

DIET-RELATED PLUMAGE ERYTHRISM IN THE WESTERN TANAGER AND OTHER WESTERN NORTH AMERICAN BIRDS

JOCELYN HUDON, Royal Alberta Museum, 9810 103A Avenue NW, Edmonton, Alberta, Canada T5J 0G2; jocelyn.hudon@gov.ab.ca

PETER PYLE, The Institute for Bird Populations, P. O. Box 518, Petaluma, California 94953; ppyle@birdpop.org

ABSTRACT: Consumption of the berries of two exotic bush honeysuckles (genus *Lonicera*) containing the red carotenoid pigment rhodoxanthin has resulted in abnormal erythristic plumages in several species of birds in eastern North America. Here we report 12 examples of plumage erythristm in the Western Tanager (*Piranga ludoviciana*), in both live birds (5) and museum specimens (7), that we suspect have the same etiology. The erythristic tanagers feature overtly orange to red feathers variously scattered on the head, rump, wing coverts, and/or underparts, areas of the plumage normally colored by carotenoid pigments. All were in their year of hatching, so the reddened feathers, including replaced median coverts with orange tips, represent formative plumage grown on or near the breeding grounds where berries containing rhodoxanthin are available. By contrast, adult Western Tanagers undergo body molt primarily in the Mexican monsoon region in fall and on their winter grounds in early spring where bush honeysuckles are nonexistent. We also report examples of Red-breasted Sapsuckers (*Sphyrapicus ruber*) with anomalous red pigmentation on their backs and of Cedar Waxwings (*Bombycilla cedrorum*) with orange tail bands, as previously documented in the East. In these species, the reddened areas are typically yellow or green, colors based on carotenoid pigments that can be altered through the consumption of fruits containing rhodoxanthin. We conclude that these reddened feathers are the result of the consumption of honeysuckle berries or possibly the red arils of the Pacific Yew (*Taxus brevifolia*), representing a first report of diet-related erythristm in western North America.

Consumption of the berries of two introduced species of bush honeysuckles, the Morrow's (*Lonicera morrowii*) and Tatarian (*L. tatarica*) honeysuckles, has for the last several decades resulted in altered, erythristic (reddened) plumages in birds of several species in eastern North America and the American Midwest (Mulvihill et al. 1992, Hudon and Mulvihill 2017). Here we describe probable examples of plumage erythristm (reddening) linked to the ingestion of the berries of these honeysuckles, or of the arils of the Pacific Yew (*Taxus brevifolia*), native to western North America, which harbor the same red pigment, in the Western Tanager (*Piranga ludoviciana*), Red-breasted Sapsucker (*Sphyrapicus ruber*), and Cedar Waxwing (*Bombycilla cedrorum*), representing a first report of this condition for western North America.

Many species of birds naturally deposit carotenoid pigments in their feathers to produce bright yellow to red plumage colors, or, when accompanied by dark melanic pigments, green colors. The berries of the two bush honeysuckles, uniquely among angiosperm fruits in North America, contain a carotenoid pigment of intense red hue, rhodoxanthin (Brush 1990), that can substitute for the normal, yellow carotenoid pigments in feathers, if it is ingested at or just before the time of feather molt (Witmer 1996). A recent compilation identified probable instances of diet-related plumage erythristm

in at least 15 species of birds, primarily in eastern North America but also in the American Midwest (Hudon and Mulvihill 2017). In a few of these instances, the role of rhodoxanthin from honeysuckle berries in the feather reddening is empirically well supported (Hudon and Brush 1989, Mulvihill et al. 1992, Witmer 1996, Hudon et al. 2013, 2017). The species with examples of erythristic plumages include the Northern Flicker (*Colaptes auratus*), the Cedar Waxwing, the White-throated Sparrow (*Zonotrichia albicollis*), the Baltimore Oriole (*Icterus galbula*), several species of wood warblers, the Scarlet Tanager (*Piranga olivacea*), and the Northern Cardinal (*Cardinalis cardinalis*). Photographs of reddened individuals of these species can be seen in Flinn et al. (2007), Hudon et al. (2013), and Hudon and Mulvihill (2017).

Plumage erythrism resulting from the ingestion of berries containing rhodoxanthin exhibits specific characteristics that stem from the way it is produced (Hudon and Mulvihill 2017). First, we can expect the red colors to be restricted to feathers that naturally contain carotenoids (which rhodoxanthin displaces), including those of bright yellow to red color, but also of green color in feathers that harbor dark melanin pigmentation. Second, we expect the reddened feathers to have been grown primarily in the summer and fall when berries are available for consumption (Mulvihill et al. 1992, Hudon et al. 2017). Many birds replace their body feathers in late summer, often irregularly and gradually in different body regions simultaneously (Jones 1930, Butler et al. 2002). Reddened feathers may thus appear scattered over the brightly colored areas of the plumage, resulting in a speckled look (Hudon and Mulvihill 2017). These individuals may subsequently lose the red feathers as a result of the prealternate molt in spring, depending on its extent in a given species or individual.

