ABSTRACT: During June and July 2011, I audio-recorded eight Warbling Vireos (Vireo gilvus) at widely scattered sites in eastern Boulder County, Colorado, immediately east of the steep foothills of the Rocky Mountains. All eight sang songs like those of the eastern subspecies, V. g. gilvus; immediately to the west, in the steep foothills of the Rocky Mountains, Warbling Vireos sing songs like those of the western subspecies, V. g. swainsonii. The results of these observations suggest both the presence of nominate gilvus farther west in Colorado than previously documented and a sharp demarcation between the breeding ranges of swainsonii and gilvus.

The polytypic Warbling Vireo (Vireo gilvus) is common across much of its extensive North American breeding range. Species limits are uncertain (AOU 1998), but the general consensus is that two groupings are represented: a monotypic eastern gilvus group and a polytypic western swainsonii group. The eastern and western populations—the Eastern Warbling-Vireo and Western Warbling-Vireo, respectively—are recognized by some authorities (e.g., Pyle 1997, Gardali and Ballard 2000) as subspecies groups, whereas others (e.g., Sibley and Monroe 1990, Phillips 1991) have treated them as separate species. Of particular interest is a recent study from Alberta (Lovell 2011) employing molecular, morphometric, and acoustic methods to test hypotheses about species limits within the warbling-vireo complex.

The Eastern and Western warbling-vireos are exemplary “cryptic taxa.” They are literally cryptic, drab and small, moving about slowly in dense foliage in treetops, where they are hard to study closely. Moreover, morphological differences between the two groups (summarized by Pyle 1997, Gardali and Ballard 2000) are relatively slight: Eastern Warbling-Vireos are proportionately larger-billed, larger overall, and brighter (less gray, more olive–yellow) than Western Warbling-Vireos. Unsurprisingly, the limits of the ranges of the Eastern and Western warbling-vireos have not been precisely established in the literature. According to the AOU (1998), Eastern Warbling-Vireos range west in the central Great Plains to eastern Nebraska, Kansas, and southeastern Colorado, whereas Western Warbling-Vireos occur east to southwestern South Dakota, central Wyoming, and western Nebraska.


The specimen record tells a similar story. The Denver Museum of Nature and Science (DMNS) houses 80 Colorado specimens of the Warbling Vireo (sensu lato), four of which have been identified at some point as
V. g. gilvus. Of those four, however, A. R. Phillips reassigned three to V. g. swainsonii. Thus only one of the 80 Colorado specimens in the DMNS collection is currently attributed to V. g. gilvus. It is certainly possible that additional Colorado specimens of V. g. gilvus are represented—but as yet undetected—in the DMNS collection. Greater resolution of the Warbling Vireo’s status in Colorado would be achieved by examining specimens in other collections as well.

Although weakly differentiated morphologically (see Lovell 2011), Eastern and Western warbling-vireos are well separated in other respects, including habitat (Fisher and Acorn 1998, Lovell 2011), genetics (Murray et al. 1994), molt schedule (Voelker and Rohwer 1998), and song (summarized by Gardali and Ballard 2000, Sibley 2000). Differences in song may be described as follows: (1) the song of the Western Warbling-Vireo is burrier or “less musical” overall than the relatively clear and “musical” song of the Eastern Warbling-Vireo; (2) the song of the Western Warbling-Vireo often has a break at the beginning, and the overall phrasing is choppier than that of the Eastern Warbling-Vireo; (3) the lowest-frequency phrases in the Western Warbling-Vireo’s song average slightly higher-pitched than the analogous phrases in the Eastern Warbling-Vireo’s song; and (4) the song of the Eastern Warbling-Vireo tends to end with a squeaky and relatively high-pitched note (“squirt!”), whereas the Western Warbling-Vireo’s song often ends on a buzzy and/or relatively low-pitched note. I have provided a tutorial comparing audio recordings and sound spectrograms of the songs of presumed Western and Eastern warbling-vireos in Boulder County, Colorado, at http://tinyurl.com/Floyd-Warbling-Vireos (Floyd 2010a).

