

HYBRIDIZATION IN THE BUNTINGS (*Passerina*) OF THE GREAT PLAINS

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INTRODUCTION

The Indigo Bunting (*Passerina cyanea*) breeds over most of eastern North America from southern Canada to the Gulf of Mexico and from the Great Plains to the Atlantic. The Lazuli Bunting (*P. amoena*) occupies the western complement of this range, breeding mainly west of the Great Plains from southern Canada to northern New Mexico and central Arizona and to the Pacific coast (Fig. 1).

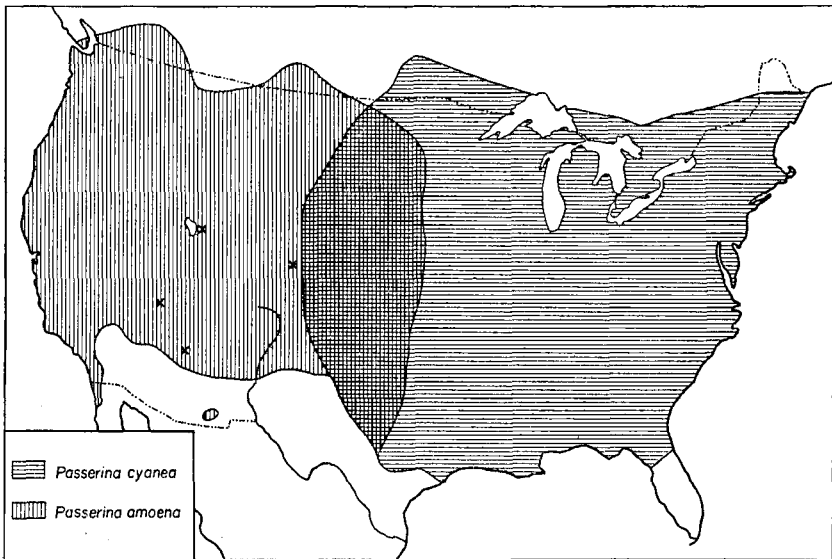


FIGURE 1. Breeding ranges of *Passerina cyanea* and *P. amoena* showing the area of overlap. Several western records of *cyanea* mentioned in the text are indicated by an X.

Both forms occur in brushy vegetation and along the edges of woodland. Their songs and calls, general behavior, and nests and eggs are extremely similar or identical. The adult males differ in color but the females are nearly indistinguishable.

The two forms were, until recently, isolated from one another by the unsuitable grassland habitat of the Great Plains. This isolation had endured at least since the Pleistocene when the glaciers divided the ancestral population as they did the populations of many other

groups of birds with similar eastern and western representatives today.

With the advent of agriculture in the plains during the past century there have been profound changes in the distribution of vegetation, and hence in the distribution of birds. The planting of trees and shrubs has greatly increased the favorable habitat for woodland and brush-dwelling species (see discussion by Sibley and West, 1959). As a result the two buntings have extended their ranges and the secondary contact between them has become extensive over a broad area in the Great Plains (Fig. 1). Because reproductive isolating mechanisms had not evolved by the time the extrinsic barrier was broken down, the two buntings have interbred. The present paper is a study of the hybridization which is now occurring in the area of overlap in South Dakota, Nebraska, Colorado and Wyoming.

MATERIALS

This study is based mainly upon 95 male specimens of *Passerina* from the states mentioned. Of these 58 are in adult plumage, 37 are subadults.

In 1955, 29 specimens were collected in Nebraska and 31 in South Dakota. In 1956, 10 were taken in Nebraska and 16 in Colorado, and in 1957, three were obtained in Nebraska. In addition three specimens from eastern Wyoming (Crook Co.) and three from the Black Hills region of South Dakota were borrowed from the Pettingill collection through the courtesy of O. S. Pettingill, Jr. Additional comparative material from states east and west of the plains was already available in the Cornell University collection.

PLUMAGE CHARACTERS OF THE MALES

Adult male Indigo Buntings in nuptial plumage are entirely deep blue above and below, the crown somewhat darker and the rump lighter than other areas. Males in their first nuptial plumage are distinguished by having *brown* primary coverts. In adult males the primary coverts are black, edged with blue. Most first year males also have some white on the lower abdomen. This white area is variable in size, sometimes extending beyond the legs but never as far forward as the breast.

The adult male nuptial plumage of the Lazuli Bunting is light turquoise blue above, the crown and rump being nearly concolor with the back. The abdomen and lower breast are white and a band of rusty (cinnamon) brown extends across the breast and down the sides. Two conspicuous white wing bars are present.

THE ANALYSIS OF HYBRIDS

When two forms differing in several characters interbreed it is usually possible to identify the parental source of a given character in the offspring. Variation in backcross products can be analyzed using a "hybrid index". This method has been described and utilized frequently in the past few years (Sibley, 1950; 1954; Sibley and West, 1958; Dixon, 1955) and was originally developed by Anderson (1949) during studies on plant hybrids.

The hybrid index is simply a synoptic description of the observed phenotypes. It is determined as follows. The principal characters by which the two parental forms differ are determined (see Table 1).

TABLE 1
DIFFERING COLOR CHARACTERS OF ADULT MALE INDIGO AND LAZULI BUNTINGS

	<i>P. cyanea</i>	<i>P. amoena</i>
1. Crown color	Deep blue-violet	Turquoise blue
2. Rump color	Azure blue	Turquoise blue
3. Wing bars	Absent	Present
4. Abdomen and lower breast	Blue	White
5. Breast band	Absent	Present

One pure parent is scored "0" on all characters. The hybrid characters are assigned as many values as there are discernible intermediate types and the other pure parent is given the character score at the upper end of the resulting scale. Values for each character of a specimen are determined and the summation of character scores is the hybrid index for the specimen (see Table 2).

