NUMBER 532 JUNE 29, 1951

OCCASIONAL PAPERS OF THE MUSEUM OF ZOOLOGY

UNIVERSITY OF MICHIGAN

ANN ARBOR, MICHIGAN UNIVERSITY OF MICHIGAN PRESS

VARIATION IN THE PAINTED BUNTING (*PASSERINA CIRIS*), WITH SPECIAL REFERENCE TO WINTERING POPULATIONS

BY ROBERT W. STORER

IN the early days taxonomists approached their subject by naming the different kinds of animals and then identifying individual specimens as belonging to a given kind. More recently, there has been a tendency to treat populations, studying first the individual variation within a population and second the variation from one population to the next. This means treating groups below the level of the subspecies, and the application of names to populations or groups of populations rather than to individuals. The actual naming of forms and the identification of individual specimens have become secondary; and it is necessary to leave individuals of intermediate populations unidentified or to assign arbitrary geographic limits to subspecies in which variation of a clinal nature occurs. The "population" approach has been made possible by the increased number of specimens in collections and by an increased application of statistical methods. Systematic studies of this nature have often added to the knowledge of such basic problems as evolution and migration.

The relative newness of this approach means that, to date, the variation in relatively few species has been thoroughly worked out; and, hence, in the absence of sufficient data on most species, curators must often continue to identify individual specimens as before.

The history of the taxonomic treatment of the Painted Bunting illustrates this difference in approach and will, I hope, emphasize some of the advantages of the use of populations rather than individuals in work of this sort.

In 1758 Linnaeus described this species as *Emberiza ciris,* basing his description on Catesby's *Fringilla tricolor* from Carolina. In 1911 Mearns[1] separated a large, pale race, *pallidior,* from Fort Clark (= Brackettville), Kinney County, Texas. From then on, individual specimens have been identified either as typical *ciris* or as *pallidior.* This has resulted in a somewhat vague idea of the variation within the species and an extremely poor idea of the breeding populations represented on the various wintering grounds. Attempts to allocate individual wintering specimens to one or the other of the two races have resulted in records of both races wintering in Veracruz, Chiapas, Yucatán, Guatemala, El Salvador, and elsewhere in Mexico and Central America. These reports may mean one of three things: first, that Painted Buntings from the entire breeding range (the Atlantic seaboard to western Texas) winter together; second, that these wintering grounds are populated with birds from areas of intergradation; or third, that some of the identifications are incorrect. The solution of this problem, which arose in connection with the determination of the status of the wintering birds of Guerrero, was the primary stimulus for undertaking this study of the Painted Bunting. The method followed has been to work out: first, the variation within a single population (that of the Atlantic seaboard); second, the geographic variation among populations in different parts of the breeding grounds of the species; and third, the use of this information in determining the wintering grounds of the various breeding populations.

A total of 871 specimens was examined. These were distributed by collections as follows: Chicago Natural History Museum, 211; United States National Museum, 193; University of Michigan Museum of Zoology, 171; Museum of Comparative Zoology, 112; Museum of Vertebrate Zoology, 51; Louisiana State University Museum of Zoology, 49; Academy of Natural Sciences of Philadelphia, 34; George M. Sutton, 28; R. W. Shufeldt, 15; and Chicago Academy of Sciences, 7. In addition, 18 specimens in the collection of the University of Kansas Museum of Natural History were measured by Mr. R. M. Mengel. I am indebted to Mr. Mengel and to the curators and owners of these specimens for permission to use the material under their care.

[1] Mearns' (1911: 217) inference that Veracruz is the type locality of the nominate race is almost certainly in error.

A geographic breakdown of the specimens examined follows:

UNITED STATES.—North Carolina, 9; South Carolina, 53; Georgia, 47; Florida, 82; Alabama, 2; Mississippi, 21; Louisiana, 62; Arkansas, 1; Oklahoma, 13; Texas, 264; New Mexico, 8; Arizona, 7.

WEST INDIES.—Bahamas, 8; Cuba, 1.

MEXICO.—Tamaulipas, 13; San Luis Potosí, 5; Veracruz, 24; Puebla, 4; Morelos, 2; Tabasco, 2; Campeche, 2; Yucatán, 64; Chiapas, 11; Oaxaca, 28; Guerrero, 42; Colima, 3; Jalisco, 2; Sinaloa, 3; Coahuila, 4; Chihuahua, 3.

