TOWARD CLARIFYING THE WYOMING RANGES OF THE *VIREO GILVUS* COMPLEX

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ABSTRACT: The Warbling Vireo (*Vireo gilvus*), generally recognized as one polytypic species, is widely distributed across North America, but differences in morphology, song, genetics, and ecology suggest the western and eastern populations may represent two species. Understanding their distributions enables tracking of range changes and other factors that might affect the conservation of populations. Therefore, I studied museum specimens, specimen data, and identifications provided by investigators recording songs to help clarify the ranges of the two taxa in Wyoming. Of 18 specimens in the U.S. National Museum collected from 1858 to 1930, I identify 15 as the western species *V. swainsoni*. These are spread over most of Wyoming, east to Crook and Albany counties. Only three represent the eastern species *V. gilvus*, two from Greybull, Big Horn Co., and one from Cheyenne. Whether the overlap represents sympatry of breeding populations in eastern Wyoming or overlap in migration remains to be determined.

The Warbling Vireo (*Vireo gilvus sensu* AOU 1998) is frequently recognized as consisting of a polytypic western species and a monotypic eastern species (e.g., Phillips 1991, Voelker and Rohwer 1998, Mountjoy and Leger 2001, Rohwer et al. 2005, Browning 2019, Lovell et al. 2021), a treatment I follow in this study. The Western Warbling Vireo, *V. swainsoni*, differs from the Eastern Warbling Vireo, *V. gilvus*, in morphology (e.g., Browning 1990, Phillips 1991, Dunn and Alderfer 2017), genetics (Lovell 2010, Slager et al. 2014, Lovell et al. 2021), breeding strategies (Voelker and Rohwer 1998), voice (e.g., Floyd 2014, Pieplow 2019), and response to cowbird parasitism (e.g., Sealy 1996, Browning 2019).

The three subspecies of *V. swainsoni* breeding north of Mexico and recognized by Browning (2019) are nominate *swainsoni* (breeding from southeastern Alaska and British Columbia to Alberta and in the contiguous U.S. west of the Cascade/Sierra Nevada divide), *leucopolius* (breeding in the Great Basin from southeastern Oregon to southern Idaho and in most of Nevada), and *brewsteri* (breeding from the eastern slope of the Rocky Mountains of the U.S. south into mainland Mexico). Birds breeding in the Rocky Mountain range of *brewsteri* were formerly included under the name *leucopolius* (Phillips 1991). The bill of these three subspecies of *V. swainsoni* is thinner than the more robust bill of *V. gilvus*. Variation within *V. swainsoni* is most noticeable in back and crown color, with *leucopolius* being the palest, nominate *swainsoni* being the most olivaceous above, and *brewsteri* having the darkest crown (Browning 2019). *Vireo swainsoni* breeds in deciduous forests and along riparian corridors at all elevations in the Rocky Mountains, whereas *Vireo gilvus* is unknown as a breeding species in montane forests of the Rocky Mountains. Several mountain ranges in Wyoming, all including some deciduous forest (Knight et al. 2014), lie east of the Rocky Mountains. In addition, cottonwood forests similar to the known breeding habitat of *V. gilvus* in South Dakota (Tallman et al. 2002) and Nebraska (Silcock and Jorgensen 2020) occur along rivers in the eastern part of Wyoming.

The poorly known breeding ranges of the Warbling Vireos in Wyoming are based on some decades-old specimens, primarily in the National Museum of Natural History (USNM), that were either misidentified or suspected to have been misidentified (Faulkner 2010). The breeding ranges, whether the taxa are recognized as constituting one species or two, thus need clarification. Much of the confusion about the inexact breeding ranges of the component taxa of the Warbling Vireo stems from the lack of specimens from Wyoming, from confusion resulting from past identifications, and from the subtlety of the physical differences (Browning 2019) between the taxa.

