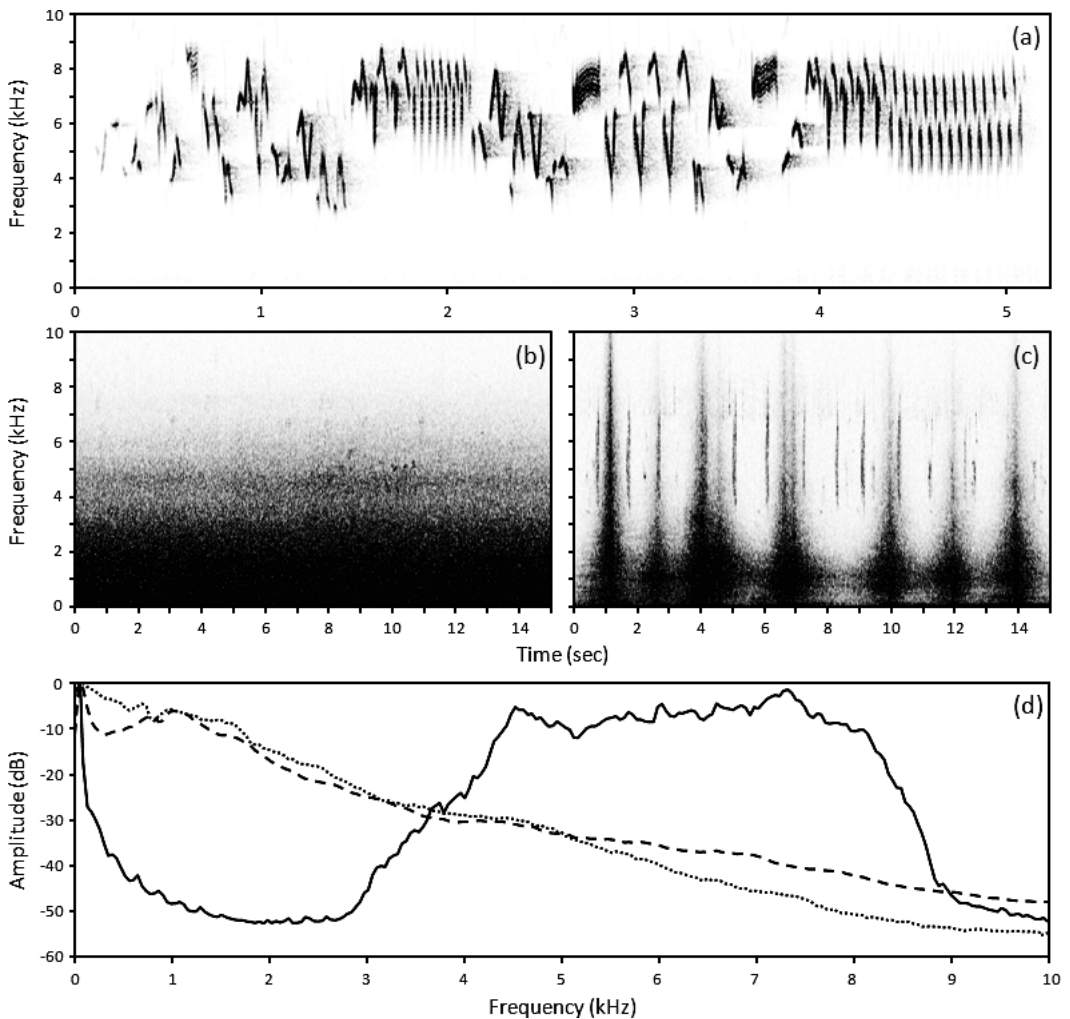
FIG. 1. Sound spectrograms of a typical song from a Pacific Wren (*Troglodytes pacificus*) (a), 15 secs of ocean noise (b), and 15 secs of highway noise (c) recorded in Pacific Rim National Park Reserve, British Columbia, Canada. Power spectra (d) are shown for a typical Pacific Wren's song (solid line), ocean noise (dotted line), and traffic noise (dashed line).

length and distance from the ocean ($r^2 = 0.09$, $n = 58$, $P = 0.02$; Fig. 3a; Table 2), a weak, non-significant effect on average number of syllables, and no effect of ocean noise on average syllable minimum frequency or song duration (Table 2). Song duration was significantly more variable within individuals near the ocean than individuals farther away (Variance-Ratio Test: $F_{10,51} = 2.68$, $P = 0.01$). The distance from the ocean showed no relationship with intra-individual variation for any other song characteristics.