CENTRAL AMERICA.—Guatemala, 39; Honduras, 10; El Salvador, 6; Nicaragua, 11; Costa Rica, 14; Panama, 1.

MOLTS AND PLUMAGES

The molts of the Painted Bunting have been described by Dwight (1900: 215–16), and to this account, I have little to add. The postjuvenal molt is nearly complete, but the brownish juvenal primary coverts are usually retained until the time of the first postnuptial molt. In some first winter specimens a few of the outer coverts have been replaced by green-edged feathers of the adult type. Most first-winter birds of both sexes also retain some of the juvenal remiges; but the six outer primaries and the four inner secondaries (including the "tertials") are, I think, always replaced.

After the postjuvenal molt there is one complete molt each year following the breeding season. The first of these annual molts results in the adult plumage. Although there is no true prenuptial molt, a few feathers may be replaced; and first-year males usually have some blue feathers on the head by the time they reach the breeding grounds in April. A few adult females may also have a blue feather or two on the head.

Seasonal variation in the color of the plumage is marked in the Painted Bunting. This is due solely to wear and fading. In contrast with males in the breeding season, adult males in fresh fall plumage are generally bluer above: the blue of the head being much darker and more purplish, the green of the back much darker and less yellow, and the rump and upper tail coverts more purple and less reddish. These seasonal differences are several times greater than any racial differences noted. This makes it necessary to use seasonally comparable birds in racial comparisons. I could find no constant racial differences in the color of the head and back, but

there is a valid racial difference in the tone of the red underparts, the western birds having a pinker and less orange hue in these feathers.

Color differences due to fading and wear in "hen-plumaged" birds are also considerable, and they are greater in both first-year males and females than they are in adult females. The color changes result from a loss of yellow on both the underparts and the upperparts. By the end of the breeding season the upperparts have become a much bluer and even a grayer green. Again, this difference is much more marked than the racial differences, which are largely confined to the amount of yellow in the underparts.

It is unfortunate that many specimens of the green-plumaged Painted Buntings which I have examined are probably wrongly sexed. Apparently, some collectors have not realized that first-year male Painted Buntings are "hen-plumaged" and for this reason have refused to believe their dissections. In one or two other instances institutions which added their own labels to the original labels on the specimens put the wrong sex on the new label.

In a series of specimens selected as probably correctly sexed, first-year males average considerably brighter and somewhat larger than adult females, which in turn average brighter and larger than do first-year females (see Table I). Thus, first-year males may usually be distinguished from first-year females on the basis of size and color characters, and adult females are the only green-plumaged Painted Buntings with a complete set of green-edged primary coverts.

From this it will be seen that, in order to compare birds from different populations, it is necessary to use birds of comparable sex and age groups. This makes it imperative that all material be sexed with the utmost care.

A minor pitfall to be avoided in working on Painted Buntings lies in a peculiarity of the green feathers of the head and back of the "hen-plumaged" birds. When these feathers are turned upside down, they appear blue instead of green; and green feathers which have dried in this position may easily be mistaken for feathers of the adult male type. The blue of reversed feathers is not so deep, however, as that in the plumage of adult males.

Frequently, adult male Painted Buntings have one or more green tail feathers. These are not necessarily an indication of immaturity but presumably result when feathers are replaced at times other than that of the

TABLE I

Age and sexual variation in the Painted Bunting

Group	Number	Wing					Tail				
		Max.	Min.	Mean±σ_m	σ	V	Max.	Min.	Mean±σ_m	σ	V
Eastern population (N. Car. to Fla.)											
Adult males	68	73.5	68.0	70.54±0.14	1.17	1.66	59.5	52.5	55.52±0.17	1.39	2.50
First-year males	23	71.5	66.5	68.37±0.23	1.11	1.62	56.5	51.5	54.05±0.27	1.28	2.37
Adult females	32	68.5	63.0	66.08±0.25	1.43	2.17	56.0	51.0	52.89±0.23	1.30	2.45
First-year females	16	68.5	63.5	65.78±0.33	1.31	1.98	54.0	49.0	51.47±0.32	1.27	2.39
Western population (Tex., Okla., N. Mex.)*											
Adult males	128	78.0	68.5	73.20±0.15	1.74	2.38	60.5	51.0	56.54±0.15	1.69	2.99
First-year males	48	74.0	66.5	71.45±0.23	1.57	2.20	59.0	51.5	55.09±0.22	1.52	2.76
Adult females	29	73.5	66.0	68.84±0.31	1.66	2.41	56.5	50.5	53.40±0.32	1.70	3.18
First-year females	15	70.0	65.5	67.90±0.37	1.44	2.12	55.0	50.5	52.56±0.32	1.27	2.42

