HYBRIDIZATION IN BUNTINGS (*PASSERINA*) IN NORTH DAKOTA AND EASTERN MONTANA

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THE Indigo and Lazuli Buntings (*Passerina cyanea* and *P. amoena*) are closely related complementary species that breed chiefly in the eastern half and western half, respectively, of the contiguous United States. Their breeding ranges overlap in the southern Great Plains, and hybridization there has been described by Sibley and Short (1959) from southern Nebraska and northeastern Colorado through the western two-thirds of South Dakota. This present study extends documentation of hybridization northward into North Dakota and eastern Montana, and discusses the identification of hybrid characteristics in buntings. Phenotypic characteristics of specimens from extreme eastern and western United States are described and compared with those from the overlap area to elucidate variations resulting from hybridization. The term hybridization as used in this paper is defined broadly as interbreeding between individuals of morphologically and genetically distinct populations and also interbreeding between hybrids and pures or between hybrids. Thus a hybrid could be F_1 (Indigo $\times$ Lazuli), a backcross ($F_1 \times$ Indigo or $F_1 \times$ Lazuli), or a specimen representing any combination of Indigo and Lazuli genes.

Both species occur around brushy vegetation along the edges of woodlands. Their songs and calls, general behavior, and nests and eggs are similar. Songs of the two species differ slightly, that of the Lazuli being approximately one and one-half times as fast as the song of the Indigo (Thompson 1969). In North Dakota the Lazuli's song seems to be more choppy and shorter—1 to 2 sec vs. 2 to 3 sec in the Indigo. In a few cases I noted atypical songs that turned out to be from obviously hybrid specimens.

Recently male Indigos have been recorded quite often west to the Pacific coast—in California: May 1950 (Cardiff 1951), June 1956 and 1957 (Bleitz 1958), February 1959 (Williams 1961), January 1963 (Wilbur 1963); in Washington: same bird in June and July 1958 (Calder 1966); and in Nevada: June 1940 and 1951 (Richardson 1952). Sibley and Short (1959) listed more western records including the western Great Plains. In addition, Audubon Field Notes contains several Indigo records in the far west. Lazulis have apparently been much less frequent in eastern localities, and I know of no Lazuli records east of the Mississippi River.

In North Dakota buntings nest in low dense brush (e.g. *Artemisia* and *Rosa*) near forest edges. Indigos seem to prefer brush near more mature mesic woods, where Lazulis also occur. Lazulis are also common in more xeric habitats such as draws with small stands of brush and short trees of green ash (*Fraxinus pennsylvanica*) in western North Dakota. Indigos are common only along the Sheyenne and Red Rivers, and locally uncommon to rare elsewhere (Fig. 1). Lazulis are common along the Missouri River, in the Killdeer Mountains (10 miles northwest of Killdeer), and in the Badlands. The total population of Lazulis is probably significantly larger than that of Indigos, as indicated by the Lazuli's more diffuse distribution within its range in North Dakota, and by Stewart and Kantrud's (1972) data that show 21 pairs of Lazulis and only two pairs of Indigos in 130 quarter-section sample units scattered throughout North Dakota. Woodlands along the Souris (Mouse) and James Rivers support relatively few buntings, possibly because of a scarcity of nesting habitats. Buntings are rare in the aspen parklands in north central North Dakota even in seemingly suitable habitats. Buntings apparently do not utilize appreciably shelterbelts and tree plantings in uplands, and therefore contact between Lazulis and Indigos has probably not increased significantly as a result of man's tree planting activities. The opposite may be true for flickers (*Colaptes*) and orioles (*Icterus*) (Sibley and Short 1964, Short 1965, Anderson 1971).

Materials and Methods

This study is based on males only because the great similarity of females of the two species makes identification of hybridity in females very difficult. During 1966–69 and 1971 I collected 153 male buntings, concurrent with population studies of forest-inhabiting birds, in North Dakota and eastern Montana and stored the specimens in the North Dakota State University Vertebrate Museum. The specimens include 35 adult and 5 subadult Indigos, 79 adult and 28 subadult Lazulis and Lazuli-like hybrids, and 6 adult phenotypically medial hybrids. Most specimens were collected from mid-June through mid-August, which seems to be the main nesting season of buntings in the northern plains. Specimens representing eastern populations from Illinois and Arkansas to the east coast and western populations near the west coast were examined at several museums mentioned in the Acknowledgments.

