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Western Specialty:
Pacific Wren

Photo by Ethan Monk of Walnut Creek, California:

Pacific Wren (*Troglodytes pacificus salebrosus*), Elk Meadows Road, Idaho County, Idaho, 22 June 2025.

Call notes are at least as useful in distinguishing the Winter and Pacific Wrens as their plumage. But variation in these calls and possible overlap had not been quantified until Ethan Monk and Martin Freeland addressed the question in this issue of *Western Birds*. In general, the call of the Winter Wren is significantly lower in pitch than that of the Pacific Wren. In general the trace at the fundamental frequency in the call is more symmetrical in the Winter Wren, more descending in the Pacific Wren, and that trace is usually single in the Winter Wren, doubled in the Pacific Wren. But there is overlap, potentially even within one bird's repertoire. The calls of the interior population of the Pacific Wren, described as subspecies *salebrosus*, while generally resembling those of coastal birds, may vary in the direction of the Winter Wren. Identification of vagrant wrens by call should be made only on the basis of typical calls analyzed in audiospectrograms.

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AN ANALYSIS OF PLUMAGE CHARACTERISTICS OF THE WINTER AND PACIFIC WRENS

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ABSTRACT: The Winter Wren (*Troglodytes hiemalis* Vieillot, 1819) and Pacific Wren (*T. pacificus* Baird, 1864) are closely related species occurring primarily in eastern and western North America, respectively. Recent literature on the identification of these cryptic species has focused on vocal cues, but subtle differences in plumage have also been proposed since Spencer F. Baird's original description of the Pacific Wren in 1864. The nature and consistency of these differences need quantification for plumage to be useful in identification. We analyzed 11 prospective characters, finding strong differentiation in 6: Winter Wrens show stronger pale markings on the chest, neck, mantle, and alula, and feature a paler throat and supercilium, on average, than Pacific Wrens. Two variables, relative width of pale and dark bars on the primaries and number of pale tips on the upperwing coverts, are moderately informative, whereas we found three variables—relative tone of pale barring on primaries and on secondaries, relative throat color, and crown color—to show no consistent differences. Although differences in plumage between Winter and Pacific wrens are subtle, consideration of the six informative characters should be of material use in identifying many individuals to species.

The Winter (*Troglodytes hiemalis*) and Pacific (*T. pacificus*) wrens, both formerly considered conspecific with the Eurasian Wren (*T. troglodytes*), have been treated as separate species since Toews (2007) and Toews and Irwin (2008) demonstrated genetic and behavioral (i.e., in song pattern) distinctions in a narrow area of sympatry. From the degree of sequence divergence in the mitochondrial genome, these authors estimated these taxa diverged between 2.3 and 4.3 million years ago. Drovetski et al. (2004) suggested that the Winter Wren may have shared common ancestry with the Eurasian Wren more recently than with the Pacific Wren, though Albrecht et al. (2020) and Imfeld et al. (2024) contested this hypothesis. Despite the relatively early dates of divergence among these three species, morphology in this complex is conservative, with most populations of the Winter, Pacific, and Eurasian wrens resembling one another closely in phenotype.

The Winter Wren (*sensu stricto*) includes two subspecies, one (*T. h. pul-*

lus) restricted principally to the Appalachians and the other (the nominate, *T. h. hiemalis*) breeding across much of Canada and the northeastern United States (Hejl et al. 2020). These subspecies are at best poorly differentiated, however, and diagnostic criteria distinguishing them are not well established (Pyle 2022, 2025). In the original description of *T. h. pullus*, Burleigh (1935) reported that it averages darker and redder than the nominate subspecies, but if true, this difference is extremely subtle and likely of little relevance to the question of the Winter Wren's distinction from the Pacific Wren. Moreover, the proposed geographic range of *T. h. pullus* does not approach that of *T. pacificus*, and it is at most a short-distance migrant, whereas the nominate subspecies overlaps in range with the Pacific Wren and is a long-distance migrant with clear potential for extralimital occurrence (Hejl et al. 2020).

Various authors have recognized as many as 14 (Rea 1986) or as few as five (Clements et al. 2025, Pyle 2025) subspecies of the Pacific Wren. Toews and Irwin (2020) and Clements et al. (2025) divided the Pacific Wren's subspecies into two groups: *T. p. alascensis* (Baird 1869), *T. p. meligerus* (Oberholser 1900), *T. p. kiskensis* (Oberholser 1919), *T. p. semidiensis* (Brooks 1915), *T. p. tanagensis* (Oberholser 1919), *T. p. seguamensis* (Gabrielson and Lincoln 1959), *T. p. stevensoni* (Oberholser 1930), and *T. p. petrophilus* (Oberholser 1919) constitute the "Alaska group" (*T. p.* [*alascensis* group]), whereas *T. p. pacificus* (Baird 1864), *T. p. salebrosus* (Burleigh 1959), *T. p. obscurior* (Rea 1986), *T. p. muiri* (Rea 1986), *T. p. ochroleucus* (Rea 1986), and *T. p. helleri* (Osgood 1901) constitute the "Pacific group" (*T. p.* [*pacificus* group]). The Alaska group comprises insular populations occupying islands in western Alaska and a limited area of the nearby Alaska mainland (Gibson and Kessel 1997). These birds are evidently resident: one of subspecies *alascensis* found dead at Barrow in October 1929 represents perhaps the only extralimital record for this subspecies group (Bailey 1948, Toews and Irwin 2020). Wrens on the Commander Islands of Russia belong to *T. t. pallescens,* a Siberian subspecies of the Eurasian Wren (Baird 1883), but genetic studies (Pruett and Winker 2008, Pruett et al. 2017) suggest that the Commander Islands population may in fact be more closely allied to Alaska Pacific Wrens than to other Eurasian Wrens. The Pacific group of the Pacific Wren comprises populations on Kodiak Island and the remainder of this species' range to the south and west, including both resident and migratory populations.

