

Proceedings of
the United States
National Museum



SMITHSONIAN INSTITUTION • WASHINGTON, D.C.

Volume 114

1963

Number 3471

GEOGRAPHIC VARIATION IN THE THRUSH
HYLOCICHLA USTULATA

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Introduction

Swainson's thrush, *Hylocichla ustulata*, known also in recent literature as the olive-backed thrush, is one of the most widely known of its genus. It has an extensive breeding range from Alaska across Canada to Labrador and Newfoundland. In the west it is found south through California and much of the Rocky Mountain area, and in the east it occurs as far south as the mountains of West Virginia. In its migrations it is found in wooded areas to the south of its breeding range throughout the United States, Mexico, and Central and South America to northern Argentina.

Four subspecies are listed in the American Ornithologists' Union Check List (1957, pp. 438-440): *H. u. ustulata* (Nuttall), the russet-backed form of the Pacific coast; *H. u. incana* Godfrey, recently named from Yukon; *H. u. clarescens* Burleigh and Peters, restricted by the authors to Newfoundland and Nova Scotia; and *H. u. swainsoni* (Tschudi), the olive-backed form of the trans-Canadian spruce belt. In the original descriptions and in most of the standard faunal works these races and others that have been proposed have been treated

individually with little attention to the overall picture of variation throughout the range. The present study is an attempt to evaluate the significance of color differences with particular emphasis on their value as racial characters.

Historical Summary

In early accounts of North American birds there is much confusion concerning the nomenclature of the five common smaller thrushes. Most of the names used for the present species had either a composite base or were preoccupied. Wilson (1812, pl. 43, fig. 2) illustrated the species but referred to it as a "hermit thrush," and in the accompanying text (p. 95) listed it as *Turdus solitarius*, a name antedated by *Turdus solitarius* Linnaeus of 1758 for another species. Nuttall (1840, pp. 400, 830) proposed *Turdus ustulatus* for the russet-backed population from Oregon, the first valid name for the species as a whole.

Swainson (Swainson and Richardson, 1832, p. 183) had earlier given an excellent description of an olive-backed thrush killed at Carlton House, Saskatchewan, in May 1827, but believing this bird to be the "tawny thrush" of Wilson, listed it as "*Merula Wilsonii* Bonaparte" from *T[urdus] Wilsonii* Bonaparte (1824, p. 34).

Cabanis (in von Tschudi, 1845, p. 28) perceived that Swainson had misidentified the bird from Carlton House and proposed the new name (in Mss.) *T[urdus] Swainsoni*. This is accepted as the sub-specific name for the eastern population, and is the second valid name available.

Baird (1864, pp. 18-19) treated the eastern and western groups of Swainson's thrush as separate species under the two names *Turdus swainsonii* and *Turdus ustulatus* respectively.

In the same publication (p. 12) he erected the subgenus *Hylocichla* for the small North American thrushes.

Coues (1872, pp. 72-73) listed the "olive-backed thrush" in Baird's subgenus *Hylocichla* under the name *swainsoni* and included the gray-cheeked thrush (*Hylocichla minima*) as the variety "*aliciae*, Alice's thrush," in addition to *ustulatus*.

In further studies, Baird and Ridgway (Baird, Brewer, and Ridgway, 1874, p. 7) separated the gray-cheeked thrush as a distinct species and recognized *swainsoni* and *ustulatus* as varieties of a single species for which, however, they continued to use the younger name *T. swainsoni*.

The presently accepted trinomials *Hylocichla ustulata swainsoni* (Tschudi) and *H. u. ustulata* (Nuttall) came into official use with the publication of the third edition of the A.O.U. Check-List (1910).

Oberholser (1898, p. 304) gave his attention to the population from the southern Rocky Mountain area and concluded that they were

subspecifically distinct. To this race he gave the name *Hylocichla ustulata almae*. The following year, Oberholser (1899, p. 23) divided the russet-backed population of the Pacific coast into two forms. Birds from California and interior Oregon were given the name *Hylocichla ustulata oedica*, and the nominate form *H. u. ustulata* was restricted to birds of the northwest coast region.

The A.O.U. check-list committee (1899, pp. 127, 131) rejected the first of these names and accepted the second. This acceptance, however, was temporary; the committee (1908, p. 335) later rejected both names so that neither appeared in the third edition of the A.O.U. Check-List in 1910 nor in the fourth edition in 1931.

Further investigations of these thrushes led to temporary acceptance of *almae* as a valid name by the A.O.U. committee (1944, p. 457) but it was dropped again at a later date (1953, pp. 360-361).

