Ecology Shapes Birdsong Evolution: Variation in Morphology and Habitat Explains Variation in White-Crowned Sparrow Song

Elizabeth P. Derryberry[*]

Department of Biology, Duke University, Durham, North Carolina 27708

ABSTRACT: Ecological variation appears to underlie the evolution of mating signals in many taxa, yet understanding of how this process occurs over time is limited. Here, I investigate whether changes over time in a well-studied mating signal—birdsong—are attributable to ecological factors that affect signal production and transmission. Variation in the acoustic properties of songs is thought to be affected by the mechanics of sound production as well as by features of the habitat that affect sound transmission. To determine whether these mechanisms contribute to song variation, I compare patterns of morphological and habitat variation with variation in song structure among populations of white-crowned sparrows (*Zonotrichia leucophrys*) at two time points separated by 35 years. Among contemporary (2005) populations, vegetation density and bill size explain significant variation in song structure. The direction of change in song structure between 1970 and 2005 is also consistent with the direction of change in vegetation density. These findings suggest that variation in factors that affect signal production and transmission explains significant variation in white-crowned sparrow song.

Keywords: birdsong, evolution of behavior, signal detectability, white-crowned sparrow.

Introduction

In many taxa, the evolution of mating signals appears driven by ecological factors, such as those that affect signal production and transmission (Wiley and Richards 1978; Ryan et al. 1990; Nowicki et al. 1992; Boughman 2002; Slabbekoorn and Smith 2002b; Leal and Fleishman 2004; Cummings 2007). There is increasing evidence that indirect selection on traits related to signal production, such as body size (e.g., Nevo and Capranica 1985; Ryan and Brenowitz 1985) or bill size in birds (Palacios and Tubaro 2000; Podos 2001; Ballentine 2006; Badyaev et al. 2008),

* Present address: Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana 70803; e-mail: ederry1@lsu.edu.

as well as habitat-dependent selection on signal transmission (e.g., Morton 1975; Wiley 1991; reviewed in Slabbekoorn and Smith 2002a; Seddon 2005), may drive signal evolution. However, because of a lack of long-term population studies, there is little evidence within species of correlated change over time between signal structure and factors that influence signal production and transmission. Here, I examine a well-studied mating signal, birdsong, to address the influences of morphology and environment on signal variation, as well as the correspondence between changes in these factors over time. I focus on variation in a widespread feature of song—vocal trills (i.e., repetitions of the same syllable)—because trills appear to be affected both by the mechanics of sound production (reviewed in Podos et al. 2004) and by habitat-dependent selection on sound transmission (Naguib 2003).

The Influence of Morphology on Trill Production

Songbirds often produce songs composed of pure tones across a range of fundamental frequencies (Nowicki and Marler 1988). Songbirds filter out harmonic overtones by actively modifying the resonant properties of their vocal tract (Westneat et al. 1993; Riede et al. 2006). One described motor constraint on trill production is the result of birds modulating bill gape while singing (Nowicki 1987; Westneat et al. 1993; Hoese et al. 2000; Beckers et al. 2003). When a bird sings, it opens and closes its bill to track the fundamental frequency produced by the syrinx (Nowicki 1987; Nowicki and Marler 1988) such that its bill is more widely gaped during production of high frequencies and more closed during production of low frequencies (Westneat et al. 1993; Hoese et al. 2000). There is a limit to how rapidly an individual can open and close its bill, depending on how widely the bill is open (Westneat et al. 1993; Hoese et al. 2000). Because vocal trills in particular often consist of rapid frequency-modulated notes, a trade-

off exists between trill rate and frequency bandwidth (Podos 1997; Podos and Nowicki 2004b). This trade-off results in a triangular acoustic space in which slow trills include either narrow or wide frequency bandwidths, whereas fast trills are restricted to narrow frequency bandwidths (Podos 1997). The upper boundary of this triangular distribution estimates a performance limit, and deviation from this limit may be an indicator of how well songs are performed relative to the motor constraint (Podos 2001; Ballentine et al. 2004). This measure of song performance is known as vocal deviation.

The evolution of bill size may influence the evolution of vocal deviation (Nowicki et al. 1992; Podos and Nowicki 2004a, 2004b). Large bills are closely associated with high force application potential in jaw musculature, or an ability to bite hard (Herrel et al. 2005, 2009). Biomechanical and muscle-architecture adaptations for high force application necessarily lead to reduced maximal velocities of bill movement, largely independent of overall body size (Herrel et al. 2009). Birds with larger bills are predicted to produce songs with slower trill rates or narrower frequency bandwidths (i.e., lower-performance songs; Podos 2001; Podos and Nowicki 2004b). Morphological adaptation to divergent habitats (Gibbs and Grant 1987), probably via changes in the expression of genes associated with bill development (Abzhanov et al. 2004), may lead to divergence in vocal deviation. In support of this hypothesis, morphological adaptation in several species is associated with variation in performance capabilities (Podos 2001; Ballentine 2006; Huber and Podos 2006). This hypothesis also predicts that changes in bill size over time should predict the direction of change in vocal deviation.

