WESTERN BIRDS



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Western Specialty:
Oregon Spotted Towhee



Photo by © Lukas Miller of Delta, British Columbia, Canada:

Oregon Spotted Towhee (*Pipilo maculatus oregonus*), George C. Reifel Migratory Bird Sanctuary, Ladner, British Columbia, Canada, 25 April 2023.

In this issue of *Western Birds*, we feature two articles on the Spotted Towhee from the region of Vancouver, Canada. Triana I. Hohn, Lukas Miller, and Elizabeth A. Gow report on a Spotted Towhee nest built 7 meters up off the ground, far higher than any previously reported for this species, which usually nests directly on the ground. With decades of exposure to urbanization and other large-scale human modifications of their habitat, some birds adapt, and for traditionally ground-nesting birds like the Dark-eyed Junco and Spotted Towhee, this adaptation may include nesting in more elevated situations better isolated from disturbance. Also, Max Hellicar reports on two instances of preformative molt in the Spotted Towhee that included several remiges, representing both the eccentric and typical patterns of replacement of these feathers. In examples like these, we see the evolutionary tension between the costs and the benefits of replacing flimsy juvenile feathers with sturdy feathers like those worn by adults. Both of these articles concern *Pipilo maculatus oregonus*, a distinctive subspecies differing from other Spotted Towhees nesting farther south and east by its reduced white spotting on the upperparts, less white in the tail, and more extensive deeper rufous on the sides.

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Front cover photo by © Cin-Ty Lee of Houston, Texas: Western Warbling-Vireo (*Vireo swainsoni*), Houston, Texas—well east of the species' normal range—on 28 August 2026. It was distinguished, in part, from the Eastern Warbling-Vireo (*V. gilvus*) by the metrics for wing formula that Steven G. Mlodinow and Peter Pyle detail in this issue of *Western Birds*.

Back cover photo by © Liam Hutcheson of Olympia, Washington: Great Knot (*Calidris tenuirostris*), Ellen Sands, Willapa Bay, Washington, 12 May 2026, substantiating the second of the two records of this Asian species for Washington—and representing only the fifth record from western North America south of Alaska—as Allison Anholt, Joseph B. Buchanan, Cameron D. Cox, Vanessa Loverti, Liam Hutcheson. Jason P. Loghry. and Roberta Swift report in this issue of *Western Birds*.

Western Birds solicits papers that are both useful to and understandable by amateur field ornithologists and also contribute significantly to scientific literature. The journal welcomes contributions from both professionals and amateurs. Appropriate topics include distribution, migration, status, identification, geographic variation, conservation, behavior, ecology, population dynamics, habitat requirements, the effects of pollution, and techniques for censusing, sound recording, and photographing birds in the field. Papers of general interest will be considered regardless of their geographic origin, but particularly desired are reports of studies done in or bearing on North America west of the 100th meridian, including Alaska and Hawaii, northwestern Mexico, and the northeastern Pacific Ocean.

Send manuscripts to Daniel D. Gibson, P. O. Box 155, Ester, AK 99725; avesalaska@gmail.com. For matters of style consult the Suggestions to Contributors to *Western Birds* (at https://journal.westernfieldornithologists.org/index.php/westernbirds).

WESTERN BIRDS

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IDENTIFICATION AND MOLT STRATEGIES OF EASTERN AND WESTERN WARBLING-VIREOS

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ABSTRACT: The reclassification of the Eastern (*Vireo gilvus*) and Western (*V. swainsoni*) Warbling-Vireos as separate species has stimulated interest in their identification. We examined photographs of 85 Easterns and 89 Westerns in the Cornell Lab of Ornithology's Macaulay Library, finding the ratio of the distance between the tips of primaries 6 and 5 to that between the tips of p5 and p4, the "p6:5 ratio," to be the most useful difference. A p6:5 ratio >0.90 eliminates 95% of Westerns and includes 68% of Easterns, whereas a ratio <0.73 eliminates 95% of Easterns and includes 52% of Westerns. Our results support previous reports that the Eastern molts primarily on its summer grounds, before southbound migration, but are counter to reports that all Westerns migrate before molt: 36% of adults and 39% of first-fall birds had molted or commenced molt within the breeding range. Thus retention of worn plumage in adults and juvenile greater coverts in first-year birds suggests a Western, whereas replacement of these feathers does not distinguish the species. Prealternate molt is more extensive in the Eastern than the Western, aiding identification in spring. Applying our findings to records of vagrants, we identified 12 Westerns from east of the Mississippi River and in South America and six Easterns from Alaska, Arizona, California, and the Azores that appear to represent vagrants. Distinguishing many, but not all, Eastern and Western Warbling-Vireos is possible with high-quality images in which the spacing of primaries, facial markings, molt state, and/or side coloration can be assessed.

The warbling-vireos were generally considered a single species until 2025, when the American Ornithological Society's North American Classification Committee elevated the Eastern Warbling-Vireo (*Vireo gilvus*) and the Western Warbling-Vireo (*V. swainsoni*) to full species status on the basis of a suite of concordant differences, including genetics, morphology, song, molt strategy, and response to brood parasitism (Chesser et al. 2025, Clements et al. 2025). Prior to the split, several authors had proposed or evaluated various physical dissimilarities between the two taxa, including differences in back and crown color, underpart color, and bill morphology (Ridgway 1904, Oberholser 1974, Phillips 1991, Buckley and Mitra 2003, Lovell 2010, Browning 2019, Carpenter et al. 2022, Pyle 2022a). Shortly after the split,

we reassessed identification by plumage and morphology (Mlodinow et al. 2025a, b), adding primary spacing, supercilium size, and auricular color to the suite of characters that might be helpful. Unsurprisingly, many of these evaluations arrived at somewhat divergent conclusions.

Additionally, the two warbling-vireos' molts reportedly differ, with the Eastern undergoing a partial preformative and complete prebasic molt on the breeding grounds from July to September, and the Western undergoing these molts primarily at migration stopover sites in the monsoonal region of the southwestern United States and northwestern Mexico from August to October (Volker and Rohwer 1998). Therefore, during fall migration, adult Eastern and Western Warbling-Vireos should be distinguishable by whether their plumage is worn or fresh, respectively. And first-year birds should be distinguishable by whether they had replaced or retained, respectively, juvenile greater coverts. However, the timing, extent, and location of preformative and prebasic molts in birds are highly variable, as Pyle et al. (2009, 2018) found among the warbling-vireos of both species. Both species also undergo a first and a definitive prealternate molt of some to most body feathers (Volker and Rohwer 1998), with that of the Eastern reportedly more extensive, on average, than that of the Western (Pyle 2022a).

Hoping to improve our ability to distinguish the two warbling-vireo species and to clarify differences in their molt, we reviewed photographs from the Cornell Lab of Ornithology's Macaulay Library. As part of our analysis, we also evaluate prospective vagrants that we found in the Macaulay catalog and elsewhere. We do not cover differences between these species in vocalizations, which have been addressed in other publications (e.g., Sibley and Monroe 1990, Lovell 2010, Spencer 2012, Floyd 2014, Carpenter 2022, Guo 2026).

METHODS

Examination of images in the Macaulay Library has been successfully employed for studying birds' molts, plumages, and wing morphology (Pyle 2022b, 2026a, b, Clark et al. 2024, Lee and Birch 2025). We used these images to assess 11 characters (including wing morphology, eight plumage characters, and differences in preformative and prealternate molt) that have been previously suggested for the discrimination of the two warbling-vireos. We ordered the photographs according to "best quality" and selected at least 20 images for both the Eastern and Western in each of four categories: adults in fall (September–December), first-cycle birds in fall, adults in spring (March–June), and first-cycle birds in spring, resulting in a total sample size of 174 individual warbling-vireos. See Table 1 for the sizes of the samples of each age and seasonal category. Pyle, following Pyle (2022a), aged the birds and scored their molt. We ensured that none of the images in our sample represented the same individual bird (i.e., same date and location) but, when necessary, used multiple images of the same bird to assess its age and score each plumage and molt characteristic. In three cases among our initial sample, we concluded that the species as indicated in the Macaulay Library may not have been correct. We excluded these from our analysis but give our reasoning under the Discussion to address a potential circularity bias in our method. We are, therefore, confident of the identification of all birds in our sample, all but two

Table 1 Mean Values of P6:5[a], Plumage Scores, and Number of Replaced Tertials for the Eastern and Western Warbling-Vireos by Age Class and Season

	Eastern		Western	
	First year	Adult	First year	Adult
Fall	*n* = 20	*n* = 20	*n* = 21–23	*n* = 20–22
P6:5	0.95 (0.66–1.24)[b]	0.94 (0.75–1.13)	0.72 (0.44–1.01)	0.68 (0.47–0.88)
Supercilium length	1.19 (0.50–1.88)	1.07 (0.11–2.02)	1.60 (0.70–2.50)	1.63 (0.34–2.92)
Supercilium breadth	0.83 (0.68–0.98)	0.71 (0.18–1.23)	0.95 (0.39–1.51)	1.01 (0.44–1.58)
Lateral crown stripe	2.68 (0.28–5.37)	2.65 (0.10–5.19)	2.71 (–0.19–5.62)	2.79 (0.16–5.42)
Loral stripe	4.05 (1.61–6.50)	4.30 (1.95–6.65)	2.83 (–0.35–6.00)	2.55 (–0.93–6.02)
Back color	2.63 (0.97–4.79)	2.65 (0.47–4.83)	3.26 (0.99–4.88)	2.55 (0.18–4.91)
Side color	2.37 (–0.32–5.05)	2.25 (0.55–3.95)	3.00 (1.40–4.60)	2.36 (1.32–4.46)
Crown color	2.53 (0.60–4.45)	2.05 (0.78–3.32)	3.35 (1.80–4.90)	2.68 (0.43–4.93)
Auricular color	3.28 (0.38–6.17)	3.12 (0.68–3.80)	4.00 (1.81–6.19)	3.95 (2.06–5.84)
Tertials replaced	0.32 (–0.13–1.96)	—	0.00 (0.00–0.00)	—
Spring	*n* = 20–23	*n* = 20–22	*n* = 21–24	*n* = 20
P6:5	0.99 (0.66–1.32)	1.00 (0.71–1.29)	0.74 (0.50–0.99)	0.76 (0.55–0.96)
Supercilium length	1.36 (0.58–2.14)	1.33 (0.46–2.21)	1.75 (0.98–2.52)	1.75 (1.02–2.47)
Supercilium breadth	0.82 (0.46–1.19)	0.92 (0.55–1.28)	1.03 (0.71–1.35)	1.15 (0.65–1.64)
Lateral crown stripe	2.80 (0.59–5.60)	3.27 (0.72–4.55)	3.10 (0.79–5.40)	3.00 (0.69–5.31)
Loral stripe	3.57 (1.00–6.15)	4.10 (1.68–6.52)	3.17 (0.50–5.45)	2.79 (0.52–5.06)
Back color	2.57 (0.77–4.36)	3.09 (0.55–5.63)	2.29 (0.21–4.38)	2.30 (0.57–4.03)
Side color	2.52 (0.73–4.32)	3.00 (1.74–4.26)	2.00 (0.40–3.56)	2.10 (0.66–3.54)
Crown color	2.91 (1.02–4.81)	3.18 (0.72–5.65)	2.79 (1.02–4.56)	3.10 (0.72–5.85)
Auricular color	2.38 (0.03–4.79)	2.67 (0.85–4.48)	3.71 (1.39–6.03)	3.58 (2.04–7.16)
Tertials replaced	2.09 (–0.32–4.49)	2.00 (–0.23–4.14)	1.92 (–0.44–4.27)	1.15 (–0.48–2.78)

[a]See text for definition.

[b]95% confidence limits.

of which were photographed within the expected range of each species; the two vagrants are discussed further below.

The Eastern Warbling-Vireo is monotypic whereas the Western Warbling-Vireo is polytypic. From the broad geographic range of images in our sample, our analysis undoubtedly included both *V. s. swainsoni* and *V. s. brewsteri*, but we did not attempt to separate these (cf. Pyle 2025, who lumped these two subspecies on the basis phenotypic characters assessed in photographs of live birds). The locations associated with our sample excluded the much larger-billed *V. s. victoriae* of Baja California Sur, Mexico, and *V. s. sympatricus* of Puebla, Mexico, the latter a taxon of unclear taxonomic affiliation (Mlodinow et al. 2025b).

We specifically selected images in which the morphology of the primaries could be accurately assessed, and we excluded from our sample birds undergoing active molt of primaries. Our preliminary examination of wing morphology indicated that "on the folded wing of a Western Warbling Vireo, the distance between the tip of p6 and that of p5 is usually shorter than the gap

between the tip of p5 and that of p4, so that p6 – p5 < p5 – p4, whereas in the Eastern Warbling Vireo these distances are equal, so that p6 – p5 = p5 – p4 (Mlodinow et al. 2025a, b; primaries numbered innermost to outermost, from p1 to p10). To test this hypothesis, we examined the ratio of p6 – p5:p5 – p4 (the "p6:5 ratio") by following the methods of Lee and Birch (2025), who used similar ratios to identify *Empidonax* flycatchers. We imported the images of warbling-vireos into a photo-processing program, enlarged them, and then measured the distances between each set of primaries with a ruler on the monitor screen. The benefit of using ratios over actual distances is that ratios eliminate the factor of enlargement as a variable as well as reducing bias due to the angle of the wing relative to the photographer (Lee and Birch 2025). When the p6:5 ratio could be calculated from measurements of multiple images of the same bird, we either selected the image in which the wing was most perpendicular to line of sight or took a mean of several measurements, which varied by no more than 10% of each other.

In the warbling-vireos, the longest primary is often p7, with p8 and p9 progressively shorter among the outer primaries, and p6, p5, and p4 shorter to varying degrees among the inner primaries (Figures 1–4). In some birds,

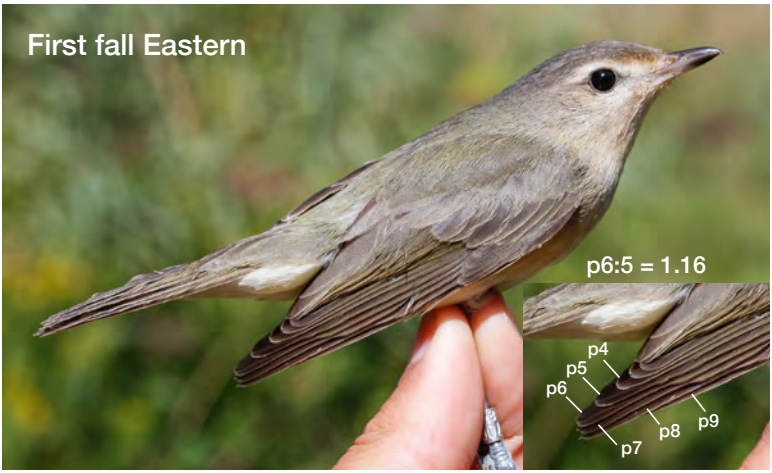


FIGURE 1. First-fall Eastern Warbling-Vireo captured for banding in Ontario, 6 September 2013, in which the ratio of the spacings between the tips of primaries 6, 5, and 4 (p6 – p5/p5 – p4, or "p6:5 ratio") is 1.16, which is diagnostic of the Eastern within our sample. Note that in this case p7 and p6 are about the same length. The bird's supercilium, with a length of 1.2 eye diameters and breadth of 0.8 eye diameters, also support its identification as the Eastern. The medium rating for darkness of the auriculars (score 3) is neutral, and the pale lores (score 1) are more typical of the Western. All marks rarely align, but the spacing of the primaries is generally the most reliable criterion. The greater coverts have been replaced, a pattern shown in our sample of photographs of southbound migrants by 100% of the Eastern Warbling-Vireos but only 39% of the Westerns. The greater coverts contrast slightly with the primary coverts, implying the bird was in its first fall. Photo used by license agreement from the Macaulay Library (ML373224281).

Photo by James Kennerly

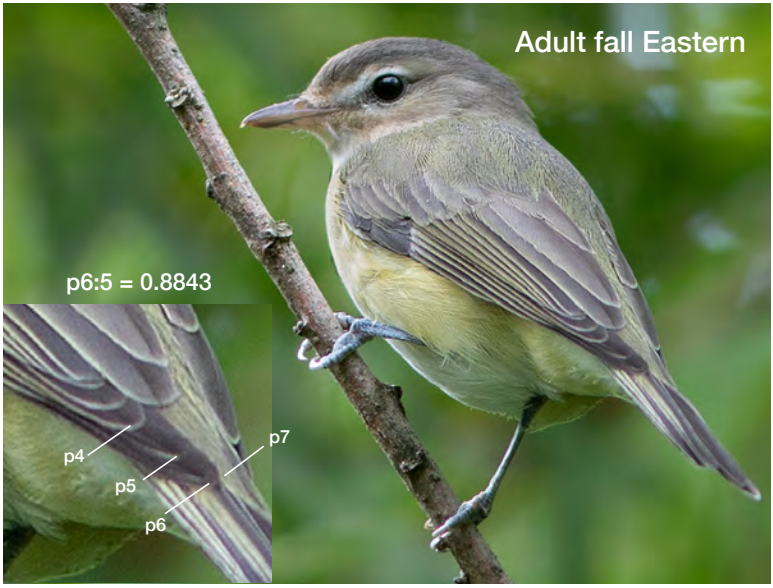


FIGURE 2. Fall adult Eastern Warbling-Vireo, photographed in Quebec on 6 September 2019. The p6:5 ratio of 0.883 is in the zone of overlap between the Eastern and Western. In this case, the tip of p7 extends a short distance beyond that of p6. The ratios of supercilium length and breadth, both 0.3, strongly support the identification as the Eastern as well, while the moderately pale loral stripe (score 2) and moderately dark auriculars (score 4) are neutral. The dusky primary coverts and broad and truncate (squared) outer primaries indicate an adult in fresh plumage. Photo used by license agreement from the Macaulay Library (ML176004381).

Photo by Suzanne Labbé

the tip of p7 falls short of the tip of p6, whereas in others the tip of p7 extends sufficiently beyond that of p6 that it creates a gap that could be confused with that between p6 and p5 (Figure 5). In such cases, however, the ratio of p7 – p6 to p6 – p5 (p7:6) is always less than 0.5, which is below the lowest end of the confidence interval for the p6:5 ratio in our sample (0.505; Table 1) and should preclude confusion due to potential misidentification of the primaries (see Lee and Birch 2025 for further discussion of this issue).

Using the same sample of images, we scored eight plumage variables, the selection of which was based on proposed differences between these two taxa in the published literature noted above. We assessed the length and breadth of the supercilium by measuring these dimensions and the vertical and horizontal diameters of the eye (excluding the orbital ring), with a tape measure on the monitor screen after importing Macaulay images into a photo-processing program and enlarging them. We define "supercilium length" as the ratio of measured supercilium length to horizontal eye diameter and "supercilium breadth" as the ratio of measured supercilium breadth to vertical eye diameter. The use of these ratios offers the same benefits as for wing morphology. When

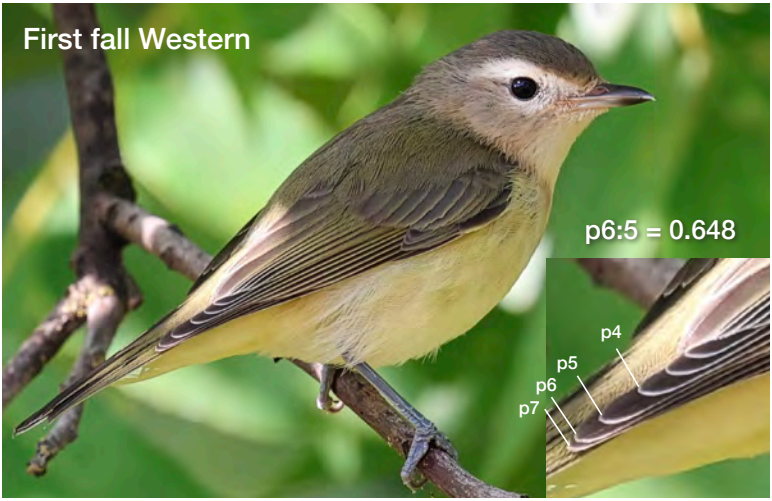


FIGURE 3. First-fall Western Warbling-Vireo photographed in California, 11 September 2024. The p6:5 ratio of 0.648 is diagnostic of the Western within our sample of photographs. The ratios of supercilium length of 1.5 and breadth of 1.3 strongly support the bird's identification as the Western, as does the pale loral stripe (score 1). The moderately pale auriculars (score 2) are neutral. The narrow and pointed primary coverts and primaries indicate a first-fall bird. The greater coverts have been replaced for migration, as seen in 39% of the immature Western Warbling-Vireos in our sample of photographs. Photo used by license agreement from the Macaulay Library (ML623623066).
Photo by Tom Uslan

the supercilium could be measured in multiple images of the same bird, we selected the image in which the head was positioned closest to true lateral.