WESTERN TANAGER: EXAMPLES PHOTOGRAPHED IN THE FIELD

Male Western Tanagers in first and definitive alternate plumages (from April to August) show variable amounts of red feathering in the head, sometimes extending to the upper breast and perhaps rarely to the mid-breast, whereas females in all plumages and males in formative plumage (from September to March) show no red in the head or at most a few red feathers on the forehead and elsewhere on the head in older females (Hudon 1999). The remainder of the plumage, including most of the upperparts and underparts and the tips of the median and greater wing coverts (wing bars), is primarily black and olive-green to yellow, without red or orange (Hudon 1999).

We first became aware of fall Western Tanagers with anomalous orange-toned feathers a few years ago, when Tim Reeves shared images of an odd tanager he and others observed at Berg Park in Farmington, San Juan Co., New Mexico, on 13 September 2016. The individual had orange to red feathers scattered over much of its body, including its crown, sides of the head, nape, rump, throat (moustachial area), upper chest, belly, and lower flanks, in areas otherwise yellow to greenish yellow (Figure 1A). Orange coloration also extended to the tip of the median coverts of its upperwing (upper wing bar). The reddish feathers gave the bird an overall orange glow.

More recently, another erythristic Western Tanager came to light when, on 25 September 2020, Nathan French, and subsequently Becky Turley, observed

DIET-RELATED PLUMAGE ERYTHRISM IN SOME WESTERN BIRDS

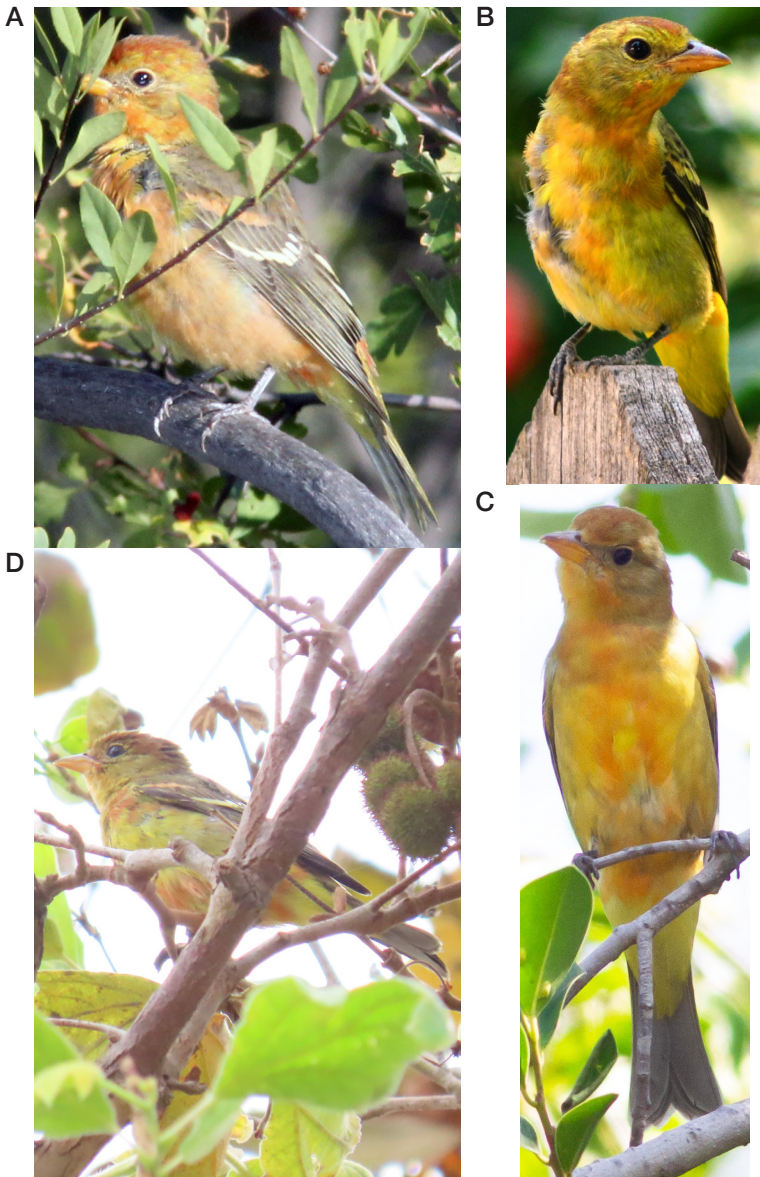


FIGURE 1. Western Tanagers with aberrant reddened feathers. A, Berg Park, Farmington, New Mexico, 13 September 2016. B, Thompson Falls, Montana, 18 August 2015. C, Coronado Golf Course, Coronado, California, 25 September 2020. D, along the West San Gabriel River Parkway Nature Trail in Lakewood, California, 26 September 2020.

