THE RELATIONSHIPS AND EVOLUTION OF THE
DENDROICA CORONATA COMPLEX

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THE *Dendroica coronata* complex is generally considered as consisting of two distinct but closely related and essentially allopatric species, the Myrtle Warbler (*D. coronata*) and Audubon's Warbler (*D. auduboni*). The breeding range of *D. coronata* is the boreal forest of northern North America, and that of *D. auduboni* is the cordilleran forests of the western part of the continent. In Alberta, British Columbia, and perhaps southeastern Alaska, their ranges are in contact and the two forms interbreed. Although specimens were collected from the area of interbreeding as long ago as 1891 and hybridization between the two forms has been alleged since 1909 (Taylor, 1911), no complete study of the complex has previously been made, and only a few minor details have been published (Taverner, 1918; Cowan, 1955).

MATERIALS AND METHODS

The study of the interbreeding of *coronata* and *auduboni* was preceded by an investigation of plumage and mensural variation of the *D. coronata* complex outside the area of southeastern Alaska, British Columbia, and Alberta (Hubbard, 1967). That study involved 1,731 specimens (543 *D. coronata*, 1,072 *D. auduboni*, 35 *D. a. auduboni-D. a. nigrifrons*, and 81 *D. a. nigrifrons*) taken in the breeding season and 26 specimens of the resident *D. a. goldmani* of Chiapas and Guatemala. The breeding season is considered to be the period from 1 June (15 May in the Pacific Northwest and parts of northern North America) through the completion of the postnuptial molt. Also studied in that context were 500 juvenile specimens, including 219 *D. coronata*, 260 *D. a. auduboni*, 4 *D. a. auduboni-D. a. nigrifrons*, and 17 *D. a. nigrifrons*.

The study of interbreeding was based on 338 specimens of breeding adults and 63 juveniles taken in southeastern Alaska, British Columbia, and Alberta. I took 175 of the adult specimens along two transects through the Canadian Rockies (discussed later under Transects) and elsewhere in southeastern British Columbia and southwestern Alberta. Specimens were grouped into 15 regional samples (Figure 1) and separated into female, first-year male, and adult male categories. First-year males are usually distinguishable from adult males by their worn flight feathers and their brownish rather than blackish (or blackish edged with gray) remiges, rectrices, and especially
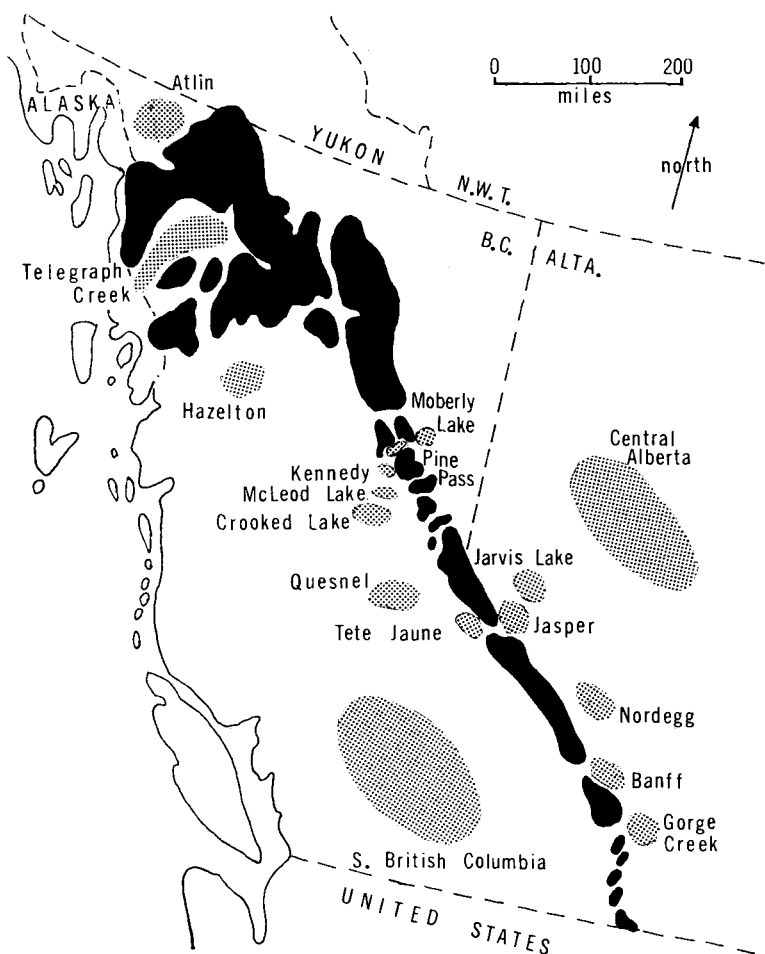
Figure 1. Regional specimen samples used in the analysis of interbreeding between *Dendroica coronata* and *D. auduboni*. The black area is unforested habitat.

primary coverts and alula. Winglength was treated separately in all three categories as small and consistent differences are evident between them, although only female and adult males differ significantly at the 0.05 level. In plumage characters the age classes of males were combined except for the analysis of tail pattern, which is the only respect in which the two differ. Aging of males and plumage analyses were carried out under direct natural lighting or under a Tensor high-intensity lamp with a 60-watt bulb.

The analysis of interbreeding between *coronata* and *auduboni* is based primarily on six plumage characters of breeding-plumaged males, wing pattern, tail pattern, throat color, auricular color, and the presence or absence of a supraloral spot and postocular line. The characters of this plumage complex were analyzed through the so-called

"hybrid" index approach (discussed later under Character Indices). Samples from the area of interbreeding were compared both among themselves and with samples from "pure" populations of *coronata* and *auduboni*. The latter are represented by aggregates that total a minimum of 200 and 385 specimens, respectively.

Other plumage differences between *coronata* and *auduboni* were found to be highly subjective, subtle, or inconsistent (Hubbard, 1967) and were discarded for the purpose of this study. Males of *coronata* average darker gray with broader blackish streaking on the dorsal surface than *auduboni* males and tend to have a larger throat patch and a smaller breast patch. Juveniles and females also show average or greater than average differences, but neither category was represented by enough specimens to provide a sound basis for comparison. Juvenile *coronata* tend to be darker brown than *auduboni* with heavier blackish streaking both dorsally and ventrally. Female *coronata* are darker brown above than *auduboni* and in the Alberta area they tend to have grayish rather than brownish crowns. *Coronata* females are also more heavily streaked than female *auduboni* and they tend to show the facial pattern of male *coronata*, although more subtly, and they, like the respective males, have white rather than yellow throats.

Mensural analysis of interbreeding is confined to a comparison of winglength (chord) among samples. Body weight is of limited value because so few weights are available from *coronata* populations. Culmen and tarsus lengths were found to offer no sound basis for separating *coronata* and *auduboni* and are also omitted. Standard statistical tests and methods used in this study are given in Steel and Torrie (1960); significance is at the 0.05 level of probability.

I spent the period 29 May to 28 June 1965 in Alberta and British Columbia collecting specimens and other data in the areas of suspected interbreeding between *coronata* and *auduboni*. My itinerary for this period is as follows (Figure 1): 29 May–2 June—Gorge Creek, the University of Alberta Biological Station, 20.5 miles west of Turner Valley in the foothills of the Rockies, Alberta; 3–4 June— Cottonwood Creek campground, just east of Jasper, Alberta; 4–7 June—Jarvis Lake, just north of Hinton, Alberta; 7–8 June—Cottonwood Creek campground; 8–9 June— near Tete Jaune Cache, British Columbia; 10–12 June—near Quesnel, British Columbia; 12–13 June—Crooked Lake campground, north of Prince George, British Columbia; 13–16 June—McLeod Lake area, Whisker Point campground, British Columbia; 16–19 June—Pine Pass area, from Kennedy to Mount Le Moray, British Columbia; 19–20 June—between Moberly Lake and Chetwynd (Little Prairie), British Columbia; 21 June—21 miles south of Grand Prairie, Alberta; 22–25 June— Edmonton, Alberta; 24 June—Nestow, Alberta; 25–26 June—Nordegg area, west of Red Deer, Alberta; 26–28 June—Gorge Creek, Alberta.

Transects in the Area of Interbreeding

With the general knowledge that *coronata* breeds to the east and north of the Canadian Rockies and *auduboni* breeds to the south and west, it was decided to set up transects that spanned these mountains and connected the provinces of Alberta and British Columbia. Where such transects could be established depended on the accessibility and nature of the populations on either side of this range. After sampling populations in the area of Calgary, Alberta, near the Trans-Canada Highway, I decided to concentrate on the two more northerly roads across the Rockies: Pro-

Moberly
Lake

Dawson Creek

Chetwynd

Grand
Prairie

0   25   75
MILES

Lesser
Slave Lake

Kennedy

McLeod Lake

ALBERTA

ROUTE
97

Prince
George

N

ROUTE 16

Jarvis
Lake

Hinton

Edmonton

JASPER

Tete
Jaune

Jasper

PARK

Nordegg
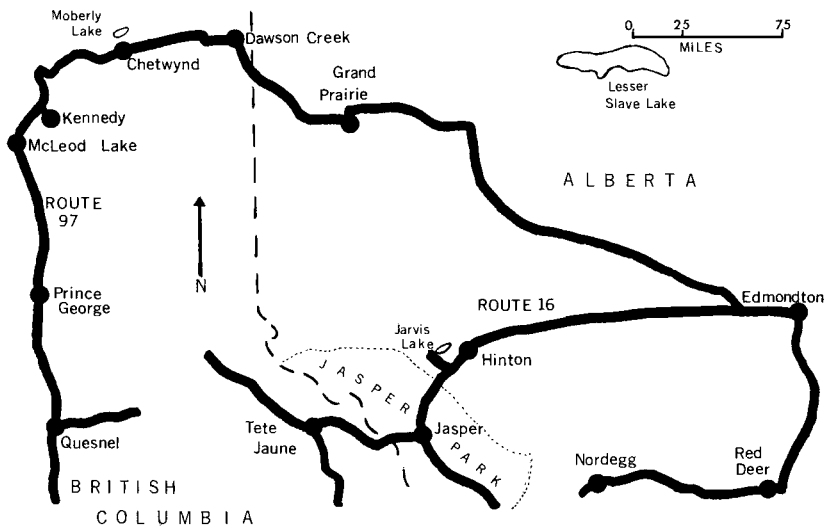
Red
Deer

Quesnel

BRITISH

COLUMBIA

Figure 2. Area of field work in east-central British Columbia and west-central Alberta. The Jasper transect is along Route 16 between Edmonton, Alberta, and Quesnel, British Columbia. The Pine Pass transect has the same end points but is along Route 97.

vincial Highway 16 which crosses the mountains at Yellowhead Pass west of Jasper, Alberta, and Provincial Highway 97 which crosses them at Pine Pass, northwest of Prince George, British Columbia (Figure 2).

Jasper transect.—This transect follows Provincial Highway 16 from the region of Edmonton, Alberta, through the Rockies into British Columbia and then it skips across to Quesnel in the central part of the province. The actual crossing of the Canadian Rockies is along the Athabaska and Miette river valleys in Alberta, over Yellowhead Pass (elevation 3,729 feet) into British Columbia, and thence along the Fraser River valley to the vicinity of Tete Jaune Cache. This stretch is a corridor of coniferous forest, approximately 75 miles long and generally 5 to 7 miles wide, that penetrates mountains rising 10,000 to 13,000 feet above sea level. Northeastward lies forested central Canada, while westward the corridor broadens and divides around other mountain masses to connect with the forested plateau of interior British Columbia.

As no collecting was permitted along this transect in Jasper National Park on the eastern slope of the Rockies, or to the west in Mt. Robson Provincial Park, samples were taken just east of the mountains at Jarvis Lake (elevation 4,200 feet), which is just north of Hinton, Alberta, and westward near Tete Jaune Cache (elevation 2,400 feet) in British Colum-

bia. In addition, specimens were collected at the end points of the transects near Quesnel (elevation 2,500 feet) and in the Edmonton area (elevation 2,185 feet).

Pine Pass transect.—Topographically this transect resembles the Jasper one, except the passage through the Rockies is shorter and more constricted and the mountains are not so high. The transect is along Provincial Highway 97 (the John Hart Highway) between Prince George and Dawson Creek, both in British Columbia. The passage through the Rockies from the south is along the Misinchinka River valley, over Pine Pass (elevation 2,850 feet) and then along the Pine River. This constitutes a corridor of coniferous forest approximately 50 miles long and 2 to 4 miles wide. South along this transect, collection stations were established at Kennedy (just at the edge of the Rockies), McLeod Lake, and Crooked Lake (all at 2,400 feet above sea level), and Quesnel at the southern end. The latter served as the anchor point for this as well as the Jasper transect. East of the Rockies collecting was done in the Chetwynd (Little Prairie)-Moberly Lake area (elevation 2,400 feet) and near Edmonton. The latter, called the "Central Alberta" sample, served as the eastern anchor point for both transects. Additional collecting was done elsewhere in the area encompassed by the transects, and along the eastern slopes of the Rockies west of Red Deer (Nordegg sample) and southwest of Calgary, Alberta (Gorge Creek sample).