We limited our comparisons to three units, corresponding to the subspecies groups delineated in Clements et al. (2025): the Winter Wren, Alaska-group Pacific Wren, and Pacific-group Pacific Wren. We do not consider the Eurasian Wren, including *T. t. pallescens*.

Although Toews (2007) and Toews and Irwin (2008) proposed that distinguishing these taxa by morphology is difficult or impossible and did not attempt to identify plumage characters relevant to their identification, several subsequent authors—most notably Leukering and Pieplow (2010), Sibley (2010), Pyle et al. (2011), and Pyle (2022)—have tentatively proposed grounds for the differentiation of these taxa on the basis of plumage. In addition, some earlier works on taxa then considered subspecies in this complex (e.g., Ridgway 1904, Rea 1986) presented features relevant to the discrimination of the Pacific and Winter (*sensu stricto*) wrens as species. In this analysis, we assess the reliability of published and novel criteria for the identification of these species by plumage.

METHODS

We examined images of 560 wrens from the Cornell Lab of Ornithology's Macaulay Library. These included 234 individuals each of the Winter Wren and the Pacific group of the Pacific Wren, as well as 92 Alaska Pacific Wrens, of which fewer high-quality images are readily available. All selected photographs were taken at locations where only one species is expected; we excluded those from the Rocky Mountains of eastern British Columbia where both may occur (Toews 2007). Photos of Pacific-group Pacific Wrens came from 10 states/provinces, those of Winter Wren from 28 states/provinces, spanning as much of each group's distribution as possible. To attain a reasonably large sample, we were not able to limit our investigation to photos from the breeding grounds and breeding season only, but the typical nonbreeding ranges of these taxa are also spatially segregated to a great degree, and we likewise excluded from our analyses areas of potential overlap in the nonbreeding season (i.e., from south-central California east through central Texas). To avoid duplications of individuals, we used only one photo from each location unless the photos were taken ≥5 years apart. All selected photos were of high resolution, taken in good lighting, and clearly showed a view of the bird in profile or nearly in profile, in order to allow consistent assessment of the plumage features detailed below. Juveniles were excluded, and we combined images of formative and basic plumages as these are similar within each species and difficult to distinguish in the field (Pyle 2022). Additionally, we examined all specimens of these species housed at the California Academy of Sciences, San Francisco.

For most analyses we used photos only, as in comparison to the single set of specimens we examined, our photographic dataset was much more extensive, more geographically diverse, and more readily permitted examination of certain plumage features such as the chest pattern, damaged in some specimens. A limitation of reliance on photographic data is the difficulty of evaluating absolute color, as factors like ambient lighting and camera settings may affect the apparent color of birds in photos quite strongly; we address this by examining only three traits that involve absolute color, all of which were suggested by prior authors (Ridgway 1904, Rea 1986, Sibley 2010, Leukering and Pieplow 2010, Pyle 2022). Two of these (throat color and supercilium color) merely require differentiation between rich rufous-brown and whitish. This determination may be made with confidence in most images, variations in extrinsic factors like lighting notwithstanding. The third feature, crown color, proved problematic to assess in photos because of the confounding effects of lighting and image quality; therefore, our conclusions related to this single trait are informed principally by examination of specimens (see Results). Mensural characteristics are treated in Hejl et al. (2020) for the Winter Wren, in Toews and Irwin (2020) for the Pacific Wren, and in Pyle (2022) for both; we did not re-examine these. Pacific-group Pacific Wrens and Winter Wrens overlap broadly in all measurements (table 46 in Pyle 2022), precluding any usefulness in the field.

The following eleven features were assessed in all photos. We selected these either because our previous experience suggested that they could be relevant or because they have previously been proposed to be of use in distinguishing

the Winter and Pacific wrens (Leukering and Pieplow 2010, Sibley 2010, Pyle et al. 2011, Pyle 2022, A. Birch pers. comm.). They are represented visually in Figure 1 and their frequencies are presented in Table 1.

1. *Absolute throat color.* In the Winter Wren, the throat may typically be pale off-white in color, whereas in Pacific Wren, the color of the throat may average richer and darker, approaching a warm brown. We assessed throat color as whitish, rufous, or indeterminate.

2. *Relative throat color.* In the Winter Wren, the throat may be contrastingly paler than the breast; in the Pacific Wren, the breast and throat may be concolorous. We assessed the relative colors of these two regions as contrasting, similar, or indeterminate.

3. *Supercilium color.* The Winter Wren may typically show a paler, cream-colored supercilium, in comparison to the more richly rufous-tinged supercilium possibly characteristic of the Pacific Wren. We categorized supercilium color as whitish, rufous, or indeterminate.

4. *Crown color.* The Winter Wren may show a colder, grayer brown tone on the upperparts, especially on the crown; the Pacific may show a warmer rufous tint. We categorized crown color as cold, warm, or indeterminate. This feature is often challenging to evaluate in photos, and many images were assessed as indeterminate.

5. *Neck pattern.* In the Winter Wren, the area immediately posterior to the auriculars may feature distinct pale streaking; in Pacific Wren, it is often unmarked. We assessed this area as featuring discernible streaking, lacking discernible streaking, or indeterminate.