Oberholser (1932) named the interior subspecies *leucopolius*, which he confined to the Warner Valley in southeastern Oregon. Despite Sibley's (1940) and Miller's (1941) having extended its range as far east as western Wyoming, the AOU (1957:476) considered that *swainsoni* occurred in "central Wyoming (Ft. Sheridan)" and did not mention either *leucopolius* or *V. g. gilvus* for the state. The range of *leucopolius* was later confined to the Great Basin (Browning 1990, Phillips 1991), a region including part of southeastern Oregon, southern Idaho, most of Nevada, and western Utah. Confining the range of *leucopolius* to the Great Basin implies a northward extension of the breeding range of *brewsteri*. Sibley (1940) and Miller (1941) had not considered *brewsteri* to breed in the Rocky Mountains, as Phillips (1991) and Browning (2019) recognized. Thus the birds once identified as *leucopolius* in Wyoming are currently known as *brewsteri*. Other sources (e.g., Phillips 1991, Gardali and Ballard 2000) likewise lack details on the distribution of the subspecies of Warbling Vireos in Wyoming.

The first report of a warbling vireo (here in lower case meaning either species) in Wyoming was its listing under the heading *V. gilvus* by Knight (1902). Grave and Walker (1913:69) considered *swainsoni* common and widespread in Wyoming while casting doubt on the occurrence of *gilvus*. Fuller and Bole (1930) listed three specimens (two adults, one juvenile) collected near Chugwater (Platte County) on 1 September 1923 that had been identified as *V. g. swainsoni* by H. C. Oberholser (Steve Rogers pers. comm.). According to Phillips (1991), on the basis of a specimen from Cheyenne, *V. gilvus* "possibly" breeds in southeastern Wyoming. Although this specimen was collected in early June, Phillips (pers. comm., ca. 1990) was uncertain of its breeding status. The specimen lacked fat, implying it was not migrating, although the absence of migration does not confirm breeding. On the basis of unpublished genetic data (Carpenter 2019), *V. s. brewsteri* breeds on the eastern slope of the Laramie Mountains approximately 190 km north-northwest of Cheyenne. Voelker and Rohwer (1998) plotted on their range map only *V. swainsoni* as breeding in Wyoming.

In the latest detailed treatment of the birds of Wyoming, Faulkner (2010) concluded that all of the specimens in various museums identified as *gilvus* from the western half of the state had been misidentified. Furthermore, some specimens collected during the breeding season from the same location were sometimes identified as *V. gilvus* and later reidentified as *V. swainsoni*, or identified as *V. swainsoni* and later reidentified as *V. gilvus*.

Two major mountain ranges in eastern Wyoming are the Bighorn Mountains and the Black Hills, both of which are surrounded by lower elevations that might support distributional enclaves of one of these species. A distribu-

tional enclave is a peripherally isolated population completely surrounded by populations of a close relative (Arntzen 1978). The Bighorn Mountains, a spur of the Rocky Mountains, extend 320 km northwest/southeast in south-central Montana and north-central Wyoming. Much of the Bighorn Mountains in Wyoming straddles the boundary between Bighorn and Sheridan counties. The Black Hills straddle the South Dakota and Wyoming border in Crook and Weston counties (Figure 1). Canterbury et al. (2013) considered 71% of the avifauna of the Bighorn Mountains to consist of western-oriented species, 22% of eastern-oriented species, and the relative frequency of western-oriented species in the Bighorn Mountains and Black Hills to be fundamentally similar. Populations of *V. s. brewsteri* breed east of the Rocky Mountains in the Black Hills (AOU 1957, Browning 2019, and references therein) and the Pine Ridge area of western Nebraska (Silcock and Jorgensen 2020). A disjunct population of *V. swainsoni* also occurs in the Cypress Hills of southeastern Alberta (Lovell 2010, Lovell et al. 2021).

Because of confusion in identifications of specimens and sometimes of audio recordings, here I present information toward clarifying the geographic breeding ranges of these two cryptic species of vireo.