VEGETATION IN THE AREA OF INTERBREEDING

The following résumé is based on my own observations supplemented freely with the work of Munro and Cowan (1947), Cowan (1955), Salt and Wilk (1958), and Canada Department of Forestry (1963).

The area in which *D. coronata* and *D. auduboni* interbreed is the meeting and mingling place of the northern, or boreal forests, and the western, or cordilleran forest. In climax form both these forests are dominated by conifers, but of different species and sometimes of different genera. In the boreal forest of Alberta and British Columbia the main climax species are white spruce (*Picea glauca*), black spruce (*P. mariana*), and, mainly east of Alberta, balsam fir (*Abies balsamea*). Common subclimax species are paper birch (*Betula papyrifera*), alder (*Alnus tenuifolia*), jack pine (*Pinus banksiana*), lodgepole pine (*P. contorta*), mainly near the Rockies, and aspen (*Populus tremuloides*). Aspen is especially common in western Alberta and northeastern British Columbia, either in large stands or interspersed by prairie. There coniferous forest is spotty in distribution, although it is extensive in the foothills and it forms a fairly broad corridor from the Rockies to Lesser Slave Lake and beyond.

In the cordilleran forest of the interior of British Columbia, spruces and Douglas fir (*Pseudotsuga menziesii*) are the dominant climax species and lodgepole pine and aspen are common subclimax forms. The spruces are two types: a western form of the white spruce (*P. g. albertiana*) and the Engelmann spruce (*P. engelmannii*). The latter usually grows at higher elevations, but it both overlaps and hybridizes with white spruce, and the two are often difficult to distinguish. West of the coast range is a dense, mesic forest dominated by Sitka spruce (*P. sitchensis*), Douglas fir, and other species, but this habitat appears to be unsuitable for warblers of this complex. In southern British Columbia are open forests of ponderosa pine (*Pinus ponderosa*) inhabited by *D. auduboni*. Although a great deal of forest has been cleared in British Columbia, it is still abundant and virtually ubiquitous below timberline.

In the Canadian Rocky Mountains, boreal and cordilleran forests are intermixed, but again Engelmann spruce and such western species as alpine fir (*Abies lasiocarpa*) and pines (*Pinus albicaulis, P. monticola*) are found mainly at higher elevations. Perhaps the commonest and most important habitats for this complex of warblers are the extensive coniferous forests of spruce, Douglas fir, and lodgepole pine. Timberline is perhaps 8,000 feet in the Jasper area and 5,000 feet in the Pine Pass areas.

NOTES ON *D. coronata* COMPLEX IN AREA OF INTERBREEDING

Warblers of this complex seem to require coniferous habitats for breeding, although they are found in many types and in adjacent or mixed broadleaf trees as well. I found them equally common in jackpine woodland, open lodgepole pine forests, and in denser spruce-Douglas fir forests. Throughout the study area they were one of the commonest birds, and as many as three or four singing males could be heard from one spot. Perhaps the only exception to this was in the Pine Pass area of British Columbia, where they seemed to be uncommon. That area features dense undergrowth, tall forests, and rough terrain, and these factors plus a seasonal waning of territorial song may have created an erroneous impression of scarcity.

Although warblers of this complex generally sang and foraged high in the trees, they could be lured within collecting range by squeaking. Males responded most readily, and females, which were seldom seen except at dawn and dusk, were generally driven off by the males if they did respond.

Although I was not able to record vocalizations with sound equipment, I took notes on them throughout the study area. As many others have noted, the call notes of the two forms differ enough in quality to be readily distinguishable. The note of *coronata* is a low "chuck," that of *auduboni* a drier "check." Most of the birds I heard in the area of interbreeding

TABLE 1

METHOD OF SCORING CHARACTERS USED IN THE ANALYSIS OF INTERBREEDING BETWEEN
D. CORONATA AND *D. AUDUBONI*

Character	Typical coronata (score 0)	coronata-auduboni (score 1)	Typical auduboni (score 2)
Throat color	White	Mixed yellow and white	Yellow
Auricular color	Blackish	Mixed gray and blackish	Gray
Supraloral spot	Conspicuous	Faint	Absent
Postocular line	Conspicuous	Faint or broken	Absent
Wing pattern	2 wing bars (white)	Intermediate	Single wing patch (white)
Tail pattern (value)[1]			
adult male	3.49 or less	3.5 to 4.49	4.5 or more
first-year male and female	3.0 or less	3.01 to 3.49	3.5 or more

[1] Values for tail pattern explained in text.

sounded like one form or the other, but some were typical of neither. I generally noted songs as "languid" and "colorless" in quality with a change of pitch and pattern toward the middle and often a quickening of pace. A typical song might be transcribed as "tur, tur, tur, tee, tee, tee, tee." Although the pattern varied, warbler songs throughout the study area sounded much the same to me. In Michigan *coronata* impressed me as having a higher pitched, thinner, and more stereotyped song than that of the *auduboni* I am familiar with in Arizona and New Mexico. This area of study offers promise for future investigation, but any differences that may exist in vocalizations are apparently insufficient to prevent interbreeding.

CHARACTER INDICES

The character index is adapted from a method developed by Anderson (1949) and used in many other studies under the designation of "hybrid index." In this approach one selects a series of characters in which two forms differ and intergrade and assigns each character at least three numerical values, one for each "pure" expression and one (or often more) for the intermediate state(s). For example *coronata* and *auduboni* differ and intergrade in throat color, which is white or yellow respectively, or a combination of white and yellow in intergrades. In this study the numerical values for throat color are zero for white, 1 for intermediate, and 2 for yellow. In the same way, the remaining five plumage characters are scored zero for the "typical" state of *coronata*, 1 for intermediate, and 2 for "typical" *auduboni* (Table 1). Thus, a "pure" specimen of *coronata* should theo-

TABLE 2

FREQUENCY OF ATYPICALLY[1] PLUMAGED BREEDING MALE *CORONATA* OUTSIDE
CORONATA-AUDUBONI INTERGRADE AREA

Population	Sample size	Per cent atypical[1] specimens				
		Post-ocular	Auric-ular	Throat color	Wing pattern	Supra-loral
Alaska	37	2.7	0	5.7	16.2	0
Northwest Territories	10	10.0	0	10.0	40.0	0
Manitoba, Saskatchewan	16	0	12.5	12.5	13.3	0
James Bay	24	0	0	4.2	20.8	0
Lake Superior	21	0	0	0	15.8	4.8
Michigan	20	5.9	0	0	20.0	0
Southern Ontario	15	6.7	0	6.7	6.7	0
Quebec	20	0	0	5.0	15.0	0
Northeast U.S.A., Nova Scotia, New Brunswick	21	0	4.8	9.6	30.0	0
Newfoundland, Labrador	16	0	0	0	12.5	0
overall coronata	200	2.0	1.5	5.0	18.0	0.5
(chi-square		5.46	19.0	6.23	5.99	7.91)
(probability, 9 degrees		<0.9	0.025	<0.750	<0.750	<0.750)
(of freedom		>0.750		>0.500	>0.500	>0.500)

[1] Atypical specimens are those which score 1 or 2 in a character.

retically score zero in each character and a "pure" specimen of *auduboni*
should score 2. Actually even in populations far removed from the area
of interbreeding, some specimens do not conform to this theoretical value.
Such variability is neither unexpected or unnatural, and so long as it is

TABLE 3

FREQUENCY OF ATYPICALLY[1] PLUMAGED BREEDING MALE *AUDUBONI* OUTSIDE
CORONATA-AUDUBONI INTERGRADE AREA

Population	Sample size	Per cent atypical[1] specimens			
		Post-ocular	Auric-ular	Throat color	Wing pattern
Northwest coast	26	4.0	7.1	0	11.5
Cascades	25	0	4.0	4.0	0
Eastern Oregon	46	0	11.1	4.6	0
Northern Rockies	24	0	13.4	0	4.0
Northern California	18	0	5.6	0	0
Great Basin	54	3.7	5.6	1.9	1.9
Eastern Utah	32	0	0	3.1	0
Black Hills	33	0	3.0	0	5.9
Southern Rockies	22	0	0	0	0
Sierra Nevada	34	0	5.9	3.0	3.6
Southern California	35	0	0	2.8	0
Mogollon Plateau	40	0	2.5	0	0
overall auduboni	389	0.8	4.8	1.8	2.1
(chi-square		1.22	11.78	6.14	21.29)
(probability,		>0.995	<0.5	<0.9	<0.05)
(11 degrees of freedom			>0.25	>0.750	>0.025)

[1] Atypical specimens are those which score 0 or 1 in a character.

TABLE 4

FREQUENCY OF LIGHT SUPRALORAL SPOT IN BREEDING MALES OF THE *AUDUBONI*
GROUP OUTSIDE INTERGRADE AREA OF *CORONATA-AUDUBONI*

Form and population	Sample size	Per cent of sample
auduboni		
Southern British Columbia	13	38.5
Northern Cascades	26	34.6
Northwest coast	26	30.8
Northern California	18	38.9
Northern Great Basin	46	33.0
Northern Rockies	24	20.8
Black Hills	33	27.3
Southern Rockies	21	23.4
Southern Great Basin	54	33.3
Sierra Nevada	33	30.3
Southern California	35	22.9
Mogollon Plateau	45	24.4
Southeastern Arizona	43	25.6
overall auduboni	417	29.0
(chi-square 3.49, 12 degrees of freedom, *P* greater than 0.995)		
nigrifrons	27	22.2
goldmani	13	0

taken fully into account a valid basis remains for this type of analysis. In essence this means the avoidance of a stereotypic concept of "pure" populations. This is done through a detailed study and documentation of variation and by the computation and analysis of character indices not only from populations in the area of interbreeding, but from those outside it as well. Variation in character states in the extralimital populations is documented and discussed later under *Intergradation and possible introgression in individual characters* and is summarized in Tables 2 through 8.

In a given sample one can use the index for a character separately or combine it with the other indices and compute a single mean index for the entire character complex. By treating characters separately one can demonstrate the behavior of each as it intergrades along a transect. By combining characters one demonstrates intergradation in the entire complex of characters. Each method of treatment provides information, and each has been used in this study as a means of better understanding intergradation.

Throat color.—As is well-known, *coronata* typically has a white throat and *auduboni* a yellow one. In *auduboni* the yellow varies somewhat in intensity, and frequently it is paler, sometimes whitish, on the chin. In *coronata* the white of the throat generally borders the posterior portion of the auriculars, giving the throat patch a somewhat greater width posteriorly than in *auduboni*. This difference is not constant, as many *auduboni* have this region streaked or entirely whitish rather than gray. Intermediate

TABLE 5

FREQUENCY OF ATYPICAL[1] TAIL PATTERN IN BREEDING *CORONATA* OUTSIDE
CORONATA-AUDUBONI INTERGRADE AREA

Population	Adult male		First-year male		Female	
	Sample size	Per cent atypical	Sample size	Per cent atypical	Sample size	Per cent atypical
Alaska	14	21.4	19	19.0	15	13.3
MacKenzie Delta	3	33.3	9	0	3	33.3
Southern Yukon	10	10.0	5	40.0	4	0
MacKenzie	8	62.5	5	40.0	7	0
Southern Manitoba	2	0	8	12.5	5	0
Western Hudson Bay	1	0	5	0	4	0
Western James Bay	7	0	9	0	10	0
Lake Superior	8	0	15	0	16	0
Quebec	6	16.7	16	0	20	0
Southern Ontario, Michigan	21	4.8	27	0	7	0
Southern Maritimes, Northeastern U.S.	20	10.0	33	9.1	24	0
Northern Maritimes	20	0	21	0	24	0
overall coronata	120	11.0	172	7.0	139	2.2
Chi-square	26.18		26.69		20.30	
Probability	<0.010		<0.010		<0.05	
(11 degrees of freedom)	>0.005		>0.005		>0.025	

[1] Atypical specimens are those which score 1 or 2 in tail pattern.

expressions in throat color are several, ranging from a few pale yellow feathers in an otherwise white throat to an intensely yellow throat bordered by white.

Auricular color.—In *coronata* the auricular region is generally black or blackish. In *auduboni* this area is gray, although it may be blackish anteriorly. In all *coronata* and many *auduboni* the loral area and the area under the eye are also blackish and both forms have the eyelids whitish. Auriculars that are intermediate may be grayish streaked with black or blackish streaked with gray. Light dusky auriculars occur with some regularity in *auduboni* (Table 3) but very rarely in *coronata* (Table 2).

Supraloral spot.—*D. coronata* generally has a conspicuous white supraloral spot. This conspicuous spot is absent in *auduboni*, but 25 to 35 per cent of the males in all *auduboni* populations have at least an indication of a whitish, light grayish, or yellowish supraloral spot (Table 4), which here is defined as an intermediate condition.

Postocular line.—In *coronata* usually a whitish postocular line extends at least half the length of the auricular region, but this is lacking in *auduboni*. The intermediate condition is a faint or broken whitish postocular line.