For two of the five characters (crown and rump) only one intermediate color type was found in the hybrids. For the other three characters (wing bars, underparts, breast band) three gradations could be easily separated. Characters expressed as in eastern (*e.g.* New York) *P. cyanea* were assigned a score of "0". Those expressed as in western (*e.g.* California) *P. amoena* were scored "2" for crown and rump color and "4" for wing bars, underparts and breast band. The following table provides synoptic descriptions of the hybrid recombination types for each of the five characters in adult males (Table 2).

The subadult males presented a slightly different problem. In the first nuptial plumage males of *cyanea* normally retain some white feathers on the abdomen. However, because they retain the brown

TABLE 2
HYBRID INDEX VALUES OF COLOR CHARACTERS

<i>Crown:</i>	0 = deep blue, as in pure <i>P. cyanea</i> . 1 = intermediate between deep blue and turquoise blue. 2 = turquoise blue, as in pure <i>P. amoena</i> .
<i>Rump:</i>	0 = deep blue, as in pure <i>P. cyanea</i> . 1 = intermediate between azure blue and turquoise blue. 2 = turquoise blue, as in pure <i>P. amoena</i> .
<i>Wing Bars:</i>	0 = absent, as in pure <i>P. cyanea</i> . 1 = slight indication of wing bars. 2 = intermediate between the two extremes. 3 = wing bars nearly as complete as in <i>P. amoena</i> . 4 = two white wing bars, as in pure <i>P. amoena</i> .
<i>Abdomen and Lower Breast:</i>	0 = blue, as in pure <i>P. cyanea</i> . 1 = approximately one-fourth of the area white. 2 = approximately half of the area white. 3 = approximately three-fourths of the area white. 4 = white, as in pure <i>P. amoena</i> .
<i>Breast Band:</i>	0 = absent, as in pure <i>P. cyanea</i> . 1 = a slight tinge of rusty color on the breast. 2 = intermediate extent of rusty color on breast. 3 = breast nearly as extensively rusty as in <i>P. amoena</i> . 4 = rusty brown breast band as in pure <i>P. amoena</i> .

primary coverts of the juvenile plumage until the first post-nuptial molt, such birds are easy to age. Adults have black primary coverts. We have segregated our specimens into adults and subadults on the basis of the primary coverts. In the adults the color of the abdomen is scored as in Table 2. For subadults this character is omitted because it would not be possible to decide whether white in the abdomen was the result of immaturity or of hybridization with *amoena*. Thus adult males of pure *amoena* have a summated score of "16" (=2+2+4+4+4) and the subadult males have a summated score of "12" (=2+2+4+4). Hybrid scores range between "0" and "16" for adults and "0" and "12" for subadults.

In the hybrids, *cyanea* and *amoena* characters occur in many recombinations. Many specimens were found to be like one of the parental types except for one or two characters. In otherwise pure *amoena* the wing bars may be basally dark or tinges of violet in the crown or azure in the rump may occur. The breast band may be incomplete and the underparts clouded with blue. In otherwise pure *cyanea* the influence of *amoena* genes is indicated in adults by the presence of white on the underparts, rusty brown feathers in the

breast region, traces of wing bars and tinges of lighter blue on the crown and rump.

FEMALES

Only five females were collected during the three summers of field work. This small number was the result of selective collecting of males when given a choice, and the fact that the females are relatively inconspicuous.

These five birds seem to be *P. amoena*, although some may be hybrids. The fact that we cannot distinguish hybrid females helps to emphasize the similarity of the females of *cyanea* and *amoena*. The same situation occurs in two other groups which hybridize widely across the Plains, namely, the Baltimore and Bullock's Orioles (*Icterus g. galbula* and *I. g. bullockii*) and the Rose-breasted and Black-headed Grosbeaks (*Pheucticus ludovicianus* and *P. melanocephalus*). In these two, the males are strikingly different in color, the females extremely similar.

HISTORY OF THE SITUATION

As previously mentioned the modifications of the plant environment by human land-use activities have permitted the two buntings to extend their ranges and to overlap. In 1900, Burnett reported a spring flock of migrant Indigo Buntings in Colorado and expressed the opinion that habitat changes would permit the species to move westward. This prophecy has been amply vindicated by breeding records of the Indigo Bunting in Colorado in 1954 (Baily) and 1955 (Hering). In the Cornell University collection there is an adult male bunting (No. 21594) taken by J. D. Webster in Weber County, Utah, on August 12, 1945 (see map, Fig. 2). The specimen was indexed at "14", appearing like *amoena*, but with traces of *cyanea* in the restriction of the wing bars and the intermediate rump color. Wells (1958) has found Indigo Buntings apparently breeding in Washington County, Utah. Dr. William H. Behle informs us that Indigo Buntings are "exceedingly rare in Utah and are known only from the extreme southwestern part of the state."

A pair of apparently pure Indigo Buntings was found breeding at 4875 feet elevation near Flagstaff, Arizona, by Dearing and Dearing (1946). Lazuli Buntings were found nearby. A male Indigo Bunting was found mated with a female Lazuli Bunting in Soledad Canyon, Los Angeles County, California, by Bleitz (1958) in June, 1956. The nest of this pair contained two bunting eggs and a cowbird egg.

Incubation was apparently normal, but the eggs did not hatch. In June, 1957, a male Indigo Bunting was again observed in the same area (Bleitz, *loc. cit.*). This bird was singing but apparently was unmated when secured as a specimen on June 10. The specimen was examined by us and found to be an adult male which shows possible effects of hybridization in the lightness of the rump color and in the length (69.1 mm. chord) of the wing, which is intermediate. The tarsal length (17.2 mm.) is also intermediate, although the difference between the two species in this measurement is so small as to make this intermediacy unimportant. In other measurements (bill 7.7 mm., tail 52.2 mm.) and in the other color characters the specimen is similar to eastern *cyanea*. Another recent western record of *cyanea* is that of Boag (1958) who recorded two male Indigo Buntings singing in an area where Lazuli Buntings are noted as "common". This was 20 miles west of Turner Valley at the base of the Rocky Mountains in southwestern Alberta. One male was taken, and the specimen was obtained from Mr. Boag for examination. The specimen proved to be a subadult and showed no indications of hybridization. Measurements of the specimen (Univ. Alberta collection, No. 929) were as follows: wing length 66.1 mm., tail length 50.7 mm., bill length 7.8 mm., and tarsal length 17.8 mm.

