The Auk 127(1):156–161, 2010

BIRDSONG DIFFERS BETWEEN MERCURY-POLLUTED AND REFERENCE SITES

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Abstract.—Mercury is a toxic heavy metal that can cause obvious physiological and reproductive problems in animals. Very little is known, however, about its subtle behavioral effects. We examined whether birds that inhabited mercury-contaminated sites exhibited differences in singing behavior compared with birds at uncontaminated reference sites nearby. We recorded the songs of 3 oscines, the Carolina Wren (*Thryothorus ludovicianus*), House Wren (*Troglodytes aedon*), and Song Sparrow (*Melospiza melodia*), and 1 suboscine, the Eastern Phoebe (*Sayornis phoebe*). Spectrographic analysis revealed that songs of oscines living on contaminated sites contained a lower diversity of note types and were sung at lower tonal frequencies than songs of birds on reference sites. Additionally, both species of wren tended to sing shorter songs. By contrast, the songs of Eastern Phoebes did not differ between contaminated and reference sites, suggesting that mercury may affect singing behavior only in species that learn their songs. Such alterations in song could have important implications for the fitness of songbirds in polluted areas. Our results highlight the importance of considering behaviors in evaluations of contaminant effects. *Received 25 November 2008, accepted 19 August 2009.*

Key words: communication, developmental stress, heavy metal, mercury, song.

Los Cantos de Aves Difieren entre Sitios Contaminados con Mercurio y Sitios de Referencia

Resumen.—El mercurio es un metal pesado tóxico que puede causar obvios problemas fisiológicos y reproductivos en los animales. Sin embargo, se conoce muy poco acerca de sus efectos sutiles sobre el comportamiento. Examinamos si aves que habitaban sitios contaminados con mercurio exhibían diferencias en el comportamiento de canto en comparación con aves de lugares cercanos no contaminados de referencia. Grabamos los cantos de tres oscinos (*Thryothorus ludovicianus*, *Troglodytes aedon* y *Melospiza melodia*) y de un suboscino (*Sayornis phoebe*). Análisis espectrográficos indicaron que los cantos de los oscinos de los sitios contaminados presentaban una menor diversidad de tipos de notas y eran emitidos a frecuencias tonales más bajas que los cantos de los sitios de referencia. Además, *T. ludovicianus* y *T. aedon* tendieron a presentar cantos más cortos. En contraste, los cantos de *S. phoebe* no difirieron entre los sitios contaminados y los de referencia, lo que sugiere que el mercurio podría afectar el comportamiento de canto sólo en las especies que aprenden sus vocalizaciones. Estas alteraciones en el canto podrían tener implicaciones importantes para la adecuación de las aves que viven en ambientes contaminados. Nuestros resultados resaltan la importancia de considerar los comportamientos en las evaluaciones de los efectos de los contaminantes.

Mercury is a toxic metal that accumulates in animal tissue and biomagnifies as it moves up food chains. The most bioavailable form, methylmercury, concentrates at the top of food webs and can cause severe damage to the nervous system in animals (Wolfe et al. 1998). Although physiological problems caused by exposure to mercury are well documented in birds, subtle behavioral changes have largely been neglected (but see Heinz 1979, Nocera and Taylor 1998, Bouton et al. 1999). However, behavioral abnormalities may be more indicative of toxicological problems than chemical, physical, or morphological parameters because behaviors depend on the integration of complex developmental and physiological pathways for proper expression (Gorissen et al. 2005).

Research on the mechanisms of singing has revealed that subtle alterations can result from stressors such as food limitation (Spencer et al. 2003), disease (Garamszegi et al. 2004), and environmental pollutants (Markman et al. 2008). Such stressors may undermine developmental processes important for successful song acquisition (e.g., Nowicki et al. 2002) or directly alter song production in adults (e.g., Garamszegi et al. 2004). To our knowledge, only one study has explicitly examined song in relation to heavy-metal exposure (Gorissen et al. 2005). In that study, male Great Tits (*Parus major*) near a metal smelter exhibited reductions in both total amount of song and repertoire size (Gorissen et al. 2005). Because song plays a critical role in both mate attraction

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The Auk, Vol. 127, Number 1, pages 156–161. ISSN 0004-8038, electronic ISSN 1938-4254. DOI: 10.1525/auk.2009.09058

and territory defense, contaminant-induced changes such as those reported by Gorissen et al. (2005) could severely depress male reproductive success. Song is therefore a potent mechanism through which contaminants such as mercury could affect fitness.