Wing pattern.—In both *coronata* and *auduboni* usually four to five greater and middle secondary coverts (numbers 4 or 5 through 9) are replaced in the spring molt, thus producing characteristic wing patterns in

TABLE 6

FREQUENCY OF ATYPICAL[1] TAIL PATTERN IN BREEDING *AUDUBONI* OUTSIDE *CORONATA-AUDUBONI* INTERGRADE AREA

Population	Adult male		First-year male		Female	
	Sample size	Per cent atypical	Sample size	Per cent atypical	Sample size	Per cent atypical
Southern British Columbia	6	16.7	10	10.0	15	6.7
Northwest coast	11	9.1	19	10.6	19	15.9
Cascades	11	0	17	5.9	11	18.2
Northern Idaho	2	0	8	0	10	0
Cypress Hills	6	0	3	0	8	0
Northern Rockies	8	12.5	16	0	28	3.8
Eastern Oregon	35	8.6	40	2.5	25	0
Northern California	15	0	17	0	18	5.6
Sierra Nevada	37	2.7	40	10.0	37	2.7
Southern California	20	15.0	19	5.3	21	9.5
Great Basin	23	8.7	36	2.8	32	6.3
Black Hills	18	0	6	0	10	10.0
Eastern Utah	7	0	10	20.0	10	10.0
Southern Rockies	25	4.0	18	11.1	14	7.2
Mogollon Plateau	25	4.0	19	0	17	0
Santa Catalina Mts.	15	6.7	26	0	20	20.0
Chiricahua Mts.	11	9.1	10	0	10	10.0
overall auduboni	275	5.8	314	4.8	305	6.9
Chi-square	19.47		15.78		15.16	
Probability	<0.25		<0.5		<0.75	
(16 degrees of freedom)	>0.10		>0.25		>0.50	

[1] Atypical specimens are those which score 0 or 1 in tail pattern.

the two forms. In *coronata* the tips of both sets of coverts are white, while the intervening distal edges of the greater coverts are usually grayish. This forms two white bars on the wing. In *auduboni* the tips of the coverts are also white, but the distal edges of the greater coverts are edged with white rather than gray, giving the effect of a white patch on the wing. The intermediate conditions involve the edges of the greater coverts being grayish-white or a mixture of the two. This character is much more variable in *coronata* (Table 2) than in *auduboni* (Table 3).

Tail pattern.—All members of the *D. coronata* complex have white markings on the inner, subdistal margins of the outer two to six pairs of rectrices. I have arbitrarily scored the amount of white on a tail feather as: ⅛ (a tiny spot or marginal edging), ¼ (small spot or marginal blotch), ½ (moderate spot or marginal blotch), ¾ (large marginal spot or blotch), and 1 (very large marginal blotch). This system reveals large areas of joint nonoverlap between *coronata* and *auduboni* when age and sex are taken into account. Thus in adult males 91.5 per cent of *coronata* have four or fewer rectrices (average 3.2) marked with white compared to 98.5 per cent of *auduboni* (average 4.9) having five rectrices so marked. First-year males and females may be grouped together, and about 95 per cent of

coronata have three or fewer (average 2.6 to 2.7) white-marked pairs of rectrices compared to about 95 per cent of *auduboni* with four or more (average 4.4) marked with white. On the basis of these data the categories and values of typical *coronata*, typical *auduboni*, and intermediates were derived (Table 1; also Tables 5 and 6).

Correlation of plumage characters.—Short (1965), in considering possible correlation between characters used to study hybridization, questions the validity of treating characters as separate entities if they are constantly associated. Actually for the purpose of detecting hybrids it does not matter whether or not characters are correlated so long as they are reliable and have intermediate states. Whether or not characters are correlated becomes significant, however, when trying to determine the degree of hybridity in individuals or populations. In spite of the highly subjective nature of such determinations and the general lack of knowledge of the genetics of natural hybridization in birds, some evaluation of the correlation of characters is both desirable and possible.

Given two characters that have several states each, one can predict, on the basis of random assortment, with what frequency any pairing of the states of these characters will occur. This is done simply by determining the relative frequencies of the states of each character in the population, and then multiplying the frequencies of the appropriate character states by each other. For example, if character A has two states and each occurs in equal numbers, and character B has similar parameters, the frequency of any given pairing of character states is 50 per cent times 50 per cent, or 25 per cent, if assortment is random. On the other hand, if characters are absolutely correlated, then certain pairings will appear with 100 per cent frequency and others will be entirely absent. This admittedly overly-simplified model affords some avenue of approach to the problem of correlation of characters.

One way of determining the degree of association between characters is to calculate the frequency with which two characters are scored the same. In this study this means determining the frequency with which the combinations 0-0, 1-1, and 2-2 occur. In theory if two characters are absolutely correlated, only these combinations will appear. In randomly assorting pairs of characters such combinations will appear at some frequency less than 100 per cent. This type of analysis was carried out with 117 phenotypically introgressed specimens from the hybrid zone. All characters were used except the supraloral spot, which shows a high degree of overlap between *coronata* and *auduboni*.

In comparing the 10 possible combinations of characters, it was found that the observed frequency of association was invariably closer to the

TABLE 7

SHIFTS IN THE FREQUENCY OF MALE PHENOTYPES ALONG TRANSECTS THROUGH THE AREA OF *CORONATA-AUDUBONI* INTERGRADATION

Transect and population		Per cent of phenotypes		
	Sample size	Pure *coronata*	*coronata-auduboni*	Pure *auduboni*
Pine Pass transect				
Central Alberta	19	63.2	36.8	0
Moberly Lake	11	18.2	81.8	0
Pine Pass	12	8.3	91.7	0
Kennedy	15	0	86.7	13.3
McLeod Lake	13	0	84.6	15.4
Crooked Lake	12	0	66.7	33.3
Quesnel	20	0	65.0	35.0
Jasper transect				
Central Alberta	19	63.2	36.8	0
Jarvis Lake	25	20.0	80.0	0
Jasper Park	16	0	100.0	0
Tete Jaune	17	0	82.4	17.6
Quesnel	20	0	65.0	35.0

values predicted on the basis of random assortment than those based on nonrandom assortment. In most cases the observed values were somewhat higher than the predicted random values, and in five cases these ranged from a third to a half higher than expected. This suggests some tendency toward association (perhaps due to linkage or pleiotropy), but the degree of deviation is far short of an indication of strong correlations between characters. Thus separate treatment of characters is justified.

RESULTS

The analysis of populations along both transects clearly demonstrates intergradation between *D. coronata* and *D. auduboni* in both plumage characters and in winglength. The pattern of intergradation of plumage characters is much the same in both transects: the populations in the interconnecting valleys and passes of the Rockies are highly hybrid while those of either side are much less so. Thus the cline of intergradation is steep, although still apparent at the end points of the transects, up to 300 air miles apart.

Jasper transect.—Along this transect (Figures 3, 4) plumage intergradation is steepest in the essentially intermediate population of the Jasper Park region (combined score 1.00). All of the specimens, including females, show some evidence of introgression (Table 7), and many cannot be called closer to one form or the other. Eastward in the sample from Jarvis Lake, the overall degree of hybridity in the population drops considerably (combined score 0.36) and most of the specimens are nearer *coronata* (Table 3). West of Jasper in British Columbia a rather sharp
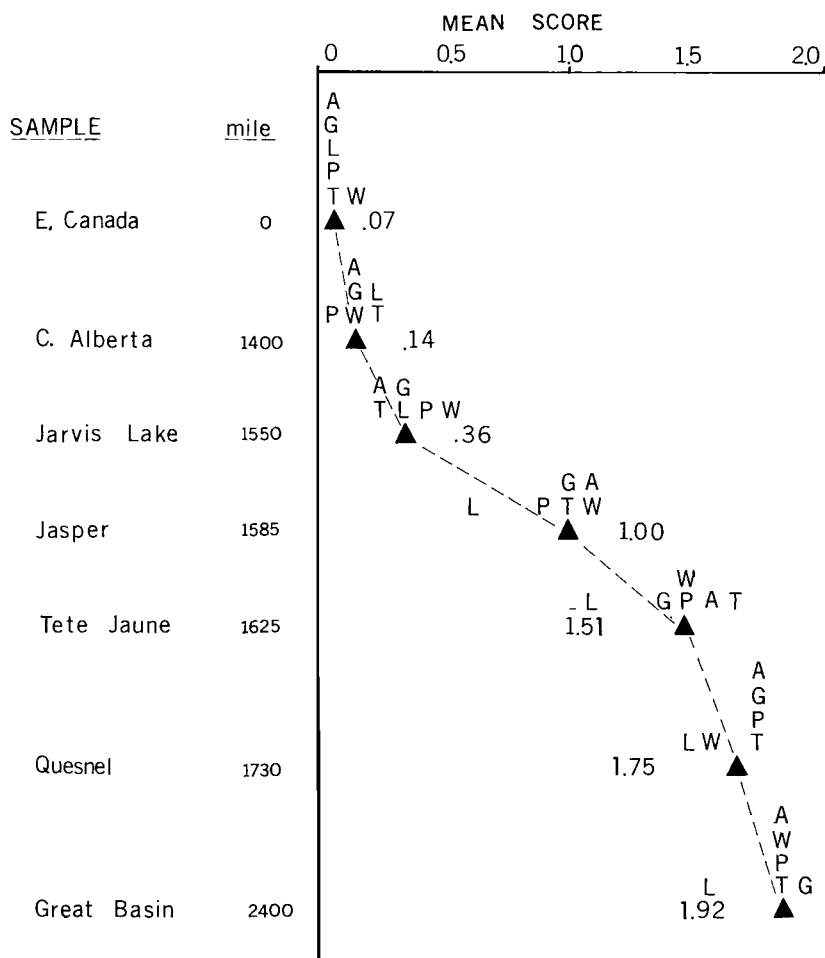
MEAN   SCORE

		MEAN SCORE			

```
              0        0.5        1.0        1.5        2.0
SAMPLE     mile
                      A
                      G
                      L
                      P
                      T W
E. Canada    0        ▲  .07
                       \ A
                        \G L
                      P W T
C. Alberta   1400     ▲    .14
                        A G
                        T\L P W
Jarvis Lake  1550      ▲    .36
                                 G A
                             L  P T W
Jasper       1585               ▲   1.00
                                            W
                              _ L      \G P A T
Tete Jaune   1625            1.51      ▲
                                                 A
                                                 G
                                                 P
                                         L W \   T
Quesnel      1730               1.75       ▲
                                                    A
                                                    W
                                                    P
                                          L      \T G
Great Basin  2400              1.92       ▲
```

Figure 3. The intergradation of male plumage characters along the Jasper transect. Key: A, auricular color; G, throat color; L, supraloral spot; P, postocular line; T, tail pattern; W, wing pattern. The mean index for all six characters is given for each sample (number and triangle).

drop in hybridity is seen in the sample from Tete Jaune Cache (combined score 1.51), although not quite to the degree in the equivalent population east of Jasper (i.e. Jarvis Lake). The sample from Quesnel shows a further decrease in hybridity (combined score 1.75), but most specimens are still not "pure" *auduboni* (Table 3).

Except for that of adult males, the winglengths of samples along this transect show gradual intergradation (Figure 4). The winglength of adult

males from central Alberta and the Jarvis Lake area remains significantly shorter (at the 0.05 level) than those of males from farther west. This may be due in part to small sample size. Populational variation in winglength might be expected to be high in a hybrid situation, but such is not the case in either transect (Figure 4). Perhaps the intergradation of this character is due as much to common selective pressures as to hybridization.

Pine Pass transect.—In this transect (Figures 4, 5) the center of intergradation is in the 50-mile stretch along the Hart Highway from the Kennedy turnoff to Mount Le Moray, in short the Pine Pass area (combined score 0.77). Most specimens from this sample are introgressed (Table 7), although the population is slightly closer to *coronata*. To the east at Moberly Lake a marked shift toward *coronata* occurs, but intergradation is still evident (combined score 0.34). Southwestward the samples at Kennedy and McLeod Lake show a parallel drop in hybridity and are closer to *auduboni* (both score 1.56). Finally the Crooked Lake sample has a somewhat higher percentage of "pure" *auduboni* (Table 3), but it too is hybrid in nature (combined score 1.65). Gradual intergradation in winglength is evident along the transect (Figure 4).

Intergradation elsewhere in the study area.—Three samples (Table 8) from the area south of Jasper also show the effects of interbreeding and intergradation. A sample of ten males from Banff National Park area has a combined score of 1.57, which indicates a high degree of hybridity but a closer resemblance to *auduboni*. Banff is about 100 miles south of of the Jasper area and also on the eastern slope of the Canadian Rockies. A sample of 20 males from the Gorge Creek area, in the foothills southwest of Calgary, has a combined score of 1.54, which is very similar to that of the Banff area. Finally a sample of nine males from Nordegg, in the foothills northwest of Calgary and west of Red Deer, has a combined score of 0.44, which shows a marked shift toward *coronata*. These three samples show that a transition occurs from *coronata* to *auduboni* in the area between Nordegg and the Banff-Gorge Creek area, within a maximum distance of approximately 70 miles.

