COMPARISON OF THE SONGS OF CASSIN'S AND PLUMBEOUS VIREOS

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ABSTRACT: We compared the songs of Cassin's (*Vireo cassinii*) and Plumbeous (*V. plumbeus*) Vireos to determine if there are characteristics that could allow one to confidently distinguish between these species by song. Using recordings made in the breeding season and within the undisputed breeding ranges of each species, away from the zone of contact, we compared five characteristics of a song: phrase length, rate of phrase delivery, proportion of frequency-modulated (buzzy) phrases, proportion of doubled phrases, and midpoint frequency between the highest and lowest frequencies of a phrase. Among these, the only character in which the species differed significantly was the average midpoint frequency of song phrases. Despite overlap between the species in the distribution of average midpoint frequency, a criterion of 3215 Hz allowed ~84% of the vireo songs in our sample to be identified correctly. We also tabulated expected proportions of true and false positive species identifications based on the full range of average midpoint frequencies likely to be encountered, finding that values >3410 Hz have a >95% probability of representing Cassin's Vireo, and values <3050 have a >95% probability of representing the Plumbeous Vireo. Various field guides show conflicting breeding ranges for these species, and there are many field reports of both vireos outside their known breeding ranges in the breeding season. Given that visual identification of these birds in the field can be difficult when individuals are in faded spring/summer plumage, song may allow us to better define the actual limits of these species' breeding ranges.

Song is a defining characteristic of many bird species, sometimes playing an important role in promoting reproductive isolation between closely related sympatric species (Sabbekoorn and Smith 2002). Differences in song can also be a significant aid to field identification of such species. Borror (1972) and James (1981) quantitatively compared the songs of the Cassin's, Plumbeous, and Blue-headed Vireos (*Vireo cassinii*, *V. plumbeus*, and *V. solitarius*, respectively), prior to the elevation of these taxa from subspecies to full species status. Borror (1972) noted no significant difference between the songs of Cassin's and Plumbeous Vireos in terms of length of song phrases, rate of phrase delivery, song frequency, number of syllables per phrase, or repertoire size. James (1981) also compared the length of phrases, repertoire size, and frequency, as well as noting the proportion of frequency-modulated elements (often referred to as "buzzy" notes). James noted an apparently significant difference in frequency, with the frequency halfway between the highest and lowest frequencies of a phrase of Cassin's higher, on average, than that of the Plumbeous. In neither study, however, were sample sizes robust. Borror's (1972) comparisons were based on four Cassin's Vireo recordings from Flathead Lake, Montana, and six Plumbeous Vireo recordings, three each from the Catalina Mountains of Colorado and Portal, Arizona. James (1981) used five Cassin's recordings, all from British Columbia, and just two Plumbeous recordings, one each from Texas and Arizona. Some field guides have noted this difference in the songs' frequencies (Sibley 2014, Pieplow 2019), and some (Floyd 2008, Sibley 2014, https://www.allaboutbirds.org/guide/Cassins_Vireo/sounds) have also suggested that the song of the Plumbeous Vireo includes a higher proportion of frequency-modulated phrases. However, the small sample sizes of Borror (1972) and James (1981) and the anecdotal nature of field guide comments do not allow one to infer that song characteristics can be used to distinguish these species, either in the field or from recordings. Hedley (2016) analyzed the repertoire and syntax of Cassin's Vireo song thoroughly but did not compare them with those of the Plumbeous Vireo. Martindale (1980) also studied repertoire and syntax, but of the Blue-headed Vireo only.

Current published range maps disagree considerably about the exact limits of the breeding ranges of Cassin's and Plumbeous Vireos, especially in northeastern California, parts of Wyoming, and central Montana. For example, Sibley (2014) showed the breeding range of the Plumbeous Vireo extending into northeastern California, including areas of southern Modoc County and northern Lassen County, while Dunn and Alderfer (2017) and Goguen and Curson (2012) showed the Plumbeous Vireo's range extending no farther north in California than just south of Lake Tahoe. Sibley (2014) and Dunn and Alderfer (2017) showed most of Wyoming and south-central Montana as within the breeding range of the Plumbeous Vireo, while Goguen and Curson (2012) showed the range extending barely into south-central Wyoming, and into small, isolated portions of northeastern Wyoming and southeastern Montana. Faulkner (2010) also showed the Plumbeous Vireo breeding in Wyoming in the south and in patches throughout the eastern parts of the state. The range maps proposed by Johnson (1995), based on genetic analyses, show the southern tip of the Sierra Nevada in California as the only likely area of sympatry. Johnson (1995) collected specimens from northeastern California where sources differ on the breeding ranges of these two species, and he identified those birds as Cassin's Vireos from genetic data. Sibley (2014) and Dunn and Alderfer (2017) showed no areas of sympatry between these species in Montana, but Marks et al. (2016) showed their ranges overlapping in portions of five Montana counties (Judith Basin, Meagher, Wheatland, Gallatin, and Park).