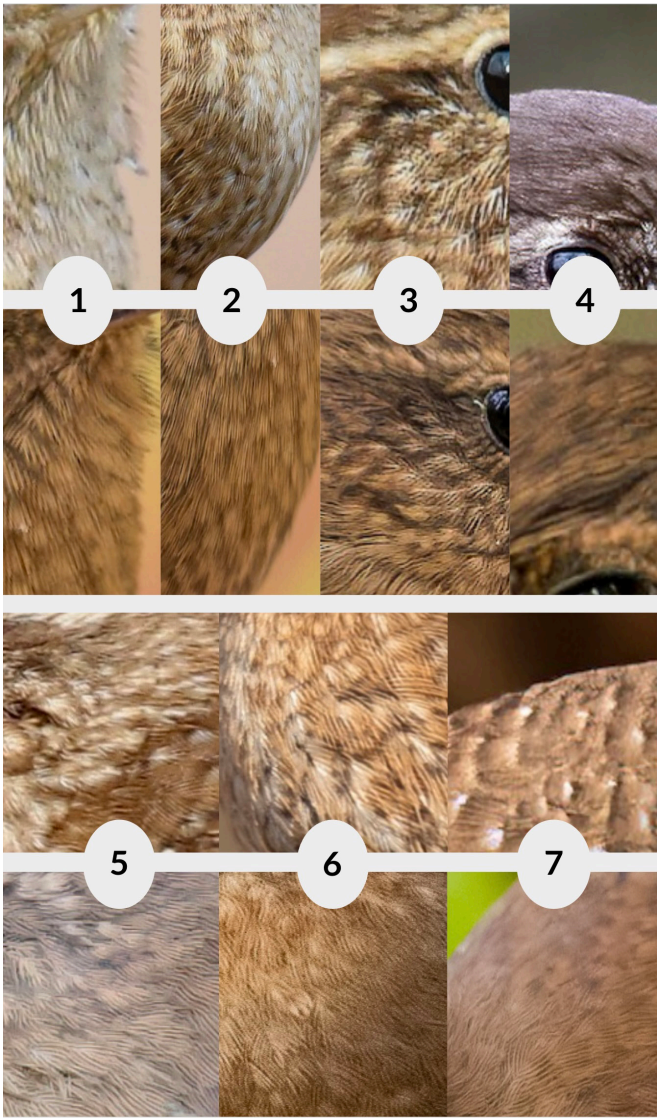
6. *Breast pattern.* In the Winter Wren, the sides of the upper breast may feature fairly prominent black-and-white checkering, much as with the pattern of the mantle described below. Pacific Wrens generally show more evenly rufous and less strongly marked sides to the upper breast. We assessed checkering in this region as bold, faint/absent, or indeterminate.

7. *Mantle pattern.* In the Winter Wren, some dorsal contour feathers may feature contrasting black centers and whitish subterminal bands, creating fairly distinct black-and-white checkering on the reddish brown background of the mantle; in the Pacific Wren, the mantle is typically uniform rich reddish-brown or has at most indistinct dark scaling but no bold checkering. We assessed checkering on the back as bold, faint/absent, or indeterminate.

8. *Alula pattern*. The Winter Wren may more frequently show strong pale barring on the alulae; the alulae of the Pacific Wren may average less distinctly marked. We assessed whitish barring on the alula (excluding the pale tip) as present, absent, or uncertain (i.e., obscured by other feathers).

9. *Number of pale tips to upperwing coverts.* Prominent white tips to some upperwing coverts occur in both species but may be more numerous in the Winter than in the Pacific. We recorded the number of prominent white tips but for most statistical analyses (see below), transformed this variable into a dichotomous categorical variable (for consistency with the 10 other categorical variables). We categorized wings as heavily marked (>5 white tips visible), lightly marked (≤5 white tips), or indeterminate.

10. *Relative tone of pale barring on primaries and on secondaries.* Leukering and Pieplow (2010) suggested that the tone of the pale markings on the primaries of the Winter Wren is notably whiter than that of the pale markings



(continued on next page)

FIGURE 1. Examples of traits potentially relevant to wren identification examined in our study, with the posited Winter-associated character state above and the corresponding proposed Pacific-associated character state immediately below. 1, Throat color; 2, contrast between throat and breast; 3, supercilium color; 4, crown color; 5, neck pattern; 6, breast pattern; 7, mantle pattern; 8, alula pattern; 9, number of pale tips on upperwing coverts; 10, contrast between pale barring on primaries and on secondaries; 11, relative width of pale and dark bars on primaries.

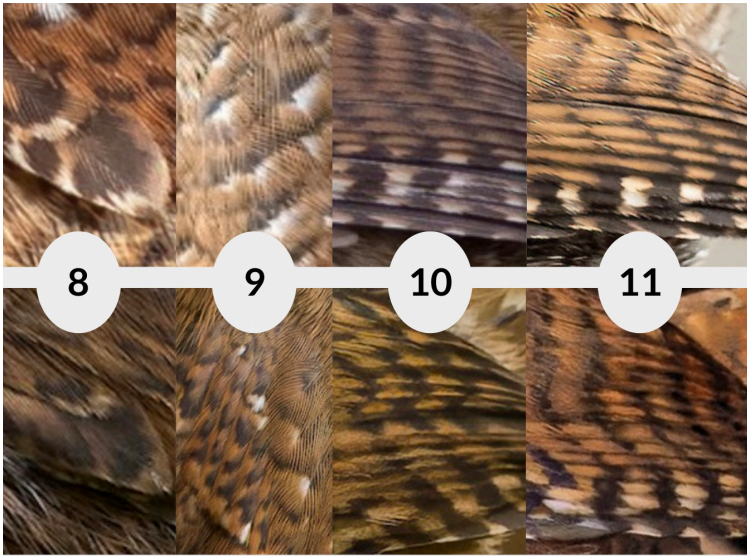


FIGURE 1 (*continued from previous page*).

on the secondaries, whereas in the Pacific Wren, the tones of the pale markings in these two feather groups are similar. We recorded the contrast in color between the pale markings on the primaries and secondaries as perceptible, imperceptible, or uncertain.