The few specimens from south of Gorge Creek are typical *auduboni* except for an apparently "pure" adult male *coronata* taken 5 June 1965 at Waterton Park, Alberta. Although this bird had enlarged testes, it may have been a late northward migrant. Birds such as this may occasionally breed outside their normal range and thus provide an additional source of gene exchange.

These two forms doubtlessly intergrade elsewhere. Particularly suggestive of this are populations in northwestern British Columbia and adjacent southeastern Alaska (Table 8). In a sample of nine *auduboni*
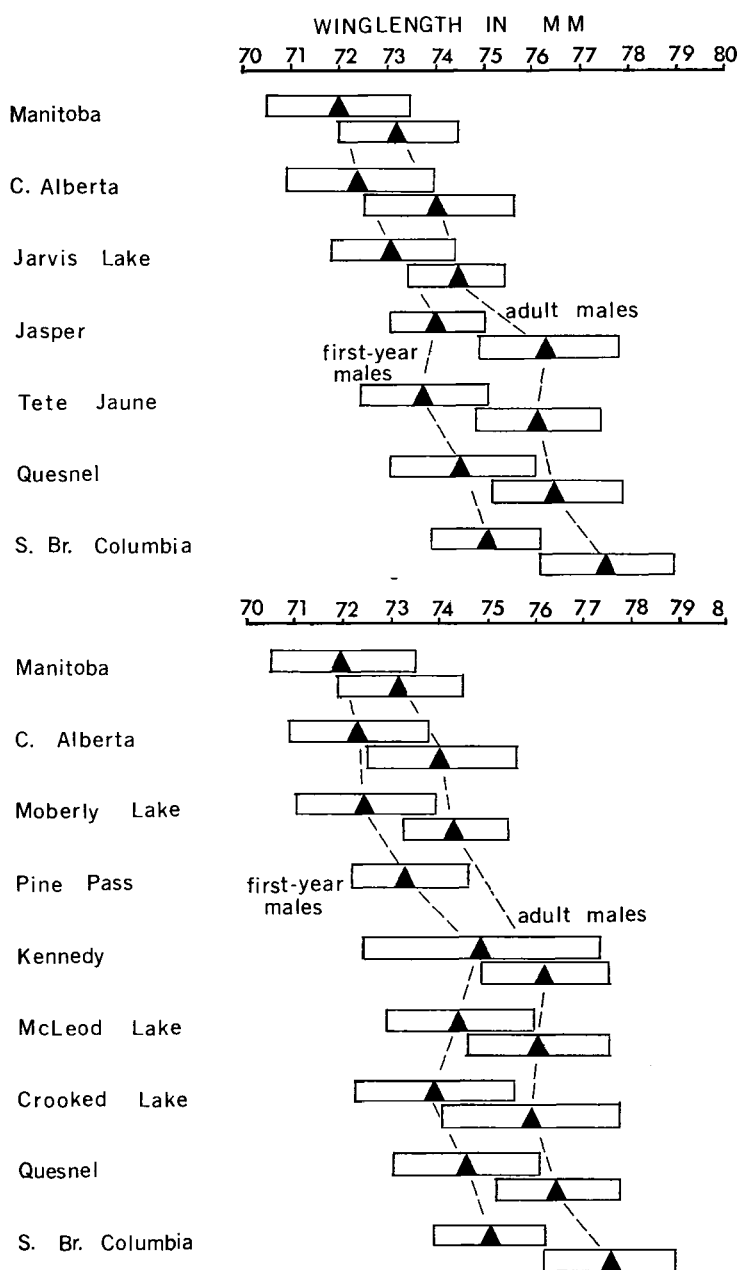
WINGLENGTH IN   M M

Figure 4. The intergradation in male winglengths along the Jasper and Pine Pass transects. The triangles indicate sample mean; the open rectangles indicate $1 \pm$ SD.
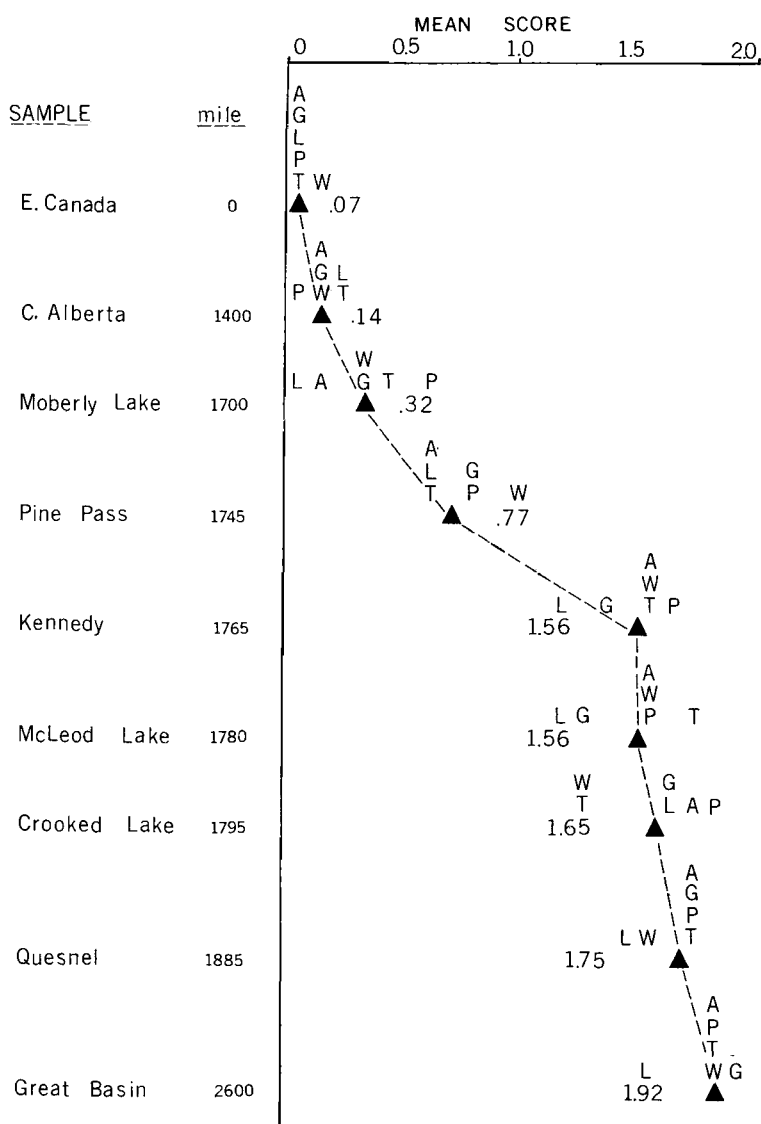
Figure 5. The intergradation of male plumage characters along the Pine Pass transect. Key: A, auricular color; G, throat color; L, supraloral spot; P, post-ocular line; T, tail pattern; W, wing pattern. The mean index for all six characters is given for each sample (number and triangle).

TABLE 8

CHARACTER INDICES[1] OF SAMPLES OF PURE *CORONATA*, PURE *AUDUBONI*, AND
CORONATA-AUDUBONI INTERGRADES

Form and population	Sample size	Auricular	Throat color	Wing pattern	Supraloral	Postocular	Tail pattern	Overall
coronata								
E. North America	75	0.01	0.04	0.19	0.08	0.05	0.04	0.07
Great Lakes	64	0.00	0.03	0.17	0.10	0.08	0.01	0.06
Central Canada	27	0.10	0.11	0.18	0.04	0.11	0.19	0.12
Alaska	37	0.00	0.05	0.19	0.00	0.03	0.24	0.08
auduboni								
Cypress Hills	10	1.70	2.00	2.00	1.70	1.80	1.90	1.85
S. British Columbia	15	1.90	2.00	1.93	1.62	1.93	1.87	1.87
Northern Idaho	10	1.90	2.00	1.90	1.60	1.80	2.00	1.87
Northwest coast	24	1.91	2.00	1.95	1.67	2.00	1.86	1.90
Cascades	24	1.92	2.00	1.96	1.62	2.00	1.82	1.89
Great Basin	54	1.98	2.00	1.98	1.69	1.94	1.96	1.92
coronata-auduboni								
Atlin	21	0.24	0.10	0.15	0.10	0.15	0.34	0.18
Telegraph Creek	14	0.33	0.08	0.42	0.00	0.18	0.43	0.24
Central Alberta	19	0.16	0.11	0.11	0.26	0.00	0.21	0.14
Moberly Lake	11	0.18	0.36	0.36	0.00	0.64	0.40	0.32
Jarvis Lake	25	0.24	0.32	0.56	0.36	0.45	0.21	0.36
Nordegg	9	0.44	0.89	0.22	0.22	0.33	0.47	0.43
Pine Pass	13	0.66	0.83	1.00	0.67	0.83	0.62	0.77
Jasper Park	17	1.16	1.05	1.11	0.68	0.95	1.04	1.00
Tete Jaune	17	1.65	1.41	1.53	1.18	1.53	1.77	1.51
Kennedy	14	1.60	1.47	1.60	1.29	1.73	1.69	1.56
McLeod Lake	13	1.62	1.38	1.62	1.23	1.62	1.87	1.56
Crooked Lake	12	1.83	1.75	1.33	1.75	1.92	1.33	1.65
Hazelton	9	1.67	1.78	1.56	1.33	1.44	2.00	1.63
Banff Park	10	1.60	1.81	1.72	1.09	1.36	1.84	1.57
Gorge Creek	20	1.43	1.52	1.65	1.35	1.65	1.63	1.54
Quesnel	25	1.80	1.80	1.64	1.52	1.88	1.88	1.75

[1] Character indices are for adult males in breeding populations and are scored on the basis of 0 (typical *coronata*), 1 (intermediate *coronata-auduboni*), and 2 (typical *auduboni*).

from the Hazelton area only two specimens are "pure," and the overall character score is 1.63. Of 35 male *coronata* from farther north, many show evidence of intergradation. For example three specimens from British Columbia (Atlin, Telegraph Creek) and two from Petersburg, Alaska have pale yellow in the throat. The degree of hybridity (combined scores 0.18 to 0.24) in these populations is somewhat higher than that in central Alberta. Interbreeding in northwestern British Columbia probably occurs in the upper reaches of the valleys of the Iskut-Nass and perhaps Skeena-Stikine Rivers. Other probable areas of hybridization include the valleys of the Kachika Findlay and Peace Rivers in Northeastern British Columbia and forested passes in the Rockies between Pine Pass and the Alberta-British Columbia border.

Intergradation and possible introgression in individual characters.—As already mentioned some variation in character indices is evident even in

"pure" populations of *coronata* and *auduboni*, and atypicalness or "foreign traits" may be found in places far removed from the zone of interbreeding (Tables 2–7). A logical assumption in such cases is that atypicalness is the result of genetic exchange between the two entities, or in short, introgression. Before attributing all such cases of atypicalness to introgression, one must consider the possibility that some of it is the result of intrinsic, natural variation. After all, if genomes of forms are similar enough to permit interbreeding and backcrossing, then they may also be similar enough to produce parallel variation independently. Thus indiscriminantly attributing all foreign traits to introgression is unjustified. This is particularly true in cases where variation in so-called "pure" populations is unstudied, and purity is assumed *a priori*.

Assuming that either or both introgression and natural variation may produce atypicalness in pure populations, the question arises as to how to distinguish the two. The answer is that no certain way of doing so exists and that regardless of one's methodology, there is ample room for error in interpreting variation. This study takes the position that introgression should show a gradient of decreasing frequency of atypicalness with increasing distance from the area of interbreeding. Further, this gradient should be evident from a lack of homogeneity among samples as predicated by the results of chi-square testing with a probability level of 0.05. Thus a gradient distribution and a heterogeneous occurrence (chi-square probability of less than 0.05) of atypicalness among samples are regarded as evidence of introgression.

The following account of intergradation and possible introgression in individual characters uses the terms "hybrid zone" and "introgression zone." These refer to the study area in southeastern Alaska, British Columbia, and Alberta and denote the pattern of hybridity in that area (Figure 6). Thus, the hybrid zone includes those samples, mainly in the mountains, that are nearly intermediate (0.75 to 1.25) in their overall character scores, and the introgression zone includes the less introgressed samples (scores 0.14 to 0.42 and 1.51 to 1.75) outside the hybrid zone. The introgression zone may be referred to as eastern and western, designations that refer respectively to the *coronata* and *auduboni* "sides" of the study area. In the absence of samples from some areas, the distribution of hybrid and introgression zones has been extrapolated. "Pure" populations are those from outside the study area. Individual and overall character indices for all the following samples are given in Table 8.