Much of this uncertainty may be due to the fact that Cassin's Vireos in faded spring and summer plumage can be quite pale (Heindel 1996, Heindel and Heindel 2004, Sibley 2014), making field identification of all individuals in this season problematic. Therefore, we analyzed song recordings from the known breeding ranges of each species to determine if one may use song to more consistently differentiate these species and to resolve some of these uncertainties about the breeding ranges.

METHODS

Recordings

We used recordings from the Macaulay Library (www.macaulaylibrary.org), and from www.xeno-canto.org that were made within each species' undisputed breeding range during the breeding season (Figure 1; Tables 1

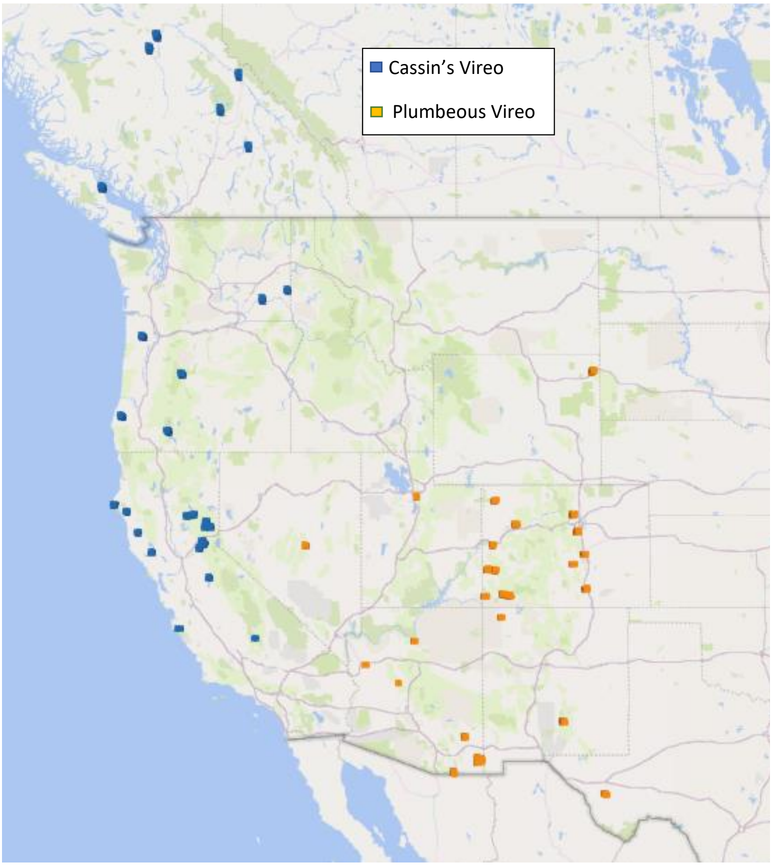

Figure 1. Locations of recordings analyzed for differences between the songs of the Cassin's and Plumbeous Vireos.

and 2), included at least eight consecutive phrases, and were of good quality (signal-to-noise ratio of approximately 5:1 or better). We also eliminated any recordings of songs elicited by a broadcast, which could have influenced the song given in response. For Cassin's Vireo, we used only recordings made between 15 April and 15 July. Because Cassin's Vireo migrates through much of the breeding range of the Plumbeous Vireo, and because both vireos are known to sing during migration (Pieplow 2019), we restricted the dates of Plumbeous Vireo recordings used to 15 May to 15 July. In total, our dataset included 64 songs, from 32 individuals of each species.

Spectrographic Analysis

We used the software Raven Pro 1.6 (Cornell Laboratory of Ornithology) to make spectrograms and to measure the characteristics of each song. We

