

# THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

*Published by the Wilson Ornithological Society*

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VOL. 87, No. 2

JUNE 1975

PAGES 145-302

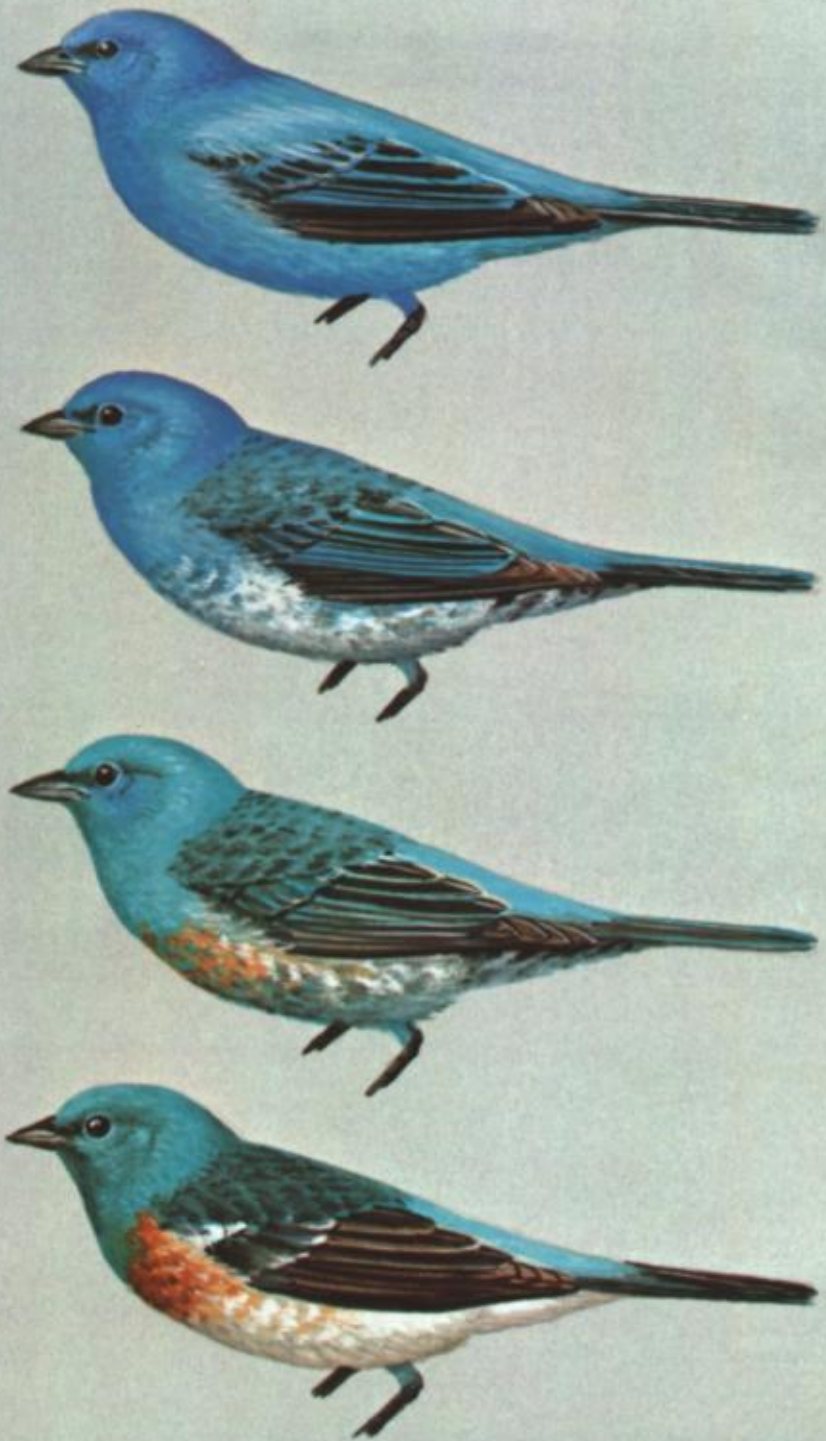
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## A BEHAVIORAL AND MORPHOLOGICAL STUDY OF SYMPATRY IN THE INDIGO AND LAZULI BUNTINGS OF THE GREAT PLAINS

STEPHEN T. EMLÉN, JAMES D. RISING, AND WILLIAM L. THOMPSON

Eastern and western counterpart taxa (species and near-species) in several avian genera meet and interbreed in the Great Plains of North America (Sibley 1961, Mengel 1970). Among these are the Lazuli Bunting (*Passerina amoena*) of the west and the Indigo Bunting (*P. cyanea*) of the east. Information on the interactions of these buntings in the Plains region was largely anecdotal until studied by Sibley and Short (1959) in South Dakota, Nebraska, Kansas, Colorado, and Wyoming. From this study, which showed that a number of specimens from the Plains were intermediate in plumage, Sibley and Short concluded that hybridization between the forms was common. Nonetheless, as conclusive evidence of extensive introgression between the species was lacking, they (1959:461) suggested that final assessment of the evolutionary status of the 2 *Passerina* required more information on “. . . pairing, mate-selection, and habitat preference of the two forms in the area of hybridization and overlap.”