In the field the distance between the tips of bill and tail (with the specimen gently extended to its total length) and the weight were determined. The following linear measurements were taken after the specimens had been preserved by injection with formalin: the chord of the wing, the tail from its insertion to the tip of the longest rectrix, the bill from the anterior edge of a nostril to the tip of the upper mandible, and the tarsus from the joint between the tibiotarsus and tarsus to the joint at the bases of the toes. These measurements (except bill) are those described by Pettingill (1970). Determining tarsal length was facilitated and made more consistent by measuring to the axis of the hallux positioned at a right angle to the tarsus. This technique is valid only for birds with an incumbent hallux.

TABLE 1

HYBRID INDEX FOR ADULT MALE BUNTINGS[1]

Character	Description	Score
Upper breast	Blue, as in Indigo	0
	Traces of rusty	1
	One-half blue, one-half rusty	2
	Traces of blue, or slight restriction by blue	3
	Rusty, as in Lazuli	4
Abdomen and lower breast	Blue, as in Indigo	0
	Traces of white	1
	One-quarter white	2
	One-half white, one-half blue	3
	One-quarter blue	4
	Traces of blue	5
	White, as in Lazuli	6
Wing bars	Absent, as in Indigo	0
	Traces of white (not buffy white) bars	1
	Medial, with blue patches or bands between white tips and dark bases of middle secondary coverts, or in adults restricted by dark bases	2
	Traces of blue between white tips and dark bases of middle secondary coverts[2]	3
	White, as in Lazuli	4
Head[3]	Deep blue, as in many Indigo	0
	Close to deep blue	1
	Medial	2
	Close to turquoise blue	3
	Turquoise blue, as in many Lazuli	4

[1] The index is for the fully nuptial plumage. See text for explanation.
[2] This description is true of many western subadult Lazulis that should therefore be scored 4 for this character.
[3] Head color scores are not included in hybrid index scores for buntings.

A hybrid index or compound character index was devised to describe quantitatively plumage pattern and color (Table 1). The hybrid index method has been used previously to describe hybridization between various species in mid-North America (Sibley and Short 1959, 1964; West 1962; Short 1965). Short (1965) and Hubbard (1969) describe and discuss the method which, briefly, involves assigning a score of 0 (zero) to a character (e.g. breast color) as expressed in one species and a maximum score (e.g. 4) to the character as expressed in the other species. Intermediate scores (i.e. 1–3) represent supposed effects of hybridization. In this way several characters are scored, and the sum of these character scores (CS) for a specimen is the hybrid index score (HIS) for that specimen. Thus as Table 1 shows, the HIS for a pure Indigo is ideally 0 (0 + 0 + 0) and for a pure Lazuli is ideally 14 (4 + 6 + 4). Hybrids would then have scores of 1–13.

MALE PLUMAGES

Major differences between the adult male Indigo and Lazuli plumages are, respectively, blue vs. rusty upper breast, blue vs. white abdomen, no white wing bars vs. white wing bars, and dark blue vs. light blue head and neck. Scores for phenotypically pure and hybrid characters are given in the hybrid index (Table 1). The plumages of the two species differ

in other ways, but only those differences that proved valuable in describing hybridization are discussed here. Subadults (approximately 1-year-old birds in their first breeding season) and adults differ in color of several characters, but are best distinguished by the primary coverts, which are brown in subadults and black with blue margins in adults.

The characters used in obtaining hybrid index scores (HIS) were the colors of the upper breast, abdomen, and middle secondary coverts (wing bar). Head color was not used because it is too variable (see Table 4). Rump color was not scored because it is too similar in the two species to be of much value.

Several complications arose during scoring the abdomen and middle secondary coverts. These resulted in part from a delay in the completion of the Indigo's prenuptial (prealternate) molt of the winter (basic) plumage far into the breeding season. The Indigo adult winter plumage includes white abdominal feathers, and frequently not all of these are molted until late summer. Abdomens of nuptial Indigos with such white feathers must be scored 0; otherwise the presence of Lazuli genes would be falsely indicated. That the presence of such white feathers results from a delayed prenuptial molt is shown by the following percentages, which are monthly percentages of eastern U.S. adult male Indigos having worn brown margins on any of the proximal three pairs of secondaries, or white abdomens, or whitish tips on worn middle secondary coverts (all these are winter characters): May, 71 (74 of 105); June, 69 (36 of 52); July, 54 (29 of 54); and August, 42 (10 of 24). These monthly proportions are not all the same ($P < 0.025$, $\chi^2 = 10.87$ with 3 df). Thus at no time during the breeding season do all adult male Indigos possess the fully nuptial plumage, as Dwight (1900: 214) also noted.