Influence of Traffic Noise.—We found a significant positive relationship between average song duration and distance from the highway

($r^2 = 0.08$, $n = 52$, $P = 0.05$; Fig. 3b; Table 2). Distance to the highway did not have a significant effect on the average number of syllables, the average syllable minimum frequency, or the average syllable length of Pacific Wrens. We found no significant intra-individual variation for any of the response variables in relation to distance to the highway.

DISCUSSION

By studying variation in the songs of Pacific Wrens in relation to the singing birds' proximity to noise sources of roadsides and shorelines, we found that wrens sing significantly longer syllables and
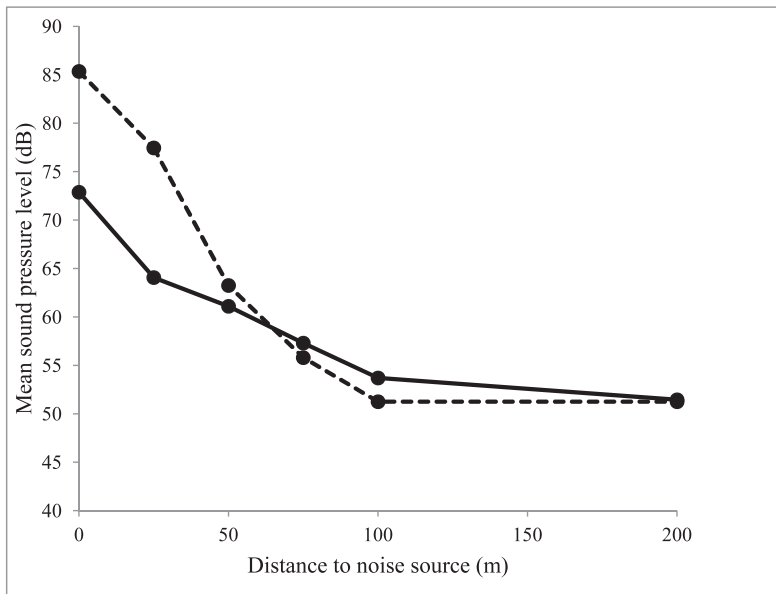
FIG. 2.   Mean sound pressure levels (dBA) corresponding to varying distances from the ocean (solid line) and the highway (dotted line). Values at each distance are means from transects retreating from each source of noise ($n = 2$, except for 0 m and 25 m from ocean where $n = 4$ and 3, respectively).

with significantly more variable song durations near the ocean. Wren songs also varied with proximity to roadside: wrens sing significantly shorter songs near the highway. Therefore, our investigation reveals that the songs of Pacific Wrens show an influence of a natural noise source, the sound of the ocean surf, and an effect of an anthropogenic noise source, the sound of traffic, although the latter effect was opposite to the direction that we predicted.

Influence of Ocean Noise on Wren Song.— Average syllable length was higher for songs of individuals that were recorded near the ocean. This finding supports our prediction and previous studies that have found that prolonged signals increase the ability of a receiver to detect a signal (Lengagne et al. 1999). We found no significant relationship between song duration and distance to the ocean. Pacific Wrens that were recorded near the ocean did not have songs that contained more syllables than those birds singing in quieter environments. Although increasing syllables are hypothesized to increase redundancy of a signal and improve the amount of information being transmitted in a noisy environment, we found only a non-significant pattern of higher syllables near the shoreline, even though ocean noise was often loud enough to disrupt normal human conversation. In other species (e.g., King Penguins) the number of syllables per call increased as wind speed increased, starting at a wind speed of 8 m/s (Lengagne et al. 1999). Similarly, Chaffinches in noisier habitats increased serial redundancy to effectively transmit their message (Brumm and Slater 2006). The faster tempo of Eastern versus Western Willets provides another consistent

TABLE 1.   Song characteristics of Pacific Wrens recorded at Pacific Rim National Park Reserve, British Columbia, Canada ($n = 63$).