Table 1 Metadata for Cassin's Vireo Recordings

Recording[a]	Latitude	Longitude	Date	Recordist
ML11895	46.865	−117.162	17 Jun	Stein, Robert
ML22925	36.397	−121.576	24 Apr	Fish, William
ML22929	40.017	−121.000	1 Jun	Fish, William
ML22956	38.920	−120.781	13 May	Fish, William
ML22957	39.431	−123.323	10 Jun	Fish, William
ML48865	39.586	−120.551	10 Jun	Moyer, David
ML67833	49.792	−125.001	20 May	Gunn, William
ML105665	43.086	−124.059	8 Jun	Keller, Geoffrey
ML105683	42.625	−122.116	10 Jun	Keller, Geoffrey
ML118826	40.315	−124.314	20 May	Keller, Geoffrey
ML118837	38.777	−122.743	21 May	Keller, Geoffrey
ML144046	39.776	−120.472	30 May	Little, Randolph
XC136030	36.313	−121.571	1 Jun	Sullivan, Brian
XC16529	45.491	−123.220	6 Jun	Jones, Don
XC16530	44.354	−121.549	8 Jun	Jones, Don
XC181413	40.101	−123.796	17 May	Cannizzaro, Eric
XC195840	52.821	−119.244	27 Jun	Webster, Richard
XC195911	51.900	−120.036	28 Jun	Webster, Richard
XC196045	50.899	−118.814	28 Jun	Webster, Richard
XC34873	46.595	−118.214	24 May	Brooks, Tayler
XC379329	35.968	−118.418	9 Jul	Benner. Lance
XC418150	53.517	−123.062	1 Jun	Dyck, Jeff
XC477500	53.867	−122.757	28 May	Bradley, David
XC497904	39.588	−120.292	16 May	Pandolfino, Ed
XC497906	39.087	−120.589	11 May	Pandolfino, Ed
XC497907	39.059	−120.572	27 May	Pandolfino, Ed
XC497913	39.165	−120.660	26 Jun	Pandolfino, Ed
XC497915	39.178	−120.644	26 Jun	Pandolfino, Ed
XC497917	39.689	−120.473	14 Jun	Pandolfino, Ed
XC497933	39.087	−120.597	27 May	Pandolfino, Ed
XC59027	39.943	−121.312	30 May	Owens, Luke
XC76908	37.977	−120.373	16 Apr	Fisher, Stuart

[a]Each recording represents one individual. ML, Macaulay Laboratory; XC, Xeno-canto.

chose to measure phrase length, song rate (number of phrases per minute), proportion of phrases that included frequency modulation ("buzziness"), proportion of phrases that were doubled (a phrase composed of two distinct parts with a very short pause in between; Figure 2), and average frequency at the midpoint of each phrase. Following the method of James (1981), we defined the midpoint frequency as the frequency halfway between the highest and lowest frequencies of a phrase, ignoring harmonics when present (Figure 3). For this, we used the selection box tool in Raven Pro 1.6 to determine the high and low frequencies of each phrase, then calculated the midpoint frequency as [(high – low)/2] + low. We then averaged the midpoints of each phrase to obtain a mean midpoint frequency for each recording. To avoid bias in making these measurements, we coded all songs before analysis so that the location of the recording was unknown during analysis.

Table 2 Metadata for Plumbeous Vireo Recordings

Recording[a]	Latitude	Longitude	Date	Recordist
ML11900	39.457	−105.105	22 Jun	Davis, L. Irby
ML11901	33.169	−105.781	25 May	Allen, Arthur
ML11905	35.085	−113.889	18 May	Stein, Robert
ML25178	31.863	−109.199	16 Jun	Barker, Harriette
ML40616	31.914	−109.319	1 Jun	Keller, Geoffrey
ML50222	37.441	−108.242	7 Jun	Keller, Geoffrey
ML109026	31.417	−110.274	19 May	Keller, Geoffrey
ML131237	30.692	−104.124	29 May	Andersen, Michael
ML186615	37.383	−107.926	16 Jun	Pieplow, Nathan
ML188813	40.450	−108.523	21 May	McGuire, Bob
ML202863	35.897	−111.875	14 Jun	Robbins, Mark
ML203254	31.429	−110.289	23 Jun	Robbins, Mark
ML203282	31.784	−109.304	25 Jun	Robbins, Mark
XC104898	39.029	−108.630	15 Jun	DeFonso, Eric
XC109269	39.701	−107.668	31 May	Spencer, Andrew
XC13651	38.219	−108.520	29 May	Spencer, Andrew
XC139887	44.463	−104.392	26 May	Leite, Gabriel
XC14274	31.885	−109.176	7 Jul	Parrish, Chris
XC179453	34.486	−112.553	24 May	Riegner, Micah
XC184593	40.573	−111.775	30 Jun	Avery, Tim
XC205477	38.241	−108.843	23 May	DeFonso, Eric
XC205865	37.363	−108.952	31 May	DeFonso, Eric
XC21768	31.905	−109.280	14 Jul	Parrish, Chris
XC323425	31.872	−109.235	11 Jun	Webster, Richard
XC324861	40.003	−105.288	26 Jun	Floyd, Ted
XC325471	37.601	−104.785	13 Jun	Riffe, Sue
XC372339	40.009	−105.286	27 May	Floyd, Ted
XC374081	38.729	−104.840	2 Jun	Wistrand, Matt
XC481057	39.012	−116.378	10 Jun	Wilcox, Bobby
XC48193	32.650	−109.817	7 Jun	Olmstead, Scott
XC5564	36.669	−108.305	23 Jun	Jones, Don
XC5565	38.408	−105.317	26 Jun	Jones, Don

[a]Each recording represents one individual. ML, Macaulay Laboratory; XC, Xeno-canto.