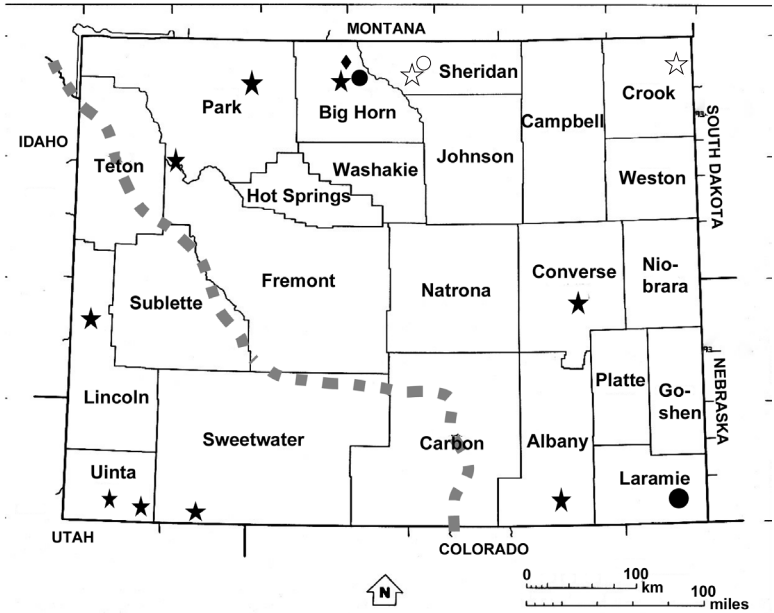

FIGURE 1. Locations of Wyoming specimens of the Warbling Vireo in the U.S. National Museum of Natural History: stars, *Vireo swainsoni*; circles, *V. gilvus*. Filled symbols, verified specimens; open symbols, unverified specimens. Filled diamonds. territorial singing of *V. swainsoni*; open diamonds territorial of singing *V. gilvus*. Dashed gray line, approximate location of Continental Divide.

METHODS

Queries in March and July 2019 of www.vertnet.org, a website through which specimen data on organisms held in hundreds of museum collections can be searched, yielded 65 specimens from Wyoming collected in June and July, the months the species breeds in Wyoming (Faulkner 2010). Of these 65, 44 were collected from 1858 to 1950, whereas 11 were collected after publication of Faulkner's (2010) *Birds of Wyoming*. Because of the difficulty of distinguishing the taxa composing the warbling vireo and lack of a detailed accounting of the basis for the identifications, annotations of subspecies on these specimens' labels are unreliable.

To assess the situation independently, I examined 18 specimens of adult warbling vireos from Wyoming borrowed from the National Museum of Natural History (USNM), all collected from 1858 to 1930 on dates from 24 May to 21 July. Three had been collected in late May, the rest in June and July. These specimens were not examined by Faulkner (pers. comm., 2021). I compared their crown and back colors with those of three specimens of *V. gilvus* from New Jersey and Wisconsin and three of *V. swainsoni leucopolius* from Nevada and Idaho. I assessed colors visually at a northeast-facing window on a sunny day in indirect sunlight. This technique yields results comparable to quantitative methods (Aldrich 1951, Browning 1993, 1994, Armenta et al. 2008, Lovell 2010, Paxton et al. 2010). Using dial calipers, I measured each specimen's wing chord, bill width, and bill depth at the anterior edge of the nostril to the nearest tenth of a millimeter.

I identified specimens to species on the basis of a suite of characters (Lovell 2010) including back color and especially crown color and measurements of wing and bill (e.g., see Gardali and Ballard 2000, Browning 2019). One or two characters, especially mensural ones, could be insufficient for conclusive identification (e.g., Browning 2019). Measurements of bill width from the eastern U.S. (= *V. gilvus*) were equal to or greater than 4.0 mm, whereas those of males from the western U.S. (= *V. swainsoni*) were less than 3.7 mm. Except for extremes, measurements of bill depth (e.g., Gardali and Ballard 2000, this study) are not as reliable a distinguishing feature as bill width. According to Phillips (1991:156), the species differ in the relative lengths of certain primaries: in *V. swainsoni*, "primary 9 is usually near the length of #4 (sometimes shorter); #10 variable, sometimes over 15 mm," whereas in *V. gilvus*, "primary 9 often as near to length of #5 (or nearer) as to #4; #10 ca. 13–15 mm long." Fortunately, most specimens of *V. gilvus* can be distinguished from all subspecies of *V. swainsoni* by back color, especially crown color, and the shape of the bill (slender in *V. swainsoni*, broad and deep in *V. gilvus*; Figure 2).

