#### SUMMARY

The above data indicate that the Caspian Tern has been a fairly constant nesting species in Utah for many years. Breeding colonies have been noted on Rock Island, Utah Lake, and Hat Island, Great Salt Lake. The size of the colonies has varied greatly from year to year, depending largely on the degree to which they have been disturbed by visitors to the islands as well as by nesting gulls. The birds apparently arrive in Utah about the middle of April and commence their nesting activities about a month later. Should their breeding grounds be left unmolested it is likely that they will remain here as a nesting species.

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# RACIAL DIFFERENTIATION IN PASSERELLA (MELOSPIZA) LINCOLNII

#### WITH FOUR ILLUSTRATIONS

# By ALDEN H. MILLER and T. T. MCCABE

An initial interest in Lincoln Sparrows (*Passerella lincolnii*) occasioned by the finding of significant size differences has led us to inquire into the nature of races in this geographically variable species or rassenkreis. First, we desired to learn the degree to which certain variable characters were correlated in individuals. Could we expect constant linkage of characters in either the genetic or physiologic sense? Second, having found no correlation in many instances, it seemed important to analyze the mosaic of structural variants which characterize a geographic race. Questions arise whether natural race units truly exist in nature and, if they do, whether they are as neatly circumscribed as usually acclaimed. Third, we wished to point out certain types of individual variants, colonial differentiations and incipient geographic variation which might lead in the course of time and further change to the establishment of geographic races of the level of differentiation commonly accorded nomenclatural recognition. Fourth, it seemed desirable to describe geographic trends that like the characters of individuals, often are not correlated, one trend running as a geographic cross current relative to another.

Lincoln Sparrows contrast with Song Sparrows, Passerella (Melospiza) melodia, and Fox Sparrows, Passerella iliaca, with regard to degree of geographic differentiation. The genera Melospiza and Passerella have been merged by Linsdale (Univ. Calif. Publ. Zool., 30, 1928, pp. 367-369; Condor, 30, 1928, pp. 349-351) in the interests of larger generic groups among the North American fringillids. Melodia and iliaca are two of the largest rassenkreise on the North American continent, each comprising over fifteen geographic races. Lincolnii has but three races, although it occupies a territory roughly equal to that of *iliaca*. Comparing in another direction, Passerella georgiana is undifferentiated geographically. Can it be said that lincolnii and georgiana are less plastic than iliaca or melodia? If they are, can one assume greater genetic variation, or potential for genetic variation, in *iliaca* and *melodia*? Before granting the existence of such inherent plasticity some other factors should be considered: (1) Migration is more prevalent and involves longer journeys in lincolnii than in melodia and iliaca (some exceptions), allowing more chance for mixture of breeding populations that might be in process of differentiation. (2) Lincolnii does not inhabit insular regions to so great an extent as do melodia and iliaca, especially in the northwest coastal region. (3) Lincolnii appears to be more restricted to a certain type of meadow-bog habitat whereas *iliaca* occurs in dry chaparral regions, in timberline scrub thickets, or in beaver swamps and streamside meadows, depending upon the race and population involved. *Melodia* may frequent salt water marshes. fresh water marshes, brushy canyon bottoms, etc. Lincoln Sparrows seem less versatile ecologically. This quality is, in one sense, a sort of lack of plasticity and may be genetically transmitted.

#### MATERIALS

We are indebted to the following persons for opportunity to study Lincoln Sparrows either in their personal collections or in the collections in their charge: Mr. J. D. Figgins, Colorado Museum of Natural History; Mr. J. H. Fleming, personal collection and that of the Royal Ontario Museum; Dr. Herbert Friedmann, United States National Museum; Mr. Lyndon L. Hargrave, Museum of Northern Arizona; Mr. Randolph Jenks; Mr. Joseph Mailliard; Dr. H. C. Oberholser, Bureau of Biological Survey; Mr. James L. Peters, Museum of Comparative Zoology; Mr. Kenneth Racey; Mr. James Stevenson; Mr. Harry S. Swarth, California Academy of Sciences; Mr. P. A. Taverner, Canadian National Museum; and Mr. E. R. Warren, Colorado College Collection.

Additional material in the Museum of Vertebrate Zoology and the McCabe collection brings the total of birds examined to 1078. Of this number about 40 per cent are birds collected on the breeding grounds. Birds were not considered to be "breeding" until after May 20 and in some cases even later. Most of the August birds were considered breeding except individuals taken late in the month without trace of molt. Limits of the winter period were arbitrarily set at November 1 and March 15; a few exceptions were made.

## THE PRINCIPAL VARIABLE CHARACTERS

Coloration of the head and back.—In the feathers of the dorsum three color areas have been analyzed independently.

The black or dark-brown shaft streaks on the back have been assigned to three categories: broad, moderate, and narrow. Width of shaft streaks in feathers of the pileum is not linked with width of shaft streaks in the back feathers, and may be quite opposite. Slight differences of color in this stripe probably involve as great a differ-

ence in pigment deposition as striking differences in lighter hues (Rensch, Kurze Anweisung für Zoologisch-systematische Studien, 1934, p. 81), but are hard to evaluate.

The buff margins near the tip vary in width, in contrast, and, in essential color, from light tan toward yellowish, toward ruddy, or toward neutrality.

The intervening brown areas have been divided into two groups with several categories. The ruddy series starts with brown, followed by moderately ruddy and ruddy. The yellow series starts with the same brown, followed by moderately yellow and yellow.

Deceptive effects of contrast and of the relative strengths of colors may be created in many ways, including wear and fading. Especially striking is the "crushed glass" effect of marginal whitening, with its brilliant contrast, which may result from wear soon after molt and disappear with the extreme wear of breeding time.

Coloration of the underparts.—In some instances the colors of the underparts vary in agreement with those of the dorsal surface. A bird with yellow type of back usually has a decidedly yellow infusion in the breast band and on the sides, but brownand ruddy-backed birds are alike beneath. There is in the breast of *lincolnii* no counterpart of the differentiation in marking and color encountered in *iliaca* and *melodia*.

