GEOGRAPHIC VARIATION IN THE *DENDROICA CORONATA* COMPLEX

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THE *Dendroica coronata* (L.) complex consists of the Myrtle Warbler (*D. coronata*), which breeds in the boreal forests of North America, and Audubon's Warbler (*D. auduboni* Townsend), which breeds in the forests of western North America. Although the two are generally regarded as distinct species, they intergrade in southwestern Canada and should be considered as a conspecies, or better, as two semispecies (Hubbard, 1969). Besides the nominate forms, one other has been named in the Myrtle group (i.e., *hooveri* McGregor) and three in the Audubon group (i.e., *memorabilis* Oberholser, *nigrifrons* Brewster, and *goldmani* Nelson). The last revisions were by Godfrey (1951) in the *coronata* group and by Oberholser (1921) in the *auduboni* group.

The present paper is the outgrowth of a comprehensive analysis of geographic and other types of variation (Hubbard, 1967), which was done prior to study of the interbreeding of the two semispecies groups (Hubbard, 1969). My object here is to describe salient features of the geographic variation in each of these groups and to assess the named forms (no new forms are proposed). For a more detailed review of variation in this complex the reader is referred to my 1967 work, available from University Microfilms, Ann Arbor, Michigan.

In extending formal, subspecific recognition to populations I followed the suggested criteria of Mayr et al. (1953), in accepting as valid those entities that are separable *inter se* on a 75 per cent from a near 100 per cent (or 90 from 90 per cent) basis. A further requirement is that the probability of correct segregation within a random sample be 95 per cent or better. While recognizing the need for certain minimum and arbitrary standards in the application of formal names to populations, I also feel that in some cases what might be termed "infra-subspecific" variation can be usefully singled out. For example, by being able to identify distinctive extremes that characterize certain populations one may gather information on dispersal, molt cycles, and other aspects of the biology even though the populations in question are not "good" subspecies. Such infra-subspecific entities can be designated by breeding range rather than by a formal name and thus provide the practical benefits of the subspecies concept without further burdening scientific nomenclature.

Males in breeding plumage of the races of the *Dendroica coronata* complex (from top): *D. c. coronata, D. c. auduboni, D. c. nigrifrons, D. c. goldmani.* Watercolor by Theodore R. Miley.

