

TYPE I AND II SONGS OF TOWNSEND'S WARBLERS IN OREGON AND WASHINGTON

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ABSTRACT: Songs of four populations of Townsend's Warbler (*Setophaga townsendi*) studied in Oregon and Washington were of two types. Each population had one song-type with one song that was used early in the breeding season (type I) and a different song-type with one song delivered pre-dawn after pairing, during territorial contests, and often with chip-like call notes (type II). Both types were sung after dawn. Type I songs differed markedly from population to population. The boundaries between songs of adjacent populations were sharp, indicating a system of dialects, unlike many wood-warblers. In contrast, type II songs of all populations were recognizably similar.

Many wood-warblers (Parulidae) sing more than one song, and these can be grouped into two categories based on the context in which they are delivered (Spector 1992). First-category songs are defined as the songs that predominate early in the breeding season before pairing. Second-category songs are defined as the songs delivered pre-dawn after pairing and the usual song used in territorial contests with other males. Second-category songs also tend to be delivered near the periphery of a territory and are often accompanied by chip-like call notes.

The terminology describing the two song categories for various wood-warblers is confused. For example, in the Chestnut-sided Warbler (*Setophaga pensylvanica*) the terms "accented ending" and "unaccented ending" have been used (Byers 1995). For the Black-throated Green Warbler (*S. virens*) the terms are "type A" and "type B" (Morse 1967), for the Hermit Warbler (*S. occidentalis*) "type I" and "type II" (Janes and Ryker 2006). Spector (1992) suggested the terms "first category" and "second category" when species are compared.

Songs of the various species of wood-warblers that follow this pattern can be identified to category either by the structure of the individual song ("form-encoded" songs) or by the manner of delivery ("performance-encoded" songs; Byers 1995). In a species with form-encoded songs, an individual song or set of songs is restricted to a specific context. Thus a single song can be classified as either first or second category by its form. In a species singing performance-encoded songs, individual songs cannot be unambiguously classified. The determination is based on how the song is used. In the American Redstart (*S. ruticilla*), Grace's Warbler (*S. graciae*), and Yellow Warbler (*S. petechia*), for example, first-category singing consists of a repeated series of the same song (Lemon et al. 1985, Staicer 1989, Spector 1991). This song may not be the same for all males in a population. Second-category song bouts, in contrast, often consist of a medley of several songs.

Townsend's Warblers (*S. townsendi*) employ two song categories (Wright et al. 1998), but much about the species' singing behavior remains to be described. Bent (1953), Stein (1962), Borror and Gunn (1985), and Wright et al. (1998) described its songs in general, but type I (first category) and type II (second category) songs have not been clearly identified. Borror and Gunn

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(1985) noted that the songs of Townsend's Warblers vary considerably both within and between populations, contributing to uncertainty in the categories and use of song. We identify the type I and II songs of four populations of Townsend's Warbler in Oregon and Washington and examine geographic variation within each song-type.

METHODS

Townsend's Warbler frequently hybridizes with the Hermit Warbler (Jewett 1944, Rohwer and Wood 1998). For purposes of this study we sought to avoid the complexities likely to be encountered where hybrid birds are common. Two of the study sites were located in areas distant from contact areas between Hermit and Townsend's Warblers. One in Washington, the "Okanogan County site," included western Okanogan County, extreme northern Chelan County, and eastern Whatcom County. The second site was located in the Ochoco Mountains of Crook County, Oregon. We studied two additional sites closer to zones of hybridization, but none of the birds recorded or observed in the area showed features of hybrids. One site was located along the White River and Buck and Crystal creeks on the north slopes of Mount Rainier in Pierce County, Washington. The site is approximately 40 km north of the hybrid zone identified by Rohwer and Wood (1998). The fourth site, "Deschutes County," was located in western Deschutes County and the extreme northwest corner of Klamath County, Oregon. The site included Odell Butte, Royce Mountain, Davis Mountain, Brown Mountain, and Lookout Mountain. It is located adjacent to a zone of hybridization, and in it we observed three singing male Hermit Warblers but no hybrids. Singing in this area differed markedly from that in nearby populations where hybrids are common, and the singing of Townsend's Warblers did not appear to be affected by the proximity of Hermit Warblers.