Analytical Methods

Given the currently limited number of suitable recordings available from each species ($n = 32$ for each), we adopted a parametric approach to estimating intraspecific variation in song characteristics and overlap between species. We represented intraspecific variation with box plots, and modeled the potential for overlap between species under the assumption of normal (Gaussian) variation in song characteristics. We modeled the natural logarithm of the average midpoint frequency by using a normal distribution with mean and standard deviation μ_C and σ_C for Cassin's Vireo, μ_P and σ_P for the Plumbeous Vireo. We then used the parametric 95% confidence interval for each mean to estimate 95% confidence intervals on the proportion of individuals that would be identified correctly (true positives) and incorrectly (false positives) given any particular cutoff in average midpoint frequency that might be used as a threshold for distinguishing these two species. To determine how indi-

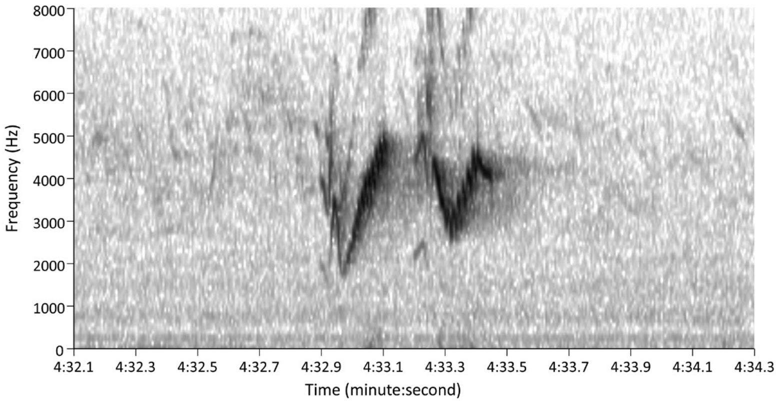

FIGURE 2. Example of a doubled phrase (Cassin's Vireo recorded in Monterey County, California, 24 April by William Fish; Macaulay Library 22925).

vidual recordings affected the optimal cutoff for species identification, and the number of individuals correctly identified, we used leave-one-out cross-validation. Specifically, we withheld each bird in turn from the estimation of the model's parameters (μ and σ), and used the resulting model to identify the species of the bird withheld. Finally, we used logistic regression to test whether the probability of correctly identifying an individual varied with the number of song phrases analyzed for that individual.

RESULTS

Of the characteristics we measured, phrase length, song rate, proportion of frequency-modulated phrases, and proportion of doubled phrases (Figure

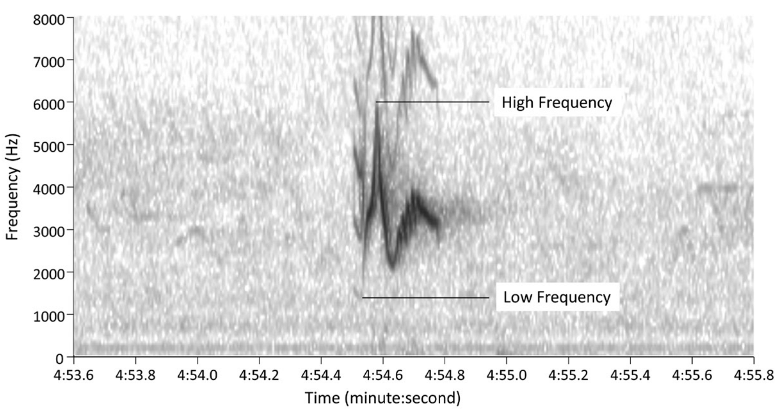

FIGURE 3. Example of determination of a midpoint frequency (Cassin's Vireo recorded in Monterey County, California, 24 April by William Fish; Macaulay Library 22925).

4a–d) in Cassin's and Plumbeous Vireo songs all overlapped broadly (Table 3). The average midpoint frequency of songs overlapped the least, with Cassin's Vireo songs being generally higher in frequency than Plumbeous Vireo songs (Figure 4e; Table 3). Of the first four characteristics, phrase length showed the least overlap; however, this was due to the greater incidence of doubled phrases in Cassin's songs (21 of 32, 66%), while Plumbeous Vireo songs more rarely included doubled phrases (8 of 32, 25%).

