VARIABILITY IN COMMON CALL NOTES OF THE WINTER AND PACIFIC WRENS

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ABSTRACT: We analyzed 175 calls of 91 individual Winter (*Troglodytes hiemalis*) and Pacific (*Troglodytes pacificus*) wrens by measuring characteristics such as peak frequency, frequency range, and complexity. We found considerable overlap in most measurements, but metrics such as peak frequency and trace shape are useful for distinguishing the two species. With these results, we recommend a standard for acceptance of extralimital Winter and Pacific wrens through evaluation of spectrograms quantifying the call's peak frequency (higher in the Pacific, lower in the Winter), the shape and symmetry of the trace at the lowest frequency (more symmetrical in the Winter), and whether the lowest-frequency trace is tightly coupled with a second trace (favoring the Pacific).

In 2010, on the basis of genetic data and bioacoustics, Chesser et al. (2010) reclassified the Winter Wren (*Troglodytes hiemalis*) and Pacific Wren (*T. pacificus*) as species, splitting them from what is now known as the Eurasian Wren (*Troglodytes troglodytes*). Differences in song between the two North American taxa aligned closely with genetically distinct clades and were important in establishing that the two represent distinct species. Thus differences in song between the two taxa have been well described (Kroodsma 1980, Toews and Irwin 2008). Many authors have noted average differences between the two species' calls, particularly the call commonly transcribed as "chimp" or doubled as "chimp-chimp" (Ellison 1994:254). But none has studied the differences systematically or thoroughly explored variation in each species' calls (e.g., Pieplow 2009, Leukering and Pieplow 2010, Hejl et al. 2020), despite this call's often being regarded as the most distinctive difference between the two species (e.g., Sibley 2010).

Calls of the Pacific and Winter wrens are presumably innate (Hejl et al. 2020); therefore, in addition to being among the most distinctive differences between the two species, at their most typical, calls are likely the most valuable identification criteria. Toews et al. (2025) presumed these wrens' song to be learned, and patterns of juveniles' dispersal and song learning are unknown or unpublished, making it conceivable that a Pacific or Winter wren could sing a heterospecific song. Yet, troublingly, since 2010 some wrens in western North America and especially in California have been heard giving calls ambiguous by currently published descriptions (e.g., Benson et al. 2025). Because of this, together with known limited hybridization between the two species (Toews and Irwin 2008, Mikkelsen and Irwin 2021), a better understanding of the range of variation possible in the calls of each species will be invaluable. Here we examine the commonly given call note of each species and establish its range of variation. We then provide guidelines for evaluation of extralimital records of each taxon by call.

METHODS

Definition of Terms

High-quality audiospectrograms of Pacific and Winter Wren calls look like vertical stacks of repeated shapes (see Figure 1). Each individual shape is called a "trace." The lowest-frequency trace of a Pacific or Winter Wren call is said to be at the fundamental frequency, and harmonics are whole-number multiples of that fundamental frequency. Because it is at the lowest frequency, and thus appears at the bottom of a spectrogram, we define and measure the fundamental frequency and traces closely clustered with it as the "bottom component." The bottom component is nested below an often longer trace or cluster of traces that includes the first harmonic (i.e., the trace at twice the frequency of the fundamental frequency). We refer to the first harmonic and any traces clustered with it as the "second component" (Figures 1, 2). Finally, if present and distinct, the first well-defined trace or cluster of traces above the second component we refer to as the "third component." Higher frequencies were often not resolvable, and we did not analyze any traces above the third component (Figure 1). We merge individual traces of the second and third harmonics into a single "component" when they are poorly defined, largely inseparable, and of similar shape. But we always refer to the often shorter, quieter trace(s) that cluster together below the second component as the bottom component, even if they are well defined and separate (Figure 1).

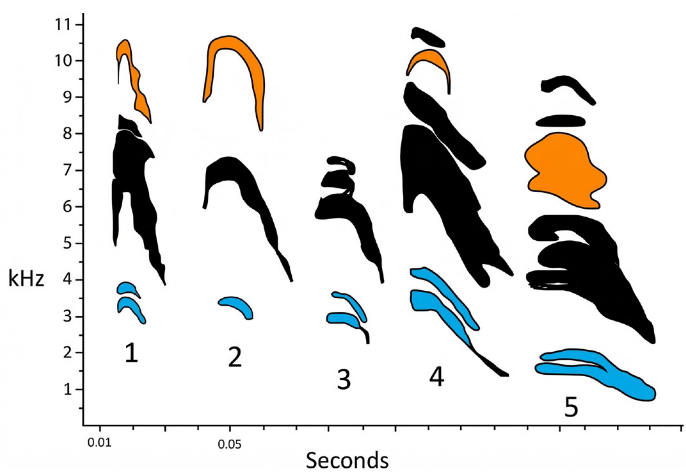

Figure 1. Variability in Pacific Wren calls. Blue, bottom components; orange, third components; black, second components and other unmeasured traces above the third component. From left to right: (1) typical-sounding Pacific Wren recorded in Sonoma Co., California (#29, Table 1); (2) typical-sounding Pacific Wren recorded in Idaho Co., Idaho, in the range of *T. p. salebrosus* (#37, Table 1); (3) presumed Pacific Wren recorded near Calgary, Alberta, near the contact zone (#26, Table 1); (4) typical-sounding Pacific Wren recorded in Cochise Co., Arizona (#20, Table 1); (5) atypical-sounding Pacific Wren recorded in Los Angeles Co., California (#1, Table 1).

Audio by Jim Holmes, Ethan Monk, J. Smith, Micah Riegner, and Lance A. M. Benner

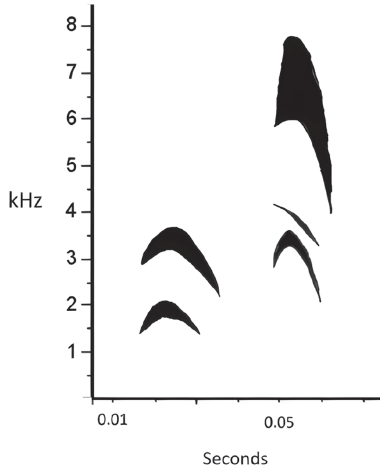

Figure 2. Representations of the bottom and second components of typical "check" or "chimp" calls of the Winter Wren (left) and Pacific Wren (right), drawn on the basis of the median measurements of 175 calls selected for our primary analysis to encompass a broad representation of the ranges of the two species.