Wing length.—This dimension is the most satisfactory quantitative character. Differences in averages of adjoining races amount to about 5 per cent with the total range of individual variation in a race no more than 7 per cent. We have measured wings of both sides and averaged them to arrive at a figure for each individual. The measurement was taken without straightening the primaries artificially.

Other measurable characters.—Tail length usually is closely correlated, individually and racially, with wing length. Races differ in average tail length to the same degree (5 per cent) but individual variation is higher with a range of 10 per cent. Because of the correlation with wing and because of the greater individual variation, tail measurements may be set aside as having no additional significance.

Tarsal length varies individually to the extent of about 10 per cent with averages of adjoining races and populations differing no more than about  $2\frac{1}{2}$  per cent. Bill length, measured from the nostril, is similar in its variations but it is not correlated individually, nor necessarily racially, with the tarsus. Tarsal and bill lengths do not correlate individually to a high degree with wing length. We have not been able to see any important variations in bill shape or in relative toe and claw length comparable to the pronounced differentiations in congeneric relatives.

# THE TRANSCONTINENTAL BOREAL AREA (P. L. LINCOLNII)

Newfoundland and Newfoundland Labrador region.—Breeding birds of this region tend to be ruddier on the back and longer-winged than those from western regions in the area. The highest percentage of ruddy-backed birds occurs here, the ruddy category diminishing from 58 to 31 to 8 to 4 per cent in regions progressively farther westward (see table 1). Wing measurements of males average 2 mm. longer than those of the adjoining Quebec-New Brunswick-Nova Scotia region. To show the nature of this geographic differentiation graphs have been constructed setting forth the frequency distribution of size and color categories. The graphs show that correlation (linkage) of these two features is lacking (fig. 26). The heterogeneity of the population is apparent; nevertheless, it is no greater than in many other populations in the rassenkreis. Tail and tarsal length are slightly greater than in western regions, whereas bill length is not greater than in areas immediately to the west. Tail correlates with wing but tarsus does not.

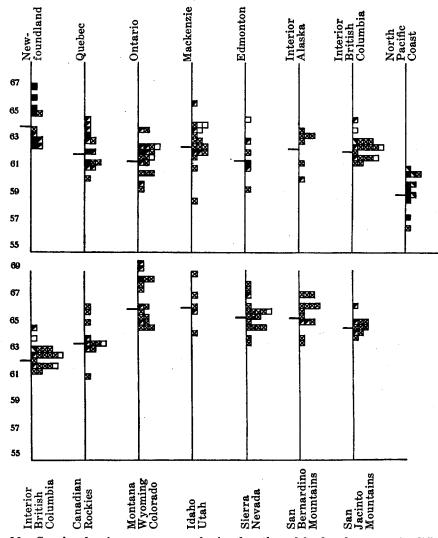


Fig. 26. Graphs showing occurrence of wing length and back color types in different regions. Each square denotes a breeding male bird. Black squares represent ruddy back; half black squares, moderately ruddy; squares with crosses, brown; open squares, gray-brown. Vertical positions of squares indicate wing length in millimeters. Heavy lines at left of vertical lines mark average wing length.

Practical means for the separation of birds from the Newfoundland and Quebec regions or the Newfoundland and Ontario regions do not exist. Separation on the basis of wing or color of back or the two in combination can effect only about sixty per cent segregation. This is below the limit of nomenclatural practicability. Nevertheless, the Newfoundland population presents all qualities of a weak geographic race. If its condition were slightly more homogeneous and there were a little greater segregation of characters geographically, a clearly defined geographic race would result. The northeastern maritime area, which is a region where many animals are represented by distinct races, supports a group of Lincoln Sparrows which seem either to be evolving into a race from individual variants or which represent a race once existent that is being obliterated by intermixture from the west. The hypothesis THE CONDOR

that this is a nascent race is preferred by us because the characters of the birds of this region are not unknown in birds from the opposite side of the continent. If these character types once were limited principally to the east coast, it is unlikely that they could have become so widely and generally dispersed at the present time.

An interesting group of twelve September and October birds from New England gives every indication of representing the Newfoundland breeding population in southward migration. In this group seven ruddy individuals are included and the wing average for males is equivalent to the average for Newfoundland breeding birds.

Quebec-New Brunswick-Novia Scotia region.—The sample from this area (see map, fig. 27) in some respects is intermediate between those of Newfoundland and Ontario. The latter is more nearly typical of populations from the remainder of the transcontinental boreal area. In the Quebec region wing length, and also bill and tarsal length, drop nearly to the value for Ontario birds, but the percentage of ruddy types is half way between the Ontario and Newfoundland groups. Diminution in the ruddy category occasions an increase in the moderately ruddy and brown categories (see table 1). The most instructive fact in connection with this intermediate population is that back and wing alterations have not been coincident geographically, the wing changing more abruptly than the back color in the westward direction. Such a condition is entirely possible since the characters are not linked.

	TA	BLE 1			
Distribution of	back types in per	cent (tra	anscontinental	boreal an	ea),
	including both	males and	i fem <b>ale</b> s		
Region	Number of individuals	Ruddy	Moderately Ruddy	Brown	Gra
lewfoundlend	12	58	33	8	

individuals	Ruddy	Ruddy	Brown	Gray-brown
	58	33	8	0
16 ·	31	44	25	0
24	8	80	54	8
22	4	18	65	13
28	4	21	47	28
. 11	0	18	82	0
- 28	4	21	65	10
	individuals 12 16 24 22 28 11	individuals         Ruddy           12         58           16         31           24         8           22         4           28         4           11         0	individuals         Ruddy         Ruddy           12         58         33           16         31         44           24         8         30           22         4         18           28         4         21           11         0         18	individuals         Ruddy         Ruddy         Brown           -         12         58         33         8           -         16         31         44         25            24         8         30         54           -         22         4         18         65            28         4         21         47           -         11         0         18         82

Ontario region.—The sample from this region comes largely from eastern Ontario, south nearly to Toronto which marks the southern limit of breeding in this sector. As a population characteristic of interior continental regions the group contains a few birds with backs classified as gray-brown. This means that these birds are distinctly grayer than the brown type, not only as regards the basal brown areas of the feathers but also with respect to the margins. There is nowhere a population predominantly of this gray-brown type, but the condition is limited to the interior of the continent. Nowhere in the transcontinental boreal area do birds average smaller with regard to wing and tail than in the Ontario region. But minimum size of bill and tarsus is not encountered here.