Photos by Tim Reeves (A), Jim Greaves (B), Nathan French (C), and Joyce Brady (D)

a tanager with a “reddish/orange wash on the head, belly, and upper wingbar” at the Coronado Golf Course in Coronado, San Diego Co., California (<https://ebird.org/checklist/S74050728>, <https://ebird.org/checklist/S74060848>; Figure 1C). Like the previous bird, this individual exhibited orange feathers over much of the normally yellow to yellow-green areas of its plumage, including the crown, sides of the throat, marginal lesser coverts at the bend of the wing, and within the breast, belly and undertail coverts, as well as the tips to the median coverts. At the time of the observation, the bird could be seen eating berries (though not of bush honeysuckles), and other Western Tanagers were nearby. The following day, on 26 September 2020, Joyce Brady reported (<https://ebird.org/checklist/S74103327>) a third tanager with orange feathers over much of its body, including the tips of the median coverts, along the West San Gabriel River Parkway Nature Trail in Lakewood, Los Angeles Co., California (Figure 1D). Finally, a search of the Macaulay Library image catalog and <https://ebird.org> turned up other Western Tanagers with atypical reddened feathers, including one photographed by Jim Greaves in Thompson Falls, Sanders Co., Montana, on 18 August 2015 (Macaulay Library image ML119879281; Figure 1B). The bird, a particularly bright hatching-year male, exhibited orange feathers scattered over much of the normally yellow sections of its plumage, including orange-tinged tips to the outer median coverts. Also, Tom Crabtree photographed an erythristic tanager at Sawyer Park, Deschutes Co., Oregon, on 12 September 2015 (<https://ebird.org/checklist/S24921607>).

We could find no mention in the literature of Western Tanagers with reddened feathers in areas of the plumage other than the head as part of the normal, or even extreme, variation in fall birds, i.e., as examples of phenotypic plasticity in this species. Probably because of this, most of these individuals were initially speculated to be hybrids between the Western and Summer (*P. rubra*) tanagers, as males and many females of the latter species can have red body plumage in the fall. But hybridization with the Summer Tanager is quite uncommon in the wild (see Pandolfino et al. 2010). We found only two well documented instances of probable hybridization between the Western and Summer tanagers. A male Summer Tanager seemingly bred with a female Western Tanager in Colfax, Placer Co., California, in 2006, resulting in probable hybrids (Pandolfino et al. 2010). Then a male resembling a Western Tanager with a slightly oversized bill and generally orange plumage, associating with female Summer Tanagers, was first discovered by Brian Gatlin at Red Rock State Park, Yavapai Co., Arizona, in 2006, relocated in 2008, and photographed on 25 May 2009 (Gatlin 2009). The five tanagers we report here did not exhibit the odd characteristics of these apparent hybrids or characteristics suggesting hybridization with another species. Indeed, we might expect a bird that was the product of past, or cryptic, hybridization between the two species to show red in areas of the plumage that are red in the Summer Tanager but don't bear carotenoids in the Western Tanager (e.g., the centers of back or flight feathers or coverts) and for the red to be more evenly distributed over the body. Except for the presence of red to orange feathers, the birds appeared perfectly typical of the Western Tanager in structure and plumage.

A far more likely explanation for the reddish feathers is that these individuals, like many birds in eastern North America, ingested berries of introduced bush honeysuckles or other berries containing rhodoxanthin during the fall

molt. It should come as no surprise that the phenomenon of diet-related plumage erythrism was first described and characterized in eastern North America and the American Midwest. First introduced to eastern North America in the late 1700s, Morrow's and Tatarian honeysuckles were actively disseminated there in the 1960s, promoted as providing food and cover to wildlife (Edminster and May 1951, Witmer 1996), and have since become naturalized, even invasive, in many states (Williams 2005). But the Tatarian honeysuckle also grows in a number of western states, particularly in the north (Alaska, Washington, Oregon, northern California, Idaho, Montana, Wyoming, Utah, and Colorado), as well as in British Columbia, Alberta, and Saskatchewan in Canada (see maps in Catling et al. 2016, Hudon and Mulvihill 2017, Klinkenberg 2020), while the Morrow's honeysuckle currently exists in several counties in Wyoming, Colorado, and New Mexico (see map in Hudon and Mulvihill 2017). These honeysuckle species are not known from the southwestern United States or northwestern Mexico. In moist, shady habitats throughout the Northwest the red arils of the Pacific Yew, like those of other members of the gymnosperm genus *Taxus*, offer another potential source of rhodoxanthin (Kuhn and Brockmann 1933, Maoka et al. 1996). Western Tanagers are well known to consume a variety of fruits, notably in mid to late summer (Bent 1958). Beal (1907) found that nearly 18% of the material in the stomach content of 46 Western Tanagers from California between April and September consisted of fruit. As expected for diet-related erythrism, the affected feathers are also ones that naturally contain carotenoids in the species, i.e., feathers that normally have yellow or greenish tones in fall Western Tanagers, as on the crown, head, underparts, rump, tips to the median coverts, and the marginal lesser coverts located near the bend of the wing. The reddened feathers were also scattered about the birds' plumages, often a hallmark of diet-related plumage erythrism.