We scored the remaining six plumage features, distinctness of the lateral crown stripe and loral stripe (absent or incomplete to distinct), extent and hue of green in the back (gray with little or no green to bright green), extent of yellow in the sides (white with little or no yellow to bright yellow), crown color (pale to dark), and auricular patch (pale or absent to dark and distinct), on a scale from one to five. See Figure 6 for examples. We calculated means and ranges (based on 95% confidence intervals) for the p6:5 ratio, supercilium length and width, and the six plumage scores (Table 1).

We also recorded the extent of molt on the basis of the replacement of greater coverts and tertials. In vireos, the greater coverts are replaced synchronously, resulting in either no coverts replaced or all coverts replaced during the preformative molt (Pyle 2022a). For birds in their first fall and first spring, we recorded whether the greater coverts were juvenile or formative. For adults in fall, we recorded whether the plumage was fresh or worn, indicating that prebasic molt had taken place before fall migration, or would take place after, respectively. We also scored the number of tertials (one to three, numbered proximally from s7 to s9) that had been replaced in molt, for both age groups in both seasons. The sequence of tertial replacement s8–s9–s7, found in the majority of birds (Pyle 2022a), prevails in the warbling-vireos as well.

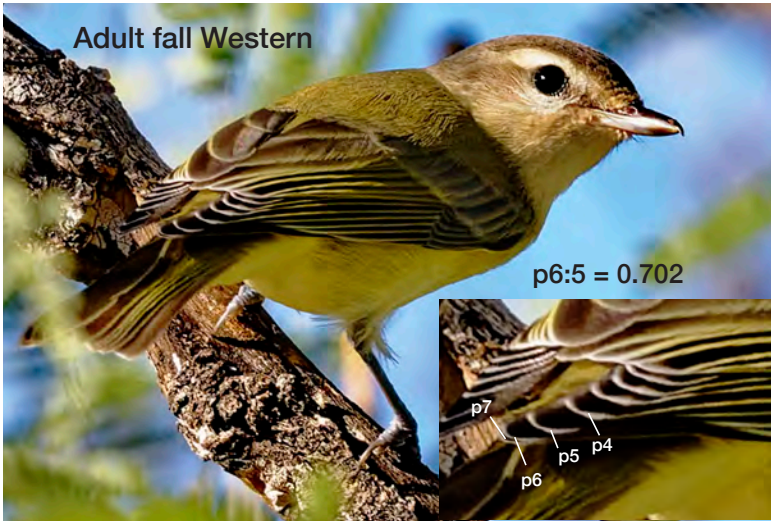


FIGURE 4. Fall adult Western Warbling-Vireo, photographed in Pima County, Arizona, on 13 September 2022. The p6:5 ratio of 0.702 is diagnostic of Western within our sample of photographs; p7 extends a short distance beyond p6. The pale loral stripe (score 1) supports the identification, the dark auriculars (score 5) are somewhat supportive, and the supercilium ratios (length 1.3, breadth 0.8) are neutral. The dusky primary coverts with olive edging and the broad, blackish, and truncate outer primaries indicate an adult in fresh plumage. Photo by an anonymous photographer used by license agreement from the Macaulay Library (ML484054071).

We evaluated records of possible vagrants of both species for which photographs were available to us from the Macaulay Library or elsewhere. These included all reports in eBird.org of birds identified as either the Western or "Eastern/Western" Warbling-Vireo recorded east of the Mississippi River, and all reports in eBird of birds identified as either the Eastern or "Eastern/Western" Warbling-Vireo recorded west of the Cascade Mountains or in the states of Nevada, California, and Arizona. We also considered records of possible vagrants from outside of continental North and Middle America, including South America, the western Palearctic, and the islands of western Alaska. Additionally, we reviewed all images of all birds photographed in the United States from December through February. We did not otherwise actively search for misidentified warbling-vireos in the Macaulay Library, e.g., during migration periods.

RESULTS

Among the characters examined (except molt), we found few substantial differences between first-cycle birds and adults of either warbling-vireo species, so we generally pooled our findings for the two age groups. We did detect seasonal differences within a species, however, and present our findings for some characters separately for fall and spring. The means of the two

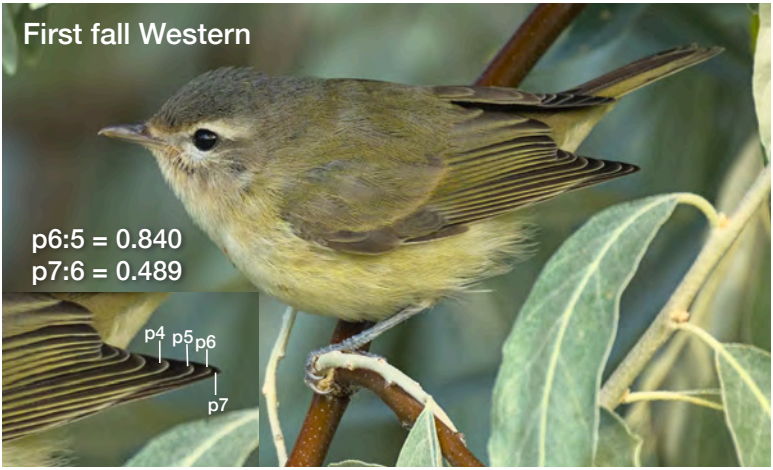


FIGURE 5. First-fall Western Warbling-Vireo photographed in Washington State, 13 September 2024. The p6:5 ratio of 0.804 is within the zone of overlap between the Eastern and Western but favors the Western. In occasional birds, such as this one, the tip of p7 extends sufficiently beyond that of p6 that it creates a gap large enough to potentially be confused with that between the tips of p6 and p5. In such cases, however, the ratio of p7 – p6/p6– p5 is always less than 0.5 (0.49 here—the highest value for this ratio in our data set), which is below the low end of the confidence interval for the p6:5 ratio in our sample (0.51; Table 1). This criterion should preclude confusion due to potential misidentifcation of the primaries. The juvenile greater coverts with pale tips have been retained, creating an indistinct wing bar and contrasting with replaced lesser coverts and scapulars, a pattern that is nearly diagnostic of migrant first-fall Westerns within our data set. Other characters supporting the identification include ratios of supercilium length (1.5) and breadth (1.0), pale lores (score 1), and dark auriculars (score 5). Photo used by license agreement from the Macaulay Library (ML 623680517).

Photo by Bartholomew Birdee

species' ratios for p6:5 and supercilium length and breadth differ distinctly but we failed to find useful differences in back color, lateral crown stripe, or fall crown color (Table 1).

Spacing of Primaries

On a warbling-vireo's folded wing, the longest primary can be either p6 or p7; if p7, the tip extends only a short distance beyond p6 (see Methods). In the Eastern, the distance between the tip of p6 and that of p5 (p6 – p5) is commonly greater than or equal to the distance between the tip of p5 and that of p4 (p5 – p4), so that p6:5 is commonly ≥1.0, whereas in the Western Warbling-Vireo p6:5 is nearly always <1.0 (Table 1, Figures 1–5). Differences in p6:5 values differed little by season (Table 1). For both seasons combined, for the Eastern (n = 85) the mean is 0.95 ± 0.12 (standard deviation; 95% confidence limit 0.71–1.18), whereas for the Western (n = 89), the mean is 0.73 ± 0.11 (95% confidence limit 0.50–0.96). On the basis of these confidence limits, 48% of the Easterns and 48% of the Westerns in our sample could be

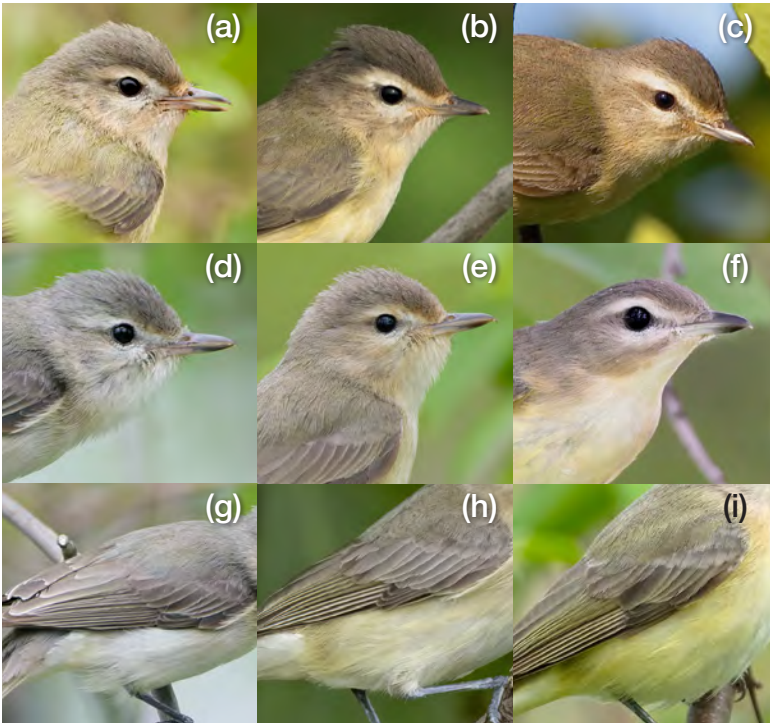


FIGURE 6. Examples of variation in the plumage of the warbling-vireos, scored on a scale from 1 to 5. Top row (all are Western Warbling-Vireos,), loral stripe (a) pale (score 1), (b) medium (score 3), (c) dark (score 5). Middle row (all are Eastern Warbling-Vireos), auriculars (d) pale (score 1), (e) medium (score 3), (f) dark (score 5). Bottom row (all are Eastern Warbling-Vireos), sides (g) with little or no yellow (score 1), (h) medium yellow (score 3), and (i) bright yellow (score 5). Photos used by license agreement from the Macaulay Library; (a) Marky Mutchler, ML493687391; (b) Darren Clark, ML607003811; (c) DigiBirdTrek CA, ML160944351; (d and g) Roy Chatburn, ML583166041; (e) Ankur Dave, ML634173927; (f) Marky Mutchler, ML641316717; (h) Iris Kilpatrick, ML617956826; (i) Don Danko, ML231812731.

identified by this metric alone. A p6:5 ratio >0.90 eliminates 95% of Westerns and includes 68% of Easterns, whereas a ratio <0.73 eliminates 95% of Easterns and includes 52% of Westerns.

Supercilium

On average, the Eastern has a shorter and narrower supercilium than does the Western, irrespective of age class and season, but in both species the supercilium is longer and broader in spring than in fall (Table 2).

Supercilium ratios of the two warbling-vireos overlap more than do the primary-spacing ratios. Nonetheless, the following criteria should be useful

Table 2 Mean Supercilium Length[a] and Breadth[b] in the Eastern and Western Warbling-Vireos by Species and Season

	Eastern		Western	
	Supercilium length	Supercilium breadth	Supercilium length	Supercilium breadth
Fall	1.1 ± 0.4[c] (0.3–2.0)[d]	0.8 ± 0.2 (0.4–1.2)	1.6 ± 0.6 (0.5–2.7)	1.0 ± 0.3 (0.4–1.5)
Spring	1.4 ± 0.4 (0.5–2.2)	0.9 ± 0.2 (0.5–1.2)	1.8 ± 0.4 (1.0–2.5)	1.1 ± 0.2 (0.7–1.5)

[a]Measured supercilium length/horizontal eye diameter.
[b]Measured supercilium breadth/vertical eye diameter.
[c]Standard deviation.
[d]95% confidence limits.

for identifying the Eastern in spring and the Western in fall. In spring, a supercilium length of ≤1.0 (i.e., less than the horizontal diameter of that bird's eye) rules out the Western in our sample (32% of Eastern; 0% of Western). In fall, ratios strongly favoring the Western include a supercilium breadth ≥1.1 (34% of Western; 5% of Eastern) and a supercilium length ≥1.9 (33% of Western; 5% of Eastern). Also in fall, the combination of a supercilium length ≥1.7 and a breadth ≥1.1 eliminates the Eastern in our sample (21% of Western; 0% of Eastern).

Loral Stripe

On average, the Western has the loral stripe weaker than in the Eastern, though these differences are more pronounced in fall. A weak loral stripe strongly suggests the Western in fall but is not as indicative in spring (Table 3).

Auricular Color

The auriculars average paler in the Eastern than in the Western, especially in spring. We scored only 2% of Westerns but 17% of Easterns as having very pale auriculars (score of 1) in both spring and fall. We found very dark auriculars (score of 5) on 0% of Easterns versus 21% of Westerns in spring, and on 11% of Easterns versus 36% of Westerns in fall.

Crown Color

The crown color of the two species is very similar in spring, but in fall, the Eastern has a paler crown on average (Table 3). In fall, we assigned a score of 4 or 5 (indicating a dark crown) to only 8% of Easterns versus 44% of Westerns, while we assigned a score of 1 or 2 (indicating a light crown) to 59% of Easterns and 23% of Westerns.

Table 3 Percent Frequency of Scores of Strength of the Loral Stripe in the Eastern and Western Warbling-Vireos by Species and Season

	Fall		Spring	
	Eastern	Western	Eastern	Western
Weak (score 1)	3	43	7	19
Intermediate (score 2–4)	34	35	44	60
Strong (score 5)	63	22	49	21

Side Color

In fall, the color of the warbling-vireos' sides is similar, but in spring, the Eastern averages brighter or yellower. In spring, we rated 27% of Easterns as having bright sides (score of 4 or 5 on a scale of 1–5) compared to only 2% of Westerns. Dull sides (score of 1 or 2) are less useful, represented by 75% of Westerns and 42% of Easterns.

Potentially Helpful Combinations

Several of the above characters can be combined to aid identification. In the fall, we found the combination of pale to intermediate lores (score of 1–3 on 1–5 scale) and a supercilium breadth of ≥1.1 in 0% of Easterns and 30% of Westerns, whereas we found a supercilium length of ≤1.0 combined with relatively pale auriculars (score of 1–3 on 1–5 scale) in 0% of Westerns and 16% of Easterns. In spring, the combination of pale auriculars (1–2 on a scale of 1–5) and a supercilium breadth of <1.0 appeared in only 2% of Westerns versus 25% of Easterns.

Molt

The photographs we reviewed of warbling-vireos in fall were all taken just before or during migration in Canada or the United States. Among the adult Easterns in fall, 17 of 20 (photographed from 1 September to 5 October) were in freshly molted plumage, whereas three (photographed 2–4 September) were in worn plumage and had not yet undergone most or any of their prebasic molt (Figure 7). Two of these birds, in Michigan and Ohio, may still have been on or near their breeding grounds (and so still had the opportunity to molt prior to migration), whereas one in Texas was south of the breeding range and presumably was a molt migrant (Figure 7). Among adult Westerns, 8 of 22 (36%) birds, recorded from 16 September to 20 November in Alaska (2), Washington (1), California (3), New Mexico (1), and Arizona (1, Figure 7), were in fresh plumage and had molted somewhere within the breeding range, whereas the remaining 13 (59%; recorded from 2 to 30 September) were in worn plumage and were undergoing molt migration (Figure 7).

Among first-fall birds, none of 20 Easterns had retained juvenile greater coverts, whereas 14 of 23 Westerns (61%) had done so (Figure 8). Among first-spring birds, only four of 24 Westerns (17%) and none of 23 first-spring Easterns had retained the juvenile greater coverts (Figure 9). The seasonal difference within the Western (61% to 17%) results from many birds replacing the juvenile greater coverts during preformative molt on the molting or wintering grounds.

With respect to the tertials, fall adults had either replaced or retained all three feathers (s7–s9), coinciding with whether or not the bird has undergone its prebasic molt (see above). Among first-fall birds, none of 23 Westerns and three of 20 Easterns (15%) had replaced juvenile tertials with formative tertials. Of these three Easterns, one each had molted one (s8), two (s8–s9), or three (s7–s9) tertials (Table 1, Figure 7), for a mean of 0.3 tertials replaced per individual. Among adults in spring, 17 of 20 Easterns (85%) had replaced one to three tertials during the definitive prealternate molt, with a mean of 1.96 tertials replaced, and 16 of 20 Westerns (80%) had replaced a mean of

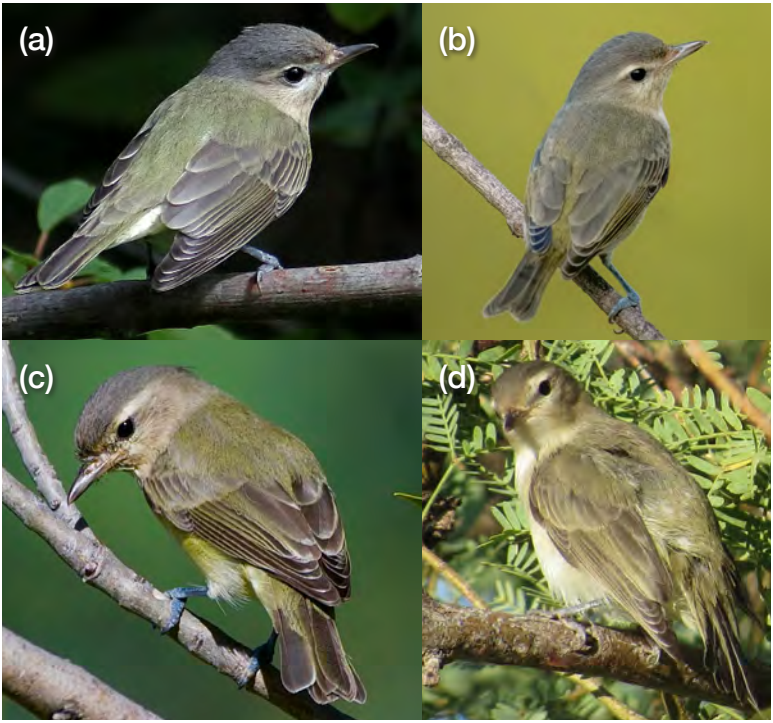


FIGURE 7. Adult warbling-vireos showing fresh and worn plumage during fall migration. (a) Eastern Warbling-Vireo in fresh plumage, Ontario, 11 September 2023; (b) Eastern Warbling-Vireo in worn plumage, Texas, 2 September 2023; (c) Western Warbling-Vireo in fresh plumage, Arizona, 16 September 2022; (d) Western Warbling-Vireo in worn plumage, Arizona, 30 September 2019. All but one Eastern in our sample had undergone a complete prebasic molt prior to fall migration, the exception being the bird from Texas (b), that was south of the breeding grounds in worn plumage. Note that the worn Eastern (b) had replaced all three tertials (s7–s9) and the worn Western (d) had replaced only two tertials (s8 and s9) during the previous prealternate molt. Photos used by license agreement from the Macaulay Library; (a) John Cameron, ML 608729100; (b) Bob Hurst, ML 608467919; (c) Tim DeJonghe, ML484725571; (d) Vincent Maglio, ML 179731601.

1.15 tertials (Table 1, Figure 9). Eight adult Easterns (40%) but only one adult Western (5% of our sample) had replaced all three tertials (Figures 7 and 9).

Assessing the replacement of tertials during the first prealternate molt is complicated, as during a suspended preformative molt they may be replaced at stopover locations or on the winter grounds, and so appear fresher than those replaced on the breeding grounds. Thus whether a tertial is formative or first alternate may be unclear (Pyle 2022c). Among first-spring birds, 20 of 23 Easterns (87%) had replaced a mean of 2.1 tertials and 20 of 24 Westerns (83%) had replaced a mean of 1.9 tertials during either the preformative and/

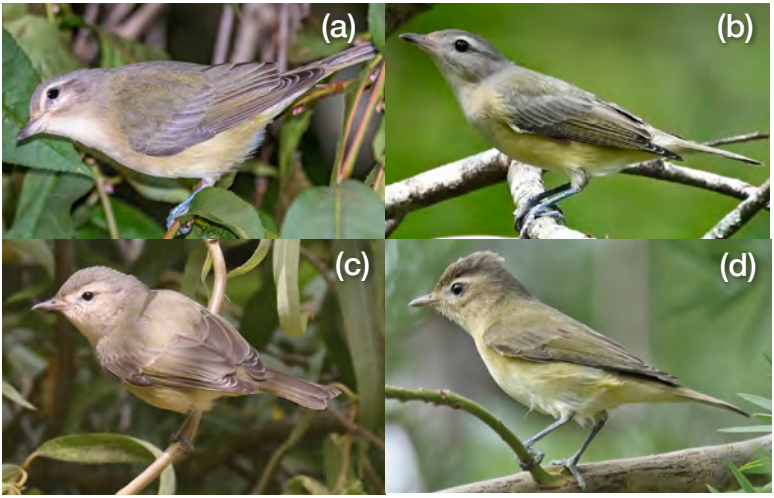


FIGURE 8. First-fall warbling-vireos showing variation in replacement of the greater coverts and tertials during the preformative molt. (a) Eastern Warbling-Vireo that has replaced its juvenile greater coverts but retained juvenile tertials, New York, 9 September 2018; (b) Eastern Warbling-Vireo that has replaced its juvenile greater coverts and one of its tertials (s8), Alabama, 7 September 2021; (c) Western Warbling-Vireo with retained juvenile greater coverts and tertials, California, 17 September 2022; (d) Western Warbling-Vireo that has replaced its juvenile greater coverts but retained its juvenile tertials, California, 13 September 2022. As expected, all four of these birds have retained juvenile primaries and rectrices that are narrow, tapered at the tips, and more worn than in adults that had replaced these feathers. Photos used by license agreement from the Macaulay Library; (a) Alan Schroeder, ML114492951; (b) Joe Wujcik, ML367558161; (c) "Pair of Wing-Nuts," ML485488091; (d) George Nothhelfer, ML483892481.

or the first prealternate molt (Table 1, Figure 8). Thirteen of the 23 first-spring Easterns (57%) and 11 of the 24 Westerns (46%) had replaced all three tertials. In eight Easterns and 10 Westerns, the middle tertial (s8) was more worn than the inner (s9) and/or outer (s7) tertial, indicating that molt was suspended after s8 was replaced, whereas in five Easterns and one Western, s8 was much fresher than both s7 and s9, indicating that it had been replaced twice and so, by definition, was a first alternate feather, provided that the tertials were replaced in the order s8–s9–s7 during the preformative molt (Figure 8, Pyle 2022c).