It has been remarked by many writers (e.g., W. M. Tyler in Bent 1950) that warbling-vireos are as easy to hear as they are hard to see. Thus audio recordings of warbling-vireos might serve as a useful proxy for occurrence data based on photographic or specimen records. In particular, differences in song—if spectrographically diagnosable and verifiably correlated with geographic variation in morphology—could provide a means for better resolution of the range limits of the two groups. Additionally, spectrographic analysis of song in the contact zone, assuming a contact zone exists, could be useful for determining taxonomic limits within the warbling-vireo complex.

Boulder County, Colorado, provides an especially propitious venue for studying variation and contact between populations in the warbling-vireo complex. From west to east, the county drops an impressive 2700 m. The transition between “eastern” and “western” landscapes is abrupt and dramatic, with typical “eastern” and “western” bird communities occurring within a few kilometers of one another.

METHODS

Applying the method of convenience sampling (see McCormack and Hill 1997), I searched for and attempted to make audio recordings of presumed Eastern Warbling-Vireos in Boulder County. I made the recordings depicted in Figures 1 and 2 with a “flower pot mic” (see Evans 2005), and those depicted in Figures 3–9 with an Olympus VN-8100PC recorder (see Floyd 2012b). I analyzed the songs on the basis of sound spectrograms generated
RESULTS

Field Observations from and Sound Recordings Obtained in the Lowlands of Boulder County, Colorado

In June and July of 2011, I made the following observations in the lowlands of eastern Boulder County.

At Walden Ponds on the afternoon of 9 June 2011, I saw a warbling-vireo that, on the basis of visual characters, I tentatively identified as an Eastern Warbling-Vireo. Within a minute of the initial detection, the bird began to sing; its song sounded to me like that of the Eastern Warbling-Vireo. I returned to the site on the morning of 11 June 2011 and obtained audio recordings of two warbling-vireos, one of which sounded typical of the Eastern Warbling-Vireo.

Figure 1. Songs of a warbling-vireo recorded at 40.0449° N, 105.1923° W at Walden Ponds, near Boulder Creek, Boulder County, Colorado, 11 June 2011. (a) This song is a bit less “exuberant” than that often uttered by the Eastern Warbling-Vireo but otherwise typical. Note the relatively smooth and continuous song delivery, the relatively low-pitched baseline phrases in the song (compare with Figure 9), and the high-pitched terminal note. (b) Song cut off at the beginning, but the terminal 1.25 sec, shown here, is entirely typical of the Eastern Warbling-Vireo; note especially the vigorous delivery and the high-pitched terminal note. The sound beginning at 1.40 sec is the song of a distant Red-winged Blackbird (*Agelaius phoeniceus*).

by Audacity (http://audacity.sourceforge.net), but the sound spectrograms reproduced here were generated by Raven (http://birds.cornell.edu/brp/raven).
Warbling-Vireo, the other atypical. Sound spectrograms of the apparently atypical songs show a mix of slightly aberrant (Figure 1a) and typical (Figure 1b) Eastern Warbling-Vireo song-types. M. O’Brien and N. Pieplow (pers. comm.) identified the songs as those of the Eastern Warbling-Vireo, despite my equivocation when I heard the bird in the field. Sound spectrograms of the other bird’s songs (Figures 2a, b) are typical of the Eastern Warbling-Vireo, consistent with my impressions from the field.

At White Rocks on the morning of 19 June 2011, I heard two warbling-vireos whose songs seemed a perfect match for the Eastern Warbling-Vireo. I returned to the site on the morning of 22 June and obtained an audio recording of what I assume was the first bird I had heard on 19 June (on both mornings, a bird was singing from the same perch). Sound spectrograms of this bird’s song (Figures 3a, b) are consistent with the song of the Eastern Warbling-Vireo. I did not obtain audio recordings of the other warbling-vireo I had heard there on 19 June.

Near Greenlee Preserve on the morning of 21 June 2011, I heard a warbling-vireo whose song sounded typical of the Eastern Warbling-Vireo. I briefly heard what I presumed to be the same bird on the morning of 23 June. I did not hear the bird again after that date, despite repeated visits to the site, and I did not obtain an audio recording of it.
At Pella Crossing on the morning of 25 June 2011, I heard and recorded two warbling-vireos. In the field, the song of the first bird sounded typical of the Eastern; I thought the second bird was an Eastern Warbling-Vireo, too, although I judged its song to be less typical than that of the first bird. Sound spectrograms of the first bird’s song (Figures 4a, b) are consistent with the song of the Eastern Warbling-Vireo. Sound spectrograms of the second bird’s songs reveal some that are typical of Eastern Warbling-Vireo (Figure 5a) as well as others that are less typical but probably within the eastern subspecies’ range of variation (Figure 5b).