The South River in Virginia was contaminated with industrial mercury between 1929 and 1950 (Carter 1977). Elevated levels of mercury occur in the blood and feathers of resident birds, including a majority of the terrestrial songbird species breeding within 50 m of the river (Cristol et al. 2008). We studied 4 species of songbirds that had blood mercury levels similar to those reported to cause behavioral abnormalities in a well-studied waterbird, the Common Loon (*Gavia immer*; 3.0 ppm threshold; Evers et al. 2008). Mean levels of contamination in our study species in 2005–2006 were as follows: Carolina Wren (*Thryothorus ludovicianus*), 4.69 $\mu g\ g^{-1}$ ($n = 49$); Eastern Phoebe (*Sayornis phoebe*), 3.24 $\mu g\ g^{-1}$ ($n = 7$); Song Sparrow (*Melospiza melodia*), 2.69 $\mu g\ g^{-1}$ ($n = 18$); and House Wren (*Troglodytes aedon*), 2.47 $\mu g\ g^{-1}$ ($n = 26$). In every species, blood mercury levels on contaminated sites were, on average, an order of magnitude higher than those of birds on reference sites (Cristol et al. 2008).

Most research on song has been conducted with oscine passerines, the majority of which show a substantial dependence on learning for proper song acquisition (reviewed in Saranathan et al. 2007). Three of our study species, the Carolina Wren, House Wren, and Song Sparrow, are oscines. By contrast, the few suboscine species with well-studied songs have revealed little evidence of learning. Instead, such birds, including the Eastern Phoebe, seem predisposed to a developmentally fixed pattern of song acquisition (reviewed in Saranathan et al. 2007). By including a suboscine in our study, we hoped to gain insight into whether mercury might disrupt processes involved in song learning.

We tested the hypothesis that the songs of birds living on mercury-contaminated sites would differ from those on uncontaminated reference areas. We did not make specific predictions about which elements would be affected or in which direction they would differ, because it is not yet possible to identify which components of song are the most vital to reproductive success or the most difficult to perform in our study species. Instead, we examined parameters of song that have proved to be of biological interest in other studies.

Methods

Song recordings.—From 7 June to 12 July, 2006, we recorded singing male Carolina Wrens ($n = 11$), House Wrens ($n = 10$), and Song Sparrows ($n = 9$) at 11 sites along the contaminated South River, a tributary of the Shenandoah River that flows through Augusta and Rockingham counties, Virginia (centroid of study sites: 38°10′N, 78°59′W). Eleven additional Song Sparrows were recorded from 6 April to 14 June, 2007, at 8 contaminated sites (13 total sites for both years). During the same periods, we recorded reference songs of 10 Carolina Wrens, 8 House Wrens, and 20 Song Sparrows ($n = 12$ in 2006, $n = 8$ in 2007) on 9 sites with no history of mercury contamination (on the South River above the point of contamination and on 2 nearby tributaries, the North and Middle rivers; as in Cristol et al. 2008). Eastern Phoebes were recorded the following year, from 13 May to 19 June, 2008 (10 from 7 contaminated sites and 7 from 6 reference sites). Although males were not color-banded, every effort was made to ensure that only 1 individual in a given area was sampled. Each of our individual sites was several kilometers away from any others. Multiple individuals were recorded at the same site only when each could be heard singing simultaneously (thus confirming the existence of >1 individual) or when recordings were made sufficiently far apart that we could safely assume 2 distinct territories. We pooled recordings from different years because we found no significant variation in mercury level between years in the wren species studied (D. A. Cristol unpubl. data).