We suggest that many individual birds can be identified to species by means of a parametric model of the average midpoint frequency in each species (Figure 5), with varying trade-offs in utility and accuracy depending on the specific frequency chosen for identification purposes. For example, the average midpoint frequency for all Cassin's Vireo songs in our sample was >3000 Hz, or >8.01 on the log-transformed axis of Figure 5a, and a Gaussian curve fit to these data suggested that few Cassin's Vireos should be expected to sing songs with an average midpoint frequency <3000 Hz. If we were to classify every song with an average midpoint frequency >3000 Hz as the song of a Cassin's Vireo, we would achieve a high rate of true positive classifications for this species (0.99), but at the expense of an unfortunate rate of false positives (0.59), because more than half of the Plumbeous Vireos we sampled also sang songs with an average midpoint frequency >3000 Hz (Figure 5). Given our samples and modeling approach, the tradeoff between true and false positives for each species (Figure 6a) suggests that 3215 Hz is the optimal average midpoint frequency for maximizing the proportion of individuals (of both species) classified correctly (Figure 6b, Appendix at www.westernfieldornithologists.org/archive/V51/Pandolfino-Ray-vireos).

With 3215 Hz as the cutoff, our model categorizes over 84% of Cassin's Vireos (95% CI = 74–91%) and 84% of Plumbeous Vireos (75–91%) correctly, leaving 16% of Cassin's Vireos (9–25%) classified incorrectly as Plumbeous Vireos and 16% of Plumbeous Vireos (9–26%) classified incorrectly as Cassin's Vireos. Table 4 shows how the expected (mean) fraction of true and false positives varies for each species when different threshold frequencies are selected, and the Appendix offers an extended tabulation of these means and their 95% confidence intervals (which illustrate how thresholds correspond to the fraction correctly identified). Leave-one-out cross-validation resulted in a similar optimum cutoff frequency (mean = 3215, range 3205–3225) and classification success (84% of Cassin's Vireos and 78% of Plumbeous Vireos

Table 3 Comparison of Characteristics of Songs of the Cassin's and Plumbeous Vireos[a]

	Cassin's		Plumbeous	
Character	Mean	StDev	Mean	StDev
Phrase length (sec)	0.36	0.05	0.31	0.03
Song rate (phrases/min)	33	10	28	6
Frequency-modulated phrases	63%	17%	52%	19%
Doubled phrases	12%	14%	3%	5%
Midpoint frequency (Hz)	3404	185	3045	173

[a]n = 32 for each species.