Along South Boulder Creek on the morning of 26 June 2011, I recorded two warbling-vireos. My experiences with these two birds were analogous with my experiences the morning before at Pella Crossing. The first bird I heard along South Boulder Creek sounded typical of the Eastern Warbling-Vireo, and sound spectrograms of that bird’s songs (Figures 6a, b) are consistent with it. The second bird sounded more problematic in the field, but sound spectrograms of that bird’s songs reveal that my assessments in the field may have been affected by substantial noise from the nearby creek. Spectrographically, this bird’s songs are either typical of (Figure 7a) or only somewhat aberrant for (Figure 7b) the Eastern Warbling-Vireo.

Figure 3. Songs of a warbling-vireo recorded at 40.0465° N, 105.1446° W at White Rocks, near Boulder Creek, Boulder County, Colorado, 22 June 2011. Both songs are typical of the Eastern Warbling-Vireo. (a) Includes calls of a Red-winged Blackbird (whistled down-slip beginning at around 0.20 sec) and an Eastern Kingbird (Tyrannus tyrannus; buzzy notes at around 0.80 sec and 2.75 sec); (b) includes song of a Western Wood-Pewee (Contopus sordidulus), extending from around 0.35 to 0.85 sec.
Along Coal Creek on the morning of 2 July 2011, I recorded a warbling-vireo which sounded to me like an Eastern. Sound spectrograms of its songs (Figures 8a, b) confirm that they are consistent with the Eastern Warbling-Vireo. The locations of these presumed Eastern Warbling-Vireos (ten birds heard, of which I obtained audio recordings of eight) are shown in Figure 10. Note that all ten were in riparian habitat just east of the steep foothills of the Rocky Mountains. Nine birds were along or within 500 m of creeks, and one was in wooded habitat near the edge of a lake. Four of the ten birds were along or near Boulder Creek; two were along or near South Boulder Creek; two were along or near St. Vrain Creek; and two were in the Coal Creek drainage (including the one at Greenlee Preserve). Thus I documented two or more apparent Eastern Warbling-Vireos within all four of the primary drainages of Boulder County.

Field Observations in the Mountains of Boulder and Teller Counties, Colorado

For comparative purposes, I recorded a presumed Western Warbling-Vireo in spruce–fir habitat at an elevation of 2750 m in mountainous Teller County on the morning of 28 June 2011. In the field, the bird sounded like
a Western Warbling-Vireo. Sound spectrograms of its songs (Figures 9a, b) confirm that they are consistent with that form.

On various occasions during June and July 2011, in Boulder County’s mountains and steep foothills I heard or saw warbling-vireos that I assumed were Western. Their songs were indistinguishable to my ears from those of the individual from Teller County (Figures 9a, b); if seen well enough, they looked like Western Warbling-Vireos (per Pyle 1997). In Boulder County, the boundary between the eastern lowlands (consisting of grasslands and broadleaf riparian woodland) and western foothills (consisting of pine, spruce, and fir forests) is abrupt and dramatic; see Figure 10. The Boulder County landscape thus differs from that described by Lovell (2011), who studied Eastern and Western warbling-vireos across a more gradual ecotone from aspen parkland (favored by the Eastern) to mixed conifer woodlands (preferred by the Western).

In late May and early June 2012 (i.e., nearly one year following the detections reported above), I audio-recorded several Western Warbling-Vireo songs in the mountains and foothills of western Boulder County (Floyd 2012a–c), as well as additional Eastern Warbling-Vireo songs in the lowlands.
just east of the Boulder County foothills (Floyd 2012a–c). These very anecdotal detections in 2012 further support an abrupt demarcation between the two subspecies’ ranges at the interface of the central Rocky Mountains and southern Great Plains.