All four birds shown in Figure 1 as well as the individual photographed in Oregon had the tapered rectrices and lightly worn outer primaries that indicate juvenile feathers retained into fall of hatching-year birds (Pyle 1997). The olive and yellow tones to the body feathers indicate that all five birds had undergone some or all of their preformative molt, the molt that replaces the juvenile plumage, since juveniles tend to be brownish and have streaks to the breast. In addition to the body plumage the birds had replaced median coverts during the preformative molt, as juvenile coverts are much weaker and have paler whitish or whitish-buff tips. The brighter yellow-green heads and rumps and broad colorful tips to the replaced median coverts also indicate that all five birds were males (Pyle 1997); formative median coverts are often tipped pale yellow in hatching-year females and bright yellow in hatching-year males, as shown by these birds, helping to clarify their sex. By contrast, the outer greater coverts, where visible in images of these birds, appeared to be juvenile, as expected in many migrating hatch-year Western Tanagers (Pyle 1997, Butler et al. 2002).

WESTERN TANAGER: MUSEUM SPECIMENS

To study erythrism in the Western Tanager further, we examined 475 specimens of this species held at the California Academy of Sciences (CAS; 330 specimens examined by Pyle) and the Royal Alberta Museum (PMA; 145 specimens examined by Hudon). We found at least six specimens (1.3% of

all birds) showing anomalous, often scattered red feathers, birds that stood out for their redness among the other Western Tanagers in the collections (Figures 2 and 3). Since these specimens included older (>50 years old) examples, whose colors could have changed slightly with time (see Armenta et al. 2008), we made sure to visually compare the erythristic birds to specimens of comparable age. Color changes associated with specimens' aging should not lead to a variegated or speckled look as in most of these examples or lead to an increase in the red of feathers colored by carotenoids (Armenta et al. 2008). All six of these birds, as well as an additional specimen from the Natural History Museum of Los Angeles County (LACM 122206), were hatching-year birds in formative plumage collected between 2 August and 8 September (Table 1, Figure 2). The specimens at CAS and PMA represent 6.5% of the 93 specimens in formative plumage. Like those of the birds photographed in the wild, the reddened feathers were often scattered throughout the body and in most cases included the tips of formative median coverts. In addition, three specimens (CAS 27550, 59902, and 53030) had replaced the inner one to three greater coverts, and the tips to one or more of these formative coverts were also tinged reddish. On the basis of the specimens' labels, plumage brightness, and color of the formative median coverts, four of the specimens were male and three were female (see Table 1). The reddened feathers of the males appeared overall to be brighter and redder than those of the females, which were duller orange, tinged olive or brownish. None of the specimens at CAS in juvenile (7), definitive basic (11), or alternate (226) plumage we examined had anomalous red feathers other than perhaps some males in alternate plumage with red breast feathers, supporting our inference that erythristic feathers appear primarily, if not solely, on birds in formative plumage.

The red/orange coloration in all 12 birds we report thus appears on individuals that had recently completed or largely completed their preformative molt. So far as known, the preformative molt of body feathers occurs on or near the breeding grounds, soon after the birds leave the nest, peaking in late July and August, and then declining through the end of September. By contrast, adults undergo the bulk of their body-feather molt in late August and early September, usually at stopover locations in the Mexican monsoon region of the southwestern United States and northwestern Mexico, away from the breeding grounds (Butler et al. 2002, Pyle et al. 2009), although molting adults have also been reported in southern California in mid-August (Unitt et al. 2020), and a small proportion of adults appear to molt on or near breeding grounds (Pyle et al. 2018). Therefore, during fall migration through the western United States, first-year Western Tanagers are in fresh formative plumage, except for retained juvenile flight feathers and some coverts, whereas most adults are in worn alternate plumage. By early September, furthermore, nearly all adult Western Tanagers have already passed through southern California (Butler et al. 2002). The apparent lack of reddened feathers on second-year specimens in alternate plumage indicates that reddened formative feathers are typically lost during the first prealternate molt, which occurs on the winter grounds (Pyle 1997; pers. obs.).

The timing and location of the preformative molt of juvenile Western Tanagers largely coincides with the availability of berries containing rhodoxanthin. In eastern North America, Morrow's and Tatarian honeysuckles