Mackenzie region.—The drainage of the Mackenzie River from Great Slave Lake northward constitutes an area fairly well represented in our assembled breeding series. Unfortunately no satisfactory representation from Saskatchewan and western Manitoba is at hand. The precise limits of the breeding range in these provinces still need to be determined. The gap in distribution shown in our map is certainly not a real one.

Wing and tail length in the Mackenzie region is slightly greater than in the Ontario region but bill and tarsus are slightly shorter. The wing length frequency graph leaves little doubt that the difference in average wing length is real, that is, it is not the result of chance sampling, for the representation is uniformly higher than the Ontario group. The Mackenzie region is high in brown-backed types. These differences are of little consequence except as they illustrate slight changes in the mosaic of characters in different localities.

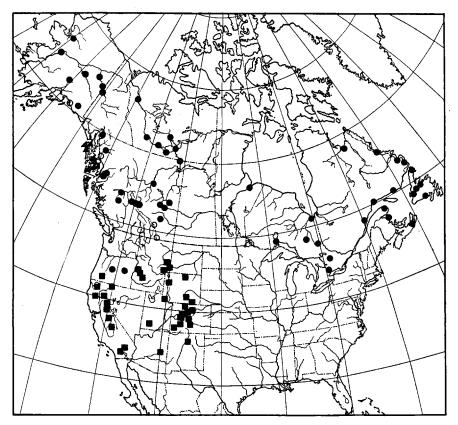


Fig. 27. Localities from which breeding Lincoln Sparrows were examined. Dots represent P. l. lincolnii; triangles, P. l. gracilis; squares, southern montane race; circles, intermediates.

Edmonton-Peace River region.—A small number of skins, most of them from near Edmonton, Alberta, demonstrate the trend of variation in the southwest sector of the plains of Canada. Averages for wing, tail, tarsus and bill are low, but the sample is not adequate to rule out error in sampling. This small region has been combined with the region along the east face of the Canadian Rockies for purposes of back color analysis. Combined they display the peak of occurrence of the gray-brown back type. Ruddy and moderately ruddy categories remain about the same as in the Mackenzie region, brown declining on account of the increase in gray-brown.

The occurrence of the largest proportion of gray-brown birds in this region is suggestive of light-colored plains races of other birds that have differentiated here. It presents a case of slight differentiation, even less than in the Newfoundland region, in which a special phase of coloration attains a frequency no greater than 28 per cent and in which there are no parallel size differences. Nevertheless the character, appearing in these low percentages, is correlated geographically just as are other more prevalent characters in other areas. Is this condition not another potential race? Is it in process of accentuation, and if so, through what mechanism?

Interior Alaskan region.—This region comprises chiefly the Yukon Valley and the mountains south of it but does not include the immediate coast from Prince William Sound southward. The sample from this region is small. In measurements it agrees with the Mackenzie group and the predominance of brown-backed types is even greater. There is complete absence of the gray-brown plains type.

Interior British Columbian region.—This comprises the intermontane section from the Cariboo district north to the Skeena River; our specimens are chiefly from the Cariboo district in the valley of the middle section of the Fraser River. Perhaps because of the restriction of the area, the range of variation in wing length is relatively small. Averages for wing, tarsus and bill are similar to the Mackenzie group and the occurrence of back color types is almost identical. One moderately yellowbacked individual occurs. Thus the Mackenzie River Valley, the interior of Alaska, and the interior of British Columbia form an immense area within which only the slightest geographic variability can be detected.

East face of Canadian Rockies.—The population from Jasper Park southward is characterized by large size which is associated with its position adjacent to the even larger montane groups south of the United States border. Wing and tail reach average values comparable to those for the Newfoundland region, and tarsus and bill show some increase. Although the size in this group may be characterized as intermediate, it is distinctly closer in this respect to populations north of it than to those to the south. Coloration is mentioned in connection with the Edmonton-Peace River region.

Summary of conditions in the transcontinental boreal area.—Of the variable characters studied none seem to be linked (correlated) in the individual except wing and tail length. Wing length decreases westward to Ontario, then increases to a uniform level in the Mackenzie, interior Alaskan and interior British Columbian regions. It seems to be low in the vicinity of Edmonton but increases in the Canadian Rockies, particularly southward near the international boundary. Tail length correlates geographically with wing. The tarsus and bill decrease in length westward to Mackenzie, Alaska, and British Columbia, then increase slightly in the southern Canadian Rockies. Ruddiness of back decreases westward to Ontario, though less rapidly than does wing length, then diminishes slightly to a nearly uniform level in the other regions. Gray-brown back appears only in the interior of the continent with greatest concentration in Alberta. Incipient racial differentiation is suggested in Newfoundland and Alberta.

This in brief is the nature of the mosaics of characters in the different regions, and the various geographic trends. There is no mystic cohesion that makes this entire aggregation a precise unit. Like most geographic races it is nothing but a summation of many individual genetic patterns. It has somewhat indefinite limits of variability and the summation of patterns, or average, is correlated to greater or lesser degree with geographic area.

The limits of variability include individuals with ruddy, moderately ruddy, brown and gray-brown backs; individuals with narrow or moderately broad dorsal stripes; males with wings usually (90 per cent) no longer than 64.5 mm. nor less than 60.0 mm.; females with wings usually no longer than 61.0 mm. nor less than 58.0 mm.