Field studies of sympatric populations of closely related forms are of interest because they permit assessment of the “interspecific” roles of cues used primarily for “intraspecific” communication. The *Passerina* are ideal for such studies: the males are strikingly different in appearance, and are easily separable in the field; the songs differ both in structure and cadence, and the importance of these parameters has been well documented (Thompson 1968, 1970, Emlen 1972); the agonistic and courtship behavior of these birds is well understood (Thompson 1965, Emlen 1972) making it possible to interpret both interactions between birds in the field and responses of individuals to song playback experiments. Field observations on habitat separation and territory overlap can provide additional information on the ecological similarity of sympatric forms.



Representative *Passerina* from the Plains. Top: "pure" Indigo male from Niobrara, Nebr. Middle: two presumed hybrid males from Chadron, Nebr. Bottom: "pure" Lazuli male from Shoshoni, W

If mating among the buntings is non-random, the situation would be especially intriguing since one feature commonly believed to mediate gene flow is song, and previous studies have shown that details of *Passerina* song are learned (Rice and Thompson 1968, Emlen 1972). We thus could examine the evolutionary significance of a "cultural" trait in determining gene frequencies.

With these objectives, we examined both "mixed" and "pure" bunting populations, looking for patterns of variation in morphology, ecology, song, and behavior. Our results permit us to speculate on the significance of song for recognition (and thus potentially for species segregation), on the duration of the critical periods for learning the utterance and recognition of song, and on the relative frequency and success of mixed matings. This, in turn, yields a better understanding of the selective pressures in operation and of the current status of bunting evolution in the Plains.

#### MATERIALS AND METHODS

*Study localities.*—The Niobrara River in northern Nebraska flows west to east through a region where the ranges of Indigo and Lazuli buntings overlap. From 22 June through 4 July 1969 we examined 3 populations near Niobrara, 3 near Valentine, and 2 near Chadron, all along the Niobrara in Nebraska, and 1 population west of the Niobrara drainage, near Shoshoni, Wyoming (Fig. 1). Thompson obtained additional song data on Indigo Buntings from Iowa, and on Lazuli Buntings from Colorado.

Our 3 study sites in Knox Co. were: 6.6 km N Niobrara; 15 km W Niobrara; and .8 km S Verdel. The dominant arboreal vegetation was cottonwood (*Populus cf. deltoides*), elm (*Ulmus americana*), and willow (*Salix* sp.), with ash (*Fraxinus* sp.), oak (*Quercus macrocarpa*), and box elder (*Acer negundo*) also present. The understory was sparse, and the buntings were found along field-woods interfaces.

In Cherry Co. we studied buntings at Fort Niobrara National Wildlife Refuge, 21.7 km E Valentine; .8 km N Valentine, along Minnechaduzza Lake and Creek; and 50 km west of Valentine, 13.3 km S Nenzel. The predominant trees were cottonwood, elm, ash, and willow. Oak and box elder were also present. North of Valentine, along north-facing bluffs facing the Niobrara, the vegetation was rank and included such species as birch (*Betula papyrifera*), hornbeam (*Ostrya virginiana*) and pine (*Pinus ponderosa*), attesting to the more xeric nature of such areas. Underbrush was short, due in part to grazing and, just north of Valentine, to a city park. Buntings were abundant and held territories along the woods-field edge.

In Dawes Co. we studied buntings 10 km S Chadron, adjacent to a small reservoir and creek; and 10 km ESE Chadron, along Little Bordeaux Creek. The former site was more mesic, with tall cottonwoods and willows, some ash, and rank understory. The Little Bordeaux Creek locality was overgrazed, with significant understory restricted to draws where plum (*Prunus*), nettles (*Urtica*), ragweed (*Ambrosia*), and daisy fleabane (*Erigeron*) were common. Scattered ash, elm, and willow grew in open stands.

In Wyoming, our study site was 30 km N Shoshoni, along the Wind River. The buntings were found in a narrow band of trees (primarily cottonwoods) with spear grass (*Stipa*) understory, bordered by sage (*Artemisia*).