Recordings were made using a portable cassette recorder (Marantz PMD 201; Marantz America, Itasca, Illinois) with a shotgun microphone (AKG SE 300 B; AKG Acoustics, Vienna). Each bird was located by sight within 50 m of the river and recorded for 2–10 min. All 3 of our oscine study species typically alternate between multiple song types; thus, it is unlikely that we recorded any individual's entire repertoire. By contrast, Eastern Phoebes sing only 2 discrete song types, both of which were recorded for 16 of the 17 individuals sampled.

Song analysis.—Songs were analyzed with the RAVEN bioacoustics program, version 1.2 (Cornell Lab of Ornithology, Ithaca, New York), using the default combination of settings (smoothed spectrogram, bandwidth = 93.8 Hz, hop size = 0.005 s). For all species, we first determined the number and distribution of strophes within the longest continuous bout of singing for each individual. We defined a strophe as a single burst of song lasting several seconds and followed by a gap of approximately the same length. A continuous series of strophes constituted a bout of singing. We analyzed spectrograms for a number of discrete song characteristics that fell into two categories: macro- and microparameters.

Macroparameters involved multiple strophes and did not require examination of individual notes. We quantified the rate of singing as a measure of total song output, and average strophe length as a measure of investment in song production and quality. Rates of singing have been linked to male quality in several studies (reviewed in Podos et al. 2004). Additionally, song output and strophe length are two parameters that have previously been measured in relation to heavy metal contamination (Gorissen et al. 2005), allowing for ease of comparison with the present study.

We also measured several microparameters involving the individual notes within strophes. For the 3 oscine species, measurements were made with respect to the most-repeated element of each song type because this represented the single note type in which the bird invested the most time. We defined the most-repeated element as the note type that was repeated the most times within a strophe, excluding entrance notes (see Fig. 1). We also measured peak frequency (defined as the tonal frequency at which the maximum amplitude occurred), number of repeats, and internal rate (defined as the amount of time between 2 successive notes) of the most-repeated element in each song. The number of different note types within each song type served as an estimate of overall complexity. For Song Sparrows, which have more varied song structure, we measured additional parameters associated with the buzz note because this consistent element is readily comparable across individuals. For the buzz note, we measured the dominant frequency, bandwidth, and duration, which have all been measured in a number of other studies (e.g., Wood and

