PACIFIC COAST AND SOUTHWEST INTERIOR POPULATIONS OF THE HUTTON'S VIREO DIFFER IN BASIC SONG PARAMETERS¹

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Abstract. Comparisons of song parameters, including syllable length and maximum and minimum frequency, from six populations of the Hutton's Vireo (Vireo huttoni) show differences in syllable length and minimum frequency measurements. Specifically, syllables produced by Pacific coastal birds tend to be shorter than those from southwest interior populations, although these differences are not statistically significant at the pairwise-comparison level. Syllables produced by most coastal populations have significantly higher mean minimum frequencies when compared with those from interior populations. Differences between songs of coastal and interior populations are consistent with genetic differences that separate the two groups. Differences in song may be attributed to the acoustical properties of coastal versus interior hab-

Key words: Hutton's Vireo, Pacific Coast, song, Vireo huttoni.

The Hutton's Vireo (Vireo huttoni) is a sedentary songbird inhabiting pine (Pinus spp.) and oak (Quercus spp.) woodlands and mixed evergreen forests. It occurs along the Pacific Coast of North America from southwestern British Columbia to Baja California, and in the southwest interior from central Arizona, southwestern New Mexico and western Texas, southward through Mexico to northern Guatemala. Being largely non-migratory, populations of the Hutton's Vireo are isolated by intervening deserts and water barriers. Specifically, the Sonoran, Mojave, and Great Basin Deserts separate coastal from inland birds, and the Chihuahuan Desert separates populations from southern Arizona and northwestern Mexico from those of west Texas and northeastern Mexico. To the north, the straits of Juan de Fuca and Georgia reduce contact between birds of southern Vancouver Island and mainland British Columbia.

Unique among all North American vireos, the Hut-

ton's Vireo sings a monosyllabic song that consists of

a single syllable that is often repeated many times until

METHODS

Most of the song material used was acquired as previously recorded material. Recordings were provided by the Royal Ontario Museum (Toronto, Ontario), Cornell University's Library of Natural Sound (Ithaca, New York), the Florida Museum of Natural History (Gainesville, Florida), and the Ohio State University Borror Laboratory of Bioacoustics (Columbus, Ohio), as well as from the personal holdings of D. Innes, G. Lasley, J. Davis (recorded by C. Tenney and D. Drynan), C. Hill (recorded by S. E. Campbell), and R. D. James.

To increase sample sizes of birds from British Columbia (BC), songs were recorded in July 1997, on the endowment lands belonging to the University of British Columbia (V. h. huttoni) and on southern Vancouver Island (V. h. insularis). These songs were recorded with a Sony ProWalkman (WM-D6C), and a Sony Electret condenser stereo microphone (ECM-MS907) in a Sony parabolic reflector (PBR330). Each male was located by brief playback of previously recorded song or recorded as encountered singing. We tried to record entire song bouts (15-180 sec) for each male found. In total, our sample included the songs from 91 individuals. The number of different syllables from each bird ranged from 1 to 19 (average = 3). Examples of syllables found in each population are shown in Figure 1.

Song samples were divided into six groups based on current subspecies ranges and political boundaries (Fig. 1). Songs from Pacific Coast populations were divided into four groups: (1) Vancouver Island, (2) mainland BC, (3) Washington and Oregon, and (4)

a new syllable is sung. In a recent study on the song of the Hutton's Vireo, Baril (1998) found that birds from the Pacific Coast have more syllables in common than they do with birds of the southwest interior and vice versa. Here, we measured three song parameters including syllable length and maximum and minimum frequency to determine whether songs from coastal populations differ in structure from those of southwest interior birds.

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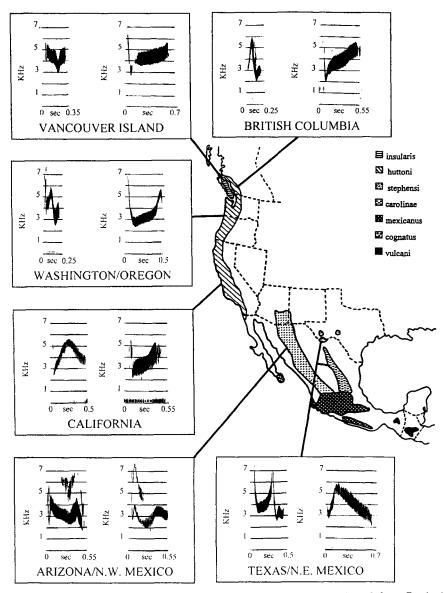


FIGURE 1. Distribution of *Vireo huttoni* showing subspecies boundaries (adapted from Davis 1995) with examples of syllables from each population sampled.

California. Subspecies from the southwest interior and northern Mexico, for example *V. h. carolinae* and *V. h. stephensi*, were divided into two groups based on their respective geographic ranges.

We analyzed song using a Kay Elemetrics DSP Sona-Graph 5500, which displayed song in real time on wideband (400 Hz) and narrowband (59 Hz) settings within a 0-8.0 kHz frequency range. Measurements of syllable length (sec) and maximum and minimum frequencies (Hz) were made for every different syllable produced by each bird. Different syllables, also known as syllable "types," were identified by vi-

sual comparison based on their overall shape, frequency range, and length (following Lynch and Baker 1986, Lang and Barlow 1987, 1997). A representative syllable for every syllable type sung by each bird was chosen for measurement. The syllable was selected at random by allowing the recording to run several syllables into the song until the song stabilized and produced a clear signal on the sonograph.