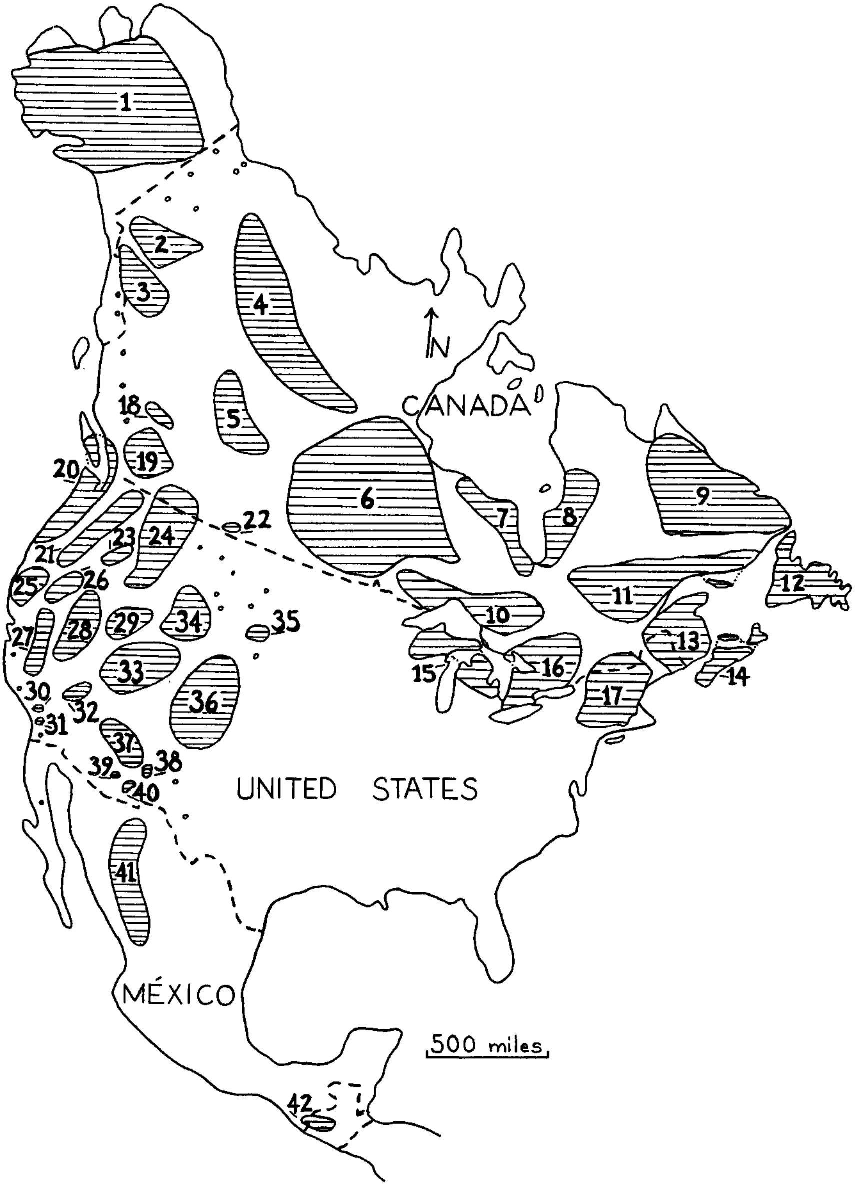

FIG. 1. Geographic samples used in analysis of mensural characters in the *Dendroica coronata* complex. Numbers 1 through 17 are *coronata* group and 18 through 42 the *auduboni* group (nominal designations of numbers in TABLE 1).

MATERIALS AND METHODS

This study is based on 350 specimens in winter plumage, 563 juveniles (none available of *goldmani*), and 2,069 specimens taken in the breeding season. The breeding season is arbitrarily considered to be 1 June (15 May in the Pacific Northwest and northernmost North America) through the time of the end of the postnuptial molt and applies to specimens taken in suitable breeding areas. For various analyses specimens were segregated into juveniles (includes both sexes), first-year males (i.e., males that have completed the postjuvenal but not the first postnuptial molt), adult males (i.e., males that have completed at least one postnuptial molt), and females. First-year males were found to be about 90 per cent separable from adults on the basis of their generally browner (and more worn) remiges, rectrices, and especially primary coverts and alular feathers (verified by juveniles and skull-aged specimens); adults have these feathers more blackish, often with grayish edgings, and less worn. Although similar differences exist in females, the segregation of age classes was not attempted because the differences are much more subtle and less consistent.

Breeding specimens within each of the two semispecies were segregated into the smallest geographic samples possible for a preliminary multivariant analysis of linear measurements, with subsequent recombination of certain samples to better study and present the data (Fig. 1). Linear measurements used were lengths of wing (chord), tail, culmen (nostril to tip), and tarsus, all but the last using established methods. The tarsus was measured from the posterior depression of the tibio-metatarsus joint to the proximal base of the hallux, *provided* that the latter was positioned 90 ± 45 degrees relative to the tarsometatarsus (positions outside that range were found to alter tarsus length by 1 to 2 mm). In spite of these qualifications most specimens were measurable for tarsus length, and this method of measurement was found to be faster than and as accurate as the traditional one. Wing and tail length were found to be strongly correlated, and as a result only wing length was used in the mensural analysis on an absolute basis.

Body weight of breeding males was also used to compare samples, those of females being excluded as too variable due to variation in weight of gonads and gonadal products (Hubbard, 1967). Body weight was found to vary independently of the linear measurements used above and is treated separately.

The amount of white in each rectrix was scored as follows: a very small spot or narrow marginal edging (0.125); a small spot or narrow marginal blotch (0.25); a medium spot or small marginal blotch (0.5); a large spot or medium marginal blotch (0.75); or a large marginal blotch (1.00). The values for each pair of rectrices were summed to obtain the score of white in the tail of each specimen and these were used to compare sample means.

Statistical procedures follow Steel and Torrie (1960) and other specified sources. Variances were calculated for samples of six or more specimens, and differences between sample measurements are accepted as significant when at or greater than the 0.05 level of probability.

RESULTS AND DISCUSSION

Coronata Group

This group breeds from New England, eastern New York, southern Ontario, central Michigan, southern Manitoba, southern Saskatchewan, central Alberta, northern British Columbia, and southeastern Alaska northward to tree line (Fig. 1) and is migratory throughout its breeding range. Intergradation with the *auduboni* group occurs in southeastern Alaska, central and eastern British Columbia, and southwestern Alberta and is discussed elsewhere (Hubbard, 1969).

Within the *coronata* group I found geographic trends in the variation of both color and pattern of plumage and in mensural characters. Plumage characters which vary are extent of black in the breast of breeding males, color and extent of streaking on the upperparts of breeding females, the color of the upperparts of winter-plumage specimens, and extent of white in the outer rectrices. Mensural characters which vary are body weight of breeding males and lengths of tarsus and wing. Purported differences in the hue of the yellow rump (Oberholser, 1918), color of the upperparts of juveniles (Oberholser, 1918; Godfrey, 1951), and of the extent of dorsal streaking in winter plumage (Godfrey, 1951) were not substantiated.