The Influence of Habitat on Trill Transmission

For acoustic signals such as birdsong, the density of vegetation in a habitat may affect both temporal and spectral characteristics. Slowly repeated notes and low frequencies are less affected by the reverberation and frequency-dependent attenuation generated by sound-reflecting surfaces such as vegetation (Morton 1975; Wiley and Richards 1978; Richards and Wiley 1980; Brown and Handford 2000), so these features should be associated with denser habitats. In support of this prediction, birds living in habitats with denser vegetation tend to have songs with more slowly repeated notes and lower frequencies than do birds living in open grassland habitat (reviewed in Slabbekoorn and Smith 2002a; Naguib 2003; Kopuchian et al. 2004; Seddon 2005; Baker 2006; van Dongen and Mulder 2006). This hypothesis also predicts that changes in vegetation density over time should predict the direction of change in temporal and spectral characteristics of song.

In this study, I examine the relationship between mor-

phology, habitat, and vocal trill structure in white-crowned sparrows (*Zonotrichia leucophrys*). I first examine whether variation in bill size and in vegetation density explains variation in trill structure within a time point. I predict that songs with lower-performance trills will be associated with large-billed birds and that trills produced at slower rates and with lower-frequency characteristics will be associated with denser vegetation. I then compare changes in trill structure with changes in bill size and in vegetation density using two time points separated by 35 years. I predict that vocal deviation will increase (i.e., performance will decrease) if bill size increases over time and that trills will decrease in rate and in frequency if vegetation density increases over time.

Material and Methods

Song Samples

Most male white-crowned sparrows sing a single song type, and most males within a location share the same song type. Locations tend to have distinct song types, known as song dialects (Marler and Tamura 1962).

Between 1969 and 1971, white-crowned sparrows were recorded across their range in the western United States (Baptista 1975, 1977; Orejuela and Morton 1975). From these recordings, I made use of songs from 170 males recorded in 15 locations (range: 5–30 males per locality). Herein, I refer to these recordings as the 1970 songs. To examine song evolution within this species, I returned to these sites between 2003 and 2006 and recorded the songs of 205 males (range: 5–35 males per locality). I refer to these recordings as the 2005 songs because most were recorded in 2005.

Most of the 15 locations are geographically dispersed (table A1 in the online edition of the *American Naturalist*), and the sparrows at each location have distinct song types (fig. A1 in the online edition of the *American Naturalist*). Males recorded at each time point within each location are certainly different individuals because the mean life span of white-crowned sparrows is less than 2 years and the longevity record in this species is 13.3 years (Chilton et al. 1995).

All songs were digitized with 16-bit precision at a 25-kHz sampling rate and high pass filtered at 1,500 Hz to eliminate noise below the frequency range of white-crowned sparrow song using Syrinx 2.2b (Burt 2001) and an Echo Digital Audio sound card. I chose one song per male for analyses because the characteristics of individuals' songs are highly stereotyped and repeatable (Nelson et al. 1996). Sound quality of historical and current recordings did not differ significantly in terms of frequency modulation, sound dropout, or background noise (Derryberry

2007). Spectral and temporal measurements contemporary with historical recordings also did not differ substantially from measurements made in 2005 on the same songs (see, in the online edition of the *American Naturalist*, app. A; table A2). Altogether, these results indicate that differences between historical and current songs are real and not the result of differences in recording equipment or quality.

Acoustic Measurements

I analyzed five aspects of trill acoustic characteristics: rate, maximum frequency, minimum frequency, frequency bandwidth, and vocal deviation. All acoustic measurements were taken using SIGNAL (ver. 3.1) digital signal processing software (Beeman 1999). Trill rate was calculated as the number of notes produced per second from time waveforms. I measured the maximum and the minimum frequencies of the trill at -36 dB relative to the peak amplitude frequency in the song from digital spectrograms (256-pt transform, frequency resolution: 97.7 Hz). The frequency bandwidth of each trill was calculated as the difference between the maximum and the minimum frequencies.

Following Podos (1997), I calculated an upper-bound regression for the plot of frequency bandwidth as a function of trill rate for all songs from 1970 and 2005 ($n = 375$; fig. A2 in the online edition of the *American Naturalist*). This method estimates an upper boundary for a triangular distribution of data (Blackburn et al. 1992). I binned songs by trill rate in 5-Hz categories and then selected the songs representing the maximum frequency bandwidth within each trill rate bin. A regression was performed on this subset of songs ($n = 10$ bins), and the resulting equation is the upper-bound regression ($y = -53.86x + 4,257.2$). Following Podos (2001) and Ballentine et al. (2004), I calculated vocal deviation as the orthogonal distance between each song and the upper-bound regression.

Morphological Measurements

Study skins of white-crowned sparrows were collected in 1959 in the counties of six of the 15 locations in this study (table A1). I took bill length (exposed culmen), width (at the nares), and depth (at the nares) on 75 of the male study skins (range: 5–20 males per location). I took the same measurements on live males captured on their territories after I recorded their song in 2005. I measured males from the same six locations, as well as males captured in one additional location. Because I was unable to take some measurements on a few individuals, there were minor differences in sample size for some measures. I took all bill measurements on both the study skins and the live males by using the same pair of calipers (SPI 2000).

Habitat Measurements

To assess vegetation density on white-crowned sparrow territories, I used point sampling from aerial photography. I used aerial photographs because I was interested in changes in vegetation density within habitats that white-crowned sparrows typically occupy. Point sampling from aerial photographs has proven an efficient and accurate means of assessing temporal variation in vegetation (Fensham and Fairfax 2002; Fensham et al. 2002; Clark and Hardegree 2005).