Nomenclaturally this aggregation breeding in the transcontinental boreal area may be termed *Passerella lincolnii lincolnii*. The original description of *Fringilla lincolnii* by Audubon (Ornithological Biography, 2, 1834, 539-541) was based on a specimen from Canadian Labrador (near mouth of Natashquan River, Quebec). This locality is well within the breeding area of the race as here conceived. Delimitation of the breeding area of *P. l. lincolnii* along its western and southwestern borders will be explained as the adjoining races are discussed.

		its in Millime					
(Numbers in parentheses indicate number of specimens)							
Breeding males							
Region	Wing	Tail	Tarsus	Bill length			
Newfoundland	63.8(11)	55.7(10)	20.8(10)	8.0(10)			
Quebec	61.8(15)	55.2(13)	20.8(15)	7.8(14)			
Ontario	61.8(19)	54.6(6)	20.2(6)	7.8(6)			
Mackenzie	62.4 (18)	55.4 (18)	19.7 (18)	7.7 (18)			
Interior Alaska	62.2(7)						
Edmonton-Peace River	61.3(6)	54.7(6)	19.5(6)	7.7(6)			
Interior British Columbia	62.2 (20)	56.4 (19)	19.9 (20)	7.7 (20)			
Southern Canadian Rockies	63.2 (11)	57.2 (11)	20.0(11)	7.8(11)			
North Pacific coast	59.0 (12)	58.0 (9)	19.2(10)	7.5 (10)			
Montana-Wyoming-Colorado	65.9(18)	59.9(19)	20.4 (19)	8.0(11)			
Idaho-Utah	65.9(5)		20.4(5)				
Sierra Nevada	65.8 (24)	59.3(16)	20.4 (19)	8.0(17)			
San Bernardino Mts.	65.2(15)	60.2 (13)	20.0(16)	8.0(6)			
San Jacinto Mts.	64.3(10)	58.1 (5)	19.8 (18)	8.0(7)			
Breeding females							
Ontario	59.3(5)						
Mackenzie	59.1 (8)		**********				
Interior British Columbia	59.1 (8)	53.1(6)	19.2(7)	7.6(8)			
North Pacific coast	56.9(14)	52.4 (8)	19.1 (13)	7.6(7)			
Southern Canadian Rockies	59.9(6)			**********			
Montana-Wyoming-Colorado	61.5(10)	55.7(8)	20.1(9)				
Sierra Nevada	61.1(7)	55.9(13)	19.8(16)	8.0(18)			
San Bernardino Mts.	62.0(7)	58.2(7)	19.7 (7)				
San Jacinto Mts.	62.4 (6)		19.0(7)	7.9(5)			

# TABLE 2

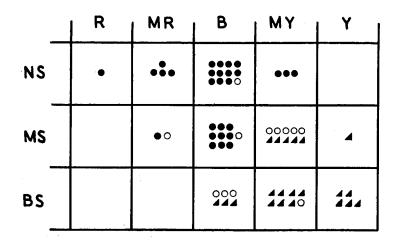
#### THE NORTHERN PACIFIC COAST AREA (P. L. GRACILIS)

Lincoln Sparrows breed in the southern Alaskan archipelago and south at least as far as the Queen Charlotte Islands. Brooks and Swarth (Pac. Coast Avif., No. 17, 1925, p. 59) state that the species is "Rather rare on Vancouver Island; breeds locally in the mountains at the southern end of the island, probably at sea level at the northern end." McCabe has found that the birds do not breed at Bella Coola, British Columbia, at sea level, though they may in the coast range near-by at high elevations. The area under consideration is limited on the basis of available specimens to the archipelago from Queen Charlotte Sound north to Glacier Bay, Alaska, and east to include the mainland coast and the large river valleys and inlets. It does not include the highly elevated regions of the coast range mountains. There appears to be a continuous distribution of breeding Lincoln Sparrows northward and eastward into the interior of Alaska and British Columbia at a few points. But, some degree of isolation, ecologic and geographic, is provided by the mountains. Complete isolation from the interior may have existed during all or part of Pleistocene time.

The characters of the birds of this area display the same correlations found in P. l. lincolnii. Yellow and moderately vellow backs which replace ruddy and moderately ruddy backs show no linkage with size or with broad stripe, a category of stripe width not encountered in other areas but found in a large percentage here. The same range of individual size variation is encountered, but the actual values are all lower (2-5 per cent). The diminution in size compared with the adjacent interior of British Columbia is relatively abrupt, as is also the shift from ruddy types to yellow types (see fig. 26).

Differentiation of the birds of this area is sharper than that in any of the regions in the transcontinental boreal area. It has gone farther and involves more characters than the incipient differentiation in Newfoundland. Nevertheless, there is no one character that is present at all uniformly throughout the group. Most of the birds show a combination of broad stripe and yellowish or brown back color that, together with prominent light-colored edgings, make up a back pattern of strong contrasts. The median feather stripe is black and there is always some crowding together of stripes on the pileum that nearly obliterates the median gray crown region. Although these characters are not linked, rarely are enough of them absent that doubt arises concerning the origin of the individual from this breeding area.

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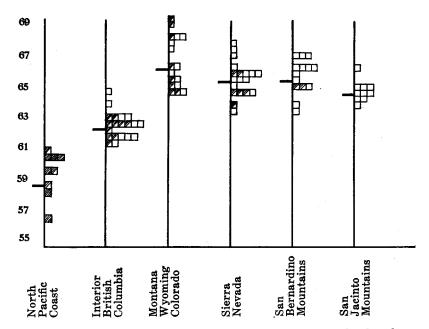


Fig. 28. Upper. Graph showing association of stripe and color characters in individuals of *P. l. gracilis* and adjacent populations of *P. l. lincolnii*. R, ruddy; M R, moderately ruddy; B, brown; M Y, moderately yellow; Y, yellow. N S, narrow stripe; M S, moderate stripe; B S, broad stripe. Triangles are breeding individuals from north Pacific coast area (gracilis); dots are breeding individuals from british Columbia; circles are late spring migrants from vicinity of Bella Coola, British Columbia.