In breeding-plumaged males the black on the breast varies from streaking to solid, with the former extreme predominating in the northwest (Alaska, Yukon, and British Columbia) and the latter in Labrador-Newfoundland. In northwestern males (81 specimens in 3 samples) 56 to 66 per cent were streak-breasted and the remaining 34 to 44 per cent were mottled with black on the breast. In the Prairie Provinces the streak-breasted type composed 20.5 per cent in a sample of 29 males, while 79.5 per cent were mottle-breasted. Farther east, 10.5 per cent of 151 males were streak-breasted, 74.7 per cent mottle-breasted, and 14.8 per cent solid-breasted, except in Labrador-Newfoundland (14 males) where none was streak-breasted and 50.0 per cent each were mottle- and solid-breasted. From these data two points can be made: one, no geographic area can be characterized by a single breast type; and, two, only solidly black-breasted males are confined to an area discrete enough to be useful in reliably segregating specimens. Thus, solid-breasted males may be said to originate in eastern North America, east of the Prairie Provinces, with a confidence level of 100 per cent. In my sample of males some 15.0 per cent are of this type and can thus be assigned geographically on this character.

In breeding-plumaged females the upperparts vary from light brown (occiput light gray) with light streaking to dark brown with heavy streaking; the light brown type predominates in the west and the dark brown in the east. In northwestern females (39 specimens in 3 samples) the light brown type composed 72.7 to 76.5 per cent, while zero to 5.0 per cent were dark brown and 22.3 to 23.5 per cent were intermediate. In Alberta the light brown type constituted 68.0 per cent of 25 specimens and 32.0 per cent were intermediate. Farther east the light brown type was 4.9 to 12.5 per cent (73 specimens in 3 regional samples), while 65.8 to 68.8 per cent were dark brown and 18.7 to 29.3 per cent were intermediate. While most specimens in regional samples fall into one or the other extreme of this character and show a geographic tendency in the trend of variation, 23.5 to 34.2 per cent of the specimens in each sample fall in the opposite extreme and intermediate categories. This means that no sample or area can be characterized by a single plumage type. Furthermore, of the two extremes only the dark brown type is sufficiently limited in its distribution and frequency to be useful in reliable segregation of specimens. Thus, females with dark brown, broadly streaked upperparts may be attributed to North America, east of Alberta; in my samples the confidence level of this segregation is 97 per cent, and 37 per cent of female specimens may be identified in this way.

In the color of the upperparts winter-plumaged specimens vary from light to dark brown, with or without a rufescent wash. Study of this character is made difficult because of the problem of obtaining winter specimens from known breeding areas. In my analysis I used 40 specimens taken in late summer and autumn, and segregated by sex and age classes, from Alaska and northwestern British Columbia, compared to 80 from southeastern Canada and the adjacent United States. In the northwestern sample 92.5 per cent of the specimens fell into the categories of light, rufescent brown or dark brown, while the remaining 7.5 per cent were either light brown or dark, rufescent brown. By comparison 68.7 per cent of the eastern specimens fell into the first two categories (i.e., light, rufescent brown and dark brown), whereas 12.5 per cent were light brown and 18.8 per cent were dark, rufescent brown. These comparisons show different frequencies of color types between the two samples, but complete overlap exists among the types. The degree of overlap is such that reliable segregation of specimens on a geographic basis is not possible.

The final plumage character in which I found geographic variation is the amount of white in the outer rectrices, with the average scores in northwestern populations being higher than those in more easterly ones. In adult males from Alaska, the Yukon, British Columbia, and MacKenzie the values are 3.2 to 3.6, compared to 3.0 to 3.1 in more eastern samples. In first-year males from the northwestern area the values are 2.7 to 3.2 compared to 2.5 to 2.7 eastward except for 2.9 on the western side of Hudson Bay. In females the northwestern values (excluding MacKenzie which is 2.5) range from 2.7 to 2.8, compared with 2.4 to 2.6 eastward except for 2.8 in southern Manitoba. The differences are relatively minor and overlap occurs in means of first-year males and females, as well as in individuals of all samples. Further, some inconsistency exists in the area from MacKenzie to Hudson Bay, perhaps due to introgression with *auduboni*. Thus, in spite of trends in average differences no effective separation of populations is possible on the basis of this character.