Selection of Recordings

For this study, we used only recordings of the typical and commonly heard call, often transcribed as "check" or "chimp" and often doubled. While most such calls are short, clipped, emphatic, and brief, some are distinctly longer and have a wheezy quality. We excluded these wheezy calls from our analysis. Recordings were sourced from Xeno-Canto (https://www.xeno-canto.org), the Cornell Lab of Ornithology's Macaulay Library (https://www.macaulaylibrary.org), our own collections, and via personal communications (see Table 1). Our primary analysis encompassed 82 calls from 45 individual Pacific Wrens and 83 calls from 40 individual Winter Wrens. Recordings were selected with the goal of ensuring seasonal and geographic diversity and for general clarity. We did not include extralimital individuals in this analysis. Winter Wren recordings were selected with the goal of sampling throughout the geographic range of *T. h. hiemalis,* and Pacific Wren recordings aimed to sample across the geographic range of the "Pacific group" of subspecies (*sensu lato*, i.e., Pyle 2022). To compare Pacific Wrens from the western part of their range with Pacific Wrens from the northeastern, interior corner of their range, our primary analysis included recordings of 12 individuals made during the breeding season in the range Phillips (1986) assigned to *T. p. salebrosus* ("interior Pacific Wrens") in northeastern Oregon, Idaho, and Montana and of 16 individuals recorded during the breeding season in western British Columbia, western Washington, western Oregon, and northern California ("western Pacific Wrens"). We loosely defined the breeding season as May through August.

We then undertook a secondary analysis in an attempt to better understand variability within the calls of each species. This analysis used six calls from three Pacific Wrens and four calls from two Winter Wrens, found via personal communications and searching Xeno-Canto (see Table 1). These calls were not included in the primary analysis. These recordings were selected not to account for geographic or seasonal diversity but instead to represent individuals giving notably atypical calls. We inferred that the birds' identity was adequately established, usually because the same birds were also recorded giving calls more easily ascribable to either species by previously published descriptions. We concluded that most recordings of Pacific/Winter Wrens giving atypical calls were not safely assignable to species by previously published descriptions, limiting the size of the sample suitable for the secondary analysis. Also, the Pacific and Winter wrens hybridize to a limited extent (Toews and Irwin 2008, Mikkelsen and Irwin 2021), so a bird capable of giving relatively standard Pacific or Winter Wren calls in addition to more intermediate/ambiguous calls as included in the secondary analysis may not necessarily represent a Pacific Wren or Winter Wren as we have identified it. Instead, these birds may be best considered capable of producing Pacific Wren-like calls, or capable of producing Winter Wren-like calls.

The ranges of measurements reported in the primary analysis may be expanded significantly by the inclusion of results from the secondary analysis. These new measurement ranges provide a more comprehensive understanding of how Pacific and Winter wrens (assuming each bird in the secondary analysis is identified correctly) may sound.

For all audio, we did not distinguish between lossy (e.g., .mp3) and lossless (e.g., .wav) audio formats, despite the lower quality and loss of data with lossy audio (MacPhail et al. 2023). Our samples would have been much smaller if we had used only lossless audio.

Analysis of Recordings

We analyzed all recordings in Raven Pro 1.6.5 (Charif et al. 2010), measuring each call's duration (sec), lowest frequency (Hz), and peak frequency (the frequency at which call energy is highest/the spectrogram is darkest colored, in Hz). Within each call, for each well-resolvable component, we measured its lowest frequency, central frequency, highest frequency, peak frequency, duration, and peak power density (decibels relative to full scale [dBFS] per second), as defined by Charif et al. (2010). Additionally, if a bottom component consisted of multiple discrete traces, we measured these values for each trace. As a quality-control measure, we calculated the signal-to-noise ratio (dB) for the entire call. The signal-to-noise ratio measures the relative strength of a call against background noise. Recordings with low signal-to-noise ratios are more difficult to analyze, and the tails of traces often appear shortened, blending into the background. In other words, the signal-to-noise ratio provides a numerical measure of how distinct the call appears on a spectrogram.

To generate the values listed above, we annotated the entire call and well-resolvable individual components in Raven. That is, we drew selection boxes as tightly as possible around the call and individual components. In response to prompts, Raven then automatically calculated the values listed above for the various "boxed" regions.

Because individual traces and, correspondingly, what we term components can vary significantly in shape from bird to bird and often within a single call, to better quantify the components' shapes we assigned a number (a "shape score") to each (Figure 3). If the component reached its highest

Table 1 Audio Recordings Analyzed for Differences between and Variation within the Pacific and Winter Wrens

	Source[a]	State/ Province	County	Date	Recordist
Winter Wren					
1	XC344954	VA	Albemarle	2016 Dec 02	Ross Gallardy
2	XC 341249	DE	New Castle	2016 Oct 29	Ted Floyd
3	XC339641	IL	DuPage	2016 Oct 21	Matt Wistrand
4	XC208172	PA	Allegheny	2014 Dec 27	Ted Floyd
5	XC175234	MN	Goodhue	2014 Apr 18	Jonathon Jongsma
6	XC860389	NH	Hillsborough	2024 Jan 06	Molly Jacobson
7	XC5769	SC	Richland	2002 Mar 09	Robin Carter
8	XC62503	WI	Vilas	2010 Sep 10	Todd Wilson
9	XC71095	PA	Montgomery	2005 Oct 18	Paul Driver
10	XC71769	NM	Bernalillo	2011 Feb 20	Cole Wolf
11	XC92154	LA	Vermilion	2011 Dec 28	Daniel Lane
12	XC93786	TX	Camp	2012 Jan 29	L. G. Price
13	XC112578	QC	La-Haute-Côte-Nord	2012 Sep 01	Martin St-Michel
14	XC163933	VT	Windsor	2014 Jan 09	Kyle
15	XC171202	AZ	Yavapai	2014 Mar 23	Micah Riegner
16	XC202335	NE	Lincoln	2014 Nov 12	Brooks Rownd
17	XC207348	KS	Hodgeman	2014 Dec 21	Jeff Calhoun
18	XC207349	KS	Hodgeman	2014 Dec 21	Jeff Calhoun
19	XC211193	SC	Richland	2014 Nov 10	Paul Marvin
20	XC211197	SC	Richland	2014 Nov 10	Paul Marvin
21	XC216439	LA	Bossier	2013 Dec 01	Terry Davis
22	XC216450	LA	Caddo	2013 Dec 14	Terry Davis
23	XC251804	NM	Sandoval	2015 Jan 04	Nancy Hetrick
24	XC297043	TX	Kimble	2015 Dec 20	Eric Hough
25	XC321847	AZ	Cochise	2016 Jan 22	Richard E. Webster
26	XC348983	FL	Marianna	2016 Dec 16	Paul Marvin
27	XC357377	VA	Roanoke	2017 Mar 01	Thomas Gray
28	XC455125	KS	Sumner	2019 Feb 04	Ves
29	XC513215	VA	Fairfax	2019 Dec 23	Bobby Wilcox
30	ML170010011	ME	Sagadahoc	2019 Jul 26	Gordon Smith
31	ML364936531	ON	Nipissing	2021 Jun 28	Lisa Cancade Hackett
32	ML474975771	NS	Kings	2022 Aug 13	George Forsyth
33	ML622032554	QC	Les Basques	2024 Jul 31	Guillaume Perron
34	XC216440	LA	Bossier	2013 Dec 21	Terry Davis
35[b]	ML123931581	TX	Harris	2018 Nov 17	Cin-Ty Lee
35[b]	Pers. comm.	TX	Harris	2018 Nov 17	Cin-Ty Lee
36	XC260207	ON	Haliburton	2015 Jul 14	Iain
37	XC190106	BC	Peace River	2014 Jun 18	Richard E. Webster
38	ML638862606	QC	Kamouraska	2025 Jun 27	Jean-Daniel Fiset
39	ML635305759	PA	Chester	2024 Dec 14	Barry Blust
40	ML634552130	NY	Monroe	2025 Apr 20	Chris Wood
41	ML631410005	VT	Bennington	2025 Feb 26	Eric Seyferth
42	ML623106559	ME	Hancock	2024 Aug 30	Scott Dresser
43	ML584728801	VT	Rutland	2023 Jun 14	Joel Tilley
44	ML471513861	NY	Tompkins	2022 Jul 31	Andrew Spencer