TABLE 1 Frequencies by Percentage of 11 Plumage Traits in the Winter Wren and Two Subspecies Groups of the Pacific Wren[a]

	Pacific (Pacific)	Pacific (Alaskan)	Winter
Relative tones of primary and secondary barring	86 / 12 / 2	93 / 4 / 3	92 / 6 / 2
Patterned alula	21 / 78 / 1	19 / 65 / 6	86 / 11 / 3
Patterned mantle	7 / 79 / 14	24 / 58 / 18	71 / 15 / 14
Patterned breast	19 / 80 / 1	27 / 72 / 1	92 / 8 / 0
Patterned neck	16 / 84 / 0	22 / 76 / 2	94 / 5 / 1
Patterned upperwing coverts	18 / 73 / 9	16 / 69 / 15	49 / 36 / 15
Color contrast between throat and breast	31 / 66 / 3	35 / 59 / 6	52 / 38 / 10
Cold crown	72 / 22 / 6	89 / 6 / 5	73 / 26 / 1
Pale throat	24 / 71 / 5	55 / 41 / 4	86 / 10 / 4
Pale supercilium	43 / 56 / 1	35 / 59 / 6	95 / 3 / 2
Relative width of pale and dark primary bars	48 / 14 / 38[b]	45 / 16 / 39[b]	39 / 30 / 31[b]

[a]For each combination of taxonomic category and trait, the percent frequency of the feature potentially associated with the Pacific Wren is listed first, followed by that of the reciprocal feature potentially associated with the Winter Wren, followed by that of cases where no determination could be made.

[b]The third number indicates the percent frequency of cases in which the width of pale and dark bars in the primaries were approximately *equal*, not incapable of being measured.

11. *Relative width of pale and dark bars on primaries.* Counterintuitively, the Winter Wren may show pale bars on the primaries that are on average narrower than the intervening dark zones, whereas in the Pacific Wren the pale bars may be slightly wider than the dark zones. We categorized the contrast in the width of these zones as pale > dark, pale < dark, and pale ≈ dark. This variable is ternary, unlike the 10 described above, which are binary, and was the only variable we could assess for all 560 wrens.

For all statistical analyses we used R version 4.4.1 (R Core Team 2024). For all binary variables we used Fisher's exact test for pairwise comparisons evaluating differences in each plumage character between all combinations of the three taxa under investigation. For the single ternary variable we used the chi-squared test. For each trait, the test considered the subset of the dataset from which individuals that could not be assessed for the feature in question were culled. We applied a Bonferroni adjustment for multiple comparisons to our set of 33 resulting *p*-values (Table 2). To supplement our computational assessment of the degree to which the 11 plumage traits differentiate the three categories being compared, we applied a permutational multivariate analysis of variance (PERMANOVA) and a nonmetric multidimensional scaling (NMDS) ordination in two dimensions, both using Gower dissimilarities (Maechler et al. 2025, Oksanen et al. 2025).

To assess whether, at the level of the individual, having one heterospecific trait was positively associated with having others, we used Pearson's correlation coefficient to quantify the degree of association among Winter Wren-like traits within the Pacific and Alaska groups combined, and the degree of association among Pacific Wren-like states in the Winter Wren. That is,

Table 2 Results of Statistical Comparison of Differences in the Frequencies of 11 Plumage Traits in the Winter Wren and Two Subspecies Groups of the Pacific Wren[a]

	pacificus vs *hiemalis*		*alascensis* vs *hiemalis*		*pacificus* vs *alascensis*	
	p-value	Odds ratio	*p*-value	Odds ratio	*p*-value	Odds ratio
Relative tones of primary and secondary barring	1	0.760	1	0.893	1	0.679
Patterned alula	**<0.0001**	64.1	**<0.0001**	0.0568	1	0.362
Patterned mantle	**<0.0001**	108	**<0.0001**	0	1	0
Patterned breast	**<0.0001**	106	**<0.0001**	0.0493	1	0.510
Patterned neck	**<0.0001**	161	**<0.0001**	0.0180	0.03	2.89
Patterned upperwing coverts	0.01	2.06	1	0.841	1	1.73
Color contrast between throat and breast	1	1.21	1	0.706	1	0.875
Cold crown	1	0.745	1	0.440	1	0.328
Pale throat	**<0.0001**	12.5	0.03	2.89	1	1.18
Pale supercilium	**<0.0001**	10.3	**<0.0001**		1	0.575
Relative width of pale and dark primary bars[b]	0.05	$\chi^2 = 17.2$ (df = 2)	<0.1	$\chi^2 = 7.07$ (df = 2)	1	$\chi^2 = 4.87$ (df = 2)

[a]Except in the last row, the statistics reported are from Fisher's exact tests. Highly significant values of Bonferroni-adjusted *p* are **bolded**, as are the labels of the corresponding traits; marginally significant ones are underlined.

[b]Statistics reported are from chi-squared tests (see Methods), and the chi-squared statistic is reported in place of an odds ratio.

we assessed the extent to which Winter Wren characters in the Pacific Wren dataset are attributable to a small number of individual Pacific Wrens that resemble Winter Wrens in multiple traits, or to a larger number of individuals that resemble Winter Wrens in fewer traits. And vice versa for the extent of Pacific-associated traits in the Winter Wren dataset. To examine potential systematic variation in the plumage characteristics in question *within* each of the three groups (e.g., of the kind that might be observed if substantial geographic variation exists within any of the three groups), we did latent-class analyses of each of the three groups with all plumage variables included as categorical predictors. We used the package poLCA (Drew et al. 2011) with a maximum of 5000 iterations to generate models that divided each group into one through six classes, each class representing a group of individuals posited to share combinations of plumage character states. We assessed each model's fit with Bayesian and Akaike information criteria. This procedure is based on those suggested by Drew et al. (2011).