TABLE 1

WING LENGTH (MM) IN BREEDING SAMPLES OF THE *DENDROICA CORONATA* COMPLEX

Semispecies groups	Adult males			First-year males			Females		
Sample	no.	mean	S.D.	no.	mean	S.D.	no.	mean	S.D.
Coronata group									
1. Alaska	14	77.1	1.8	23	75.3	1.3	16	72.9	1.1
2. Yukon	13	76.5	1.6	12	74.5	1.3	9	72.3	0.9
3. Northwest British Columbia[1]	13	76.8	1.1	24	75.0	1.4	27	71.4	1.2
4. MacKenzie	9	74.7	0.8	7	72.7	0.8	9	69.7	1.1
5. Central Alberta[1]	8	74.1	1.6	9	72.4	1.7	9	69.0	1.8
6. Manitoba	5	73.0	—	12	72.0	1.6	11	68.4	1.7
7. West James Bay	9	74.3	1.7	7	72.5	1.3	8	69.3	0.9
8. East James Bay	6	74.9	1.5	11	71.8	0.9	14	69.3	1.5
9. Labrador	12	74.5	1.5	4	71.8	—	12	69.7	1.4
10. Central Ontario	11	73.9	1.7	15	71.7	1.4	16	69.0	2.4
11. Quebec	9	74.0	1.2	19	72.6	1.2	16	69.3	1.1
12. Newfoundland	6	74.7	2.4	8	72.5	1.6	10	70.1	2.3
13. New Brunswick	5	73.0	—	12	71.3	0.9	13	68.7	1.5
14. Nova Scotia	9	74.1	2.0	10	72.4	1.2	10	67.9	1.3
15. Michigan	12	73.0	1.0	20	71.7	1.7	9	68.3	0.7
16. Southeast Ontario	11	73.3	1.5	10	71.6	2.0	8	68.3	1.0
17. Northeast United States	7	74.1	1.3	15	72.1	1.9	13	68.6	1.3
Auduboni group									
18. Central British Columbia[2]	10	76.5	1.3	15	74.5	1.6	2	72.6	—
19. Southern British Columbia	8	77.7	1.4	12	75.2	1.3	18	71.6	1.6
20. Northwest Coast	13	76.6	1.3	21	74.0	1.4	24	71.4	1.4
21. Cascades	13	78.0	1.6	17	75.1	1.4	12	73.3	1.6
22. Cypress Hills	6	78.0	1.3	7	77.3	1.4	11	73.5	1.7
23. Northeast Oregon	14	77.9	1.6	10	76.3	1.2	7	73.8	0.8
24. Idaho	7	79.4	1.6	18	75.9	1.5	22	73.3	1.0
25. Northwest California	12	79.0	1.5	14	76.4	1.9	17	73.9	1.3
26. Northeast California	14	79.6	1.9	17	76.4	1.1	10	73.4	1.9
27. Sierra Nevada	30	79.7	1.5	41	77.1	1.8	47	74.4	1.8
28. Western Nevada	13	80.3	1.8	9	76.8	0.8	8	74.8	1.6
29. Northeast Nevada	7	80.5	2.3	10	77.1	1.6	12	74.4	1.6
30. San Bernardino Mts.	17	79.7	1.3	12	78.0	2.1	10	74.3	1.8
31. San Jacinto Mts.	7	80.0	1.3	7	76.5	1.2	12	76.6	1.4
32. Southern Nevada	8	80.0	1.4	8	77.8	1.7	10	73.5	1.8
33. Utah	14	80.3	1.2	19	77.5	1.3	15	74.3	2.0
34. Northwest Wyoming	14	80.2	1.2	16	77.6	1.4	27	74.6	1.5
35. Black Hills	17	81.4	0.5	8	78.6	1.0	13	76.5	1.4
36. Southern Rockies	31	80.7	1.8	22	77.9	1.2	20	75.1	1.6
37. Central Arizona	15	80.7	1.3	12	78.8	1.1	11	76.0	1.8
38. Mogollon Mts.	11	80.8	1.9	9	78.9	1.4	10	75.4	1.5

[1] Intergrades toward *auduboni*.
[2] Intergrades toward *coronata*.

TABLE 1 (Cont'd.)

Semispecies groups	Adult males			First-year males			Females		
Sample	no.	mean	S.D.	no.	mean	S.D.	no.	mean	S.D.
Auduboni group (Continued)									
39. Santa Catalina Mts.	18	81.8	1.7	27	79.5	1.4	19	76.4	1.8
40. Chiricahua Mts.	10	81.1	0.6	9	79.3	1.8	10	77.3	1.4
41. Sierra Madre Occidental	35	83.0	2.4	20	80.0	1.2	24	77.8	2.2
42. Chiapas-Guatemala[3]	9	84.4	1.6	6	81.3	1.5	11	78.9	1.5

[3] Includes specimens taken throughout the year.