(*continued*)

	Source[a]	State/ Province	County	Date	Recordist
Pacific Wren					
1[b]	XC610353	CA	Los Angeles	2020 Dec 19	Lance A. M. Benner
2[b]	Pers. comm.	CA	Los Angeles	2021 Jan 20	Naresh Satyan
3	XC354539	NM	Eddy	2017 Feb 03	Matt Baumann
4	XC401689	CA	Los Angeles	2018 Feb 03	Lance A. M. Benner
5[b]	XC154689	CA	Los Angeles	2013 Nov 17	Lance A. M. Benner
6	XC490933	WA	King	2018 Jul 25	Steve Hampton
7	XC550930	WA	King	2020 Apr 19	Bruce Lagerquist
8	XC602829	WA	San Juan	2020 Aug 13	Steve Hampton
9	XC602839	WA	San Juan	2020 Aug 16	Steve Hampton
10	XC706135	BC	Victoria	2022 Mar 04	Barry Edmonston
11	XC162163	WA	Spokane	2013 Dec 31	Garrett MacDonald
12	XC163178	OR	Tillamook	2013 Feb 08	Paul Marvin
13	XC201358	WA	Thurston	2014 Oct 31	Micah Riegner
14	XC349619	MT	Missoula	2016 Mar 04	Thomas Magarian
15	XC363871	CA	Humboldt	2017 Jan 27	Paul Marvin
16	XC419952	CA	Santa Cruz	2018 Jun 09	Thomas G. Graves
17	XC422034	BC	Fraser-Fort George	2018 Jun 23	Jeff Dyck
18	XC630096	CA	Yolo	2021 Feb 04	Steve Hampton
19	XC76204	WA	King	2011 Apr 20	Andrew Spencer
20	XC112411	AZ	Cochise	2012 Nov 04	Micah Riegner
21	XC156281	AZ	Cochise	2013 Nov 30	Micah Riegner
22	XC934084	BC	Fraser Valley	2024 Sep 15	Justin Flint
23	ML66274581	ID	Ada	2017 Aug 11	Jason Talbot
24	ML345780231	ID	Kootenai	2021 May 30	Andrew Emlen
25	ML612734147	MT	Glacier	2021 Jul 17	Marky Mutchler
26	ML633747631	AB	Calgary	2025 Apr 14	J. Smith
27	ML634315119	MT	Missoula	2025 Apr 23	Shane Slater
28	ML171177901	CA	Sonoma	2019 Aug 01	Teresa & Miles Tuffli
29	ML157910701	CA	Sonoma	2019 May 10	Jim Holmes
30	ML466771301	OR	Tillamook	2022 Jul 22	Cliff Cordy
31	ML170859781	OR	Benton	2019 Jul 24	Bob Nieman
32	Pers. recording	ID	Idaho	2025 Jun 22	Ethan Monk
33[c]	Pers. recording	ID	Idaho	2025 Jun 22	Ethan Monk
34	Pers. recording	OR	Wallowa	2025 Jun 19	Ethan Monk
35	Pers. recording	OR	Wallowa	2025 Jun 19	Ethan Monk
36	Pers. recording	OR	Wallowa	2025 Jun 19	Ethan Monk
37	Pers. recording	ID	Idaho	2025 Jun 22	Ethan Monk
38	Pers. recording	MT	Sanders	2025 Jun 28	Ethan Monk
39	ML635562395	OR	Tillamook	2025 May 06	Jeff Bleam
40	ML637344112	CA	Sierra	2025 Jun 06	Skyler Bol
41	ML638211639	BC	Comox-Strathcona	2025 Jun 28	Daniel Donnecke
42	ML639387282	WA	Clark	2025 Jun 25	Isaac Lang
43	ML639398447	WA	Clallam	2025 Jul 19	Gregory Irving
44	ML32400541	WA	San Juan	2016 Aug 11	Dave Slager
45	ML409291201	WA	Island	2016 Aug 02	Aidan Place
46	ML65621101	OR	Polk	1995 May 31	Gregory Budney
47	ML638781212	CA	Sonoma	2020 Sep 18	Colin Meusel

[a]XC, https://xeno-canto.org; ML, https://www.macaulaylibrary.org/.

[b]Recording contains atypical calls used only in the secondary analysis of intraspecific variation.

[c]Recording contains calls of two individuals.

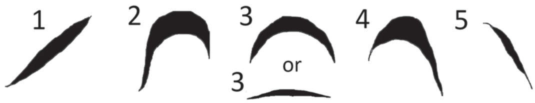

Figure 3. Scale from 1 to 5 of scores describing the shapes of traces within spectrograms of calls of the Pacific and Winter Wrens.

frequency at its end point, and its frequency was lowest at the beginning, so its shape resembled a forward slash ("/"), we assigned it a shape score of 1. If a component's beginning and end were at the same frequency (i.e., its shape resembled "∩" or "—"), we scored it as 3. If the component's frequency was highest at its beginning and its lowest at its end, so that its shape resembled a backslash ("\"), we scored it as 5. Intermediate shapes were assigned intermediate values accordingly. For the bottom and second components, we also measured the interval from the trace's beginning to the point of highest frequency ("left-time") and the interval from the point of highest frequency to the trace's end ("right-time"). Note that the distance and quality of a recording can affect the appearance of the shape of a trace, especially as these values are measured from the very leftmost and rightmost ends of each trace.