In succeeding studies, Burleigh and Peters (1948, p. 118) separated the breeding birds of Newfoundland and Nova Scotia under the name *clarescens*, and Godfrey (1951, p. 173) described *Hylocichla ustulata incana* for the breeding population found from eastern Alaska and western Mackenzie south to northern British Columbia and northern Alberta. These two forms were added in the fifth edition of the A.O.U. Check-List (1957, pp. 439-440) to typical *ustulata* and *swainsoni* of the two previous editions.

Status of Proposed Names

In considering the dorsal coloration of Swainson's thrush across its entire breeding range in North America from Alaska to Newfoundland and southward in the Rocky and Appalachian Mountains, two distinct patterns are observable. The population from Alaska to the southern Rockies is definitely grayish above with several seasonal and sexual variations that approach the reddish olive of the eastern group. There is a weak color cline in which birds from the southern Rockies appear paler than birds from Yukon and Alaska, but I consider this tendency too slight to warrant nomenclatural recognition. Recently collected material from Idaho and eastern Washington are practically indistinguishable from birds collected during the last few years in northwestern Yukon. The type of *almae* from Nevada has been considered as a representative of *swainsoni*, but critical examination shows it to be a somewhat atypical specimen of the western population. At any rate, it is definitely a gray bird when compared with specimens from the eastern population. A specimen from Mountain City, Nev., is also definitely gray, as are specimens from southern Idaho and northwestern Utah. For this reason, the bird from Franklin Lake, Nev., described by Oberholser as *almae* will have to be considered the type of the grayish western population and the

subspecies described as *incana* by Godfrey will have to be considered a synonym of it.

From the Athabaska River eastward, the population exhibits a reddish-olive coloration dorsally, noticeably richer and warmer than in the Alaskan and Rocky Mountain group. I have not been able to separate specimens taken in the Atlantic maritime area (*H. u. clarescens* of Burleigh and Peters) from birds of the interior even on a conservative 75 percent basis (Rand and Traylor, 1950). For that reason I believe that *H. u. clarescens* Burleigh and Peters must be considered a synonym of *H. u. swainsoni* (Tschudi).

Topotypical material from the exact type locality of *swainsoni* is unavailable, but specimens from Cypress Hills, Fort Chipewyan, and the Athabaska River strongly indicate that the breeding population from Carlton House, Saskatchewan, is not the grayish race of the mountains and foothills to the west.

Birds from California and southern Oregon northward along the river bottoms, slopes, and ravines east of the Cascades to northern Washington are definitely paler and less rufescent than the russet-backed thrushes of the northwestern coastal forests; the name *H. u. oedica* Oberholser, therefore, should be used for this population. This usage will automatically restrict the nominate race *H. u. ustulata* (Nuttall) with type locality Fort Vancouver, Wash., to the area west of the Cascades in northwestern Oregon and thence northward along the coast to Juneau, Alaska.

Specimens from the Warner Mountains of California are unavailable to me, but earlier authors (Grinnell and Miller, 1944) referred to this section of the state as an area of intergradation between the California race of Swainson's thrush and a darker or grayer race. It seems reasonable to believe that the latter is *H. u. almae*.

This paper is based in the main on study of 442 specimens in the United States National Museum. Additional material was borrowed from other museums. The sources and numbers of these additional specimens and the abbreviations used in designating collections in the text are: Cornell University (CU), 3; National Museum of Canada (NMC), 37; Geological Survey Museum of Canada (GSMC), 12; Victoria Memorial Museum (VMM), 3; and the Ira N. Gabrielson collection (ING), 16. All specimens not otherwise designated are from the U.S. National Museum.

Prolonged study of the material showed that the only valid criterion for separating the several races in question is the color of the upperparts. Ventral coloration is mentioned in the literature as being of racial significance, but I have found that it is not reliable in delimiting the races. Wing, tarsal, and culmenal measurements taken of samples throughout the population showed no significant differences.

Magnification of $\times 10$ in a binocular microscope was used in examining feathers for wear and abrasion.

For their many helpful comments and suggestions while the study was in progress I would like to express my appreciation to Dr. John W. Aldrich, Dr. Harry C. Oberholser, and Mr. Herbert G. Deignan. To Dr. Alexander Wetmore I am particularly indebted for the time and effort he has spent in helping me revise the final manuscript.