Mensural variation.—In analyzing body weights I was hampered by the lack of data, and conclusions are necessarily tentative. In comparisons of the only two sizable samples, I found a significant difference to exist between the means of eight males from Alaska (weight 13.5 ± 0.7 grams) and that of 13 from Michigan (weight 11.8 ± 0.4 grams). Among the few other weights available, those from Ontario and the northeastern United States were similar to the Michigan series and those from the Yukon and northwestern British Columbia were similar to the Alaskan ones. However, three weights from Quebec are intermediate (range 12.4 to 13.1 grams), which may suggest that weight increases from south to north rather than just northwestward. Obviously more data are needed to properly assess this character.

For the tarsus a slight increase in mean length occurs from southern Canada and the adjacent United States northward to Labrador-Newfoundland on the east and Alaska-Yukon-British Columbia on the west, although locally the variation becomes mosaic rather than geographic in distribution. The means in southern areas are 16.9 to 17.7 mm in males compared to 17.5 to 18.1 mm in the northwest and 17.9 to 18.2 mm in Labrador-Newfoundland (females average smaller in size but show parallel trends). No reliable segregation of populations is possible on the basis of this measurement because of overlap and the slight differences involved.

One finds that wing lengths of populations from the northwest (Alaska, the Yukon, MacKenzie Delta, and northwestern British Columbia) average larger than those to the east (Table 1). In adult males the means are 76.5 to 77.1 mm in the northwest and 73.0 to 74.9 mm to the east; in first-year males 74.5 to 75.3 mm in the northwest, 71.3 to 72.7 mm to the east; and in females 71.4 to 72.9 mm to 67.9 to 70.1 mm.

I compared the group of easterly specimens with that from the northwestern and found that the separability in adult males (east versus northwest) is 70.7 per cent from 20.6 per cent, in first-year males 94.3 per cent from 36.9 per cent, and in females 91.1 per cent from 30.6 per cent. This degree of separability (confidence level 95 per cent) falls far short of the 75 from ca. 100 per cent (or 90 from 90 per cent) levels suggested by Mayr et al. (1953), and even on a less reliable basis of segregation (confidence level 75 per cent) the maximum separability is still only 89.5 to 83.1 per cent in easterly specimens and 61.7 to 86.1 per cent in the northwestern ones. Obviously separation of populations of wing length is not possible in the *coronata* group on a reliable and large-scale basis.

Summary of variation and nomenclatural conclusions.—This review of geographic variation reveals the existence of several characters in the *coronata* group which reliably distinguish populations (confidence level of 95 per cent or more), including longer wing in northwestern North America, and shorter wing, more extensively black breast in breeding males, and darker brown upperparts with heavier streaking in breeding females in more easterly North America. Other characters show minor differences, overlap, or other factors which negate their value in separation of populations, and include the color of the upperparts in winter plumage, amount of white in the outer rectrices, weight (data incomplete and inconclusive), and tarsus length. The reliable characters, even when combined (on the basis of random association), do not produce a sufficient level of separability to justify subspecific recognition of two populations, i.e., at least 75 per cent from about 100 per cent (or 90 from 90 per cent). In eastern populations the segregation by breeding plumage characters and wing length is 75.5 per cent in adult males, 96.1 per cent in first-year males, and 97.1 per cent in females, compared to 20.6 per cent, 36.9 per cent, and 30.6 per cent in the respective categories in northwestern populations, which are solely separable by wing length. Thus the separation of the latter population as a formal subspecies is unwarranted, and the name *hooveri* (McGregor, 1899) is considered a synonym. Nevertheless, the fact remains that the specified portions of the specimens from the two areas are reliably separable, and as segregation of such specimens may be of value, it is provided for in the key included in this work.

Auduboni Group

The breeding range of this group is from central British Columbia, southern Alberta, and extreme southwestern Saskatchewan southward to northern Baja California, central Durango, and westernmost Texas, with a disjunct, resident population in extreme southeastern Chiapas and the adjacent highlands of Guatemala (Fig. 1). Except for the last, all populations are thought to be migratory, or at least are not known to be resident. Geographic variation exists in plumage color and pattern and in measurements.

Plumage variation.—In breeding plumage, males from north of the Mexican border are gray above streaked with black, and white below with the breast streaked to solidly black. The loral and anteriormost auricular areas are blackish, and the areas posterior to the auriculars and posterior to the yellow crown patch are gray or grayish white. Over much of the western United States, southwestern Canada, and Baja California this plumage varies only slightly, with males from the Southern Rockies and Black Hills southward averaging somewhat more extensively black on the underparts than those to the north and west. The increase in extent of black is gradual over most of this extensive area, but in the southernmost Southwest a marked increase occurs in the extent of black not only on the underparts but also on the sides of the head and in the dorsal streaking as well. This increase is most apparent in adult males of the Chiricahua and Huachuca Mountains of Arizona, but it also exists in first-year males from those areas and in males from northward to the Mogollon Plateau of Arizona and New Mexico (and occasionally farther). In the increased melanism specimens from the two Arizona mountain areas often are intermediate between more northern populations and those of the Sierra Madre Occidental. The latter are even more extensively black below, with heavier dorsal streaking, more blackish heads (lores, forehead, auriculars), and have the post-coronal and post-auricular patches whitish rather than grayish in color. Except for narrow intergradation through the Chiricahua and Huachuca Mountains, the Sierra Madrean population shows a discontinuity with both northern and southern populations in characters of the male breeding plumage.