In this study adult Indigos that had not completed the prenuptial molt were identified by the presence of ragged brown margins on any of the proximal three pairs of secondaries. Of 158 birds with such secondaries from eastern states, 76 had white feathers on the abdomen. Adult Indigos with the fully nuptial plumage have black proximal secondaries with smooth and broad blue margins. Of 90 specimens with such secondaries from eastern states, only two had white abdominal feathers left from the winter plumage. This association of white feathers on the abdomen with worn brown proximal secondaries and the decreasing percentages of adult birds having such feathers from May through August indicate that these characters result from a delayed or incomplete prenuptial molt, not from introgression (flow of genes resulting from hybridization) from the Lazuli. Lazulis have no obvious prenuptial molt, as specimens I studied had no new feathers in the spring or summer; all

feathers were very worn. Therefore in Indigo-like hybrids a delayed or reduced prenuptial molt could result from introgression from the Lazuli, but this would not be the case for Indigos far from the overlap zone. Abdomens with white feathers are typical of most subadult Indigos, and were also assigned scores of 0.

Problems with scoring middle secondary coverts also resulted from a delayed prenuptial molt in the Indigo. Middle secondary coverts of the Indigo's winter plumage have brown to whitish tips separated from black bases by blue bands. Whitish tips would form a wing bar resembling that of the Lazuli. These feathers of the Indigo's winter plumage can be identified in the spring and summer by their worn brown margins, and must be scored 0.

In adult Lazulis the middle secondary coverts occasionally have traces of blue on the margins, which resemble the blue margins of the Indigo's middle secondary coverts. Such feathers in Lazulis were indexed as pure (CS = 4) unless the blue margins extended between the white tips and brown bases. In subadult Lazulis such blue on the margins is typically more extensive, but was also assigned a score of 4. Occasionally in adults but more often in subadults the wing bars are very narrow, which may result from wear or from introgression from Indigos. In the latter case black or blue bases extend farther toward the feather tips than in pure Lazulis.

The preparation of Lazuli museum skins sometimes produces apparent Indigo-like characters. Failure to extend the neck to its normal length may allow the blue throat to restrict the rusty band. Also, disarranged blue feathers of the sides of the neck may restrict the breast band laterally.

RESULTS

Distribution of hybridization.—Nuptial plumages of adult male buntings from eastern and western United States exhibit little variation in the color and pattern of the upper breast, abdomen, and wing bars. Almost all specimens had HIS of either 0 (pure Indigo) or 14 (pure Lazuli). Of 227 eastern adult Indigo only two had HIS greater than 0 (1 and 2), which resulted from whitish tips on otherwise black and blue greater secondary coverts. Of 94 subadults four had HIS of 1 or 2 resulting from white wing bars. Many subadults had buffy tips on the greater secondary coverts, which were assigned CS of 0. Of 127 western adult Lazulis only three had HIS less than 14 (13), which resulted from restrictions of the upper breast in one, and traces of blue in the wing bars of the other two.

In the northeastern half of North Dakota 30 adult and three subadult male buntings were collected; all were phenotypically pure Indigo (Fig.