Visher (1909) found Indigo Buntings breeding in the Black Hills of South Dakota and our own work indicates that *cyanea* may breed in eastern Wyoming. It should be pointed out that all recent records of "*cyanea*" west of the Plains are likely to be hybrids and that sight records are not satisfactory as the basis for records of "pure" Indigo Buntings in such areas.

The eastward movement of the Lazuli Bunting has also been documented. In 1888, Cooke found Lazuli Buntings in the summer at Vermillion, southeastern South Dakota. The first definite published evidence of *amoena* deep within the normal range of *cyanea* was the first hybrid taken by Breckenridge (1930) along the western border of Minnesota (Marshall Co.) on June 26, 1929. A second hybrid was collected in Cherry County, Nebraska on June 1, 1932 by Youngworth (1932). On July 4, 1933, a pair of *amoena* was found at Yankton, in southeastern South Dakota (Youngworth, 1934), and in June 1935, a male Lazuli was seen in Day County in northeastern South Dakota (Youngworth, 1935). The dates indicate that these birds were probably on their breeding grounds.

The Lazuli Bunting was recorded as a spring migrant at Hastings, Nebraska at least as early as May 7, 1933 (Swenk, 1933). In May,

1938, a "wave" of migrating Lazuli Buntings was recorded at Hastings (Staley, 1938; Jones, 1938). The first record near Omaha was on May 11, 1940 (Nebraska Ornithologists' Union, 1940) and on May 29, 1940, Whelan (1940) found the species near Lincoln. The second record east of Lincoln was at Omaha on May 21, 1944 (Haecker, 1944). The reports of spring migrants at Hastings were regular during the years since approximately 1933, as indicated by the annual reports published in the Nebraska Bird Review. In 1945 a dead Lazuli Bunting was found in Lincoln on May 6 (Jones, 1945) and the editor noted in connection with the record that, "In recent years reports of Lazuli Buntings in eastern Nebraska have become more frequent."

In spite of these numerous records of migrants there have been no breeding records of *amoena* yet reported in eastern Nebraska although we have found indications of hybridization as far east as Blair on the eastern border and at Crete, near Lincoln. It seems probable that the *amoena* which migrate through eastern Nebraska mostly swing westward before stopping to nest. In North Dakota the easternmost record obtained by Pettingill and Dana (1943) was a pair at Kenmare, Ward County, on June 19. Tordoff (1956) indicates that the Lazuli Bunting is a common transient and probably breeds in extreme western Kansas, but there are no actual nesting records. It is rare in eastern Kansas on migration.

For western Oklahoma there is again evidence of hybridization. Sutton (1938) states that in the same region in which hybrids between the Baltimore and Bullock's Orioles were collected, the Indigo Bunting and the Lazuli Bunting "were actually found to be inter-breeding."

THE ANALYSIS OF COLOR

Each of the 95 male specimens was indexed by the method previously described. Twenty-four were indexed at "0" as phenotypically pure *P. cyanea* and six were indexed as pure *P. amoena*. The remainder, more than two-thirds of the total, showed evidence of hybridization. The maps, Figures 1 and 2, indicate the distribution of hybrids and pure types.

Pure *cyanea* were obtained as far west as Crook, Colorado, on the South Platte River, at Valentine, Nebraska, on the Niobrara River, at Willson, Crook County, Wyoming, and at Rapid City, South Dakota.

Pure *amoena* were found at Rapid City, Mobridge, and Bridger Creek in South Dakota and at Chadron, Nebraska. Previously cited