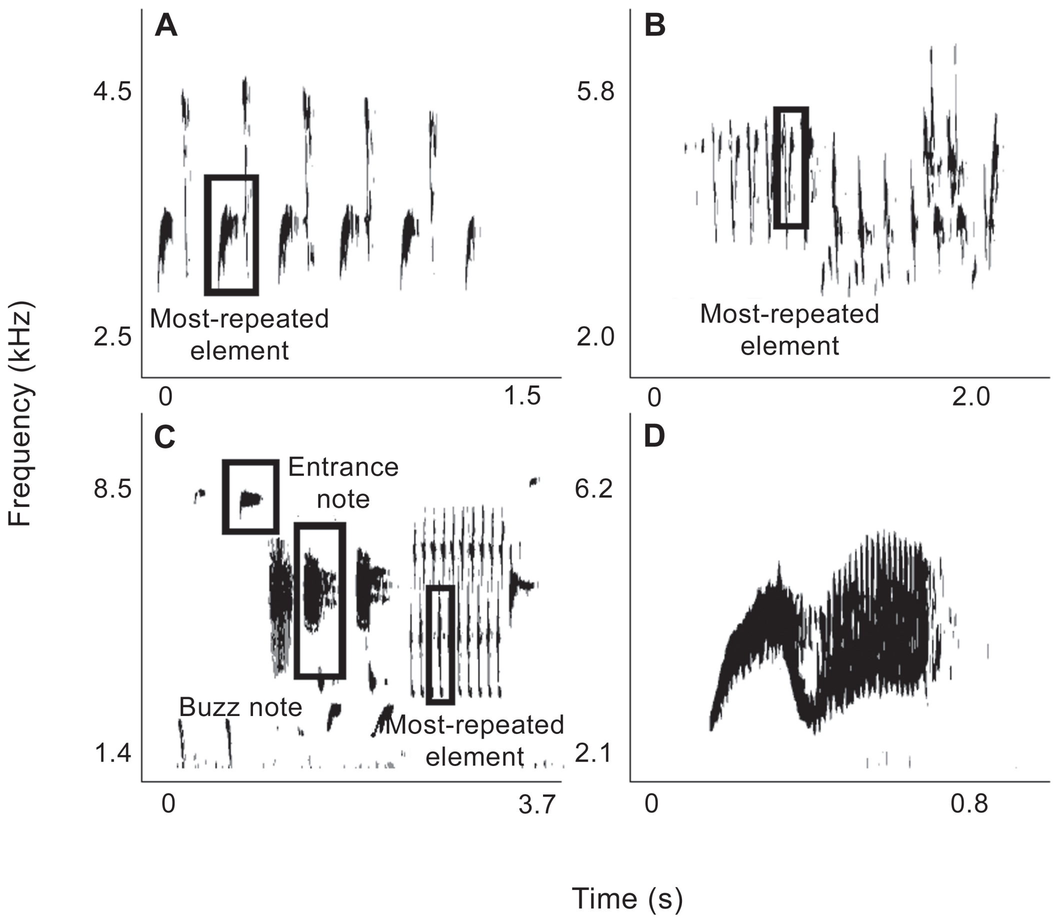

Fig. 1. Examples of spectrograms representing 1 strophe of (A) Carolina Wren, (B) House Wren, (C) Song Sparrow, and (D) Eastern Phoebe songs. The major components of the song, as well as the specific notes measured, are highlighted.

Yezerinac 2006). The simple structure of the Eastern Phoebe song precluded analyses involving particular elements or quantification of complexity. Instead, we measured the dominant frequency and bandwidth of 2 entire strophes.

Mercury levels.—We did not take tissue samples from our study subjects, but Tree Swallows (*Tachycineta bicolor*) were well sampled at nearly all sites as part of another study. Because Tree Swallows exhibited mercury levels of comparable magnitude to those in the focal species (mean contamination = 3.66 μg g^{-1}; n = 79; Cristol et al. 2008), we used Tree Swallow mercury levels as a proxy for the relative contamination of each study site. Blood of adult Tree Swallows was sampled and analyzed for total mercury concentration following the methods of Brasso and Cristol (2008). In 2006, 267 adult Tree Swallows were sampled at 24 of the 29 sites at which recordings were made during 2006–2008. The mean number (± SD) of Tree Swallows sampled at each site was 11.2 ± 8.5 on contaminated sites ($n = 10$) and 11.1 ± 9.1 on reference sites ($n = 14$). The mean blood mercury level for all Tree Swallows at each site was used to characterize that site.

Land cover analysis.—Because differences in acoustic environment have been linked to differences in singing behavior (Patricelli and Blickley 2006), we used geographic information systems software (ARCVIEW, version 9.2; ESRI, Redlands, California) to analyze habitat structure across the 29 sites at which recordings were made. We examined digital orthophoto quarter-quad images and delineated study sites by creating circular buffers around the midpoint of each site with a variable radius that encompassed the upstream and downstream boundaries. Relative proportions of each major habitat type (developed, forest, field) were then determined using the National Land Cover Database (see Acknowledgments).

Statistical analyses.—We measured multiple song traits across Carolina Wrens ($n = 6$ song traits), House Wrens ($n = 6$ song traits), Song Sparrows (n = 9 song traits), and Eastern Phoebes (n = 4 song traits) to examine potential differences between mercury-contaminated and reference birds. We then performed principal component analysis (PCA) on each set of variables common to a particular species. Because we measured the same suite of parameters for both species of wrens, these 2 species were examined in a single analysis. By contrast, for Song Sparrows and Eastern Phoebes, for which different variables were measured, we ran 2 additional PCAs. We then used linear models, with mercury status (contaminated or reference), species (wrens only), and a mercury status × species interaction (wrens only) as factors, to determine whether any of the principal components (PCs) were associated with mercury contamination.

We regressed tonal frequency for all oscine individuals recorded at a given site against the average mercury level at the same site (based on Tree Swallow blood samples; see above). Frequency was normalized separately for each oscine by calculating *z* scores using each species' mean frequency and standard deviation. To reduce the effect of aberrant individuals, we included only those sites with ≥2 recordings from a species.