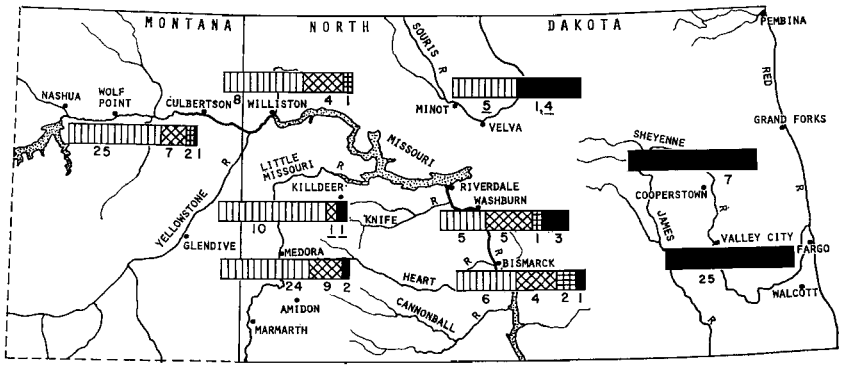

Fig. 1. Phenotypic composition of bunting populations. Solid black = Indigo (Hybrid index score, HIS, = 0), horizontal-vertical crosshatching = medial hybrids (HIS = 5–8), diagonal crosshatching = Lazuli-like hybrids (HIS = 10–13), and vertical hatching = Lazuli (HIS = 14). Sample sizes are given beneath each rectangle. Underlined numbers represent sight records selected as necessary for additional documentation.

1). Of the adults 13 still had worn brown inner secondaries of the winter plumage, and seven of these 13 had white on the abdomen. All were assigned HIS of 0 (see plumage section above for rationale). Of the 17 with nuptial blue and black inner secondaries none had white on the abdomen.

Other collections include the following: along the Missouri River in mid-North Dakota (including the Knife River) 4 Indigos, 3 medial hybrids (HIS = 5–8), 9 Lazuli-like hybrids (HIS = 10–13), and 11 Lazulis; in southwestern North Dakota 2 Indigos, 9 Lazuli-like hybrids, and 24 Lazulis; in and near the Killdeer Mountains (8 miles northwest of Killdeer) 10 Lazulis; and along the Missouri River near Williston and in Montana 1 Indigo, 3 medial hybrids, 11 Lazuli-like hybrids, and 33 Lazulis (including two Lazulis collected near Glendive). No apparent backcrosses to Indigo or Indigo-like hybrids were seen or collected. Locality and ecological data are given in more detail in Table 2.

Analysis of hybrid plumage characteristics.—All six hybrids with medial HIS of 5–8 have very similar plumages. These birds may be first generation (F_1) hybrids because they are (1) phenotypically medial, (2) all very similar as F_1 hybrids are generally (Mayr 1963: 112; for examples see Johnsgard 1971), and (3) phenotypically disjunct from all other hybrids (HIS = 10–13) collected in this study. All have very worn feathers as in Lazulis and therefore apparently lacked a prenuptial molt, as do

TABLE 2

LOCALITY AND ECOLOGICAL DATA FOR COLLECTIONS[1]

Locality name and description	No. of occurrences of hybrid index scores
Valley City	
Sheyenne riverine forests, 11 mi NNW Valley City to 14 mi W Walcott	0 (25)
Cooperstown	
Sheyenne riverine forests, 7 mi SE to 20 mi NNW Cooperstown	0 (6)
Tree planting, 11 mi S Grand Forks	0 (1)
Velva	
Souris riverine forests, 4 mi NW to 24 mi ENE Velva	0 (1), 0 (4), 14 (5)
Bismarck	
Missouri riverine forests, 9–14 mi SE Bismarck	7 (2), 10 (1), 11 (1), 12 (1), 13 (1), 14 (5)
Beaver Creek, 2 mi SE Linton	0 (1), 14 (1)
Washburn	
Missouri riverine forests, 9–14 mi SSE Washburn	0 (1), 6 (1), 13 (2), 14 (3)
Knife riverine forests, 3 mi NNW Stanton and 2 mi SW Hazen	0 (2), 10 (1), 13 (2), 14 (2)
Riverdale	
Missouri riverine forests	0 (1), 14 (6)
Williston	
Missouri riverine forests	5 (1), 12 (1), 13 (3), 14 (8)
Killdeer	
Forested Killdeer Mountains, 8 mi NW Killdeer	0 (1), 11 (1), 14 (7)
Little Missouri riverine forests, 19 mi W Grassy Butte	14 (3)
Amidon	
Small deciduous woods and brush along creeks	
2 mi SW South Heart, along Heart River	0 (1), 14 (3)
2 mi E and 7 mi S Belfield	12 (1), 14 (3)
11 mi N Medora	0 (1)
1–3 mi SW and 6 mi S Medora	13 (1), 14 (6)
Small deciduous woods and brush along creeks in scattered Ponderosa Pine forests, 10 mi NW Amidon	12 (3), 13 (4), 14 (11)
Brush at edge of a cottonwood grove, northwest side of Marmarth	14 (1)
Montana	
Missouri riverine forests	
20 mi ESE Culbertson	14 (2)
8 mi W Culbertson	13 (2), 14 (7)
5 mi ESE Wolf Point	13 (1)
2 mi SE Wolf Point	7 (1), 11 (1)
16 mi SE Nashua	14 (1)
10 mi SE Nashua	0 (1), 13 (2), 14 (4)
6–7 mi SSE Nashua	8 (1), 14 (9)
6 mi S Nashua	13 (1)
13 mi NNE and 8 mi N Glendive	14 (2)