Syllable lengths and frequencies from the six geographic regions were compared using a one-way analysis of variance (ANOVA) to determine whether or not they were significantly different from one another (Zar

Size of syllable n syllable n birds Minimum frequency^a Population recorded pool types Syllable length (sec) Pacific Coast populations Vancouver Island (V.I.) 19 50 23 $0.30 \pm 0.14 (44)$ $2,026 \pm 569 (44)$ Mainland BC 35 15 0.30 ± 0.13 (27) $2,068 \pm 306 (28)$ 6 Washington/Oregon (WA/OR) 17 8 17 0.27 ± 0.07 (17) $2,247 \pm 356 (17)$ California (CA) 13 33 22 0.30 ± 0.09 (28) $2,200 \pm 296$ (28) Southwest interior populations Arizona and NW Mexico (AZ) 19 68 31 0.34 ± 0.08 (68) $1,865 \pm 344 (68)$ $0.34 \pm 0.08 (50)$ Texas and NE Mexico (TX) 26 $1,779 \pm 286 (50)$

TABLE 1. Number of birds recorded, syllable pool size, total number of syllable types, and mean \pm SD (n)syllable lengths and minimum frequencies from populations of the Hutton's Vireo.

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56

1984). If the ANOVA showed statistically significant differences among populations, pairwise comparisons were then conducted using Tukey's test to determine which populations were significantly different from one another. All analyses were done with Minitab release 12 (1998).

RESULTS

Between-population comparisons showed statistically significant differences in mean syllable length (P <0.03) and minimum frequency ($\dot{P} < 0.001$). We observed no statistically significant differences in our comparisons of maximum frequency.

No pairwise differences in mean syllable length were found using Tukey's method. However, coastal birds appear to have shorter syllables compared to interior populations (Table 1). Most pairwise comparisons for mean minimum frequency indicated significant differences between coastal and interior populations. Also, all pairwise comparisons among coastal populations and between southwest interior populations were not statistically significant. Mean minimum frequencies showed that, in general, coastal birds have higher minimum frequencies than those from the interior (Table 1).

DISCUSSION

In addition to the structural differences in song between Pacific coastal and southwest interior populations, genetic structuring among these two groups also has been observed. Results from an allozyme study in which 33 loci were sampled (Cicero and Johnson 1992) showed that populations from California (V. h. huttoni) and Arizona (V. h. stephensi) differ by a fixed allele difference at the Gpi locus and had a high mean F_{ST} of 0.614. Another recent study based on neutral mtDNA control region sequences showed that although coastal and interior populations share a common haplotype, coastal and interior populations are each defined by a unique haplotype (Baril 1998). The genetic differences between coastal and interior populations are most likely due to random drift resulting from their disjunct distribution due to intervening deserts; an isolation which may date to at least the late Wisconsin, ca. 18,000 years before present (Cicero and Johnson 1992, Baril 1998). In contrast, the differences in song may result from both a combination of memetic drift (Lynch and Baker 1994) and selection (Morton 1975, Wiley and Richards 1982).

Two important factors in the evolution of bird song are the quality of sound transmission and the acoustical background of a particular environment (Marler 1960, Morton 1975). The acoustical properties of a particular habitat may selectively promote structural changes in song to maximize its effectiveness in a particular environment (Marler 1960, Morton 1975). Although the Hutton's Vireo has a broad latitudinal distribution, it appears to favor similar habitats throughout its range. In the northern parts of its distribution, this species occurs in tall Douglas-fir (Pseudotsuga menziesii) forests with sparse undergrowth, and forages mostly in lower strata and scrub, as well as in dense second growth woodlands characteristic of edge habitats (Campbell et al. 1997). On Vancouver Island and in limited areas on the adjacent mainland British Columbia, V. huttoni also inhabits open madrone (Arbutus menziesii) and Garry oak (Quercus garryana) woodlands. The understory, scrub, and arid open-canopy forests occupied by this bird in the north are comparable to habitats found in California and the southwest interior states and neighboring northern Mexico. There, in the southern parts of its range, the Hutton's Vireo occurs in arid, open-canopy forests dominated by live oaks (Quercus spp.), Ponderosa pine (Pinus ponderosa), juniper (Juniperus spp.), and madrone (Davis 1995).

Although the northern and southern habitats of the Hutton's Vireo share some vegetational elements, their extremes are different; the north offers more mesic, high-canopy closed forests, contrasting with the arid woodlands and scrub habitat of the south. The acoustical properties of coastal forests may be promoting the production of syllables with higher minimum frequencies, whereas the dry, open habitats of the south and interior may favor the production of lower frequency syllables. This trend also has been documented in the Rufous-browed Peppershrike (Cyclarhis gujanensis; Tubaro and Segura 1995) and the Rufous-collared Sparrow (Zonotrichia capensis; Tubaro et al. 1993), who exhibit higher minimum frequencies in more me-

a Population pairs with significantly different mean minimum frequencies (using Tukey's test): WA/OR-AZ, CA-AZ, BC-TX, CA-TX, WA/OR-TX, V.I.-TX; all other population comparisons were not significantly different.

sic and densely vegetated areas compared to more open habitats. Although we have shown that there are differences in minimum frequency between Pacific Coast and southwest interior populations, whether the birds can detect these subtle differences in song has yet to be determined. Whether or not regional environmental conditions can help explain the vocal differences observed between Pacific Coast and southwest interior populations awaits a detailed study of song from these regions which would attempt to demonstrate correlations between habitat parameters and song properties in specific habitats.

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