RESULTS

Of the eleven traits evaluated in photographic analyses, three showed no statistically significant differentiation among any of the three groups we examined—the Winter Wren, the Pacific group of the Pacific Wren, and the Alaska group of the Pacific Wren. Two showed at most moderately statistically significant differentiation in certain comparisons, and six showed sufficiently substantial differentiation to be useful in the diagnosis of Pacific and Winter wrens to species.

The traits in which we found minimal differentiation (i.e., all pairwise comparisons returned $p = 1$ after Bonferroni correction) were (1) contrast between primaries and secondaries in tone of pale barring, (2) contrast in color between throat and breast, and (3) crown color. Most individual Pacific-group Pacific Wrens and Winter Wrens in our samples shared the same phenotype with respect to these three characters. Traits showing moderate differentiation were (1) relative width of pale and dark bars on the primaries and (2) number of pale tips on the upperwing coverts. For the latter trait the difference between Winter and Pacific-group Pacific wrens was statistically significant ($p = 0.01$) and in the former trait it was marginally significant ($p = 0.05$), but—again—the two groups' distributions of frequencies of these traits overlapped by more than 50%. Moreover, it is possible that the formative and definitive plumages differ in the width of dark bars on the primaries (Taylor 2012, Pyle 2022). The other two pairs (Pacific-group vs. Alaska-group Pacific Wrens and Alaska-group Pacific Wrens vs. Winter Wrens) did not show statistically significant differentiation with respect to these two characters. In any case, all five of the traits discussed so far are unlikely to be of service in differentiating Winter and Pacific wrens because of the great breadth of overlap.

In the remaining six characters, however, the Winter and Pacific wrens diverged consistently. These were (1) neck pattern (presence/absence of discernible streaking), (2) breast pattern (bold vs. faint or absent checkering), (3) mantle pattern (bold vs. faint or absent checkering), (4) absolute throat color (whitish vs. rufous), (5) alula pattern (whitish barring present/absent, excluding tip), and (6) supercilium color (whitish vs. rufous). In all of these cases, the

proportion of Winter Wrens displaying the Pacific-associated character state was ≤15% and the proportion of Pacific-group Pacific Wrens displaying the Winter-associated character state was ≤24%. With respect to Alaska-group Pacific Wrens, the proportion displaying the Winter Wren-associated character state was ≤27% for four of the six characters, the exceptions being throat and supercilium color, in which overlap with the Winter Wren was more extensive (55% and 35%, respectively). Pairwise comparisons of the Winter Wren with each group of the Pacific Wren identified statistically highly significant ($p < 0.001$) differences in the frequencies of all these traits, with the lone exception—again—of throat color in the comparison of Alaska-group Pacific Wrens with Winter Wrens. Differences between Pacific-group and Alaska-group Pacific Wrens did not rise to the level of statistical significance for any character except neck pattern, where the tendency of Alaska-group birds to show a more patterned neck than Pacific-group wrens was marginally significant ($p = 0.03$).

Our PERMANOVA returned a highly significant group effect ($R^2 = 0.48$, $F = 260.67$, $p < 0.001$), and our NMDS similarly produced a visually clear clustering of individuals by species (Figure 2, NMDS stress = 0.156). NMDS stress reports the goodness-of-fit of a two-dimensional representation of higher-dimensional data on a 0–1 scale, with lower stress (as seen in our ordination) corresponding to a better fit. While these tests confirm that the differences in plumage of Winter and Pacific wrens are sufficiently consistent

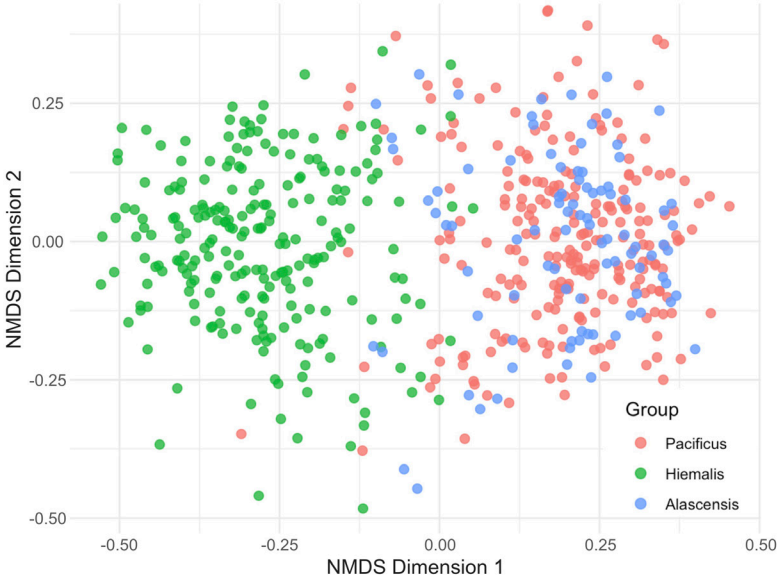


FIGURE 2. Values of Gower dissimilarity in 11 plumage traits of the Winter and Pacific wrens, plotted in a nonmetric multidimensional scaling (NMDS) ordination. Separation between the Pacific Wren (Pacific and Alaska groups, taken together, in blue and red) and the Winter Wren (green) is fairly clear, although the zone of overlap is wide. Stress = 0.156.

to be detected with very high confidence in statistical analysis, we caution that this does not directly imply separability in the field.

Nevertheless, in general, we found that overlap between Winter and Pacific wrens with respect to the six plumage features detailed above is limited; as a result, when taken together, they may permit the identification of these species. Figure 3 summarizes the differences in these six plumage characters.