Throat color.—In the hybrid zone scores of this character are 0.83 at Pine Pass and 1.05 at Jasper. This drops to 0.32 to 0.36 just east and northward, except at Nordegg where it is a highly intermediate 0.89. In
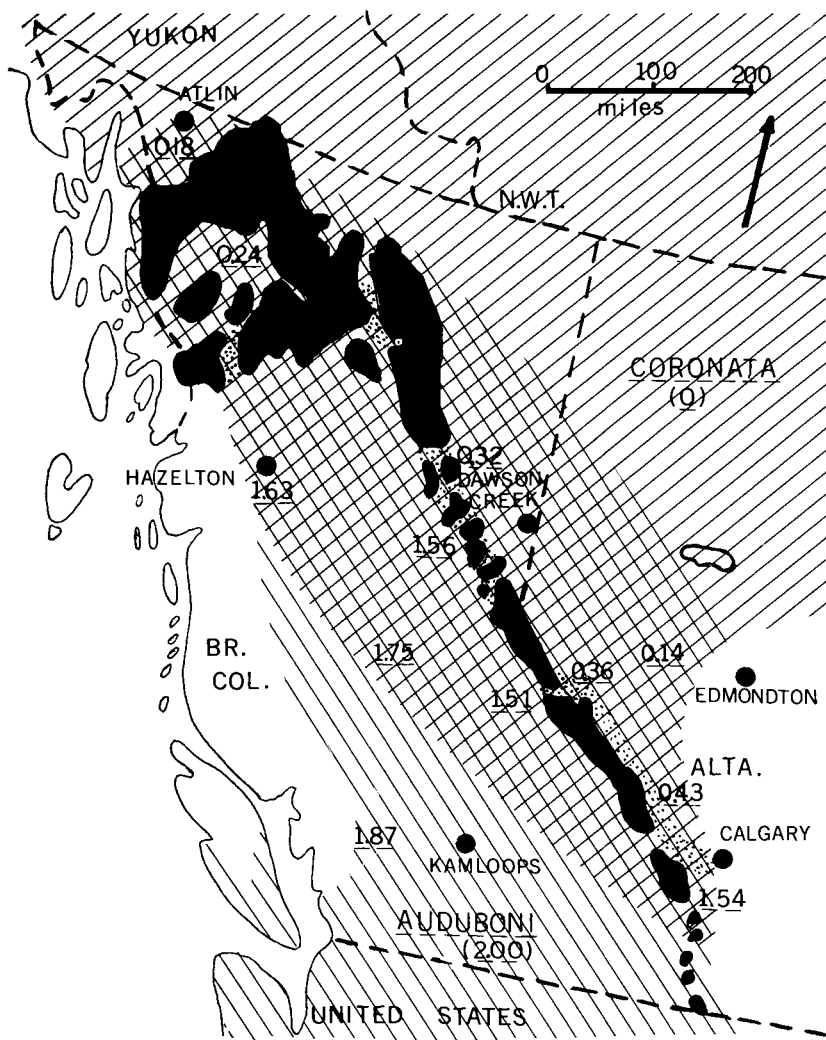
Figure 6. The area of interbreeding between *Dendroica coronata* and *D. auduboni*. The hybrid zone is stippled and the introgression zone is crosshatched (see text for explanation). The black area is unforested habitat, and the numbers are selected sample means for plumage characters.

northwestern British Columbia and central Alberta it further decreases to 0.08 and 0.11. "Pure" *coronata* populations score 0.03 to 0.05, except in central Canada where the score is 0.11. Just west of the mountains and at Gorge Creek the scores are 1.38 to 1.52 and this rises to 1.75 to 1.80 in the remaining part of the western introgression zone. From southern

British Columbia and the Cypress Hills south, throat color scores 2.00 in *auduboni* populations. Introgression cannot be demonstrated statistically on the basis of a gradient concept anywhere outside the study area (Tables 2 and 3), although some suggestion of it occurs in eastern to central Canada.

Postocular line.—In the hybrid zone this character scores 0.83 at Pine Pass and 0.95 at Jasper. It then drops off to 0.33 to 0.64 just east of the mountains. In northwestern British Columbia it is 0.15 to 0.18, in central Alberta zero, and in pure *coronata* 0.03 to 0.11. In the western part of the introgression zone it is 1.36 to 1.73 except for 1.88 at Quesnel and 1.92 at Crooked Lake. Except for the Cypress Hills and northern Idaho (which are both 1.80), values are 1.93 to 2.00 in *auduboni*. Again no statistical basis exists for suggesting introgression outside the study area (Tables 2 and 3).

Wing pattern.—Scores in the hybrid zone are 1.00 at Pine Pass and 1.11 at Jasper. In the eastern introgression zone only the scores from Jarvis Lake (0.56), Moberly Lake (0.36), and Telegraph Creek (0.42) are significantly higher than the values of 0.17 to 0.19 in pure *coronata*. In ten regional samples of *coronata* from Alaska to eastern North America, specimens with atypical wing pattern comprise up to 40 per cent of all specimens, with the average per sample 18 per cent (Table 2). A chi-square test reveals no gradient in atypicality and therefore no reason exists to speculate that this phenomenon is due to introgression from *auduboni*. In the western part of the zone of introgression this character scores 1.63 to 1.72, except for 1.33 at Crooked Lake. In pure *auduboni* the scores range from 1.90 to 2.00 and the chi-square value reveals heterogeneity among the samples (Table 3). As the heterogeneity seems to stem from the high percentage of intermediate specimens from the northwestern U. S., (11.5 per cent compared to average of 2.1 per cent), introgression in wing pattern is weakly suggested in that area.

Auricular color.—In the hybrid zone this character scores 0.66 at Pine Pass and 1.16 at Jasper. Eastward and northward it scores 0.16 to 0.24, except for 0.44 at Nordegg and 0.33 at Telegraph Creek. In the western introgression zone the value is 1.60 to 1.67 except for 1.43 at Gorge Creek, 1.80 at Quesnel, and 1.83 at Crooked Lake. *D. auduboni* values range from 1.90 to 1.98, except for 1.70 at Cypress Hills. Values from *coronata* populations are near zero, except for central Canada which is 0.10. A chi-square test of *coronata* samples shows heterogeneity to exist among them, apparently as the result of the latter sample (Table 2). As the area (Saskatchewan, Manitoba) is adjacent to the area of interbreeding, a basis exists for suspecting introgression in auricular color in that area. *Auduboni* is not introgressed (Table 3).

Supraloral spot.—In the hybrid zone this value is 0.67 and 0.68 and it is 0.36 at Jarvis Lake, 0.26 in central Alberta, and 0.22 at Nordegg. Elsewhere in the eastern introgression zone and in *coronata* populations it is zero to 0.10. In the western introgression zone it is 1.09 at Banff, 1.18 at Tete Jaune, and 1.23 to 1.33 in most other populations. At Quesnel it is 1.52 and at Crooked Lake 1.75, both of which are near the normal values of 1.60 to 1.70 in pure *auduboni*. In 13 populations of *auduboni* the percentage of specimens atypical in this character varies from 22.9 to 38.9, with the average 29.0 (Table 4), but the chi-square value offers no statistical justification for suggesting gradient introgression in this character. *Coronata* is not introgressed in this character either (Table 2).

Tail pattern.—The scores in the hybrid zone are 0.62 at Pine Pass and 1.04 at Jasper. In the eastern zone of introgression values are 0.34 to 0.47 (0.21 at Jarvis Lake and in central Alberta). In *coronata* from eastern North America these values are 0.01 to 0.04, but in central Canada and Alaska they are 0.19 to 0.24, and thus more similar to some intergrade populations than those further east. A chi-square test on *coronata* populations reveals heterogeneity (Table 5), and the trend of atypicalness shows that specimens from northwestern North America generally have more white in the tail than those from further east. This is suggestive of introgression in the former area, but certain difficulties exist in interpreting the situation. For example, 13.3 to 21.4 per cent of all specimens from Alaska have more-than-average amounts of white in the tail, but in the MacKenzie Delta only adult males and females (both 33.3 per cent) show this. Above-average white is found in males of the MacKenzie (40 to 62.5 per cent), southern Yukon (10 to 40 per cent), and locally in eastern North America (e.g. 9.1 to 10 per cent in Maritimes), but not in females. As these patterns are both variable in themselves and not strictly gradients, caution is necessary in attributing the increase in extent of white in the tail of northwestern populations to introgression. In the western introgression zone, low scores are found at Kennedy (1.69), Crooked Lake (1.33), Gorge Creek (1.63), and Tete Jaune (1.77), but the others are in or near the normal range of *auduboni* (1.82 to 2.00). No statistical evidence exists for suggesting introgression of tail pattern in *auduboni* (Table 6).

Atypicalness in Central American races of D. auduboni.—Two races of the *auduboni* group occur in the highlands of Central America, *D. a. nigrifrons* in the Sierra Madre Occidental (Chihuahua, Durango) and possibly the Nevado de Colima in Jalisco, and *D. a. goldmani* in western Guatemala and adjacent Chiapas (Volcán Tacaná). Both are similar to *D. a. auduboni*, but are darker and have somewhat longer wings. In addi-

tion both show departures in other characters that might be thought of as an approach to *coronata*. These areas of approach include less white in the tail, more white in the throat, darkened auriculars, and darker brown coloration in juvenile, female, and winter plumages. In addition *nigrifrons* shows a high frequency (22 per cent of 27 specimens) of light lores in breeding males (as does *auduboni*), but *goldmani* shows none in 13 specimens.

In the amount of white in the tail *auduboni* averages 4.9 in adult males and 4.4 in first-year males and females compared to values of 4.6, 3.8, and 4.3 in *nigrifrons* and 4.4, 3.8, and 3.8 in *goldmani*. In percentage of atypicalness in this character, *auduboni* is 4.9, 4.8, and 6.9 in the respective categories. *Nigrifrons* is 29.3 in adult males and 22.2 in first-year males, *goldmani* is 66.7 and 33.3, and both are zero in females. Thus only males of the Central American races average less white in the tail than *D. a. auduboni*.

In the amount of yellow in the throat, both *nigrifrons* and *goldmani* average less than *auduboni*. This is most evident in juveniles, immature females, and breeding birds. For example breeding males of *nigrifrons* tend to have whitish chins and an indication of whitish latero-posterior patches on the throat, and these are even more marked in *goldmani*. The darker auriculars of southern races are part of the cline of increasing melanism (especially marked in breeding males), which includes much of the upperparts, lower breast, and flanks. In juvenile, female, and winter plumages, the southern races are darker brown than *auduboni*. In fact, with the reduction of yellow in the throat of juveniles and females, some specimens (especially of *nigrifrons*) are very similar to *coronata*.

We cannot assume that the similarities between *coronata* and the southern races of the *auduboni* group are due to introgression, because there is no evidence of widespread introgression in the intervening populations of *auduboni*. More likely any approach by *D. a. nigrifrons* and *D. a. goldmani* to *D. coronata* is the result of intrinsic variation and parallelism rather than of introgression.

Recapitulation.—Interbreeding between *D. coronata* and *D. auduboni* occurs along the axis of the Canadian Rockies and probably in the mountains of northern British Columbia and adjacent southeastern Alaska. Two transects across the Rockies showed essentially intermediate populations in the Pine Pass area, British Columbia, and in Jasper National Park, Alberta. The straightline distance across the areas occupied by these populations is about 35 miles (40–70 road miles). A marked decrease in the level of intergradation occurs in populations immediately adjacent to these areas although intergradation is still quite evident there, and it

persists in most characters across an area of 200 to 300 miles. In populations of *coronata* and *auduboni* from outside the area of southeastern Alaska, British Columbia, and Alberta, introgression is apparent only in one or two of the six plumage characters analyzed. In *coronata* the sample from Saskatchewan and Manitoba appears to be somewhat introgressed in respect to auricular color, and samples from northwestern North America show greater than normal amounts of white in the tail. The latter shows some departure from a gradient distributional pattern and in some sex/age classes, and thus it may not be strictly attributable to introgression. In *auduboni* introgression in wing pattern appears to exist in the Pacific Northwest and perhaps other northern populations. No statistical evidence suggests introgression in any other characters outside the study area, but an average of 18 per cent of "pure" *coronata* are atypical in wing pattern, as are 29 per cent of "pure" *auduboni* in loral color. Although Central American races of *auduboni* (*nigrifrons* and *goldmani*) show an approach to *coronata* in some characters, the absence of widespread introgression in intervening *auduboni* suggests this is due to parallelism rather than to introgression.

DISCUSSION

While *D. coronata* and *D. auduboni* clearly intergrade through intermediate populations in the Canadian Rockies and probably also in the mountains of northern British Columbia, the transition between them is abrupt and intergradation is restricted to a few hundred miles or less in most characters. The implications of these findings are that the two forms interbreed and backcross freely where their ranges meet, but that away from this periphery factors are operating that prevent massive introgression. Other than natural selection, the most likely factors to account for reduced introgression would be a recent and/or limited area of contact between the two forms.

On the assumption that the mountain corridors through which interbreeding now occurs were once glaciated barriers separating these two forms (discussed further under Evolution), the establishment of interbreeding may be dated on the basis of deglaciation. Judging from the events in the cordilleran United States (Richmond, 1965), these corridors probably became free of ice as much as 10,000 years ago, and certainly by the beginning of the altithermal period, which started 6,500 years ago (Deevy and Flint, 1957). Even allowing a thousand years or more for the establishment of forest and populations of warblers in these corridors, interbreeding has obviously been possible for several thousand years. This being the case, then recency of contact can hardly be regarded as a factor in the curtailment of intergradation between the two taxa.