To account for hidden complexity, i.e., individual, non-discrete traces subsumed within the components, we counted the number of well-defined rightmost points on the spectrogram of each call (see Figure 4). Additionally, we measured the range of frequencies spanned by the bottom and second components at the time they reach their highest frequency ("height"). This

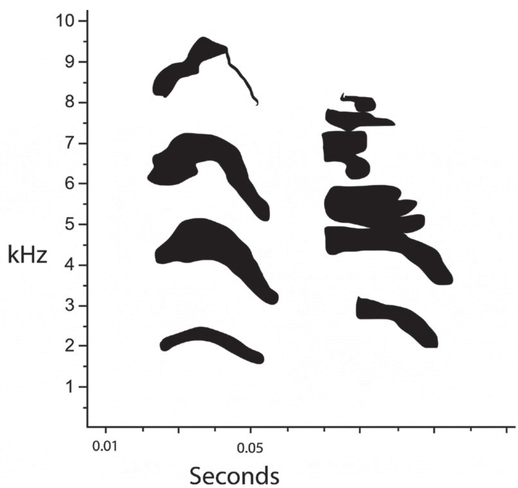

Figure 4. Representations of two calls made by a wren at the University of California, Riverside, Riverside County, California. Peak frequencies of 4875.0 (left; ML509689271) and 6843.8 Hz (right; ML510579921). These calls would be assessed as having four and nine rightmost points, respectively. For a photograph of the bird, see Figure 5 in Freeland et al. (2026).

Audio by Curtis Marantz (left) and Christine Dean (right) was done by measuring from the point of highest frequency in the component down vertically to the point at which the line of measurement exits the component. Height is equal to the hertz spanned by the vertical line.

Statistical Methods

Basic summary statistics were calculated for all measurements. We used the median and interquartile range (IQR) as measures of average and spread, preferring these to the mean and standard deviation because they are more resistant to the influence of outliers. In the evaluation of interspecific differences, we used two-tailed, two-sample *t*-tests to assess whether measurements differed significantly and imported all measurements into Past5 (Hammer 2025). In Past5, using all measurements, we ran a principal component analysis (PCA) with correlative matrices and iterative imputation, and otherwise represented various data graphically to inspect them for difference visually. PCA is a technique that mathematically simplifies large datasets into simpler variables. By plotting the two most informative of these (PC1 and PC2), we can more easily inspect the data for differences. Additional graphic representations, primarily box and whisker plots, we generated in Microsoft Excel. We looked particularly for measurements with a median value outside the range of the same measurement in the other species.

RESULTS

Primary Analysis: Interspecific Differences

Measurements of Winter and Pacific wren calls are reported in Tables 2 and 3. Pacific and Winter Wren calls in their entireties were found to differ significantly ($p < 0.01$) in duration, lowest frequency, and peak frequency. In the bottom component, Pacific and Winter Wren calls differed significantly in lowest frequency, central frequency, highest frequency, peak frequency, and duration. In the second component, the two species differed significantly in all recorded measurements except central frequency. In the third component,

Table 2 Quantification and Comparison of Entire Calls of the Pacific and Winter Wrens

	Winter Wren				Pacific Wren			
	Median	Interquartile range	Min	Max	Median	Interquartile range	Min	Max
Lowest frequency (Hz)	1289.8	226	670.2	2646	2117.6	711.4	1128.8	3069.1
Peak frequency (Hz)	3750.0	485.7	2718.8	6546.1	6890.6	665.0	4593.75	8062.5
Duration (sec)	0.049	0.010	0.026	0.083	0.034	0.008	0.020	0.050
Shape score[a]	2.7	0.4	1.9	4	4.4	0.5	3.3	5

[a]A representation of the shape of the call's traces; lower values represent a rising pitch, intermediate a peaking or flat pitch, and higher values a falling pitch. These values, summarizing the entire call, are averages of numbers assigned to individual traces within the call; see Methods.

Table 3 Quantification and Comparison of the Components[a] of Pacific and Winter Wren Calls

	Winter Wren			Pacific Wren		
	Bottom component	Second component	Third component	Bottom component	Second component	Third component
Lowest frequency (Hz)						
Median (IQR[b])	1283.7 (255.7)	2088.1 (467.6)	4013.9 (502.3)	2114.8 (723.6)	3991.0 (695.1)	8066.7 (1417.8)
Min, max	670.2, 1587.6	1629.2, 2946.7	2266.7, 4768.8	1128.6, 3069.1	2116.8, 8921.3	6192.7, 10013.6
Highest frequency (Hz)						
Median (IQR)	2036.5 (200.5)	3880.1 (430.9)	5639.8 (529.6)	4071.2 (578.3)	7957.0 (1189.7)	10240 (2275.6)
Min, max	1651.8, 2504.5	2320, 4615.8	4320, 6497.4	2678.4, 7731.8	4756.9, 10740.5	7178.2, 11535.2
Central frequency (Hz)						
Median (IQR)	1781.3 (187.5)	3562.5 (344.5)	5081.8 (618.9)	3421.9 (340.1)	6804.5 (430.1)	8957.8 (1808.8)
Min, max	1406.25, 2153.3	1875, 4218.8	3703.71, 5770.9	2203.1, 4921.9	4312, 9843.8	6718.359, 10680.5
Peak frequency (Hz)						
Median (IQR)	1781.3 (187.5)	3656.3 (344.5)	5081.8 (667.2)	3281.3 (258.4)	6890.6 (870.6)	9302.3 (2153.3)
Min, max	1406.3, 2153.3	1968.8, 4218.8	3703.7, 6000	2156.3, 3750	4593.8, 9937.5	6546.1, 10875
Duration (sec)						
Median (IQR)	0.035 (0.013)	0.045 (0.016)	0.038 (0.019)	0.023 (0.013)	0.031 (0.007)	0.018 (0.006)
Min, max	0.014, 0.059	0.024, 0.081	0.015, 0.067	0.007, 0.069	0.015, 0.050	0.009, 0.032
Shape score[c]						
Median (IQR)	3.0(0.6)	3.8(0.4)	2.3(0.9)	4.3 (0.7)	4.4 (0.5)	4.2 (0.8)
Min, max	1, 4	3, 4	1, 4	3, 5	3, 5	3, 5
Left-time[d] (sec)						
Median (IQR)	0.013 (0.006)	0.017 (0.007)		0.006 (0.003)	0.007 (0.004)	
Min, max	0.006, 0.029	0.007, 0.027		0.0003, 0.023	0.0003, 0.012	
Right-time[e] (sec)						
Median (IQR)	0.016 (0.010)	0.025 (0.012)		0.019 (0.012)	0.023 (0.008)	
Min, max	0.007, 0.041	0.013, 0.059		0.004, 0.037	0.014, 0.036	
Height (Hz)						
Median (IQR)	332.7 (219.2)	581.4 (468)		1009.5 (485.9)	2035.2 (1494.2)	
Min, max	65.3, 1968.6	219.8, 1587.6		295.1, 1683.9	417.3, 3470.6	

[a]Defined as individual traces that are poorly defined and of similar shape, so that they appear to cluster tightly; see Methods.