DISCUSSION

Encouragingly, our analysis of photographs suggests several characteristics or combinations of characteristics that distinguish a subset of the two warbling-vireo species. We then used our findings to assess the validity of records of vagrants of each species.

Molt

Volker and Rohwer (1998) reported that all adult Eastern Warbling-Vireos molt on their breeding grounds, before fall migration, whereas all adult West-

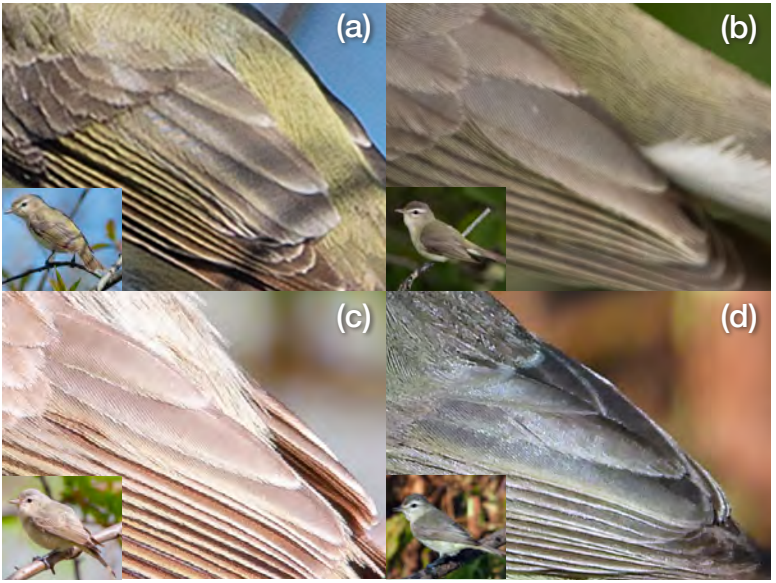


FIGURE 9. Spring warbling-vireos showing variation in replacement of the tertials during the first and definitive prealternate molts. (a) Adult Eastern Warbling-Vireo with three replaced alternate tertials, Michigan, 5 May 2019; (b) adult Western Warbling-Vireo with one replaced alternate tertial (s8) and two retained basic tertials, Idaho, 2 June 2022; (c) first-spring Eastern Warbling-Vireo in which s7 and s9 are formative (replaced the previous fall) and s8 is alternate (replaced once in fall and again in spring), Massachusetts, 8 May 2022; (d) first-spring Western Warbling-Vireo that had replaced all three tertials during the preformative molt (but none during the first prealternate molt), with s8 more worn than s7 and s9, reflecting the sequence of replacement and possibly a suspension of molt, California, 18 May 2021. In each case these patterns support the identification; see text and Pyle (2022c) for discussion of molt terminology in migratory birds in which the tertials are replaced in these patterns during the preformative and prealternate molts. Photos used by license agreement from the Macaulay Library; (a) Jocelyn Anderson, ML156639701; (b) Darren Clark, ML459525131; (c) Pavel Hanc, ML 445877871); (d) James Maley, ML345203711.

ern Warbling-Vireos molt south of the breeding range, at stopover locations or on the winter grounds. Our results indicate that this is largely true of the Eastern (with only one exception among a sample of 20), whereas in the Western, 36% of the adults in our sample of 22 had undergone a complete prebasic molt prior to departure from the breeding range. Similarly, during the preformative molt, all 20 first-fall Easterns had replaced wing coverts prior to fall migration whereas in the Western 39% of 24 individuals had replaced them and 61% had retained them for migration. This supports the conclusion of Pyle et al. (2009, 2018) that the timing and location of the prebasic molt in the warbling-vireos, as well as other species that undergo molt migration, is variable. The decision of an adult to molt before or after migration may correspond to whether it bred successfully as well as the availability of food

resources on its summer grounds (Pyle et al. 2009, 2018). These factors can vary from year to year for both species, but especially for the Western, for which food resources in the breeding range typically diminish during late summer. Examples demonstrating that the Eastern occasionally undergoes molt migration include one in our sample that was in worn condition in central Texas (ML622985289) and one undergoing molt photographed in Alabama (Mlodinow et al. 2025a). Conceivably, molt migration might be less adaptive in those portions of the Western's range that are relatively wet in summer (e.g., western Washington) and more adaptive in those parts of the Eastern's range that are relatively dry in summer (e.g., eastern Colorado). In any case, with rare exceptions, retention of worn plumage in fall adults and retention of juvenile greater coverts in first-fall birds indicates a Western, whereas replacement of these feathers cannot be used to distinguish the species, as Voelker and Rohwer (1998) inferred. Voelker and Rowher (1998) based their analysis largely on birds undergoing active molt (of which adults are difficult to locate on migration), whereas our analysis also incorporates plumage wear, which may account for the difference in our conclusions.

Both species undergo a prealternate molt (Voelker and Rohwer 1998, Pyle 2022a) that includes at least some body feathers. Our results regarding changes in the coloration of the sides (see above), typically the last feathers to be replaced in a molt, suggest that this molt may include most or all body feathers in the Eastern but not in the Western. In the Eastern, the loral stripe averages less distinct in spring than in fall, the opposite in the Western. This discrepancy may imply prealternate molt of these feathers in the Eastern, whereas in the Western it may be due instead to wearing of pale fringes from unmolted loral feathers in some birds. Likewise, the auriculars becomes paler in spring in the Eastern, likely a result of prealternate molt, whereas they remain similar year round in the Western, perhaps signifying lack of feather replacement. These suppositions, along with more tertials being replaced during the definitive prealternate molt in the Eastern than in the Western, imply a more extensive prealternate molt in the Eastern than in the Western, as Pyle (2022a) suggested. As many Westerns molt later in the summer or fall than do the Easterns, and on molting grounds following southbound migration, by spring, the Eastern's plumage is more worn and a more extensive prealternate molt may be more adaptive.

Among first-spring warbling-vireos, both species had replaced a similar number of tertials, but their disparate wear patterns indicated that the feathers had been replaced at various times between fall and spring. Pyle (2022c) discussed similar patterns of replacement in first-year Summer Tanagers (*Piranga rubra*) and Indigo Buntings (*Passerina cyanea*) and distinguished the formative and first alternate feathers on the basis of a fixed replacement sequence of the middle tertial (s8) followed by the inner (s9) and outer (s7) tertials. Under this interpretation, among the photographs we studied, the Eastern Warbling-Vireo had replaced a mean of 2.1 tertials during the preformative molt, compared to a mean of only 0.3 tertials replaced during this molt prior to fall migration. Eight of 23 first-spring Easterns (35%), furthermore, showed s8 older than s7 and/or s9, indicating replacement in late fall rather than spring. These results indicate that many first-year Eastern Warbling-Vireos replace the tertials at stopover locations or upon arrival at the winter

grounds in late fall, following replacement of body feathers and wing coverts on or near the breeding grounds and thus can suspend the preformative molt for migration.

Most first-year Western Warbling-Vireos appeared to have replaced most tertials during the preformative molt on molting grounds or shortly after arrival on the winter grounds in fall, as expected (Voelker and Rohwer 1998). But 10 of 24 (42%) had suspended molt of the tertials at some time over the winter after s8 but before s7 and/or s9 had been replaced. In five of 23 first-spring Easterns (22%) but only one of 24 first-spring Westerns (4%), s8 had been replaced for a second time, further supporting the conclusion that the prealternate molt averages more extensive in the Eastern than in the Western Warbling-Vireo. Exposed to intense sun, the tertials protect the remaining remiges, a selective force that may drive replacement of these feathers twice in the bird's first year, during both the preformative and first prealternate molts (Pyle 2022a, c).

There are instances in which molt patterns can be helpful in the identification of the warbling-vireos. Adults that migrate in fall in worn plumage and first-cycle birds that retain their juvenile greater coverts during fall migration or later can be identified as the Western with a high degree of confidence. Juvenile greater coverts can be recognized by being relatively worn and often showing pale tips that result in a faint wing bar, along with molt limits or contrasts between juvenile greater coverts and replaced lesser and median coverts of the formative plumage (Pyle 2022a; compare Figures 5 and 8). Neither adults in fresh plumage, nor first-fall birds that have replaced greater coverts for fall migration, can be confidently identified by molt patterns alone, although the great majority of Easterns should show these plumage states.

In spring, the prealternate molt being more extensive in the Eastern than in the Western results in some average plumage differences that could be useful for identification. Some Eastern Warbling-Vireos of both age classes replace feathers of the sides with brighter yellow feathers, whereas in the Western Warbling-Vireo these feathers appear not to be replaced and thus are more worn and faded (less yellowish) than in fall. Lack of molt may also result in the lores being darker in spring in the Western than in the Eastern, which may show fresher and paler-fringed feathers of the alternate plumage in this region. These differences can contribute to the identification of some spring birds, as mentioned above. In adults, the replacement of three tertials during the definitive prealternate molt appears to be a useful average character for identification, having occurred in 40% of adult Easterns but in only one adult Western in our sample. Likewise, all three tertials replaced once and with the middle feather (s8) replaced for a second time may be useful for identifying some first-spring birds, having occurred in 22% of the Easterns but only 4% of the Westerns in our sample.

A Summary of Identification Criteria

Marks that are often of use for identifying any given warbling-vireo include spacing of the primaries, differences in molt status, supercilium length and breadth, brightness of yellow on the sides (spring only), and the darkness of the auriculars, lores, and crown (see Figure 10 for examples of a typical Eastern and Western). We found that back color and the presence or absence of



FIGURE 10. Only a minority of each species of warbling-vireo is "typical" in all the features that we quantified. However, these two birds, an adult Eastern Warbling-Vireo on the top (a) and a first-fall Western Warbling-Vireo on the bottom (b), are nearly exemplary. Note that the Western but not the Eastern has retained the juvenile greater coverts and that this Eastern is quite bright yellow for a spring bird, brighter than any spring Western in our sample. We scored these birds as follows: with the score for the Eastern given first: p6:5 ratio 1.045 and 0.723, supercilium length 1.2 and 1.7 eye diameters, supercilium breadth 0.7 and 1.3 eye diameters, auricular color 2 and 3 , lore intensity 3 and 1. Photos used by license agreement from the Macaulay Library; (a) Don Danko, ML231812731, Franklin Co., Ohio, 7 May 2020; (b) Marc Kramer, ML644087559, St. Paul Island, Alaska, 27 September 2023.

Table 4 Mean Score of Auricular Color[a] in the Eastern and Western Warbling-Vireos by Species and Season

	Eastern	Western
Fall	3.1 ± 1.4[b]	4.0 ± 1.0
Spring	2.5 ± 1.0	3.7 ± 1.0

[a]On a scale of 1 to 5 from light to dark.
[b]Standard deviation.

Table 5 Mean Score of Crown Color[a] in the Eastern and Western Warbling-Vireos by Species and Season

	Eastern	Western
Fall	2.3 ± 1.1[b]	3.1 ± 1.0
Spring	3.0 ± 1.0	2.9 ± 1.0

[a]On a scale of 1 to 5 from light to dark.
[b]Standard deviation.

Table 6 Mean Score of Side Color[a] in the Eastern and Western Warbling-Vireos by Species and Season

	Eastern	Western
Fall	2.4 ± 1.3[b]	2.7 ± 1.0
Spring	2.8 ± 1.1	2.1 ± 0.8

[a]On a scale of 1 to 5 from duller to brighter or yellower.
[b]Standard deviation.

a lateral crown stripe are not useful criteria. Detailed photographs are likely needed for definitive identification, especially those that provide a lateral view of the wing and head and a crisp image of the primaries.

When these marks are assessed, it is important that the effects of lighting and perspective be recognized. For instance, high-contrast lighting may cause the crown and auriculars to appear darker, an abundance of light reflected off green leaves may make the sides appear brighter yellow, and the loral stripe may seem less evident when the bird is looking away and darker when the bird is looking toward the observer. Furthermore, the bird's posture and attitude may alter some characteristics. For example, the breadth of a warbling vireo's supercilium may increase when its crown feathers are raised. The apparent p6:5 ratio may vary from photo to photo by up to 10%, so a bird should be assessed in multiple photographs, preferably with the bird at differing angles. When judging the spacing of the primaries, observers need to be aware that the longest primary may be p7, not p6, and when a bird's state of molt is evaluated, the bird should be aged first (see figures for tips on age determination in spring and fall).

The most useful characters for identification, by species and season, are as follows. Percentages represent the proportion of birds with the specified feature among the sample of photographs we examined, representing 20–24 individuals of each season and age class.

Favoring the Eastern in fall

1. p6:5 > 0.89—0% of the Western and 67% of the Eastern.
2. Pale auriculars (score of 1)—2% of the Western and 17% of the Eastern.

Favoring the Western in fall

1. p6:5 < 0.72—0% of the Eastern and 41% of the Western.
2. Supercilium breadth ≥ 1.1—5% of the Eastern and 34% of the Western.
3. Supercilium length ≥ 1.9—5% of the Eastern and 33% of the Western.
4. Supercilium length ≥ 1.7 and breadth ≥ 1.1—0% of the Eastern and 21% of the Western.
5. Weak loral stripe (score of 1)—3% of the Eastern and 43% of the Western.
6. Pale to intermediate lores (score of 1–3 on 1–5 scale) *and* a supercilium breadth ≥ 1.1—0% of the Eastern and 30% of the Western.
7. Adult migrating in worn plumage—5% of the Eastern and 64% of the Western
8. First-fall bird with retained juvenile greater coverts—0% of the Eastern and 61% of the Western.

Favoring the Eastern in spring

1. p6:5 > 0.89—2% of the Western and 76% of the Eastern.
2. Supercilium length ≤ 1.0—0% of the Western and 32% of the Eastern.
3. Pale auriculars (score of 1)—2% of the Western and 17% of the Eastern.
4. Bright side color (score of 4 or 5)—2% of the Western and 27% of the Eastern.
5. Supercilium breadth < 1.0 combined with pale auriculars (score of 1–2)—2% of the Western and 25% of the Eastern.
6. Adult with three replaced tertials—5% of the Western and 40% of the Eastern.
7. First-year bird with s8 replaced twice—4% of the Western and 22% of the Eastern.

Favoring the Western in spring

1. p6:5 < 0.71—0% of the Eastern and 39% of the Western.
2. Dark auriculars (score of 5)—0% of the Eastern and 21% of the Western.
3. First-year bird with retained juvenile greater coverts—0% of the Eastern and 17% of the Western.

In this study, we did not evaluate bill morphology or song characteristics. Additionally, although average differences in bill length and depth between the Eastern and Western Warbling-Vireos are long established (Ridgway 1904, Phillips 1991, Pyle 2022a), we chose not to pursue these characters as substantial overlap in both length and depth has been demonstrated (Lovell 2010, Carpenter et al. 2022, Mlodinow et al. 2025a, b), and this character is difficult to quantify from photographs. We did note that many Easterns showed a downward bulge along the gonys that appears to be absent in most Westerns (Figure 11), and an examination of specimens may prove this apparent difference to be of value (Phillips 1991).

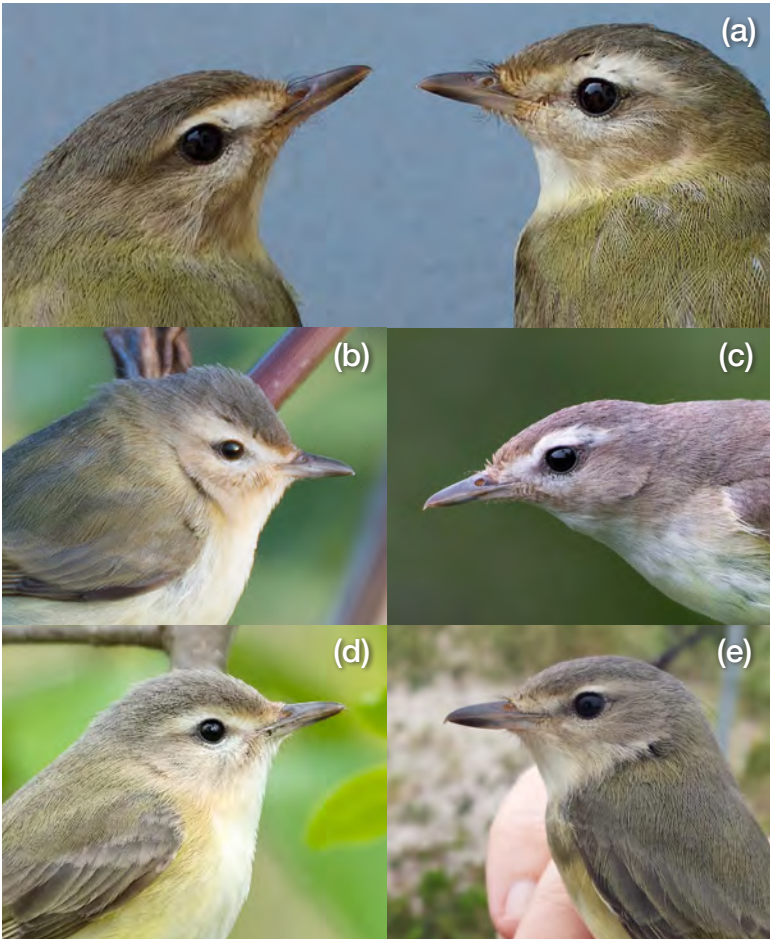


Figure 11. Bill-size variation in the Western (a–c) and Eastern (d–e) warbling-vireos. Shown are examples of each species with smaller and larger bills. The bills of Westerns that are very small and slender (e.g., b) and those of Easterns that are very stout and have a bulge to the lower mandible (e.g., e) can aid in and may be diagnostic for identification. Photos used by license agreement from the Macaulay Library; (a) Matt Brady, ML45687211, Southeast Farallon Island, California, 19 September 2010; (b) Marc Kramer, ML644087559, St. Paul Island, Alaska, 27 September 2023; (c) Tanner Martin, ML105788761, Stevens Co., Washington, 27 June 2018; (d) Don Danko, ML231812731, Franklin Co., Ohio, 7 May 2020; (e) David M. Bell, ML20122971, Halifax Co., Nova Scotia, 9 September 2015.

Possibly Misidentified Birds

For our sample, we initially selected three Eastern Warbling-Vireos so identified in the Macaulay Library and photographed well within the normal range of Eastern but later excluded them because we concluded that their identification was questionable. Here we outline our reasons to avoid potential circularity in our sample selection.

1. A first-fall bird photographed in St. Tammany Parish, Louisiana, on 27 November 2023 (https://ebird.org/checklist/S155330192) has a large supercilium (length 1.5 and breadth 1.1 eye diameters) and pale lores (score of 1), which are more consistent with the Western, while its p6:5 ratio of 0.901 is at the uppermost limit for the Western but also within the range of the Eastern. Its greater coverts were replaced, which is consistent with an Eastern but does not rule out a Western. None of the Easterns in our sample had so broad a supercilium *and* pale lores, but given its molt status and primary spacing, it may have been a Western and is thus best left unidentified. Birds such as this raise the possibility of a hybrid Western × Eastern Warbling-Vireo.

2. A first-winter bird photographed in Richmond County, Georgia, on 9 December 2019 (https://ebird.org/checklist/S62178398) was identified as an Eastern Warbling-Vireo, but we conclude that it is a Western—see discussion below under records of vagrants.

3. A first-fall warbling-vireo identified as an Eastern in Rockingham County, New Hampshire, on 29 September 2021 (https://ebird.org/checklist/S95357619) had retained juvenile greater coverts, a supercilium length of 1.5, and dark auriculars; neither the retained coverts nor this combination of supercilium length and auricular color were found in any of the other first-fall Eastern Warbling-Vireos in our sample. Its supercilium breadth (0.8) is more typical of the Eastern, however, and its p6:5 ratio of 0.817 is at the low end for the Eastern. Possibly, the bird had not yet begun its fall migration and its greater coverts could still be replaced, or the bird was a rare molt-migrant Eastern, but given these conflicting characters we prefer to leave the identification unresolved.