In earlier studies (Browning 1974, 1990), I examined specimens then available to Allan Phillips. While visiting the USNM, he borrowed breeding specimens held by major U.S. and Canadian museums. During that time, and in studies of other species, I agreed (Browning 1990) with most of Phillips's (1986) identifications, including those of vireos (Phillips 1991). Identification of audio recordings are based on determinations by the recording investigators D. Faulkner and N. Pieplow.

FIGURE 2. Comparison of the bill shapes of *Vireo gilvus* (broader, left, San Diego Natural History Museum [SDNHM] 25628, Lexington, Lafayette Co., Missouri) and *V. swainsoni* (narrower, right, SDNHM 25643, Hart Mt., Lake Co., Oregon).

RESULTS

Identifications of the 18 specimens from Wyoming I examined are listed in Table 1. The specimens I examined from near and west of the Continental Divide represent *V. s. brewsteri*. Specimens from localities farther east in Wyoming include those from Fort Steele, Greybull and the Big Horn Mountains, and the Black Hills (Table 1).

Fort Steele and Region

While employed by the Biological Survey from 1910 to 1911 (Sterling et al. 1997), Harold Elmer Anthony collected birds in Wyoming. At Ft. Steele (Carbon County) along the North Platte River in south-central Wyoming, he collected one male vireo on 25 May 1911 (USNM 228537) and another on 30 May 1911 (USNM 228538). Oberholser (1974) designated the latter as the holotype of *V. g. petrorus*, a name synonymized by Browning (1974).

In color USNM 228537 is similar to examples of *V. s. brewsteri*. In bill size, it is in the low end of the range for bill depth and width (3.2 and 3.4 mm, respectively) of specimens of *V. s. leucopolius* or *brewsteri*.

Greybull and the Bighorn Mountains

In June 1910, during his first year working for the Biological Survey (Banks 1995), Alexander Wetmore collected birds (Table 1) from Greybull (Bighorn County), a small river town southwest of the Bighorn Mountains of north-central Wyoming. He collected five (USNM) warbling vireos that are perhaps the most troublesome set of specimens from Wyoming. On 8 June 1910, Wetmore recorded in his field journal collecting two adult males that he identified as *swainsoni* near the bridge crossing the Bighorn River at Greybull

Table 1 Wyoming Specimens of the Warbling Vireo in the U.S. National Museum of Natural History

USNM number	Date	Sex	Locality	Species identification
230019	8 June 1910	♂	Greybull, Big Horn Co.	*swainsoni*
230022	10 June 1910	♂	Greybull, Big Horn Co.	*swainsoni*
230024	8 June 1910	♂	Greybull, Big Horn Co.	*swainsoni*
230021	9 June 1910	♀	Greybull, Big Horn Co.	*gilvus*
230023	10 June 191	♂	Greybull, Big Horn Co.	*gilvus*
228537	30 May 1911	♂	Ft. Steele, Carbon Co.	*swainsoni*
228538[a]	30 May 1911	♂	Ft. Steele, Carbon Co.	*swainsoni*
137815	11 June 1894	♂	Bear Lodge Mountain, Crook Co.	*swainsoni*
455069	2 June 1888	♂	Cheyenne, Laramie Co.	*gilvus*
242510	21 July 1915	♂	Laramie, Albany Co.	*swainsoni*
228540	1 July 1910	♂	8 km N Cody, Big Horn Basin Co.	*swainsoni*
A11065	3 June 1858	♀	Ft. Bridger, Uinta Co.	*swainsonii*
137813	24 May 1890	♂	Ft. Bridger, Uinta Co.	*swainsoni*
302025	2 July 1930	♂	Two Ocean Lake, Teton Co.	*swainsoni*
228541	11 July 1910	♂	Valley, Park Co.	*swainsoni*
228542	29 June 1910	♂	Pat O'Hara Creek, Park Co.	*swainsoni*
228539	12 June 1911	♂	Riverside, Carbon Co.	*swainsoni*
227034	19 July 1904	?	Sundance, Crook Co.	*swainsoni*