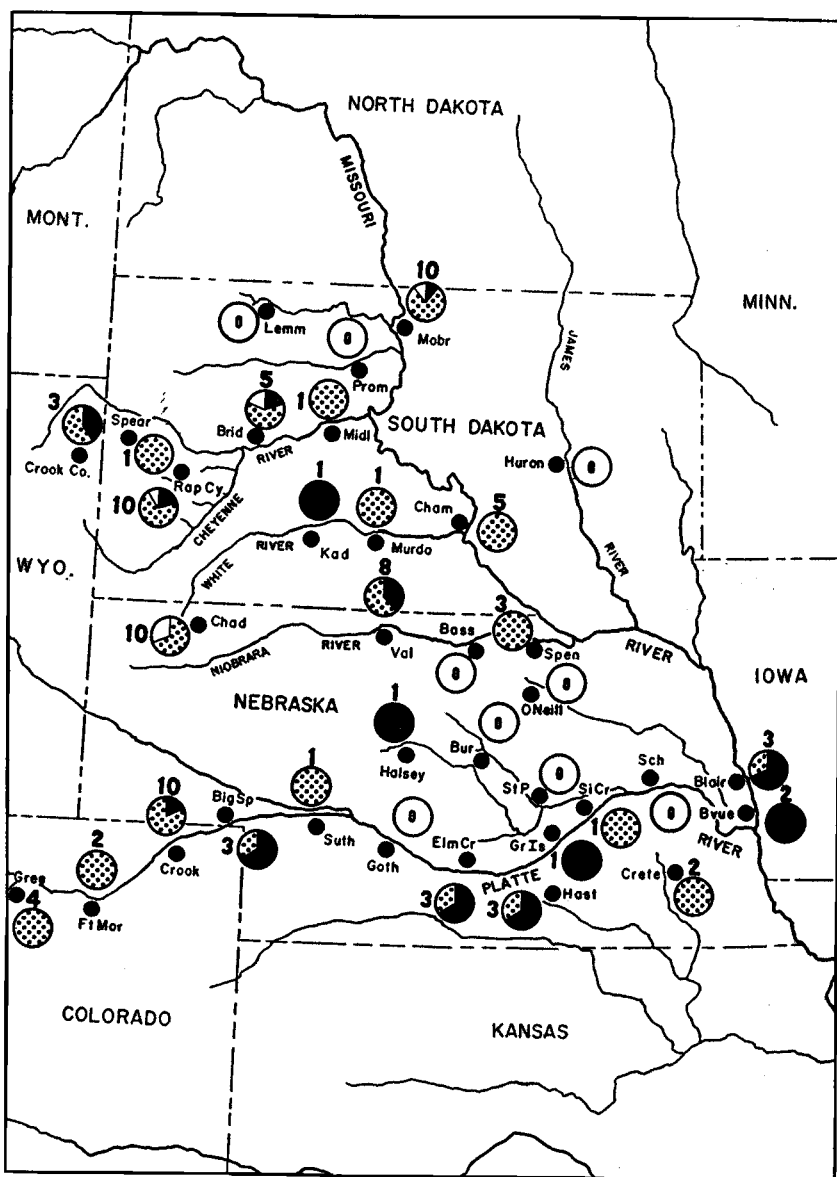


FIGURE 2. Map of the Central Plains showing collecting localities mentioned in the text. Names of the localities are abbreviations and names of nearby towns; exact locations are described in the text. Small black circles indicate the stations. The large circles contain a "0" if no buntings were taken. Numbers beside the large circles indicate the number of specimens. The proportions of pure *cyanea*, *amoena* and hybrid specimens are shown in the larger circles by black, white and dotted areas respectively.

records of probable breeding birds in eastern South Dakota, the hybrid from western Minnesota (Breckenridge, 1930) and our evidence of hybridization at Blair and Hastings, Nebraska, indicate that the zone of overlap between *cyanea* and *amoena* is possibly as much as 400 miles wide in Nebraska. As will be seen from the data the buntings occur in small, discontinuous populations because their habitat occurs in this pattern and, although hybridization is extensive, pure types of both parental forms are found throughout the overlap zone.

In the following section the localities at which specimens were collected will be considered individually.

THE PLATTE RIVER TRANSECT AND SOUTHERN NEBRASKA

During June and July, 1956, ten localities, spaced at approximately 50 mile intervals along the Platte and South Platte rivers of Nebraska and Colorado, were visited. These localities spanned 450 miles of the Platte River system from Schuyler, in eastern Nebraska, to Greeley, in north-central Colorado. Three days were spent in each locality. In order to obtain a better picture of the seasonal aspects, the localities, chosen in advance, were visited in an every-other-one sequence on the westward journey and the remaining ones were visited on the return eastward. The six easternmost localities were again visited in 1957.

In addition five other localities in southern and eastern Nebraska were visited. In the following discussions these first 15 localities will be considered in a generally east to west series. The abbreviations used in Figure 2 are indicated in parentheses.

Bellvue and Blair, Eastern Nebraska (Bvue and Blair).

Two pure *cyanea* were collected by Jerome H. Smith at Bellvue, on the Missouri River, on June 1, 1956. Three male buntings, two adults and one subadult were collected at Blair, Nebraska, June 4-6, 1957. One of these adults (C. U. No. 27610) shows the effects of introgression from *amoena*. It has traces of white on the underparts and of turquoise on the crown and rump (hybrid index = "3"). At Blair the buntings were found in fields among cottonwood saplings.

Schuyler, Nebraska (Sch).

Although favorable bunting habitat was present at this locality we neither observed nor collected one during the two visits.

Silver Creek, Nebraska (3 mi. SSW) (SiCr).

The single adult male is basically *cyanea* but shows the effects of *amoena* in the rump color. This was the only *Passerina* encountered during two visits in an area of seemingly excellent habitat.

Hastings and Crete, Nebraska (Hast and Crete).

One adult, and five subadult males were taken at these two southeastern Nebraska localities (3 mi. SSE Crete and 7 mi. S. Hastings). The adult and one subadult (from Hastings) were phenotypically pure *cyanea*. Three other subadults (2 from Crete, 1 from Hastings) were indexed as "1", showing traces of introgression from *amoena*. One subadult male from Hastings (C.U. No. 25497)

was nearly intermediate (hybrid index "5"), showing complete wing bars, indications of the breast band, and intermediate rump and crown color. Frequent reports of *amoena* at Hastings (previously cited) had indicated that hybrids might be found there, and this was verified. All buntings were taken near streams in heavy riparian cover.

Grand Island, Nebraska (7 mi. SSW) (GrIs).

A pure male (subadult) *cyanea* was obtained at this locality, which was visited during all three years for a total of nine days. Only four buntings were seen, two each in 1955 and 1956. All seemed to be pure *cyanea*.

Elm Creek, Nebraska (3 mi. SE) (Elm Cr).

Three males, two adult and one subadult, were taken in 1956. The adult showed traces of *amoena* influence in belly and rump color (C.U. No. 27386), while the others are apparently pure *cyanea*. In the meadows along the Platte five seemingly pure *cyanea* were seen in 1956, none in 1957.

Gothenburg, Nebraska (Goth).

No buntings were collected and none were seen in two visits (1956 and 1957). Seemingly good habitat exists in the riparian meadows and brushy fields near the river.

Sutherland, Nebraska (Suth and Halsey)

A single subadult male was taken one mile southeast of Sutherland, on July 6, 1956. Included with the specimen from this locality is an adult male taken June 13, 1955, two miles west of Halsey, Thomas Co., Nebraska (northeast of Sutherland). The subadult was intermediate in crown and rump color but was otherwise like *cyanea*. The adult was a pure *cyanea* ("0"). During visits to Sutherland in 1956 and 1957 no other buntings were found although numerous brushy fields and riparian meadows seemed to provide favorable habitat. Only one pair of buntings was seen near Halsey, in a clearing in the Nebraska National Forest (Bessey Division).

Big Springs, Nebraska (8 mi. W) (Big Sp).

Three males, two adults and one subadult, were taken in dense cover along the river in 1956. No others were seen. The adults are pure *cyanea* ("0") while the subadult has an intermediate rump color and a hybrid index of "1".