Vagrants

Using these criteria, we evaluated records of vagrants of which photographs were available to us from the Macaulay Library or elsewhere. The 12 vagrant Westerns and 6 vagrant Easterns that we accept are listed in Tables 7 and 8, respectively, along with the supportive and contradictory criteria. Examples of five of these suspected vagrants are shown in Figure 12.

There is one additional record of the Western Warbling-Vireo from the eastern U.S. that we did not review, based on a specimen (Tall Timbers Research Station 1047) collected as a tower-kill casualty in Tallahassee, Florida, 29 October 1956. This bird was initially identified by Allan R. Phillips (Phillips 1991), and the identification was later reviewed and supported by Henry Stevenson (Stevenson and Anderson 1994).

Most of these vagrant Western Warbling-Vireos were identified as such by the observers. The exceptions were the bird in Georgia (identified as an Eastern; see Misidentified Birds, above) and the birds in Ecuador and Kentucky, which had not been identified to the species level. The Ecuador record

Table 7 Vagrants of the Western Warbling-Vireo[a]

Location, date, and source[b]	Age and molt	p6:5 ratio	Supercilium	Lores	Auriculars
Fire Island Lighthouse, Suffolk Co., Long Island, New York, 29 Sep 1998 (Buckley and Mitra 2003)					
	first fall, **juv. coverts retained**	0.885	length 1.3, *breadth 0.8*	medium (3)	medium (3)
NE of Marlboro, Stark County, Ohio, 17–22 Nov 2008 (S277054973, S128340353)[c]					
	first fall, *juv. coverts replaced*	**0.596**	*length 1.0,* *breadth 0.8*	medium (3)	medium (3)
Bon Portage Island, Shelburne Co., Nova Scotia, 24 Oct 2013 (S15576234)[b]					
	first fall, *juv. coverts replaced*	**0.625**	*length 1.0,* *breadth 0.7*	medium (3)	medium (3)
Dade County, Florida, 15 Dec 2015–22 Jan 2016 (S103028555, S101976136, S52440159, S26500024)					
	winter adult, coverts replaced	0.833	**length 2.0**, breadth 0.9	**pale (1)**	medium- dark (4)
Jardín Botánico de Quito, Pichincha Province, Ecuador, 11 Apr 2017 (S35871298)					
	first spring, **juv. coverts and tertials retained**	0.794	**length 1.5, breadth 1.3**	medium (3)	**pale (1)**
Prinzy Swamp Nature Park, Richmond Co., Georgia, 9 Dec 2019 (S62178398)					
	first winter, **juv. coverts retained**	**0.726**	**length 1.5, breadth 1.3**	**pale (1)**	**medium- dark (4)**
Escambia Co., Florida, 11 Dec 2022 (S123825798)					
	first winter, **juv coverts retained**	**0.713**	n/a[d]	n/a	**dark (5)**
Cape May, Cape May Co., New Jersey, 18–21 Dec 2022 (S124275843, S124254725, S124306712)					
	first winter, **juv. coverts retained**	0.836	**length 1.7,** *breadth 0.7*	**pale (1)**	**medium-dark (4)**
Pea Island, Dare Co., North Carolina, 5 Dec 2023 (S155797525)					
	first winter, **juv. coverts retained**	**0.642**	**length 2.0, breadth 1.2**	n/a	n/a
New Haven, New Haven Co., Connecticut, 16 Dec 2023–6 Jan 2024 (S158308227, S158283933)					
	first winter, **juv. coverts retained**	**0.672**	length 1.2, *breadth 0.7*	**pale (1)**	**dark (5)**
Florida Atlantic University, Palm Beach Co., Florida, 27 Nov–3 Dec 2024 (S203830594, S204176937)					
	fall adult	n/a	**length. 1.6,** breadth 1.0	*dark (5)*	medium (3)
Eva Bandman Park, Jefferson Co., Kentucky, 28 Nov 2025 (S286553933)					
	fall adult, coverts replaced	0.934	**length 1.4,** breadth 1.0	**pale (1)**	**dark (4 or 5)**

[a]Boldface, characters that support the identification; italics, contradictory characters.

[b]Sources prefixed with "S" are eBird checklists accessible by appending the entire code onto "https://ebird.org/checklist/."

[c]Identified as the Western Warbling-Vireo because of the very small value of p6:5 in spite of other conflicting characters.

[d]n/a, not assessable.

represents the first of either species in South America (Mlodinow et al. 2025b; Figure 12). Lacking photographs, we did not evaluate reports of two other Western Warbling-Vireos from eastern North America—one from Ontario, 2 November 2009 (https://ebird.org/checklist/S41616262) and one from Florida, 15–16 March 2019 (https://ebird.org/checklist/S53929591, https://

Table 8 Vagrants of the Eastern Warbling-Vireo[a]

Location, date, and source[b]	Age and molt	p6:5 ratio	Supercilium	Lores	Auriculars
Peachtree Valley, Monterey Co., California, 24 Oct (S97803473, S97804606)					
	first fall, **juv. coverts**		**length. 1.0,**		
	replaced	**(1.042)**	**breadth 0.8**	n/a[c]	*dark (5)*
Cienega National Conservation Area, Pima Co., Arjzona, 30 Jun 2014 (S18957138, S18956900)					
	first spring, juv. covs.		**length 1.2,**	**medium-**	
	replaced	n/a	breadth 1.0	**dark (4)**	**medium pale (2)**
Gambell, St. Lawrence I., Alaska, 12 Sep 2018 (S48776031, S48475204, S70861592, S51745916)					
			length 2.0,		
	adult, **coverts replaced**	**1.029**	**breadth 0.8**	**dark (5)**	medium (3)
Lake Havasu City, Mohave Co., Arizona, 1 May 2019 (S55660082)					
	spring adult, one tertial		**length. 1.0,**		
	replaced	**1.241**	**breadth 0.8**	medium (3)	medium dark (4)
Corvo, Azores, Portugal, 25 Sep 2021 (Doniol-Valcroze et al. 2025)					
	first fall, **juv. coverts**		**length. 1.2,**		
	replaced	n/a	**breadth 0.7**	**dark (5)**	medium-dark (4)
Corvo, Azores, Portugal, 9 Oct 2024 (Doniol-Valcroze et al. 2025)					
	first fall, **juv. coverrts**		**length. 0.8,**		
	replaced	n/a	breadth 0.9	medium (3)	**pale (1)**

[a]Boldface, characters that support the identification; italics, contradictory characters.

[b]Sources prefixed with "S" are eBird checklists accessible by appending the entire code onto https://ebird.org/checklist/.

[c]n/a, not assessable.

ebird.org/checklist/S54000891. Our analysis implies that any warbling-vireo east of the Mississippi River in November or December should be identified carefully, as the Western Warbling-Vireo fits a general pattern of western passerines occurring in eastern North America during late fall migration (Farnsworth and Iliff 2012).

The bird in Monterey County, identified as an Eastern Warbling-Vireo by the observers, represents, to our knowledge, the only potentially acceptable record of that species for California. We concur with the identification as the Eastern on the basis of supercilium size (length 1.0 and breadth 0.8) and dark lores (5). The spacing of the primaries was difficult to evaluate from photographs because of the angles of the wings and obstructing vegetation, but from three images (ML389366471, ML389366491, and ML389366551) we tentatively estimated ratios of 1.06, 1.04, and 1.03, all exceeding the maximum ratio observed for the Western in our sample. The bill also looks large from above (ML389365171) and large and with a bulge to the lower mandible in images showing it in profile (e.g., ML389365161, ML389366471). The Eastern Warbling-Vireo in Pima County, Arizona, was recorded singing a song typical of the Eastern, and it matches our criteria for this species as well. A warbling-vireo in Mohave County, Arizona, 1 May 2019, was identified as a Western in eBird, but we are confident that it was an Eastern by the criteria presented in Table 8.

We propose that the bird at Gambell, Alaska, is an Eastern primarily on the basis of the spacing of its primaries: the mean value of p6:5 in five measurements from different photographs is 1.03, and all five of the ratios (0.92,

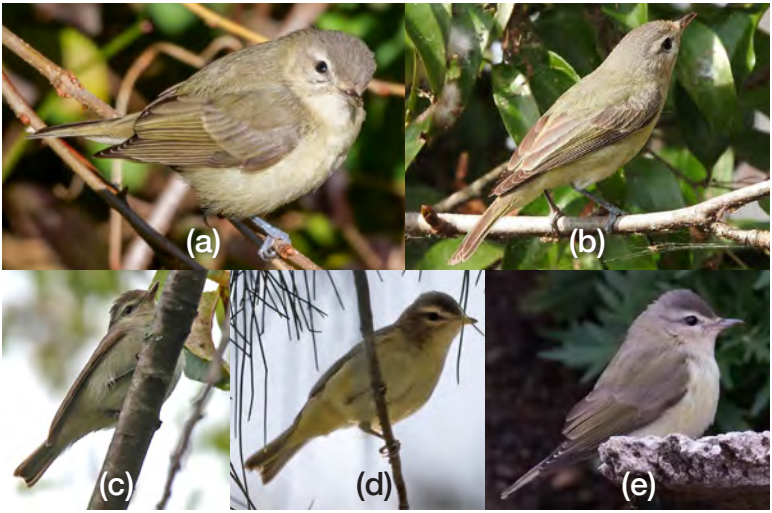


Figure 12. Examples of apparent vagrant warbling-vireos. See Tables 7 and 8 for details. Photos used by license agreement from the Macaulay Library. Western: (a) Roger Horn, ML514865991, Cape May Co., New Jersey, 20 December 2022; (b) Milton Hobbs, ML192334641, Richmond Co., Georgia, 9 December 2019; (c) Roger Ahlman, ML54158341, Jardín Botánico de Quito, Ecuador, 11 April 2017. Eastern: (d) Paul Fenwick, ML389365221, Monterey Co., California, 19 November 2021; (e) Gary Rosenberg, ML291622921, Gambell, St. Lawrence Island, Alaska, 12 September 2018.

0.98, 1.10, 1.11, and 1.04) are well above the maximum of 0.89 for the Western in our sample. We scored its lores as dark (5), which favors the Eastern, and the moderately dark (3) auriculars are unremarkable for either species. The scores for its supercilium are inconclusive, with the length of 2.0 being more typical of the Western and the breadth of 0.8 more typical of the Eastern.

Two birds on the Atlantic islands of the Azores were not identified to species by Doniol-Valcroze et al. (2025) and represent the only records of a warbling-vireo for the western Palearctic. Unsurprisingly, their characters supporting their identification as the Eastern Warbling-Vireo. The identification of the bird in 2021 is the more tenuous of the two, as the photos available to us were less than ideal. Nonetheless, the apparent supercilium length of 1.2 and breadth of 0.7 and dark lores (score of 5) would have eliminated all but 2 of the 43 fall Westerns we examined. The second bird is an Eastern by its supercilium size (length 0.8, breadth 0.9) and pale auriculars (score of 1); only 2 of 43 (5%) of the Westerns in our fall sample had a supercilium length ≤0.8, and only 1 of 42 (2%) had such pale auriculars; none showed that combination of features. Both birds had replaced all greater coverts, consistent with first-fall Easterns but not fully eliminating first-fall Westerns. Unfortunately, none of the photographs available to us of this second bird allowed for analysis of spacing of the primaries.

A bird captured for banding on Southeast Farallon Island, California, 5 September 2018 (https://ebird.org/checklist/S48321597) was identified by the

observers as an Eastern Warbling-Vireo. It was aged in the field as a first-fall bird, but we believe it is an adult. It was in fresh plumage, which fits the majority of adult Easterns but we also found such in 41% of the adult Westerns in our sample. The bill appears very large, the basis on which the identification as the Eastern largely rested. No photographs are available from which the bird's wing morphology can be analyzed. Characters that point away from an identification as the Eastern include supercilium size (length of 1.5 and width of 1.0 eye diameters) and exceptionally dark lores. The lores are darker and bolder than the postocular stripe, and the back seems quite intense olive-green, both of which are atypical of either warbling-vireo species. Possibly, this bird was a hybrid between a warbling-vireo and a Red-eyed Vireo (*Vireo olivaceus*) (McKee et al. 2016).

CONCLUSION

Distinguishing many Eastern and Western Warbling-Vireos from each other is possible but doing so without a specimen requires high-quality images that allow for the assessment of primary spacing, facial markings, molt state, and/or side coloration. Photographs should be evaluated with an eye to potentially confounding factors such as lighting, perspective, and a proportionally long p7. The application of the criteria we have outlined should improve determination of these species' ranges. Nevertheless, many warbling-vireos will remain unidentifiable by these criteria, and the possibility of hybrids (Lovell et al. 2021, Carpenter et al. 2022) should be considered, especially where the species' ranges meet along the Great Plains–Rocky Mountains interface.

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IT'S A TRAP—THE CASE OF THE BUTTE CREEK TERRITORY OF THE NORTHERN SPOTTED OWL

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ABSTRACT: In the Pacific Northwest region of the United States, forests within the range of the Northern Spotted Owl (*Strix occidentalis caurina*) have changed dramatically over the last two centuries. It began with the loss of frequent fires that indigenous communities set annually to manage their natural resources. This change was exacerbated a century later with the advent of effective fire suppression by the United States Forest Service. A once diverse forested landscape maintained by frequent fires became more uniform. In recent times, urbanization and widespread timber harvesting largely confined remaining owl habitat to federally managed public forest lands. In some places there was less than historically existed and in other places, more. These changes can create ecological traps—areas of low-quality habitat that are occupied for various reasons—where long-term persistence is not possible. A recent (2024) article in *Western Birds* focused on a Northern Spotted Owl territory that produced three young two years after a large, severe wildfire. Our paper broadens the time perspective for that territory and tells a more holistic story of how the owls occupied it prior to and after the fire. The rapid change in this territory, now unoccupied, is an example of a site-level ecological trap for the Northern Spotted Owl, while the slow forest changes from fire exclusion that preceded the fire exemplify a landscape-scale trap.

Northern Spotted Owls (*Strix occidentalis caurina*) can live up to 21 years in the wild (Davis et al. 2016). They prefer to nest and roost in older Douglas-fir (*Pseudotsuga menziesii*) or mixed-conifer forests with closed canopies for cover and multiple layers of trees for thermoregulation. They nest in tree cavities or structures and forage in the canopy, among fallen trees, and along stands' edges (Forsman et al. 1984, Solis and Gutiérrez 1990, Thomas et al. 1990). In fire-prone areas of the subspecies' range, such as the Klamath Mountains region, the habitat's quality and the owls' fitness benefit from a certain amount of forest heterogeneity caused by frequent fire (Ward et al. 1998, Franklin et al. 2000, Franklin and Gutiérrez 2002). These fires create and maintain other forest cover types intermixed with forest in which the owls nest or roost, allowing them to find food closer to the nest and to spend more energy on successful reproduction than on foraging. In the portions of the Northern Spotted Owl's range where fire is less frequent, forest heterogeneity is less important and the owls prey primarily upon species that inhabit the cover type in which they nest and roost (Forsman et al. 2004).

The forests of the Pacific Northwest that the Northern Spotted Owl inhabits have changed dramatically over the past two centuries and continue to change at an accelerating pace (Hagmann et al. 2017, Halofsky

et al. 2020, Knight et al. 2022, Hoecker et al. 2026). Changes began in the early 19th century when annual fires set by indigenous populations managing their natural resources were ended by expanding western settlements (Huntsinger and McCaffrey 1995, Anderson 1996). The heterogeneous and biodiverse forest landscapes these fires created and maintained (Taylor and Skinner 1998) began to fill in with trees once held at bay by frequent burning. In these previously fire-tended systems, denser forest types in which the Northern Spotted Owl prefers to nest and roost began to slowly spread into and replace other less dense forest types or open areas (Agee and Edmonds 1992, Skinner 1995, Taylor and Skinner 2003). A century later an era of aggressive fire suppression (Loveridge 1944) began exacerbating this process of forest homogenization. Shortly thereafter, an era of industrial timber harvesting reduced remaining Northern Spotted Owl habitat to about half of its former range and largely confined it to federally managed public lands that had been established as forest reserves in the late 19th century (Thomas et al. 1990). Now, we are witnessing an increase in the frequency and extent of large wildfires, causing alarming changes to what habitat remains (Miller et al. 2012, Davis et al. 2017, 2022).

These changes, especially those caused by the logging that sparked the "Timber War" (Petach 2024), which then led to the listing of the Northern Spotted Owl under the Endangered Species Act and the Northwest Forest Plan, left indelible marks and confounding dilemmas. Both the Northwest Forest Plan (USDA and USDI 1994) and the recovery plan for the Northern Spotted Owl (USFWS 2011) recognized that in the portions of the owl's range that formerly burned frequently fires had been excluded for over a century and that active forest management would be required to restore those landscapes. Yet, over three decades later, little has been accomplished and a debate for or against this restoration still rages (Spies et al. 2019, Lindenmayer et al. 2025), a debate fueled by the past and focused on the most obvious change: rapid forest loss. Meanwhile, a slower, less obvious change caused by fire exclusion and spread of forest has garnered little attention. Both, however, can affect the Northern Spotted Owl adversely.

Disturbances responsible for large-scale rapid loss of nesting and roosting forest, whether wildfires, timber harvesting, or other agents, can reduce the owl's populations. In northern California, moderate to severe fires can reduce the owls' survival while having varying effects on recruitment (Rockweit et al. 2017). Persistence in a territory decreases and displacement increases with a fire's severity and extent within a territory (Rockweit et al. 2024). Alternatively, lack of disturbance in historically disturbance-prone forests allows for dense stands to encroach into other forest types and openings that represent good prey habitat, thus lowering the quality of the habitat and the fitness of the owls in it (Franklin et al. 2000). The ability of a territory to support long-term survival and reproduction depends on the proper balance and juxtaposition of both types of forest cover through time. Too much or too little of one or the other can produce an ecological trap and, over time, a population sink.

An ecological trap can be defined as an area that has been altered such that long-term survival and/or reproduction is no longer possible, but the inhabitants remain because some habitat-selection cues persist for a while or because of strong site fidelity (Battin 2004, Merkle et al. 2022). The scale of a

trap can range from a single territory (Gullion 1967) to a landscape (O'Neil et al. 2020). The concept originated over a half-century ago when Gullion (1967), studying the effects of forestry practices on the Ruffed Grouse (*Bonasa umbellus*), found adults' survival was lower at sites of perennial drumming. Dwernychuk and Boag (1972) found that California Gulls (*Larus californicus*) and Ring-billed Gulls (*L. delawarensis*) frightened away American Crows (*Corvus brachyrhynchos*), allowing Lesser Scaups (*Aythya affinis*), Mallards *(A. platyrhynchos*), Northern Pintails (*A. acuta*), Gadwalls (*Mareca strepera*), American Wigeons (*M. americana*), and White-winged Scoters (*Melanitta deglandi*) to successfully hatch eggs, but the gulls then consumed all the hatched ducklings! Ganey et al. (1997) speculated that the creation of openings in forest suitable for the Mexican Spotted Owl (*Strix occidentalis lucida*) might attract Great Horned Owls (*Bubo virginianus*), which might prey upon the Spotted Owls. And finally, Comfort et al. (2016) cautioned that intensely burned territories might become ecological traps because they could increase Northern Spotted Owls' exposure to predators or the elements.

In the summer of 2020, California experienced its largest wildfire on record, the August Complex Fire, which burned about 418,000 ha of forest in the Mendocino, Six Rivers, and Shasta–Trinity national forests (Safford et al. 2022). Chi (2024) reported a pair of Spotted Owls that two years after the fire hatched three young and fledged two. This observation was in the historical Butte Creek territory, which burned intensely. Chi concluded that intensely burned forest may be essential to the Northern Spotted Owl and that high-quality conditions for nesting and roosting persist in a different form after the fire. Here, we offer a longer perspective on the owls' use of this territory before and after the fire by examining forest growth, disturbance, and habitat trends in it. Evidently, the August Complex Fire set an ecological trap in the Butte Creek territory and some (but not all) Northern Spotted Owl territories within its footprint.

