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ANALYSIS OF PLUMAGE VARIATION IN THE CANADA WARBLER

By John H. Rappole

The plumages of the Canada Warbler (*Wilsonia canadensis*) have been described in detail by Oberholser (1974), Dwight (1900), Roberts (1936), and others. Although Oberholser (1974:793) presents information on 10 different plumages in the bird, the Canada Warbler is generally considered to be dimorphic with "adult male" and "female" type plumages (e.g., Verner and Willson 1969, Rohwer et al. 1980). The male plumage is gray above and yellow below with a series of black streaks across the breast. The female plumage is similar except the breast streaking is gray (see Peterson 1980:234). The species is considered to be monotypic throughout its geographic range (A.O.U. 1957:518).

As part of a study of transient migrants, I examined a number of Canada Warblers and discovered considerable variation within the major plumage types. The purpose of this paper is to describe, categorize, and evaluate the significance of plumage variation in the Canada Warbler.

METHODS

Field work for this study was done at the Welder Wildlife Foundation, 48 km N of Corpus Christi, Texas, from 15 Aug.–23 Oct. 1973; 4 Mar.–24 May 1974; 20 Aug.–13 Nov. 1974; 29 Mar.–27 May 1975 (Rappole 1978) and in the Tuxtla Mountains of southern Veracruz, Mexico from Aug. 1973–May 1975 (Rappole et al. 1979).

Birds were captured in mist nets (12 m × 2.6 m × 30 mm mesh) and each was examined for plumage aberrancies. Age in fall birds was determined by degree of skull pneumatization following a method similar to that of Schneider (1981) except that ethanol was used for wetting skull feathers. Wing chord measurements were taken as described by Oberholser (1974) to the nearest millimeter. I captured, banded, and released 634 birds and collected 87 birds.

I examined an additional 54 specimens of known age and sex from the Bell Museum of Natural History, University of Minnesota and the University of Georgia Museum of Natural History. The total specimen sample was divided into 6 categories on the following basis: (1) testes reported present, skull pneumatized, captured Aug.–Oct. = adult male, Basic plumage; (2) testes reported present, skull not completely pneumatized, captured Aug.–Oct. = immature male, Basic plumage; (3) testes reported present, skull pneumatized, captured Mar.–Jun. = adult male, Alternate plumage; (4) ovary reported present, skull completely pneumatized, captured Aug.–Oct. = adult female, Basic plumage; (5) ovary reported present, skull not completely pneumatized, captured Aug.–Oct. = immature female, Basic plumage; (6) ovary reported present, skull completely pneumatized, captured Mar.–Jun. = adult female, Alternate plumage.

TABLE 1. Description and assigned scores for color characters used in analysis of plumage variation in individual Canada Warblers of different age, sex, and plumage status.

Character and Score	Description
Crown	
0	Yellowish-green or yellowish brown.
1	Gray tinged with yellowish-brown or green.
2	Gray tinged with yellowish-brown or green, some black flecks.
3	Gray flecked with black.
4	Black edged with gray.
Forehead	
0	Yellowish or yellowish-green.
1	Yellowish-green tinge on gray.
2	Gray or yellowish-green flecked with black.
3	Gray flecked with black.
4	Black.
Side of Neck	
0	No defined spots along border between gray nape and yellow throat.
1	Defined grayish spots along border between gray nape and yellow throat.
2	Defined black spots along border between gray nape and yellow throat.
3	Black border between gray nape and yellow throat.
Cheek	
0	Mostly yellowish.
1	Gray tinged with yellow.
2	Gray.
3	Black and gray.
4	Black.
Breast	
0	No gray or black on breast.
1	Some ill-defined grayish streaks.
2	Distinct grayish or grayish-black streaks.
3	Grayish or blackish streaks with more or less well-defined black spots.
4	Black streaks.

Wing chord measurements of the specimens in the different age, sex, and plumage categories were compared statistically. Plumage characters were analyzed using an index type scoring method similar to that used by Short (1965) (Table 1).

RESULTS

Plumage scores of males in both Basic and Alternate plumage individuals varied from a strongly male-like score of 19 to a score of 6 well within the female range (Table 2). Females in Alternate plumage varied from a score of 3 to a male-like score of 13.

The main differences among the four Basic plumages (Fig. 1) are

TABLE 2. Analysis of color and pattern variation in individuals of different sex, age, and plumage categories in Canada Warblers.