Crook, Colorado (5 mi. ESE) (Crook).

In early July, 1956, buntings were common at this locality and six adult and four subadult males were collected. One adult and one subadult are pure *cyanea* ("0") and one adult (C.U. No. 27400) is nearly pure *amoena* ("15") except for a partly clouded breast band. Of the others four are close to *cyanea* (ad. "1", "1"; subad. "1", "3"), two are close to *amoena* (ad. "13", "14") and one subadult is almost exactly intermediate in all characters ("7").

Large elms and other trees were present with brushy fields in the wide bottom lands along the river. All buntings were taken in the bottom lands and the males, of varying phenotypes, were found on adjacent territories. No differences in habitat preference associated with color type were found.

Fort Morgan, Colorado (8 mi. WNW) (FtMor).

Two male buntings, both showing evidence of hybridization, were collected

near Fort Morgan. One, an adult, has an index of "8", the other is a subadult and is close to *cyanea* ("2") but has traces of wing bars and a rump of intermediate color. No other buntings were noted in the meadows and woodland edges along the river.

Greeley, Colorado (7 Mi. SW) (Gree).

Four male hybrids (2 ad., 2 subad.) were taken here in 1956. One, a subadult (C.U. No. 27405), is mainly *cyanea* but shows *amoena* influence in the breast band and rump color. It has an index of "2", while the others are closer to *amoena*, the other subadult being indexed at "9", the adults at "13" and "14".

Buntings were common at this locality, especially in brushy fields near the river and both *amoena*-like and *cyanea*-like individuals were seen in addition to the ones collected. All males noted were singing and seemed to be on territories.

THE NIOBRARA RIVER TRANSECT

The Niobrara River flows west to east near the northern border of Nebraska. Three collecting localities were established in its drainage system.

Spencer, Nebraska (5 mi. SSE).

Three adult buntings were taken along the Niobrara River at the edges of oak woodland and fields. All are hybrids and close to *cyanea*, two with indexes of "1", the third has an index of "3".

Valentine, Nebraska (9 mi. ENE) (Val).

This area proved to be of special interest. The eight males collected included five adults and three subadults. Three of the adults are pure *cyanea* ("0") and one adult and two subadults are nearly pure *cyanea* ("1", "1", "2"). These have traces of wing bars and the one indexed at "2" also has turquoise in the rump. The other two specimens index at "9" (subad.) and "14" (ad.). The "9" specimen has a restricted breast band and wing bars and the crown color is intermediate. The "14" bird is close to *amoena* but the crown color is darker and the breast band smaller.

Most of the buntings were found along the weedy edges of hayfields near the river. In one 300 yard strip of such habitat six males were taken. A pure *cyanea* (C.U. No. 25502) was collected from a singing post on a bush only a few minutes after the nearly pure *amoena* ("14") (C.U. No. 25500), also singing, had been collected from the same bush. The other hybrid ("9") (C.U. No. 25503), which approaches *amoena* in color, was taken while singing in an area between the territories of two pure male *cyanea* (C.U. No. 25506 and 25507).

Chadron, Nebraska (Chad).

Six adults and four subadults were taken near Chadron. One was collected two miles northeast of Chadron, the other nine were taken along Little Bordeaux Creek, six miles southeast of Chadron. Most were found in brushy upland fields near open woodland.

One subadult (C.U. No. 25518) has an index of "6" and is intermediate in the extent of the breast band and in rump color. The crown is as in *amoena* but the wing bars are indicated only by faint traces, thus being more like *cyanea*. Of the other nine, three are pure *amoena*, four are nearly pure *amoena* but show slight traces of *cyanea* in breast band, rump and crown color. The remaining two are intermediate with indexes of "11" (ad.) and "9" (subad.).

SOUTH DAKOTA

The South Dakota localities do not form as complete a pattern, and fewer specimens are available. Eight localities are represented by specimens. Of these, four are represented by small samples, and four by single specimens. Each of the single specimens is included with the specimens from the major locality nearest that where it was taken.

Chamberlain, South Dakota (10 mi. S.) (Cham, Murdo).

Three adults and two subadults were taken in fields along the White River near its junction with the Missouri. One adult was taken west of Chamberlain, 10 mi. SSE Murdo, on the White River. All show evidence of hybridization. One adult (C.U. No. 25546) is nearly pure *cyanea* ("1") but has a lighter rump. The Murdo adult (C.U. No. 25551) is close to *cyanea* ("3") but has wing bar traces, some white on the belly and an intermediate rump. Another (C.U. No. 25547) is almost pure *amoena* ("14") but the crown is intermediate and the breast band is restricted. The other adult indexes at "10" and one of the subadults also at "10". The other subadult is exactly intermediate with an index of "6" (C.U. No. 25548).

Mobridge, South Dakota (9 mi. NNE) (Mobr).

Seven adult and three subadult males were collected on open, brushy hillsides and in meadows near the Missouri River.

One of the subadults (C.U. No. 25544) is a pure *cyanea* ("0") and one adult (C.U. No. 25535) is a pure *amoena* ("16"). The other eight specimens are close to *amoena* but all show evidence of *cyanea* in one or more characters.

Bridger Creek, South Dakota (Brid, Kad and Midl).

Four adults and one subadult were taken at this locality nine miles south-southeast of Howes, Meade County. In addition, one adult was taken six miles south of Kadoka, on the White River, and one subadult was taken on the Cheyenne River, in Haakon County, 45 miles north of Midland. At Bridger Creek a pure *cyanea* and a pure *amoena* were taken in a field, both having sung from the same tree within a few minutes of one another. The other three tend toward *amoena*, the subadult being nearly pure ("11" with the only evidence of *cyanea* influence being slightly restricted wing bars, while the two adults index at "10" and "12" and have indications of *cyanea* genes in the crown, rump, breast band and wing bars. Several other males, all seemingly *amoena*, were observed on song posts. The adult taken near Kadoka is a pure ("0") *cyanea*. The subadult from the Cheyenne River north of Midland has wing bars and crown color intermediate and breast band traces (index "4"), but otherwise is like *cyanea*.