METHODS

Study Area

The Butte Creek territory lies within the Mendocino National Forest (Figure 1), which was once inhabited by diverse indigenous peoples, including the Yuki, Wailaki, Nomlaki, Patwin, and Pomo (Dugas et al. 2014). The territory, defined by a circle of radius 2092 m (1375 ha) around the 2022 nest, contains a core area defined by a circle of radius 1126 m (398 ha). Aerial imagery from the 1940s shows a road into the territory but no apparent sign of logging. Commercial timber harvesting began in the 1970s and ended by the mid-1980s. At that time, about 13% of the territory and 10% of the core area had been thinned or clearcut. From at least the 1950s to 2020, the territory had largely avoided fire. In 1988 the Butte Fire burned 6.5 ha within a previously harvested area on the northwestern edge of the territory. In 1990 the Carpenter Fire burned 15 ha, also within an area previously harvested on the southern edge of the territory. Then in 2020 the August Complex Fire burned the entire territory, the majority at high severity (Figure 1). Only one small (and ephemeral) patch of interior forest suitable for nesting or roosting (>30 m from the patch's edge) remained

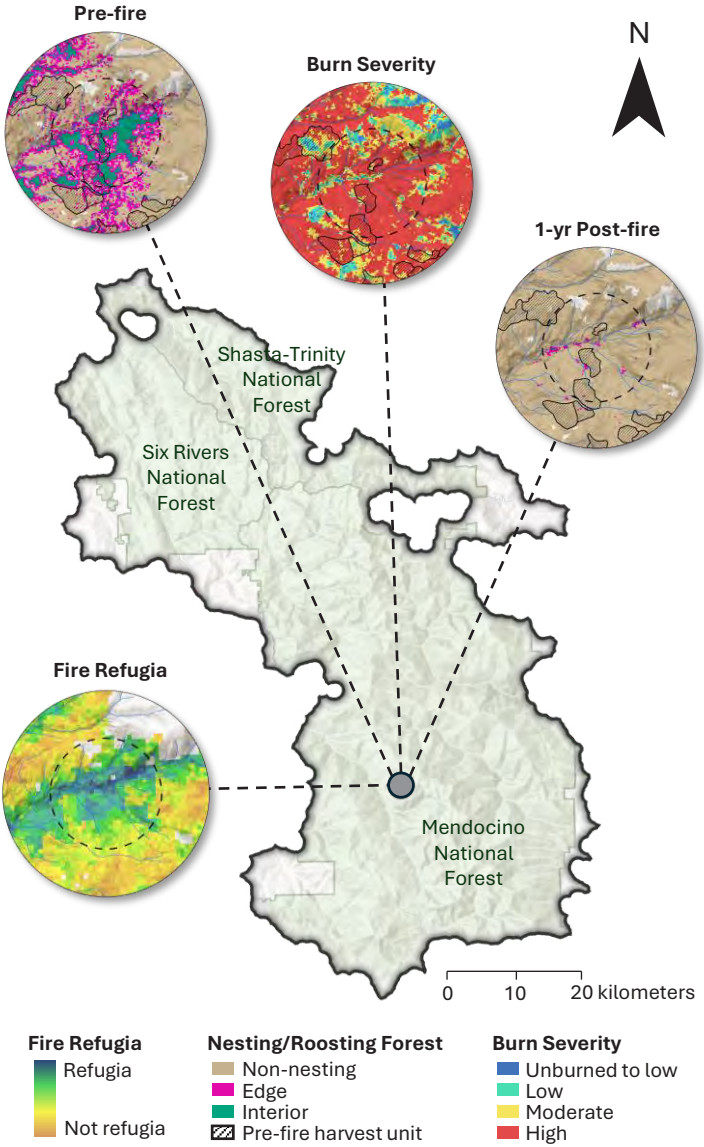


FIGURE 1. Location of the Butte Creek territory (1375 ha) of the Northern Spotted Owl within the perimeter of the August Complex Fire. The dashed circle within the territory indicates the core area (398 ha) within it.

in the core area and within a fire refugium (Krawchuk et al. 2020, Lesmeister et al. 2021: fig. 2). Small nonforested (rock, meadows, etc.) or less densely forested areas burned at low severity, including two areas previously logged (Figure 1).

Northern Spotted Owl Surveys

Pre-fire surveys of the Butte Creek territory, following the USFWS (1992, 2012) protocol, date back to the 1970s and took place intermittently thereafter. A combination of vocal lure (callback) surveys and passive acoustic-recording surveys has been done every year since the fire (2021–2025). In 2022, over 20 pellets were collected from the fledglings' roost tree and examined for prey content. Within the August Complex Fire's footprint generally, passive acoustic monitoring under the Northwest Forest Plan continued from 2023 to 2025 (Kantor et al. 2022, Lesmeister and Jenkins 2022). Locations for this territory are documented in California's database of Spotted Owl observations (CDFW 2019).

Forest and Habitat Monitoring

We evaluated changes from 1986 to 2025 on the basis of long-term habitat-monitoring data from throughout the Northern Spotted Owl's range. These data consist of annual time series of Landsat-based forest maps (30-m pixel resolution) and habitat maps (100-m resolution), developed through machine-learning methods trained on locations of Northern Spotted Owl nests and pair roosts (Glenn et al. 2017, Davis et al. 2022). Maps of forest types (suitable for nesting, roosting, or dispersal) are based on stand structure and tree-species composition. Habitat maps are consistent with "high-value habitat" as defined in recovery actions 9 and 10 (USFWS 2011). They are based on the extent and spatial arrangement of nest- or roost-suitable forest at multiple spatial scales, including abiotic factors (e.g., topography and climate). We also examined landscape maps representing large areas (25-km radius, ~1964 km^2) covered with enough forest (≥40% cover) to facilitate the owls' movement across the landscape (Davis et al. 2011:40–41).

At the finest spatial scale (core area), light detection and ranging (lidar) data (1-m resolution) from 2018 were used to map the crowns of trees >24 m in height, a height that, according to local height-to-diameter relationships, corresponds with nest- or roost-suitable forest (Forest Vegetation Simulator 2026). Maps of the annual normalized burn ratio, produced from Sentinel 2 satellite imagery (20-m pixel resolution), were used to determine whether the trees were alive or dead before and after the fire. This ratio is a multispectral index that ranges from –1 to +1. Values below zero indicate dead vegetation. Values closer to 1 indicate living vegetation (see figure 3 in Miller and Thode (2007), in which the values are expressed on a scale from –1000 to +1000). The relationship between canopy cover of live trees (based on lidar mapping) and the normalized burn ratio showed that when this ratio equals zero, canopy cover is 4–10% (mean 7%), a ratio of 0.4 equates to canopy cover of 36–42% (mean 39%), and a ratio >0.6 represents a mean canopy cover >60% (Lesmeister et al. 2019: fig. 3). Each tree was assigned a mean annual normalized burn ratio, where a value >0.6 represents living trees with canopy cover >60%, values between 0.4 and 0.6 represent 40–60% live tree cover, values between 0.15 and 0.4 represent 15–40% live tree cover, values between 0 and 0.15 represent 0–15% live tree cover, and values <0 represent 100% dead trees.

RESULTS

Surveys

This territory was first surveyed in 1975, when one pair of Spotted Owls was noted. A pair with three young was found the following year (1976). Subsequent surveys took place in 1977 (species detected), 1980 (pair with two young), 1982 (species detected), 1990 (pair with one young), 1992 (pair with two young), 2002 (pair with young), 2006 (pair with two young), and 2008 (pair with one young). There are no records of this territory being surveyed again until the first year following the fire (2021), when one adult male was observed. A pair that produced three young and fledged two was documented the following year (Chi 2024). During that same year four-noted hoots from both a male and a female were detected by an autonomous recording unit placed near the historical nest tree and approximately 390 m uphill and south of the new nest tree. Examination of Spotted Owl pellets from the fledglings' roost tree did not reveal an abundance of small mammal bones, and all cranial bones found belonged to the Dusky-footed Woodrat (*Neotoma fuscipes*). All pellets contained insect exoskeletons. In 2023, a single male was detected aurally once during a callback survey. It was never detected during two other night visits, stand searches, or follow-ups. No Spotted Owls were detected by autonomous acoustic recorders placed within 200 m of the nest tree and recording for six weeks during the breeding season in both 2023 and 2024, or during six callback surveys in 2025.

Within the August Complex Fire's footprint, annual rangewide passive acoustic monitoring detected Spotted Owls in 9 of 13 (69%) 5-km^2 hexagons in which four autonomous recording units had been deployed. These included a pair about 21 km north-northeast of the Butte Creek territory, in an area that burned with mixed severity (Figure 2). The following year (2024), Spotted Owls were detected in 4 of 9 such hexagons surveyed (44%), including a pair in the same hexagon as in 2023. In 2025, the owls were detected in 2 of 7 hexagons surveyed (29%), including one pair in a hexagon about 20 km to the south that had also burned with mixed severity. The northerly hexagon with two back-to-back years (2023 and 2024) of recording units detecting a pair was surveyed in 2025 by local biologists and the pair was confirmed, marking three consecutive years of pair occupancy. In 2025 this hexagon contained 115 ha of habitat in refugia that survived the fire (Figure 3). In all three of these years this same monitoring also detected Great Horned Owls throughout the fire's footprint. A Barred Owl (*Strix varia*) was detected in 2023 in the northern portion of the fire (Six Rivers National Forest), but no Barred Owls were detected in the vicinity of the Butte Creek territory.

Forest and Habitat Monitoring

Prior to the August Complex Fire, the extent of forest suitable for Spotted Owl nesting or roosting within the Butte Creek territory was increasing at a rate of 0.13 ± 0.07% (95% confidence interval) per year; within the core area it was increasing by 0.21 ± 0.10% per year (Figure 4a). The immediate effect of the fire was a decrease of 97.7% in such forest at the territory scale and 96.1% within the core area. By the fifth year post-fire (2025), these losses had increased to 99.3% and 98.9%, respectively, owing to trees' delayed mor-

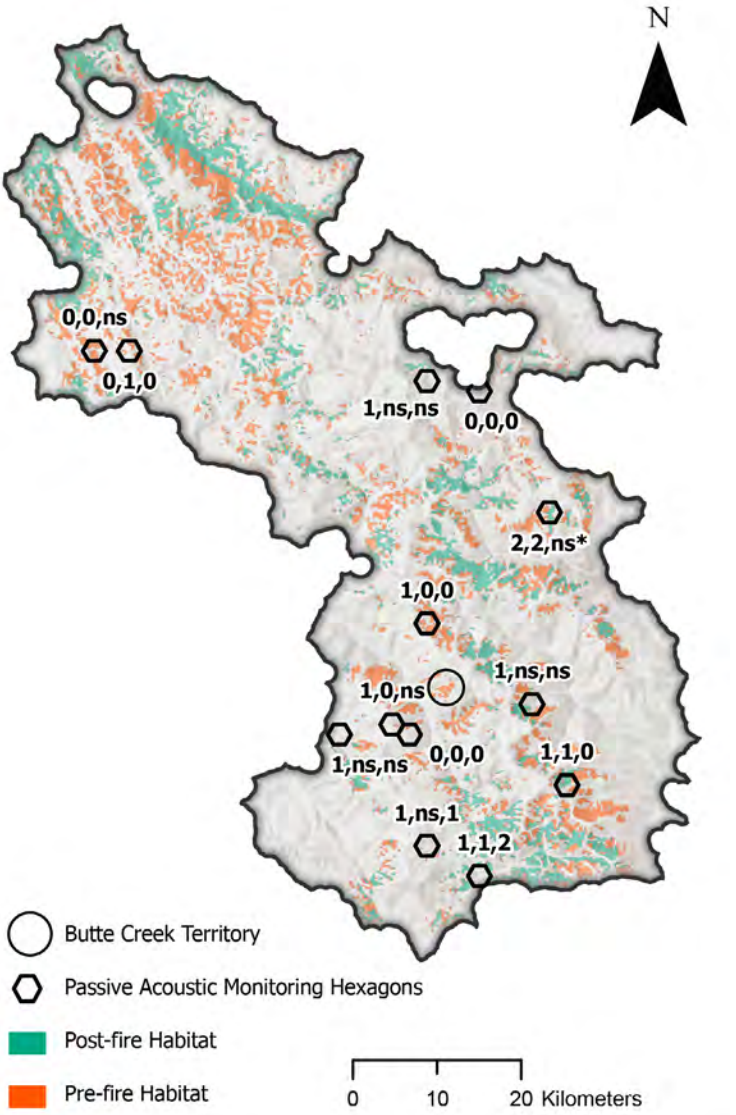


FIGURE 2. Detections of the Northern Spotted Owl within the perimeter of the August Complex Fire by passive acoustic monitoring under the Northwest Forest Plan from 2023 to 2025. The three numbers associated with each hexagon represent the results for each year (2023, 2024, 2025), where 0 = no owls detected, 1 = a single owl detected, 2 = a pair detected, and ns = not surveyed by this technique. The asterisk (*) represents a pair detected through callback surveys in a hexagon unsurveyed that year by an autonomous recording unit. Pre-fire habitat represents habitat lost from the fire; post-fire habitat represents habitat remaining in 2025.

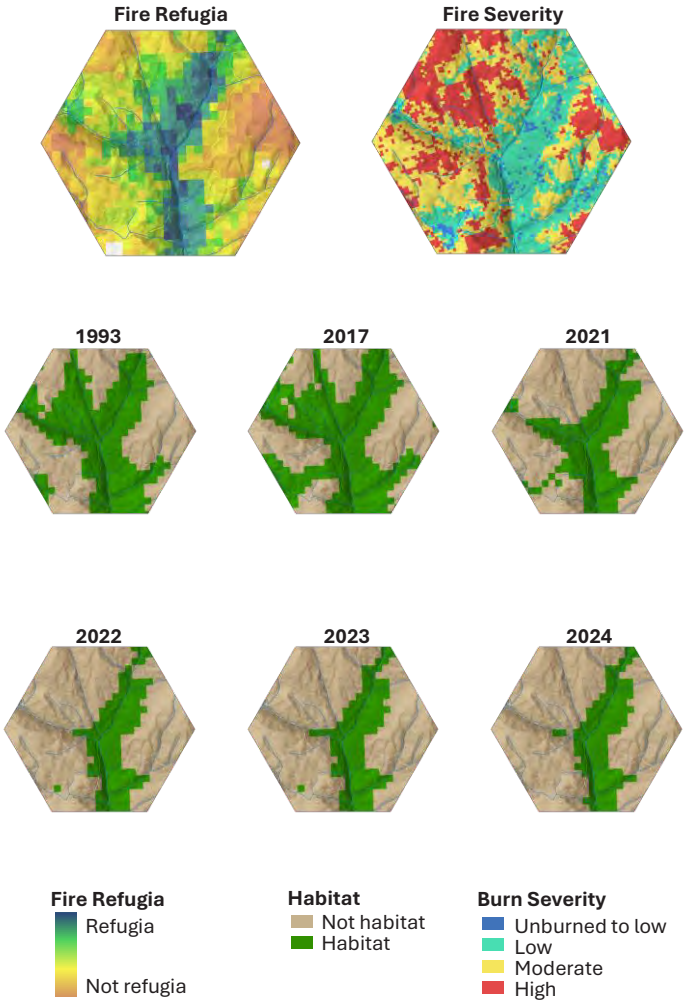


FIGURE 3. Distribution of habitat suitable for the Spotted Owl in a 500-ha hexagon monitored by passive acoustic recording 3 to 5 years after the August Complex Fire. Over time, the habitat conformed to topo-climatic fire refugia and, without disturbances, expanded outward into nonrefugial areas (1993 to 2017). The post-fire maps (2021–2024) show the effect of trees' delayed mortality from the fire and how wildfires can realign Spotted Owl habitat with fire refugia.

tality. In 1993 (the first year of habitat mapping) the forest in this territory contributed to 245 ha of habitat suitable for long-term occupancy by a pair (Glenn et al. 2017). From 1993 to 2020, suitable habitat within the territory increased by 24%, but it was completely removed by the fire. At the landscape scale (the footprint of the August Complex Fire) habitat had increased, over

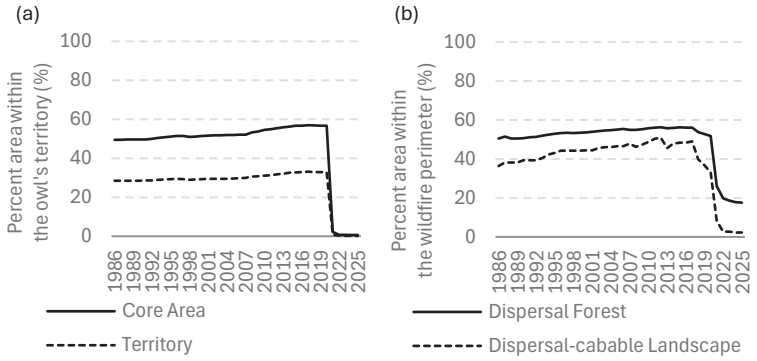


FIGURE 4. (a) Trends in the extent of forest suitable for Spotted Owl nesting or roosting within the Butte Creek territory. (b) Trends in the extent of forest and of landscape suitable for Spotted Owl dispersal in the August Complex Fire's footprint.

this same interval, by 27.7% and the carrying capacity for Spotted Owl pairs had increased by 4.2%, on the basis of Glenn et al. (2017). The notable difference between the gains in habitat and carrying capacity has to do with the spatial pattern of the gains, which essentially expanded from source patches within fire refugia. This expansion offered only more space use for existing territories, not an equivalent percentage of new territories. The effect of the fire, after 5 years, was a 54.3% loss of habitat, but a 30.4% reduction in carrying capacity. Before the fire, the area of suitable habitat nearest the Butte Creek territory's activity center was slightly over 2 km away (Pinto Creek). After the fire, the distance increased to 3 km in 2021 and 4 km by 2025.

Also, we analyzed forest suitable for Spotted Owl dispersal at the scale of the August Complex Fire. Prior to the listing of the Northern Spotted Owl as threatened in 1990, it covered slightly over half of this future fire's footprint. Post-listing, it began increasing at an average rate of 0.29 ± 0.10% per year until 2005, when damage from insects began increasing above background levels (Figure 4b). From 2006 to 2017 such forest increased at an average rate of 0.07 ± 0.17% per year, essentially remaining stable as recruitment was balanced with losses from disturbances. A notable decrease from 2017 to 2020 coincided with a significant increase in tree mortality related to insects (CFPC 2018). The immediate effect of the August Complex Fire was a decrease of 49.7%, and by the fifth year the loss had reached 66.1%. The landscape suitable for dispersal generally followed the same trend as forest suitable for dispersal. It increased monotonically from 1986 to 2007, followed by a period of instability until 2017, when it began to decrease rapidly. This decrease was initially related to insects and drought, then followed by the August Complex Fire. The area suitable for dispersal within the fire's footprint had increased from 36% in 1986 to 51% by 2017 but was slightly over 2% in 2025.

Within the core area of the Butte Creek territory, approximately 12,000 large live trees, median height 41 m, constituted the forest suitable for the owl's nesting or roosting (Figure 5). The largest trees (99th percentile) occurred within fire refugia. Before the fire, 95% of trees had mean normalized burn

ratios above 0.6. In the first-year post-fire, no trees with a ratio >0.6 remained. About 3.7% had ratios >0.4. This proportion declined to 1.2% in the second year post-fire and to 0.6% by the third, where it remained until 2025. The tree in which the owls nested in 2022 was in an area where the normalized burn ratio was 0.15–0.4 in 2021, 0–0.15 in 2022, then <0 subsequently. The nearest distance from the nest tree of 2022 to trees with ratios >0.4 in 2021 was about 40 m. This distance increased to about 200 m in the following years.

DISCUSSION

Almost two-thirds of the August Complex Fire's 4180-km² footprint had not experienced a wildfire since 1878 (Safford et al. 2022, CALFIRE 2025). Prior to the 2020 fire, forest suitable for the Northern Spotted Owl's nesting

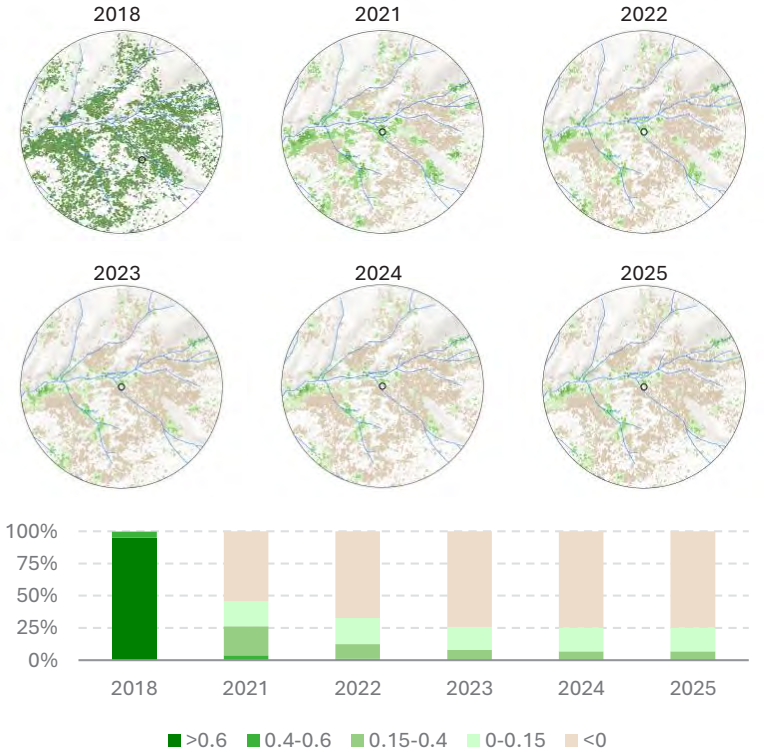


FIGURE 5. Changes in the coverage of live and dead large tree crowns within the Butte Creek core area before and after the August Complex Fire. The black hollow dots represent nest trees' locations before (2018) and after the fire. Nesting was observed in 2022 but not in the years following. Values are the mean normalized burn ratio of tree crowns, representing the percentage of live tree cover, shown in shades of green to tan (live to dead).

or roosting was expanding steadily. Additional forest suitable for dispersal was displacing other cover types (Figure 4). Prolonged exclusion of fire from this landscape, formerly burned annually by indigenous peoples, set a "slow" landscape-scale ecological trap (Figure 6). Over time, this trap likely lowered the owls' fitness in several territories. Not only does fire exclusion have the potential to lower their fitness, it also increases the risk of severe fire and large-scale loss of habitat (Safford and Stevens 2017), setting the stage for "fast" site-level ecological traps (Figure 6).