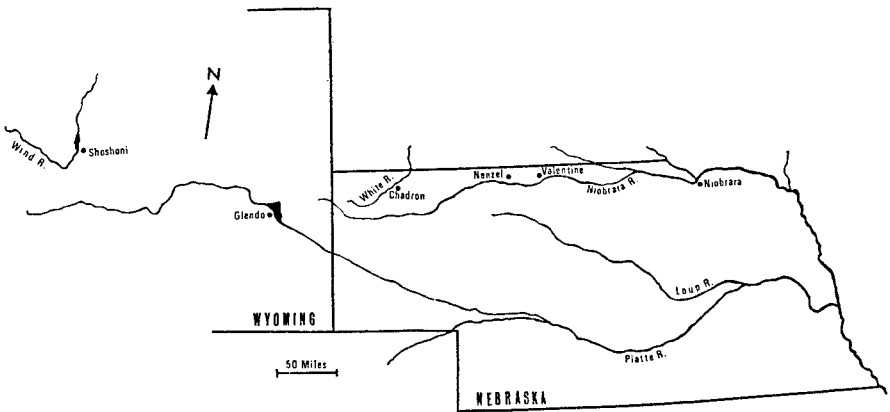


FIG. 1. Localities (mostly along the Niobrara River) at which *Passerina* were studied in 1969: Niobrara, Nebraska (23–25 June); Valentine, Nebraska (25–28 June); Chadron, Nebraska (29–30 June); Shoshoni, Wyoming (1 July).

*Study of song.*—At each locality, Thompson recorded the songs of territorial male buntings using a Shure 545 Unidyne III dynamic microphone and a Uher 4000 Report-S tape recorder at a speed of  $7\frac{1}{2}$  i.p.s. (19 cm p.s.). Several songs were recorded for each bird, and one judged to be typical was selected for detailed analysis.

Sound spectrograms were made with a Kay Electric Company model 6061-B Sonagraph, using the high shape and wide band settings. Four song features were examined in detail: 1, *figure morphology*—the detailed structure of the individual song figures; 2, *repetition index*—a measure of the tendency for song figures to be repeated in pairs or triplets, and defined as the total number of figures in a song divided by the number of different types of figures; 3, the *frequency of buzzes* in the song; and 4, *temporal intervals* between successive figures within a song.

Song features of populations from the main study localities were compared with one another and with song data from Indigo Buntings in Michigan (Thompson 1968, 1970) and New York (Emlen 1972) and Lazuli Buntings from Utah and Pacific states (Thompson 1968). Since songs of Indigo Buntings from Knox and Cherry cos. showed no significant differences from more eastern populations, these data were pooled for some of the analyses. Similarly, for certain analyses, songs of Lazuli Buntings from Shoshoni and Colorado were pooled with those of more western populations.

In the analysis of figure morphology, song figures of birds of *P. cyanea* or intermediate plumage were compared with the catalog or “dictionary” of figures compiled from eastern populations published earlier (Thompson 1970). Thompson compiled a catalog of *P. amoena* figures using songs from birds far west of any reported zone of sympatry. This catalog, which will be published separately, was used for comparison with the *P. cyanea* catalog, with the songs of *P. amoena* (by plumage) from along the Niobrara, and with the songs of males with intermediate plumage.

*Study of behavior.*—Emlen gathered data on territorial behavior of males and performed playback experiments to determine each individual’s responsiveness to Lazuli and Indigo song types. At each locality, sketch maps were made of the territories of singing

males, and notes kept of all border encounters and male-female interactions observed. At Chadron, we made a special effort to locate and collect females with mates and to determine the stage of breeding of such pairs.

For playback experiments, we used a Uher 4000-Report L tape recorder, a Nagra DH portable amplifier, and an Atlas WT-2 speaker connected to the amplifier by 30.5 m of cord.

The test songs were recorded from birds outside the zones of sympatry. The Indigo Bunting song used was from a bird recorded in Tompkins Co., New York; the Lazuli Bunting song was a recording made in central California. Each test tape contained the single song (Fig. 2) repeated at 12 sec intervals, a singing rate well within the typical range for *Passerina*.

Each bird was exposed to both test songs and the results were compared by a paired statistical test. This decreases variance caused by extraneous factors such as differences in responsiveness at different stages in the reproductive cycle, or inter-individual differences in the quality of response. In the areas of allopatry, the test song of the unlike form was presented first; in zones of possible sympatry (Valentine and Chadron) the sequence of presentation was randomized. If the first test song produced no response, the second song was played after a pause of 10 to 30 min. If the territorial male showed any sign of responding to the first test, the second test was conducted at approximately the same time on the following day. We took this precaution because previous experiments with *P. cyanea* have shown that the birds habituate to repeated song playback (Emlen 1972).

We initiated experiments only when the territorial male was known to be in the vicinity of the speaker. In practice, the speaker was placed on the ground directed upward near the presumed center of a territory or adjacent to a principal song perch. The tape recorder was turned on and the test song allowed to play for a period of 3 min measured from the time the bird made its first response to the playback. If no response occurred after continuous playback for 6 min, the experiment was terminated and given a zero score.