Rapid City, South Dakota (Rap Cy and Spear).

Eight specimens (4 ad., 4 subad.) were taken in 1955 in the vicinity of Rapid City. In addition, two adults collected near Rapid City in 1948, and one adult taken in the Black Hills near Spearfish, South Dakota, were borrowed from the Pettingill collection.

Along Elk Creek, 11 miles north of Rapid City, buntings were quite common in 1955 and six specimens were collected in wooded, grassy areas along the creek. Of these one adult is pure *cyanea* ("0") and one subadult is pure *amoena* ("12"). The other four are hybrids. Two subadult hybrids were collected in brushy fields along Box Elder Creek, six and one-half miles north of Rapid City.

The two Rapid City area specimens in the Pettingill collection are adults, one is a pure *cyanea* from South Canyon and the other a nearly pure *amoena* ("15") from Dark Canyon. Both localities are at the eastern edge of the Black Hills. In 1955 apparently pure *amoena* were seen at the mouth of South Canyon but no *cyanea* were noted. The songs of both forms were heard in this area and seemed identical to all members of the party.

The Spearfish adult in the Pettingill collection is close to *amoena* ("14") but has restricted wing bars and a restricted breast band.

Crook County, Wyoming (Crook Co.)

One adult and two subadult buntings taken in June, 1949, in this eastern Wyoming county were borrowed from the Pettingill collection. Two are from 1 mi. SW Willson, one from 2½ mi. NSundance. The adult is pure *cyanea* and the subadults are hybrids with indexes of "4" and "9". These specimens, in an area where *amoena* would be expected to be the dominant form, indicate that the area of overlap probably extends well into Wyoming.

WEIGHTS AND MEASUREMENTS

The weights and measurements of the plains buntings, and of eastern (New York, Michigan) *cyanea* and western (California, Utah) *amoena* samples, indicate the following:

- (1) Mensural differences exist between *cyanea* and *amoena* from eastern and western North America.

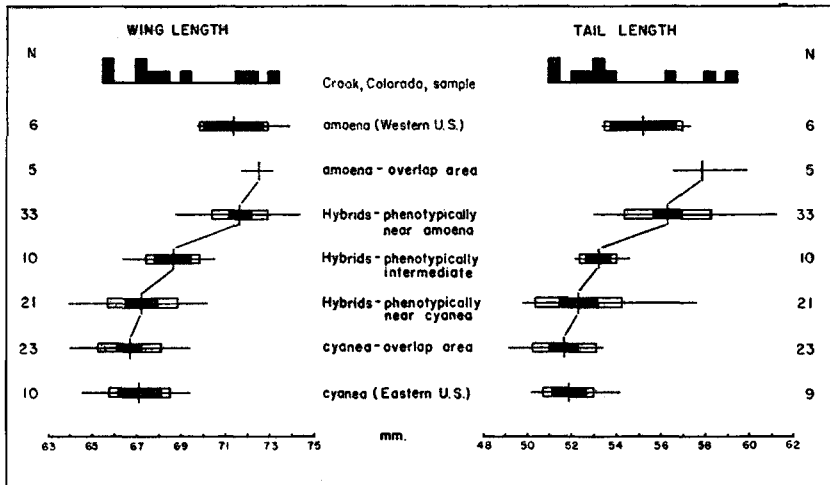


FIGURE 3. Statistical analysis of wing length and tail length of *P. cyanea*, *P. amoena* and hybrids. Histogram of the sample from one locality shown at the top with each square representing a specimen. Horizontal lines represent the range; rectangles indicate one standard deviation from the mean and the solid black marks twice the standard error of the mean. The means are indicated by vertical lines.

(2) Similar differences exist between pure ("0") *cyanea* and pure ("16" adults and "12" subadults) *amoena* from the plains.

(3) Hybrids are intermediate between the parental forms in weights and measurements.

(4) There is a correlation between the color pattern (i.e., the hybrid index) and the measurements and weights of the hybrids.

These points are illustrated in Figures 3-5 and are discussed below.

Differences Between cyanea and amoena. It is apparent from Figure 4 that *cyanea* is somewhat smaller than *amoena*. While weights were unavailable for far eastern or western buntings, the difference between the two forms in the plains, and the greater wing and tail lengths of *amoena* (see Amadon, 1943, for correlation between wing length and body size) indicate that *amoena* is the larger form. Differences exist in tarsal length and bill length (from nostril), in addition to the wing length (chord) and tail length differences shown in Figure 3. The bill of *cyanea* is slightly larger than that of *amoena* (mean = 7.63 mm. in *cyanea*, 7.27 mm. in *amoena*, for 10 and 8 males respectively). The eastern *cyanea* also has a slightly longer tarsus (mean = 17.39 mm.) than has *amoena* (mean = 16.77 mm., with same N as for bill length). (See Figures 4 and 5 for bill length and tarsal length respectively.)

Differences in Plains Buntings. An average difference in weight of slightly over one gram exists between "pure" ("0") *cyanea* and

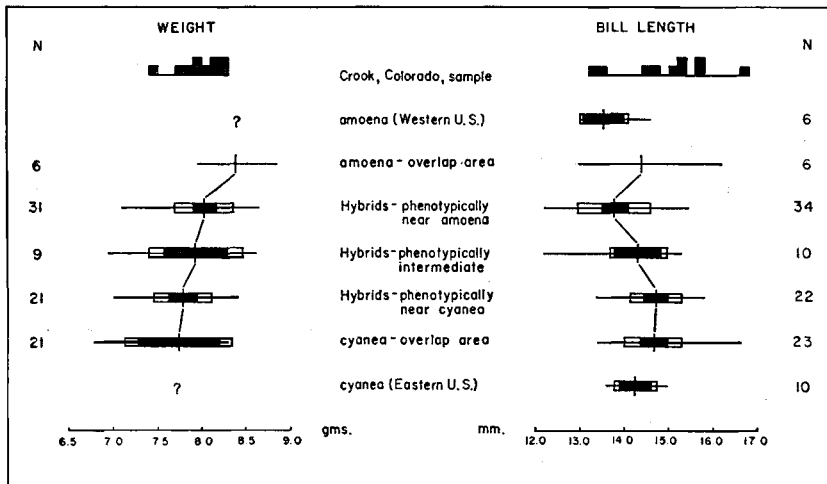


FIGURE 4. Statistical analysis of weight and bill length of *P. cyanea*, *P. amoena* and hybrids. See Figure 3 for explanation.