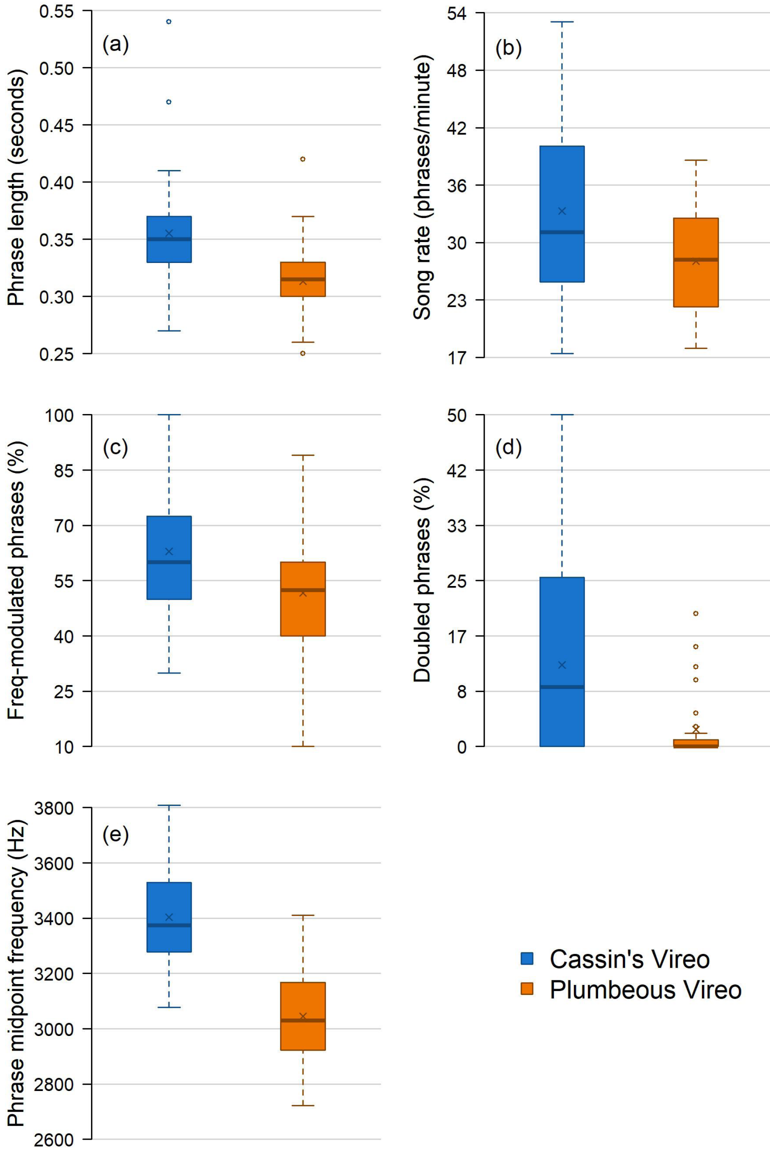

FIGURE 4. Box plots comparing characteristics of the songs of the Cassin's and Plumbeous Vireos. (a) Phrase length, (b) song rate, (c) percent of phrases frequency modulated (buzzy), (d) percent of phrases doubled, (e) average of midpoint between highest and lowest frequency of phrases. Boxes, interquartile range; black line within boxes, median; whiskers, 3× interquartile range; circles, outlying values.

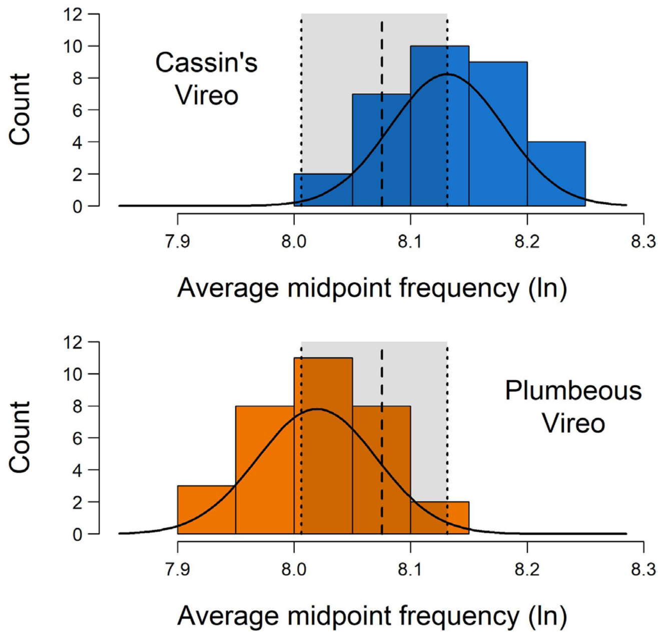

FIGURE 5. Variation in the average midpoint frequency of songs of Cassin's and Plumbeous Vireos, shown as observed (histograms) and as modeled (curves). Vertical dashed lines indicate the natural logarithm (ln) of 3215 Hz, the value for midpoint frequency cutoff that maximizes true positive identifications across both species. Vertical dotted lines indicate ln(3000) and ln(3400) Hz, used to exemplify dual cutoffs that increase true positive identifications for one or the other species (see text), at the expense of leaving a large proportion of individuals of each species unidentified (shaded regions).

were correctly identified under this model). In our logistic regression of true positive classifications, the success of categorization was not related to the number of song phrases analyzed per individual (df = 62; p = 0.635). The average difference between the two species was consistent regardless of the number of phrases analyzed (Figure 7). It is possible that using samples with a very large number of consecutive phrases (>50) might produce a higher rate of successful classification, but we had too few samples in that range to draw a firm conclusion.

Two thresholds could be employed to reduce the proportion of misclassified birds, at the expense of leaving unidentified the birds with average midpoint frequencies that lie between the two values. For example, we could classify all birds with average midpoint frequencies <3000 Hz as Plumbeous Vireos, and all those with average midpoint frequencies >3400 Hz (>8.13 on the log-transformed axis of Figure 5a) as Cassin's Vireos. With these values as thresholds, about 43% of Plumbeous Vireos would be identified, including about 41% true positives (below the 3000-Hz threshold) and about 2% falsely

Table 4 Expected Probability of Correct (True Positive) or Incorrect (False Positive) Identifications of the Plumbeous and Cassin's Vireos with Various Thresholds of Phrase-Midpoint Frequency in Songs[a]