If the bird did respond, detailed notes were taken of its behavior during the 3 min of playback and 6 min immediately following playback. The behavior was scored according to 2 predetermined scales of responsiveness. The first evaluates the maximum intensity of the response on a scale ranging from 0 (no reaction) through a graded series of "alarm," "approach," and "attack" responses, to a value of 7 (a fully submissive response to the experimental song). In the second scale, each of 8 components of the agonistic repertoire is scored separately (as 0, 1, or 2) according to its frequency of occurrence. These values then are summed to give a 0 to 16 scale which is less dependent upon the subjective weighing of one posture or call over another. (Details of the derivation of these scales and arguments of their relative merits may be found in Emlen 1972.) The data were compared by the Wilcoxon Matched-Pairs Sign-Rank Test (Siegel 1956).

*Morphological study.*—Rising collected specimens at each locality, making a special effort to collect individuals for which we had obtained playback observations. Fifty-three huntings (all adults) were collected: 5 definite pairs, 34 other males, and 9 other females. Study skins of these specimens are at Cornell University (CU nos. 34218 to 34270). All these birds were in presumptive breeding condition (males with testes enlarged; most females with oviducts and/or ova enlarged, or a brood patch present).

In the analyses, these 53 bunting specimens, plus those collected by Sibley and Short (1959) and a few specimens from the University of Kansas Museum of Natural History

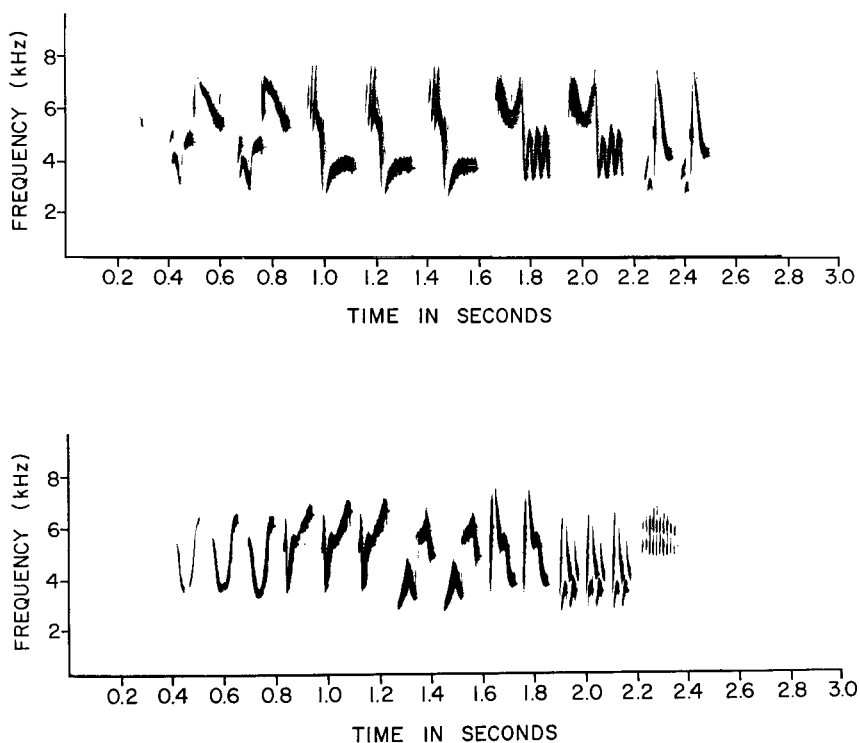


FIG. 2. Test songs of Indigo Bunting (top) and Lazuli Bunting (bottom) used in song playback studies.

(KU) comprise the "Plains sample." To provide standards against which these Plains specimens could be viewed, random sets of Indigo Buntings from Ontario and New York, and of Lazuli Buntings from British Columbia, California, and Utah were examined from the collections at Cornell University and the Royal Ontario Museum (Toronto).

Variation in color and pattern was assessed by use of subjective multistate categories (Appendices 1 and 2). Some of the characters used to assess differences in coloration reflect variation in the blue colors which apparently can be dietarily influenced (Emlen pers. obs.). Nonetheless, these features (forehead, throat, and rump color) can consistently be used to separate wild-taken specimens of the basically cobalt-blue Indigo Bunting from the turquoise-blue Lazuli Bunting. In assessing the blue of specimens, long series (including eastern and western reference birds) were laid out under the same fluorescent lights. The range of coloration within the eastern reference birds was taken to be representative of that of Indigo Buntings, and that of western birds as representative of Lazuli Buntings. Each of the specimens from the Plains sample was compared against the standards and scored according to the criteria in the appendices.