[b]IQR, interquartile range.

[c]On a scale of 1 to 5, a value of 1 represents an ascending contour, a value of 5 represents a descending contour; see Methods, Figure 3.

[d]"Left-time," the interval from the trace's beginning to its point of highest frequency.

[e]"Right-time," the interval from the point of the trace's highest frequency to its end.

they differed significantly in all measures except lowest frequency. With respect to the shape of the components, the bottom and second components in each species differed significantly from those of the other in left-time but not right-time measurements, and the calls overall differed significantly in their average shape scores.

In all three components, bottom, second, and third, the ranges of central and peak frequency of the two species' calls did not overlap (Figure 5), but all other measurements did. Most overlapping measurements had medians that fell outside the range of the same measurement in the other species. The exceptions were the entire call's lowest frequency, entire call's duration, bottom component's lowest frequency (in the Winter Wren only), bottom component's duration, second component's duration, third component's duration (Pacific Wren only), bottom component's left-time (Pacific Wren only), and height of the second component (Pacific Wren only). In the PCA generated in Past5 with these data the Pacific and Winter wrens clustered largely separately (see Figure 6).

Various measures showed the calls of the Pacific Wren to be more complex on average than those of the Winter Wren, despite superficially appearing less complex. In other words, there are possibly more and/or denser traces within the call of the Pacific Wren. The number of individual traces within each call, estimated by the number of distinct right points, averaged five for both species, whereas the number of right points in the bottom and second components was two (IQR = 0) for the Winter Wren and four (IQR = 1) for the Pacific Wren (Figures 1, 7). Most revealingly, 38 of 40 Winter Wrens included in the primary analysis showed a single trace in the bottom com-

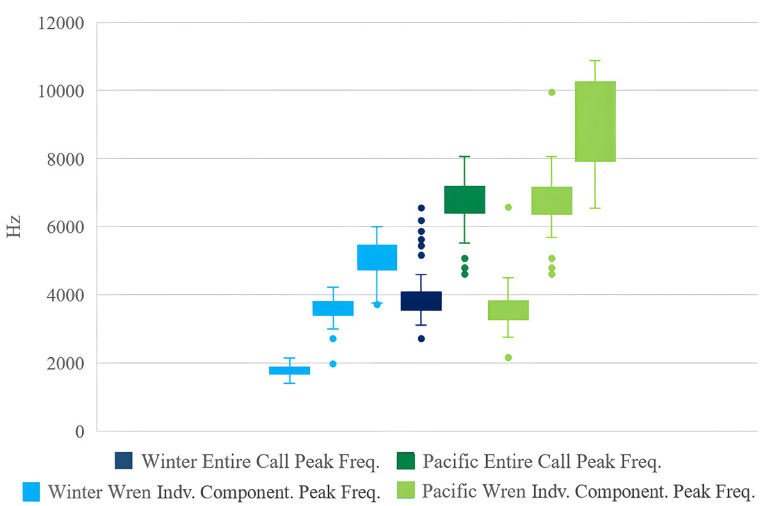

Figure 5. Peak frequencies of all measured components (bottom, second, and third, respectively) and entire call in the Pacific and Winter wrens, from our primary analysis of 175 calls selected to encompass a broad representation of the ranges of the two species.

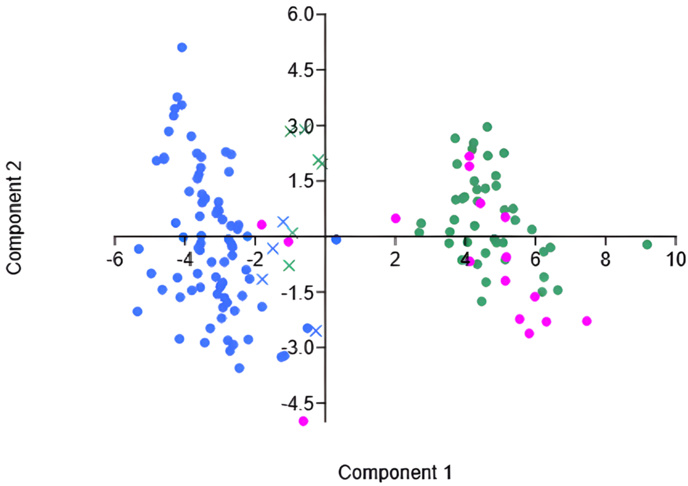

Figure 6. Principal-component analysis of all Winter (blue) and Pacific Wren calls (green, western or coastal segment of range; pink, interior segment of range) analyzed, including the 10 atypical calls selected for our secondary analysis. Dots are calls included in the primary analysis of 175 calls selected to encompass the range of both species, while crosses are from the secondary analysis of 10 additional calls selected to include atypical variants. Principal component 1 is driven primarily by frequency-based quantities such as entire call low and peak frequency; loadings for temporal variables are strongly negative. Contrastingly, principal component 2 is driven primarily by temporal variables, with duration and right-time particularly heavily loaded. Because the methods for selecting the recordings in primary and secondary analyses differed, calls marked with crosses are significantly overrepresented in this principal-components analysis.

ponent, whereas only 10 of 45 Pacific Wrens did: most Pacific Wrens instead showed two traces in the bottom component (Figures 1, 2). In Pacific Wren calls with two traces in the bottom component, the median peak frequency and average shape score for the lower trace were 3281 (IQR = 258) and 4.3, respectively; for the upper trace, 3816 (IQR = 605) and 4.5.

Among the Pacific Wren calls showing a single trace in the bottom component, nine of ten were recorded in the breeding season (May 30–July 19). Seven of ten were from the interior section of the species' range, and only one of these seven was recorded outside of the breeding season.