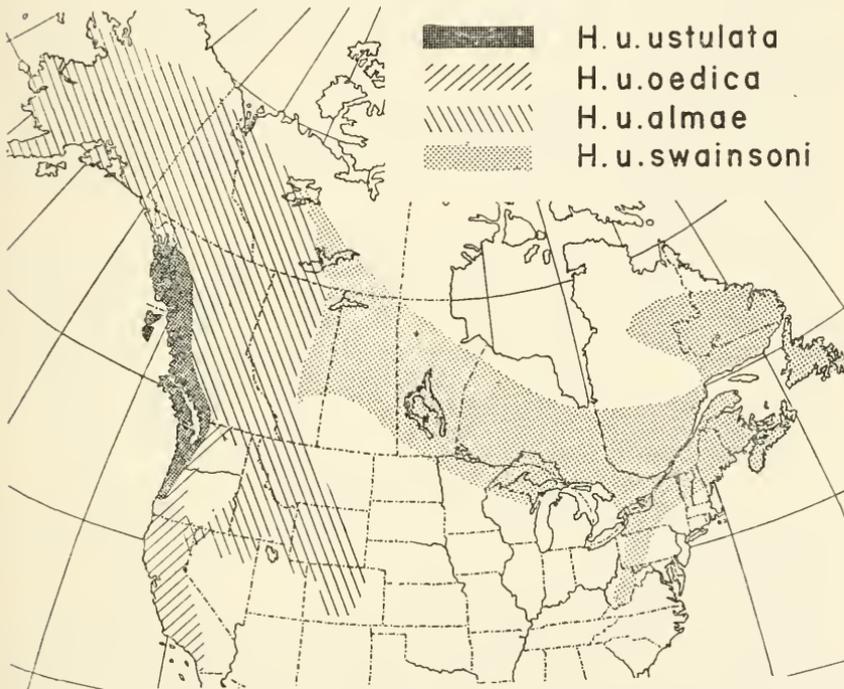


FIGURE 1.—Ranges of the subspecies of *Hylocichla ustulata*.

Dr. Herbert Friedmann allowed me to use specimens under his care in the U.S. National Museum collection.

The following persons loaned specimens: Dr. Ira N. Gabrielson; Dr. Kenneth C. Parkes, Cornell University; Dr. W. Earl Godfrey, National Museum of Canada, Geological Survey Museum of Canada, and the Victoria National Museum.

I also wish to express my appreciation to Dr. Brina Kessel, University of Alaska, and to Dr. Allan R. Phillips of Mexico City for their cooperation.

The Subspecies of *Hylocichla ustulata**Hylocichla ustulata ustulata* (Nuttall)

Turdus ustulatus Nuttall, Manual of ornithology of the United States and Canada, ed. 2, vol. 1, pp. vi, 400, 1840. (Forests of Oregon=Fort Vancouver, Wash.)

In breeding season the upperparts of the adult are a rather brownish umber, considerably brighter and richer than the same plumage of *oedica* and lacking the olive of *swainsoni*. They could under no circumstances be confused with the ashy gray upperparts of *almae*. The deep russet of fall and winter birds is the distinguishing characteristic of this race and sets it apart from the grayer, more subdued russet of *oedica*.

Breeding range is west of the cascades from northwestern Oregon to Juneau, Alaska. Winter range is mainly to western mainland of Mexico; one specimen is in the U.S. National Museum, from Tres Zapotes, Veracruz.

The following specimens were examined:

BREEDING: ALASKA: Sheep Creek, 1; Sitka, 3. BRITISH COLUMBIA: Howe Sound, 1; Port Moody, 2; Queen Charlotte Island, 3; Wellington, 2. WASHINGTON: Cathlamet, 1; Clallam County (Lake Sutherland), 1; Granville, 2; Neah Bay, 3; Vancouver, 1. OREGON: Multnomah County (Sauvies Island), 1 (ING); Portland, 1 (ING).

MIGRANT: WASHINGTON: Bumping Lake, 1; Carson, 1; Ellensburg, 1; Suez, 1. CALIFORNIA: Pacific Grove, 2; Placerita Canyon, 1; Stanford University, 1. MEXICO: Veracruz, (Tres Zapotes), 1.

Hylocichla ustulata oedica Oberholser

Hylocichla ustulata oedica Oberholser, Auk, vol. 16, no. 1, p. 23, January 1899. (Santa Barbara, Calif.)

Hylocichla ustulata ustulata (Nuttall) (part).

Adults in breeding plumage are similar to *ustulata* except that the upperparts are considerable paler and grayer. Compared with *swainsoni* they are more buffy, less olivaceous above. Fall and winter birds are slightly darker than those taken in the summer.

Breeding range is from California (except the southeastern part) and southwestern Oregon (Klamath Mountains), north along the east slopes of the Cascades to northern Washington. Winter range is in Baja California, Arizona, and southern Mexico.