We measured the chord of the longest unflattened wing feather, length of the longest rectrix, tarsal length (diagonal distance between the tibiotarsal-tarsometatarsal joint and

the last undivided scute), length of the horny bill (anterior edge of the nostril to the tip), and the bill width (greatest width of the upper mandible).

We pooled the 5 mensural and 6 plumage characters and analyzed overall phenetic variation using principal components analysis (PCA) based on the matrix of correlation coefficients among the 11 characters (Sneath and Sokal 1973:245-247; for a fuller discussion of multivariate techniques and their use in studies of this type, see Rohwer 1972). First-year males (which can be identified by the color of the primary covert feathers) were not analyzed by PCA since assessment of abdomen color, and often of other features, is impossible. For the females, the matrix of 5 measurements and 3 color features was similarly analyzed. This multivariate procedure is useful for arranging or ordering the individuals along uncorrelated (orthogonal) axes, simultaneously considering variation in all the characters among all the individuals. A weakness of this approach is that discrimination is not maximized, so we also analyzed these matrices using discriminant function analysis (DFA), another multivariate technique (Sneath and Sokal 1973:400-405), using the following as reference samples: 27 males from New York and Ontario versus 27 males from British Columbia, California, and Utah; and 18 females from Ontario versus 11 females from British Columbia and California. For DFA only the 5 mensural features were used, thus giving an estimate of phenetic separation that is independent of plumage characteristics, and permitting the inclusion of first-year males. In both PCA and DFA analyses, missing mensural data (e.g., features that were broken and could not be measured) were estimated by regression analysis using the other measurement that best predicted the size of the deleted characteristic. There were no missing features in the reference samples, and not more than one for any other specimen. Specimens missing plumage character index values were not used in PCA.

## RESULTS

### *Morphology*

Both the PCA and the DFA clearly separate the Plains buntings into 2 clusters that correspond to nominant Indigo and Lazuli buntings (Figs. 3, 4, 5, and 6). In the PCA plot for males (Fig. 3) several of the specimens from Nebraska and Colorado fall between the reference Indigo and Lazuli clusters that separate along the component I axis, apparently reflecting differences in wing, tail, and culmen lengths in addition to the plumage color features. Of these, birds C, D, and N are clearly intermediate in plumage. Birds B and M may also be intermediate, but are close to Lazuli, and G, H, and E are perhaps intermediate, but close to Indigo. Birds A, J, and O all appear by eye to be of Lazuli plumage, and F, L, and K all appear by eye to be Indigo Buntings. None of the females is intermediate on the PCA plot (Fig. 4).

Insomuch as there is considerable subjectivity involved in assigning the character index scores and possible circularity in interpreting them, we sought to discriminate further between the buntings using DFA based *only* on the 5 mensural features. These features discriminated between the reference samples with but slight inconsistency or error: 1 of the 27 (3%) reference