Aerial photographs from the appropriate time frame were available for five of the 15 study locations (table A1). Each location had two photographs: one that approximated the time of the 1970 recordings (hereafter, historical photos) and one that approximated the time of the 2005 recordings (hereafter, current photos; see, e.g., fig. A3 in the online edition of the *American Naturalist*). Historical photos were within 6 years of the 1970 recordings (range: 1963–1972). Current photos were taken in either 2003 or 2004, except the current Tioga Pass aerial photo taken in 1993. So that differences in resolution between current and historical aerial photos could be resolved, current photos were rescaled to match historical photos.

Point samples were taken within 1,000-m^2 areas centered on the GPS point at which each bird was recorded in 2005. This size area is the mean territory size for white-crowned sparrows (Patterson and Petrinovich 1978). Because territory coordinates were available only for 2005 recordings, historical and current photos were both sampled at the site of 2005 territories. This sampling method makes the assumption that birds in 1970 held territories in more or less the same areas as birds in 2005. None of the hypothetical 1970 territories estimated this way occurred in habitat atypical of white-crowned sparrows (e.g., on completely bare or completely forested ground), so this assumption is credible. This procedure was a conservative approach because any shift in territories between 1970 and 2005 would obscure a relationship between habitat and song. Vegetation was sampled at 100 uniformly distributed points within each 1,000-m^2 point-sampling area, using a 100×100-m grid layered on top of the digital, scanned version of the aerial photograph in Adobe Photoshop (ver. 4.0). All images were analyzed by an independent researcher blind to the vocalization data.

The dominant vegetation type at each sampling point was categorized as (1) lacking vegetation (typically structures, roads, parking lots, water, or sand), (2) grassland (typically a light color), (3) scrubland (characterized by shrubs and small trees; more textured than grassland but

Table 1: Results of ANOVA examining change in trill structure over time

Variable (Hz)	Historic ($n = 170$; mean $\pm$ SD)	Current ($n = 205$; mean $\pm$ SD)	Rate	$F_{(1, 373)}$	P	Direction[a]
Trill rate	11.8 $\pm$ 8.3	10.3 $\pm$ 8.2	.001	11.8	.0007[b]	Decreased
Maximum frequency	5,633 $\pm$ 731	5,964 $\pm$ 661	.003	21.1	.0001	Increased
Minimum frequency	2,804 $\pm$ 361	2,784 $\pm$ 267	.0002	3.0	.08	No change
Frequency bandwidth	2,829 $\pm$ 625	3,216 $\pm$ 759	.003	28.3	.0001	Increased
Vocal deviation	14.7 $\pm$ 11.1	9.1 $\pm$ 12.2	.001	21.6	.0001	Decreased

[a] Direction of significant change over time.

[b] Bonferroni-corrected $\alpha = 0.01$.

without visible individual canopies; usually darker than grass), or (4) forest (individual canopies visible; dark hue). From these data, the percentage of each vegetation category present was calculated. Percentage scrubland was the sole vegetation density index used in subsequent analyses because of the biology of white-crowned sparrow singing behavior.

White-crowned sparrow males defend territories that include shrubs and grass, with a few shorter trees from which they sing (Dewolfe and Dewolfe 1962). Singing from an elevated height of one to several meters means that songs encounter little vegetation when the receiver is a countersinging male. However, receivers may also be females (i.e., potential mates) or fledglings (e.g., in a learning-sensitive phase) hidden in grass or shrubs; thus, scrubland is the vegetation type most likely to degrade relevant song transmission in white-crowned sparrows.

Statistical Analyses

Variables were log or inverse transformed when necessary to meet model expectations. All analyses were conducted in SYSTAT (ver. 10) or JMP (ver. 6.0).

Acoustic Variation. To assess changes in trills over time, I performed ANOVAs. I calculated a rate of change for each trill variable, following methods described by Lynch (1990). This dimensionless measure of change allows one to compare the rate of change across variables.

Testing the Influence of Morphology on Trill Production. I used bill depth and bill width as a proxy for bill strength (Podos 2001; Herrel et al. 2005). I evaluated the relationship between bill size and vocal deviation within 2005 songs by using regression analysis. I could not evaluate this relationship within 1970 songs because the bills of birds recorded in 1970 were not measured.

I next examined the relationship between changes in bill size and vocal deviation over time. The time span of these two changes is different by approximately 11 years (see "Discussion" for implications). Because museum skins may shrink over time (reviewed in Winker 1993), I first

compared bill length, depth, and width between the two time periods by using two-tailed *t*-tests to determine whether there was any indication of an overall reduction in bill size. I used ANOVAs to determine whether vocal deviation and bill size changed over time in the subset of six locations. For this set of locations, I also calculated the rate of change for morphological and trill variables.

Testing the Influence of Habitat on Trill Transmission. I performed regression analyses with trill rate, maximum frequency, and minimum frequency as the dependent variables and percent scrub as the independent variable to examine the current relationship between vegetation density and trill structure. I could not evaluate the historical relationship because I did not know the exact territories of birds recorded in 1970.

I then compared changes in vegetation density with changes in trill structure between 1970 and 2005. I used a pairwise ANOVA to analyze change in vegetation density because scrub density estimates were taken from the exact same points in space at two separate times. I analyzed change in trill variables by using ANOVAs for the appropriate subset of five locations. For this set of locations, I also calculated the rate of change for habitat and trill variables.

Relationship between Measures of Morphology and Habitat. Adaptation to different ecologies may involve selection on phenotypic traits involved in food acquisition, such as bill morphology (e.g., Gibbs and Grant 1987; Greenberg and Droege 1990; Grenier and Greenberg 2005). I therefore tested for a correlation between the measures of bill size and vegetation density used in this study. Bill size is not correlated with percent scrub cover (linear regression: $R^2 = 0.04$, $n = 37$, $P = .2$), and I treat these variables separately.