The following specimens were examined:

BREEDING: WASHINGTON: Yakima, 1; Yakima County, (Big Klickitat), 1; Yakima County, (Ahtanum), 1; Mount St. Helens, 2; Wenatchee Lake, 1; Entiat, 1; White Salmon, 1. OREGON: Crater Lake, 1; Drew, 1. CALIFORNIA: Aptos, 1; Milpitas, 1; Nicasio, 1; San Diego County, 1; Santa Barbara, 1; Santa Cruz, 1.

MIGRANT: ARIZONA: Fort Huachuca, 1. MEXICO: Baja California (Salton River [thus on label]), 1; Chiapas (Chieharras), 1.

Hylocichla ustulata swainsoni (Tschudi)

T[urdus] Swainsoni Cabanis Mss. in von Tschudi, Untersuchungen über die Fauna Peruana, part VI, Ornithologie, pp. 187-188, 1845 [probably December]. New name for *Merula Wilsonii* Swainson, nec *T[urdus] Wilsonii* Bonaparte. (Carlton House, Saskatchewan River, Saskatchewan, lat. 53°).

Hylocichla ustulata clarescens Burleigh and Peters, Proc. Biol. Soc. Washington, vol. 61, p. 118, June 16, 1948. (Glenwood, Newfoundland).

Resembles *H. u. almae* Oberholser in the nuptial plumage except that the upperparts are decidedly more reddish, less grayish, olive; sides of head and breast are more buffy and spotting of breast paler. In autumn plumage it is separable by the deep reddish olive of its upperparts, distinctly different from the grayish to brownish olive of *almae* at the same season of the year. Compared with *ustulata* and *oedica*, *swainsoni* may always be separated by the olive suffusion of its upperparts, a characteristic that is lacking in the Pacific coast races, which are much more russet in coloration.

Breeding range is eastern Alberta (Athabaska River) eastward to Newfoundland and south in the mountains to West Virginia. Winter range, based on specimens examined, is Mexico (Veracruz, Tabasco, Tres Marias Islands); Central America (Costa Rica, Guatemala, Panama); South America (Colombia); West Indies (Bahamas). Recorded in migration in most of the States south of its breeding range. Occasional records in migration from west of the Rocky Mountains (Idaho, Washington, Oregon, British Columbia).

The following specimens were examined:

breeding: ALBERTA: Athabaska delta, 3; Athabaska River (East Branch), 1; Fort Chipewyan, 2. LABRADOR: Chateau Bay, head, 1; Eagle River, 1; Lake Melville (Etagaulet Bay), 3; Moisie Bay, 1 (NMC); Lac Marchant (Moisie Bay), 1 (NMC); Northwest River, 3. MAINE: Fort Kent, 6. MANITOBA: La Pas, 2 (NMC); Oxford House, 1; Seven Sisters, 1 (NMC); York Factory, 3. NEW BRUNSWICK: Grand Manan, 1. NEW YORK: Franklin County, 1 (CV). NEWFOUNDLAND: Badger, 2; Corner Brook, 1 (ING); Gander River, 15 mi. below Glenwood, 1 (ING); Glenwood, 2; Norris Point (Bonne Bay), 1; Bay of Islands (North Arm), 1; South Brook, 1; Stephenville, 1; Tomkins, 2; White Bear River (12 miles up), 2. NOVA SCOTIA: Cape Breton Island (Ingonish), 4; James River, 3. ONTARIO: Kapuskasing, 1 (GSMC); Lac Seul, 1 (GSMC). PENNSYLVANIA: Tamarack Swamp, 3. QUEBEC: Blue Sea Lake, 3 (ING); Mistassini Post, 1 (NMC); Notre Dame de la Dore, 1 (NMC); Pt. au Maurier, 1 (NMC); St. Felicie, 5 (NMC). SASKATCHEWAN: Cypress Hills, 1 (NMC); Cypress Lake, 3 (GSMC). WISCONSIN: Outer Island, 3; Hebster, 1.

MIGRANTS: ALABAMA: Barachias, 1. ALBERTA: Athabaska Landing, 1; Athabaska River (30 mi. above landing), 1. BRITISH COLUMBIA: Moose Lake, 1; Okanogan Landing, 2. COLOMBIA: Bogotá, 1; Saóta, 1. COSTA RICA: Bonilla, 4; Coliblanco, 1; Hacienda Santa María, 1; Santa María de Dota, 1. DISTRICT OF COLUMBIA: 18. DELAWARE: Cedar Branch, 1. FLORIDA: Franklin County, 4. GEORGIA: Athens, 4; Atlanta, 1; Commerce, 1; Danielsville, 1; Decatur, 1; Grady County, 2; Young Harris, 1. GUATEMALA: Coban, 1. IDAHO: Moscow, 4; Potlatch, 3. ILLINOIS: Cook County (Glenwood), 4; Grand Crossing, 1. INDIANA:

Wheatland, 1; Vincennes, 1. KENTUCKY: Brandenburg, 1; Middleboro, 2; Uniontown, 1. MANITOBA: Duck Mountain, 1 (NMC); Shoal Lake, 1 (GSMC); Thicket Portage, 2 (NMC). MARYLAND: Finzel, 2; Kensington, 1; Laurel, 7; Montgomery County, 1; Ocean City, 1; Plummers Island, 2; Riggs Mill, 1. MEXICO: Chiapas (Comitan), 1; Tabasco (Teápá), 2; Tres Marias Islands, 2; Veracruz (Volcán San Martin), 1. MINNESOTA: Fort Snelling, 1. MISSISSIPPI: Cat Island, 1; Deer Island, 4; Gulfport, 9; Horn Island, 1; Saucier, 2. MONTANA: Little Missouri River, 1; Terry, 1. NEW YORK: Essex County (Lake Placid), 1; Ulster County (Slide Mountain), 1. NORTH CAROLINA: Asheville, 1; Bethel, 1; Clinton, 1; Mitchell, 1; Statesville, 1. NORTH DAKOTA: Fairmount, 1. OKLAHOMA: Tulsa, 3. ONTARIO: Lac Seul, 1 (GSMC); Norfolk County (Long Point), 1 (NMC); Ottawa, 1 (NMC). PANAMA: Chiriqui Province, 1. PENNSYLVANIA: Carlisle, 2. QUEBEC: Blue Sea Lake, 2 (ING); Hudson Heights, 1 (NMC); Lake Albanel, 1 (NMC). RHODE ISLAND: Johnston, 1. SASKATCHEWAN: Cypress Lake, 4 (GSMC). SOUTH CAROLINA: Bennettsville, 1; Chester, 1. SOUTH DAKOTA: Hill City, 1. TENNESSEE: Hornbeak, 2; Reelfoot Lake, 2; Roan Mountain, 2; Waynesboro, 1. TEXAS: Castle Mountain, 1; Tacosá, 1. VIRGINIA: Alexandria, 3; Alexandria County [thus on label], 1; Arlington, 1; Chesterfield County Court House, 1; Falls Church, 3; Four Mile Run, 1; Gainesville, 1; Giles County, 1; Lexington, 6; McLean, 2; Mount Vernon, 1; Richmond, 1; Shenandoah National Park, 1; Williamsburg, 1. WASHINGTON: Pullman, 1; Tunk Mountain, 1. WEST VIRGINIA: Enon, 1. WEST INDIES: Swan Island, 1. WISCONSIN: Alden, 1; Milton, 1; Outer Island, 2. WYOMING: Moran, 1; Teton Mountains, 1.

Hylocichla ustulata almae Oberholser

Hylocichla ustulata almae Oberholser, Auk, vol. 15, no. 4, p. 304, October 1898. (Humboldt Mountains, across from Franklin Lake, Nev.)

Hylocichla ustulata incana Godfrey, Canadian Field Nat. vol. 65, no. 5, p. 173, September-October 1951 [Feb. 21, 1952]. (Lapie River, Canol Road, mile 132, Yukon Territory.)

Hylocichla ustulata swainsoni (Tschudi) (part).

Adults in breeding season are distinctly grayer, less olivaceous above than *H. u. swainsoni* (Tschudi). Fall birds tend to be more grayish to brownish olive, less reddish olive than the eastern population. Sides of head and breast usually paler, and spotting of breast darker than *swainsoni*.

Breeding range is Alaska (except southeastern coast), Yukon, western Mackenzie, west-central Alberta, south through the mountains to Colorado and northwestern Utah. Few winter specimens are available, but fall and spring records indicate a heavy migration along the Mississippi Valley. The most abundant records during migration occur in the southeastern and Gulf States where some birds probably spend the winter (Saucier, Miss., Dec. 2, 1935). Only one wintering specimen has been identified from outside the United States: Costa Rica (Bonilla), April 13, 1908. Extremely rare in migration along the Atlantic coast.