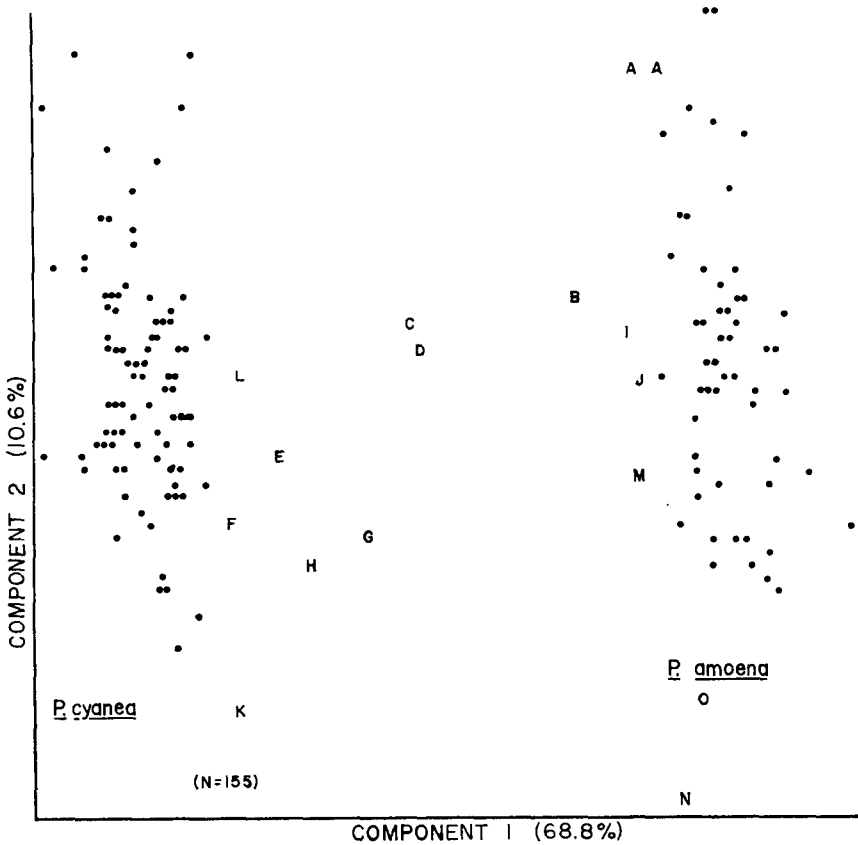


FIG. 3. A 2-dimensional view of the phenetic position of 155 male buntings on principal components 1 and 2 extracted from the matrix of correlations among 11 characters. Together, components 1 and 2 account for 79.4% of the total variance. The letters indicate the position of specimens singled out for discussion in the text: **A**, Shoshoni, Wyo. (1969); **B**, CU 25516, 10 km ESE Chadron (1955); **C**, CU 34251, 10 km S Chadron (1969); **D**, CU 27395, Crook Co., Colo. (1955); **E**, CU 27392, Crook, Colo. (1955); **F**, CU 27612, Blair, Nebr. (1955); **G**, 34257, 10 km S Chadron (1969); **H**, CU 27401, Goodrich, Colo. (1955); **I**, Royal Ontario Mus. 70815, Nicasio, Calif.; **J**, CU 25505, 15 km ENE Valentine, Nebr. (1955); **K**, ROM 72898, Cobourg, Ont.; **L**, CU 25501, 15 km ENE Valentine (1955); **M**, CU 27396, Goodrich, Colo. (1955); **N**, CU 34247, 10 km S Chadron (1969); **O**, CU 34245, 10 km ESE Chadron (1969). All birds collected in 1955 are from Sibley and Short (1959).

Indigo males could not be separated from the Lazuli males; all of the Lazuli males could be discriminated from Indigo males; all of the reference females were correctly differentiated (Figs. 5 and 6). The histogram of the discriminant scores of all male birds from the Great Plains (obtained by multiplying



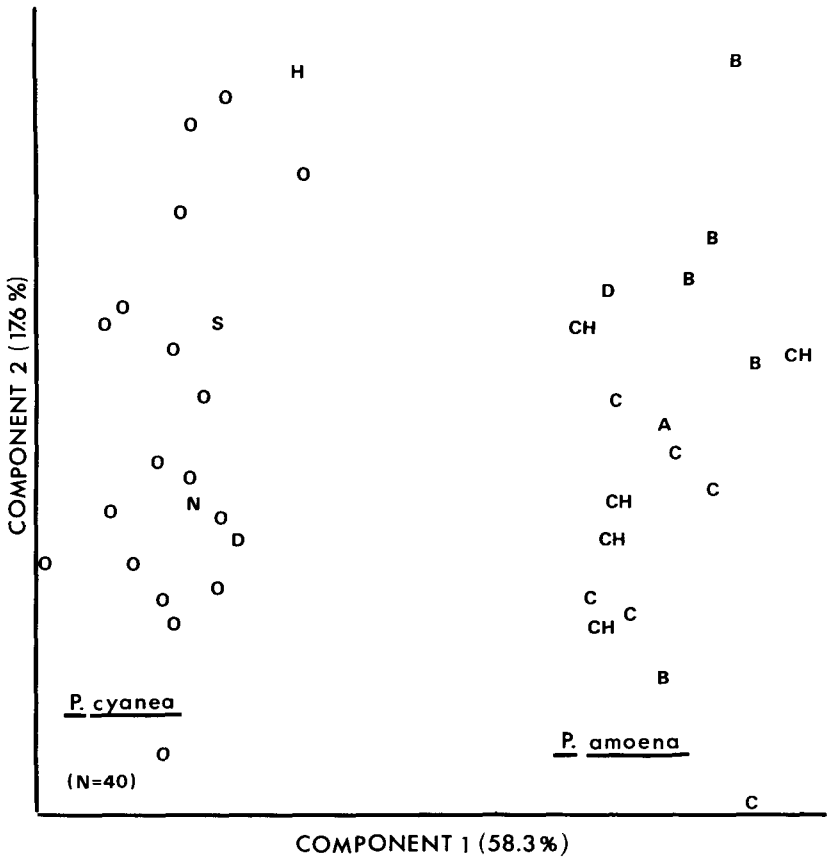


FIG. 4. A 2-dimensional view of the phenetic position of 40 female buntings on principal components 1 and 2 extracted from the matrix of correlations among 8 characters. Together, components 1 and 2 account for 75.9% of the total variance. The letters refer to the following localities: A, 10 km SE Chadron (1955); B, British Columbia; C, California; D, 10 km ESE Chadron (1969); CH, 10 km S Chadron (1969); H, 25 km E, 25 km S Hoxie, Sheridan Co., Kans.; N, 13.3 km S Nenzel, Nebr.; S, 6.6 km N, 1.6 km E St. Francis, Cheyenne Co., Kans.; O, Ontario.