Five years after the August Complex Fire, it appeared that Spotted Owls no longer occupied the Butte Creek territory. We contend that the August Complex Fire set a "fast" ecological trap by rapidly reducing the amount of forest that provided the owls cover from predators and the elements. The Butte Creek pair, remaining in their territory, were able to find temporary refuge in a small ephemeral patch of interior forest with a suitable nesting cavity nearby. A diffuse edge of the forest suitable for nesting and roosting (Comfort et al. 2016) and the increase in prey that normally follows a forest disturbance (Carey et al. 1992, Culhane et al. 2022) likely created conditions conducive for foraging and reproduction. The lack of sufficient closed-canopy forest, however, likely increased the owls' vulnerability to predation, and at least one of their offspring was preyed on by a mammal (Chi 2022).

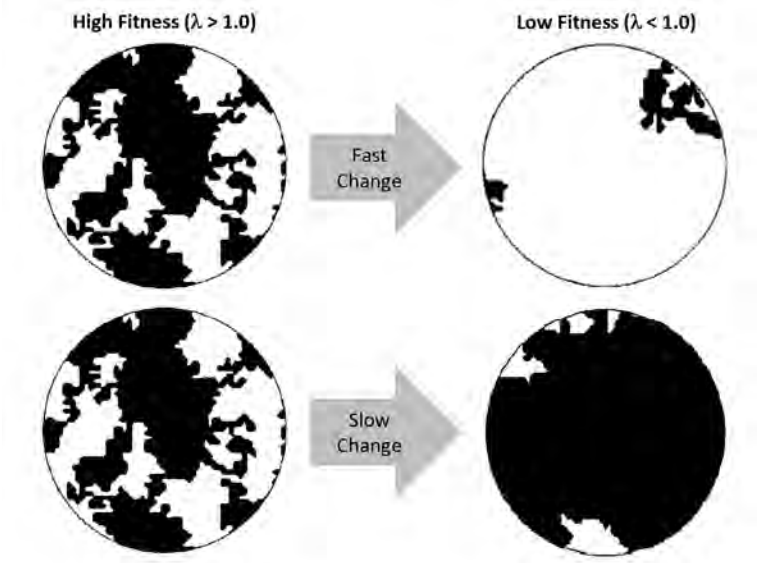


FIGURE 6. Spotted Owl territories (circles of radii 0.71 km) from Franklin et al. (2000: fig. 10), illustrating two types of ecological traps. The top circles illustrate a rapid loss of nesting/roosting forest resulting in a territory in which survival is low (< 1.0). The bottom circles illustrate how slow gains in nesting/roosting forest, owing to prolonged periods of fire exclusion, may also result in low fitness because of a low rate of reproduction. Black areas, nesting/roosting forest; white areas, other vegetation types. Graphics used with permission from A. Franklin.

With every passing year, accumulating tree mortality tightened the "noose." Favorable habitat disappeared, and the Spotted Owls were no longer able to find adequate cover and shelter. Eventually, they likely succumbed to these pressures or moved elsewhere.

Documentation of the Pacific Fisher (*Pekania pennanti*) near the nest (Chi 2022) hints that it may have been responsible for predation of one of the three hatchlings. While the fisher is an opportunistic forager and doesn't specifically target the Spotted Owl, the remains of birds and eggshell fragments have been found in its scat (Zielinski et al. 1999). In California, Pilgrim et al. (2023) found DNA of raptors and cavity-nesting birds in fisher scat, but it was unknown if it was from eggs, nestlings, or adults. While there are no published accounts of a fisher preying on a Northern Spotted Owl, during a nearby long-term study of the owl's demography, one was observed entering a nest—being defended by the male owl—that subsequently failed (Mark Higley pers. comm.). The female owl was not seen again after this encounter. Also, in 2022, automated recording units detected a Great Horned Owl, known to prey on juvenile Spotted Owls (Forsman 1976, Marcot and Gardetto 1980), and in 2024 they detected a pair within the core area.

In addition to exposure to predators, the combination of climate and extent of suitable forest, rather than these factors individually, is an important factor explaining variation in the Spotted Owl's survival (Franklin et al. 2000). The species is less heat tolerant than many birds (Weathers et al. 2001). Ganey et al. (1993) found that Great Horned Owls were better at thermoregulation than Mexican Spotted Owls. Ting (1998) found that Northern Spotted Owls appear heat intolerant and select forest with a multilayered structure that provides stable, cooler microclimates. Therefore the loss of such forest where owls can thermoregulate may also depress their survival (Barrows and Barrows 1978), even without an increase in predation.

Finally, the type of forest disturbance matters less than what remains and where it remains after the disturbance. In the case of the Butte Creek territory, Spotted Owls persisted and reproduced years after the territory and core area were disturbed by pre-fire timber harvesting. This harvesting changed only a small portion of the territory and left enough suitable forest to support survival. Intermixed with this forest accommodating nesting and roosting were other types of forest that supported prey populations. Nesting/roosting forests were concentrated within fire refugia, which support their development and maintenance, and where they are naturally more resilient to fires. What little forest suitable for nesting and roosting that remained in the territory following the fire, remained in fire refugia.

SUMMARY

In July 2023, three years after a fire had killed 99% of the forest suitable for nesting and roosting, the last detection of a Spotted Owl within the Butte Creek territory was recorded. A male at the territory's southeastern edge, it had presumably dispersed from an active territory about 5 km to the northeast (see Figure 2). Chi's (2024:300) statement, "It appears that the high-quality conditions for nesting and roosting observed at this site in 2002 (unmanaged from 2002 to 2022) persisted in a different form after the territory burned in 2020"

was perhaps premature. Contrary to the perspective that this territory was "unmanaged" for two decades before the fire, the management decisions to actively suppress fires and limit the amount of active forest management allowed under the Northwest Forest Plan (USDA and USDI 1994) may have contributed to the loss of habitat in this territory, which burned with such high intensity.

Chi (2024:300) also suggested an unrecognized benefit of fire-killed forest is that it may be essential to the Spotted Owl after a wildfire, stating that it is "regularly undervalued, overlooked, and routinely removed." However, burned forest's potential benefits to the Spotted Owl have been recognized since the early 1990s (Carey et al. 1992) and are a focus of active research. On federally managed forests, only a small fraction (4.9%) of burned forest has been removed (Zuspan et al. 2024). Forest managers are beginning to better understand the important role of burned forest, not only for the Spotted Owl but for biodiversity in general (Spies et al. 2012). Additionally, as wildfires burn ever more frequently, more extensively, and more severely, as has been predicted (Davis et al. 2017) and observed (Cova et al. 2025), forest managers are realizing the consequences of excluding fires from landscapes that once burned regularly. While new knowledge is being incorporated into how burned landscapes are managed, adoption of indigenous peoples' knowledge and practices can help restore a balance (Charnley et al. 2007).

The Butte Creek territory provides an example of a site-level ecological trap set by a rapid change in habitat conditions caused by a large wildfire. The slow (at least over a century) increase of dense forests regionally represents a landscape-scale ecological trap. The focus on the adverse effects of forest change on the Northern Spotted Owl has mostly been on the former and has ignored the latter. Active forest management that aims to restore the former balance of forest suitable for nesting and roosting (within fire refugia) and other forest types (outside of such refugia) can defuse existing traps and may be beneficial to the Northern Spotted Owl, or at least neutral (Franklin et al. 2000, Halofsky et al. 2024, Lesmeister et al. 2025).

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We acknowledge Tonja Chi for documenting and highlighting the Northern Spotted Owl's use of burned forest. It was the catalyst needed to elicit the broader story of a century or more of fire exclusion and its effect on the once diverse forests inhabited by this bird and hosts of other species. Long-term monitoring and research for the Northwest Forest Plan made telling that story possible. We also thank Jeremy Rockweit, Alan Franklin, and Brandon Collins for improving this paper through their helpful reviews.

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RECORD HIGH SPOTTED TOWHEE NEST IN METRO VANCOUVER, BRITISH COLUMBIA

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ABSTRACT: Most bird species evolved nest characteristics such as height or type of materials that match their life history and niche requirements. Many species, including the Spotted Towhee (*Pipilo maculatus*), commonly nest on the ground or in low shrubs. Urban environments, which comprise many novel anthropogenic structures and related pressures, can alter bird behaviors, including nest-site selection. As part of a multi-year field study in Metro Vancouver, British Columbia, Canada, we located a Spotted Towhee nest that was 7.0 m high. This nest was 2 m higher than the highest nest previously documented in the literature and was much higher than the mean nest height of 0.2 m (median = 0 m) that we have observed in this region. This discovery suggests that the Spotted Towhee's nest-site selection may be more plastic than previously documented and highlights a need to consider factors, particularly in human-modified environments, that influence nest-site selection.

Nest-site selection is influenced by various interacting environmental conditions, resource availability such as food and available nesting material, and the density of both conspecifics and predators (Mainwaring et al. 2014). Urban environments are highly heterogeneous and may have abundant and stable resources capable of sustaining high densities of adult birds (Batáry et al. 2017, Wilson 2025). When the density of conspecifics is high, breeding pairs may be forced to occupy territories whose quality in one or many attributes, such as nesting habitat, is lower (Pulliam 2000). In urban environments where natural nest sites may be limited or absent, birds may take advantage of the many novel structures that resemble natural nesting sites, such as crevices and holes of pipes, poles, bridges, buildings, and even machinery (Reynolds et al. 2019, Liu and Li 2024). While cavity nesters show great plasticity in nest-site selection, many North American passerine species typically build open-cup nests on the ground. This guild is often considered relatively intolerant of urban environments because of the vulnerability of ground nests to disturbance by human activity, vegetation management (e.g., mowing), as well as synanthropic or domestic predators (Chace and Walsh 2006, Reynolds et al. 2019, Minias and Janiszewski 2023). Instances of nonpasserine ground-nesting species nesting in locations such as balconies, windowsills, and rooftops, prompted by a lack of available undisturbed ground and/or predation pressures, have long been documented for species such as the Killdeer (*Charadrius vociferus,* Ankney and Hopkins 1985) and Common Nighthawk (*Chordeiles minor*, Brigham 1989).

Evidence of ground-nesting passerines using anthropogenic structures has not been frequently reported. Several shrub- or ground-nesting species, such as the Dark-eyed Junco (*Junco hyemalis*, Bressler 2020) and the Blue-crowned Laughingthrush (*Pterorhinus courtoisi*, Zhang et al. 2017), however, have been documented building nests at greater heights in areas with more human activity. Higher renesting in direct response to human disturbance at a nest site is also known, as in the Emei Shan Liocichla (*Liocichla omeiensis*, Zhang et al. 2023) and the Great Gray Shrike (*Lanius excubitor*, Antczak et al. 2005). Additionally, anecdotal evidence implicates domestic cats as accounting for a case of the Spotted Towhee building an atypically high nest (Cohen 1899), which suggests predators affect nest height. The Spotted Towhee is a ground-nesting sparrow in the family Passerellidae that breeds through much of western North America from southwestern Canada to Guatemala (Bartos Smith and Greenlaw 2020). Typically, it builds its nests on or close to the ground: previous studies have found between 69% and 92% of Spotted Towhee nests to be on the ground (Baumann 1959: $n = 11$, Davis 1960: $n = 25$, Bartos Smith and Greenlaw 2020: $n = 344$). The highest Spotted Towhee nest on record was at 5.0 m, found within a wildlife refuge surrounded by agriculture in the Sacramento Valley, California (Small 2005). Here we document a Spotted Towhee nest >7 m high in an urban green space in Metro Vancouver, British Columbia, Canada, and discuss why typical ground- or shrub-nesting birds may opt to nest at greater heights.

METHODS AND RESULTS

Since 2022, we have studied the reproductive ecology of Spotted Towhees across five sites of varying habitat types and degrees of urbanization in Metro Vancouver (see Hohn et al. 2025 for descriptions of study sites). We visited each study site one to three times per week for the duration of the breeding season (March–August) from 2022 to 2025 to find and monitor nests, capture adults with mist nets, and resight color-banded individuals. After successfully locating a nest, we continued to monitor it every 3 to 7 days. Once the chicks had fledged or the nest had failed from either abandonment or depredation, we took a series of nest-site measurements, including height from the ground to the base of the nest.

Through a total of four breeding seasons from 2022 to 2025, we found 407 Spotted Towhee nests across the five sites. The mean height of Spotted Towhee nests across all sites was 0.2 m ± 0.5 (standard deviation) and the median was 0 m (i.e., nest built directly on the ground). Of all located nests, 72.7% (296/407) were found on the ground, 21.9% (89/407) were built off the ground but under 1 m in height, and only 5.4% (22/407) were more than 1 m high. One nest found at Terra Nova Rural Park and Natural Area in Richmond (49.172°, –123.196°), however, was a clear outlier, located 7.0 m high. The next highest nests were 4.0 m and 2.5 m above ground. This park is a 39-ha green space with a paved roadway that separates the rural park region, a recreational and small-scale agricultural land, from the natural area, an ecological preserve with one walking trail (Hohn et al. 2025, Figure 1). The site-specific mean and median nest heights at Terra Nova (84 nests, mean = 0.2 m ± 0.8, median = 0) were similar to those at each of the other four study sites.

The nest built 7 m above ground was in a row of decorative western red



FIGURE 1. Aerial view of Terra Nova Rural Park and Natural Area in Richmond, British Columbia (scale: 1:1500, www.arcgis.com/home/item.html?id=10df2279f9684e4a9f6a7f08febac2a9). The green space's boundary is indicated in black. The Fraser River and Vancouver International Airport lie to the north, the Richmond city center to the east. The approximate area used by the pair of Spotted Towhees that built a nest 7 m high is encircled in purple.

cedar (*Thuja plicata*) trees that separates a small regularly mowed orchard from a steep water-filled ditch that parallels a roadway (Figure 2). On the basis of time spent in the area during field work and lidar-derived land-cover maps (Latifovic 2020), we estimated that 85% of the ground in a 50-m radius



FIGURE 2. Higher-resolution view of the approximate territory of the pair of Spotted Towhees that built a nest 7 m high. The nest's location is encircled in purple (scale: 1:15, www.arcgis.com/home/item.html?id=10df2279f9684e4a9f6a7f08febac2a9).

Photo by Finola Fogarty

surrounding this nest (i.e., about the size of a Spotted Towhee territory) was accessible to human foot traffic. A regularly mowed lawn under routinely pruned orchard trees surrounded the nest, alongside several roads and driveways that lead to buildings (Figure 2). Our team used a telescoping pole fitted with a custom-built camera to view the contents of this nest (Figures 3 and 4). The nest was built against the trunk of a domestic western red cedar and supported by a platform of dense branches (Figure 4). All three nestlings successfully fledged at ~11 days post-hatching (a typical clutch size and length of the nestling period for this species and park).

In subsequent seasons, we found two additional nests on this territory. One was built 2.41 m high in the outer branches of an orchard tree prior to the trees being pruned that season. The other was built on the ground near the base of an orchard tree within the only unmowed area of grass in the orchard. This patch of <2 m^2 was left unmowed because of an active beehive.

DISCUSSION

While our findings on the Spotted Towhee's nest heights generally align with previous literature, the nest at 7 m was 2 m higher than any previously recorded for the species. Several hypotheses may account for selection of this site. First, the height at which a female constructs her nest may be driven by prior weather patterns such as total or average precipitation. Being built off the ground allows a nest to dry faster after a rain and prevents water from pooling



FIGURE 3. Observation of the 7-m Spotted Towhee nest (approximate location encircled in purple) by means of a telescoping pole with a custom-built camera transmitting to a cellphone app.

Photo by Finola Fogarty

within it, to the detriment of the eggs and/or nestlings (Deeming 2023). This may be particularly important for a typically ground-nesting species in an urban landscape where absorption or drainage may be compromised because of more extensive impervious surfaces or altered hydrology (Fletcher et al. 2024). While urban hydrology could affect nest placement, it seems unlikely



FIGURE 4. Three Spotted Towhee nestlings (estimated to be six days old) in the 7-m nest viewed through the camera on the telescoping pole.

Photo by Elizabeth Gow

to be the main driving factor, as we found mean and median nest height to be similar to those reported in other studies in drier and less urban settings.

Second, urban environments may have abundant and stable resources capable of sustaining a high density of adult birds (Batáry et al. 2017, Wilson 2025). The density of Spotted Towhees we observed at Terra Nova appears to be high relative to estimates elsewhere in the species' range (Birds Canada 2018), suggesting the towhees perceive its habitat quality as high (Bock and Jones 2004). The habitat surrounding the 7-m nest, however, is highly disturbed, lacking ideal nesting locations, comprising mostly roadways, mowed vegetation, and pruned trees, which all pose risks to nests and fledglings (Stanton et al. 2018, Reynolds et al. 2019). The microclimate at the few undisturbed sites was likely not ideal for nesting. The ditch was steep and full of water. The ground under the row of cedar trees was bare, and the foliage on the trees' lower branches was sparse.

Although in our study we did not quantify predation explicitly, that factor may have influenced the selection of this nest site. Urban areas typically have a greater abundance of small and medium predators, including feral and domestic cats, which are associated with proximity to and density of residential buildings (Flockhart et al. 2016, Wilson 2025). Wildlife perceives humans and predators similarly, contributing to changes in behavior such as nest-site selection (Frid and Dill 2002). It is unlikely that the activities of our research team contributed to the selection of this particular nest site, as this nest was the first we located in this territory during our study. Beyond being perceived as a threat, human activity can also destroy nests during mowing, removal, or trampling of vegetation. For a ground-nesting species like the Spotted Towhee, human activity could contribute to selecting nest sites in denser vegetation, in less accessible areas, or at greater heights when suitable ground sites are unavailable. The towhees' using other, more typical

sites within this same territory in subsequent years supports the hypothesis that a lack of ground area inaccessible to human disturbance contributed to the selection of the record-high nesting site.

Urbanization alters the type and quantity of suitable resources available to birds. This new record for nest height in the Spotted Towhee expands understanding of the species' natural history. It also demonstrates that individuals may have behavioral flexibility to adapt to changing environments like cities (Wong and Candolin 2015, West-Eberhard 2024).

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CONCURRENT ECCENTRIC AND TYPICAL REPLACEMENT SEQUENCES DURING PREFORMATIVE MOLT IN THE SPOTTED TOWHEE

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ABSTRACT: Molt is a crucial component of the avian annual cycle, and precise knowledge of its extent, sequence, timing, and duration is key to understanding a species' life history. Differences in molt patterns allow individuals of most temperate-zone songbird species to be categorized as first-cycle or older. The extent of molt, however, can vary among individuals of a species, and knowledge of the frequency of unusually extensive or limited molts is critical for accurate age determination. During banding of 100 first-year Spotted Towhees (*Pipilo maculatus*) on Vancouver Island in autumn 2025, I noted two individuals in which the preformative molt was exceptionally extensive. In these individuals, up to six primaries, five secondaries, and seven primary coverts had been renewed. The patterns of these feathers' replacement had evidently followed eccentric and typical sequences concurrently, a combination previously documented in only seven North American passerine species. These results improve our understanding of molt in the Spotted Towhee and suggest that extensive replacement of juvenile flight feathers could improve the birds' fitness by furnishing higher-quality feathers that may enhance flight performance, thermoregulation, and resistance to wear, potentially providing an adaptive advantage in abrasive environments.

Accurately determining the age of birds is critical for numerous components of population-level analyses, such as breeding success and survival rates (Martin 1995). Age-related differences in plumage characteristics and molt patterns allow accurate discrimination of first-cycle birds from older individuals in most temperate-zone passerines. The majority of North American passerines undergo a partial preformative molt (renewing some but not all feathers) in their first year of life, and a complete prebasic molt (renewing all feathers) following the annual breeding season thereafter (Pyle 1997a, 2022a). Within a species, the extent of renewal of wing feathers during a preformative molt can vary considerably, both from individual to individual and from region to region (Mulvihill 1993, Pyle 1997a, Howell et al. 2003, Jenni and Winkler 2020a).