[a]Holotype of *Melodivireo gilvus petrorus* Oberholser (1974) examined in earlier studies (Browning 1974, 1990).

(Figure 1), and he collected three more birds in the vicinity of Greybull on 10 and 11 June 1910, all of which he also identified as *swainsoni*.

I found that three of these specimens (USNM 230019, 230022, 230024) have the dorsal color and bill size and shape (small and slender) of *V. swainsoni*, in agreement with J. W. Aldrich's previous identification of them as western warbling vireos. But the other two specimens (USNM 223021 and 230023) are near the high end of the range for bill depth (4.0, 3.7 mm) and wing chord (71.0, 72.5 mm) for a warbling vireo so are more typical of *V. gilvus*. Measurements of *V. s. brewsteri* and *V. gilvus* overlap, but the crown and back color of these two specimens agree with specimens of typical *V. gilvus* from east of Wyoming. Aldrich had also identified them as *gilvus*. There are no reports of warbling vireos from Greybull via https://ebird.org, but recently the area has drawn only light attention from birders (no hotspot at eBird and no hotspot with over eight checklists or a warbling vireo within 36 km).

Sheridan County

According to AOU (1957:476), subspecies *swainsoni* breeds in "central Wyoming (Ft. Sheridan)." I presume this was a mistake for the town of Sheridan in north-central Wyomng, as there is no evidence for a locality named Fort Sheridan anywhere in Wyoming (T. Rea, pers. comm., 2020). (A Camp Sheridan was established in 1886 near the northern boundary of Yellowstone National Park, in far northwestern Wyoming. That site was renamed Fort Yellowstone in 1891 and abandoned in 1918 [Frazer 1965]. Fort Yellowstone is about 354 km west of Sheridan.) The only specimens of warbling vireo from Sheridan County are two collected by Aldrich at Smiths Creek, about 6

km northwest of Dayton, on 31 July 1930 (Carnegie Museum of Natural History P162981 and P162982). That locality, at 1370 m in the eastern foothills of the Bighorn Mountains, is 24 km northwest of Sheridan. Aldrich (1935) mentioned the more unusual species he collected in the Bighorn Mountain region, apparently omitting the warbling vireo because of its abundance. The specimens, which I have not examined, are annotated as "*swainsoni* W.E.G." (Stephen P. Rogers pers. comm., 2020). The initials are those of W. Earl Godfrey, who worked under H. C. Oberholser at the Cleveland Museum of Natural History (Andy Jones pers. comm., 2020) from 1942 through 1945 (Houston and Gosselin 2003), when Godfrey likely identified the Dayton specimens as *swainsoni*. Whether the undated identifications were made before or after 1944, when *leucopolius* was recognized by the AOU (1944), is unknown.

Black Hills

A possibly disjunct population of *V. swainsoni* breeds in the Black Hills of Wyoming and South Dakota (e.g., Browning 2019). Carpenter (2019) reported the alleles of vireos from the Black Hills to be more similar to those of *brewsteri* and stated that birds from there do not represent a hybrid population of *V. swainsoni brewsteri* and *V. gilvus*. I tentatively identify as *V. swainsoni brewsteri* a specimen from Sundance (Crook County) in the Black Hills (Table 1).