each measurement by its discriminant weight (Appendix 4) and obtaining a single value for each specimen to indicate its position) shows the scores to be distributed roughly bimodally. About 5% of the male specimens are "misidentified" (i.e., are placed differently than their plumage features would indicate), a percentage similar to the number misidentified in the reference samples. The DFA (Fig. 5) suggests that there has been a shift toward Indigo-like buntings at Valentine since 1955—as indeed the plumages of the

buntings suggest. Four of the 6 birds (from the total 101) that are "intermediate" on the DFA were taken at Little Bordeaux Creek, 10 km ESE Chadron; these specimens all appear by eye to be Lazuli Buntings. However, all but one are first-year males and thus it is hard to assess their plumage features accurately. None of the birds that appears to be a hybrid on the basis of plumage is intermediate on the DFA. Thus, while there does appear to be some independence of plumage and size of the males, both the PCA and the DFA suggest that only a few specimens from the Plains fall outside of the phenotypic ranges of Indigo and Lazuli buntings. The DFA additionally suggests that the plumage patterns have not been grossly misinterpreted: the basic Indigo-Lazuli separation is preserved, with relatively few individuals intermediate.

None of the 11 females from the Plains falls outside the statistical limits of reference Indigos or Lazulis. But 5 specimens are close enough to deserve mention. Three, all from 10 km S Chadron, have "borderline" *P. amoena* scores (CU 34255, 34258, and 34263). These all appear to be typical Lazuli Buntings by plumage and cluster with Lazuli females in the PCA (Fig. 4). The fourth specimen (CU 34246) taken at Little Bordeaux Creek scored as a borderline Indigo by DFA but was identified as a Lazuli by PCA and plumage inspection. The 5th female (KU 54644) was collected in Sheridan Co., Kansas in 1966. It clustered with Indigo Buntings by PCA and plumage, yet fell within the Lazuli range by DFA.

The small numbers of female specimens make it difficult to interpret these results although they suggest, as with the males, some independence of plumage and size. The distribution of discriminant scores of the 11 females from the Plains is unimodal (Fig. 6); most of the "intermediate" specimens are from the Chadron region (plus KU 54644), and could well be of mixed parentage.

#### *Song Variation*

*Song figures.*—East and west of the zone of sympatry (Chadron, Nebraska), buntings sang Indigo or Lazuli song figures which were essentially the same as those of birds from populations in the main parts of their respective ranges. The 31 Indigo Buntings from eastern Nebraska and Iowa sang a total of 63 song figure types of which 49 matched up perfectly with counterparts in Thompson's (1970) catalog of *P. cyanea* songs from Michigan. Thirteen additional figures were variants showing only slight differences from those described previously. Only one song figure was so distinctive that it could not be identified with a counterpart from the Michigan population, and it seems to represent a composite of 2 Michigan figures.