We grouped land-cover classifications as either developed (developed open, low-, medium-, high-intensity), forest (deciduous, evergreen, mixed), or field (pasture–hay, cultivated crops). We then compared the percentages of each habitat type between contaminated and reference sites using two-sample *t*-tests. All statistical analyses were performed using R (R Development Core Team, Vienna; see Acknowledgments) or MINITAB, version 15 (Minitab, State College, Pennsylvania).

Results

When the songs of both wren species were included in a PCA (Table 1), the first component, which explained 44% of the variance, partitioned the variation attributable to species differences, as indicated by a significant species effect (PC1: $F = 57.67$, df = 1 and 33, $P < 0.001$). Mercury status (contaminated or reference) and the mercury status × species interaction were not significant. By contrast, PC2 (Table 1), which accounted for 23.6% of the variance and loaded positively for the number of note types per song, average strophe length, and peak frequency of the most-repeated element, resulted in a significant effect of mercury status ($F = 15.35$, df = 1 and 33, $P < 0.001$), which indicates that it captured the variance related to site contamination. The lack of significance of the species × mercury status interaction indicates that songs of the 2 wren species did not respond differently to living on a contaminated site. Post hoc tests revealed that wren songs on contaminated sites had lower PC2 scores than those on reference sites (Tukey's HSD, $P < 0.001$), which indicates that contaminated wrens sang shorter songs with fewer note types and lower tonal frequencies.

The PCA conducted on 9 parameters measured in Song Sparrows (Table 2) produced a component (PC3) that loaded positively for the peak frequency and bandwidth of the buzz note, as well as the number of note types per song. This PC revealed a significant effect of mercury status, such that birds on contaminated sites produced songs that contained fewer note types and lower-frequency, shorter-bandwidth buzz notes ($F = 8.36$, df = 1 and 37, $P = 0.006$). By contrast, neither PC1 nor PC2 reflected variation that was significantly associated with a site's mercury status (PC1: $F = 0.30$, df = 1 and 37, $P = 0.59$; PC2: $F = 0.90$, df = 1 and 37, $P = 0.35$).

The PCA conducted on Eastern Phoebe songs produced 2 components that, together, accounted for 71% of the variance in the data (Table 3). PC1 loaded for longer strophes with higher bandwidth that were sung at a higher rate, whereas PC2 loaded positively for peak frequency. However, linear models revealed no effect of mercury contamination on either PC1 ($F = 0.61$, df = 1 and 14, $P = 0.45$) or PC2 ($F = 1.06$, df = 1 and 14, $P = 0.32$).

Tonal frequency was related to mercury status in all 3 oscine species. We therefore used analysis of covariance to further test for species-level differences in the response to mercury contamination. Neither the elevation ($F = 0.42$, df = 1 and 3, $P = 0.74$) nor the slopes ($F = 0.52$, df = 1 and 2, $P = 0.60$) differed among species, but tonal frequency declined significantly with increasing mercury

Table 1. (A) Eigenvalues and variances explained for principal component analysis on song characteristics measured for Carolina and House wrens.

Component	Eigenvalue	Proportion of variance	Cumulative proportion
PC1	2.647	0.441	0.441
PC2	1.418	0.236	0.677

(B) Factor loadings for each variable on principal components 1 and 2.

	PC1	PC2
Rate	−0.528	0.159
Number of repeats	0.555	−0.064
Number of note types	−0.316	0.653
Peak frequency of most-repeated element	0.289	0.490
Strophe length	0.362	0.549
Strophe rate	−0.314	0.046

Table 2. (A) Eigenvalues and variances explained for principal component analysis on song parameters measured for the Song Sparrow.

Component	Eigenvalue	Proportion of variance	Cumulative proportion
PC1	2.323	0.258	0.258
PC2	1.707	0.190	0.448
PC3	1.386	0.154	0.602

(B) Factor loadings for each variable on principal components 1, 2, and 3.