Other Wyoming Localities

Between the Black Hills and Big Horn Mountains, Faulkner (pers. comm., 2020) recorded singing *V. gilvus* at Gillette (Campbell County). Whether or not the population of *V. swainsoni* breeding in the Bighorn Mountains is disjunct from *V. gilvus* can not be said until the species breeding immediately adjacent to those mountains can be ascertained. Specimens from west of the Bighorn Mountains are *V. s. brewsteri* (Figure 1). For example, those from Pat O'Hara Creek (USNM 228542) and Cody (USNM 238540), both in Park County, owing to their small bills and coloration, represent *V. s. brewsteri*, contrary to Aldrich's 1945 identifications. A specimen (USNM 228541) from Valley, a locality southwest of Cody and at 2133 m elevation near the Continental Divide, is more similar to *gilvus* in size but in color to *V. s. brewsteri*. Though Aldrich identified it as *gilvus*, I tentatively consider it an example of *V. s. brewsteri*.

DISCUSSION

On the basis of my identifications of USNM specimens and audio recordings by others, I infer that *V. gilvus* most likely breeds in southeastern Wyoming and probably in the regions below the Black Hills west to at least Campbell County. Breeding of *gilvus* in the Sheridan region and elsewhere in the vicinity of the Bighorn Mountains is suspected on the basis of sound recordings but unsubstantiated. The breeding range of *brewsteri* includes the Black Hills in northeastern Wyoming, the Bighorn Mountains, and eastern and western slopes of the Rocky Mountains across Wyoming (Figure 1). Nevertheless, representation by specimens is geographically spotty and

most specimens are decades old, lacking information on molt, reproduction, habitat, and other data that would allow breeding ranges to be described more precisely.

Western Wyoming

Sibley (1940) and Miller (1941) referred to an unspecified number of specimens from western Wyoming in the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley. The only specimens from Wyoming in MVZ are an adult and an immature from South Pass in Fremont County and one immature from near Green River Lakes in Sublette County, all collected in late August or early September 1939, thus outside the months of breeding (Faulkner 2010), a fact perhaps considered by the AOU (1944) when it defined the breeding range of *leucopolius*. I have not verified the identity of the three MVZ specimens, but it is unlikely that Sibley or Miller was mistaken in assigning the specimens to a western subspecies.

Fort Steele and Region

One documented change in habitat is deforestation through cutting of the lodgepole pine used by the railroad for lumber, fences, and other structures for the former Ft. Steele. The affected regions later regrew with aspen and second-growth pine (Cary 1917). Changes in habitat at Fort Steele and elsewhere may have led to changes in breeding distributions but are beyond the scope of this paper.

Greybull and the Bighorn Mountains

Greybull represents a site of apparent contact through migration or breeding where the interaction between the eastern and western taxa might profitably be studied. Aldrich did not publish on the Greybull specimens, but it is plausible that he left notes on them. Files in the office of the Biological Survey in the Division of Birds (USNM) were customarily maintained by investigators who often stored measurement sheets and notes to be consulted by anyone at some later date. Unfortunately, through multiple reorganizations and chronic under-funding, those files have been disrupted (T. Chesser pers. comm., 2020) so it is no longer possible to know what Aldrich might have noted. Furthermore, the significance of the Greybull specimens has apparently gone unappreciated by investigators after Aldrich, including Browning (1974, 1990) and Phillips (1991), both whom had ample access to USNM specimens.

Was early June too early for the Greybull birds to be breeding? Late May to mid-July is the interval reported for egg dates from an unspecified location in Montana (Gardali and Ballard 2000) and unspecified localities in Montana and Wyoming (Johnsgard 2009) that might represent either western or eastern vireos. In the Bighorn Mountains, warbling vireos are fairly common from May to October, with breeding confirmed by young begging on 11 July 1976 at Tongue River Canyon (Canterbury et al. 2013).

Might the birds Wetmore collected at Greybull have been migrants or representatives of a population breeding along the Bighorn and Greybull rivers? Unfortunately, the labels on Wetmore's specimens do not offer clues about re-

production. Some may have been on their way to breed in the nearby Bighorn Mountains where *V. swainsoni* is currently reported (https://ebird.org) or to Sheridan County, where *V. gilvus* breeds (see beyond), or still farther north.