Plumage character	Average score and range for individuals					
	Alternate plumage		Basic plumage			
	Male (65)[1]	Female (18)	Adult male (7)	Adult female (10)	Immature male (19)	Immature female (22)
Crown	3.8[2] (2–4)[3]	1.8 (0–3)	2.9 (0–4)	1.4 (1–2)	0.7 (0–2)	0 (0)
Forehead	3.9 (2–4)	1.4 (1–3)	2.7 (0–4)	1.0 (0–2)	0.6 (0–2)	0.1 (0–2)
Side of neck	2.7 (2–3)	0.2 (0–2)	2.6 (1–3)	0.5 (0–1)	1.4 (0–2)	0.3 (0–3)
Cheek	3.0 (2–4)	1.3 (0–3)	3.1 (2–4)	1.4 (1–2)	1.1 (1–2)	0.8 (0–2)
Breast	3.8 (3–4)	1.8 (1–3)	3.9 (3–4)	2.2 (1–3)	3.0 (3)	1.3 (0–3)
Total score	17.2 (11–19)[4]	6.5 (3–13)	15.2 (6–19)	6.5 (4–9)	6.8 (4–10)	2.5 (0–9)

[1] Sample size.
[2] Average score.
[3] Range of scores.
[4] Average and range of total scores for individuals within each plumage category.

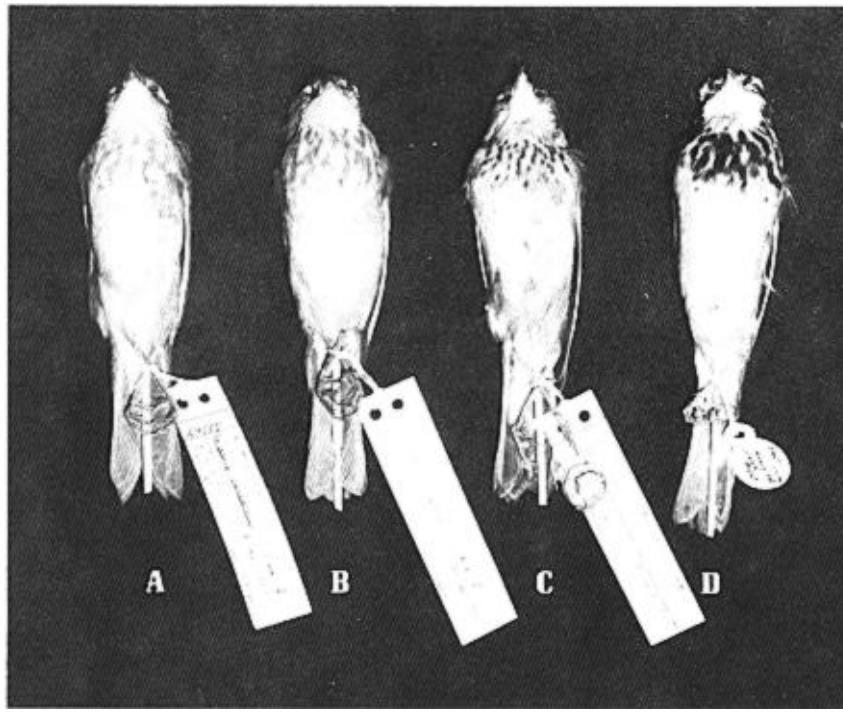

FIGURE 1. Plumages of the Canada Warbler. A—immature female, Basic; B—adult female, Basic; C—immature male, Basic; D—adult male, Basic (note that a fifth plumage type, adult male, Alternate, is very similar to D but distinguishable—see Table 3).

TABLE 3. Key to Canada Warblers in Basic plumage.

1. (a) Necklace (breast markings) of thick (1–2 mm) black streaks. Forehead black or blue-gray flecked with black. Skull completely pneumatized. ..... adult male (Fig. 1D).[1]
   (b) Necklace not as above. ..... 2.
2. (a) Necklace of distinct black or grayish spots. Forehead usually (84%) yellowish-green. Skull not completely pneumatized (Jul.–Nov.). ... immature male (Fig. 1C).
   (b) Necklace of mostly grayish streaks. ..... 3.
3. (a) Skull completely pneumatized (Jul.–Nov.). Generally (90%) with some black in necklace. Forehead grayish, sometimes tinged with yellow.[2] ..... adult female (Fig. 1B).
   (b) Skull not completely pneumatized (Jul.–Nov.). Generally (77%) without black in necklace. Forehead yellowish-green (95%). ..... immature female (Fig. 1A).