Also distinctive is the resident population of Chiapas and Guatemala, in which males in breeding plumage are solidly black above, or black with a few gray streaks or smudges, with the post-coronal and post-auricular patches markedly white. The underparts are somewhat less extensively black than those of Sierra Madrean males.

In winter plumage adult males from north of the Mexican border have the upperparts extensively gray, washed with light to moderately dark-brown, and the black marking of the underparts (obscured by buff tips in fresh plumage) are in the form of spots or mottling. First-year males are browner, less gray above and have the ventral black markings as streaks. Females resemble first-year males but are more diffusely and less darkly streaked and in first-year plumage have reduced or no yellow in the throat. North of the southernmost Southwest little geographic variation exists in these plumages, although adult males become slightly more extensively black below as one progresses southward. In southern Arizona, and at least occasionally farther northward, occurs a definite shift toward the winter plumages that characterize the birds of the Sierra Madre Occidental, with the populations of the Chiricahua and Huachuca Mountains constituting intergrades in winter plumages between the Sierra Madrean populations and those to the north.

Adult males in winter plumage from the Sierra Madre Occidental are more extensively gray above with heavier black streaking than those from farther north, and the uneven brown wash that may be present is darker brown. The underparts are much more extensively black (with a variable buff wash in fresh plumage) and the face is blackish. First-year males and females are darker brown above, heavier streaked, and more extensively black below than their northern counterparts. Specimens of this population are highly separable from those farther north, except for a few of the intergrade specimens from southernmost Arizona.

Also distinct and highly separable in winter plumage is the population of the Chiapas-Guatemalan area. Adult males differ from all others in having the winter plumage identical to the breeding plumage, thus lacking any trace of buff or brown. First-year males and females resemble each other and their counterparts from the Sierra Madre Occidental, differing from the latter in their more richly brown, less sooty upperparts and more extensive streaking on the occiput.

Females in breeding plumage show a pattern of geographic variation that parallels that of the breeding plumage of males and winter plumages. The same pattern of geographical variation also exists in the juvenal plumage as far as is known, but in the absence of specimens from the Chiapas-Guatemalan area the situation there remains to be clarified. In each of these plumages no significant geographic variation exists in populations north of the Mexican border except in southernmost Arizona (occasionally elsewhere in the Southwest), where intergradation from northern plumage types toward that of the Sierra Madre Occidental occurs. For example, north of the intergrade area the upperparts of juveniles vary from light gray to buffy brown and the blackish streaking is narrow above and below. In the Sierra Madre Occidental the upperparts are a darker, more rufescent brown, lacking any grayish cast, and the streaking is darker, broader, and more extensive. Interestingly, the Sierra Madrean juveniles are virtually identical to those of the *coronata* group except for being more extensively streaked above and relatively larger in size. I presume that Chiapas-Guatemala juveniles will be found to be similar to those of the Sierra Madre Occidental.

Geographic variation was found to exist also in the amount of white in the outer rectrices. North of the Mexican border the average scores of white in the tail of 14 samples showing no introgression with *coronata* were 4.9 to 5.1 in adult males, compared to 4.6 in the Sierra Madre Occidental and 4.4 in the Chiapas-Guatemalan area. In first-year males showing no introgression from the north the values are 4.2 to 4.7, compared with 3.8 in both the Sierra Madre Occidental and Chiapas-Guatemalan area; females from the respective areas score 3.7 to 4.6, 4.3, and 3.8. These figures show that males of the Mexican-Guatemalan area average less white in the tail than those from farther north, but in females considerable overlap exists. No effective separation of populations is possible on this basis because of the amount of individual variation.

Mensural variation.—In the *auduboni* group at least local geographic trends are evident in body weight and lengths of culmen, tarsus, and wing. Slightly lesser values of weight are evident in 4 of 5 western United States samples (range of means 11.9 to 12.2, ± 0.7 to 1.0 grams) compared to 5 Rocky Mountain and Southwest samples (range of means 12.5 to 13.0, ± 0.6 to 1.5 grams), but differences are not significant and one western sample (northwestern California—12.6 ± 0.6 grams) overlaps the eastern range. The Sierra Madre sample (mean 12.7 ± 0.7 grams) and the one Guatemalan weight (13.0) are similar to more northern values and suggest a general homogeneity in this character in the *auduboni* group.