[1] The number to the left of each parenthesis is the hybrid index score and the number in each parenthesis is the number of specimens with that hybrid index score. Underlined numbers represent sight records that were added only as necessary for additional documentation. Hybrid index scores for sight records are approximate.

TABLE 3

CHARACTER SCORES OF BUNTINGS

Locality	Breast					Abdomen							Wing bars				
	0	1	2	3	4	0	1	2	3	4	5	6	0	1	2	3	4
Eastern U.S.[1]	321					321							315	3	3		
Eastern ND	33					33							33				
Bismarck	1	2	1	2	7	1				2	3	7	1		2	3	7
Washburn	4			4	6	3				1	1	9	3		2	1	8
Williston		1		2	10				1			12		1		3	9
Killdeer					10							10					10
Amidon	2			7	26	2						33	2			6	27
Montana	1	2	1	5	26	1				1	1	32	1		2	2	30
Western U.S.[2]				1	126							127				2	125

[1] Abbreviations: U.S. = United States, ND = North Dakota.
[2] Adults only.

Lazulis. Abdomens are largely white (CS = 4, 4, 4, 3, 4, 5) mottled with blue, with the white extending as far anterior as in pure Lazulis. This dominance by white may result from a combined effect of a delayed prenuptial molt of the white underparts of the winter plumage of Indigos and the white abdomen characteristic of the Lazuli during the entire year. White may thus not be entirely caused by Lazuli genes for a white abdomen, but partially by Lazuli genes for an absence of a prenuptial molt (or lack of genes for a prenuptial molt like the Indigo's). The greater secondary coverts are tipped with white, forming a very narrow white wing bar on each wing. In two hybrids the bar is absent apparently because of wear. All middle secondary coverts have white tips separated from dark bases by blue bands (CS = 2, 2, 2, 1, 2, 2). These white tips form a wing bar that is approximately half as broad as in the Lazuli; but in two hybrids the wing bar is narrower apparently because of wear. Head color is intermediate (CS = 2, 1, 1, 2, 2, 1). The upper breasts are predominantly blue in five hybrids, and entirely blue in the other (CS = 0, 1, 1, 1, 1, 1). Breast bands are thus more similar to the Indigo's and abdomens are more similar to the Lazuli's, while wing bars and heads are nearly medial. These hybrids are very similar to one described by Breckenridge (1930) collected 26 June 1929 in Marshall County, Minnesota. Judging from Breckenridge's description the scores for upper breast, wing bars, and abdomen would be 1, 2, and 4, respectively.

Of 29 Lazuli-like specimens that appear to be hybrids, only four can be assuredly identified as such. Of these four, two have almost entirely white abdomens and also white upper breasts with rusty scarcely evident. The blue throat only slightly restricts the white upper breast. White up-

TABLE 4

PERCENT FREQUENCIES OF HEAD SCORES OF BUNTINGS

	0	1	2	3	4	(Sample size)
Atlantic coast States	19.1	80.9				(162)
Michigan and Illinois to Alabama and Mississippi	33.6	66.4				(125)
Minnesota to Arkansas	14.3	85.7				(14)
North Dakota Indigo (HIS[1] = 0)	42.5	57.5				(40)
Medial hybrids (HIS = 5–8)		50.0	50.0			(6)
Lazuli-like hybrids (HIS = 10–13)		3.4	10.3	72.4	13.8	(29)
North Dakota and eastern Montana Lazuli (HIS = 14)			10.3	66.7	23.1	(78)
Alberta to Arizona and New Mexico			27.5	66.7	5.9	(51)
Pacific coast states			19.4	62.2	18.4	(98)