Sheridan County

In 2019, warbling vireos at Sheridan were singing songs typical of *V. gilvus* (J. L. Canterbury pers. comm., 2019) but in 2020 were recorded singing songs typical of *V. swainsoni brewsteri* (D. W. Faulkner pers. comm., 2020). The number and behavior of the individuals singing is unknown. The situation might be an example of sympatry or overlap in migration.

Black Hills

A possibly disjunct population of *V. swainsoni* breeds in the Black Hills of Wyoming and South Dakota (e.g., Browning 2019). Carpenter (2019:36) reported the alleles of vireos from the Black Hills to be more similar to those of *brewsteri* than to those of *gilvus* and that the birds there do not represent a hybrid population.

Most specimens available for distributional and taxonomic studies are not recently collected and frequently many decades old. A better understanding of any species of bird, including the warbling vireos, requires newer specimens for many reasons (e.g., Remsen 1995, Peterson and Navarro-Sigüenza 2017), including filling geographic gaps with specimens accompanied by data on habitat, reproduction, and other information, including audio recordings.

Several regions of Wyoming clearly need further study, especially those where both species have been detected. Specifically, information from the Bighorn Mountains would be instructive. Likewise, it would be useful to confirm what species of vireo breeds between Sheridan and the Black Hills and to clarify the situation in the Black Hills. Information on the birds and breeding habitat from localities south of the Black Hills to Laramie County and west to at least western Sweetwater County would fill some gaps.

Collecting genetic samples and recording vocalizations along with voucher specimens would be very helpful. Study of specimens in the Denver Museum of Nature and Science (mostly collected in Fremont County) could contribute to understanding the two species of vireo. Combining genetic, vocal, and morphological information would also help identify problematic birds, such as any originating from the narrow hybrid zone (Lovell 2010, Lovell et al. 2021) in Alberta (which might migrate through Wyoming).

Establishing a baseline for the distribution of the warbling vireos in Wyoming will help in clarifying their taxonomic relationships as well as provide basic information for management of habitat and conservation (e.g., Gill 2007, Tietze 2018, Winker 2018).

ACKNOWLEDGMENTS

Special thanks to Christopher Milensky and Carla Dove for the loan of and additional information concerning the USNM specimens. Stephen P. Rogers (Carnegie Museum of Natural History, Pittsburgh) provided information on the Aldrich specimens from Sheridan County and other vireo specimens. I thank Arielle Helpern and Bethany Lindbloom of Southern Oregon University for receiving and housing

the loan of specimens and providing a place to compare them. Much appreciated is VertNet for specimen data. Thank you to Andy Jones (Cleveland Museum of Natural History) for additional information on the Sheridan specimens, Tom Rea (Wyoming historian) for information on the nonexistence of Ft. Sheridan, and Jackie Canterbury for reading the manuscript and for information on Sheridan vireos. Nathan Pieplow, Ted Floyd, and especially Douglas W. Faulkner's useful comments and information on audio recording and his comments on an earlier draft are appreciated. Alan Contreras provided information on forts in Wyoming and helpful comments on a later draft. Valuable recommendations concerning the manuscript from Grant Ballard, Daniel D. Gibson, Peter Pyle, and Philip Unitt are greatly appreciated.

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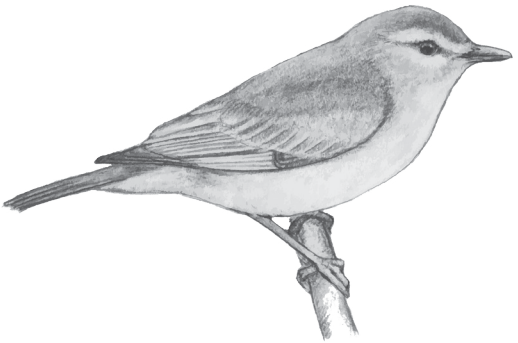
Accepted 12 March 2021



Warbling Vireo

Sketch by Bryce Robinson