Although our sample is small, the calls of western and interior Pacific Wrens might differ in several other ways. A measurement of complexity, the number of rightmost points, was 6 (IQR = 3.25) for breeding western Pacific Wrens and 4 (1.25) for breeding interior Pacific Wrens. The number of rightmost points in the bottom and second components combined was 4 (2.25) for breeding western Pacific Wrens and 2.5 (1) for breeding interior Pacific Wrens, whereas it was 4 (1) and 2 (0) for overall samples of Pacific and Winter wrens. Additionally, *t*-tests suggested significant difference between these two subsets of the Pacific Wren in the left-time values for the bottom and second

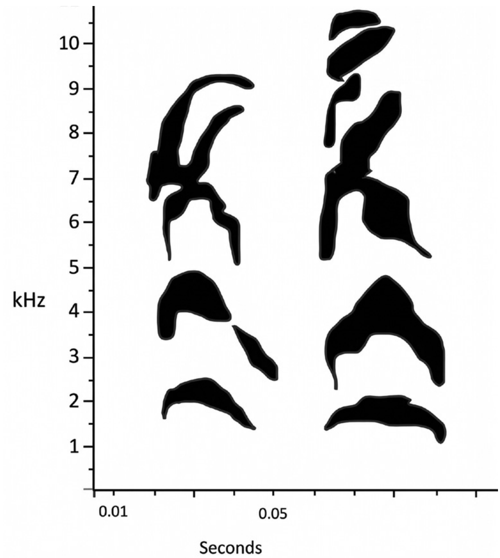

FIGURE 7. Variability in Winter Wren calls. Left, ML190186441; right, ML471513861 (#44, Table 1).

Audio by Jay McGowan and Andrew Spencer.

components ($0.01 < p < 0.05$). However, a PCA comparing individuals of both groups included in the primary analysis did not show clear differentiation.

Secondary Analysis: Intraspecific Variation

The secondary analysis was based on recordings of wrens whose specific identity was reasonably established but were giving atypical calls. The measurements of the calls included in the secondary analysis expand several of the ranges from our primary analysis, lessening these measurements' utility for discriminating the two species (Tables 4 and 5). This additional sample increased the upper limit of all measurements of frequency of Winter Wren calls, and decreased the lower limit of several frequency ranges in Pacific Wren calls, most notably the peak frequency of all three components (Tables 4 and 5). Ranges of measurements that reflect traces' shape and complexity (left-time, right-time, height, occurrence of two traces in the bottom component, etc.) were generally unaltered by inclusion of calls in the secondary analysis. Nevertheless, a single Pacific Wren's third component received a shape score of two, expanding the range of shape scores of that component. As expected, calls of two of the three presumed Pacific Wrens in the secondary analysis showed two traces in the bottom component, and those of the third individual also suggested this feature. As expected, calls of the two Winter Wrens in the secondary analysis had only a single trace in the bottom component.

In the PCA plot (Figure 6), although most calls from the primary analysis

Table 4 Minimum and Maximum Values of Characteristics of Calls of Five Pacific and Winter Wrens Selected to Include Unusual Variants

	Winter Wren (n = 4)		Pacific Wren (n = 6)	
	Min	Max	Min	Max
Lowest frequency (Hz)	819.1	1760	1156.3	1875.8
Peak frequency (Hz)	4031.3	**6656.3**[a]	**4031.3**[a]	7312.5
Duration (sec)	0.035	0.047	0.032	**0.060**[a]
Shape score[b]	2.8	4	**3.3**[a]	4.125

[a]Values that extend the range in Table 2 are in **bold**.

[b]On a scale of 1 to 5, a value of 1 represents an ascending contour, a value of 5 represents a descending contour.

Table 5 Minimum and Maximum Values by Component of Ten Calls of Five Pacific and Winter Wrens Selected to Include Unusual Variants

	Winter Wren			Pacific Wren		
	Bottom Component	Second component	Third Component	Bottom Component	Second component	Third Component
Lowest frequency (Hz)	819.1, **1760**[a]	2006.8, **3340.5**[a]	4832.8, **5477.1**[a]	1156.3, 1875.8	2544.0, 3035.2	**3854.4**[a], 6440.1
Highest frequency (Hz)	2322.6, **2573.3**[a]	4753.7, **5115.6**[a]	7143.5, **7908.6**[a]	**2184.2**[a], 2454.8	4830.8, 5637.8	**5704.5**, 7791.4
Central frequency (Hz)	1968.8, **2250.0**[a]	3962.1, **4565.0**[a]	5906.3, **6750**[a]	**1968.8**[a], 2454.8	**4218.8**[a], 4909.6	**4781.3**[a], 7149.0
Peak frequency (Hz)	2153.3, **2325.6**[a]	4031.3, **4737.3**[a]	5437.5, **6937.5**[a]	**1968.8**[a], 2325.6	**4125.0**[a], 5340.2	**4593.8**[a], 7149.0
Duration (sec)	0.017, 0.042	0.028, 0.045	0.020, 0.033	0.032, 0.050	0.042, 0.050	0.032, **0.057**[a]
Shape score[b]	3, 4	4, 4	1, 4	4, 4	4,4	**2**, 4
Left-time[c] (sec)	0.008, 0.019	0.010, 0.022		0.007, 0.013	0.005, 0.021	
Right-time[d] (sec)	0.007, 0.018	0.015, 0.027		0.020, 0.031	0.025, 0.042	
Height (Hz)	288.8, 672.0	315.0, 1120.0		544.0, 644.5	993.1, 1856.0	

[a]Values that extend the range in Table 3 are in **bold**.

[b]On a scale of 1 to 5, a value of 1 represents an ascending contour, a value of 5 represents a descending contour.

[c]"Left-time," the interval from the trace's beginning to its point of highest frequency.

[d]"Right-time," the interval from the point of the trace's highest frequency to its end.