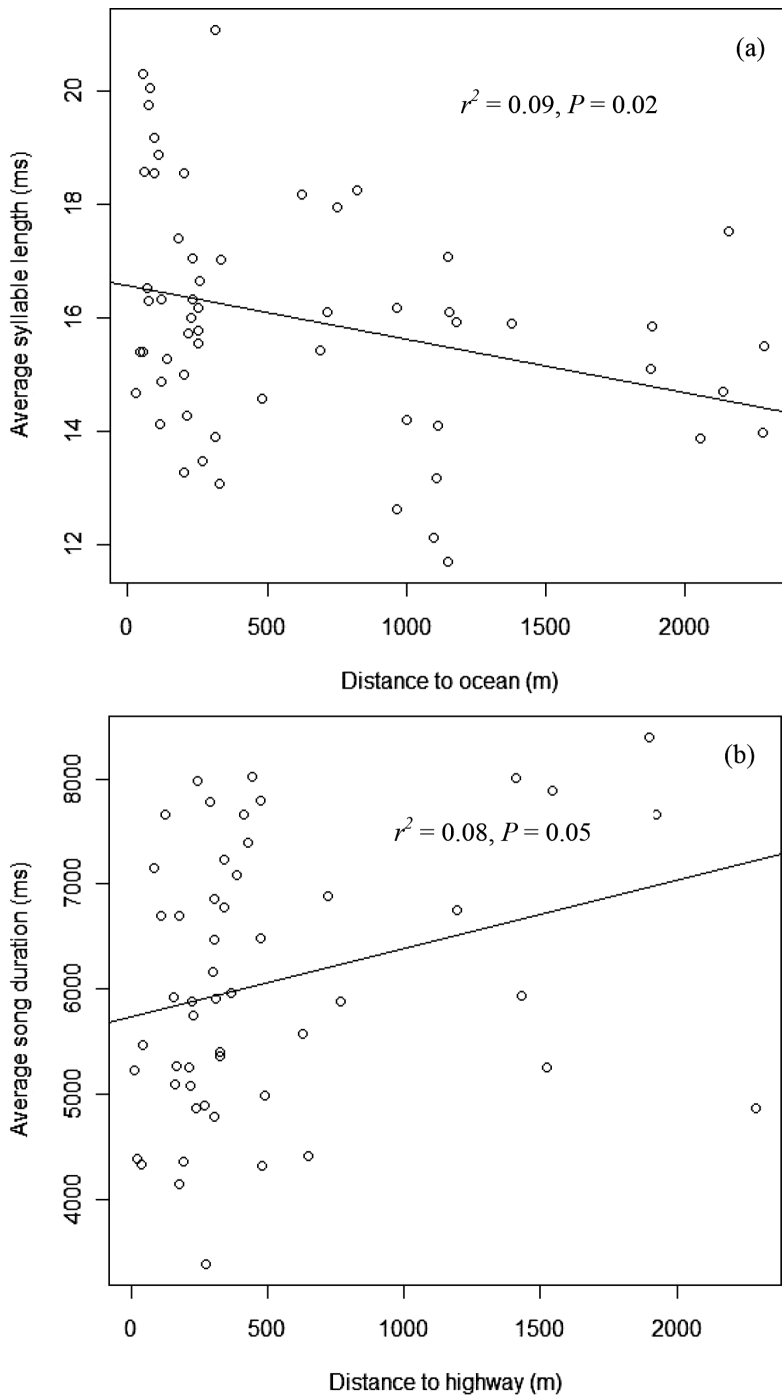| Song characteristic	Mean ± SE	CV (%)
Syllable Length (ms)	16.01 ± 0.25	13
Song Duration (ms)	6222.91 ± 185.61	24
Syllable Minimum Frequency (Hz)	5387.81 ± 19.65	3
Number of Syllables (per song)	159.92 ± 4.56	23

FIG. 3.   Linear regression plots showing (a) a significant negative relationship between the average syllable length of Pacific Wrens' songs and distance from the ocean (regression equation: Syllable length = 16.5846–0.0009 distance to ocean) and (b) a significant positive relationship between the average song duration of Pacific Wrens' songs and distance from the highway (Song duration = 5735.5671 + 0.6478 distance to highway).