To identify type I and II songs, we recorded the singing of Townsend's Warblers in several contexts. See Spector (1992) for a review of the use of song by wood-warblers.

We recorded the singing of Townsend's Warblers between 2 May and 2 July 2009 with either a Marantz PMD660 or a Marantz PMD670 coupled with a Sennheiser ME-62 microphone in a 61-cm parabolic reflector. Additional recordings of the Deschutes County population had been made in 2007. Songs were analyzed from spectrograms generated by Raven version 1.2.1 (Cornell Laboratory of Ornithology, Ithaca, NY). Phrases and syllables are shown in Figure 1. We assessed variation in song among populations with a Kruskal-Wallis test.

RESULTS

We recorded songs of 239 Townsend's Warblers in four populations: 96 in Crook County, 69 in Deschutes County, 40 in Pierce County, and 34 in Okanogan County. Two distinct songs predominated within each population, one from each song category.

At least in the Deschutes and Crook County populations, males sang

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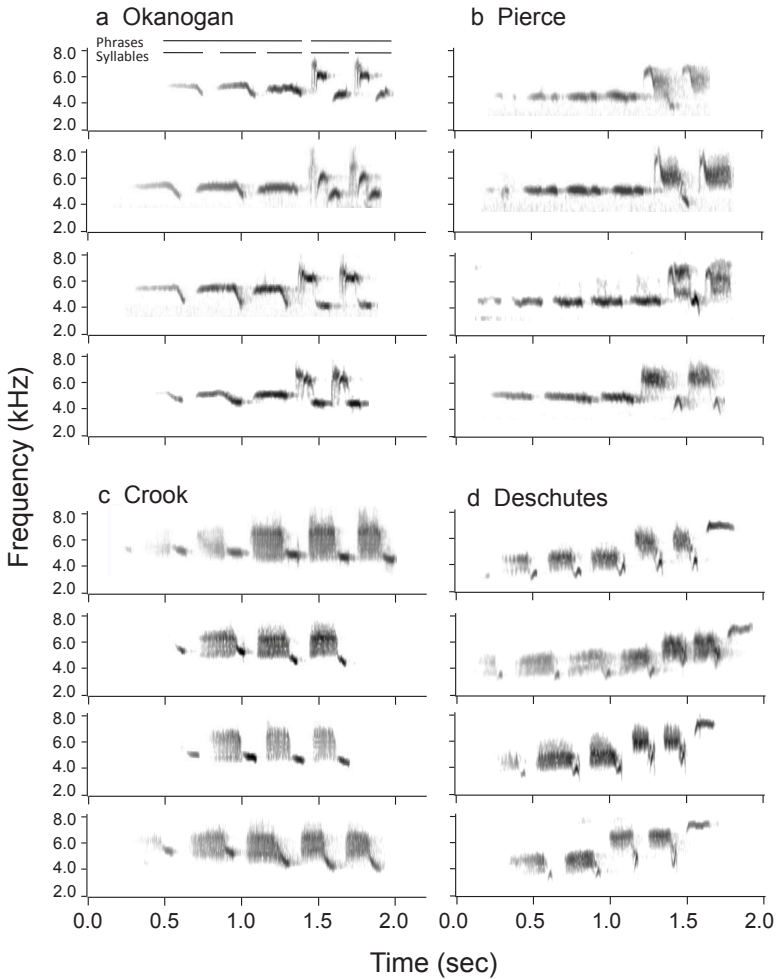


Figure 1. Examples of Type I songs of Townsend's Warblers at four sites, 2009: (a) Okanogan County, Washington, (b) Pierce County, Washington, (c) Crook County, Oregon, and (d) Deschutes County, Oregon.

one song, which we identify as the type I song, early in the season before females were observed in early May. The only circumstances when the other song was heard at this time involved encounters (chases and fights) between males. We were unable to visit the two Washington sites during the brief period between the arrival of the males and that of the females. The type I song was also common later in the breeding season after dawn.