Much of the variation in culmen length in the *auduboni* group is mosaic rather than clinal in nature, although certain populations are distinguishable compared to others. For example, in the Chiapas-Guatemalan area culmen length averages significantly larger (value 7.9 ± 0.2 mm in females and first-year males, 8.1 ± 0.1 mm in adult males) than in the Sierra Madrean population (females 7.2 ± 0.3 mm, males 7.4 ± 0.2 mm). Among the northern populations values vary widely (7.1 to 7.9 in females, 7.1 to 8.1 mm in males), but the pattern of variation is mosaic and no effective separation is possible *inter se* or when compared with more southerly populations.

A gradual cline of increasing tarsus length exists from the north to the south, but as in culmen length local digressions and mosaic variation are present. For example, minimum values are in the Northwest Coast sample (17.7 to 18.0, ± 0.4 to 0.5 mm, depending on age and sex) compared to miximum values (18.9 to 19.4, ± 0.5 to 0.6 mm) which occur in the Chiapas-Guatemalan area. Because of intergradation, overlap, and variability, no segregation of populations is possible on this basis.

A generally orderly and gradual cline of increase of wing length occurs from the Northwest Coast southward to the Chiapas-Guatemalan area (Table 1). Differences in the means of these two extreme areas are 7.3 to 7.8 mm and are highly significant, but because of the gradual nature of intergradation, no line can be made that will separate adjacent populations on a reliable and large-scale basis. Even when populations from geographic extremes are compared one finds that separation is not highly effective. For example, the values in the Chiapas-Guatemalan sample average larger than all other *auduboni* samples, but no significant differences exist between that sample and those from the Sierra Madre Occidental, Southwest, Southern Rockies, and the Black Hills. North of the Mexican border the effective separation of populations is equally untenable because of the very broad overlap, and the small average differences between extremes.

Interestingly, I found no differences between migratory and non-migratory populations in relative lengths of the "wingtip" (i.e., the ratio of the length of the primaries posterior to the tips of the secondaries on the folded wing to the length of the total wing.). For example, this ratio is 24.5 per cent in adult males of the resident Chiapas-Guatemalan population compared to 24.1 per cent in the highly migratory Black Hills population.

Summary of variation and nomenclatural conclusions.—This review of geographic variation reveals the existence of plumage characters which reliably and on a large scale distinguish several populations at the level of formal subspecies. These characters include the extent of black in male plumages, color of the upperparts and amount of streaking in breeding, winter, and juvenal plumages, and the color of the post-auricular and post-coronal patches in breeding males. These characters involve stepped or broken clines of increasing melanins in the plumage (decreasing in the post-auricular and post-coronal patches) from north to south. Clines of increasing tarsus and wing lengths occur over the same area but no steps or breaks exist that permit effective separation of adjacent (and many distant) populations. Also the weak clines or locally mosaic variations in the amount of white in the outer rectrices, body weight, and culmen length are generally ineffective in separating most populations although the last effectively separates breeding birds of the Chiapas-Guatemalan area from those of the Sierra Madre Occidental. Populations meriting formal, subspecific recognition are *goldmani* (Nelson, 1897), resident of the Guatemalan highlands and adjacent Chiapas (Fig. 1, sample 42); *nigrifrons* (Brewster, 1889), breeding in the Sierra Madre Occidental of Chihuahua and Durango (Fig. 1, sample 41); and *auduboni* (Townsend, 1837), breeding from Baja California and the Southwest northward (Fig. 1, samples 18 through 40), intergrading with the preceding in the Chiricahua and Huachuca Mountains of southern Arizona. The name *memorabilis* (Oberholser, 1921) applied to the breeding birds of the Southern Rockies, etc., is not recognizable because of broad intergradation in wing length and plumage characters with northwestern populations. However, infra-subspecific segregation of long- and short-winged extremes of the interior and the Northwest Coast populations, respectively, may be useful and is provided for in the key.

KEY

This key is intended both as a summary of taxonomically useful geographic variation and as a synopsis of populations, named and otherwise, which can be reliably segregated on such bases. Segregates which are worthy of formal subspecific recognition are identified only by name, whereas infra-subspecific ones are identified by breeding range with names that have been applied to them in quotes. The intergrade populations which bridge *coronata* and *auduboni* and those which bridge *auduboni* (*"memorabilis"*) and *nigrifrons* are not included. Characters given here yield identifications which have a 95 per cent or better probability of accuracy.