[1] Males in Alternate plumage in contrast to those in Basic, generally lack yellow edgings on gray and black feathers of crown, back, neck, and breast presumably because of feather wear.

[2] Females in Alternate plumage are indistinguishable to my eye from adult females in Basic plumage.

summarized in the key in Table 3. Using this key 93% (54 of 58 birds) of the total specimen sample of birds in Basic plumage would have been correctly identified to age and sex on the basis of plumage alone. Use of skull pneumatization information increased the accuracy to 56 of 58 birds (97%).

Three individuals (.4%) of the total sample of banded birds and specimens examined (775 individuals) had aberrant plumages. One immature male had throat, breast, and forehead flecked with black and yellow, and a gray rather than white crissum. One adult female in Basic plumage had cream color in all areas which would normally be yellow. Areas of gray color and the pattern of necklace and face are normal in this bird. One adult male in Alternate plumage had pale yellow from necklace to crissum instead of normal bright yellow. Other areas of this bird's plumage were normal in coloration.

The wings of males averaged 5–6% longer than those of females, but there was considerable overlap (Fig. 2). The wings of 89% of fall males were 65 mm or longer, while all fall females in the specimen sample had wings 62 mm or less in length. Wing length of 98% of spring males was 64 mm or more while a bird with a chord of 61 mm or less was a female for 92% (11 of 12) of the spring sample. Fall birds in Basic plumage tended to have longer wings than spring birds of the same sex in Alternate plumage (1%). Remiges were molted only during the pre-Basic molt, so the spring birds had 7–8 months more wear on the wings than fall birds. However, I was unable to distinguish birds hatched the previous year from older birds in Alternate plumage based on degree of wing wear (cf. Rohwer et al. 1980:420–421).

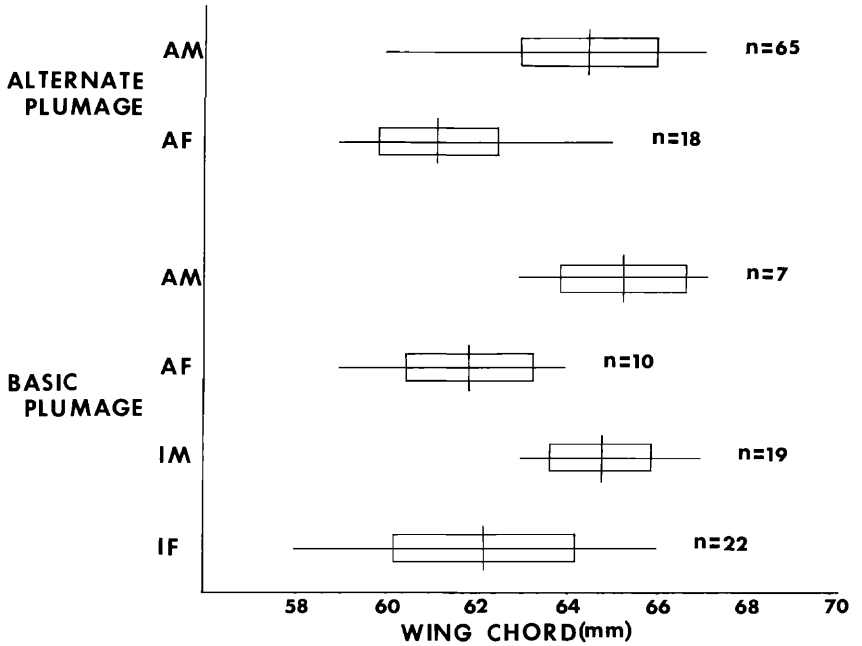

FIGURE 2. Comparisons of wing measurements for Canada Warblers in different age, sex, and plumage categories. (Horizontal line = mean, vertical line = range, rectangle = one standard deviation.)

DISCUSSION

The Canada Warbler is polymorphic with respect to plumage coloration. This conclusion is suggested not only by my data but by the description of the different plumages of this species in Oberholser (1974) and other meticulous works where both the norm and the range of variation within the main plumage categories are described in detail. The Canada Warbler has five separable post-Juvenal plumage types: Adult male—Basic, Adult male—Alternate, Adult female—Basic and Alternate, Male—first Basic, Female—first Basic. However, there are several variants within each major type which resemble norms of other plumage types—males that resemble females (2.7% of specimen sample), immatures that resemble adults (2.4%), females that resemble males (3.5%), etc.