TABLE 2.   Results of linear or multiple regression models for associations between distance to noise source (m; ocean surf or highway noise) and syllable length (ms), song duration (ms), syllable minimum frequency (Hz), and number of syllables (per song) of Pacific Wrens' songs along with corresponding F values of full models, P values, and r^2 values. Degrees of freedom for regressions with ocean and highway are 1,56 and 1,50, respectively.

Noise source	Regression equations	F	P	r^2
Ocean	Syllable length = 16.5846–0.0009 Distance to ocean	5.72	0.020	0.09
	Song duration = 6561.5072–0.4092 Distance to ocean	1.98	0.17	0.03
	Syllable minimum frequency = 5370.0000 + 0.0315 Distance to ocean	0.97	0.33	0.02
	Number of syllables = 134.3344–0.0123 Distance to ocean + 3.8652 Decimal hour	2.92	0.093	0.05
Highway	Syllable length = 15.6400 + 0.00002 Distance to highway	0.001	0.98	<0.01
	Song duration = 5735.5671 + 0.6478 Distance to highway	4.09	0.049	0.08
	Syllable minimum frequency = 5413.4264–0.0340 Distance to highway	0.89	0.35	0.02
	Number of syllables = 110.3000 + 0.0087 Distance to highway + 4.6780 Decimal hour	1.16	0.29	0.02

response to natural noise, with higher redundancy (Douglas and Conner 1999). The number of syllables in the songs of singing Pacific Wrens was moderately variable among individuals (CV = 23% of mean; Table 1), so this may have contributed to why we were unable to detect an effect of either noise source on this song characteristic.

We found no significant relationship between distance to ocean and syllable minimum frequency. Low-frequency signals experience greater acoustic interference from low-frequency noise than do high-frequency signals (Rheindt 2003, Parris and Schneider 2009). Given that Pacific Wrens' songs have relatively high frequency characteristics overall (Fig. 1), it is possible that the low-frequency noise from the ocean and the highway does not mask their songs, which would provide an explanation for the lack of observed effect in syllable minimum frequency.

We had predicted that there would be greater intra-individual variation in all song characteristics for wrens recorded near sources of noise but found that there was only greater intra-individual variation in song duration for individuals near the ocean (within 100 m) compared to far away from the ocean (>100 m). Although this was not tested, the within-individual variation in song duration may be because of interruptions in singing caused by crashing waves and hence analogous to the hypothesized function of shorter songs in Eastern Willets that can then be transmitted between the crashing of waves (Douglas and Conner 1999). In the case of Pacific Wrens, songs are generally much longer (up to 10 secs; Toews and Irwin

2012) than those of Willets and many other species, so varying song length during the waves would also ensure transmission of at least part of the song. The highly variable song length of birds singing at the ocean may help to explain why we did not find a significant change in song length as a function of distance to the ocean.

Influence of Traffic Noise on Individual Song Components.—The positive relationship between distance to the highway and average song duration could be because of traffic noise interrupting the songs of wrens singing near the highway; although this was not tested. Contrary to this, distance to ocean had a negative, albeit not significant, relationship with song duration. The difference in the direction of the effects could be because the wave frequency is longer than the traffic frequency, and therefore wrens can sing longer songs in between crashing waves. The absence of significant influence of highway noise on other song characteristics measured may have been because the traffic along Trans-Canada Highway 4 was not frequent or loud enough to cause the birds to adjust their songs more extensively. Many studies that have found significant impacts from traffic noise on bird song were evaluating busy highways carrying 30,000–50,000 vehicles/day (e.g., Rheindt 2003, Parris and Schneider 2009), compared to the highway in this study that carried many fewer vehicles/day during the peak period of Pacific Wrens singing and during the park's busiest month (unpubl. road count data, Pacific Rim National Park Reserve, 2011). It is also possible that vehicular speed contributed to the lack of significant influence of