[1] HIS = hybrid index score, based on upper breast, wing bars, and abdomen.

per breasts are atypical of Lazulis, and did not occur in any buntings examined except these two Lazuli-like hybrids. Blue bands are obvious in the middle secondary coverts. In the other two hybrids rusty on the upper breast is much more obvious, but its extent is reduced considerably by the blue throat. Blue is also present on the mostly white abdomen and tips of the middle secondary coverts. The hybridity of other apparent hybrids is questionable because they are so similar to the Lazuli, but seems confirmed by the rarity of their hybrid characteristics in western Lazulis. In all these birds blue flecks occur in the upper breast or middle secondary coverts, while abdomens are entirely white. Often the white wing bar of the middle secondary coverts appears reduced by dark bases, but this could result from feather wear rather than from hybridization.

Character gradients.—Scores of all three characters change from Indigo-like to Lazuli-like in the same localities (Table 3). Such a concordant change in expression is expected in zones of hybridization between two well-differentiated gene pools in secondary contact. This contrasts with discordant or independent geographical variation in areas of intergradation between geographical races in primary contact (Wilson and Brown 1953). Increased variability of expression is also obvious, and indicates effects of hybridization (Mayr 1963: 380) with the production of F_1 hybrids and backcrosses, rather than a smooth and continuous intergradation with no increased variability. Scores of head color (Table 4) of North Dakota Lazuli-like specimens (HIS = 10–14) and Indigos (HIS = 0) are not intermediate between western and eastern U.S. populations. Thus no clines in head color between pure and hybrid populations are obvious from these data.

Linear measurements and weight.—Two measurements of color patterns were obtained from Lazuli-like buntings. The blue throat was measured from the lower mandible's posterior edge in between the two rami along the medial line to the posterior edge of the blue. The rusty upper breast was measured along the medial line from its anterior to posterior edge. The means ± 1 SD (in mm) for throat lengths of 17 Lazuli-like hybrids and 48 overlap (North Dakota and Montana) Lazulis are 28.05 ± 2.75 and 26.13 ± 1.88 respectively, and for breast length 13.64 ± 2.77 and 16.13 ± 2.63 respectively. In both measurements Lazuli-like hybrids and overlap Lazulis are significantly different ($P < 0.025$). Thus the group of birds determined to be Lazuli-like hybrids by the hybrid index method was intermediate between the Lazuli and the Indigo in both measurements.

Comparisons of breast and throat measurements of North Dakota and western Lazulis are spurious because of differences in the preparation of specimens. Most North Dakota specimens were preserved whole by injection with formalin and dried while extended to their total length. Many Lazuli study skins at other museums were shorter because heads were tucked in close to the body, which greatly shortened the length of the blue throat and to a lesser degree the length of the rusty breast.

In all five linear measurements and weight, North Dakota adult male Indigos and Lazulis are significantly different ($P < 0.025$). Lazulis have longer wings, tails, and total lengths, and greater weights, while Indigos have longer bills and tarsi (Fig. 2). Medial hybrids (HIS = 5–8) are significantly different ($P < 0.05$) from Indigos in all measurements except total length and weight, and from Lazulis in all except bill, tarsus, and weight. Lazuli-like hybrids (HIS = 10–13) are not significantly different from Lazuli, although they are slightly intermediate in all characters (except wing in which Lazulis and Lazuli-like hybrids are equal). Thus size measurements correlate roughly with plumage characteristics, as the measurements grade from one pure plumage phenotype through the hybrids to the other pure plumage phenotype (Fig. 2).

Subadult and adult male buntings differ in some measurements, and should therefore not be pooled. Five subadult Indigos have significantly shorter wings and tarsi than 29 adults, and 16 subadult Lazulis have significantly shorter wings, tails, and total lengths than 38 adults ($P < 0.05$).