Results

Trill Structure Has Changed Significantly over Time

Trill structure changed significantly between 1970 and 2005 (table 1). Trill rate slowed. Maximum frequency and

frequency bandwidth increased, while minimum frequency did not change significantly. Vocal deviation decreased (i.e., the performance of trills increased across populations). For those trill variables that changed, the rate of change is of the same magnitude across variables.

3.18, $n = 160$, $P = .002$; Bonferroni-corrected $\alpha = 0.016$). There was no corresponding significant change in vocal deviation between 1970 and 2005. Bill depth changed 10 times faster than vocal deviation.

Evidence for the Influence of Morphology on Trill Production

As predicted, white-crowned sparrow males with deeper bills sang significantly lower-performance trills (linear regression: $R^2 = 0.09$, $n = 66$, $P = .02$). The relationship between bill depth and vocal deviation is triangular in distribution, such that males with relatively shallow bills sang within a wide performance range while males with relatively deep bills were restricted to low-performance songs (fig. 1). Counter to predictions, there was no significant relationship between bill width and vocal deviation (linear regression: $R^2 = 0.001$, $n = 56$, $P = .78$).

I compared the direction of change in bill depth between 1959 and 2005 with the direction of change in vocal deviation between 1970 and 2005 (table 2) for the subset of six locations. I did not examine change in bill width because the current relationship between bill width and vocal deviation was not significant. Bill depth decreased over time. The reduction in bill depth over time was probably a result of actual changes rather than museum preservation because the bill did not decrease in all dimensions: bill length did not change, and bill width increased (two-tailed t-test: length: $t = 0.67$, $n = 162$, $P = .51$; width: $t =$

Evidence for the Influence of Habitat on Trill Transmission

As predicted, slower trill rates and lower minimum frequencies are associated with denser vegetation (linear regression: trill rate: $R^2 = 0.15$, $n = 84$, $P = .0003$; minimum frequency: $R^2 = 0.1$, $n = 84$, $P = .0035$). The relationship between scrub density and both trill rate and minimum frequency is a triangular distribution (fig. 2). On territories with dense vegetation, only slow trills and low minimum frequencies are found, while the full range of trill rates and minimum frequencies is found on more open territories. In contrast, there is no relationship between trill maximum frequency and scrub density ($R^2 = 0.01$, $n = 84$, $P = .52$; Bonferroni-corrected $\alpha = 0.016$).

I compared the direction of change in scrub density with the direction of change in trill rate and minimum frequency over time (table 3) for the subset of five locations. Scrub density increased over time. As predicted by an increase in scrub density, both trill rate and minimum frequency decreased over time. Scrub density and trill rate changed at a similar rate, while the rate of change for minimum frequency was twice as fast.
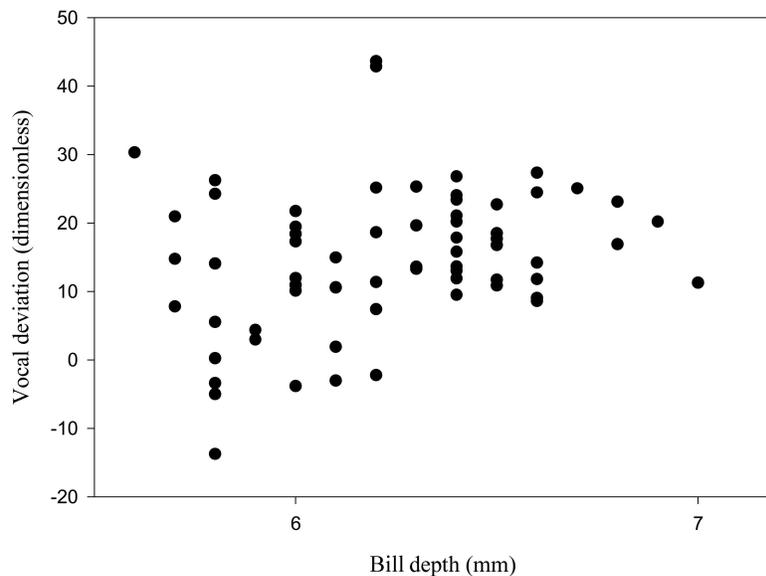
Figure 1: Scatterplot of the relationship between bill depth and vocal performance in white-crowned sparrows.

Table 2: Results of ANOVAs examining variation in bill depth and in vocal deviation over time

Variable	Historic (mean ± SD)	Current (mean ± SD)	Rate	F	P	Direction[a]
Bill depth (mm)	6.4 ± .4	6.2 ± .3	.002	10.5[b]	.002	Decreased
Vocal deviation	14.7 ± 10.7	14.4 ± 10.8	−.0002	.04[c]	.85	No change

[a] Direction of significant change over time.

[b] df = 1, 160.

[c] df = 1, 171.

Discussion

Variation in song among populations and over time appears to be shaped by variation in both morphology and habitat. Within contemporary (2005) populations, larger-billed males tend to sing lower-performance trills, and males on more densely vegetated territories tend to produce trills at slower rates and with lower minimum frequencies. The direction and rate of change in trill structure between 1970 and 2005 are also consistent with the direction and rate of change in vegetation density over time. In interpreting these results, there is the possibility of a confounding effect of evolutionary history among populations, but such an effect would obscure rather than highlight patterns of evolution across the species. Although the historical data are less direct than the contemporary data, these are the first data provided for how these characters may change over time and thus provide a good first look at these evolutionary processes. Taken together, these results suggest that morphology and habitat may shape signal variation within a species and that changes in habitat may underpin signal diversification over time.