On the other hand, the extent of contact between *coronata* and *auduboni* is clearly limited, as interbreeding occurs only through the corridors that penetrate (or flank in southwestern Alberta) the montane barrier that separates them (Figure 6). Of the approximately 600 miles of potential interface between the two forms, only about 15 per cent actually allows contact in suitable habitat. The rest is montane rock, glaciers, tundra, and other unforested environments. As populations that occupy these corridors are small, one would expect that the larger, less hybrid populations beyond the mountain would have the effect of swamping out foreign genes before they penetrate deeply into pure populations. This may well be true to some extent, but one wonders why a more gradual cline of intergradation has not been established after thousands of years of interbreeding. The steepness of the cline is particularly puzzling in small and insular populations north and east of the mountains (e.g. Telegraph Creek, Moberly Lake), which in theory should be more affected by the influx of foreign genes and thus more hybrid than less insular and larger populations. Such is not the case, either in these areas or in general east of the Rockies, where populations are both relatively smaller and less continuous than those to the west. In view of these inconsistencies, to assume that the steepness of intergradation between *D. coronata* and *D. auduboni* is due solely to their limited contact and the effects of swamping is untenable. Natural selection must also be a factor.

In questions of evolutionary relationships merely to establish that selection is operating is insufficient; also necessary is the elucidation of selection's extent and pattern, even in the absence of other knowledge about it. Basic to this elucidation is a knowledge of gene flow, which is the basis for the definition of species and conspecies. Unfortunately an understanding of gene flow, and consequently the extent and pattern of selection, does not necessarily arise from a study of gross character intergradation. Without an understanding of the genetic bases and behavior of gross characters we are uncertain as to the relation of their intergradation to the process of gene flow.

Even so, this inability to relate the two poses no real problem in cases where the blending of characters is gradually clinal, for merging is evident even without invoking gene flow. On the other hand, in steeply clinal intergradations a knowledge of gene flow, and hence of the extent and pattern of selection, is critical, because if we operate on the strict assumption that such a cline represents strong counterselection, we ignore the possibility of an undercurrent of undetected gene flow. For example, in studies of intergradation of two forms of lizard (genus *Cnemidophorus*) in the southwestern United States, an analysis of gross characters showed only limited interbreeding and a narrow zone of intergradation (Zweifel,

1962), which suggested that both counterselection and species reenforcement were occurring. On the other hand, an analysis of serum proteins of the two forms showed broader intergradation (Dessauer et al., 1962), thus illustrating gene flow that would have otherwise been undetected. Obviously an evaluation of evolutionary relationships based only on the intergradation of gross characters would have been inaccurate, because such intergradation did not accurately reflect the full extent of gene flow between the two forms. This is not to say that an undetected undercurrent of gene flow actually *does* exist between *coronata* and *auduboni*, but rather that such an undercurrent *may* exist. The uncertainty of the situation makes unwise any unreserved postulation of gene flow on the basis of intergradation of gross characters.

Aware of possible undetected gene flow, one must still conclude that some degree of selection is operating to maintain the phenotypic differences between *coronata* and *auduboni*. Precisely what selective forces are involved, or what the selective advantages of the two genotypes are, is obscure. One is at a loss even to say whether selection is operating on phenotypically obvious characters or ones that are not presently apparent. In fact little substance can be offered, except that a positive correlation appears to exist between phenotypes and habitat; *coronata* is favored in boreal forest, *auduboni* in cordilleran forest, and intergrades in a mixture of the two types.

In spite of an ignorance of the selective mechanisms involved, the evolutionary interrelationships of *D. coronata* and *D. auduboni* are worth pondering, particularly the question, are they one or different species? As has already been mentioned, the concept of gene flow is basic to the definition of a species, which, broadly stated, is a group of populations among which a genetic continuum exists. Thus the question posed above becomes one of whether a genetic continuum exists between *coronata* and *auduboni*.

In terms of the more striking evidence, no well-defined genetic continuum appears to exist between *D. coronata* and *D. auduboni*. After all, intergradation is steep, and outside the immediate area of contact the effects of interbreeding seem to dissipate within a relatively short distance. This seems to indicate that selection is operating against foreign genes and removing them before they achieve widespread penetration. If this is the case, then one can hardly claim that the two forms are truly genetically continuous. On the other hand the question has already been raised as to how accurately the intergradation (or lack of it) reflects gene flow. In theory an undercurrent may exist that is not being detected, and hence an erroneous conclusion could be reached in regard to the extent and pattern of counterselection. In addition the probability also exists that some dilution of gene flow is occurring as the result of swamping outside the

narrow interface between the two forms. Combining uncertainty as to the amount of gene flow with the probability of swamping, it becomes impossible to take a position that suggests a total absence of genetic continuity or that all possible dilution of gene flow is due to counterselection.

Even taking the situation at face value and assuming that a large part of any dilution of gene flow is primarily due to counterselection, it would appear that the latter is not extremely rigorous. If it were, one would expect that by now it would have succeeded in eliminating the tendency toward interbreeding, as very strong selection on genomes adjacent to the hybrid zone should have a feedback effect on the more peripheral hybrid populations and reenforce specific differences. That this has not happened is evident, even though the populations that would have to be reenforced are relatively small in size. As a consequence of the lack of intensive (enough) selection, interbreeding and backcrossing have continued, and in so doing have continued to provide the potential for gene flow. That some gene flow is occurring as a result of this is evident from the intergradation of characters in the study area and, in a few cases, beyond it. Thus the question becomes one of the quantity of gene flow between these two forms rather than one of its existence.

In terms of a black-and-white assessment of evolutionary status, the situation in the *D. coronata* complex is paradoxical. Evidence allows both for the existence of gene flow and for the operation of counterselection, and as a consequence the nature of any genetic continuity that may exist is extremely conjectural. Thus, to judge the situation only in terms of species or conspecies would be arbitrary, for elements of both categories are present. Instead, it would seem better to recognize that shades of gray do exist, to continue the metaphor, and to accept them as such. Mayr (1963) has already proposed to apply the term semispecies to forms that have attributes of both species and conspecies, and I would adopt this term to designate the relationships of *D. coronata* and *D. auduboni.* To do otherwise would be a less accurate reflection of their relationship.

Other examples among birds that show a similar steepness of intergradation between interbreeding forms are shown in Table 9. In terms of distance over which intergradation occurs, perhaps the shortest on record is that in certain Mexican wrens (*Campylorhynchus rufinucha humilis-C. r. nigricaudatus*) in which this is a mere 20 miles (Selander, 1965). Even in the rather widely intergrading North American flickers (*Colaptes auratus-cafer*), the major shift between forms may be in as little as 100 miles (Short, 1965).

The taxonomic treatment of these and similar situations varies both with the data and the systematist. Most workers seem to feel that highly

TABLE 9

SOME EXAMPLES OF INTERBREEDING FORMS IN WHICH INTERGRADATION IS
STEEPLY CLINAL IN NATURE

Form and authority	Zone of intermediacy	Zone of intergradation
Campylorhynchus rufinucha humilis-C. r. nigricaudatus (Selander, 1965)	6½ miles or less	20 miles
Parus bicolor-P. atricristatus (Dixon, 1955)	less than 40 miles	
Sphyrapicus varius nuchalis-S. v. daggetti (Howell, 1952)	less than 40 miles	
Rhamphocelus flammigerus-Rh. icteronotus (Sibley, 1958)	less than 50 miles	
Dendroica coronata-D. auduboni (this study)	ca. 35 miles	200 to 300 miles
Junco hyemalis-J. oreganus (Miller, 1941)	ca. 100 miles	
Corvus corone-C. cornix (Mayr, 1963)	30 to 150 miles	
Pheucticus ludovicianus-Ph. melanocephalus (West, 1962)	100 miles	200 miles
Icterus galbula-I. bullockii (Sibley and Short, 1964)	ca. 125 miles	200 miles
Pipilo erythrophthalmus-P. e. maculatus group (Sibley and West, 1957)	several hundred miles	
Colaptes auratus-C. cafer (Short, 1965)	100 to 150 miles	

introgressive connecting populations are more significant than steep clines of intergradation, and hence they tend to lump the interbreeding forms. Another element interprets the evidence more conservatively and opts to split such groups. Not only would a semispecific designation more accurately reflect relationships in many cases, but it would also tend to reduce the area of conflict between extremes of taxonomic approach. The semispecies concept could also be applied to insular and other allopatric forms with the view of associating evolutionary groups. In terms of nomenclature, the semispecies can be recognized within the framework of the present trinomial system. For example, the *D. coronata* complex could be designated:

> *Dendroica coronata coronata*
> *Dendroica (coronata) auduboni*
> *Dendroica (coronata) nigrifrons*
> *Dendroica (coronata) goldmani*

In cases where several semispecies and their races are included in a single species complex, different units could be designated with nonfixed superscripts, as:

> *Passerculus sandwichensis oblitus*
> *Passerculus sandwichensis rufofuscus*
> *Passerculus (sandwichensis)*[a] *princeps*
> *Passerculus (sandwichensis)*[b] *rostrata*
> *Passerculus (sandwichensis)*[b] *guttatus*

THE POSSIBLE EVOLUTION OF THE *Dendroica coronata* COMPLEX

The differentiation of *coronata* and *auduboni* was probably attained during a period in which ancestral populations became isolated in and closely adapted to their present habitats of boreal and cordilleran forests, respectively. A likely time for this to have occurred would have been during the glacial advances of the latter half of the pleistocene. Before exploring this possibility, a brief sketch of the Tertiary history of coniferous forest in North America seems in order.

At the beginning of the Tertiary period in North America the coniferous elements of the present day cordilleran and boreal forests were apparently confined to the extreme north. Southward, forests were dominated by temperate to tropical broadleaf genera, and conditions suitable for palms and cycads existed as far north as southeastern Alaska, the Prairie Provinces, and even Greenland (La Motte, 1952). By Eocene time conifers of several genera, including *Picea, Abies,* and *Pinus,* were present as far south as Colorado in a flora consisting mainly of temperate broadleaf trees plus several cycads and palms (Brown, 1934).

Subsequent floras from the same general area, including Oligocene Florissant flora (MacGinitie, 1953) and the probably Pliocene Creede flora (Stewart, 1940) show the progressive loss of broadleaf trees and the rise of conifers to produce a flora similar to that of the region at present. Concomitant with the appearance and rise in dominance of conifers, a shift is suggested toward lessened and/or seasonally distributed moisture conditions, which may have been a major causative factor in the gradual establishment of coniferous forests in this area.

Westward, fossil floras show a similar appearance and ascendancy of conifers, but with a more retarded and less complete loss of broadleaf trees. Northward, a gradual and parallel loss of subtropical and temperate broadleaf trees and an increasing dominance of conifers also occurred which was due perhaps as much to decreasing temperatures as to decreasing mesicness. How far conifers penetrated southward in the Tertiary period is unknown, but the present adaptive radiation of pines in Mexico (Martínez, 1945) suggests that at least *Pinus* (along with many temperate angiosperms) reached Middle America well before the end of this period. In the eastern United States *Pinus* is known from an Eocene deposit in Virginia and a Pliocene deposit in Alabama (La Motte, 1952) and its radiation in the southeast is also suggestive of a pre-Quaternary appearance and differentiation in that area.

The gradual increase in aridity of the interior part of the continent through the Tertiary period is thought to have caused the retreat of coniferous forests to higher elevations in the cordilleran region and to
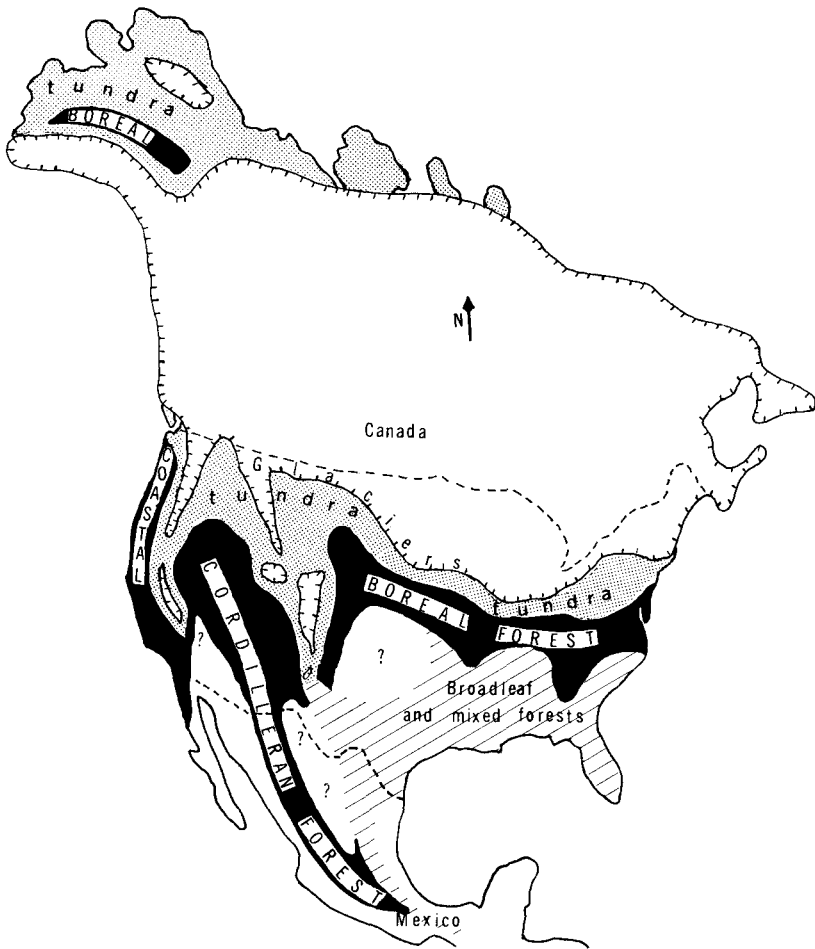
Figure 7. A postulated distribution of certain vegetational types in North America during maxima of the Illinoian and Wisconsin glaciations (diagrammatic rendition), including coastal, cordilleran, and boreal coniferous forests. The boreal area in Alaska was probably woodland, and the areas with question marks were probably woodland or savanna. Glacial boundaries are for the Wisconsin and are from various sources including Wright and Frey (1965) and Hopkins (1967). Lowered sea level not indicated at the continental periphery.

higher latitudes in the boreal region. By middle Pliocene time, conditions of aridity increased to the point of possibly duplicating those of today, and boreal and cordilleran forests may have had a distribution similar to that of the present. In upper Pliocene time there began a shift toward less arid and perhaps cooler conditions, which culminated in the first glacial advance

(the Nebraskan glaciation) of the Pleistocene period, thus beginning a new phase in this history of coniferous forests on this continent and in Eurasia.