An eccentric molt is an incomplete molt that includes the renewal of outer primaries and inner secondaries to varying extents but not a block of consecutive inner primaries and outer secondaries. Sometimes the outer primary coverts are replaced, but usually most to all primary coverts are retained (Pyle 1997a, 2022a). During eccentric molts, the primary and secondary feathers are molted distally (Gargallo 2013, Pyle 2022b). In contrast, a typical preformative molt follows the sequence of the prebasic molt, in which primaries and primary coverts are molted distally, secondaries (among s1–s6) are molted proximally from the outermost, and tertials are molted bilaterally from the middle feather (Pyle 2022b). The only feathers that may be retained are among the outer primaries and primary coverts and the inner secondaries. As yet, concurrent eccentric and typical sequences during the preformative

molt have been documented in only seven species of North American passerines (Pyle 1997a, Small et al. 2013). When birds are aged by molt, precise knowledge of the species' strategy and extent of molt is essential to quantifying the prevalence of unexpected patterns.

Dwight (1900) recognized the presence or absence of a molt limit (a discontinuity between different generations of feathers) between the primary and greater secondary coverts as a reliable criterion for determining age in the Eastern Towhee (*Pipilo erythrophthalmus*). This limit results from a partial preformative molt that includes the greater secondary coverts but not the primary coverts. Sibley (1950) and Davis (1957) confirmed the same criterion in the other member of the Rufous-sided Towhee complex, the Spotted Towhee (*P. maculatus*). In first-year birds, the retained juvenile primary coverts are brownish and contrast with the renewed blackish (male) or slaty (female) greater secondary coverts. In adults, after the complete prebasic molt, these feathers are uniformly blackish or slaty across both tracts. Pyle (1997b) reported the preformative molt of these towhees to include all greater secondary coverts (except occasionally the outermost) and 1–3 tertials. Later, Johnson et al. (2013) showed that in a small proportion of Eastern Towhees the preformative molt could also be eccentric, as did Fettig and Hathcock (2015) for the Spotted Towhee, finding up to three outer primaries, three inner secondaries, and two outer primary coverts renewed.

Here, I present evidence of incomplete preformative molt consistent with having followed eccentric and typical replacement sequences concurrently in two Spotted Towhees on Vancouver Island in autumn 2025.

METHODS

Between 21 July and 18 October 2025, in accordance with the Canadian Migration Monitoring Network Protocol (Hussell and Ralph 2005), Spotted Towhees were captured during standardized banding at Rocky Point Bird Observatory's Rocky Point (48.321°, –123.547°) and Pedder Bay (48.350°, –123.578°) field stations in British Columbia, Canada. The banders mist-netted daily at both sites, with 13 nets at Rocky Point and 15 at Pedder Bay. Nets were opened 30 minutes prior to sunrise, operated for 6 hours, and checked and cleared every 20 minutes. All birds were captured under appropriate permits and in strict adherence with legal and ethical requirements.

The towhees' ages were determined by the presence or absence of molt limits in the wing coverts, with the extent of skull ossification used as a supplementary criterion when time allowed (McKinney 2004, Fettig and Hathcock 2015, Pyle 2022a). The birds were sexed by plumage color (Sibley 2014, Pyle 2022a). In the sample, I included only first-year birds in formative plumage. To document patterns of extensive feather replacement, I photographed the wings of the individuals in which any primary coverts had been renewed. Visible primaries and primary coverts are numbered distally (p1–p9 and pc1–pc8), and secondaries are numbered proximally (s1–s6). All individuals were of the subspecies *oreganus* on the basis of the extent of white on the scapulars, wing coverts, and rectrices (Pyle 2022a).

RESULTS

Two of 100 first-year Spotted Towhees captured from 4 September to 10 October had undergone a preformative molt more extensive than documented in prior literature (Pyle 1997a, Fettig and Hathcock 2015). A first-year female banded at Rocky Point on 23 September 2025 had replaced feathers in patterns that I inferred to have followed both eccentric and typical sequences. On the right wing, p1–p5 were retained and p6–p9 renewed; s1 and s2 were renewed, s3 retained, and s4–s6 renewed; pc1–pc3 were renewed, pc4 retained, and pc5–pc8 renewed (Figure 1). On the left wing, replacement of the primaries was symmetrical, but s1 and s2 were retained, s3 renewed, s4 retained, and s5 and s6 renewed; pc1–pc3 were renewed, pc4–pc5 retained, pc6 renewed, and pc7–pc8 retained (Figure 2). Similarly, a first-year male banded at Pedder Bay on 9 October 2025 had molted in patterns consistent with both eccentric and typical sequences. On the right wing, p1–p4 were retained and p5–p9 renewed; s1 was renewed, s2 retained, and s3–s6 renewed; pc1–pc4 were retained and pc5–pc8 renewed. On the left wing, p1–p3 were retained and p4–p9 renewed; s1 was renewed, s2 and s3 retained, and s4–s6 renewed; pc1 was renewed, pc2 retained, and pc3–pc8 renewed.

DISCUSSION

This study documents the most extensive instances of preformative molt yet recorded in the Spotted Towhee, with up to six primaries, five secondar-



FIGURE 1. Right wing of Spotted Towhee 3051-00417, a first-year female in formative plumage, banded at Rocky Point, British Columbia, on 23 September 2025, exhibiting a mix of renewed and retained feathers. The patterns of replacement are consistent with both eccentric and typical sequences. Primaries and secondaries (among p1–9 and s1–6) are labelled, with renewed remiges denoted by asterisks; those lacking an asterisk are retained juvenile feathers.

Photo by Max Hellicar



FIGURE 2. Primary coverts on the left wing of Spotted Towhee 3051-00417, a first-year female in formative plumage, exhibiting a mix of renewed (denoted by asterisks) and retained feathers, banded at Rocky Point, British Columbia, on 23 September 2025.

Photo by Max Hellicar

ies, and seven primary coverts renewed, expanding the upper bounds of the extent of preformative molt in each of these feather tracts and increasing the sample size of molt examined in the species (Pyle 1997a, Fettig and Hathcock 2015). Notably, I provide the first documentation of concurrent eccentric and typical replacement sequences during the preformative molt in the species. These patterns occurred in two individuals, representing 2% of the first-year Spotted Towhees examined on Vancouver Island in autumn 2025. In both individuals, although replacement of outer primaries, inner secondaries and outer primary coverts followed an eccentric sequence, replacement of the outer secondaries and inner primary coverts was consistent with the typical sequence (Figure 1).

With any unexpected pattern of replacement, the possibility of a feather's accidental loss and adventitious replacement (Humphrey and Parkes 1959) should be considered. In the cases of the two towhees I describe, multiple factors signify that these molt patterns arose intrinsically (Jenni and Winkler 2020b). Simultaneous loss of numerous remiges reduces a bird's flight capability and therefore probability of survival. Additionally, the similarity in replacement patterns between the left and right wings of each towhee is unlikely to have arisen by accident. Furthermore, the patterns of feather replacement in these Spotted Towhees are similar to those in other species in which concurrent eccentric and typical sequences have been identified.

In New Mexico, Fettig and Hathcock (2015) reported an eccentric preformative molt in one first-year male Spotted Towhee among a sample of 30 individuals in formative plumage. It had renewed p7–p9 (right wing) and p7–p8 (left wing), s4–s6 on both wings, pc8–9 (right wing) and pc7 (left wing), representing the first documented eccentric molt in the species. Also within the Rufous-sided Towhee complex, Johnson et al. (2013) recorded three of

27 formative-plumaged Eastern Towhees to have undergone an eccentric preformative molt, including a variable extent of outer primaries and inner secondaries but no primary coverts. Tattoni et al. (2022) detailed the renewal of remiges during eccentric preformative molt in five California (*Melozone crissalis*) and two Canyon Towhees (*M. fusca*). None of these, however, had renewed any primary coverts. During their first year of life, most temperate-zone passerines do not molt their primary coverts (Pyle 1997a, Jenni and Winkler 2020a), which are the feather tract least commonly renewed during the preformative molt (Kiat and Izhaki 2017). Those that do molt primary coverts, however, tend to replace them only when primaries are also being renewed, but may not molt the primary covert that corresponds with each renewed primary (Westphal et al. 1976, Gargallo and Clarabuch 1995), a pattern consistent with my findings (Figure 2).

Among 54 species of North American passerines that can undergo incomplete preformative molt, Pyle (1997a) found eccentric sequences in 46, typical sequences in eight, and both concurrently in six. Of these six species, the Blue Grosbeak (*Passerina caerulea*), Lazuli Bunting (*P. amoena*), Varied Bunting (*P. versicolor*), Carolina Wren (*Thryothorus ludovicianus*), House Finch (*Haemorhous mexicanus*), and Song Sparrow (*Melospiza melodia*), only 5–16% of individuals that had molted in an eccentric sequence had also replaced some feathers in the typical sequence (Pyle 1997a). Later, Small et al. (2013) found concurrent eccentric and typical sequences of replacement during preformative molt in 8% of the Field Sparrows (*Spizella pusilla*) they examined. The Spotted Towhee becomes the eighth North American passerine species, and the third in the family Passerellidae, in which both replacement sequences are documented.

Even within a species, passerines' preformative molt may range from partial to complete (Pérez and Brandolin 2024). Subspecies or populations may differ in the extent of this molt, as in the Song Sparrow (Hudson et al. 2008). Johnson et al. (2013) predicted, on the basis of their findings in the Eastern Towhee, that further examination of the Spotted Towhee would reveal eccentric preformative molt in a small percentage of birds, which my findings, along with those of Fettig and Hathcock (2015), support. Although a complete preformative molt has never been recorded in the Rufous-sided Towhee complex, the extent of replacement documented suggests the possibility warrants consideration. Although the presence or absence of molt limits is considered a reliable method to age Rufous-sided Towhees (Johnson et al. 2013, Fettig and Hathcock 2015), I encourage banders to check flight feathers for evidence of extensive preformative molt, and the extent of skull ossification (McKinney 2004, Pyle 2022a) may be useful for confirming the age of apparent adults in autumn. Despite iris color having long been regarded as a basis for assessing age in the Spotted Towhee (Davis 1957), Hohn et al. (2025) found extensive overlap in iris color among demographic groups, lessening its reliability as a criterion for age. Therefore, molt limits, and the patterns and extent of molt from which they arise, are important considerations in assessment of a Spotted Towhee's age.

When birds undergo preformative molt, they attain higher-quality plumage, which may improve their fitness (Kiat and Izhaki 2016, Podlaszczuk et al. 2016). Juvenile feathers grown in the nest are simpler in structure, having

fewer barbs per unit length, and are typically weaker than the feather generations succeeding them (Kiat and Izhaki 2016, Podlaszczuk et al. 2016). This is because nestlings prioritize fast growth of the juvenile plumage at the expense of feather quality (Butler et al. 2008). Therefore, in species that retain juvenile plumage beyond the preformative molt, those feathers' lower quality may impair fitness (Podlaszczuk et al. 2016). Feathers with greater structural quality improve flight performance and thermoregulation (Nilsson and Svensson 1996, Swaddle et al. 1996) and better resist wear and abrasion (Dawson et al. 2000). The adaptive value of an extensive preformative molt may be particularly pronounced in species exposed to conditions that accelerate feather wear and weaken feathers' structural integrity, such as abrasive vegetation and intense solar radiation (Willoughby 1991, Pyle 1998, Jenni and Winkler 2020a). The renewal of flight feathers in first-year Spotted Towhees, which inhabit thickets that are often abrasive (Bent 1968), may improve the birds' fitness by reducing the proportion of weaker feathers that have been exposed to substantial wear and increasing the proportion of fresher, higher-quality feathers.

Molt is an energetically and nutritionally costly process (Murphy and King 1992). There is a limit to the number of feathers first-year birds can replace without significantly compromising other needs (Delhey et al. 2020). Alternatively, variation in the preformative molt's extent may be neutral, arising and persisting in the absence of strong selective pressures. Wolfe et al. (2021) suggested that the pervasiveness of preformative molt in passerines is not currently adaptive, representing a vestigial trait, potentially leaving its extent somewhat unconstrained by contemporary selection. Variation in the extent of molt may also arise from constraints associated with time and resource availability (Delhey et al. 2020).

The southern subspecies of the Spotted Towhee average slightly greater in extent of preformative molt than those in the north (Pyle 1997b). Therefore, the incidence of extensive preformative molt at the northern edge of the species' range (Sibley 2014) is noteworthy, paralleling reports in Song Sparrow (Hudson et al. 2008). With the Spotted Towhee consisting of 21 recognized subspecies (AviList Core Team 2026), of which only one is represented in this study, further research, particularly farther south, may reveal extensive preformative molt to be more frequent in the species than previously reported.

Documentation of unusual molt patterns improves understanding of their prevalence, and improved knowledge on the variation in species-specific molt patterns enhances the accuracy of age determination. In turn, accurate age determination improves avian population monitoring and conservation.

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NOTES

FIRST TWO RECORDS OF THE GREAT KNOT (*CALIDRIS TENUIROSTRIS*) FOR WASHINGTON

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ABSTRACT: We document the first two records of the Great Knot (*Calidris tenuirostris*) for Washington, which also represent the second and third records of the species during spring migration in the Pacific Americas Flyway south of Alaska. The first Great Knot, which was in breeding plumage, was observed 15–20 May 2024, the second, in basic plumage, 12–18 May 2026. Both were at Willapa Bay: the one in 2024 was seen initially south of the mouth of North River Cove and subsequently at Ellen Sands, a high-tide roost site. The one in 2026 was observed at Ellen Sands on four dates. It is likely that the two Great Knots overwintered in northwestern Mexico and migrated northward with Red Knots (*C. canutus*).

With an estimated population of 425,000 individuals in the East Asian–Australasian Flyway (Hansen et al. 2016, 2022), the Great Knot (*Calidris tenuirostris*) breeds, migrates, and winters entirely within the Eastern Hemisphere (Cramp and Simmons 1983). The species breeds in alpine areas in the northeastern Russian Arctic and spends the boreal winter along the coasts of Pakistan, southern China, southeast Asia, and Australia (Cramp and Simmons 1983, Tomkovich 1997, Lisovski et al. 2016). The Great Knot's major stopover sites in the East Asian–Australasian Flyway, notably those in the Yellow Sea, are well documented (Chan et al. 2019). Except in western Alaska, where the Great Knot occurs semi-regularly (Kessel and Gibson 1978, Roberson 1980, Kessel 1989, Paulson 1993, Gibson and Byrd 2007), vagrants to the Western Hemisphere have been documented rarely. Here we report on the first documented observations of the Great Knot in Washington.

On 15 May 2024, Anholt, Buchanan, Cox, and Loverti observed a Great Knot at Willapa Bay, Pacific County, Washington (Figures 1, 2). It was foraging with a flock of about 150 Red Knots (*C. canutus roselaari*) on silty mudflats approximately 800 m south of the east side of the mouth of North River Cove in the northern part of the bay (46.726° N, 123.880° W). We observed the Great Knot from 20 m with spotting scopes from an airboat stopped on the mudflats. We watched it for about 5 minutes until it departed with the Red Knots to a new foraging location. On 20 May 2024, Anholt observed it at Ellen Sands, a shoal on which shorebirds roost at high tide in northern Willapa Bay (46.672° N, 123.964° W), implying that it remained at Willapa Bay for at least 6 days.



FIGURE 1. Great Knot observed south of North River Cove, in Willapa Bay, Washington, on 15 May 2024. This bird was foraging with a group of Red Knots when first observed. For much of the time it was observed, its feathers were erected, as can be seen in the image.

Photo by Cameron Cox

On 12 May 2026, Buchanan, Hutcheson, Loghry, and Swift also observed a Great Knot at Ellen Sands (Figures 3, 4). When Hutcheson saw the bird initially, it alternated between roosting and foraging among a group of ≥100 Red Knots in the interior of the shoal. The knots remained at Ellen Sands throughout the high tide. During three subsequent visits to Ellen Sands on 14, 17, and 18 May, the Great Knot



FIGURE 2. Great Knot in flight at Willapa Bay, Washington, on 15 May 2024. This represents the first record for Washington and the second observation during spring migration in the Pacific Flyway south of Alaska.

Photo by Cameron Cox



FIGURE 3. Great Knot in flight at Ellen Sands, a shoal in northern Willapa Bay, on 12 May 2026. This represents the second record for Washington and the third observation during spring migration in the Pacific Flyway south of Alaska.

Photo by Liam Hutcheson

was always seen roosting with Red Knots, indicating a minimum stopover period of 7 days. It was not found on 19, 20, 21, or 26 May.

The Great Knot observed in 2024 was similar in size, profile, and posture to the Red Knots with which it was foraging, but its bill was slightly longer (Figures 1, 2). It was in alternate plumage and had several distinctive plumage features: the back and breast were heavily marked with black, darker than the head, nape, or throat; the belly was white with dark chevrons or triangles that were slightly more pronounced on the flanks than on the belly; and the scapulars had distinct rufous banding. The head had a mix of light and dark feathers that resulted in a moderate gray appearance. The Great Knot observed in 2026, in contrast, was in basic plumage. The belly was



FIGURE 4. Great Knot foraging at Willapa Bay on 14 May 2026. In contrast to the Great Knot observed in 2024, this individual was in basic plumage.

Photo by Jason Loghry

white with sparse dark gray spots and chevrons on the sides. The throat, nape, back, and ear coverts were finely speckled with dark gray and light markings. The crown was slightly darker than the nape. The scapulars and coverts were gray with white margins and dark central shafts. The coverts were heavily worn as in spring migrant Red Knots in western Washington (Figures 3, 4). Shorebird biologists working in the East Asian–Australasian Flyway examined our photographs and concurred that the knot observed in 2026 was in first-year plumage, having hatched in 2025 (D. Rogers, C. Hassell, P. Battley, pers comm.).

Battley et al. (2006) reported that Great Knots appear to undergo a presupplemental molt in the Yellow Sea before moving north to breeding grounds in northeastern Russia. During that time the rufous-colored scapulars increase through molt, and the breast darkens slightly because of wearing off of the white tips on the black feathers. The Great Knot we observed in 2024 did not appear to be in presupplemental molt, which would have made it look brighter (Howell 2010), nor were its white feather tips worn.

Great Knots are known to associate with other shorebird species—including the Red Knot—during the nonbreeding period (Choi et al. 2015). They consume a variety of food items, but bivalves are considered an important if not an essential food source (Zhang et al. 2011). Migrating Red Knots in Washington also appear to favor bivalves (J. Buchanan pers. obs.), and they and the Great Knot were actively foraging on bivalves when our first observation was made.

The Great Knot's status is of growing conservation concern. While some analyses indicate seemingly stable abundance, information from Australia is uncertain, possibly because of high variability in the data (Clemens et al. 2016). More recently, the International Union for Conservation of Nature listed the species' status as endangered (www.iucnredlist.org.). Since the turn of the century, sites of major migratory stopovers along the East Asian–Australasian Flyway (e.g., in Korea and China) have been substantially altered or degraded through elimination of vast amounts of coastal habitat (Choi et al. 2015, Moores et al. 2016, Studds et al. 2017). Moreover, annual survival rates of the Great Knots that migrate through the Yellow Sea have declined abruptly, presumably in response to habitat loss (Piersma et al. 2016, Peng et al. 2023).

South of Alaska, as of July 2026, there were two records of the Great Knot from British Columbia (13 May 1987 at Boundary Bay and 15 January 1998 at Iona Island; https://bcrarebirdrecords), one record from coastal Oregon during autumn migration (1–17 September 1990; https://oregonbirding.org), and single records from West Virginia (13 and 14 August 2007 from Winfield Locks; https://ebird.org/checklist/S18542374) and Maine (23 July 2016 from Seal Island National Wildlife Refuge; https://ebird.org/checklist/S30822170). The Washington Bird Records Committee reversed its decision on an earlier report from western Washington from 6 September 1979 (https://wos.org/records). That committee accepted the 2024 observation of a Great Knot in Washington, and its review of the 2026 report is pending. The Western Hemisphere's remaining records from spring and summer (Kessel and Gibson 1978, Roberson 1980, Kessel 1989, Gibson and Byrd 2007, https://eBird.org, accessed 23 July 2026) are from the coast of and islands in the Bering Sea. The records of the Great Knot from Washington are the first documented for the state and are the second and third spring records in the Western Hemisphere south of Alaska.

Although it is uncertain how the Great Knots made their way to Washington, the following hypothesis seems probable. Red Knots that migrate along the Pacific coast of North America breed in northwestern Alaska and at Wrangel Island, Russia (Carmona et al. 2013). The mainland coast of Russia near Wrangel Island is within or adjacent to the breeding range of the Great Knot (Tomkovich 1997, Lisovski et al. 2016). It seems likely that the Great Knots we observed joined Red Knots somewhere in the far north, perhaps at a staging area, and then migrated to overwintering areas in northwestern Mexico (Carmona et al. 2013) or elsewhere along the flyway. Given

that the timing of the Great Knot's northbound migration (Tomkovich 1997; but see Lisovski et al. 2016) is like that of the Red Knot (Buchanan et al. 2017) and both species prefer bivalve prey (Booth and Buchanan 2020), we might expect that Great Knots would migrate north with Red Knots or at least stop at locations they favor.