	Fraction below threshold identified as Plumbeous		Fraction above threshold identified as Cassin's	
Threshold frequency (Hz)	True positive	False positive	True positive	False positive
3000	0.406	0.01	0.99	0.594
3020	0.452	0.014	0.986	0.548
3040	0.498	0.02	0.98	0.502
3060	0.544	0.026	0.974	0.456
3080	0.59	0.034	0.966	0.41
3100	0.634	0.044	0.956	0.366
3120	0.676	0.056	0.944	0.324
3140	0.714	0.07	0.93	0.286
3160	0.752	0.088	0.912	0.248
3180	0.786	0.108	0.892	0.214
3200	0.816	0.132	0.868	0.184
3220	0.844	0.158	0.842	0.156
3240	0.868	0.188	0.812	0.132
3260	0.89	0.22	0.78	0.11
3280	0.91	0.254	0.746	0.09
3300	0.926	0.292	0.708	0.074
3320	0.94	0.332	0.668	0.06
3340	0.952	0.372	0.628	0.048
3360	0.96	0.416	0.584	0.04
3380	0.97	0.458	0.542	0.03
3400	0.976	0.502	0.498	0.024

[a]See Appendix at archive.westernfieldornithologists.org/V51/Pandolfino-Ray for additional values, 95% confidence intervals, and values with the two species considered simultaneously.

identified as Cassin's Vireo (above the 3400-Hz threshold), leaving about 57% of Plumbeous Vireos not identified at all (Figure 5, Appendix). Similarly, about 51% of Cassin's Vireos would be identified, including about 50% true positives (above the 3400-Hz threshold) and about 1% falsely identified as the Plumbeous Vireo (below the 3000-Hz threshold), leaving 49% of Cassin's Vireos unidentified (Figure 5, Appendix). If one raises the threshold for Plumbeous or lowers the threshold for Cassin's, more birds will be identified, but at the cost of higher rates of misidentification. To ensure that at least 95% of all birds identified as Plumbeous Vireos are true positives, there must be no more than 5% false positives. In this case, our analysis suggests a midpoint frequency cutoff of 3050 Hz (Appendix), which results in fewer than 5% (95% CI = 1.0–4.8%) false identifications of Cassin's Vireos as Plumbeous Vireos. To ensure 90% or 99% true positives for the Plumbeous Vireo, our analysis suggests cutoffs of 3110 or 2940 Hz, respectively (Appendix). To ensure 90%, 95%, or 99% true positives for Cassin's Vireo, our analysis suggests cutoffs of 3340, 3410, or 3540 Hz, respectively (Appendix).

DISCUSSION

Whenever a single historical species is broken up, issues of range limits and identification of birds out of range become more consequential to birders and to ornithologists. When the species are easily differentiated in the field visually or through vocalizations, resolving range limits and identifying wayward birds is usually straightforward. In the case of the Solitary Vireo complex, the three species can be differentiated visually in the field when in relatively fresh plumage. However, distinguishing the Blue-headed from Cassin's or Cassin's from the Plumbeous can be difficult when the birds are in faded spring/summer plumage (Heindel 1996, Heindel and Heindel 2004, Sibley 2014). Heindel (1996) noted that, regardless of plumage wear, normal individual variation and the quality of light during observation renders field identification of some birds impossible.

In many field identification challenges (e.g., *Empidonax* flycatchers), vocalizations are helpful. In the case of this vireo complex, some sources suggest that a slower rate of song delivery and fewer frequency-modulated (buzzy) phrases allow the Blue-headed to be distinguished from the other two species (James 1981, Heindel and Heindel 2004, Sibley 2014, Dunn and Alderfer 2017, Pieplow 2017). Distinguishing Cassin's from the Plumbeous Vireo by song is considered more difficult, but some authors have suggested that the song's frequency and/or the proportion of buzzy phrases may be useful (James 1981, Sibley 2014, www.allaboutbirds.org/guide/Cassins_Vireo/sounds). However, only James (1981) showed any data, and those data were based on very few samples. Indeed, Floyd (2008), Dunn and Alderfer (2017), and Pieplow (2019) cautioned that differences in song may not be useful for differentiation between those species.

From the average midpoint frequency most of these vireos can be identified as the correct species. However, the broad overlap in midpoint frequency means that one must weigh various factors in choosing the criteria for identification. If one wants to identify Cassin's Vireos confidently from a sample of unknowns, one should use a higher frequency as the threshold (3410 Hz for at least 95% true positives), though it will leave more birds unidentified. Conversely, a lower threshold is appropriate if the goal is to confirm Plumbeous Vireos (3050 Hz for at least 95% true positives). Given a clear recording of several consecutive song phrases, the Appendix at https://archive.westernfieldornithologists.org/archive/V51/Pandolfino-Ray-vireos can be used to quantify confidence in species identity.