Morphology Influences Variation in Trill Production

Results presented here provide some support for the hypothesis that bill size influences trill production (Podos 2001; Podos and Nowicki 2004*a*). As predicted, birds with deeper bills tend to produce lower-performance songs (fig. 1); however, there is no relationship between bill width and vocal deviation. The relationship between bill depth and vocal deviation features unequal variances across the range of bill size, such that males with larger bills are limited to producing lower-performance songs, while smaller-billed males produce songs within a wider performance range. While potential vocal performance is predicted to vary linearly with bill size, realized songs may vary from this linear relationship (Podos et al. 2004).

A correlation between bill size and vocal deviation also occurs in at least two other species of songbird, the medium ground finch (*Geospiza fortis*; Podos 2001) and the swamp sparrow (*Melospiza georgiana*; Ballentine 2006). In these species, realized vocal performance is closer to potential vocal performance, such that smaller-billed birds sing high-performance songs and larger-billed birds sing low-performance songs. Differences among the three species in the relationship between bill size and vocal deviation are likely not due to a difference in the range of bill size examined. While the range of bill depth reported by Podos (2001) is from 9 to 15 mm (6 mm), both this study and that of Ballentine (2006) examined bill size within a 2-mm range. Instead, differences among the three species suggest that other sources of selection may act on vocal deviation. The tighter relationship between bill size and vocal deviation in swamp sparrows may be indicative of sexual selection acting on song performance. Female swamp sparrows prefer males that sing higher-performance songs (Ballentine et al. 2004), and smaller-billed birds in this species tend to produce high-performance songs even though they are capable of producing low-performance songs.

Because the mechanical constraint on trill performance acts as a potential limit on trill diversification, a decrease in bill size should release mechanical limitations and expand the range of potential performance phenotypes (Podos et al. 2004). While bill depth decreased over time among white-crowned sparrow populations, vocal deviation did not change. However, the magnitude of change in bill depth was 0.2 mm, which would not map onto a difference in vocal deviation among current males (fig. 1). Thus, the amount of change in bill size over time may not have been enough to change limitations on vocal deviation. One restriction to interpreting these results is the difference in when recordings and study skins were collected (1970 vs. 1959, respectively). Such a difference could obscure the relationship between bill size and vocal deviation over time. Overall, results support the idea that bill morphology, specifically bill depth, may act as a limit on the performance of trills in contemporary populations, but it is unclear whether these two traits coevolve in this species.

Habitat Influences Variation in Trill Transmission

Results presented here support the hypothesis that habitat influences variation in both spectral and temporal characteristics of song (Morton 1975; Wiley and Richards 1978). As predicted, slower trill rates and lower minimum frequencies are associated with more densely vegetated
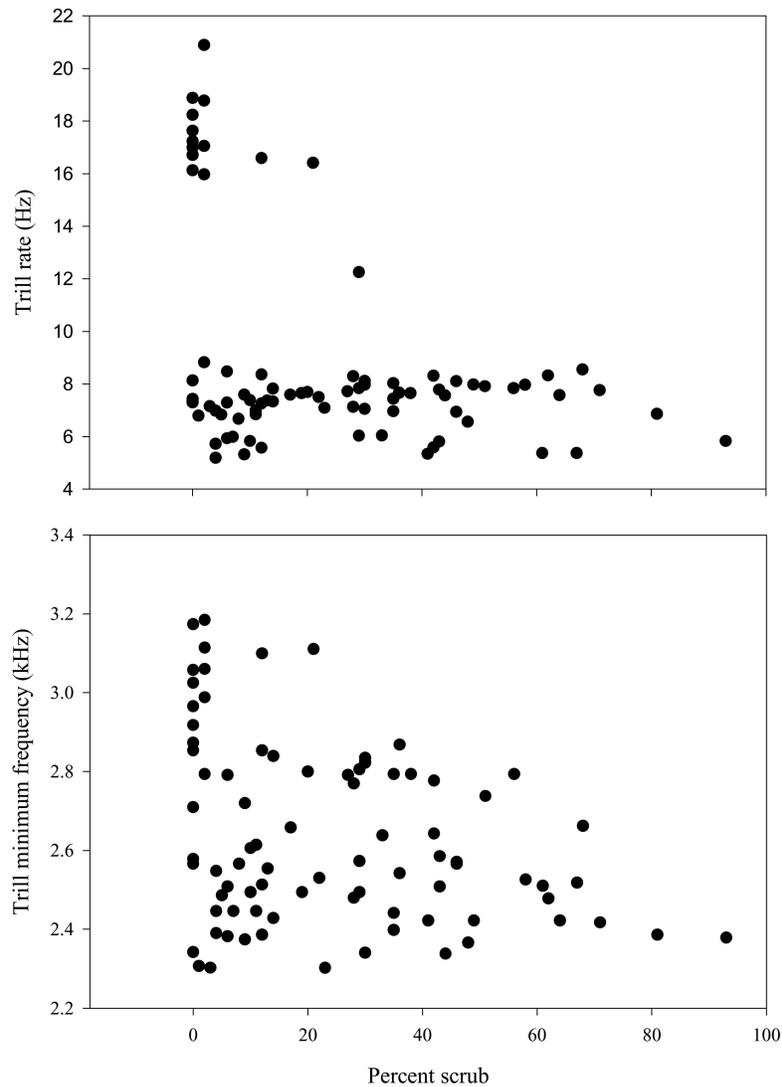
Figure 2: Scatterplot of the relationship between trill rate and minimum frequency and the percent of scrubland on a bird's territory.