The following specimens were examined:

BREEDING: ALASKA: Anchorage, 3 (ING); Bettles, 2; Circle, 7; Circle (20 miles above), 2; Eagle (mountains near), 1; Fairbanks, 2 (ING); Fort Egbert, 1; Katmai National Monument, Brooks Lake, 1 (ING); Kushkokwim River (North Fork), 1;

Robinson River, 2; Toklat River (head of), 1. ALBERTA: Grimshaw, 1 (NMC); Joussard, 7 (NMC); Slave River, 4 (intermediate). BRITISH COLUMBIA: Creston, 1; Hazleton, 1; Moose River (head of South Fork), 1; Summit Lake (12 miles north), 3 (NMC); Trail, 1 (VMM). COLORADO: Avolo, 2; Clear Creek, 1. IDAHO: Bovill, 1; Clearwater County (Headquarters), 2; Coeur d'Alene, 1; Harvard, 2; Idaho County (Whitebird Summit), 1; Inkom, 2; Latah County (East Fork Meadow Creek), 1; Latah County (Princeton), 1; Moscow Mountain, 1; Potlatch, 1; Priest River, 1; Shoshone County, Avery, 2; Shoshone County (Dismal Lake), 1; Shoshone County (Lookout Pass), 1. MACKENZIE: Fort Norman, 2; Fort Simpson, 1; Fort Providence, 1; Great Slave Lake, 1; Nahanni River (mouth of), 1. MONTANA: Crazy Mountains, 2; Flathead Lake, 1; Ward Peak, 1. NEVADA: Franklin Lake, 1; Mountain City, 1. OREGON: Disaster Peak, 1; Jordan Valley, 2. WASHINGTON: Anatone, 1; Ferry Lake, 4; Swan Lake, 6. WYOMING: Greybull, 1. YUKON: Haines Road (mile 130), 1 (NMC); Lake Laberge, 1; Lake Marsh, 2; Lapie River (Canol Road, mile 132), 5 (NMC); Old Crow, 5; Stoney Creek, 1 (NMC).

MIGRANTS: ALASKA: Savage River (McKinley Park), 1 (atypical). ALBERTA: Athabaska Landing, 1; Athabaska River (30 miles above landing), 1; Banff, 1; Red Deer River, 1 (GSMC). BRITISH COLUMBIA: Babine Mountains, 1; Nulka Lake, 1; Okanogan Landing, 1; Telegraph Creek, 1 (slightly intermediate towards *ustulata*). COSTA RICA: Bonilla, 1. GEORGIA: Athens, 2; Decatur, 1; Stone Mountain, 1. IDAHO: Bonneville County (Gray), 2; Hope, 1; Lewiston, 1; Moscow, 25; Potlatch, 2; Silver, 1; Washington County (Cambridge), 1. ILLINOIS: Cook County (Glenwood), 9; Iroquois County (Papineau), 1; Will County (Braidwood), 1. KENTUCKY: Middlesboro, 1; Uniontown, 1. LOUISIANA: New Orleans, 2. MANITOBA: Grand Rapids, 1. MISSISSIPPI: Bay St. Louis, 1; Cat Island, 1; Deer Island, 2; Gulfport, 2; Saucier, 1. MONTANA: Fort Logan, 1; Glendive, 1; Johnson Lake, 1; Madison River, 1; Terry, 1. NORTH CAROLINA: Asheville, 1. NORTH DAKOTA: McHenry (near Bantey), 1. TENNESSEE: Roan Mountain, 1. UTAH: Utah County (Scofield Reservation), 1. VIRGINIA: Mount Vernon, 1. WASHINGTON: Blue Mountains, 1; Pomeroy (16 mi. south), 1 (ING); Tunk Mountain, 1; Uniontown, 1. WYOMING: Fort Steele, 2. YUKON: Laird River and Alaska Highway, 1 (NMC); Tagish Road (mile 19), 1 (NMC).

Geographic Variation

Adult males in fresh plumage: *Hylocichla ustulata ustulata*: The upperparts are bright russet in color; they are similar in hue but darker in value than the Dresden Brown of Ridgway (1912). Examples of specimens with this plumage selected at random from the U.S. National Museum collection are 360036, 262522, and 262231. *H. u. oedica*: Has the upperparts somewhat darker than the Deep Olive of Ridgway. Examples are 262230 and 134188. *H. u. almae*: The upperparts are brownish olive above. This color is quite near the Olive of Ridgway. Examples selected at random from the main series are 298158, 341604, 420836, 465075, and 465333. *H. u. swainsoni*: Characterized by a much more reddish-olive overcast to the upperparts, nearest the Raw Umber of Ridgway. Examples are 342628, 458080, 466952, and 466953.

Subadult males in fresh plumage: *Hylocichla ustulata ustulata* and *H. u. oedica*: Similar to adults in fresh plumage. *H. u. almae*: Slightly

more reddish olive above than adult males. Nearest the Medal Bronze of Ridgway. Specimens of *almae* exemplifying this plumage are 193042, 419145, and 425279. *H. u. swainsoni*: Subadult males in fresh plumage are not too different from adult males; in series they appear to be somewhat less bright reddish olive above. Examples are 271375, 301600, 349253, 361680, 393349, and 458079.