highway noise on most wren song characteristics, since the posted speed limit is 80 km/h and this portion of the highway is meant as more of a scenic drive than a high-traffic commuting route. Finally, the peak in traffic is likely not overlapping with the maximum period of Pacific Wrens singing, which is at dawn. For these reasons, we do not interpret the general lack of effect of traffic noise on Pacific Wrens' songs as evidence that traffic noise does not influence bird song; instead, our results suggest that lower traffic volumes have less influence on bird songs than the well documented effects of high traffic volumes at other sites.

Future Studies.—Future studies could examine densities, pairing, and reproductive success of individuals found in noisy environments near the ocean. It is possible that despite adjustments to the songs and singing behavior of Pacific Wrens, the songs may not be sufficient for effective communication or may result in reduced attractiveness to females. A study of Ovenbirds (*Seiurus aurocapilla*) in two territories of varying noise levels but otherwise equal habitat quality found there were significantly more inexperienced first-year breeders and less pairing success in the noisy territories (Habib et al. 2007). It is also possible that these wrens changed their songs in ways that we did not measure. An additional avenue of research would be to examine whether Pacific Wrens adjust their vocal amplitude in the face of ocean and traffic noise. This phenomenon, known as the Lombard effect, is common in birds, humans, and monkeys (Junqua 1992, Brumm and Todt 2002, Brumm et al. 2004). Nemeth et al. (2013) found that increasing singing frequency was effective in mitigating acoustic masking but that the greatest effect came from the associated increase in amplitude.

ACKNOWLEDGMENTS

LITERATURE CITED

BRADBURY, J. W. AND S. L. VEHRENCAMP. 2011. Principles of animal communication. Second Edition. Sinauer Associates, Sunderland, Massachusetts, USA.

BRUMM, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. Journal of Animal Ecology 73:434–440.

BRUMM, H. AND H. SLABBEKOORN. 2005. Acoustic communication in noise. Advances in the Study of Behavior 35:151–209.

BRUMM, H. AND P. J. B. SLATER. 2006. Ambient noise, motor fatigue, and serial redundancy in chaffinch song. Behavioral Ecology and Sociobiology 60:475–481.

BRUMM, H. AND D. TODT. 2002. Noise-dependent song amplitude regulation in a territorial songbird. Animal Behavior 63:891–897.

BRUMM, H., K. VOSS, I. KOLLMER, AND D. TODT. 2004. Acoustic communication in noise: regulation of call characteristics in a New World monkey. Journal of Experimental Biology 207:443–448.

CATCHPOLE, C. K. AND P. J. B. SLATER. 2008. Bird song: biological themes and variations. Cambridge University Press, Cambridge, UK.

CHESSER, R. T., R. C. BANKS, F. K. BARKER, C. CICERO, J. L. DUNN, A. W. KRATTER, I. J. LOVETTE, P. C. RASMUSSEN, JR., J. V. REMSEN, J. D. RISING, D. F. STOTZ, AND K. WINKER. 2010. Fifty-first supplement to the American Ornithologists' Union check-list of North American birds. Auk 127:726–744.

DABELSTEEN, T. AND N. MATHEVON. 2002. Why do songbirds sing intensively at dawn? A test of the acoustic transmission hypothesis. Acta Ethologica 4:65–72.

DOUGLAS III, H. D. AND W. E. CONNER. 1999. Is there a sound reception window in coastal environments? Evidence from shorebird communication systems. Naturwissenschaften 86:228–230.

EDWARDS, D. 2005. Pacific Rim National Park Reserve carnivore-human interaction research project report. Progress Report prepared for Pacific Rim National Park Reserve of Canada, Long Beach, USA.