*The higher standard deviations and coefficients of variation in the western population reflect the greater geographic variation within this population (see Table II).

annual molt. An adult male (U.S.N.M. No. 144,193) taken by Nelson and Goldman on April 15, 1894, at Otatitlan, Veracruz, has four fully grown red rectrices left from the fall molt. The other rectrices, all green like those of a female, are approximately 1 cm. shorter than the red ones and have not completely erupted from the sheaths at their bases. There are a few yellow feathers below, probably also replacements, but otherwise the plumage is that of an adult male.

Two specimens (U.S.N.M. No. 348,067 and M.C.Z. No. 3878) have the red of the normal adult male plumage (remiges, rectrices, back, and underparts) replaced with yellow. The former specimen is a cage bird from the National Zoological Park; the latter is from Orizaba, Veracruz, where these birds are frequently caged. According to Lee S. Crandall (*in litt.*), adult males of this species "invariably have red replaced by yellow at the first molt in captivity." He stated further that "this color can sometimes be preserved, in varying degrees, by the use of sweet red pepper and other vehicles of Vitamin A."

The intake of vitamin A, however, can play only a small part. The lack of red in females and first-year males, which presumably molt at the same time as the adult males, and the fact that adult males fail to produce normal red feathers at times other than that of the normal molt strongly indicate that a hormonal factor is involved in the production of the red pigment.

Adult females and first-year males occasionally have reddish feathers. These are most frequently on the underparts, but may occur on the back, rump, crown, or even among the remiges (as A.N.S.P. No. 121,553, male). The red on such birds is never as bright as it is on the adult males and occurs on individual feathers scattered through the plumage, producing a mottled effect. It is not, as Sharpe (1888: 615) said it was, the normal plumage of the adult female.

Coues' statement (1884: 391) that the young male is "at first like ♀; acquiring the red and blue with every possible gradation between the colors of the two sexes," has been quoted or paraphrased by several others. It is strictly applicable only to the period of the first postnuptial molt. Although young males in their first breeding season may have some blue on the head and some red on the underparts and elsewhere and adult males may have some green flight feathers and yellow feathers on the underparts, both due to replacement outside of the season of the annual molt, there is

still a very large gap between the most advanced young male and the adult with the most replaced feathers.

GEOGRAPHIC VARIATION IN COLOR

Mearns (1911: 217) described *Passerina ciris pallidior* as being larger than *P. c. ciris,* and the "adult male with underparts considerably paler vermilion red; rump and upper tail coverts paler, more purplish red" than the typical race. The females were described as "paler throughout." My own comparisons between birds of like age and sex indicate that the underparts of the adult males from central Texas and west are a pinker and less orange red than are those of the eastern birds and that the underparts of the females and first-year males of the eastern populations are yellower than are those of the Texas birds. I failed to find consistent differences between eastern and western birds in the color of the upperparts. If any such difference is present, it is greatly overshadowed by age, sex, and seasonal differences. On the basis of color, the line of demarcation between the eastern and western birds lies in eastern Texas, the birds of Louisiana being bright and those of central Texas being pale.

The buntings wintering in Florida and the West Indies agree in color with the eastern breeding population, as do nearly all of the wintering birds of the Yucatán Peninsula. The birds taken in other parts of Mexico and in Central America are, with few exceptions, like the western birds in color.

GEOGRAPHIC VARIATION IN SIZE

The necessity for comparing birds of the same sex and age group, combined with evidence that many "hen-plumaged" birds in collections have been missexed, was the reason for my selection of only adult males for the analysis of geographic variation in size. Fortunately, collectors seem to have found it difficult to resist taking adult male Painted Buntings, and this is the group best represented in collections.