Adult males in breeding plumage: *Hylocichla ustulata ustulata*: The upperparts are dull russet, similar to the Saccardo Umber of Ridgway. Specimens selected at random from this color series are 529 (ING), 286675, and 156359. *H. u. oedica*: Has the upperparts quite near the deep olive of Ridgway. Examples are 394934, 420624, and 262237. *H. u. almae*: The upperparts are dark ashy gray; Ridgway's Olive is nearest this hue. The following random samples are illustrative: 395459, 465332, 465976, 468145, 397341. The type specimen of *almae* belongs here. This specimen has caused considerable confusion in the past because it is slightly lighter in value than other, more "typical," specimens of the western population; however, the dorsal coloration is definitely Olive in hue if not in saturation. Another specimen, taken at Mountain City, Nev., a short distance from Mountain Lake, is definitely *almae*. *H. u. swainsoni*: More reddish olive above than *almae*, and its dorsal coloration falls between the Brownish Olive and light Buffy Olive of Ridgway. Samples of adult males in breeding plumage are 136319, 271370, 259580, 340549, 382036, 394307, and 4440 (ING).

Subadult males in breeding plumage: This plumage is retained by first-year birds until they have completed nesting activities. It is characterized by spotted-wing coverts. The feathers of first-year birds in breeding plumage are much more abraded than those of adults at the same season of the year because the first-year birds did not undergo a postnuptial moult during the previous fall. Two examples of *Hylocichla ustulata almae* in "typical" subadult breeding plumage are 367528 and 397342. Although they usually retain a slight reddish-olive wash above, subadult breeding specimens of *swainsoni* become so dark that they are sometimes difficult to separate from *almae*. This condition is probably responsible for the conclusion of several authors (Burleigh and Peters, 1948; Braund and McCullagh, 1940) that *incana* [= *almae*] extends all the way across northern Canada to the Atlantic coast. A warm yellowish wash at the base of the pileum is a characteristic of the eastern population and, when present, is an excellent diagnostic character in separating the two races of this particular age and plumage. Occasional birds occur in the plumage of subadults but lack the spotting of the wing coverts. The type of *clarescens* is an example of this sort. Two examples of *swainsoni* in the spotted-covert subadult breeding plumage are 382039

and 397072. Neither *H. u. ustulata* nor *H. u. oedica* is represented in the collection in this plumage.

Adult females in fresh plumage: *Hylocichla ustulata ustulata*: The upperparts are paler, slightly greener in hue than those of adult males of the same season of the year; 156436 is an example. *H. u. oedica* is not represented in the collection in this particular plumage. Specimens of *almae* of this sex and age group were not well represented in the collections which I studied, and the diagnostic coloration which is indicated below may be open to correction; the two specimens which I examined (397775 and 466951) are characterized by a pronounced grayish-olive overcast, strikingly different from other plumages of either sex or race. Females of *swainsoni*, on the other hand, are bright reddish olive above and are quite similar to the Dresden Brown of Ridgway; representatives of this group are 164179, 175847, 363970, and 375972.

Subadult females in fresh plumage: *Hylocichla ustulata ustulata* and *H. u. oedica*: None seen. *H. u. almae*: Specimens of this age and sex group possess the darkest dorsal coloration of any specimens in fall plumage; I would call it dark reddish brown, although the Brownish Olive of Ridgway is quite close but perhaps a little too saturated. 397618 and 419144 are examples of this plumage type. *H. u. swainsoni*: Specimens are quite reddish olive above; they are definitely more reddish olive above than males in fresh fall plumage, but on the other hand they are slightly paler than adult females in the fall. Some examples are 362315, 404722, 460530, and 479755.

Adult females in breeding plumage: *Hylocichla ustulata ustulata*: Similar to males but slightly richer in hue. 157768, 166909, and 156357 are examples. *H. u. oedica*: Paler and grayer than males in the same plumage; this plumage may be represented by specimens 420625, 262239, and 258364. The females of both of the following races are similar to the adult males in breeding plumage: *H. u. almae* may be represented by 242895, 269731, 367532, and 7170 (ING). *swainsoni* is represented by 348507, 382046, 425094, and 6836 (ING).

Subadult females in breeding plumage: *Hylocichla ustulata ustulata* and *H. u. oedica*: None seen. Specimens of *almae* are similar to adults but with slight reddish wash to the upperparts. They may be represented by the Brownish Olive of Ridgway, and are paler, less saturated than fall subadults females. Specimens of *swainsoni* in subadult female breeding plumage are more reddish above than adults but considerably paler than first-year males which are extremely dark in this plumage; specimens selected at random are 382042, 382049, and 397075.