DISCUSSION

My observations confirm the widespread occurrence in the lowlands of Boulder County, Colorado, of birds that sound like Eastern Warbling-Vireos. In the middle latitudes of the continental United States, the western limits of the range of the Eastern Warbling-Vireo have been characterized only imprecisely (e.g., Bailey and Niedrach 1965, AOU 1998); nevertheless, the prevailing published consensus has been that Eastern Warbling-Vireos, if present at all in Colorado, are limited to the southeastern part of the state (Bailey and Niedrach 1965; see Barrett 1998; cf. DMNS data). More recently, an emerging online “gray literature”—consisting, in the present case, of data submitted to eBird.org, xeno-canto.org, and groups.google.com/forum/#!forum/cobirds—has pointed to the occurrence of Eastern Warbling-Vireos across the eastern tier of Colorado counties and west spar-
VIREO GILVUS GILVUS IN COLORADO

Figure 7. Songs of a warbling-vireo recorded at 39.9784° N, 105.2224° W in the South Boulder Creek Management Area, near South Boulder Creek, Boulder County, Colorado, 26 June 2011. In both examples, excessive background noise (broadband “splattering,” heaviest at low frequencies) is the sound of South Boulder Creek; the bird was singing from a perch just above the creek. (a) Although obscured somewhat by creek noise, the song appears to be typical of an Eastern Warbling-Vireo. (b) The song may be atypically short for an Eastern Warbling-Vireo, but background noise may obscure the beginning of the bird’s song. In other respects, however, the song is typical of the Eastern Warbling-Vireo, consisting of sweet, continuous phrasing with a relatively low-pitched baseline and a high-pitched and ascending terminal note.

In any event, the occurrence of at least ten presumed Eastern Warbling-Vireos, eight of which I audio-recorded, is without precedent in the lowlands immediately east of the Rocky Mountains in northern Colorado. Their presence in Boulder County raises an ontological question: are they “really” Eastern Warbling-Vireos, or are they birds that merely sound like Eastern Warbling-Vireos? Either outcome would have bearing on our understanding of geographic variation and taxonomic limits in the warbling-vireo complex.

The typical songs of warbling-vireos from well within their described ranges are distinct. Thus an Eastern Warbling-Vireo in New Jersey sounds different from a Western Warbling-Vireo in Nevada. In regions of contact, however, one must be wary of two complications. First, because vireos are oscines and develop their songs in part through learning, a “good” Western Warbling-Vireo might learn the “wrong” song, i.e., that of an Eastern Warbling-Vireo singing nearby; conversely, an Eastern might sing the song of a Western. Second, there might be intermediate song types, just as one might expect
intermediate morphologies in zones of overlap; in this regard, it is worth noting that geographic variation in song phrases in the Solitary Vireo complex (*Vireo solitarius sensu lato*) appears to be clinal (James 1981). Unpublished field observations and playback experiments from Choteau, Teton County, Montana, suggest the local warbling-vireo population may be intermediate with regard to song type (D. A. Sibley, pers. comm.) In a zone of overlap zone in Alberta, however, Lovell (2011) detected no intermediate song types.

Regardless, the songs of warbling-vireos are complex and variable (Howes-Jones 1985). It might be expected that a variant or atypical song of an otherwise “normal” Western Warbling-Vireo approaches or overlaps that of the Eastern Warbling-Vireo, and vice versa.

Better understanding of the Eastern and Western warbling-vireos in or near the contact zone will require specimen-based studies. On the one hand, my study establishes the occurrence near the foothills of the Rocky Mountains of birds that sound like Eastern Warbling-Vireos. On the other, its results cannot be taken as proof that such birds “really” are Eastern Warbling-Vireos. Audio recordings alone are inadequate, in most instances, for establishing taxonomic limits in birds; evidence adduced only from audio recordings may appear persuasive, but such “proof” is based on circular reasoning. A recent and relevant case study involves the question of the taxonomic status of the “South Hills Crossbill” (*Loxia sinesciuris* Benkman), rejected as a full species by the AOU (2009) in part because audio recordings purported to refer to

**Figure 8.** Songs of a warbling-vireo recorded at 39.9776° N, 105.1139° W in the Coal Creek Open Space, near Coal Creek, Boulder County, 2 July 2011. Both songs are typical of the Eastern Warbling-Vireo. (a) A fairly faint House Wren song ends at around 0.25 sec. (b)
the taxon were not convincingly matched to specimens, i.e., vouchers of verifiable identity.