There are no data with which I am familiar on other species for comparison of plumage analysis results. However, cursory examination of specimens of other "dimorphic" species of passerines (Verner and Willson 1969, Rohwer et al. 1980) for which I have good sample sizes from Texas and Mexico indicates a comparable degree of variation with-

in the supposedly distinct "male" and "female" plumage categories (Wilson's Warbler *Wilsonia pusilla,* Northern Parula *Parula americana,* Bay-breasted Warbler *Dendroica castanea,* Chestnut-sided Warbler *Dendroica pensylvanica,* Northern Oriole *Icterus galbula,* Yellow-breasted Chat *Icteria virens,* Kentucky Warbler *Oporornis formosus*).

These observations indicate that plumage categories, e.g., "adult male, Basic plumage," are not discrete entities. There is variation within each category and overlaps between categories.

The evolutionary significance of sexual dimorphism has been studied in detail and some workers have examined the tendency of young males in some species to look like females (Rohwer et al. 1980, Rohwer 1978). However, other plumage variations, e.g., the tendency for some females to closely resemble males, have not been thoroughly examined even though knowledge of these phenomena is not new. Oberholser (1974: 791) describes females of the Hooded Warbler (*Wilsonia citrina*) that have the black throat and jugulum of the male-type plumage. "Normal" female plumage in this species is a drab greenish above and yellowish below (Peterson 1980:242).

I propose that the plumage polymorphisms found in the Canada Warbler and other species mentioned above can be attributed to the balancing effects of selection factors that favor opposing directions in the evolution of plumage coloration. These factors can be divided into those favoring a "brighter" plumage (one in which there is a large degree of contrast between colors, making the bird more visible) vs. those favoring a "duller" plumage (less contrast).

Factors favoring a "bright" plumage include: (1) intra-male competition for mates and/or territories (Wallace 1889, Rohwer et al. 1980:407), (2) epigamic selection (Darwin 1859:44, 1871:529, Hamilton and Barth 1962, Selander 1965, 1972, Lowther 1975, Fisher 1930), (3) intraspecific competition for limiting resources (Fretwell 1972:109–113, Ketterson and Nolan 1976, Schwartz 1964, Rappole and Warner 1976, 1980).

"Dull" plumage may help to reduce aggressiveness of adult males toward the dull-plumaged bird. This would be advantageous for adult females by reducing pairing time (Hamilton 1961), for unmated females entering breeding territories of mated birds, and for unmated young males (Rohwer et al. 1980). "Dull" plumages also reduce the likelihood of predation on the individual itself or on its eggs or nestlings (Darwin 1871:504).

Some selection factors, e.g., species recognition (Sibley 1957) may favor neither a "bright" nor a "dull" plumage, merely one that is different from other species.

Good data on molts and plumages of birds like the Canada Warbler have been available for a number of years. Researchers like Ridgway, Brewster, Oberholser, and Dwight were well aware of the variety and sequence of plumages demonstrated in different avian species. Yet, the possible evolutionary significance of these different plumages has not been analyzed for the most part. Although male/female dimorphism has

stimulated considerable interest, as have subadult male plumages, most other plumage strategies have not been closely examined (though see Morton 1976, Hamilton and Barth 1962). Plumage variants deserve considerably more attention as they reflect important aspects of species' biology that have been overlooked.

SUMMARY

Museum specimens of 141 Canada Warblers of known sex, age, and plumage status, and 634 wild caught individuals were examined. Analysis of the specimen sample revealed 5 visually different plumage categories: adult male—Basic, adult male—Alternate, adult female—Basic and Alternate, immature male—Basic, immature female—Basic. A visual scoring method was used to characterize variation within each of the plumage categories. The norm of each plumage type was easily separable from the norm of all other types. However there were variants within each age—sex—plumage group which resembled individuals from other groups: male-like females, female-like males, adult-like immatures. The major plumage patterns as well as the variants within each group can be explained on the basis of balancing selection forces (e.g., intrasexual competition during the breeding season, predation, epigamic selection, and intraspecific competition during the non-breeding season).

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