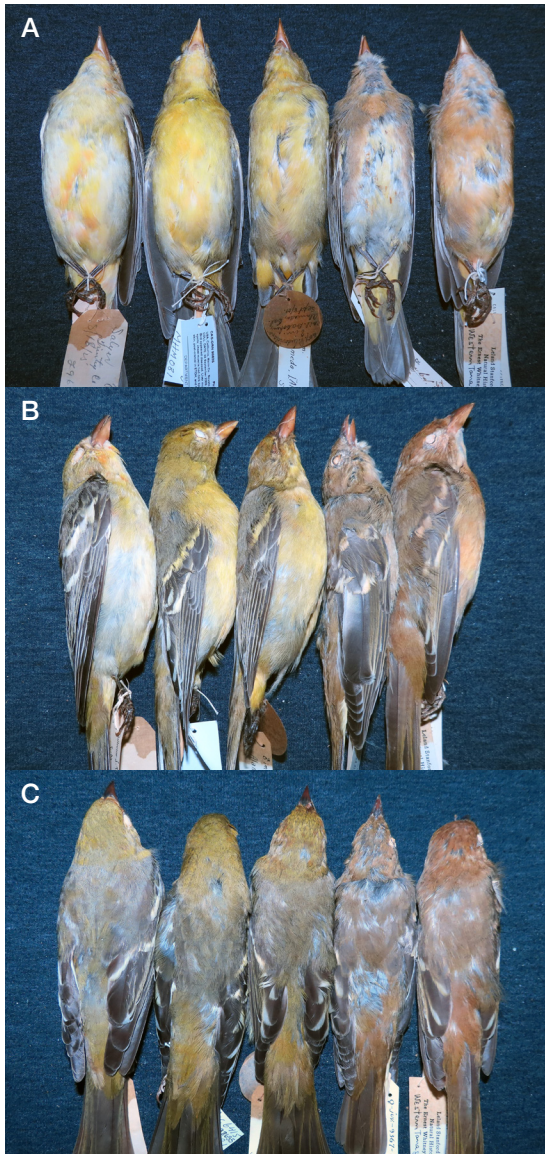


FIGURE 2. Specimens of Western Tanagers with reddened feathers. Left to right: CAS 27550, Trinity Co., California, 18 August 1925, formative-plumaged male; CAS 98635, Marin Co., California, 3 September 2009, formative-plumaged male; CAS 59902, Alameda Co., California, 8 September 1901, formative-plumaged male; CAS 53050, El Dorado Co., California, 2 August 1918, female undergoing preformative molt with about 20% of juvenile body feathers remaining; CAS 80074, Siskiyou Co., California, 1 September 1938, formative-plumaged female by plumage (sexed male on specimen label). A, underparts; B, sides; C, upperparts.

Photos by Peter Pyle

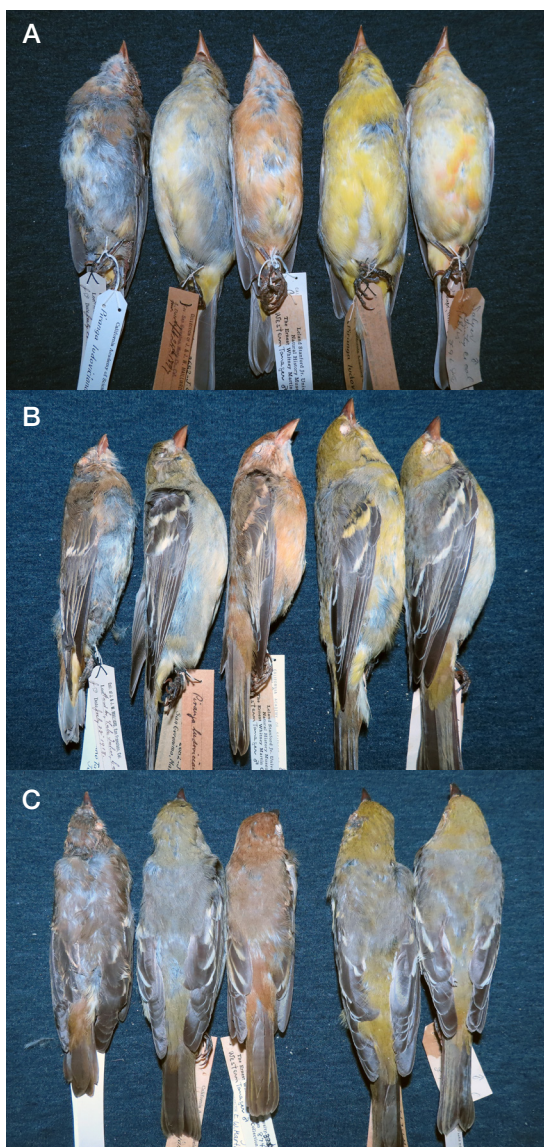


FIGURE 3. Specimens of Western Tanagers in first-year plumages, comparing females and males in typical formative plumage with those showing reddened feathers. Left to right: CAS 53030, Placer Co., California, 22 July 1918, juvenile, male according to specimen label; CAS 53017, Marin Co., California, 24 September 1897, typical formative-plumaged female; CAS 80074 (see Table 1 and Figure 2 for details), formative-plumaged female with reddened feathers; CAS 53026, Mariposa Co., California, 7 September 1917, typical formative-plumaged male; CAS 27550, Trinity Co., California, 18 August 1925, formative-plumaged male with reddened feathers. A, underparts; B, sides; C, upperparts. Note that the juvenile plumage is brown to olive and streaked (sexes are similar) and that in formative plumage males' body feathering and replaced median coverts average brighter yellow than females, although the reddened male in this figure is somewhat intermediate in plumage.