The Quaternary history of the boreal and cordilleran coniferous forests was one of displacement both latitudinally and altitudinally. During the drier interglacials, as in middle Pliocene time, the distribution of these forests was probably similar to that of today, with many disjunctions in the cordilleran region and only a narrow connection between it and the boreal forest. During the glacial periods, the boreal forest moved southward in front of the glaciers and cordilleran forest spread into lower elevations. These peregrinations of conifer forest in the Pleistocene period were probably instrumental in the development of the present differentiation in the *D. coronata* complex and many other North American birds (Rand, 1948) and other vertebrates.

Considerable evidence has been presented in support of the theory that most vertebrate speciation requires that continuous populations become separated and isolated for marked differences to accumulate (Mayr, 1963). Simply stated, vertebrate speciation is predominantly allopatric. In attempting to account for the differentiation of the *D. coronata* complex on an allopatric basis, I am assuming both that the immediate ancestors of the group inhabited coniferous forest and that differentiation occurred with the same east-west orientation we see at present.

Mengel (1964), in his study of speciation in North American wood warblers, has postulated that differentiation of *D. coronata* and *D. auduboni* may have occurred in the last (Wisconsin) glaciation as southward retreating coniferous forests became disjoined by the Great Plains into discrete segments in the eastern and in the western United States. The disjoining of such forest by the Great Plains is not tenable, in view of the thesis that more mesic conditions would have prevailed during the Wisconsin and earlier glacial periods. Thus rather than being disjunct, glacial-age coniferous forests are more likely to have been continuous across the northern plains and along the western portion to the southern plains (Figure 7).

Evidence of the existence of boreal forest in the northern plains includes fossil conifers (*Picea, Abies, Larix, Pinus*, and/or *Tsuga*) in Wisconsin deposits from central Iowa (Cushing, 1965) and southern South Dakota (Watts and Wright, 1966) and from undated, probably glacial, deposits in northeastern Kansas (Horr, 1955). In the southern high plains, similar fossil remains in Illinoian deposits in southwestern Kansas and adjacent Oklahoma (Kapp, 1965), and Wisconsin deposits in eastern New Mexico and western Texas (Wendorf, 1961) suggest a movement of cordilleran forests eastward into the lowlands during pluvial periods.
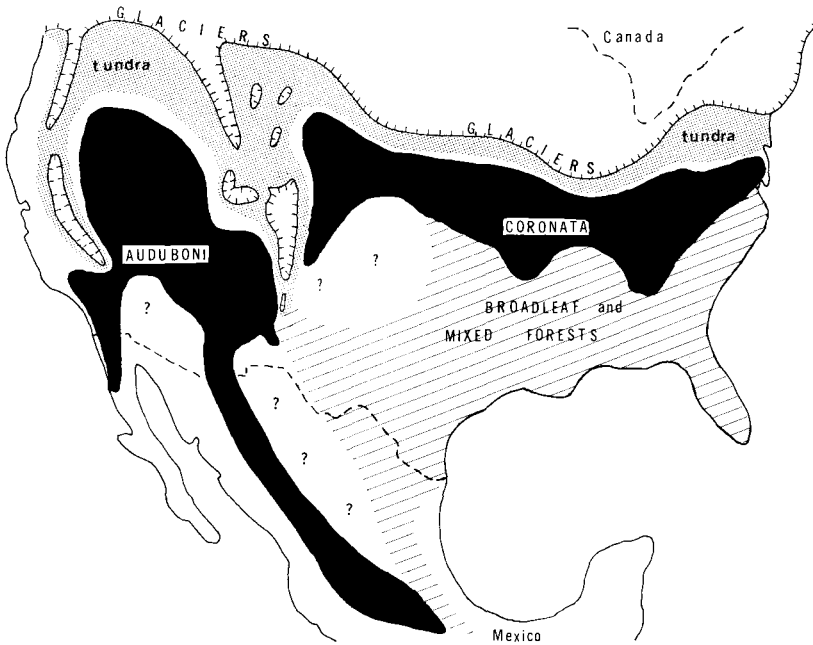
Figure 8. Model showing possible areas of differentiation of *Dendroica coronata* and *Dendroica (coronata) auduboni* in the Wisconsin glaciation (diagrammatic rendition). Other details as in Figure 7.

That this also occurred in the northern high plains and resulted in a coalescing of boreal and cordilleran forests is suggested by phytogeographical and fossil evidence. For example, the present forests of the Black Hills are a mixture of boreal forms (*Picea glauca, Betula papyrifera, Populus balsamifera,* and *Prunus pensylvanica*) and cordilleran forms (*Pseudotsuga menziesii, Pinus contorta, P. flexilis,* and *P. ponderosa*). In addition an early post-Wisconsin flora from southern Saskatchewan (Cushing, 1965) contains boreal spruces (*Picea glauca, P. mariana*) which probably migrated north from refugial forests in Montana or Wyoming, where they surely would have been in contact with cordilleran elements.

Although this evidence strongly suggests the presence of coniferous forests in the northern plains in the Wisconsin and other glacial periods, no assurance exists that these were occupied by *coronata* complex warblers. It may have been that populations of these birds were absent from this region and were instead confined to the cordilleran region and the (say) Appalachians, where differentiation did proceed at this time. The present ecological and climatic tolerance of this group of warblers argues against their absence from the northern plains, as does zoogeographic evi-

dence. For example the presence of such boreal or northeastern forms as the snake, *Opheodys v. vernalis* and the frog, *Rana sylvatica*, in the cordilleran regions suggests the range of these animals was continuous across the plains during the Wisconsin glacial period.

A somewhat different hypothesis is that the present *coronata-auduboni* differentiation stems from a disjoining of ancestral populations along the axis of the Rocky Mountains rather than the Great Plains during the Wisconsin glacial advance (Figure 8). A separation of populations could have been effected by the presence of a cap of ice and alpine tundra extending along the montane crest from southeastern British Columbia to northern or central New Mexico. Farther south and east in New Mexico and adjacent parts of Texas and Mexico a continuation of this barrier may have existed in the form of mixed forest. Such forest would have resulted from the coalescing of cordilleran forest and invading broadleaf forest from eastern (and perhaps southern) North America (Blair, 1958; Tucker and Muller, 1958). As mixed forest is not presently occupied by members of the *D. coronata* complex (e.g. in the southern Appalachians) such forests may be assumed not to have been during the Wisconsin either.

The result of this barrier of tundra and ice would have been to divide ancestral *D. coronata* stock into a pre-*coronata* population in boreal forest (boreo-cordilleran in the northern plains) east of the Rockies, and a pre-*auduboni* in the cordilleran forest west of the Rockies, but east of the Cascade-Sierra Nevada axis (Figure 8). The reason for the postulated absence of warblers of this complex on the West Coast is that the dense coastal forest that probably occupied the area would have been unsuitable habitat for these birds as it appears to be now (e.g. British Columbia).

Thus separated into two isolated populations, the process of differentiation may have occurred over the course of the tens of thousands of years that the Wisconsin glaciation endured. From time to time in this period glaciers waned to some degree, but whether the cordilleran barrier was ever dissolved to the extent of allowing recontact and interbreeding between the two forms is problematical.

With the beginning of the melting of continental and montane glaciers at the end of the Wisconsin, a change in the distribution of these warblers would have begun. Gradually the boreal forest (and *coronata*) would have spread northward to reoccupy Canada and Alaska, while southward it was dying out in the north-central United States. Along the eastern slopes of the Rockies and in the outlying ranges of the northern plains, however, remnant boreal forests may have retreated upslope, thus leaving relicts of this forest found in the flora of this region today (e.g. Black Hills, Pettingill and Whitney, 1965). Populations of *coronata* may have continued to occupy these montane forests as long as they remained co-

dominantly boreo-cordilleran in their composition. With the rise in dominance of the cordilleran forest elements, the habitat may have become progressively less suitable for the continued existence of *coronata* as a breeding bird.

With the melting of montane glaciers in southwestern Wyoming and the disappearance of mixed forest at the periphery of the southwestern plains, populations of *auduboni* probably spread eastward and northward respectively into the eastern Rockies, perhaps absorbing remnant populations of *coronata*. Gradually the spread of *auduboni* may have continued with its colonization and the establishment in the outlying ranges of the northern plains. There, too, relict populations of *coronata* may have been absorbed, as, for example, is suggested in the Cypress Hills where a slightly intergrade population of *auduboni* exists now (combined score 1.85).

As the southern range of *coronata* receded, either through extinction or absorption by *auduboni*, the extent of the interface between these two forms may have steadily declined. Perhaps contact in the early postglacial period was restricted to the area of the eastern slopes of the northern Rockies, east of the then still impenetrable glaciers that capped the mountains from northern British Columbia to the southern Alberta-British Columbia boundary. Eventually this interface may have moved northward to its present position west of Calgary, Alberta, while other contacts were established farther north with the melting of ice and the opening of montane passes.

Meanwhile the post-Wisconsin aridity and die-off of habitat in much of the lowlands of the interior and southern parts of western North America would have caused the upslope retreat of populations of the *auduboni* group (i.e. *auduboni*, *nigrifrons*, *goldmani*). Thus the previously continuous distribution southward through the highlands of central Mexico or possibly even Guatemala would have become disjunct and broken into the montane segments that we see today. Whether the races of this group arose before or after this disjunction is problematical, but from the nature of variation it seems likely that a north-south cline may have existed in the Wisconsin much as it does today. Of course over the thousands of years since disjunction occurred, selection would have been necessary to preserve the pattern of such variation.

On the basis of a study of the ecology, zoogeography, and postulated relationships within the genus *Dendroica*, the ancestor of the *D. coronata* complex may have arisen in the cordilleran region in the penultimate (Illinoian) glaciation. The mechanism may have been much the same as that which I postulate to account for the differentiation of *auduboni* in the Wisconsin. The boreal differentiate of an Illinoian disjunction (which

would correspond to *D. c. coronata*) may have been the ancestor of *D. palmarum*, a species that in juvenal plumage and certain other respects appears to be the nearest relative of the *D. coronata* complex (Hubbard, 1967). *D. palmarum* is a widespread boreal species sympatric with, but ecologically isolated from *D. c. coronata* by its preference for wetter breeding haunts and its terrestrial habits.

Assuming common ancestry of the *D. coronata* complex and *D. palmarum*, one can visualize a widely distributed, pre-Illinoian progenitor that became disjunct with that glacial advance and separated into segments east and west of the Rockies. Thus during the perhaps 75,000 years that the cold cycle of the Illinoian endured (Hopkins, 1967), differentiation may have preceded and produced the ancestor of the *D. coronata* complex in the cordilleran region and that of *palmarum* in the boreal region east of the Rockies. With the close of the Illinoian, ancestral *D. coronata* could have spread eastward through the boreal region to become widely sympatric with pre-*palmarum*. The development of sympatry may have been a factor in the present differences in ecology between the two forms, while the absence of *palmarum* from the cordilleran region may be due to the scarcity of its preferred habitat. Subspeciation in *D. palmarum* into an eastern and a western race has probably occurred in the Recent period.

Two other apparent relatives of the *D. coronata* complex are *D. striata* and *D. castanea*, which are more closely similar to each other than either is to *coronata-auduboni* or to *palmarum*. *D. striata* and *D. castanea* are breeding species of boreal forest and are widely sympatric with each other, with *D. palmarum,* and with *D. c. coronata*. Two differences between *D. castanea* and *D. striata* are that in the breeding season *D. striata* prefers smaller trees and it occurs in the Yukon and Alaska where *D. castanea* is absent. These two factors and the relationships of the two species raise the possibility that their evolution involves isolation and differentiation in the Alaskan glacial refugium.