In the Pacific Wren, across all pairwise comparisons of binary traits, the average Pearson correlation between the occurrence of a given Winter-associated state and other such traits in the same individual was 0.092. In the Winter Wren, the corresponding mean correlation for the occurrence of Pacific-associated character states was 0.100. These values are positive but low, indicating that the possession of one heterospecific trait is not a strong positive predictor of the possession of others.

However, as shown in Table 1, overlap between the Winter and Pacific wrens, even with respect to the plumage features identified as most useful in their discrimination, remained fairly extensive, and clearly no trait in isolation can diagnose either species. Combinations of these traits show the most promise in facilitating their identification. Only four of 234 Winter Wrens in our photographic dataset showed more than four (of six) Pacific-like traits, and only ten of 234 Pacific-group Pacific Wrens showed more than four (of six) Winter-like traits.

Examinations of specimens corroborated the usefulness of most features used in photographic analyses; see Figure 4. Except for juveniles and several specimens in poor condition whose plumage was difficult to assess, nearly all Winter and Pacific wrens could be correctly assigned to species by a combination of throat pattern, neck pattern, and mantle pattern, these also being the easiest features to assess on study skins. Crown color, which is the most problematic of the traits we investigated to evaluate in photos, did not differ consistently in the series of Winter and Pacific wren specimens that we examined.

In the Winter Wren, plumage scores for supercilium color (95% pale), neck pattern (94% strongly checkered), and breast pattern (92% boldly patterned) were fairly uniform. By contrast, Pacific Wrens of the Pacific group were consistently more variable: there was no feature for which more than 90% shared the same phenotype. The Alaska group of Pacific Wrens was also more variable than the Winter Wren across nearly all features examined, its plumage in general being somewhat intermediate between that of the other two groups, albeit closer to the Pacific Wrens of the Pacific group.

We did not detect geographic variation within the Winter Wren or the Pacific group of the Pacific Wren, and our sample of the Alaska group of the Pacific Wrens was too small to reveal the described geographic variation (Pruett et al. 2017). In latent-class analyses for each of the three categories, the Bayesian information criterion was lowest for the 1-class model (2588.57 for the Pacific group, 959.54 for the Alaska group, and 2173.61 for the Winter Wren) and increased monotonically thereafter, indicating no support for additional latent classes. In other words, on the basis of the characters we evaluated, the individuals in each sample are best represented as a single, homogeneous group, with no evidence suggesting distinct subgroups that can be defined by the plumage characters we assessed. The Akaike informa-

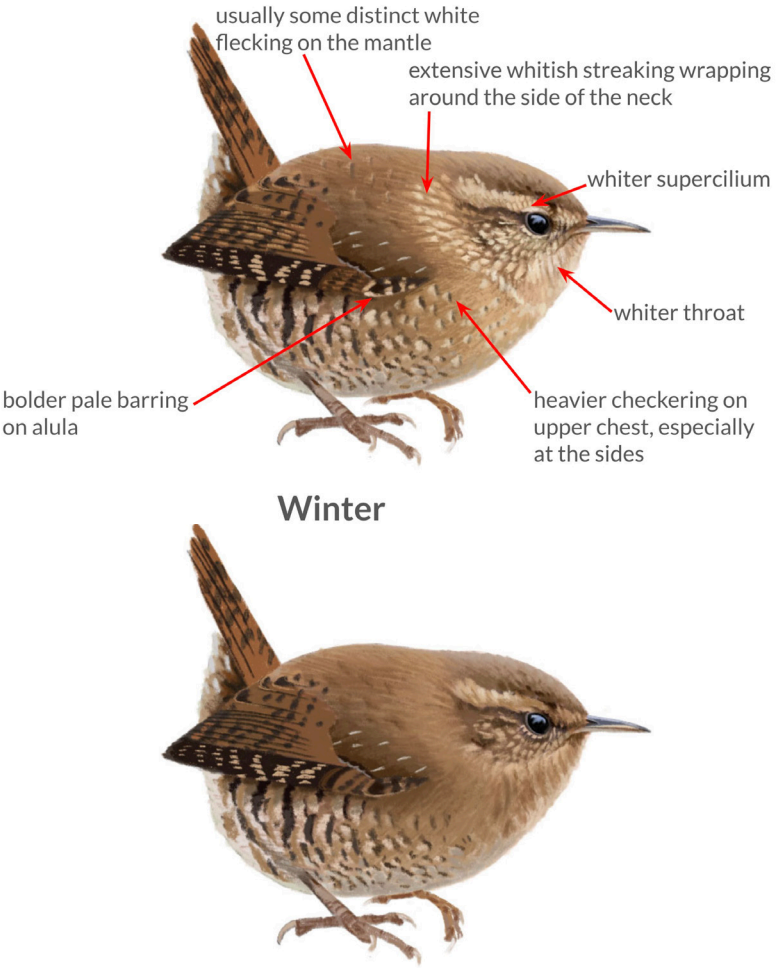


FIGURE 3. A comparison of typical Pacific-group Pacific and Winter wrens. Annotations identify the six plumage features in which these categories differ with some consistency. Alaska-group Pacific Wrens (not pictured) differ from the Winter Wren in most of the same ways, although their throats may be paler than in the Pacific group, on average, and they are also typically larger.