habitats (Wiley and Richards 1978). A pattern of association between song structure and the acoustic environment has been described in both oscines and suboscines (e.g., Wiley 1991; reviewed in Slabbekoorn and Smith 2002*a*; Seddon 2005). These studies demonstrate clearly that the physics of sound transmission affects the structure of song across distinct habitats (e.g., grassland vs. forest). My study provides additional support of this hypothesis and on a finer scale than before. Here, I demonstrate that variation in both spectral and temporal characteristics of trills maps onto variation in scrub density across individual territories within a species. This result suggests that song structure may be more locally adapted than previously expected.

Similar to other studies, my study also found that not all spectral and temporal characteristics map onto habitat differences (Date and Lemon 1993; Williams and Slater 1993; Doutrelant and Lambrechts 2001; Naguib et al. 2001). For example, I did not find a relationship between trill maximum frequency and vegetation density. Variation in the extent to which habitat shapes signal structure may be dependent on other factors acting on signal structure (Endler 1993). Maximum frequency and vocal deviation are significantly correlated ($r = -0.8$, $P < .0001$), and selection on one of these trill variables may affect the other. Variation in maximum frequency may be more influenced by variation in factors that affect vocal deviation, such as bill morphology or sexual selection, than by variation in

Table 3: Results of ANOVAs examining change in percent scrubland, trill rate, and trill minimum frequency over time

Variable	Historic (mean ± SD)	Current (mean ± SD)	Rate	F	P	Direction[a]
Percent scrub	10.8 ± 14.5	25.6 ± 22.1	.006	6.9[b]	.0001	Increased
Trill rate	10.0 ± 2.0	8.9 ± 3.8	.005	22.6[c]	.0001[d]	Decreased
Minimum frequency	2,844 ± 287	2,631 ± 225	.01	26.1[c]	.0001[d]	Decreased

[a] Direction of significant change over time.
[b] df = 1, 105.
[c] df = 1, 152.
[d] Bonferroni-corrected α = 0.025.

vegetation density. A similar pattern of association was found in the greenish warbler (*Phylloscopus trochiloides*) such that variation in the minimum frequency of this species' songs reflected variation in habitat while variation in their songs' maximum frequency did not; instead, maximum frequency was associated with an increase in song complexity potentially because of an increase in the intensity of sexual selection (Irwin 2000). Despite the lack of an association between maximum frequency and vegetation density, this study still provides some evidence that ecology shapes trill structure in white-crowned sparrows (fig. 2), particularly because changes in trill structure are consistent with changes in vegetation density over time (table 3).

Although comparative analyses have shown an association between habitat type and song structure (e.g., Wiley 1991; Badyaev and Leaf 1997; Seddon 2005), no study has documented changes in habitat and in song structure over time within a species. In rufous-collared sparrows (*Zonotrichia capensis*), Kopuchian et al. (2004) found that trill rate slowed over time in both grassland and forested habitats. While vegetation density might have increased in both habitats over time, aerial photographs were not available to measure changes in vegetation. Thus, the study presented here allows the first comparison of changes in both trill structure and vegetation density over time. I found that both trill rate and minimum frequency decreased over time in populations in which vegetation density increased. Both trill rate and vegetation density are also changing at a similar rate over time. Altogether, these findings suggest that trill structure is responsive to changes in habitat, at least across 30 generations.

These results beg the question of whether the association between trill structure and habitat is due to selection or to phenotypic plasticity. In oscines, changes in trill structure in response to changes in habitat may be mediated by cultural selection such that juvenile males preferentially copy nonreverberated songs (Hansen 1979). Another possibility is that males whose songs do not transmit well are unable to hold territories. If these males were excluded from the gene pool, then changes in song over time could

be due to changes in the frequency of occurrence of genes associated with the song template. I think it unlikely that phenotypic plasticity explains the association between habitat and trill structure in this species. Slabbekoorn and Peet (2003) found that male great tits (*Parus major*) adjust their song repertoire to match their territory's transmission properties. Because white-crowned sparrow males sing one song that is highly stereotyped and typically crystallized within their first year, it is unlikely that they can adjust their song to match their territory. It is also unlikely that males match their song to a territory because choosing a territory based on its transmission properties would have to occur through a process of trial and error. Because the median life span of males is 2 years (Morton 2002) and territories are fixed early in the breeding season (Morton 2002), males, on average, would be able to try the process of trial and error twice. This essentially stochastic process is probably not sufficient to explain the significant relationship between habitat and song.

Habitat and, to a certain extent, bill morphology appear to shape song diversification in white-crowned sparrows and have also been suggested to play a role in the evolution of mating signals in many other species of birds (reviewed in Slabbekoorn and Smith 2002a; Podos and Nowicki 2004b). The importance of ecological selection for the evolution of both acoustic and visual communication systems has also been suggested for *Anolis* lizards (Leal and Fleishman 2004), iguanian lizards (Ord et al. 2002), surfperch (Cummings 2007), cricket frogs (Ryan et al. 1990), and African cichlids (Seehausen et al. 1997), to name a few. The results presented here add to this body of research the first evidence that temporal changes in signal structure are associated with changes in habitat.