HABIB, L., E. M. BAYNE, AND S. BOUTIN. 2007. Chronic industrial noise affects pairing success and age structure of Ovenbirds *Seiurus aurocapilla*. Journal of Applied Ecology 44:176–184.

HALFWERK, W., S. BOT, J. BUIKX, M. VAN DER VELDE, J. KOMDEUR, C. TEN CATE, AND H. SLABBEKOORN. 2011. Low-frequency songs lose their potency in noisy urban conditions. Proceedings of the National Academy of Sciences 108:14549–14554.

HANNA, D., G. BLOUIN-DEMERS, D. R. WILSON, AND D. J. MENNILL. 2011. Anthropogenic noise affects song structure in Red-winged Blackbirds (*Agelaius phoeniceus*). Journal of Experimental Biology 214:3549–3556.

HU, Y. AND G. C. CARDOSO. 2010. Which birds adjust the frequency of vocalizations in urban noise? Animal Behavior 79:863–867.

JUNQUA, J. -C. 1992. The variability of speech produced in noise. Speech Processing in Adverse Conditions 43–52.

LENGAGNE, T., T. AUBIN, J. LAUGA, AND P. JOUVENTIN. 1999. How do King Penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? Proceedings of the Royal Society B 26:1623–1628.

MEDINA, L. AND C. D. FRANCIS. 2012. Environmental variability and acoustic signals: a multi-level approach in songbirds. Biology Letters 8:928–931.

MORTON, S. E. 1975. Ecological sources of selection on avian sounds. American Naturalist 109:17–34.

NEMETH, E. AND H. BRUMM. 2009. Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization? Animal Behaviour 78:637–641.

NEMETH, E., N. PIERETTI, S. A. ZOLLINGER,, N. GEBER-ZAHN, J. PARTECKE, A. C. MIRANDA, AND H. BRUMM. 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. Proceedings of the Royal Society B 280:1–7.

PARRIS, K. M. AND A. SCHNEIDER. 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. Ecology and Society 14:29.

PARRIS, K. M., M. VELIK-LORD, AND J. M. A. NORTH. 2009. Frogs call at a higher pitch in traffic noise. Ecology and Society 14:25.

POTVIN, D. A., K. M. PARRIS, AND R. A. MULDER. 2011. Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in Silvereyes (*Zosterops lateralis*). Proceedings of the Royal Society B 278:2464–2469.

QUINN, J. L., M. J. WHITTINGHAM, S. J. BUTLER, AND W. CRESSWELL. 2006. Noise, predation risk compensation and vigilance in the Chaffinch *Fringilla coelebs*. Journal of Avian Biology 37:601–608.

REIJNEN, R. AND R. FOPPEN. 1994. The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for Willow Warblers (*Phylloscopus trochilus*) breeding close to a highway. Journal of Applied Ecology 31:85–94.

R DEVELOPMENT CORE TEAM. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RHEINDT, F. E. 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? Journal of Ornithology 144:295–306.

SLABBEKOORN, H. AND A. DEN BOER-VISSER. 2006. Cities change the songs of birds. Current Biology 16:2326–2331.

SLABBEKOORN, H. AND M. PEET. 2003. Ecology: birds sing at a higher pitch in urban noise. Nature 424:267–267.

SLABBEKOORN, H. AND E. A. RIPMEESTER. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. Molecular Ecology 17:72–83.

STATSOFT, INC. 2004. STATISTICA (data analysis software system). Version 7. Tulsa, Oklahoma, USA.

TOEWS, D. P. L. AND D. E. IRWIN. 2008. Cryptic speciation in a Holarctic passerine revealed by genetic and bioacoustic analyses. Molecular Ecology 17:2691–2705.

TOEWS, D. P. L. AND D. E. IRWIN. 2012. Pacific Wren (*Troglodytes pacificus*). The birds of North America. Number 720.

WILEY, R. H. AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behavioral Ecology and Sociobiology 3:69–94.

WOOD, W. E. AND S. M. YEZERINAC. 2006. Song Sparrow (*Melospiza melodia*) song varies with urban noise. Auk 123:650–659.

ZAR, J. H. 2009. Biostatistical analysis. Fifth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.