Photos by Peter Pyle

DIET-RELATED PLUMAGE ERYTHRISM IN SOME WESTERN BIRDS

TABLE 1 Specimens of Reddened Western Tanagers Held in Museum Collections and Localization of Reddish Feathers

Catalog number ^a	Collection date	Collection locality	Sex	Plumage and localization of reddened feathers ^b
CAS 59902	8 Sep 1901	Alameda Co., California	Male	Formative plumage, Red feathers on crown (10), malar region (2), chin (2), throat (3), breast (6), mid-ventral region (8) and rump (6). Inner 3–4 greater coverts replaced, the innermost 2 slightly tinged red. Red feathers throughout occur generally symmetrically.
CAS 53050	2 Aug 1918	El Dorado Co., California	Female	Largely formative plumage. ^c Formative feathers in center breast (25%), sides (80%), flanks (80%), and rump (60%), tinged dull orange. Some juvenile rump feathers tinged orange. Median coverts dropped, the innermost 2 on each wing with erupted tips tinged orange. 1–2 juvenile greater coverts on both wings slightly tinged orange.
CAS 27550	18 Aug 1925	Trinity Co., California	Male	Formative plumage. Reddish formative feathers in malar region (2), on chin (2), mid-ventral region (13), undertail coverts (5), rump (6) and lesser coverts (3). Tips to two outermost median coverts (formative) and two innermost greater coverts (formative) tinged red on both wings; remainder of median coverts (formative) and greater coverts (juvenile) not tipped red.
CAS 80074	1 Sep 1938	Siskiyou Co., California	Female ^d	Formative plumage. Dull orange-tinged feathers on crown (most of forehead back to mid crown), malar region (half), throat (40%), breast (70%), ventral region (60%), rump (75%). Some tips to lower lesser coverts and all median coverts tinged pinkish. Orange coloration duller and browner than reddish tinged feathers of males.
CAS 98635	3 Sep 2009	Marin Co., California	Male	Formative plumage. Red-tinged formative feathers on crown (postocular ~3 feathers on each side), throat (4), breast (4), sides of lower ventral region (8), undertail coverts (3), and rump (5). No red tips to wing coverts. Red feathers throughout occur generally symmetrically except in ventral region where they are concentrated on the bird's right side.
PMA Z80.120.82	11 Aug 1975	Salmon Arm, British Columbia	Male	Formative plumage. Dull orange-tinged feathers on crown (40%, particularly forehead), malar region (60%), throat (55%), breast (75%), ventral region (20% mainly along midline), and rump (60%). Most formative median coverts orange-tipped; juvenal coverts yellow-tipped.
LACM 122206	8 Oct 2020	Los Angeles Co., California	Female	Formative plumage. Dull orange-tinged feathers on crown, malar region, throat, breast, and ventral region.

^aCAS, California Academy of Sciences; PMA, Royal Alberta Museum (formerly the Provincial Museum of Alberta); LACM, Natural History Museum of Los Angeles County.

^bNumbers in parentheses are approximate feather counts, except where percentages are given.

^cUndergoing preformative molt with about 20% of juvenile body feathers remaining.

^dSexed as male on specimen label but female by plumage and size.

typically bear fruit from late June to mid-August, so that in many states by mid-August the berries have largely withered or been stripped from the bush (Mulvihill et al. 1992, Witmer 1996; J. A. Craves pers. obs.), although berries may persist into late August to mid-September in Alberta (Hudon et al. 2013; Hudon pers. obs.). The Pacific Yew typically bears fruits slightly later in the year (late July–October; DiFazio et al. 1998, Vance and Rudolf 2008) than the honeysuckles, but still within the interval in which they could affect a Western Tanager's plumage coloration. The Pacific Yew produces arils asynchronously over a 12- to 15-week period starting in late July with no obvious peak of seed availability (DiFazio 1996). Taken together, this evidence implies that these reddened fall Western Tanagers are further examples of diet-related plumage erythrism, with the two Asiatic bush honeysuckles likely accounting for the majority of the recent examples, the native Pacific Yew accounting for older examples collected when the bush honeysuckles weren't yet widely available.

OTHER SPECIES

During our research we also became aware of other western species with abnormal reddened feathers. Prompted by a recent sighting of a Red-breasted Sapsucker with unusual redness to many of the yellowish spots the species normally displays on its back in fresh plumage (a vagrant photographed at Pincher Creek, Alberta, on 11 November 2020), we looked for examples of reddened Red-breasted Sapsuckers among the 207 specimens of this species at CAS. We found 12 such examples (Figures 4 and 5), including three of 32 specimens identified as subspecies *Sphyrapicus ruber ruber* or as intermediates (9%) and nine of 175 specimens identified as *S. r. daggetti* (5%). Of these 12, 2 were in formative, 3 were in second basic, and 7 were in definitive basic plumage. By contrast none of 60 specimens of the Red-naped Sapsucker (*S. nuchalis*) or 87 specimens of the Yellow-bellied Sapsuckers (*S. varius*) at CAS showed abnormally reddened back feathers. Surprisingly, the red on the back of many of the reddened sapsuckers was nearly as intense as that on their heads (Figure 4), unlike the orange coloration often associated with diet-related reddening. The lack of yellow pigments we speculate may be due to their quick loss to fading in the wild, as often happens with pale yellow colors, leaving the more stable rhodoxanthin. Also, because many of these specimens date from the late 1800s to early 1900s, as do those of some of the Western Tanagers, it is probable that these birds acquired their rhodoxanthin from the arils of the Pacific Yew, whose distribution in moist habitats largely overlaps that of the Red-breasted Sapsucker (but not the Red-naped or Yellow-bellied sapsuckers), rather than from the berries of bush honeysuckles whose distributions would have been more limited then. Woodpeckers are known to occasionally consume the arils of yew trees (Hudon et al. 2020), and sapsuckers have been observed foraging on yew trees in Oregon (DiFazio 1996).