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BOOK REVIEW

Birds of California's Channel Islands, by Paul William Collins, Justyn Todd Stahl, and Harry Lee Jones. Santa Barbara Museum of Natural History Monographs No. 9, Studies in Biodiversity No. 7. Two volumes, 781 pages. Hardcover, $129.00. ISBN-13: 978-0-936-49420-3. **Volume 1, Ecology, History, and Human Influence.**

The Channel Islands have long intrigued and enticed naturalists, evoking an enduring sense of adventure and discovery off the coast of southern California. Half a century in the making, with a cutoff date of 31 December 2023, *Birds of California's Channel Islands* presents a satisfyingly comprehensive treatment of this storied archipelago's avifauna. The hardcover, two-volume set is handsomely published, printed on heavy stock, and furnished in a blue, cloth-covered slipcase. The typesetting, with cyan/blue headings and black text, is neat and very readable, and the writing is, for the most part, clean and direct. Scattered small drawings by Dana Gardner and N. John Schmitt are attractive and unobtrusive. A recurring motif is the Island Scrub-Jay, aptly chosen as "the ideal ambassador for the avifauna of California's Channel Islands."

As the size, scope, and significance of this work call for a substantial review, I've chosen to cover only volume 1 here; I'll address volume 2, *Species Accounts*, and Appendix 4, *Checklist of the Birds of California's Channel Islands* in another issue of *Western Birds***.**

As stated on page 3 of the Introduction, "The intent of this book is to serve as a reference guide to the avifauna of the Channel Islands, the islands' history during the past 180 years, their status, and efforts being undertaken to preserve and conserve them." Furthermore, "Data summarized in this book should serve as a baseline against which any future stressors could be assessed, such as the introduction of novel diseases, future colonization by non-native predators or competitors, habitat change, and the effects of climate change." *Birds of California's Channel Islands* achieves these rigorous scientific objectives while also bundling in one neat package the scores of outrageous records of vagrants that function as avian catnip for so many mainland birders.

Lead author Paul Collins, curator emeritus of vertebrate zoology at the Santa Barbara Museum of Natural History, has visited each of the Channel Islands, spending the most time on little-studied Santa Rosa. Collins devoted decades to the painstaking tasks of tracking down museum records and publications, developing extensive databases, and writing the text (a paragraph on the back of Volume 2 credits his co-authors with "field contributions, editing, and e-Bird verification"). How fortunate we are that he lived long enough with the requisite fortitude and the right co-authors to see this daunting project through to its ripe and succulent fruition.

In 2023, Justyn Stahl joined the effort, bringing his 15 years of experience helping to conserve the endemic subspecies of the Loggerhead Shrike and Bell's Sparrow on San Clemente Island. Many mainland birders know Stahl best for his long (2008–2023) and enviable run of records of vagrants from the famed Lemon Tank and elsewhere on San Clemente, where he documented such gems as the Dusky Warbler, Bluethroat, and Smith's Longspur. Let us hope that any anguish Stahl might have experienced from being off the island on 25 September 2017, when a Eurasian Wryneck was photographed at Lemon Tank, has by now abated.

H. Lee Jones' personal experience across the Channel Islands is even more significant, dating to the 1970s when he earned his doctorate under Jared Diamond at UCLA with a dissertation titled, *Studies of Avian Turnover, Dispersal, and Colonization of the California Channel Islands*. In this early work, Jones demonstrated that the Channel Islands function as last-gasp havens for wayward migrants caught out over the ocean during migration, much like the famous Southeast Farallon Island

off San Francisco. Jones's contributions include records of such scarce waifs as the Chimney Swift, Scissor-tailed Flycatcher, and Golden-winged Warbler. He has also prepared annotated bird checklists and published on the natural history of the seabird colonies on the islands.

Chapter 1 of *Birds of California's Channel Islands* addresses the physical environment. The eight Channel Islands differ from each other in their geology, topography, climate, size, maximum elevation, and degree of isolation. Their distance from the mainland varies from 12 miles for Anacapa to 61 miles for San Nicolas. All islands excluding San Nicolas have offshore rocky islets that provide important roosting and nesting sites for seabirds. Current human activities vary from island to island, but conservation and restoration of their natural communities and endemic taxa have been a shared priority across all of the islands since the 1970s.

Ten pages are devoted to describing the islands' complex geologic history. In short, the four northern Channel Islands, San Miguel, Santa Rosa, Santa Cruz, and Anacapa, are products of volcanic and tectonic forces. About 19 million years ago, the Transverse Ranges Block broke free from the North American Plate and was dragged northward by the Pacific Plate. The northern part of this block embedded into the continent at Point Conception as the southern part, while being compressed, rotated clockwise by 110° so that its elevated central ridge now runs east and west, forming the Transverse Ranges onshore and the four northern Channel Islands offshore. Sea-level fluctuations associated with cycles of glaciation have caused the northern Channel Islands to repeatedly coalesce into a single mega-island, "Santarosae," that has always been separated from the mainland by a water gap of at least five miles. The southern Channel Islands, San Nicolas, Santa Barbara, Santa Catalina, and San Clemente, are more geographically isolated from each other and from the mainland than the northern Channel Islands and, unlike the northern islands, these were never connected to each other. The southern Channel Islands, which arose through volcanism and tectonic uplift, are oriented parallel to the Peninsular Ranges, as they were not subject to the tectonic rotation of the northern quartet. The authors' detailed discussions of the geology of each island and of the two major groupings of islands, explain why the landforms appear as they do today. These discussions also provide context for understanding the mix of endemic and near-endemic birds, and other life forms, found on different islands.

Maps include three pull-out overleaves: a topographic map of the islands with unlabeled submarine topography, a topographic map of the islands with labeled submarine topography, and a topographic map depicting conditions 20,000 years ago, when sea levels were 300–330 feet lower than today. The third pull-out shows that the Southern California Bight was once dotted with 26 islands that accounted for 1780 square miles (18 more islands and 1431 more square miles than in modern times). A regular-sized map shows the eight current islands as they appeared 20,000 years ago, 10,000 years ago, and as they are now. Another map shows surface ocean circulation and the mixing of the California Current, Davidson Current, and California Countercurrent in the Southern California Bight.

Surprisingly, maps that depict each island and its named/cited features are not included, so most readers will need to seek out this basic information online. The National Park Service has produced hiking maps for the four northern islands, plus Santa Barbara Island, which appear to be reasonably complete, although some holes remain (e.g., "Windmill Canyon," cited in the species account for the Northern Harrier, is missing from the hiking map of Santa Rosa Island). The Catalina Island Conservancy provides a detailed map of Santa Catalina Island. Detailed maps of San Nicolas and San Clemente islands can be found at Islapedia.com, and many cited locations on the latter island are mapped as hotspots at eBird.org. To save readers from this bother, the Santa Barbara Museum of Natural History might consider developing a set of uniform maps that could be accessed on its website. In the case

of a second print-run, two of the pull-out maps (Figures 1.1 and 1.3) could be easily combined to save money.

Chapter 2 describes the biotic environment, starting with the interplay of oceanic currents in different parts of the Southern California Bight at various seasons, which affects the distribution of seabirds on and around the islands. Northwest winds intensify in late winter and spring, driving upwelling of cold, nutrient-rich waters of the southbound California Current in the bight. These fortified waters feed the small fish and squid that support not only local breeding colonies of resident seabirds, but also a wide range of migratory seabirds and overwintering subarctic species. The narrative highlights regions of the Southern California Bight that support the greatest concentrations of seabirds: Arguello Canyon off Point Conception, waters off the west end of San Miguel Island, waters along the Santa Rosa–Cortes Ridge, and waters at the margins of submerged island shelves. The authors praise the efforts of observers to document seasonal patterns of seabird migration off the western shore of San Clemente Island (Sullivan, B. R., and Kershner. E. L. 2005. The birds of San Clemente Island. W. Birds 36:158–273) and call out for "more shore-based surveys . . . particularly on San Nicolas and San Miguel islands."

Chapter 2 discusses the main habitat types and their distribution on and around the islands: nearshore waters, rocky coastline, coastal strand, coastal salt marsh, freshwater marsh, freshwater impoundments, coastal sage scrub, coastal bluff scrub, maritime cactus scrub, island chaparral, grasslands, riparian woodland, oak woodland, island woodland (variable woodlands consisting of ironwoods, oaks, scrub oaks, etc.), conifer forest, and human-altered habitats. It lists the characteristic bird species of each island's terrestrial habitats. Provision of scientific names in Appendix 5, rather than in the text, improves the readability of these descriptions. The discussion of island chaparral notes that many birds typical of mainland chaparral, such as the California Thrasher and California Towhee, have failed to reach the Channel Islands, resulting in competitive release (allowing species to be more common in island chaparral than they are on the mainland) and increased niche breadth (changes to habitat usage by some island species in response to decreased interspecific competition).

Chapter 3 describes the prehistoric avian environment as investigated by Collins and the late Dan Guthrie, among others. The five-page chapter contains extensive data on the islands' prehistoric record, which includes seven extinct species: (two flightless sea ducks, a puffin, a flightless alcid, a gannet, an eared owl, and a condor) and an extinct subspecies of caracara. This chapter also describes ways in which the Chumash and Tongva peoples have related both spiritually and materially to the birds of the islands. The chapter is filled with interesting and relevant information, but I found it difficult to wade through because the narrative jumps around chronologically and geographically, repeats information, and discusses extirpations that have occurred much more recently than in prehistoric times. Those with an especially keen interest in prehistory should be able to overlook the organizational problems, but general readers will likely spend more time pondering Tables 1 and 2 in Appendix 1, which specify the numbers of bones recovered for each bird species on each island (amounting to more than 96,000!).

Chapter 4, Human Influences, describes the known influences of people on the islands' avifauna during the prehistoric period (pre-European contact), protohistoric period (European contact through the early 1800s), historic period/herbivore era (1850s to late 1990s), and the conservation and restoration period (1970s to present). As many as 3000 to 4000 Chumash and Tongva occupied the northern Channel Islands for 13,000 years and the southern Channel Islands for 9500 years, up until the 1820s, when those who had managed to survive epidemics of Old World diseases were removed to Spanish missions on the mainland. These tribes' lasting influences on the ecology of the Channel Islands include the translocation from the mainland

of various small mammals that in time evolved into island taxa (most famously the Island Fox) and the wiping out of "several burrow-nesting seabirds" and a large sea duck, *Chendytes lawi*.

Between the 1700s and the late 1990s, and in some respects extending to the present day, humans from various lands have exploited the Channel Islands in many ways, from commercial fishing and abalone harvesting to hunting of otters and pinnipeds to grazing of livestock to introduction of game animals for hunting to military uses, and, of course, tourism. Overlooked in the narrative are mining and, more importantly, hard-rock quarrying (most notably, the massive Pebbly Beach Quarry on Santa Catalina Island, which has supplied marine-grade riprap to coastal projects on the mainland for nearly a century). Table 4.1 lists the 19 terrestrial mammal species introduced to and, in most cases, eradicated from the various islands. This table also specifies the year that each island—except Santa Catalina with its enduring populations of Mule Deer and American Bison—was freed of herbivores.

Volume 1 is nearly error-free, but I was momentarily thrown by a claim on page 54 that "feral burrows" had been eradicated from San Miguel before recognizing this as a misspelling. In Table 7.5, the Graylag Goose should be listed for Santa Catalina, not Santa Barbara. The only other miscues that came to my attention, both in the Literature Cited, involve Robert Pyle being credited as author of one of Peter Pyle's publications, and the book authored by this father/son team being listed out of alphabetical order.

Chapter 4 goes on to describe how dumping of DDT and other organochlorine pollutants into the Southern California Bight by the Montrose Corporation during the 1950s and 1960s led to the decline and extirpation of several marine birds and terrestrial raptors from the Channel Islands. On a positive note, settlement funds from legal actions taken against Montrose have supported successful programs to reintroduce the Peregrine Falcon and Bald Eagle to the islands, to eradicate the Black Rat from Anacapa, and to improve seabirds' recruitment and productivity.

Chapter 5 describes the islands' rich ornithological history, which dates back to 1842 when William Gambel twice voyaged to Santa Catalina. Gambel was only 18 years old that year, and no record exists of him having set foot on any other Channel Island before typhoid claimed him eight years later. Synopses describe five government-sponsored surveys, undertaken by such renowned figures as William Dall, James Cooper, Henry Henshaw, John Townsend, Edgar Mearns, and Alfred Anthony. Chapter 5 refers the reader to Appendix 2, which catalogues the participants in more than 1000 ornithological expeditions to the islands (from 1842 through the early 2000s), and to Appendix 3, which lists the abbreviations used to identify more than 1600 cited observers. One is honored to see his or her own name in an ornithological lineage descended from such giants as Harold Bryant, Joseph Grinnell, Alden Miller, George Willett, A. J. Van Rossem, and the curator of ornithology and mammalogy at the Santa Barbara Museum of Natural History from 1935 to 1963, Egmont Rett. Morbidly, I checked for Ralph Hoffmann's ill-fated excursion to San Miguel Island on 23 July 1932, but apparently no bird records survived his fatal fall from a cliff while botanizing, and thus the last entry for Hoffmann is from March of that year, when he notably observed a Townsend's Solitaire above Pelican Harbor on Santa Cruz Island. I got a little misty harkening back to my own 22 visits to beloved San Nicolas Island, all but three of which took place before 11 September 2001. The U.S. Navy's subsequent ratcheting up of restrictions on civilian access to this fascinating outpost represents one of the lesser, but still unfortunate, casualties of the ever-expanding global war on everything.

Chapter 5 includes two more very useful tables, one listing the original and current names of each endemic avian taxon described from the Channel Islands and the other showing their current distribution on each island. Potential confusion arises from the last column being labeled "Mainland Species" instead of "Mainland

Subspecies" and from the term "I" (for introduced) not being explained in the notes below the table.

Chapter 5 next discusses molecular studies of the Channel Islands' endemic taxa, hinting at possible future recognition of new subspecies. It details specimen and egg collecting on the islands over time with the aid of four more tables and a histogram. The chapter concludes with a rundown of ornithological research on the islands from the late 1960s to present. Among a dizzying number of projects mentioned in this section and incorporated into the species accounts in Volume 2 are various studies of the effects of organochlorides on eggshells, multiple island-wide surveys of seabird colonies by George Hunt and others, the work of Ned Johnson on the origin and differentiation of the islands' endemic avifauna, and Jonathan Atwood's study of the breeding biology of the Channel Islands' only extant endemic bird species, the Island Scrub-Jay.

Chapter 6 lays out the methods used to put the set together, which include not only all published literature but also the extensive "gray literature" on seabirds and, to a somewhat lesser extent, landbirds. Collins diligently mined museum data to create two important databases: the Channel Islands Bird Specimen database, with records of 9119 individuals of 253 species from 38 museum collections, and the Channel Islands Egg Set and Nest database, with records of 1894 egg sets of 45 species from 39 museum collections. The final major sources of data are observers' field notes, results of banding efforts, and records from eBird.org and iNaturalist.org. Long-term trend data, presented in Appendix 1, Tables 6–10, were obtained from Christmas Bird Counts, Breeding Bird Surveys, and point-count monitoring surveys. Chapter 6 concludes by explaining the plan of the species accounts in Volume 2 and the relative-abundance codes used in the Appendix 4 checklist (both to be addressed in part 2 of this review).

Chapter 7, Results and Discussion, starts with a review of the historical record of previous compilations of bird records from the islands dating back to A. B. Howell's 1917 monograph, *Avifauna of the Channel Islands off the Coast of Southern California*. Table 7.1 summarizes the number of bird species recorded on each island after the publication of each new island-specific, or island-wide, compilation. The islands with the best observer coverage, San Clemente, Santa Cruz, and San Nicolas, average 92 more species than do the least covered, San Miguel, Anacapa, and Santa Rosa (347 to 255). Table 7.2 reports the number of species recorded per family on the Channel Islands by ecological groups.

Page 84 lists out the 32 species recorded only on a single island, including such coveted rarities as the Jouanin's Petrel, Northern Wheatear, Common Redpoll, and Cerulean Warbler. Two pages later, Table 7.3 lists the 14 species for which a sighting from the islands represents the first or second record for California. A standout among standouts is the record of an Asian Stonechat on San Clemente Island 20–21 October 1995, misidentified for years as a Vermilion Flycatcher!

Chapter 7 goes on to describe four "Characteristics of Channel Islands Avifauna," which I won't repeat here (you really should buy the set!), but one generalization is that the breeding seabirds are "diverse and abundant" (reflecting the high seasonal productivity of the waters of the Southern California Bight and the widespread availability of protected nesting sites, especially on islands and islets that lack Island Foxes), whereas the breeding landbirds are characterized as "depauperate" (attributed mainly to the failure of many mainland residents to colonize any island and to migratory species that regularly pass through the islands without staying to breed).

After a review of the source regions of vagrant birds recorded on the Channel Islands (eastern North America, central North America, southwestern U.S. and Mexico, Asian and Arctic, Pelagic) and a brief discussion of introduced species and escaped exotics, Chapter 7 dives into a thorough summary of the Channel Islands' breeding avifauna. Since the last comprehensive assessments of breeding landbirds and seabirds in 1980, 32 or 33 additional breeding species have been confirmed

(both numbers are cited) and 11 more are suspected to have nested on one or more islands. Table 7.5 shows the Guadalupe Murrelet as a new breeder, although the species account notes that in 1977 and 1978 this species (then classified as a subspecies of Xantus's Murrelet) nested on Santa Barbara Island. The listing of breeding-status codes below Table 7.5 is missing the codes for common, irregular, and uncommon, although they are defined in Chapter 6. These points aside, Table 7.5 is a useful summary of the known and suspected breeding status of each species on each island, and Table 7.6 shows the estimated size for breeding seabirds' population by island; see also Tables 3–5 in Appendix 1, which give counts of cormorants and pelicans at the islands' breeding colonies over the years. Any questions raised in these summary tables are answered in the species accounts (Volume 2).

Pages 100–102 describe changes in the breeding avifauna of the Channel Islands resulting from anthropogenic effects, especially the introduction of many non-native mammals (e.g., sheep, deer, rabbits, rats, cats), most of which were eventually removed. While many beneficial results have come about through passive recovery of habitats after removal of invasive species, the authors note, for example, that "no chaparral plants have sprouted on San Miguel since non-native herbivores were removed 50–60 years ago" with the assertion that "active restoration will be needed to assist in the reestablishment of chaparral on the island." Invasive species remain on some islands, Catalina especially, where human residents of Avalon help to maintain their populations and, at least in the case of the Mule Deer, actively oppose their removal.

The Conservation and Restoration section describes many successful programs enacted to maintain, increase, and in some cases re-establish, populations of various avian taxa affected by human-related degradation of island ecosystems. For seabirds, removal of herbivores from most of the islands has had profoundly positive effects, as has eradication of rats from Anacapa and cats from San Nicolas. Other measures that have improved conditions for burrow-nesting seabirds include establishing artificial burrows with broadcast of social vocalizations, replacing exotic plants with appropriate natives that provide better protection from avian predators, translocation of Spotted Skunks away from nesting areas, improved lighting practices for squid boats operating near the islands, and restricting human access to certain breeding areas during the nesting season. After describing actions taken to conserve the Bald Eagle, Peregrine Falcon, Island Scrub-Jay, and on San Clemente Island, Loggerhead Shrike and Bell's Sparrow, the section closes with discussions of how the effects of climate change, including increasing air and ocean temperatures, reduced precipitation, a rising sea level, increasing ocean acidification, and increasingly intense El Niño events, are likely to affect the islands' terrestrial and marine ecosystems by the end of the twenty-first century. As the authors note in conclusion, we can only wait to see how so many mercurial parameters will interact to affect the islands' bird populations. Thankfully, *Birds of California's Channel Islands* provides a full suite of benchmarks that will be invaluable to tomorrow's researchers.

Birds of California's Channel Islands not only presents a thorough and engaging portrait of the archipelago and its birdlife, it represents a consequential work of ornithological research, documentation, synthesis, and analysis undertaken on a scale seldom attempted and even more rarely achieved. As the planet's climate continues to warm, with potentially dire consequences for many insular (and mainland) bird populations, *Birds of California's Channel Islands* establishes countless points of reference against which future data from the Channel Islands can and will be evaluated. If this review has failed to persuade any reader of *Western Birds* to order a copy of *Birds of California's Channel Islands*, before the first printing runs out (only 250 sets were published!), rest assured that the upcoming review of Volume 2 will provide further encouragement.

Robert A. Hamilton

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The Santa Barbara Museum of Natural History has produced a major landmark in the ornithology of western North America in publishing *The Birds of California's Channel Islands* by Paul W. Collins, Justyn T. Stahl, and H. Lee Jones. In this issue of *Western Birds*, Robert A. Hamilton offers a review of volume 1 of this two-volume work. Volume 1 is far more than an introduction to the islands' birds, for it covers the islands' geology, paleontology, and history of human exploitation at a depth that provides a firm foundation for understanding their biology and continuing management.