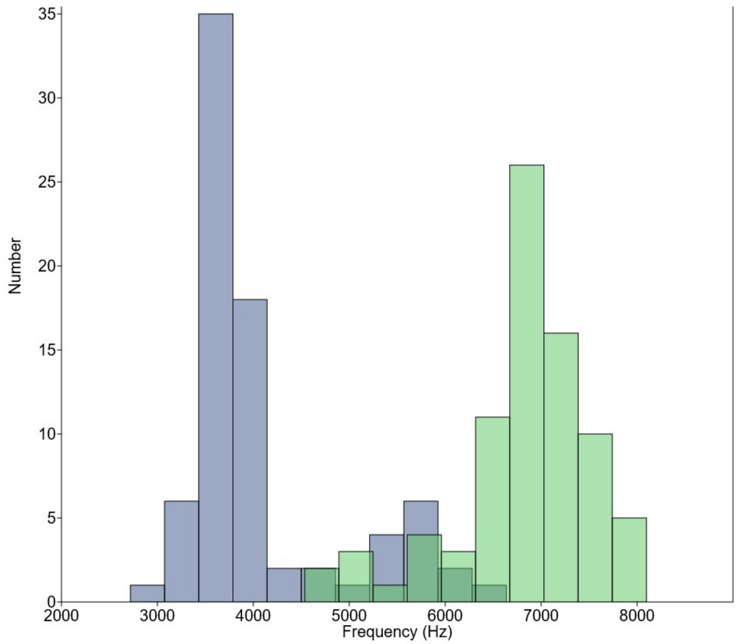

Figure 8. Peak frequency of entire call in 175 Winter and Pacific Wren calls selected to encompass a broad representation of the ranges of both species, showing a wide average difference between the two. Green bars, Pacific Wren; blue bars, Winter Wren.

cluster neatly by species, those from the secondary analysis cluster closer to or with typical Winter Wren calls, regardless of the bird's presumed specific identity.

DISCUSSION

Identification of Extralimital Wrens by Call

The typical single or double-noted calls of a Pacific Wren or Winter Wren usually identify the bird readily. Unfortunately, significant variability in the calls of both species confuses the issue. Our analysis of atypical-sounding calls suggests that, in both species, the calls' shape and complexity, as viewed by spectrogram, are less variable than their frequency. Regardless, an extralimital record of either species, based only on a reasonably adequate recording of a single or double-noted call, should be based on a typical call only. Our study suggests the following *holistic* guidelines for identifying an extralimital Pacific or Winter Wren to species conclusively. Because of variability, many Pacific and Winter Wren calls may not satisfy these criteria, though if additional information such as photographic documentation supports a specific identification, not all vocal criteria may need to be met.

Guidelines. We suggest that an acceptable extralimital Winter Wren's call should show (1) a peak frequency that is reasonably typical for the Winter Wren and reasonably atypical for the Pacific Wren (see Figures 5 and 8, Tables 2 and 3); (2) a bottom component consisting of a single trace; and (3) a bottom component that is fairly symmetrical (Figures 9, 10) or, even more favorably, has a shape score of 1 or 2 (see Figure 3).

An extralimital Pacific Wren's call should show (1) a peak frequency that is reasonably typical for the Pacific Wren and reasonably atypical for the Winter Wren (see Figures 5 and 8, Tables 2 and 3); (2) a bottom component consisting of multiple traces; and (3) a bottom component that is asymmetrical, with right-time greater than left-time to the degree reflected in Table 2 and Figures 9 and 10, and preferably with a shape scored 4 or 5 (see Figure 3).

We recommend peak frequency as a discriminator because, unlike the lowest or highest frequency, it is less likely to be obscured in recordings of poorer quality. Although the bottom component is consistently weaker than the second component, its shape is more helpful for diagnosis of species (Figure 9), as is the number of traces constituting it, usually one in the Winter Wren and usually two in the Pacific.

These criteria are conservative but may be interpreted flexibly. Under a conservative interpretation of these criteria, 65 of 83 Winter Wren calls in the primary analysis pass as that species by all three criteria, as do 60 of 82 Pacific Wren calls. In other words, approximately 22% of "typical" Winter Wren calls evaluated do *not* qualify by all three criteria, nor do 27% of "typical" Pacific Wren calls. Among Pacific Wrens breeding in the interior of North America, the failure rate was higher, with approximately half of those failing, failing on the guideline for a doubled trace in the bottom component.

Caveats. Several caveats must be considered when these guidelines are applied. First, in audio recordings of suboptimal quality, information disappears from the spectrogram. As the volume of the background noise approaches the volume of the call, for example, the edges of the spectrogram corresponding to the quieter parts of the call begin to disappear into the background, and/

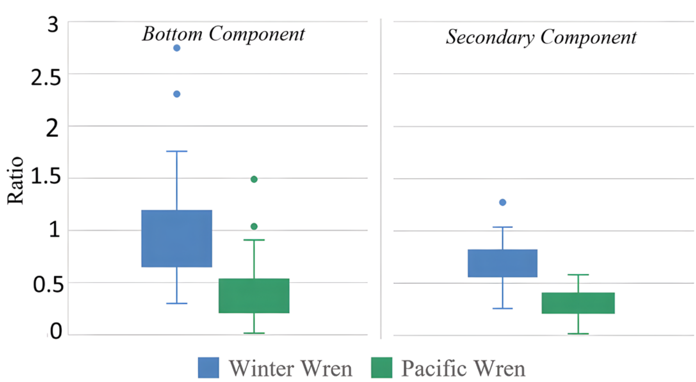

FIGURE 9. Ratios of "left-time" (the interval from the trace's beginning to its point of highest frequency) to "right-time" (the interval from the point of the trace's highest frequency to its end) in the bottom and secondary components of 175 Winter and Pacific Wren calls selected to encompass a broad representation of the ranges of both species. Note that the proportion of the call consisting of the initial rising segment averages shorter in the Pacific Wren than in the Winter Wren.

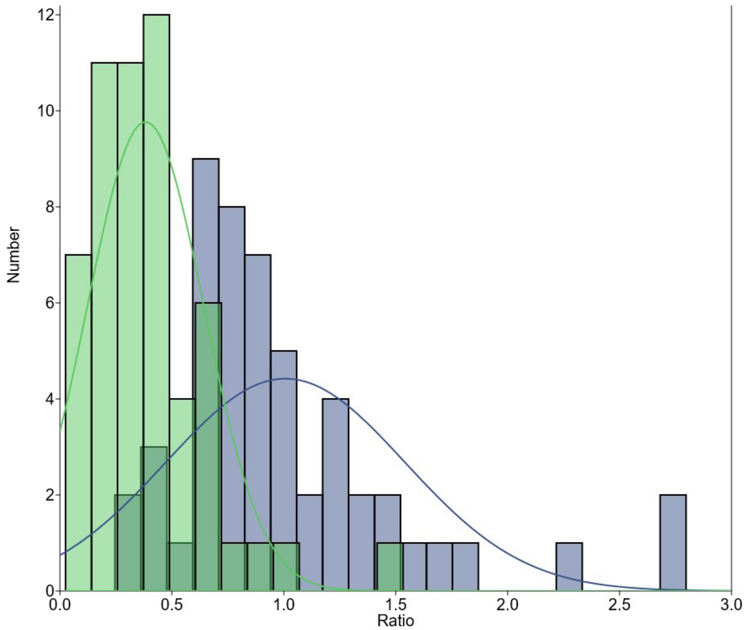

FIGURE 10. Ratios of "left-time" (the interval from the trace's beginning to its point of highest frequency) to "right-time" (the interval from the point of the trace's highest frequency to its end) in the bottom component of 175 Winter and Pacific Wren calls selected to encompass a broad representation of the ranges of both species. Green bars, Pacific Wren; blue bars, Winter Wren. The curves show normal distributions fit to the data for each species.