Birds from the following seven areas were selected as the population samples representing the various parts of the breeding range of the species: eastern North Carolina to northeastern Florida, southern Louisiana and the adjacent parts of Mississippi, southeastern Kansas and eastern Oklahoma, central northern Texas (Cooke, Shackleford, and Tarrant counties), central Texas (Bexar, Coryell, Gillespie, Hays, Kendall, Kerr, Lampasas, and

Travis counties), southern Texas (Cameron, Hidalgo, Kenedy, Kleberg, Nueces, and Webb counties), and New Mexico and western Texas (Brewster, El Paso, Hudspeth, Jeff Davis, Kinney, Reeves, Terrell, and Val Verde counties). Figures for wing (chord) and tail measurements for these populations are shown in Table II.

Birds from the following areas on the wintering grounds were used as samples for comparison with the breeding populations: southern Florida and the West Indies, the Yucatán Peninsula, eastern Mexico (the states of Tamaulipas, San Luis Potosí, Veracruz, Puebla, and Tabasco), western Mexico (the states of Sinaloa, Jalisco, Colima, and Guerrero), southern Mexico (the states of Oaxaca and Chiapas), and Central America. The figures for wing and tail length for birds of these populations are also given in Table II.

An examination of these figures shows that there is a cline of increasing wing length from North Carolina and Florida through Louisiana to central Texas, and a similar cline from south to north in Texas. The first was to be expected on the basis of Mearns' description of *pallidior,* whereas the second is rather surprising and is of considerable significance in the interpretation of the status of the birds wintering in Mexico and Central America. Tail length appears to be more variable than wing length. Whereas there is a cline in tail length parallel with the east-west cline for wing length, what geographic variation in tail length there is in Texas does not appear to be clinal in nature.

COMPARISON OF WINTERING AND BREEDING POPULATIONS

Upon comparing the wintering populations with the breeding populations it is evident that the Florida–West Indies sample, although small in numbers, agrees well in size with the North Carolina to Florida breeding sample. As there is also agreement in color characters, there can be little doubt that these two populations are the same.

The birds wintering in Yucatán, like the eastern birds, are brightly colored. They appear to have significantly longer wings than those of the southern Louisiana–Mississippi sample, but otherwise agree closely with these birds. In view of the cline of increasing wing length from south to north in Texas, it might be expected that the breeding birds from farther north in the Mississippi Valley would be longer-winged than the Louisiana–Mississippi sample used here. Thus it is likely that the breeding birds from

TABLE II

Geographic variation in wing and tail length of adult male Painted Buntings

Population	Number	Wing					Tail				
		Max.	Min.	Mean$\pm\sigma_m$	σ	V	Max.	Min.	Mean$\pm\sigma_m$	σ	V
Breeding populations											
North Carolina to Florida	68	73.5	68.0	70.54±0.14	1.17	1.66	59.5	52.5	55.52±0.17	1.39	2.50
Louisiana and Mississippi	39	75.5	68.0	71.04±0.27	1.71	2.41	58.0	51.5	55.66±0.21	1.35	2.43
Northern Texas	34	78.0	69.5	74.40±0.30	1.72	2.31	59.0	53.5	56.38±0.27	1.55	2.75
Central Texas	34	76.0	70.0	73.38±0.21	1.22	1.66	60.0	54.0	57.03±0.23	1.36	2.38
Southern Texas	25	74.0	68.5	71.26±0.28	1.41	1.98	58.0	53.0	55.54±0.22	1.13	2.03
New Mexico and western Texas	22	76.0	70.5	73.32±0.32	1.52	2.07	60.5	54.5	57.80±0.35	1.63	2.82
Kansas and Oklahoma .	13	74.5	70.0	73.12±0.33	1.19	1.63	58.0	51.0	55.54±0.51	1.83	3.29
Total western populations	128	78.0	68.5	73.20±0.15	1.74	2.38	60.5	51.0	56.54±0.15	1.69	2.99
Wintering populations											
Florida and West Indies	7	71.5	69.5	70.79			56.0	54.0	55.29		
Yucatán	39	75.0*	68.5	71.99±0.24	1.50	2.08	59.0	52.5	55.97±0.23	1.39	2.48
Eastern Mexico	28	76.0	70.0	73.07±0.28	1.50	2.05	60.0	54.0	56.50±0.27	1.38	2.44
Western Mexico	13	75.5	70.0	72.73±0.69	1.79	2.46	59.0	54.5	56.75±0.38	1.41	2.48
Southern Mexico	20	77.0	70.0	73.46±0.42	1.86	2.53	61.0	53.0	56.95±0.49	2.20	3.86
Central America	45	77.0	71.0	73.26±0.20	1.35	1.84	59.5	52.5	56.18±0.23	1.51	2.69
Central America and Mexico (exclusive of Yucatan)	106	77.0	70.0	73.22±0.15	1.54	2.10	61.0	52.5	56.52±0.16	1.66	2.94