"pure" ("16" adults, "12" subadults) *amoena* taken in the plains (Fig. 4). The wing lengths, and tail lengths of the two forms, as shown in Figure 3, differ by more than do the far eastern *cyanea* and western *amoena*. However, the plains buntings approach each other closely in bill length (mean = 7.84 mm. in 23 *cyanea*, mean = 7.70 mm. in 6 *amoena*), and also in tarsal length (mean = 17.27 mm. in 23 *cyanea*, mean = 16.87 mm. in 6 *amoena*).

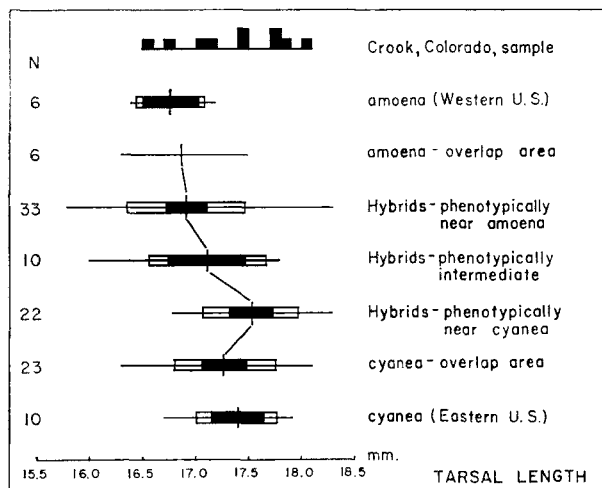


FIGURE 5. Statistical analysis of tarsal length of *P. cyanea*, *P. amoena* and hybrids. See Figure 3 for explanation.

The significance of these data is twofold. The differences between eastern *cyanea* and western *amoena* have not been lost due to swamping following widespread hybridization and backcrossing. On the other hand, selection against hybridization has not resulted in greatly increased divergence in bill length, tarsal length, wing length or tail length. Some such divergence is to be expected if selection is against the hybrids and isolating mechanisms are being reinforced, for under these conditions competition becomes effective in favoring divergence toward adaptation for different niches (see Sibley, 1957, pp. 169-170, 182-183, for discussion on this point, and Vaurie, 1951, for the fine example in *Sitta neumayer* and *S. tephronota*). In the buntings the time which has elapsed since the breakdown of isolation has apparently been too short to have resulted, as yet, in either reinforcement or swamping.

Intermediacy of Hybrids. This point is shown in Figures 3-5. The

three centrally located samples, including all hybrids and backcross individuals, are intermediate between the "pures" in all weights and measurements. This intermediacy is noteworthy (although to be expected), since the hybrids were initially identified as such on the basis of color pattern only.

Correlation Between the Hybrid Index and Weights and Measurements. The three groups of specimens between the "pure" *cyanea* and "pure" *amoena* plains samples in Figures 3-5 are hybrids grouped according to their hybrid index number. Those hybrids phenotypically nearer *cyanea* (index = 1-5 in adults and 1-3 in subadults) were placed in one group; those intermediate in color characters were placed in a second group (index = 6-10 in adults, and 4-8 in subadults; and those nearer *amoena* in color characters (index = 11-15 in adults, and 9-11 in subadults) were placed in the third group. The correlations between wing length and hybrid index is shown in Figure 3. Those individuals indexed closer to *amoena* are nearer *amoena* in wing length also, when compared with the intermediates or with *cyanea*. The phenotypically intermediate individuals are likewise intermediate in wing length between the "pures" of both parental forms from the plains. Those individuals nearer *cyanea* in hybrid index are closer to *cyanea* in wing length, compared with the other hybrids. The same situation is shown by comparing hybrid index with tail length (Figure 3), with weights (Figure 4), with bill length (Figure 4), and with tarsal length (Figure 5). The correlation is clear for weights despite the small difference in mean weights between the two forms in the plains (1.28 gms.). The small differences between *cyanea* and *amoena* in bill length and tarsal length complicate the picture slightly for these measurements. The bill length of plains *cyanea* is greater than that expected on the basis of the bill length of western *amoena*, although the difference is not large. However, the hybrids indexed near *cyanea* are longer billed than those indexed near *amoena*, and the gradient in the three hybrid groups clearly shows the correlation between hybrid index and bill length. In tarsal length, the plains *cyanea* have shorter tarsi than do eastern *cyanea*, although the difference is not large. The gradient exists in the three groups of hybrids for this character also, showing the correlation between tarsal length and hybrid index.

Variation in Linear Measurements and Weights in Locality Samples. Histograms depicting the weights and measurements of the male buntings from Crook, Colorado, (see discussion under that locality concerning the hybrid indexes of the specimens) are included in Figures 3-5. This sample is typical of the larger plains samples in that great variation is shown in all five mensural characters. The variation in wing length, tail length, tarsal length, and bill length approaches that of all the phenotypically pure *amoena* and *cyanea* specimens taken in the plains. While the variation in weight is not so great, it is nevertheless quite considerable. As we have shown the linear measurements and weights are closely correlated with color pattern (hybrid index). Statistical treatment of the samples by locality was not carried out because the small size of the samples, and the possibility of non-random mating, cast doubt on the validity of such a treatment. In regard to the latter point, if non-random mating were occurring, samples would represent a non-panmictic population. Hence, statistical treatment of the small samples available was not attempted.