Lower. Graphs showing occurrence of wing length and stripe width in different regions. Each square denotes a breeding male bird. Fully shaded squares represent broad stripe; half shaded squares, moderate stripe; open squares, narrow stripe. Vertical positions of squares indicate wing length in millimeters. Heavy lines at left of vertical lines mark average wing length.

To demonstrate the manner in which these characters occur in individuals we shall consider especially color and stripe width. Figure 28 shows the geographic distribution and association in individuals (not linkage) of these features. Brown back and moderately broad stripes are character types common to birds from interior British Columbia and this coastal area. But these two phases of the color pattern do not appear combined on individuals from the coastal area. Moderately yellow backs may appear in the interior regions, but, if so, in combination with narrow stripe. Brown back may appear on the coast, but in combination with broad stripes. We have little faith that these rules of occurrence of types would stand without exception if still more individuals were available, but they are valid generalizations and hold true in our material.

What now is the association of characters in geographically intermediate localities? The only large sample of birds that possibly could be used in this connection is a group of late spring migrants from near Bella Coola at the inner border of the coastal area in British Columbia. We presume this group represents a population about to breed in intermediate areas not far distant. In any event, in this group no combinations either of extreme coastal or extreme interior characters appear. On the correlation chart these birds are distributed so as to overlap the adjacent parts of the coastal and interior populations. Another, comparable, population of intermediates consisting of early fall migrants is at hand from the mainland coast of Alaska, chiefly the mouths of the Taku and Stikine rivers. This group is a little more predominantly of the coastal type and has some extreme examples with combinations of yellow and broad stripe.

True breeding birds from intermediate localities are scarce. Two such regions are represented. One of these is the Stikine River Valley that cuts through the coast range in central British Columbia. From Flood Glacier, at the eastern limit of the coastal area on the river (Swarth, Univ. Calif. Publ. Zool., 24, 1922, p. 138), there is one juvenile. Its dimensions fall near the upper limit of the coastal group. From Doch-da-on, just through the mountain range where interior faunal conditions prevail, there are: one adult that is broad-striped, moderately vellow and of minimum size for the coastal group; another adult that is moderately striped, brown and of size near the maximum for the coastal group and within the limits of variation of the interior population; a juvenile that is longer-winged than the maximum of coastal birds. Thus, one bird is predominantly of the coastal type, the other two nearer the mean of the interior group. One other locality on the Stikine, Sawmill Lake near Telegraph Creek, is represented by a pair of birds. This locality is still farther inland. The female is moderately yellow, narrow striped and above the maximum of coastal wing size. The male is brown, narrow striped with wing nearly equal to the average of interior birds.

Swarth (op. cit., p. 260) found Lincoln Sparrows scarce along the Stikine bypass to the interior. These few samples point to diffusion of characters from the coast eastward in an irregular fashion that results in birds and populations possessing mixtures of characters.

A second intermediate locality is the region of Prince William Sound, Alaska (Grinnell, Univ. Calif. Publ. Zool., 5, 1910, pp. 404-405). This is far northeast of the Sitkan area and different faunally. A short distance inland, in the vicinity of Mount McKinley, Lincoln Sparrows are of the interior type. The following are the combinations of principal characters in five birds from Cordova Bay, Prince William Sound:  $\delta$  brown, broad stripes, wing intermediate;  $\delta$  moderately yellow, broad stripes, wing above maximum of coastal group;  $\delta$  brown, moderate stripe, wing above average of *P. l. lincolnii*;  $\varphi$  brown, moderate stripe, wing intermediate;  $\varphi$  moder-

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ately yellow, broad stripe, wing above maximum of coastal group. Apparently any mixture of characters can occur, but in general stripe width and color partake more of the coastal type, size of the interior type. Nevertheless, two brown, moderately striped birds occur, which character combination was not encountered on the coast farther south. A specimen taken by Osgood at Cook Inlet, August 28, is in all respects well within the character limits of *P. l. lincolnii*.

The name gracilis seems to us properly applied to the coastal race (see Oberholser, Proc. Biol. Soc. Wash., 19, 1906, p. 42). Kittlitz, the describer, mentions Sitka as the locality where his bird was encountered. There is little chance that he referred to any other race than gracilis as now understood. Migrants of P. l. lincolnii are not known to us from points this far from the mainland.

Limits of variability in the race *gracilis* include individuals with yellow, moderately yellow and brown backs and those with broad or moderately broad stripes on pileum and back. Brown back and moderate stripes do not occur in combination. Males usually have wings no longer than 60.6 mm., and females no longer than 58.0 mm.

## THE SOUTHERN MONTANE AREA

This breeding area comprises the higher mountain ranges of the coast, Great Basin and Rocky Mountain series south of northern Montana, northern Idaho, and central Oregon. Lincoln Sparrows are limited to suitable meadows scattered through these ranges at elevations usually above 3000 feet and extending upward to 10,000 feet. Many of the mountain ranges are relatively dry and experience high maximum summer temperatures. The immediate habitat of the Lincoln Sparrows here is not especially different from that of populations to the northward, but precipitation in the breeding season is less than in the north Pacific coastal area and the transcontinental area exclusive of the plains. Southern outposts in the montane area are Pecos Baldy, New Mexico, the White Mountains, Arizona, and the San Jacinto Mountains, California. To the east distribution is of course sharply limited by the great plains. The western outpost is on the Yolla Bolly Mountains of California.

The chief features of birds of the area are large size and preponderance of brown, narrow-striped types in most of the subregions. Discontinuity of breeding range favors formation of colonies.