Discussion

Overlap of breeding ranges and hybridization in North Dakota and Montana apparently resulted from immigration of Indigos into Lazuli populations. Conversely apparently no Lazulis dispersed from the Mis-

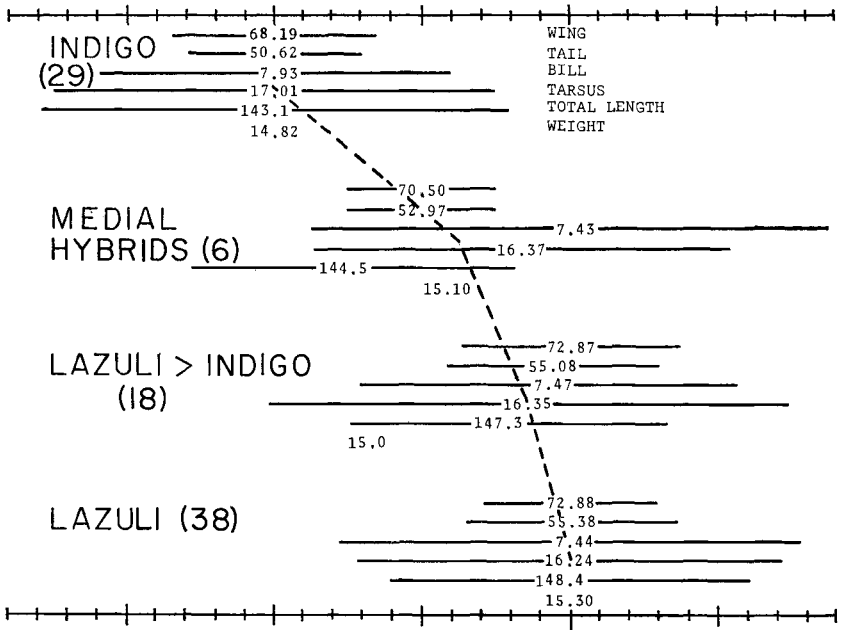

Fig. 2. Relationship of linear measurements (mm) and weight (g) to plumage of adult male Indigos (hybrid index score, HIS, = 0), medial hybrids (HIS = 5–8), Lazuli-like hybrids (HIS = 10–13), and Lazulis (HIS = 14) from North Dakota and eastern Montana. Decimal points represent graphic location of sample means, and horizontal lines represent ± 1 SD. Standard deviations for weight were too large to graph. Sample sizes are in parentheses. Buntings collected in Montana during 1971 are not included. The dashed line connects the averages of all six measurements for each phenotype. The horizontal axis assumes different scaling for each measurement.

souri to the James and Sheyenne Rivers. When hybridization occurs, there is therefore considerable introgression of Indigo genes into Lazuli-like populations, but little or no Lazuli introgression into Indigo-like populations.

The westward dispersal of Indigos may depend on available forested migratory and dispersal routes in the plains. Although buntings appear to be principally nocturnal migrants and would not necessarily remain near forests while migrating at night, they probably also migrate some during daylight when they would prefer forested habitats for foraging. Also buntings, especially subadults, might disperse considerably during the time interval between the end of spring migration and the start of breeding, as buntings breed relatively late in the season. Thus Indigos

migrating northward through eastern Kansas and eastern Nebraska would reach the Missouri River valley, and might follow its forests northwestward into western North Dakota and eastern Montana. Forests along North Dakota rivers flowing westerly into the Missouri River might provide dispersal routes into southwestern North Dakota. In contrast, buntings would not tend to disperse eastward from the Missouri River because in North Dakota and northern South Dakota the Missouri has no tributaries from the relatively treeless country to the east. Thus any Lazulis dispersing northeastward would not likely continue beyond the Missouri River, although Lazulis have apparently established a small population along the Souris River.

Two observations here may indicate that backcrossing toward the Indigo is selected against. First there was no evidence of Lazuli genes in Indigo-like populations in eastern North Dakota. Second, in overlap areas where apparently pure Indigo and Lazuli stocks occur together no backcrosses toward Indigo were seen or collected.

On the other hand, backcrosses toward Indigo may be rare simply by chance alone, as indicated in two ways by Fig. 1. First, in areas of overlap Indigos are much less plentiful than Lazulis (except in the Souris River area), and if random mating occurs hybrids would by chance breed with Lazulis rather than with Indigos. Second, backcrosses to Indigo may be absent in eastern North Dakota because Lazulis are absent, or at least very rare. The data indicate that Lazulis are so rare in eastern North Dakota that they would have almost no effect on Indigo populations. While traveling along the Sheyenne River from Valley City to Kindred 5–7 August 1968, I saw no Lazulis, but saw 79 singing Indigo-like males that showed no obvious effects of hybridization.