or the spectrogram may blur, degrading the graphic representation of the call. Components that may appear to have a shape score of 2 in a good recording may appear to have a score of 1 in a poor recording; similarly, the bottom component—consistently weaker than the second component—may vanish altogether. However, note that in Pacific Wren calls in which the bottom component is doubled (two traces rather than one), the median peak power density of each trace was similar (–38.3 and –36.9 dBFS/sec). Thus in a clear recording showing the bottom component, both traces are likely to be visible if present.

Second, in an evaluation of a spectrogram, it may be unclear if the lowest-frequency trace visible represents the bottom component, as we have described it, or instead belongs to the second component, with the bottom component too weak to be discerned. Peak power density is a measure of loudness, with higher (more positive) numbers appearing darker on the spectrogram. Average peak power densities (dBFS/sec) of the bottom, second, and third components were –36.8, –23.9, and –41.4, respectively, for the Pacific Wren, and –42.9, –28.5, and –34.2 for the Winter Wren. In other words, the bottom component is generally quieter (fainter on the spectrogram) than the second component. If the lowest-frequency trace(s) in a spectrogram are not substantially weaker than the higher-frequency traces, the bottom component is likely not visible on the spectrogram. Additionally, the average height (range of hertz spanned on the *y* axis) of the bottom, second, and third components was 1925.9, 3644.9, 1631.8, respectively for the Pacific Wren and 691.1, 1721.6, and 1582.4 for the Winter Wren. In other words, the bottom component should be significantly shorter (as measured on the *y* axis) than the second component. If the lowest-frequency trace in a recording is not substantially shorter than the component above it, the bottom component is likely not visible on the spectrogram.

Third, it is inappropriate to estimate measurements—particularly peak frequency—without a program designed for rigorous bioacoustic analyses, such as Raven. Similarly, one should look for features in a spectrogram only in applications that allow the user to magnify the spectrogram significantly. Many computer applications other than Raven may be sufficient; the user must simply be able to take a close look at the spectrogram and be able to reliably measure, for example, the peak frequency of a selection.

Fourth, it bears repeating that six of twelve interior Pacific Wrens (identified by range during the breeding season) included in this study showed only one, not two, traces in the bottom component of their calls. If this pattern proves consistent, then a bottom component consisting of two traces may not be as useful for identifying an extralimital Pacific Wren as the species-wide analysis implies, especially because it is Pacific Wrens from this area that are nearest to the normal range of the Winter Wren.

Therefore, these criteria and precautions remain insufficient for identifying some individuals. The few Pacific Wren calls from the primary analysis that clustered with Winter Wren calls were all from interior Pacific Wrens (Figure 6). Calls of ambiguous-sounding Pacific Wrens from the secondary analysis also clustered with Winter Wrens (Figure 6), raising the question whether many relatively ambiguous sounding wrens are interior Pacific Wrens. More troublingly, some individual wrens are capable of making calls that are either entirely ambiguous, or that at times are most similar to the Winter, and at other times most similar to the Pacific (see Figures 4 and 11). Mikkelsen and Irwin (2021) reported limited hybridization at the contact zone but offered no information on the appearance or sound of the hybrids. It is possible that wrens that make entirely ambiguous calls and/or calls appropriate for both species are of mixed ancestry. Alternatively, even unhybridized birds may make calls that fall outside the range of variation we confirmed. Clearly, more study is needed.

Recommendations for Future Study

Further work to establish the range of potential geographic variation in the calls of these taxa, among Pacific Wrens especially, is needed. Our study did not encompass calls of any of the Alaska subspecies (*T. p. helleri*, *alascensis*, *meligerus*, *kiskensis*, and *semidiensis*, which are mostly or completely sedentary). More geographic variation within the calls of each species may remain to be identified. Efforts to characterize the calls of Pacific Wrens breeding as isolated populations, e.g., in South Dakota and Arizona (Toews et al. 2025), are needed, as is a more comprehensive comparison of interior Pacific Wrens and coastal Pacific Wrens.

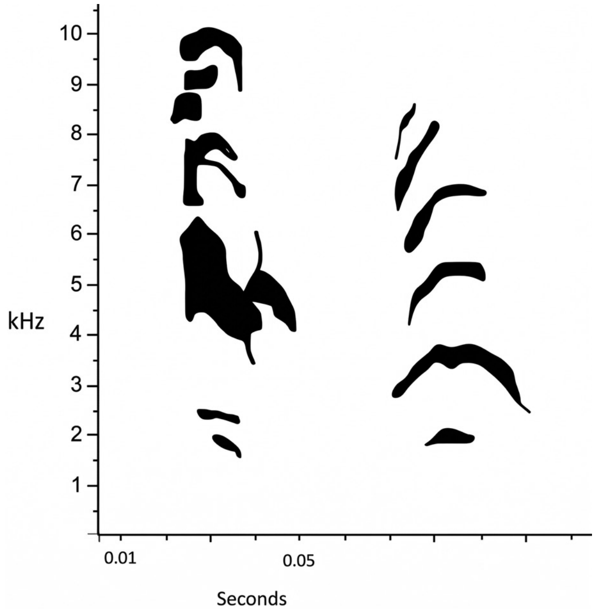

Figure 11. Two calls made by a Winter/Pacific wren at Sycamore Reservoir, Arizona, XC218679. These calls have a peak frequency of 4306.6 Hz and 3359.2 Hz, respectively. The call on the left shows two descending traces of similar size and shape at the lowest frequencies (favoring the Pacific Wren), whereas the right spectrogram shows a single, generally symmetrical trace instead (favoring the Winter Wren). Note additional "soft features," such as the size and shape of the traces centered at 5 kHz (left) and 3 kHz (right), and the call's overall complexity; compare to Figures 1, 2, and 7.

Concrete information on vocal learning in these taxa would deepen our understanding of variation in these wrens' calls, but this information is lacking. Similarly, descriptions of calls of F1 hybrids (confirmed with genetic analysis) might assist with the field identification of problem birds.

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