Montana-Wyoming-Colorado region.—Figure 26 shows the abrupt increase in wing length southward from interior British Columbia through the southern Canadian Rockies to Montana. Our Montana samples are all from southern Montana (see map) and are in no way different as regards average size from those of Colorado. Birds from Banff and Waterton Lakes, Alberta, represent a stage in intermediacy, but the principal change occurs south of these points.

Tail length is great, corresponding to wing length. Tarsal and bill length increase only to values equal to those in the Newfoundland region. There is no difference in back striping compared with the British Columbian birds and the proportions of color types is similar except for a nearly complete disappearance of the graybrown type.

We have had few fresh-plumaged Rocky Mountain birds taken on the breeding grounds. Those that are available in several instances have a cold brown hue in the back, together with narrow, relatively neutral feather margins. The result is a back pattern of extremely low contrast that we will refer to as the dull type. Since this feature is visible only in fresh plumage we have not been able to set up a separate color category for it and all birds so colored are classed merely as brown. This type of coloration is more prevalent in other regions in the montane area.

Idaho-Utah region.-An inadequate representation, chiefly from Idaho, suggests

size and color characters equivalent to the foregoing region. The Idaho specimens are from the arid mountain section of the central part of the state and are dissimilar in size to specimens from the Blue Mountains of Oregon to the west. These latter (five) average in wing length slightly less than those from the Canadian Rockies. They no more than vaguely suggest intermediacy toward the larger-sized birds south and east of them. The Blue Mountain birds therefore fall entirely within the limits of variability of *P. l. lincolnii*. Whether or not the Idaho region is irregularly connected southward into northern Nevada and northeastern California has not been determined.

Sierran region.—This comprises the entire Sierra Nevada, the southern Cascade mountains from Crater Lake, Oregon, south, and the Warner, Siskiyou and Yolla Bolly mountains of California. No differences among birds from these localities within this region have been found. All size characters average much the same as in the Montana-Wyoming-Colorado region except for a slight decrease in wing length. Back color is somewhat more predominantly brown, with further reduction in ruddy and gray-brown types (see table 3). Narrow striped birds are more abundant (see fig. 28), a trend which is carried still farther in southern California. The peculiar dull type of back frequently is seen in fresh plumages.

TABLE 3							
Distribution of back types in per cent (southern montane area),							
including both males and females							
	Number of		Moderately				
Region	individuals	Ruddy	Ruddy	Brown	Gray-brown		
Interior British Columbia	28	4	21	65	10		
Montana-Wyoming-Colorado _	25	8	24	64	4		
Sierra Nevada	31	5	18	75	2		
San Bernardino Mts.	22	0	9	91	0		
San Jacinto Mts.	16	0	25	75	0		

San Bernardino Mountain colony.—A good representation from this breeding area includes a number of August birds in fresh plumage. Wing and bill size is the same as in the Sierran region. Tail averages slightly longer and tarsus slightly shorter. The ruddy and gray-brown types are wanting and moderately ruddy types are much fewer, so that 91 per cent of the group is brown backed. The population is almost uniformly narrow striped. Nearly all fresh-plumaged birds show the dull type of back.

San Jacinto Mountain colony.—This colony, near, but distinctly isolated from, the San Bernardino locality, displays certain peculiarities that are fairly reliably attested by a group of sixteen individuals. Here there is a uniform decrease in wing size in the males. This is not reflected in females, and curiously in both this group and the San Bernardino group the females are relatively large compared to the males. Bill length is the same as in the San Bernardinos and the Sierra Nevada but the tarsus has dropped to a remarkably low figure, being even smaller than in *gracilis*! This surprisingly small tarsus is found in males and females to equal degree. Ruddy and gray- brown categories are lacking, but the figure for "moderately ruddy" increases to equal that for the Colorado birds. Back stripes are without exception narrow. Thus is culminated a trend toward narrow stripe seen first in the Sierran region. This trend is paralleled by slight decrease in wing in the same regions. Comparison should be made with the trend in *gracilis*, however, in which increase in stripe width parallels decrease in wing length.

The San Bernardino and San Jacinto colonies are good examples of local differentiation and homogeneity of character in restricted isolated localities. They do not show any differences that can reasonably be associated with the special environments of these localities. The two mountains are similar faunally and florally. One is led to suppose that the colonies were derived from small, slightly different, parental stocks that did not contain all the variety of character that may be found in large samples. Probably through isolation and interbreeding they have preserved their germ line in relatively homogeneous state. It also is possible that occasional depletion of the breeding stock has necessitated rebuilding of the population from a small residual sample (see Elton, Animal Ecology, 1927, pp. 186-187). Such circumstances would induce homogeneity and local differentiation depending on the nature of the residuum. These factors may be the explanation for the lack of ruddy and graybrown types and, coincidentally, the different average wing and tarsal lengths and percentages of moderately ruddy birds in the two colonies.

With colonial differentiation progressed thus far, the ground work is laid for insular (boreal mountain top island) races. There is nothing to prevent the agencies which have created the existing colonies from effecting an even sharper differentiation. If differentiation is carried out in this manner, natural selection need not have been a contributing factor. This does not mean that it may not have been.

Summary of conditions in the southern montane area.—Wing and tail length again appear to be linked. These dimensions constitute the most uniform character throughout the area and fairly sharply delimit montane birds from those to the northward. There is some regional and colonial differentiaton that consists in slightly reduced size toward the west. The region of most highly differentiated size (Colorado, etc.) shows least differentiation with respect to color (geographic cross-trends). The dull-colored back is more prevalent westward and, in California, southward. Narrowness of stripe shows a parallel trend. Ruddy and gray types diminish and disappear in the same directions. Tarsal length and moderately ruddy back show peculiar colonial differentiation.

The principle of character mosaic as the basis of the race concept applies to this montane group much as it did to the race *P. l. lincolnii*. The differentiation of the montane race from *lincolnii* is comparable in degree to *gracilis* with respect to dimensions and is distinctly greater than the differentiation in Newfoundland. In the matter of color the montane race is well differentiated only at its southwestern extreme.