DISCUSSION

The bunting situation in the plains is the result of a recent secondary contact between the two formerly isolated *amoena* and *cyanea* populations. The differences exhibited by the forms could only have arisen under different selective forces acting on allopatric populations. When the barrier between them was broken the forms extended their ranges and came into contact. This contact has resulted in hybridization as described. The changes which have affected bird populations in the plains include the planting of trees and shrubs in shelterbelts, around villages and buildings, and along the rivers. The control of prairie fires, which formerly burned extensive areas periodically, and the control of the rivers, which formerly flooded at intervals washing away vegetation along the banks, have resulted in more continuous riparian vegetation. It is also suggested that removal of the Indians and the buffalo from the plains played a role in increasing the habitats available for woodland birds in that region (see Sauer, 1950, for comments on these effects). Removal of the Indians aided in eliminating the prairie fires they occasionally caused. Periodic trampling of vegetation along rivers, rendering such areas unsuitable for habitation by birds, was an effect of the former huge herds of buffalo.

Natural changes which have increased suitable habitat for buntings and other woodland species of birds include the ameliorating climatic conditions in the plains and the consequent movement of trees and shrubs into the valleys of the plains.

An obvious effect of these changes is the increase in the contact area between the two buntings through the development of suitable habitat for breeding. Furthermore, shelterbelts and tree plantings provide suitable resting places for migratory birds where none previously existed. This has probably aided in the colonization of the plains by the buntings. The discontinuous distribution of the buntings in the plains suggests that stray birds may be aided in colonizing suitable areas by this means. The suggestion of Wells (1958), concerning rapid population expansion in *cyanea* following the last glaciation and opening up of the eastern woodlands, should also be taken into account when considering colonization of the plains by the buntings. Stray birds forced westward by population pressure could exploit favorable areas by such "stepping-stones" as the shelterbelts. The present discontinuous distribution of the buntings in the plains may be influencing the hybridization by limiting gene flow between disjunct populations.

In situations of this nature, the problem of proper taxonomic recognition of the hybridizing forms inevitably arises. As one of us has pointed out (Sibley, 1957), the crucial point is the effect of selection on the apparently fertile hybrids being produced. If selection is operating against the hybrids, reinforcement of isolating mechanisms should occur, resulting in further divergence of the two interbreeding forms. If selection is not operating against the hybrids, then sufficient gene exchange should result in the swamping out of the differences between the two forms as selection fashions a new adaptive combination from the variable gene pool available.

Unfortunately, the determination of the direction of selection acting on the hybrids is difficult in hybrid situations of relatively recent occurrence.

Looking at the situation from one point of view, the number of hybrids taken (66) compared to the number of "pure" individuals of both forms (29) indicates regular gene exchange of sufficient frequency to suggest that all the gene combinations of each form are available to the gene pool of the other. The continuation of such a contact will prevent speciation. On this basis, the forms can be considered conspecific.

Another point of view would stress the fact that "pures" of each form are present with the hybrids at some localities. The great amount of overlap (400+ miles) in which "pures" of both forms, as well as hybrids, are found, would be stressed also. Advocates of this viewpoint would consider the two forms separate species.

The problem in this case can be reduced to a single question, namely: is random mating actually occurring, the large area of overlap being due to the discontinuous distribution of the buntings and their habitat, or is this overlap due to the occurrence of non-random mating in which "pure" individuals of one form are tending to mate with individuals of the same form, rather than with hybrids or individuals of the other form? Our data cannot answer this question conclusively. Further study of the populations in the field should give a better basis for a taxonomic decision.

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SUMMARY

The Indigo Bunting (*Passerina cyanea*) and Lazuli Bunting (*P. amoena*) have formed a secondary contact in the plains as a result of climatic changes and man's activities, which have provided suitable habitat in a formerly unsuitable area. Over a broad area of contact and overlap specimens show that hybridization and backcrossing are occurring, and that both parental forms are present with the hybrids at some localities. The hybrid index technique indicates that 66 out of 95 specimens from 21 localities are hybrids or the result of backcrossing. The hybrids and the situation at each locality are discussed.

Measurements and weights of the specimens show that clear size differences exist between the two forms, that the hybrids are intermediate between the parental forms, and that color pattern is correlated with weights and measurements in the hybrids. No evidence is found for increased divergence of the two forms due to reinforcement of isolating mechanisms and/or the effects of competition. Neither is there clear evidence which indicates that swamping of the existing differences is in progress.

The effects of nature and man in causing the contact between the previously isolated forms are discussed. We postpone a taxonomic decision on the status of the two buntings pending the accumulation of more information, particularly in regard to pairing, mate-selection and habitat preference of the two forms in the area of hybridization and overlap. Data presented in this paper provide bases for arguing for conspecificity, as well as for maintaining the two forms as separate species.

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COLOR-DYED SHOREBIRDS

As part of a shorebird population study on the Florida Gulf coast, a large number of shorebirds were trapped, banded and color-dyed in the spring of 1959. Birds caught in May were dyed a vivid golden color; birds trapped in June were dyed scarlet, which apparently faded to pinkish within two weeks. Other colors will be used in the fall, 1959. Those observing colored shorebirds should communicate with Horace Loftin, Dept. of Biological Sciences, Florida State University, Tallahassee, Florida.

Ed. Note: Those employing a dyeing technique for marking birds should be careful to refrain from obscuring field-marks and should avoid colors that resemble or may fade or change into hues borne by other species of the group.

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Applications are invited for the post of Director of the newly-founded Institute at the University of Cape Town. The Institute is an independent organization, but the post carries academic status. Applicants should have an M.Sc. or its equivalent, preferably in zoology, and have experience in organized research. Applications giving age, marital status, qualifications, and experience, and accompanied by two recent testimonials, must reach the Chairman of the Board of Control before 1st February, 1960. Particulars regarding duties, salary, and other matters may be obtained from: C. K. Niven, Chairman, Board of Control, Amanzi, Uitenhage, Cape Province, South Africa.