Literature Cited

Abzhanov, A., M. Protas, B. R. Grant, P. R. Grant, and C. J. Tabin. 2004. *Bmp4* and morphological variation of beaks in Darwin's finches. Science 305:1462–1465.

Badyaev, A., R. L. Young, K. P. Oh, and C. Addison. 2008. Evolution on a local scale: developmental, functional, and genetic bases of divergence in bill form and associated changes in song structure between adjacent habitats. Evolution 62:1951–1964.

Badyaev, A. V., and E. S. Leaf. 1997. Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. Auk 114:40–46.

Baker, M. C. 2006. Differentiation of mating vocalizations in birds: acoustic features in mainland and island populations and evidence of habitat-dependent selection on songs. Ethology 112:757–771.

Ballentine, B. 2006. Morphological adaptation influences the evolution of a mating signal. Evolution 60:1936–1944.

Ballentine, B., J. Hyman, and S. Nowicki. 2004. Vocal performance influences female response to male birdsong: an experimental test. Behavioral Ecology 15:163–168.

Baptista, L. F. 1975. Song dialects and demes in sedentary populations of the white-crowned sparrow (*Zonotrichia leucophrys nuttalli*). University of California Publications in Zoology 105:1–52.

———. 1977. Geographic variation in song and dialects of the Puget white-crowned sparrow. Condor 79:356–370.

Beckers, G. J. L., R. A. Suthers, and C. ten Cate. 2003. Pure-tone birdsong by resonance filtering of harmonic overtones. Proceedings of the National Academy of Sciences of the USA 100:7372–7376.

Beeman, K. 1999. SIGNAL. Engineering Design, Belmont, MA.

Blackburn, T. M., J. H. Lawton, and J. N. Perry. 1992. A method of estimating the slope of upper bounds of plots of body size and abundance in natural animal assemblages. Oikos 65:107–112.

Boughman, J. W. 2002. How sensory drive can promote speciation. Trends in Ecology & Evolution 17:571–577.

Brown, T. J., and P. Handford. 2000. Sound design for vocalizations: quality in the woods, consistency in the fields. Condor 102:81–92.

Burt, J. 2001. Syrinx. University of Washington, Seattle.

Chilton, G., M. C. Baker, C. D. Barrentine, and M. A. Cunningham. 1995. White-crowned sparrow. The Birds of North America, ed. A. Poole and F. Gill. No. 183. Academy of Natural Sciences, Philadelphia; and American Ornithologist's Union, Washington, DC.

Clark, P. E., and S. P. Hardegree. 2005. Quantifying vegetation change by point sampling landscape photography time series. Rangeland Ecology and Management 58:588–597.

Cummings, M. 2007. Sensory trade-offs predict signal divergence in surfperch. Evolution 61:530–545.

Date, E. M., and R. E. Lemon. 1993. Sound transmission: a basis for dialects in birdsong. Behaviour 124:291–312.

Derryberry, E. P. 2007. Evolution of bird song affects signal efficacy: an experimental test using historical and current signals. Evolution 61:1938–1945.

Dewolfe, B. B., and R. H. Dewolfe. 1962. Mountain white-crowned sparrows in California. Condor 64:378–389.

Doutrelant, C., and M. M. Lambrechts. 2001. Macrogeographic variation in song: a test of competition and habitat effects in blue tits. Ethology 107:533–544.

Endler, J. A. 1993. Some general comments on the evolution and design of animal communication systems. Philosophical Transactions of the Royal Society B: Biological Sciences 340:215–225.

Fensham, R. J., and R. J. Fairfax. 2002. Aerial photography for assessing vegetation change: a review of applications and the relevance of findings for Australian vegetation history. Australian Journal of Botany 50:415–429.

Fensham, R. J., R. J. Fairfax, J. E. Holman, and P. J. Whitehead. 2002. Quantitative assessment of vegetation structural attributes from aerial photography. International Journal of Remote Sensing 23:2293–2317.

Gibbs, H. L., and P. R. Grant. 1987. Oscillating selection in Darwin's finches. Nature 327:511–513.

Greenberg, R., and S. Droege. 1990. Adaptation to tidal marshes in breeding populations of the swamp sparrow. Condor 92:393–404.

Grenier, J. L., and R. Greenberg. 2005. A biogeographic pattern in sparrow bill morphology: parallel adaptation to tidal marshes. Evolution 59:1588–1595.

Hansen, P. 1979. Vocal learning: its role in adapting sound structures to long-distance propagation and a hypothesis on its evolution. Animal Behaviour 27:1270–1271.

Herrel, A., J. Podos, S. K. Huber, and A. P. Hendry. 2005. Evolution of bite force in Darwin's finches: a key role for head width. Journal of Evolutionary Biology 18:669–675.

Herrel, A., J. Podos, B. Vanhooydonck, and A. P. Hendry. 2009. Force-velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation? Functional Ecology 23:119–125.

Hoese, W. J., J. Podos, N. C. Boetticher, and S. Nowicki. 2000. Vocal tract function in birdsong production: experimental manipulation of beak movements. Journal of Experimental Biology 203:1845–1855.

Huber, S. K., and J. Podos. 2006. Beak morphology and song features

covary in a population of Darwin's finches (*Geospiza fortis*). Biological Journal of the Linnean Society 88:489–498.

Irwin, D. E. 2000. Song variation in an avian ring species. Evolution 54:998–1010.