Illustrations by Andrew Birch

tion criterion, which penalizes a model's complexity less heavily, preferred a three-class solution for the Winter Wren, but support was weak and for all traits the classes' probabilities differed only minimally, leading us to prefer the parsimonious one-class solution identified by the Bayesian information

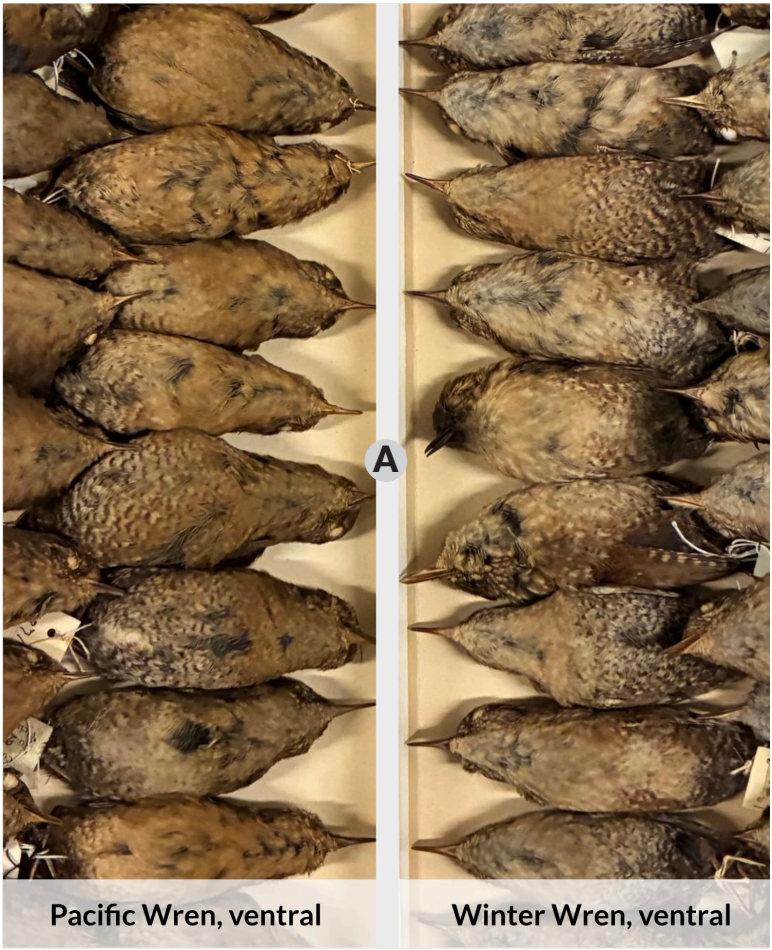


FIGURE 4. Differences in the color of the throat and breast between Pacific-group Pacific Wrens and Winter Wrens. (A) Ventrally, Pacific-group wrens are warmer, darker, and browner, while the Winter Wren is paler, colder, and whiter; (B) dorsally, the mantle of the Pacific is typically unmarked brown, while that of the Winter often shows distinct pale spangling. (*Continued on next page.*)

criterion. Thus we found no evidence of latent heterogeneity (i.e., systematic differences in plumage within a taxon) for any of the three groups.

SUMMARY

In comparison to Pacific Wrens of both subspecies groups, most Winter Wrens display stronger white streaking at the sides of the neck, more extensive

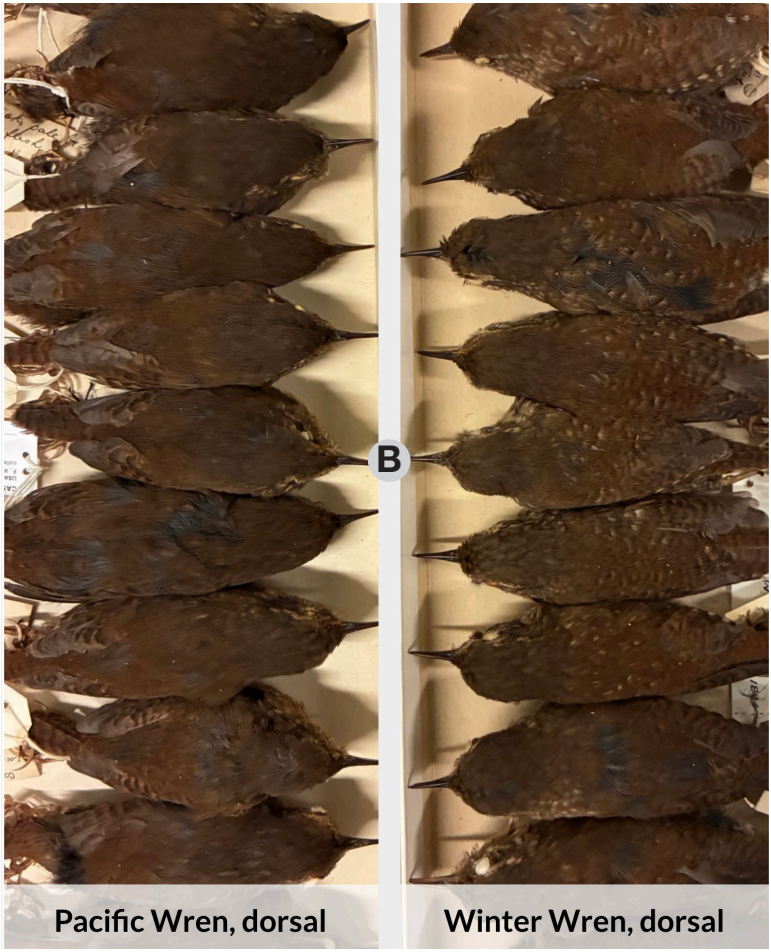


FIGURE 4 (*continued from previous page*).

and paler white marking on the alula, bolder checkering at the sides of the upper breast, checkered spangling on the mantle (in many individuals), a paler throat, and a paler supercilium, though in many cases the differences from the Winter Wren with respect to the Alaska group are somewhat less pronounced than for the Pacific group. In general, the Winter is paler and more boldly patterned, and the Pacific is darker, browner, and less boldly patterned. These results are in general agreement with some previous, albeit untested, assessments (e.g., Sibley 2010, Pyle 2022). However, it is notable that three of the six features that we identified as most reliable in differentiating Winter and Pacific wrens have not been published previously, to our knowledge. In a similar vein, several previously published marks that we investigated did

not receive support in our analyses. For example, we found that primary-bar color and relative throat color were too variable to be consistently of use in distinguishing these species, cf. Leukering and Pieplow (2010), and detected no consistent differences in crown color, cf. Sibley (2010).