	PC1	PC2	PC3
Rate	0.543	−0.072	−0.280
Number of repeats	−0.578	−0.008	0.079
Number of note types	0.322	0.335	0.466
Peak frequency of most-repeated element	−0.027	−0.441	−0.087
Strophe length	−0.127	−0.526	0.290
Strophe rate	0.367	−0.074	−0.341
Peak frequency of buzz note	0.166	−0.128	0.514
Buzz note bandwidth	0.216	0.098	0.462
Buzz note duration	0.203	−0.616	0.108

Table 3. (A) Eigenvalues and variances explained for principal component analysis on song characteristics of Eastern Phoebes.

Component	Eigenvalue	Proportion of variance	Cumulative proportion
PC1	1.656	0.414	0.414
PC2	1.198	0.300	0.714

(B) Factor loadings for each variable on principal components 1 and 2.

	PC1	PC2
Strophe length	0.581	−0.389
Strophe rate	0.616	−0.121
Peak frequency of strophe	0.105	0.815
Frequency bandwidth of strophe	0.522	0.412

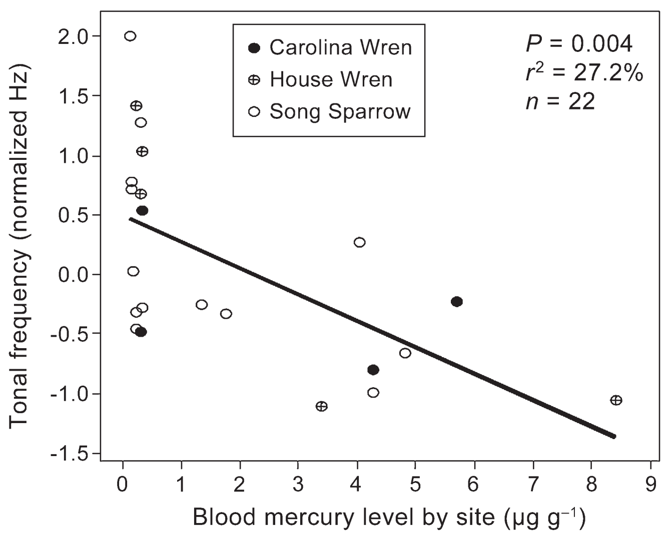

Fig. 2. Regression of site contamination level (Tree Swallow blood mercury level) plotted against normalized peak frequencies of Carolina Wren, House Wren, and Song Sparrow (buzz note). Each data point represents a site at which songs of ≥ 2 individuals of a particular species were recorded.

contamination at a site ($t = -3.31$, df = 18, $P = 0.004$, $r^2 = 0.272$; Fig. 2), which indicates that birds living at sites with higher mercury levels sang their songs at lower tonal frequencies. A comparable analysis that related number of note types to a site's mercury level resulted in a similar but nonsignificant trend (data not shown).

Land cover.—The land-cover analysis revealed no significant differences between contaminated and reference sites for the 3 predominant characteristics of habitat structure (percent developed: $t = 0.30$, df = 11, $P = 0.77$; percent forested: $t = 1.76$, df = 11, $P = 0.10$; percent fields: $t = -1.37$, df = 11, $P = 0.20$).

Discussion

In 3 of the 4 species examined, songs of birds living on mercury-contaminated sites differed from those on reference sites. Principal component analyses revealed that Carolina Wrens, House Wrens, and Song Sparrows breeding on contaminated sites all exhibited a lowered diversity of note types and sang at lower tonal frequencies than conspecifics breeding on reference sites. Additionally, the 2 wren species sang shorter strophes in polluted areas. By contrast, Eastern Phoebe song did not differ between mercury-contaminated and reference sites.

Our results suggest that living on a mercury-contaminated site affected several characteristics of oscine song. One potential explanation for these results is incidental differences in habitat structure between polluted and unpolluted areas, because the fine structure of songs often matches the acoustic environment (Patricelli and Blickley 2006). However, there were numerous contaminated and reference sites, and they did not differ significantly in their proportions of human development, forest, and fields, which suggests that our results did not arise from a systematic bias in habitat structure.

We did not measure mercury levels of the individual birds that we recorded, so we made the assumption that the degree of contamination at each site could be approximated by data from another insectivorous bird for which we have ample mercury data. Because tonal frequency differed consistently between contaminated and reference birds of all 3 oscine species, we tested the hypothesis that the tonal frequency of a bird's song was related to the relative degree of site contamination. The resulting significant negative relationship suggests that tonal song frequency varies with mercury level in a dose-dependent manner.