1. Light brown to white post-ocular line present in winter and breeding plumages; throat light brown to white in all plumages; white in outer 2 to 3 pairs of rectrices in most females and first-year males and in outer 3 to 4 in most adult males. .... *coronata*
   a. Minimum wing lengths: females—73.5 mm, first-year males—75.5 mm, adult males—78.0mm .... breeding populations of Alaska, Yukon, MacKenzie Delta, northwestern British Columbia (*"hooveri"*).
   b. Maximum wing lengths: female—69.0 mm, first-year males—72.0 mm, adult males—74.0 mm; includes all males with solidly black breasts in breeding plumage .... breeding populations from MacKenzie and northeastern British Columbia eastward to the Atlantic Coast.

1. Post-ocular line absent in winter and breeding plumage; throat yellow in breeding plumage and yellowish (at least in malar region) in winter plumage, except in some first-year females and (rarely) males which have none; white in the outer 4 pairs of rectrices in most females and first-year males and in outer 5 in most adult males (if not wing exceeds 74.5 mm in females, 78.5 mm in first-year males, 80.5 mm in adult males). 2

2. Breeding-plumaged male gray above lightly streaked with black, breast streaked to solidly black and sides streaked with black; female grayish to light brown above, lightly streaked with blackish on upperparts, breast, and sides. Winter-plumaged adult male gray above streaked with black and variably washed with light brown or light rufous brown, breast spotted or mottled with black and washed with buff; first-year male similar but more extensively brown (less grayish) above and with blackish on breast as streaks; females similar to last but streaking paler and much more diffuse .... *auduboni*
   a. Maximum wing length: females—71.0 mm, first-year males—74.0 mm, adult males—77.0 mm .... breeding populations of costal areas of British Columbia, Washington, and Oregon.
   b. Minimum wing lengths: females—76.5 mm, first-year males—78.5 mm, adult males—81.0 mm .... breeding populations of the Rockies, Black Hills, Great Basin, Sierra Nevada, and southwestern United States (*"memorabilis"*).

2. Breeding-plumaged males more extensively black above and below; females darker above and with heavier streaking above and below. Winter-plumaged males more extensively gray or black above and more extensively black below; first-year males and females darker brown above and with heavier streaking above and below than *auduboni* 3

3. Breeding-plumaged males gray above with heavy black streaking, sides and front of head washed with blackish, breast, sides, and posterior abdomen solidly black, post-auricular and post-coronal patches grayish white; female sooty to moderately

dark brown above with moderate streaking on the crown. Winter-plumaged adult male extensively gray above with considerable black streaking and variable (but usually limited) wash of dark rufescent brown, below mottled or solidly black on the breast, sides, and posterior abdomen, washed with buff; first-year male similar but less grayish, more extensively brown above and black of underparts usually as spotting; female similar to last but not as dark brown above with lighter streaking and with blackish of underparts as streaks .... *nigrifrons*

3. Breeding-plumaged males solidly black above or with limited gray streaking or mottling, breast and sides solidly black but posterior abdomen white, post-auricular and post-coronal patches white; female browner less sooty above with heavier streaking on the occiput. Winter-plumaged adult male identical to breeding male, lacking browns or buff in plumage; first-year male grayer, less brownish above with more extensive streaking than *nigrifrons*; female is richer, less sooty above with heavier streaking on the occiput than *nigrifrons* .... *goldmani*

SUMMARY

Geographic variation in plumage and measurements is discussed in the *Dendroica coronata* (L.) complex, consisting of two semispecies *coronata* and *auduboni* Townsend, particularly with reference to features which bear on segregation of populations, either as formal subspecies or as "infra-subspecies." The latter are populations that have some distinctive character(s) by which individuals can be identified, but which lack sufficient separability to warrant formal recognition. In the *coronata* group only the nominate race is formally recognized, although breeding populations of northwestern North America ("*hooveri*" McGregor) are infra-subspecifically separable from more easterly ones on the basis of extremes in wing length, i.e., long versus short. In the *auduboni* group three subspecies are recognized: *auduboni*, *nigrifrons* Brewster, and *goldmani* Nelson. Within the first, infra-subspecific segregation of breeding populations in the coastal northwest from those of the interior ("*memorabilis*" Oberholser), is possible on the basis of extremes of wing length, i.e., short versus long. Because of the largely clinal or mosaic nature of mensural variation, the characterization of the four accepted subspecies in this complex is basically on plumage characters. Plumage characters also show clinal gradation but discontinuities or steps in the clines are such that formal naming of subspecies is justifiable. The provision for the identification of infra-subspecies is to allow study of dispersal and other features in populations which have identifiable extremes but which are not sufficiently separable to warrant formal, subspecific recognition.

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