That a large part of Alaska was ice-free during the glacial periods of the Pleistocene and served as a refugium for animals and plants is well established (Hopkins, 1967). Fossils show the existence of large mammals (e.g. mammoths, bison, horses, saiga) and trees (willow, birch, alder, spruce), and doubtlessly such birds were there as gulls, alcids, and shorebirds. Although much of glacial-age Alaska (as well as the Bering landbridge and adjacent Siberia) is thought to have been tundra and grassland, some woodland is known to have existed in the eastern area along the Yukon and Tanana rivers, and it probably was present in parts of southern Alaska as well (Figure 8).

The coniferous aspect in this habitat may have consisted mainly of small or dwarfed spruces interspersed among deciduous shrubs. A true

TABLE 10

SOME EXAMPLES AMONG NORTH AMERICAN BIRDS THAT MAY HAVE DIFFERENTIATED
IN RECENT GLACIAL PERIODS

Species or complex	Area of differentiation			
	Alaskan woodland	Coastal forest	Cordilleran forest	Boreal forest
Wisconsin glaciation				
Dendroica coronata	none	none	*auduboni*[1]	*coronata*[1]
Dendroica striata	*striata*[2]	none	none	*castanea*
Dendroica virens	none	*townsendi occidentalis*	*nigrescens*[2]	*virens*[2] *chrysoparia*[2]
Junco hyemalis	none	*oreganus*[1] group	*caniceps* group	*hyemalis*[1] group *aikeni mearnsi*
Zonotrichia leucophrys[2]	*gambelii*[1,2]	*nuttalli*[1,2] *pugetensis*[1,2]	*oriantha*[1,2]	*leucophrys*[1,2]
Perisoreus canadensis	none	*obscurus* group	*capitalis*[1] group	*canadensis*[1] group
Sphyrapicus varius	none	*ruber*[1]	*nuchalis*[1]	*varius*[1]
Dendragapus obscurus	none	*richardsonii* group	*obscurus* group	none
Canachites canadensis	*atratus*	?none	*franklinii*[1]	*canadensis*[1]
Illinoian glaciation				
Dendroica coronata and allies	*striata castanea*	none	*coronata-auduboni*	*palmarum*

[1] Similar or same origin postulated by Rand, 1948.

[2] Indicates forms of other than pure coniferous forest.

spruce forest with closed canopy and large trees may also have existed in favorable sites, but it was probably very limited in extent. These refugial woodlands and forests were probably inhabited by birds, some of which probably migrated over the ice to winter in Central and South America. Assuming that forest was rare and the woodlands were brushy or open, it seems unlikely such habitat would have been suitable enough to support populations of birds like the present *D. coronata* complex. However it may have been suitable for a species like the present *D. striata*, and it is conceivable that this species not only existed in Alaska, but that it may have differentiated there in the Wisconsin. This could have been brought about by the disjunction of ancestral *D. striata-castanea* into two populations by continental glaciation, the ancestor of the afore-mentioned *D. striata* in Alaska and that of *D. castanea* east of the Rockies in the United States. Following differentiation through the Wisconsin, *D. striata* could have later moved eastward to become widely sympatric with *D. castanea* over much of northern North America, but for some unknown reason *D. castanea* did not penetrate Alaska or the Yukon.

In the same way that ancestral *D. striata* may have been disjoined and differentiated from ancestral *castanea* in Alaska in the Wisconsin, the ancestor of both may have been disjoined and differentiated in the Illinoian, from the same stock that has produced *coronata-auduboni* and

palmarum. Thus, one can visualize the progenitor for this entire assemblage as a single widespread form of boreo-cordilleran forest in the interglacial preceding the Illinoian. With the development of glacial barriers in the Illinoian this ancestor may have been disjoined into three populations: ancestral *striata-castanea* in Alaska, *coronata-auduboni* in the cordilleran region, and *palmarum* in the boreal region east of the Rockies (Figure 8). Subsequent differentiation of these forms through the Illinoian, recontact and spread in the following interglacial, more disjunction and differentiation in the Wisconsin, and final recontact and spread would have produced the situation we see today.

Also an apparent relative of this assemblage is *D. kirtlandi*, a species restricted in the breeding season to pine woodland of central Michigan. In part because of its apparently relictual distribution, an understanding of its time and place of origin is obscure. I suspect that its ancestor either split off from the main stock before the Illinoian, or that it arose by a somewhat different mechanism in or since the Illinoian.

Rand (1948) was among the first to postulate the possible role of glaciation in the differentiation of North American birds, and the present model may be regarded as an extension and an additional confirmation of that proposed by him. Although independently conceived, a close resemblance exists between models not only in many of the forms involved (Table 10), but also in the areas of possible differentiation that have been proposed. Thus his forest refugia in the Yukon-Bering Sea area, the southeastern United States, the Rocky Mountains, and the West Coast are similar to those, respectively, of Alaskan, boreal, cordilleran, and coastal forests proposed here (Figure 7). Any improvement in the understanding of the situation attained in this study is due to the accumulation of additional evidence in the last 20 years, particularly in the field of paleobotany. Another 20 years of investigation will hopefully provide an even better basis for erecting and evaluating models of Pleistocene differentiation in North American birds.

SUMMARY

The interbreeding and intergradation of *Dendroica coronata* and *D. auduboni* were studied along two transects between central Alberta and central British Columbia. Intergradation was found to occur through highly hybrid and intermediate populations in the Canadian Rockies and probably in the mountains of northern British Columbia. Outside this narrow zone (35–70 miles wide), the degree of introgression was found to drop steeply and then to disappear gradually in most characters within a few hundred miles. Introgression in auricular color and possibly in tail pattern were found in *D. coronata* at least as far as central Canada, and in wing pattern of *D. auduboni* in the Pacific Northwest.

The steepness of the cline of intergradation is thought to be due both to swamping outside the limited interface of interbreeding and to the effects of counterselection. Interbreeding has probably been possible and occurring for thousands of years, yet the effects of counterselection appear insufficient to bring about species reenforcement. This, coupled with the evidence of at least a limited amount of gene flow (some may also be undetected), suggests that these two forms are better considered semispecies rather than a conspecies or as distinct species. Their semispecific status may be recognized as follows: *Dendroica coronata coronata* and *Dendroica (coronata) auduboni*.

A model presented to account for their differentiation involves the disjunction of an ancestral form by Rocky Mountain glaciation into cordilleran (pre-*auduboni*) and boreal (pre-*coronata*) isolates in the last, or Wisconsin, glaciation. Similar but more widespread disjunction and isolation in the penultimate, or Illinoian, glaciation may have produced not only the ancestor of *D. coronata-auduboni* (in the cordilleran region), but also those of the related *D. palmarum* (in the boreal area) and *D. striata-castanea* (in the Alaskan refugium). The origin of another close relative, *D. kirtlandi*, is obscure.

LITERATURE CITED

ANDERSON, E. 1949. Introgressive hybridization. New York, Wiley.

BLAIR, W. F. 1958. Distributional patterns of vertebrates in the southern United States in relation to present and past environments. Pp. 433–477 *in* Zoogeography (C. L. Hubbs, Ed.). Amer. Assoc. Advan. Sci. Publ. 51.

BROWN, R. W. 1934. The recognizable species of the Green River flora. Washington, D. C., Geol. Surv. Prof. Paper 185–C.

CANADA DEPARTMENT OF FORESTRY. 1963. Native trees of Canada. Ottawa, Ontario, Canada Dept. Forestry, Bull. 61.

COWAN, I. McT. 1955. Birds of Jasper National Park. Ottawa, Ontario, Canadian Dept. Northern Affairs and Natural Resources, Bull. 8.

CUSHING, E. J. 1965. Problems in the Quaternary phytogeography of the Great Lake region. Pp. 403–416 *in* The Quaternary of the United States (H. E. Wright, Jr. and D. G. Frey, Eds.), Princeton, New Jersey, Princeton Univ. Press.

DEEVY, E. S., AND R. F. FLINT. 1957. Postglacial hypsithermal period. Science, 125: 182–184.

DESSAUER, H. C., W. FOX, AND F. H. POPE. 1962. Starch-gel electrophoresis of transferins, esterases, and other plasma proteins of hybrids between two subspecies of the whiptail lizard (genus *Cnemidophorus*). Copeia: 767–774.

DIXON, K. L. 1955. An ecological analysis of the interbreeding of crested titmice in Texas. Univ. California Publ. Zool., 54: 125–206.

HOPKINS, D. M. 1967. The Bering land bridge. Stanford, California, Stanford Univ. Press.

HORR, W. H. 1955. A pollen profile study of the Muscotah Marsh. Univ. Kansas Sci. Bull. 37: 143–149.

HOWELL, T. R. 1952. Natural history and differentiation in the Yellow-bellied Sapsucker. Condor, 54: 237–282.

HUBBARD, J. P. 1967. A systematic study of the *Dendroica coronata* complex. Unpublished Ph.D. dissertation, Ann Arbor, Univ. Michigan.

KAPP, R. O. 1965. Illinoian and Sangamon vegetation in southwestern Kansas and adjacent Oklahoma. Univ. Michigan Mus. Paleontol. Contrib., 29: 165–255.

LA MOTTE, R. S. 1952. Catalogue of the Cenozoic plants of North America through 1950. Geol. Soc. Amer. Mem. 51.

MACGINITIE, H. D. 1953. Fossil plants of the Florissant Beds, Colorado. Carnegie Inst. Publ. 599.

MARTÍNEZ, M. 1945. Las pináceas mexicanas. Inst. Biol. México Anales, 16: 1–345.

MAYR, E. 1963. Animal species and evolution. Cambridge, Massachusetts, Harvard Univ. Press.

MENGEL, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). Living Bird: 9–43.

MILLER, A. H. 1941. Speciation in the avian genus *Junco*. Univ. California Publ. Zool., 44: 173–434.

MUNRO, J. A., AND I. McT. COWAN. 1947. A review of the bird fauna of British Columbia. Prov. Mus. British Columbia, Publ. 2: 3–285.

PETTINGILL, O. S., JR., AND N. R. WHITNEY, JR. 1965. Birds of the Black Hills. Cornell Lab. Ornithol., Spec. Publ. 1.

RAND, A. L. 1948. Glaciation, an isolating factor in speciation. Evolution, 2: 314–321.

RICHMOND, G. M. 1965. Glaciation of the Rocky Mountains. Pp. 217–230 *in* The Quaternary of the United States (H. E. Wright, Jr. and D. G. Frey, Eds.). Princeton, New Jersey, Princeton Univ. Press.

SALT, W. R., AND A. L. WILK. 1958. The birds of Alberta. Edmonton, Alberta, Queen's Printer.

SELANDER, R. K. 1965. Hybridization of Rufous-naped Cactus Wrens in Chiapas, Mexico. Auk, 82: 206–214.

SHORT, L. L., JR. 1965. Hybridization in the flickers (*Colaptes*) of North America. Amer. Mus. Nat. Hist., Bull. 129: 307–428.

SIBLEY, C. G. 1958. Hybridization in some Columbian tanagers, avian genus *Ramphocelus*. Amer. Phil. Soc. Proc., 102: 448–453.

SIBLEY, C. G., AND L. L. SHORT, JR. 1964. Hybridization in the orioles of the Great Plains. Condor, 66: 130–150.

SIBLEY, C. G., AND D. A. WEST. 1959. Hybridization in the Rufous-sided Towhees of the Great Plains. Auk, 76: 326–338.

STEEL, G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. New York, McGraw-Hill.

STEWART, B. K. 1940. Plants ecology and paleoecology of the Creede Valley, Colorado (abstract). Univ. Colorado Studies, 26: 114–117.

TAVERNER, A. A. 1918. Addenda to the birds of Jasper Park. Canadian Alpine Club, 9: 62–69.

TAYLOR, W. P. 1911. An apparent hybrid in the genus *Dendroica*. Univ. California Publ. Zool., 7: 173–177.

TUCKER, J. M., AND C. H. MULLER. 1958. A reevaluation of the derivation of *Quercus margaretta* from *Quercus gambelii*. Evolution, 12: 1–17.

WATTS, W. A., AND H. E. WRIGHT, JR. 1966. Late Wisconsin pollen and seed analysis from the Nebraska Sandhills. Ecology, 47: 202–210.

WENDORF, F. 1961. Paleoecology of the Llano Estacado. Santa Fe, New Mexico, Mus. New Mexico Press.

WEST, D. A. 1962. Hybridization in grosbeaks (*Pheucticus*) of the Great Plains. Auk, 79: 399–424.

WRIGHT, H. E., AND D. G. FREY. 1965. The Quaternary of the United States. Princeton, New Jersey, Princeton Univ. Press.

ZWEIFEL, R. G. 1962. Analysis of hybridization between two subspecies of the Desert Whiptail Lizard, *Cnemidophorus tigris*. Copeia: 749–766.

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