Nongeographic Variation

Moult and plumages: I believe that Dwight (1900) is essentially correct in his diagnosis of the moults of Swainson's thrush. There is no prenuptial moult but some birds go through a "brightening" stage in which the upperparts acquire a rich, bright hue. At first glance, it might appear that the bird had just completed a prenuptial moult, but observation under a low-powered binocular-microscope reveals that the feathers are considerably worn. Miller (1941, p. 181) observed that some races of juncos undergo a similar brightening stage. There is a sequence of abrasion to the feathers of the upperparts that is helpful in segregating specimens in breeding plumage. Females arrive on the breeding ground later than males (sometimes as much as two weeks) and do not begin to show signs of wear until another week or ten days has passed, where as males begin to show signs of wear (sometimes going through a "brightening" stage) almost as soon as they arrive on territory. Specimens of subadult birds taken in spring migration are invariably more worn than adult birds taken during the same season. There is evidence that both age groups go through a prenuptial moult of the tail feathers (239929 and 208991), sometimes extending well into the breeding season (187190 and 187176).

Age of museum skins: Many of the specimens in the U.S. National Museum are very old. Consequently, the problem of color alteration due to age was given special attention. A series of skins known to be badly foxed were used as a control group. Foxing produces a peculiar artificially dyed appearance to the plumage that is at once apparent after a little experience is gained in recognizing this type of pigment alteration. As a secondary result of having the control series available, it was determined that several birds collected on the east coast and labelled "*ustulata*" were actually foxed specimens of *swainsoni*. These were 236009, female, Sept. 18, 1881, Highland Falls, N.Y., E. A. Mearns; and 263403, sex unknown, Sept. 21, 1897, Ariel, Amite Co., Miss., collected by A. Allison.

Ecological Comments

With the possible exception of the race *H. u. oedica*, the nest-site requirements of Swainson's thrush are almost invariably associated with the northern and mountain coniferous forest climaxes and their subclimaxes. In general, *H. u. ustulata* shows a decided preference for the deep forests of the Humid Transition Zone west of the Cascades in Oregon and Washington and the Coast Ranges of British Columbia. Here the heavy rainfall produces a rain forest of almost impenetrable undergrowth that is dominated by a climax forest of Sitka spruce,

western hemlock, western red cedar, and grand fir. Subclimax associates are dominated by Douglas-fir.

H. u. swainsoni prefers both climax and subclimax forests of the Canadian Zone. Their habitat requirements show some variation in different parts of their range, for, according to Bent (1949, p. 175), "this thrush is less common in mature dense coniferous forests than in bordering growths of smaller trees, where young balsam firs are growing up with a mixture of birches." Again, referring to northern New England, he said "they prefer the spruce and fir forests of the Canadian Zone."

H. u. almae occupies a broad range of climax and subclimax forested areas across the Canadian, Transition, and lower Hudsonian Zones. Among the dominants found in this area are black, white, and Englemann spruce and lodgepole pine.

H. u. oedica prefers the less humid areas of the Pacific Coast States and is found in the Transition Zone where yellow pine predominates and where strips of willow, cottonwood, and white alder provide nesting sites along foothill, valley, and streamside lowlands.

Summary

To reevaluate the criteria purported to be significant in segregating the various races of Swainson's thrush 513 specimens were assembled. Birds from Alaska south through the Rocky Mountains to Colorado were found to have a grayish-olive dorsal coloration, while the upperparts of birds from the Athabaska River in Alberta eastward to Newfoundland and south to West Virginia exhibited a more reddish-olive coloration.

Hylocichla ustulata oedica Oberholser is considered a valid race and as a consequence the nominate form *H. u. ustulata* is restricted to the Pacific coast from northwestern Oregon to Juneau, Alaska.

The terminal population, *H. u. clarescens*, described by Burleigh and Peters from Newfoundland, is not considered sufficiently distinct from the mainland form *H. u. swainsoni* to be given nomenclatural recognition. The subspecies *H. u. incana*, described by Godfrey in 1951 from the Yukon Territory, is considered a synonym of *H. u. almae* Oberholser, 1898.

H. u. almae does not normally occur along the Atlantic coast during migration. There are, however, a number of records from southern Illinois and the Gulf States which suggest that the Mississippi Valley may be a major flyway for this subspecies in the spring and fall.

Several specimens labelled "*ustulata*" taken along the Atlantic and Gulf coasts were found to be foxed specimens of *swainsoni*. This error suggests that all former records of the Pacific coast race taken in the east should be re-examined for possible misidentification.

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