Kopuchian, C., D. A. Lijtmaer, P. L. Turbaro, and P. Handford. 2004. Temporal stability and change in a microgeographic pattern of song variation in the rufous-collared sparrow. Animal Behaviour 68:551–559.

Leal, M., and L. J. Fleishman. 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. American Naturalist 163:26–39.

Lynch, M. 1990. The rate of morphological evolution in mammals from the standpoint of the neutral expectation. American Naturalist 136:727–741.

Marler, P., and M. Tamura. 1962. Song "dialects" in three populations of white-crowned sparrows. Condor 64:368–377.

Morton, G. A. 1975. Ecological sources of selection on avian sounds. American Naturalist 109:605–624.

Morton, M. L. 2002. The mountain white-crowned sparrow: migration and reproduction at high altitude. Studies in Avian Biology 24:1–273.

Naguib, M. 2003. Reverberation of rapid and slow trills: implications for signal adaptations to long-range communication. Journal of the Acoustical Society of America 113:1749–1756.

Naguib, M., K. Hammerschmidt, and J. Wirth. 2001. Microgeographic variation, habitat effects and individual signature cues in calls of chiffchaffs *Phylloscopus collybita canarensis*. Ethology 107: 341–355.

Nelson, D. A., C. Whaling, and P. Marler. 1996. The capacity for song memorization varies in populations of the same species. Animal Behaviour 52:379–387.

Nevo, E., and R. R. Capranica. 1985. Evolutionary origin of ethological reproductive isolation in cricket frogs, *Acris*. Evolutionary Biology 19:147–214.

Nowicki, S. 1987. Vocal-tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere. Nature 325:53–55.

Nowicki, S., and P. Marler. 1988. How do birds sing? Music Perception 5:391–426.

Nowicki, S., M. W. Westneat, and W. Hoese. 1992. Birdsong: motor function and the evolution of communication. Seminars of Neuroscience 4:385–390.

Ord, T. J., D. T. Blumstein, and C. S. Evans. 2002. Ecology and signal evolution in lizards. Biological Journal of the Linnean Society 77: 127–148.

Orejuela, J. E., and M. L. Morton. 1975. Song dialects in several populations of mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) in the Sierra Nevada. Condor 77:145–153.

Palacios, M. G., and P. L. Tubaro. 2000. Does beak size affect acoustic frequencies in woodcreepers? Condor 102:553–560.

Patterson, T., and L. Petrinovich. 1978. Territory size in the white-crowned sparrow (*Zonotrichia leucophrys*): measurement and stability. Condor 80:97–98.

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

———. 2001. Correlated evolution of morphology and vocal signal structure in Darwin's finches. Nature 409:185–188.

Podos, J., and S. Nowicki. 2004a. Beaks, adaptation, and vocal evolution in Darwin's finches. BioScience 54:501–510.

———. 2004b. Performance limits on birdsong production. Pages 318–341 *in* P. Marler and H. Slabbekoorn, eds. Nature's musicians: the science of birdsong. Elsevier Academic, New York.

Podos, J., S. K. Huber, and B. Taft. 2004. Birdsong: the interface of evolution and mechanism. Annual Review of Ecology, Evolution, and Systematics 35:55–87.

Richards, D. G., and R. H. Wiley. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. American Naturalist 115:381–399.

Riede, T., R. A. Suthers, N. H. Fletcher, and W. E. Blevins. 2006. Songbirds tune their vocal tract to the fundamental frequency of their song. Proceedings of the National Academy of Sciences of the USA 103:5543–5548.

Ryan, M. J., and E. A. Brenowitz. 1985. The role of body size, phylogeny, and ambient noise in the evolution of birdsong. American Naturalist 126:87–100.

Ryan, M. J., R. B. Cocroft, and W. Wilczynski. 1990. The role of environmental selection in intraspecific divergence of mate recognition signals in the cricket frog, *Acris crepitans*. Evolution 44: 1869–1872.

Seddon, N. 2005. Ecological adaptation and species recognition drives vocal evolution in Neotropical suboscine birds. Evolution 59:200–215.

Seehausen, O., J. J. M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277:1808–1811.

Slabbekoorn, H., and M. Peet. 2003. Ecology: birds sing at a higher pitch in urban noise—great tits hit the high notes to ensure that their mating calls are heard above the city's din. Nature 424:267.

Slabbekoorn, H., and T. B. Smith. 2002a. Birdsong, ecology and speciation. Philosophical Transactions of the Royal Society B: Biological Sciences 357:493–503.

———. 2002b. Habitat-dependent song divergence in the little greenbul: an analysis of environmental selection pressures on acoustic signals. Evolution 56:1849–1858.

van Dongen, W. F. D., and R. A. Mulder. 2006. Habitat density, song structure and dialects in the Madagascar paradise flycatcher *Terpsiphone mutata*. Journal of Avian Biology 37:349–356.

Westneat, M. W., J. H. Long, W. Hoese, and S. Nowicki. 1993. Kinematics of birdsong: functional correlation of cranial movements and acoustic features in sparrows. Journal of Experimental Biology 182:147–171.

Wiley, R. H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. American Naturalist 138:973–993.

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.

Williams, J. M., and P. J. B. Slater. 1993. Does chaffinch *Fringilla coelebs* song vary with the habitat in which it is sung? Ibis 135: 202–208.

Winker, K. 1993. Specimen shrinkage in Tennessee warblers and "Traill's" flycatchers. Journal of Field Ornithology 64:331–336.