*One 78.0.

the Mississippi Valley and the Gulf coast of Alabama, Mississippi, and Louisiana winter in Yucatán. Further, the lack of migrating specimens of this brightly colored population from southern Texas and eastern Mexico suggests that these birds migrate directly across the Gulf of Mexico to their wintering grounds in Yucatán.

The wintering populations of Mexico (exclusive of Yucatán) and Central America show no significant differences in wing or tail length *inter se*. As regards color, all birds examined from Coahuila, Chihuahua, Sinaloa, Jalisco, Colima, Guerrero, Morelos, Veracruz, Tabasco, and Chiapas agree with the pale Texas specimens. Birds from Central America and elsewhere in Mexico are predominantly pale, with some intermediate or indeterminate birds and a few bright birds which seem closer to the eastern groups. When measurement data for the western populations (Kansas, Oklahoma, Texas, and New Mexico) are combined and those of Mexico (exclusive of Yucatán) are treated similarly, a surprisingly close agreement between the two groups is apparent (see Table II). This is strong evidence that virtually all of the wintering Painted Buntings of Mexico belong to the western populations as does the great majority of birds wintering in Central America. It is probable, however, that a few Mississippi Valley birds wander south from Yucatán into Central America.

CONCLUSIONS

For purely practical taxonomic purposes, it seems advisable to recognize two races: *Passerina ciris ciris*, which is smaller and brighter (more yellowish) underneath and breeds from North Carolina and Florida to Louisiana; and *Passerina ciris pallidior*, which is larger and paler below and breeds from Kansas and central and southern Texas to eastern New Mexico, northern Chihuahua and Coahuila, and probably northern Tamaulipas. Birds from southern Texas are intermediate between the two races in size but not in color and are referred to *pallidior*. On the basis of the few specimens available, the birds from eastern Texas appear intermediate in both respects. More breeding material is needed from this area and from northern Mississippi, Tennessee, and Arkansas to determine the status of the birds of these areas. Birds from the last three states should prove bright below and somewhat larger than the birds from Louisiana.

In the past there has been a tendency to rely rather strongly on measure-

ment data for the subspecific identification of wintering Painted Buntings. This has led to some confusion, since there is considerably more overlap between the races than was formerly thought to be the case. When sufficient material of comparable age, sex, and season is available, single specimens can usually be identified on the basis of color alone. Series are often necessary if size differences are to be used.

In species in which two or more populations share a common wintering ground, there is always a possibility that some individuals, especially first-year birds, will follow individuals of other populations to their breeding grounds. The resulting interbreeding of birds from different populations tends to reduce the genetic and, hence, the morphological differences between populations, while, at the same time, it increases the genetic variability within the given population. The segregation of the three principal populations of the Painted Bunting on the wintering grounds, as well as on the breeding grounds, has probably been a factor favoring the development and maintaining of size and color differences among the three populations.

Application of statistical methods to the data obtained from the large numbers of available specimens of many species should make it possible to work out in detail the wintering ranges of the various breeding populations of many of these species, including some in which variation between populations is below the subspecific level. When this is done, the wintering ranges of many breeding populations may well prove more circumscribed than is generally thought to be the case. The results of such studies should individually provide clues to the evolution of the species concerned and collectively help trace the histories of whole bird faunas.

LITERATURE CITED

COUES, ELLIOTT
1884 Key to North American Birds. Boston: Estes and Lauriat. xxx + 863 pp.

DWIGHT, JONATHAN, JR.
1900 The Sequence of Plumages and Moults of the Passerine Birds of New York. Ann. N.Y. Acad. Sci., 13: 73–360, 7 pls.

MEARNS, EDGAR A.
1911 Description of a New Subspecies of the Painted Bunting from the Interior of Texas. Proc. Biol. Soc. Wash., 24: 217–18.

SHARPE, R. BOWDLER
1888 Catalogue of the Birds in the British Museum. 12: xv + 871 pp., 16 pls.

Submitted for publication December 11, 1950.