Sampling songs from the regions where there is uncertainty about the occurrence of these species might allow one to resolve these range issues. However, analyses of these songs may be equivocal if the two taxa are sympatric in these areas. Exposure of birds of one species to the song of the other during their song-learning period may result in songs whose midpoint frequency differs from that found outside the zone of sympatry. Also, such areas may produce some hybrid individuals that could also make the data difficult to interpret. Ideally, such studies would couple recording of song with visual identification of the individual through photographs and/or collection of specimens.

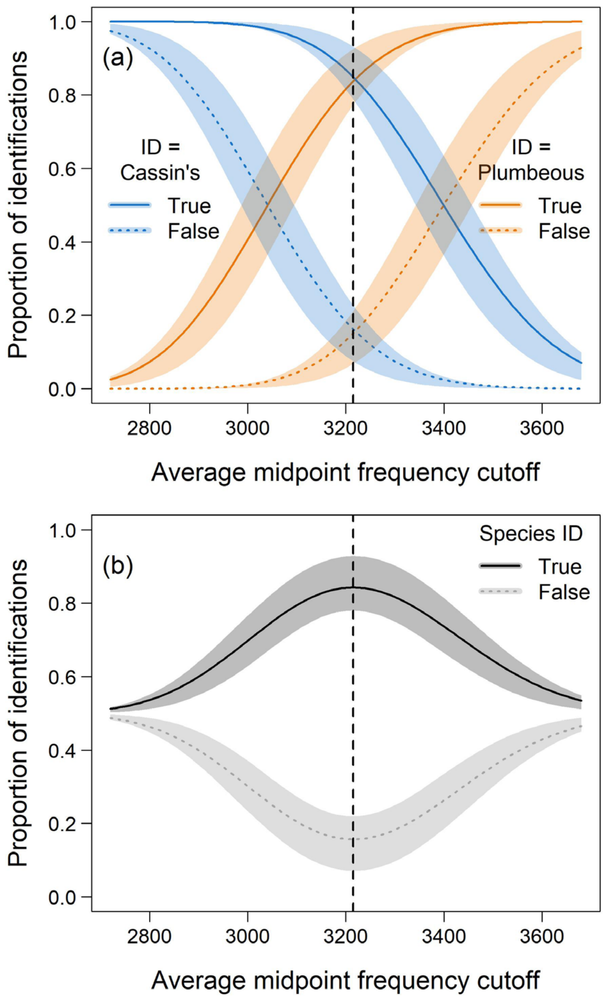

FIGURE 6. (a) Proportion of species identifications expected to be correct (true positive, solid lines) and incorrect (false negative, dotted lines) given the models in Figure 5 and a range of potential thresholds in average frequency that might be used to distinguish between the Cassin's and Plumbeous Vireos. (b) Proportion of all identifications expected to be correct (solid line) or incorrect (dotted line) on the basis of these models. Shaded regions represent parametric 95% confidence intervals, and the dashed vertical lines represent the optimal cutoff frequency (~3215 Hz) for distinguishing Cassin's from Plumbeous Vireos on the basis of the songs sampled.

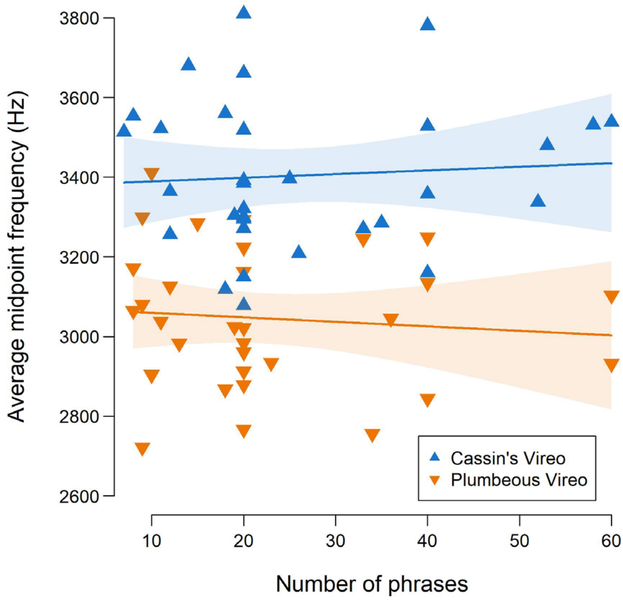

Figure 7. Linear regressions (and 95% confidence intervals) of the average midpoint frequency on the number of song phrases used to estimate average midpoint frequency, for Cassin's Vireo (blue upright triangles) and Plumbeous Vireo (orange inverted triangles).

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