Finally, we also found examples of Cedar Waxwings with orange tail tips from Idaho and Texas (Hudon and Mulvihill 2017), Alberta (PMA specimens Z06.1.11 and Z06.1.12), New Mexico (Tim Reeves pers. comm.), and a number of other western states (several eBird posts). These include juvenile birds with completely orange tail bands (Macaulay Library images ML113338651, ML177234211, ML267074161) and older birds in which only some of the



FIGURE 4. Examples of specimens of Red-breasted Sapsuckers with reddened feathers on their backs. Left to right: CAS 58110, *daggetti*, El Dorado Co., California, 3 July 1934, second basic plumage; CAS 45394, *daggetti*, Amador Co., California, 17 November 1895, definitive basic; CAS 45388, *daggetti*, Alameda Co., California, 31 October 1898, definitive basic; CAS 76033, intermediate *daggetti/ruber*, San Mateo Co., California, 12 December 1895, definitive basic; CAS 60488, *ruber*, Wrangell, Alaska, 27 June 1946, definitive basic.

Photo by Peter Pyle

tail feathers have orange tail tips (Macaulay Library images ML253034611, ML235968641), as described previously in the East (Mulvihill et al. 1992, Witmer 1996). In light of these observations, and a greater awareness of the phenomenon of diet-related plumage erythrism in the West, we expect more examples of it to come to light in western bird species in the future.

ACKNOWLEDGMENTS

We are grateful to Justyn Stahl and Louis Bevier for bringing the recent examples of tanagers with atypical red feathers to our attention. Tim Reeves, Nathan French, Joyce Brady, and Jim Greaves kindly provided high-resolution images of the reddened birds they observed. We thank Moe Flannery for providing access to the bird specimens in the collections at the California Academy of Sciences. Kimball L. Garrett found an example of a reddened tanager in the collections at LACM, and along with Ben Scott and an anonymous reviewer made suggestions to improve the article.

LITERATURE CITED

- Armenta, J. K., Dunn, P. O., and Whittingham, L. A. 2008. Effects of specimen age on plumage color. *Auk* 125:803–808; <https://doi.org/10.1525/auk.2008.07006>.
 Beal, F. E. L. 1907. Birds of California in relation to the fruit industry, part 1. U.S. Dept. Agric. Biol. Surv. Bull. 30; <https://doi.org/10.5962/bhl.title.62785>.



FIGURE 5. Red-breasted Sapsuckers showing typical plumage compared with those showing reddened feathers on their backs. Left to right: CAS 45459, *ruber*, Marin Co., California, 1 January 1898, definitive basic plumage; CAS 60488, *ruber*, Wrangell, Alaska, 27 June 1946, definitive basic; CAS 45463, *daggetti*, San Benito Co., California, 6 October 1898, formative plumage; CAS 45388, *daggetti*, Amador Co., California, 17 November 1895, definitive basic.

Photo by Peter Pyle

- Bent, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and their allies. U.S. Natl. Mus. Bull. 211; <https://doi.org/10.5479/si.03629236.211.1>.
- Brush, A. H. 1990. A possible source for the rhodoxanthin in some Cedar Waxwing tails. J. Field Ornithol. 61:355.
- Butler, L. K., Donahue, M. G., and Rohwer, S. 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): Age effects, aerodynamics, and conservation implications. Auk 119:1010–1023; <https://doi.org/10.1093/auk/119.4.1010>.
- Catling, P. M., Mitrow, G., and Ward, A. 2016. Major invasive alien plants of natural habitats in Canada. 13. Honeysuckle, Chèvrefeuille, *Lonicera* spp. Can. Bot. Assoc. Bull. 49:21–29.
- DiFazio, S. P. 1996. The reproductive ecology of Pacific yew (*Taxus brevifolia* Nutt.) under a range of overstory conditions in western Oregon. Master's thesis, Ore. State Univ., Corvallis.
- DiFazio, S. P., Wilson, M. V., Vance, N.C. 1998. Factors limiting seed production in *Taxus brevifolia* (Taxaceae) in western Oregon. Am. J. Bot. 85:910–918; <https://doi.org/10.2307/2446356>.
- Edminster, F. C., and May, R. M. 1951. Shrub plantings for soil conservation and wildlife cover in the Northeast. U.S. Dept Agric. Circular 887.
- Flinn, T., Hudon, J., and Derbyshire, D. 2007. Tricks exotic shrubs do: When Baltimore Orioles stop being orange. Birding 39(5):62–68.
- Gatlin, B. 2009. Hybrid Western × Summer Tanager (*Piranga ludoviciana* × *P. rubra*), Red Rock State Park, Yavapai County; http://www.azfo.net/gallery/2009/html1/Hybrid_Western_X_Summer_Tanager_RRSP_Gatlin_20090525.html.