In each population, the second song, which we identify as the type II song,

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was the only song delivered before dawn after the females arrived. At this time of day the song was accompanied by doubled chip-like call notes. Type II songs, without doubled call notes, were also used during counter-singing among males and during territorial contests involving chases later in the morning. After the arrival of the females, males also sang type II song after dawn, in no special context that could be identified, also without call notes.

Type I songs of individuals within each population were similar, but the song of each of the four populations was distinct (Figure 1). Type I songs consisted of a single phrase in the Crook County population and two phrases in the other three. The first (or only) phrase consisted of a series of repeated syllables. In the Crook and Deschutes County populations, the syllables consisted of a vibrato note followed by a brief tonal note of comparatively low frequency. Vibrato notes are rapid pulses delivered too fast to be distinguished individually even on a spectrogram and sound buzzy. In the Pierce and Okanogan County populations the syllables consisted of a single tonal note. The amplitude of the tonal note in many Pierce County songs varied, tending to two separate notes.

Except in the Crook County population, the introductory phrase was followed by a pair of similar syllables distinct from those of the first phrase. The syllables were poorly differentiated from the introductory syllables in some Deschutes County songs but clear in others. The majority of the males in the Deschutes County population concluded the song with a tonal note of relatively high frequency.

We encountered a boundary between the Pierce County song population and an adjacent population to the south singing a different type I song was detected. Individuals singing the different dialect were not observed to overlap spatially with the population we studied intensively. The area of the Deschutes County song was also clearly bounded by two other dialects sung to the north and southwest in hybrid zones.

Type II songs of all populations of Townsend's Warbler studied were similar, characterized by an introductory phrase consisting of one to 12 (most often two) syllables, though this phrase was lacking 4% of the time. Each syllable tended to consist of a single vibrato note. The number of syllables was similar at the Crook, Pierce, and Okanogan County sites (mean plus or minus standard deviation 2.67 ± 1.58 , 2.72 ± 1.46 , and 2.29 ± 1.19 , respectively) but was greater at the Deschutes County site (4.78 ± 2.81 ; $H = 20.91$, $P < 0.001$; Figure 2). In most songs these syllables were approximately equal in duration.

The introductory notes of type II songs were followed by a characteristic vibrato note of long duration, which was similar in all populations. In addition, songs typically ended with two similar syllables. The syllables were complex in structure, each consisting of two brief vibrato notes alternating with two tonal notes. The final tonal note within a syllable was usually lower in frequency than the first. Although terminal syllables shared a similar general structure, individual variation was apparent (Figure 2).

Type II songs varied more within a population than did type I songs. In each population the introductory syllables of type II songs of a few individuals (1–6%) were nearly tonal, and 3–10% of the individuals in each population incorporated a brief tonal note in the introductory syllables.