In Boulder County and elsewhere in Colorado, high-quality digital photographs of audio-recorded birds might help to clarify the range limits of the Western and Eastern warbling-vireos. Specimens and mist-netted birds would be better, however, as the relatively slight morphological differences between these cryptic taxa are difficult to quantify from digital photographs. Moreover, specimens of audio-recorded birds would provide genetic data that digital photographs cannot; of particular value would be nuclear DNA for determining the extent of introgression, if any, in the contact zone. The recent monograph by Lovell (2011) affirms the importance of specimen-based research for acoustic studies aimed at resolving species limits within the warbling-vireo complex.

Figure 9. Songs of a warbling-vireo recorded at 38.9268° N, 105.1005° W in spruce–fir forest in Woodland Park, Teller County, Colorado, 28 June 2011. Both songs are typical of the Western Warbling-Vireo, differing in various ways from the songs of the Eastern Warbling-Vireo. In both examples, note the break after the first phrase in the song, followed by irregular phrases with a baseline frequency slightly higher pitched than that of the Eastern Warbling-Vireo; note further that both songs peter out at the end, ending on a low-pitched note, the opposite of the high-pitched and emphatic terminal note of the Eastern Warbling-Vireo. The effect on a human listener is of a burry tone quality and a “relaxed” quality to the phrasing; also, the absence of an emphatic terminal note (“squirt!”) is characteristic. (a) The song of a Dark-eyed Junco (*Junco hyemalis*) runs to about 0.75 sec; the sounds at about 2.35 and 2.65 sec are of a wooden screen door being shut. (b) The song of a Dark-eyed Junco runs to about 0.95 sec.
Another unresolved matter is the status in Boulder County prior to 2011 of birds that sound like Eastern Warbling-Vireos. My field notes indicate no such occurrences prior to 2011. Likewise, Boulder-based natural-sounds expert N. Pieplow (pers. comm.) is unaware of occurrences prior to 2011. The summer of 2011 brought numerous “Midwestern” breeders to Boulder County; Cassin’s Sparrows (*Peucaea cassinii*) were widespread, multiple Red-headed Woodpeckers (*Melanerpes erythrocephalus*) were reported, and, most notably, Eastern Phoebes (*Sayornis phoebe*) bred or were suspected of breeding at several locations (Such and Such 2012). Perhaps the occurrence in 2011 of presumed Eastern Warbling-Vireos was linked to the broader arrival of such “Midwestern” bird species in an unusual breeding season. However, Eastern Warbling-Vireos might have been present in previous summers but simply undetected as such.

An obvious next step is to continue to monitor the status of presumed Eastern Warbling-Vireos in Boulder County and elsewhere along the eastern foothills of the southern Rocky Mountains. Such monitoring would benefit from a two-pronged approach, involving both audio recording and capture. In this scenario, individual birds would first be recorded and then collected or captured for measurements, photos, and blood-sampling; next, sound
spectrograms would be matched to individuals that could be identified by plumage, measurements, and genes. Such a sampling design is essential for avoiding the trap of circular reasoning that an Eastern Warbling-Vireo song can come only from an Eastern Warbling-Vireo.

Such an approach will also permit determination of the extent of interbreeding, if it exists, in the contact zone. That finding, in turn, would substantially advance our understanding of taxonomic limits within the warbling-vireo complex. It would also answer the question of whether song can reliably be used to identify warbling-vireos in field studies such as breeding bird atlases, point-count surveys, and the Breeding Bird Survey.

ACKNOWLEDGMENTS

I thank Jon L. Dunn, Kimball L. Garrett, Daniel D. Gibson, Scott F. Lovell, Van Remsen, David A. Sibley, and Philip Unitt for their helpful comments on an earlier draft of this paper, and I thank Michael O’Brien and Nathan Pieplow for help with analysis of the sound spectrograms. Jeff Stephenson, Zoology Collections Manager with the Department of Zoology at the Denver Museum of Nature and Science (DMNS), kindly granted me access to specimens of warbling-vireos in his care. I am especially grateful to Nathan Pieplow for creating Figures 1–9, and to Kei Sochi for creating Figure 10.

LITERATURE CITED


Accepted 17 July 2013