- Hudon, J. 1999. Western Tanager (*Piranga ludoviciana*), in *The Birds of North America* (A. Poole and F. Gill, eds.), no. 432. Birds N. Am., Inc., Philadelphia; <https://doi.org/10.2173/bna.432>.
- Hudon, J., and Brush, A. H. 1989. Probable dietary basis of a color variant of the Cedar Waxwing. *J. Field Ornithol.* 60:361–368.
- Hudon, J., and Mulvihill, R. 2017. Diet-induced plumage erythrism as a result of the spread of alien shrubs in North America. *N. Am. Bird Bander* 42(4):95–103.
- Hudon, J., Derbyshire, D., Leckie, S., and Flinn, T. 2013. Diet-induced plumage erythrism in Baltimore Orioles as a result of the spread of introduced shrubs. *Wilson J. Ornithol.* 125:88–96; <https://doi.org/10.1676/11-161.1>.
- Hudon, J., Driver, R. J., Rice, N. H., Lloyd-Evans, T. L., Craves, J. A., and Shustack, D. P. 2017. Diet explains red flight feathers in Yellow-shafted Flickers in eastern North America. *Auk* 134:22–33; <https://doi.org/10.1642/AUK-16-63.1>.
- Hudon, J., Omote, K., and Mizushima, M. 2020. Do fruits cheming the red carotenoid rhodoxanthin affect avian plumage coloration in Japan? *Ornithol. Sci.* 19:99–106; <https://doi.org/10.2326/osj.19.99>.
- Jones, L. 1930. The sequence of the molt. *Wilson Bull.* 42:97–102.
- Klinkenberg, B. (ed.) 2020. E-Flora BC: Electronic atlas of the flora of Br. Columbia. Lab for Advanced Spatial Analysis, Dept. Geogr., Univ. British Columbia, Vancouver; <https://linnet.geog.ubc.ca/biodiversity/eflora/>.
- Kuhn, R., and Brockmann, H. 1933. Über Rhodoxanthin, den Arillus-Farbstoff der Eibe (*Taxus baccata*). *Berichte der Deutschen Chemischen Gesellschaft* 66:828–841 [in German]; <https://doi.org/10.1002/cber.1933060609>.
- Maoka, T., Ito, Y., Fujiwara, Y., and Hashimoto, K. 1996. Structures and antioxidative activity of retro carotenoids from the berries of the Japanese Yew, *Taxus cuspidata*. *J. Japan Oil Chemists' Soc.* 45:641–646 [in Japanese]; <https://doi.org/10.5650/jos1996.45.641>.
- Mulvihill, R. S., Parkes, K. C., Leberman, R. C., and Wood, D. S. 1992. Evidence supporting a dietary basis for orange-tipped rectrices in the Cedar Waxwing. *J. Field Ornithol.* 63:212–216.
- Pandolfino, E. R., Risser, P., and Risser, L. 2010. First evidence suggesting hybridization between the Summer Tanager and Western Tanager. *W. Birds* 41:181–183.
- Pyle, P. 1997. Identification Guide to North American Birds, part 1. Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.
- Pyle, P., Leitner, W. A., Lozano-Angulo, L., Avilez-Teran, F., Swanson, H., Gómez Limón, E., and Chambers, M. K. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. *Condor* 111:583–590; <https://doi.org/10.1525/cond.2009.090085>.
- Pyle, P., Saracco, J. F., and DeSante, D. F. 2018. Evidence of widespread movements from breeding to molting grounds by North American landbirds. *Auk* 135:506–520; <https://doi.org/10.1642/AUK-17-201.1>.
- Unitt, P., Hargrove, L., and Clark, K. B. 2020. Overlap of molt and fall migration of the Western Tanager and Warbling Vireo in southern California. *W. Birds* 51:59–64; <https://doi.org/10.21199/WB51.1.5>.
- Vance, N. C., and Rudolf, P. O. 2008. *Taxus* L. Yew, in *The Woody Plant Seed Manual* (F. T. Bonner and R. P. Karrfalt, eds.), pp. 1092–1098. Agriculture Handbook 727. U.S. Dept. Agric. Forest Service, Washington, DC.
- Williams, C. E. 2005. Fact sheet: Exotic bush honeysuckles. Plant Conservation Alliance's Alien Plant Working Group, Washington, DC; <https://www.invasive.org/alien/fact/pdf/loni1.pdf>.
- Witmer, M. C. 1996. Consequences of an alien shrub on the plumage coloration and ecology of Cedar Waxwings. *Auk* 113:735–743; <https://doi.org/10.2307/4088853>.

Accepted 14 October 2021

Associate editor: Kimball L. Garrett