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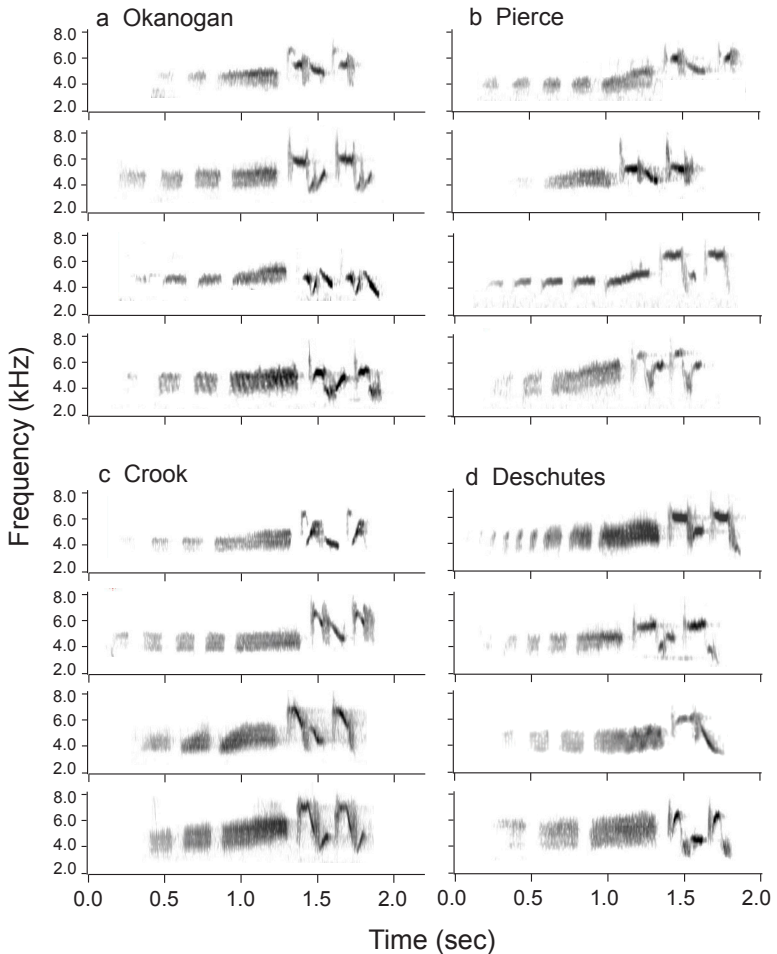


Figure 2. Examples of Type II songs of Townsend's Warblers at four sites, 2009: (a) Okanogan County, Washington, (b) Pierce County, Washington, (c) Crook County, Oregon, and (d) Deschutes County, Oregon.

DISCUSSION

The song systems of the wood-warblers are varied (Spector 1992). In some species males have a single song, while males of other species employ two or more. The songs of species with multiple distinct songs can often be grouped into two categories by context.

Within the genus *Setophaga*, all the species that have been studied to date sing songs of both first and second categories, but even within the

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genus song systems vary. Some species sing form-encoded songs, others performance-encoded songs. Furthermore, the number of songs within a song category also varies by species. Each Chestnut-sided Warbler, for example, sings several first- and several second-category songs, whereas each male Golden-cheeked Warbler (*S. chrysoparia*) tends to sing a single first- and a single second-category song (Byers 1995, Bolsinger 2000).

The Black-throated Gray (*S. nigrescens*), Grace's, Black-throated Green, Golden-cheeked, Hermit, and Townsend's Warblers constitute a clade within the genus *Setophaga* (Lovette et al. 2010). Most, including the Townsend's Warbler, share a number of similarities in singing behavior including the use of form-encoded songs (Morse 1967, Morrison and Hardy 1983, Wright et al. 1998, Bolsinger 2000, Janes and Ryker 2006). Grace's Warbler is the exception, singing performance-encoded songs (Staicer 1989).

Each male of the five species with form-encoded songs uses a single first-category song, and most, if not all, tend to rely on a single second-category song (Wright et al. 1998, Bolsinger 2000, Janes and Ryker 2006, 2011). Second-category singing of the Black-throated Green Warbler has not been described in detail.

The Townsend's Warbler is most closely related to the Hermit Warbler (Lovette et al. 1999, 2010). The two regularly hybridize where their ranges meet, and it is reasonable to expect that their song systems should be similar. The two species' first-category singing is the same, including general song form and the existence of distinct dialects. Second-category singing, however, differs markedly. Second-category songs of Townsend's Warbler of the four Oregon and Washington populations we studied, plus four others in the region as well as a population near Girdwood, Alaska, >2200 km northwest of the Okanogan study area (Janes, unpublished data), are recognizably similar. In contrast, second-category songs of the Hermit Warbler vary greatly, among both individuals and populations, with respect to both general song structure and form of the component syllables (Janes and Ryker 2006).

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