Nomenclature of the montane race.—These seems to be no name available for this race. We propose that it be called:

### Passerella lincolnii alticola, new subspecies

The limits of variability of this race include males with wing lengths usually (about 90 per cent) not less than 64.0 mm., averaging 65.2 mm., and females not less than 60.5 mm., averaging 61.5 mm. It includes chiefly birds with moderately ruddy or brown backs, rarely ruddy or gray-brown backs. The greatest number are brown-backed. Varying percentages of brown backed birds are of the dull brown type with reduced light feather margins. Birds with moderately broad and narrow stripes are included, but the latter type predominates.

We deplore the sanctity that often shrouds the type specimen in current systematic treatises. In the course of nomenclatural bickerings the type specimen has certain values which bespeak its careful preservation, but its scientific value in modern ornithology is, in our opinion, not great. The inability of a single type specimen to characterize a race mosaic is patent. There is no such thing as a specimen typical of all phases of the race or of the species. At best, a type is a form of insurance—a point of reference to turn to only in the event that the analysis of a newly described form is entirely inadequate. The type continually should be viewed in proper perspective and should not be allowed to overshadow and distort the true picture of the group of animals concerned. There is no doubt that preoccupation with the type specimen, even in familiar fields with abundant material, can create a working tradition which

disregards the complete character of the breeding population and misses the point of the study of geographic variation. Often, under modern conditions, we can imagine that a type locality without a type specimen would be a desirable arrangement where geographic races are involved.

To propose some definite type specimen we can do not more than select an individual from some one subregion in the range of the race and designate what category

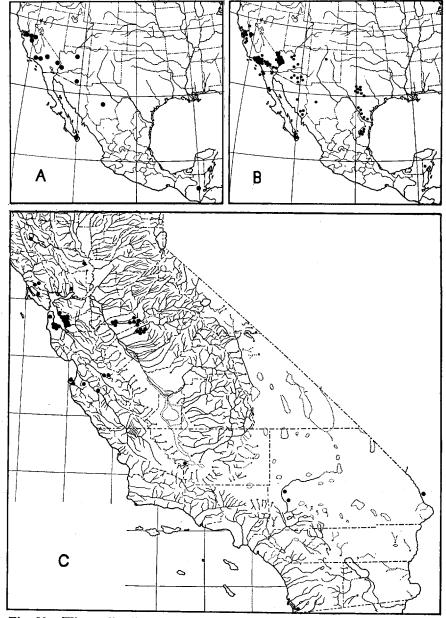


Fig. 29. Winter distribution of races of Lincoln Sparrows based on strongly characterized specimens only. Each dot represents a single individual.
A, P. l. alticola; B, P. l. lincolnii; C, P. l. gracilis.

of color, stripe width and size it represents in our concept of the race pattern. We have chosen no. 36111, Mus Vert. Zool.,  $\delta$  adult, Bluff Lake, 7400 feet, San Bernardino Mountains, San Bernardino County, California; collected August 28, 1905, by J. Grinnell. This bird had nearly finished the postnuptial molt. The tail is not yet full length but one of the wing feathers (6) that constitutes the wing tip is fully grown. Average length of the two wings is 66.5 mm., or about 1 mm. above the average for males of this colony and near the maximum. The bird is narrow striped, but not exeremely so; it is brown-backed, displaying the cold brown hue previously described, combined with lack of contrasting margins. The bill is slightly below average, the tarsus above average for the sample from this colony.

### WINTER DISTRIBUTION

Rather than court error by naming all winter specimens, we have selected for purposes of plotting the winter distribution only those birds that possessed combinations of characters which left no reasonable doubt as to breeding area to which they belonged. In no instance do we know of birds wintering on the breeding grounds. Occasionally individuals remain far north of the normal wintering range; as, for example, a bird taken at Kingston, Ontario, January 4, 1932.

P. 1. lincolnii.—Figure 29 presents a fairly complete picture of winter distribution in the western United States except for New Mexico and parts of Texas. Concentration of dots is likely to mean concentration of collecting activities. Nevertheless, the larger of the concentrations in California and Arizona, such as that along the Colorado River, we believe represent true concentrations of birds. Further collecting in Mexico doubtless would demonstrate a more general distribution than indicated.

This race has been reported by Griscom (Bull, Am. Mus. Nat. Hist., 64, 1932, p. 364) from Guatemala, but of course such a record does not preclude *alticola*, one of which we have examined from that country. Probabilities favor the occurrence of P. *l. lincolnii* as now understood south to Guatemala. We have no information regarding details of winter distribution in the eastern United States additional to that which forms the basis for statements in the latest edition of the A. O. U. Checklist (1931, p. 536). One should not be misled into supposing that Lincoln Sparrows do not winter in the southern states because of absence of record localities on our maps.

In migration *P. l. lincolnii* may appear on the southern British Columbian coast and it has been found in early spring on several of the islands of southern California.

**P. l. gracilis.**—This race is restricted chiefly to California in winter. It is most concentrated along the coast in the northern half of the state and in the Sacramento-San Joaquin Valley. Winter collections from these points are predominantly of this race whereas south of the Tehachapi strongly-characterized gracilis are almost wanting and *P. l. lincolnii* is prevalent (compare figs. 29B and 29C). Outside of California gracilis-like specimens almost always are intermediate toward *P. l. lincolnii*. Such is the case in Lower California where all the specimens of "gracilis" in the Museum of Vertebrate Zoology reported by Grinnell (Univ. Calif. Publ. Zool., 32, 1928, p. 177) fail to show enough character to warrant placing them on our map. Many of them we feel are closer to gracilis than to *P. l. lincolnii* and probably have some genetic affinity with the former. The specimens reported by Griscom (loc. cit.) from Guatemala we have not studied. It is not impossible that the race winters this far south. We must re-emphasize the fact, however, that the greatest number and the most typical individuals winter in central and northern California.