The occurrence of apparently pure Indigos within the Lazuli range indicates that isolating mechanisms have not completely broken down (see Short 1969). Ample opportunities for mixed mating exist because Lazulis breed in the same habitats as Indigos in the overlap area. Indigos should not occur with Lazulis if random mating occurs with the production of fully viable and fertile offspring, and if no immigration occurs. After many generations of hybridization and backcrossing almost all individuals should be hybrids, as appears to be the case in flickers (Short 1965). In other words, free hybridization should result in clines (character gradients) between parental populations (Mayr 1963).

Even if rapid immigration accounts for the occurrence of Indigos in Lazuli range, hybrids might be more common if free interbreeding occurs. For example, hybrid orioles (*Icterus galbula*) phenotypically similar to the Baltimore Oriole (*I. g. galbula*) are the commonest oriole phenotype

in populations along the Missouri River in North Dakota where Bullock's Orioles (*I. g. bullockii*) are very rare (Kroodsma 1970). Thus Baltimore Oriole-like hybrids are very common even where the immigration rate of Bullock's Orioles is apparently minimal.

Conversely, hybrid buntings may not be more common because of dispersal of Lazulis into areas of hybridization, which could mask or swamp effects of hybridization with Indigos. Swamping may occur because Indigos prefer more mesic woodland habitats along streams, which are not plentiful in western North Dakota. Lazulis breed both in these mesic areas and in surrounding drier habitats. Thus the very small local Indigo populations in western North Dakota occur within larger and more ecologically diffuse populations of Lazulis (as also indicated by Stewart and Kantrud's 1972 data) that might continually swamp phenotypic expressions of Indigo genes.

According to Sibley and Short's (1959) indexing, 66 of 95 buntings collected in South Dakota, Wyoming, Nebraska, and Colorado were hybrids. This apparently high frequency of hybridization contrasts with results of this study in which only 35 of 153 buntings from North Dakota and eastern Montana were indexed as hybrids. Also, many specimens as indexed by Sibley and Short would appear to be backcrosses toward Indigo or Indigo-like hybrids, while no such hybrids were collected in North Dakota. Based on my study and specimens I have seen that were indexed as hybrids by Sibley and Short, I believe that hybridization in the southern Great Plains may be less extensive than their study indicates. For example, of six specimens collected near Hastings and Crete in Nebraska, Sibley and Short indexed four as hybrids, while I indexed only one as a hybrid. (These six specimens were the only buntings of Sibley and Short's collection present in the Cornell University Museum at the time of my visit; the rest were out on loan.) The difference resulted because Sibley and Short used head and rump color, which are relatively variable in each species (see plumage descriptions above), and did not recognize that adult male Indigos often have white on the abdomen during the breeding season. Because of these differences in indexing no further comparisons of hybridization in northern and southern areas of the plains can be made, and a reappraisal of hybridization between buntings in the southern Great Plains may be advisable.

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Summary

During 1967–69 and 1971 male Indigo and Lazuli Buntings and their hybrids were collected in North Dakota and Montana and compared with buntings from extreme eastern and western United States to clarify the extent of hybridization. Identification of phenotypically pure Indigo Buntings was complicated by a delay in the completion of their prenuptial molt far into the summer, causing many of them to possess characteristics of the winter plumage that could be mistaken as indication of hybridization with Lazuli Buntings. Identification of such pure males with an incomplete nuptial plumage was accomplished by noting the presence of ragged (worn) brown margins on any of the proximal three pairs of secondaries.

Colors and color patterns of the upper breast, abdomen, and wing bars were analyzed by the hybrid index method. Population samples from eastern North Dakota were entirely Indigo. Samples from along the Missouri River in North Dakota, southwestern North Dakota, and along the Missouri River in Montana were mostly Lazuli, with a progressively lesser proportion of Lazuli-like hybrids, intermediate hybrids, and Indigos. Data of weight and several linear measurements corroborate data of the hybrid index method. Hybridization apparently resulted from dispersal of Indigo Buntings into the breeding range of the Lazuli Bunting.

The frequency of hybridization in the southern Great Plains as described by a previous study is greater than in North Dakota and eastern Montana, but may have been overestimated as shown by data in this paper.

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