DISCUSSION

The plumage of Winter and Pacific wrens differs with sufficient consistency to be at least somewhat useful in identifying most individuals to species. However, some degree of overlap in all assessed plumage characters continues to pose a challenge. It is unlikely that intermediate phenotypes are solely (or even primarily) the result of recent hybridization, as our sample did not include individuals from regions known to contain both parent species at any time of year, and hybridization appears to be limited: in a genetic analysis of 75 Winter and Pacific wrens from a segment of the contact zone, Mikkelsen and Irwin (2021) detected only two first-generation hybrids and one individual showing signs of more distant hybrid ancestry, indicating that the reproductive isolation of these taxa from one another is reasonably robust even in sympatry.

We found that the presence of one heterospecific trait in a given individual was not strongly associated with the presence of others. In other words, the occurrence of heterospecific plumage traits within each species is likely attributable to a relatively large number of individuals exhibiting a few heterospecific traits, as opposed to a small number of individuals that resemble the opposite species in multiple traits. This is perhaps encouraging, as large numbers of birds that deviate slightly from the character states expected in their species pose less of an identification challenge than small numbers that deviate more strongly and in multiple traits convergently. Moreover, it is inconsistent with the idea that variation in our dataset may be due to the inclusion of misidentified photos or highly aberrant birds, in which case nonstandard plumage traits ought to be concentrated in a small number of individuals.

Identification of Extralimital Wrens by Plumage

One of the most pressing challenges in the context of this species complex is the identification of vagrants. Over the past several decades the Winter Wren has occurred in the far western United States repeatedly (e.g., Benson et al. 2025), and at least some populations of Pacific Wren migrate moderate distances and thus might reach midwestern or eastern North America as vagrants.

We propose that a vagrant Pacific Wren of the Pacific group in midwestern or eastern North America be so identified only if it has at least five of the six plumage traits described above, and conversely with a vagrant Winter Wren in the far west. An extralimital Pacific Wren of the Alaska group seems unlikely outside the Bering Sea region, as most populations are nonmigratory island endemics or near-endemics, but in any case, conclusive identification would likely require measurements (Pruett et al. 2017, Pyle 2022). In accordance with Bergmann's Rule, Alaska-group Pacific Wrens are larger, on average, than any other members of the complex in North America. We consider these recommendations as minimum standards rather than formulae for acceptance

of extralimital records, paralleling the standards of acceptance of records on the basis of calls outlined in Monk and Freeland (2026).

In applying the plumage criteria described here to all 53 records of the Winter Wren for California accepted by the California Bird Records Committee (CBRC), we found that 28 were incapable of being evaluated because of a lack of good photos. Of the remainder, we recommend three records for re-evaluation. These three birds, along with two others for which high-quality photographs were unavailable, also gave calls inconsistent with the Winter Wren according to the criteria we propose (Monk and Freeland 2026). Figure 5 shows an example of one of these. Although in some photos it appears to show a relatively pale throat and supercilium—characteristic of the Winter Wren, though also occurring with some regularity in the Pacific Wren (see above)—it lacks the crisp pale streaking on the side of the neck that is characteristic of Winter Wren and evident in 94% of the individuals we evaluated. It has an unmarked mantle, a largely dark alula, and relatively limited patterning at the sides of the upper part of the breast, thus showing more plumage characters associated with the Pacific Wren than with the Winter Wren. We recommend that such birds be left unidentified, especially in cases like this one where the call was also atypical.

Intraspecific Variation in Plumage

Our morphological analyses proved incapable of resolving consistent geographic variation within the Winter Wren and within the Pacific group of the Pacific Wren. Although we focused on features that may be relevant in distinguishing the Winter and Pacific wrens and omitted many features that informed the description of subspecies within these groups, our analyses nonetheless included some of the criteria that Rea (1986) presented for the diagnosis of certain subspecies in the Pacific group of Pacific Wren. For example, we assessed breast pattern and supercilium color, which Rea (1986) proposed as relevant in distinguishing *T. p. muiri* from *T. p. salebrosus*. Even with respect to these criteria specifically, we still detected no consistent patterns of geographic variation, i.e., the photos and specimens we examined from the range of *T. p. muiri* did not show higher frequencies of rufous supercilium or lower frequencies of heavy chest marking than did those from the range of *T. p. salebrosus*.

We suggest that a thorough reassessment of the validity of subspecies within the Pacific group of Pacific Wren may be warranted, including examination of type specimens and assessment of an array of characteristics wider than those we examined. Although preliminary, our findings are more in accordance with those of Pyle (2025) and Clements et al. (2025), who (without published analysis) considered morphological variation in the *T. p. pacificus* group insufficient to support the recognition of multiple subspecies within that group, than with those of prior authors who recognized up to five subspecies within this group (e.g., Rea 1986, Toews and Irwin 2020).

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FIGURE 5. Two views of the same ambiguous bird, which wintered in Riverside County, California, 29 November 2022–21 January 2023 (CBRC 2022-118). With respect to plumage, it resembles the Pacific Wren more closely than the Winter Wren but is somewhat intermediate; it gave calls odd for both species and sang like a Winter Wren. Additionally, see Figure 4 in Monk and Freeland (2026).

Photos by Matthew Grube

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