Among migrants worthy of special note is one from 10 miles south of Cibola,

Arizona, on the Colorado River. It is clearly *gracilis*. Spring and fall migrant Lincoln Sparrows in the northern coast belt of California are chiefly of this race. In September *gracilis* has appeared in the Yosemite Valley, showing that the birds must move southward in the mountains, avoiding the dry, hot interior lowlands in the early fall. There is a fall migrant from Eagleville, Modoc County, California.

P. l. alticola.—This race is not concentrated like *gracilis* in winter but is scattered with *P. l. lincolnii* in the southwestern United States and Mexico. One specimen from Guatemala has been examined. Frequently this race winters in the lowlands near the mountains in which it breeds.

There are a number of examples of *alticola* that have been taken late in the fall migration or early in the spring that indicate probable wintering localities. The localities are: 10 miles east of Sanger, Fresno County, Palm Springs, Riverside County, and Los Angeles, California; Todos Santos, cape district, Lower California; 7 miles south of Bisbee and Patagonia, Santa Cruz County, Arizona.

Unequivocal examples of *alticola* sometimes appear mixed with groups of *lincolnii* in Colorado at the eastern base of the mountains in early May. Similarly, several *alticola* have been taken along the eastern and western flanks of the Sierra Nevada shortly before or after the breeding season.

### SUMMARY AND CONCLUSIONS

Analysis of the mosaic of characters in breeding populations of Lincoln Sparrows (*Passerella lincolnii*) has been made. This mosaic has no precise limitations in pattern in a given race. In passing from one geographic race area to another, different characters come into prominence in the pattern, and occasionally new characters appear in varying proportions. These shifts in pattern, these differences in summation of characters, that are geographically correlated are all that mark the races. There are no other cohesive factors (except perhaps physiologic characters) that bind individuals into race units.

Three principal races were found, one, P. 1. lincolnii, occupying the transcontinental boreal area, another, gracilis, the north Pacific coast area, and a third, alticola, heretofore unrecognized, the montane region of the western United States. Within these races incipient differentiation, correlated with geographic locality, was found that led in various stages from the level of individual variation to that of weak racial differentiation. The essential steps along the course of racial evolution seem to be illustrated. Colonial differentiation on isolated mountain tops in southern California presents a situation with potentialities for the evolution of insular races. Population fluctuations and isolation with resultant genetic homogeneity and preservation of a particular type of variant are likely factors in the establishment of the present condition and seem capable of augmenting the differentiation.

Trends of character differentiation have been traced geographically. The trend in two characters may be parallel and proceed at the same rate. More often two trends proceed at different rates and, though parallel in one region, may run counter to one another elsewhere. The large-sized *alticola* appears to controvert Bergmann's law of large-sized races in cold regions. During the breeding season *alticola* experiences greater maximum temperatures than *P. l. lincolnii* and *gracilis*. This does not rule out the possibility that a summation effect of moderate to warm daytime temperatures in northern latitudes may have more influence than the short midday maximum of the southern mountains.

Variable characters, except for wing or tail, do not appear to be linked. Birds from regions intermediate between race areas are not uniform blends of characters but usually present various mixtures of characters in the individual with the popuTHE CONDOR

lation encompassing most of the range of variation in the two races concerned. Nevertheless, each character may "blend" from one extreme manifestation to the other. This is the sort of complex to be expected if two populations, already heterogeneous and with characters inherited through many sets of factors, are thrown together and interbreed.

Winter ranges of races of Lincoln Sparrows have been mapped. The race *gracilis* has a restricted winter range. The other two races are wide spread in winter, but with local concentrations where there are favorable conditions.

The amount of individual variation (presumably genetic) in characters appears to us to be of the same order as that encountered in Fox Sparrows (*Passerella iliaca*) and Song Sparrows (*P. melodia*). In Lincoln Sparrows there is no reason to believe that in any one type of character there is less raw material in the way of variation upon which natural selection may work in the production of races. There are, however, fewer characters that differentiate conspicuously. Such characters as ventral spotting, coloration of ventral spots, bill shape, length of claw of hallux, that differentiate in races of Song Sparrows and Fox Sparrows, have not done so in Lincoln Sparrows. Yet, the reason they have not may be that there has been no selective pressure, for clearly there is some individual variation in all these features in Lincoln Sparrows.

A sort of organic selection may operate in Fox Sparrows and Song Sparrows to induce diversification. For example, Fox Sparrows by temperament (probably hereditary) may be especially given to pushing into new regions and new habitats; certainly they appear to have accomplished this. The attempt to colonize would set up new habits in the individual and throw the bird under new selective influences so that racial evolution would be relatively rapid. The Lincoln Sparrow, on the other hand, by rigidly adhering to a certain ecologic niche for purely psychologic reasons (there might be others) would not differentiate greatly even though giving rise to variants upon which selection might work. The bird is not adventurous. Species that are aggressive in the sense of range expansion, geographically or ecologically, and yet not too adaptable individually, should form large rassenkreise. We can see in the natural history of the Lincoln Sparrow, then, factors which we think are partly responsible for lesser racial differentiation compared with its generic relatives.

Museum of Vertebrate Zoology, Berkeley, California, January 17, 1935.

# CONTINENTAL LAND MASSES AND THEIR EFFECT UPON BIRD LIFE

### WITH TWO ILLUSTRATIONS

# By P. A. TAVERNER

It seems that no particular attention has ever been called to the effect that relative shape and size of the large continental land masses may have upon bird populations, especially of migratory species; yet an important relation exists between them. It is obvious that no population can increase permanently beyond the number that can be carried through the most difficult season. The amount of live stock that a ranch can carry is not measured by summer pasturage but by its winter resources. Similarly, no northern area can, except temporarily, possess more migratory birds than can be supported through the winter in southern quarters. No improvement in northern conditions can ever increase migratory bird populations