The analysis also revealed that contaminated oscines of all 3 species tended to sing a lower diversity of notes than reference conspecifics. Such results are consistent with Gorissen's (2005) finding that birds living near a metal smelter produced smaller repertoires than birds living farther from the contamination source. The co-occurrence of low tonal frequency and lowered note diversity in contaminated songbirds may not be mere coincidence. Sensory perception could be impaired in young birds on contaminated sites, causing them to hear and learn lower-frequency notes preferentially. In fact, mercury exposure has been linked to auditory impairment in the laboratory: monkeys exposed to mercury from birth exhibited an inability to perceive high-frequency sounds as adults (Rice and Gilbert 1992). Thus, it is possible that juveniles living on contaminated sites suffered from high-frequency hearing impairment, which caused them to acquire and preferentially sing lower-frequency notes. If this were the case, one might also expect a resultant decrease in overall note diversity caused by the selective discrimination of notes in the lower range of frequencies. However, other mechanistic explanations are certainly possible. For example, male Zebra Finches (*Taeniopygia guttata*) that were experimentally stressed during song learning tended to produce songs that were both lower in frequency and shorter (Spencer et al. 2003). This result is equally consistent with our findings and suggests that more generalized stress during song learning, caused directly or indirectly by mercury, could produce the observed changes in the songs of mercury-contaminated birds. A third possibility, and one that does not require that juveniles settle near their natal sites, is that mercury-contaminated adults were in poorer condition and therefore substituted lower-frequency notes, which might be easier to perform. Such physiological impairment would also provide an explanation for why contaminated male wrens sang shorter strophes, given that shorter songs may reduce metabolic costs (Eberhardt 1994; but see discussion in Podos et al. 2004).

Our analysis of Eastern Phoebe song provided an opportunity to examine the possible role of learning in the relationship between mercury and song. Kroodsma and Konishi (1991) showed that experimentally deafened nestling Eastern Phoebes produced normal songs despite the absence of auditory feedback. This suggests that environmental perturbations are unlikely to affect development of the relatively inflexible song of this species. Indeed, we found that the Eastern Phoebe, the only species of the 4 that we studied that does not learn its song, was also the only species whose song characteristics were not associated with living on a mercury-contaminated site. Although not conclusive, this result suggests that future studies could profitably address the hypothesis that mercury alters song through effects on learning. Of particular value would be experimental work aimed at pinpointing the specific developmental or physiological pathways through which mercury may alter singing behavior.

Regardless of the mechanisms underlying these differences in song, the fact that they exist at all demonstrates the potential usefulness of subtle behavioral cues in ecotoxicological studies. Song may be a more sensitive indicator of environmental stress than tissue samples, which are traditionally used to evaluate contaminant effects, because song is the result of a combination of complex behavioral and physiological pathways (Gorissen et al. 2005). Thus, future ecotoxicological studies may be able to use song to more realistically evaluate the fitness costs associated with heavy-metal contamination.

Acknowledgments

Funding was provided by E.I. DuPont de Nemours and Company, Virginia Society of Ornithology, Association of Field Ornithologists, American Ornithologists' Union, Office of Vice Provost for Research at the College of William and Mary, National Science Foundation grant UBM 0436318, and the William and Mary Undergraduate Science Education and Research Program sponsored by Howard Hughes Medical Institute. We thank the South River Science Team, R. Brasso, A. Condon, A. Dolby, R. Fovargue, S. Friedman, G. Gilchrist, M. Howie, N. Karouna-Renier, T. Meier, A. Monroe, T. Russell, J. Schmerfeld, A. White, and the many cooperative landowners of the Shenandoah Valley. Two anonymous reviewers greatly improved earlier versions of the manuscript. R, a language and environment for statistical computing, is available at www.R-project.org. The National Land Cover Database (Multi-Resolution Land Characteristics Consortium, U.S. Geological Survey) is available at www.mrlc.gov/index.php.

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Associate Editor: A. M. Dufty, Jr.