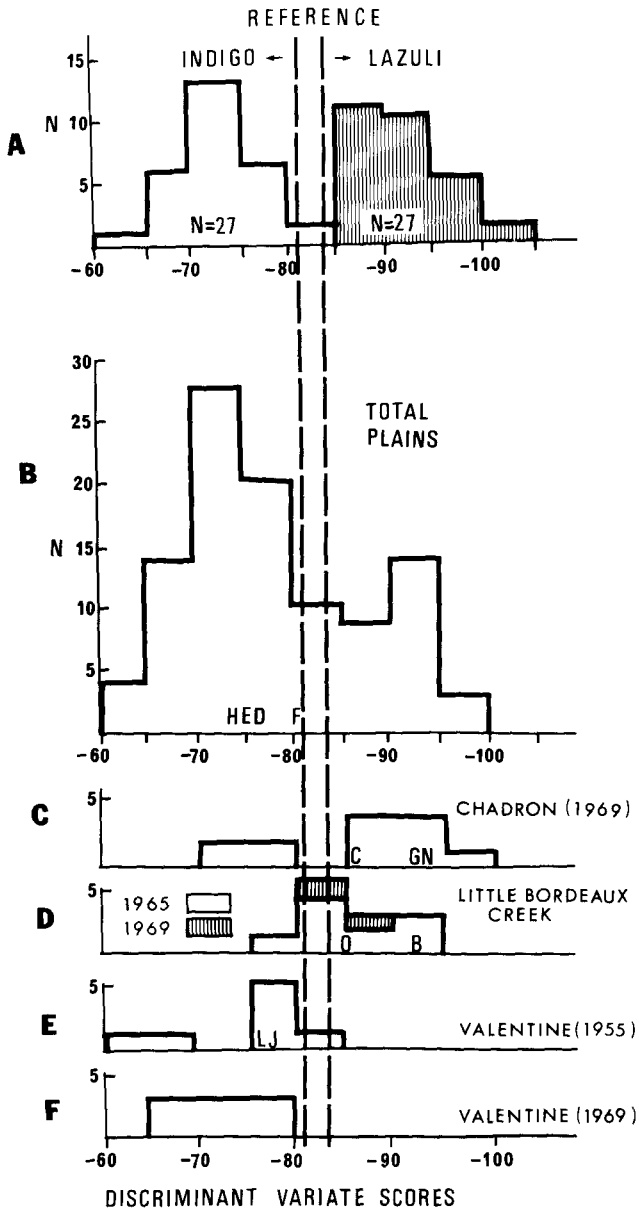


FIG. 5. Histograms of discriminant scores for male buntings. Scores for the reference specimens are plotted on the upper diagram, (A), and various combinations of the specimens from the Great Plains on the lower diagrams: (B) all 101 of the Great Plains males; (C) only the males taken 10 km S Chadron, 1969; (D) the males taken along

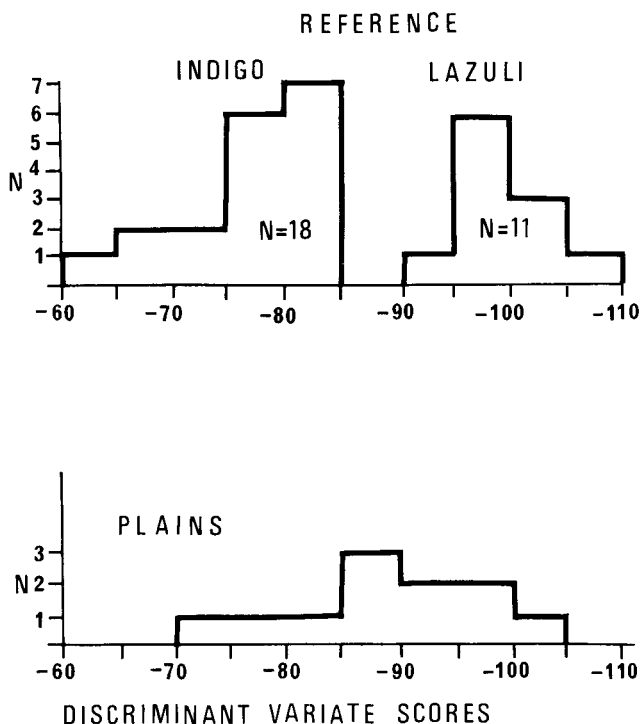


FIG. 6. Histograms of discriminant scores for female buntings. Scores for the reference specimens are plotted on the upper diagram, and those for the females from the Great Plains on the lower. The statistical lower extreme for Lazuli females is  $-89.6$ ; the statistical upper value for Indigo females is  $-87.5$ .

The 19 Lazuli Buntings in Wyoming and Colorado sang a total of 51 song figure types, 40 of which had precise counterparts in the song catalog for Lazuli Buntings recorded from farther west. Thus, in areas of allopatry, there was little tendency for the song figures of either species to deviate from more eastern or western populations or to converge upon intermediate characteristics.

At Chadron, within the zone of sympatry, the situation was different. Males with *P. amoena* plumage sang songs whose composition varied from 100%

←

Little Bordeaux Creek, 10 km ESE Chadron (1955, open; 1969, shaded); (E) males taken from the Valentine region in 1955; (F) and males taken from Valentine in 1969. The upper Indigo and lower Lazuli extremes are indicated by the dashed line. The letters inside the histograms indicate the location of certain specimens identified in Fig. 3.

TABLE 1

PERCENTAGE OF *P. CYANEA* AND *P. AMOENA* FIGURE TYPES IN SONGS OF BIRDS OF VARIOUS PLUMAGES NEAR CHADRON, NEBRASKA

<i>P. cyanea</i> plumage	% <i>cyanea</i> figure types
CU 34250	100
CU 34252	65
not collected	20
CU 34264	14
Intermediate plumage	
CU 34257	100
CU 34247	9
<i>P. amoena</i> plumage	% <i>amoena</i> figure types
CU 34249	100
CU 34254	100
CU 34260	100
CU 34243	100
not collected	100
not collected	89
not collected	88
CU 34256	87
CU 34248	80
not collected	64
not collected	55
not collected	44
CU 34259	0
CU 34245	0

Lazuli figure types to 100% Indigo types (complete song interchange). Similarly, different individuals in *P. cyanea* plumage sang songs containing varying numbers of Indigo and Lazuli figure types. Table 1 shows the song composition of all males recorded at Chadron in terms of Indigo and Lazuli figures. One bird intermediate in plumage characteristics (CU 34257) sang a song composed entirely of Indigo figures, whereas a second intermediate male (CU 34247) sang a primarily Lazuli song. Three figures not found in other Lazuli Bunting populations were sung by males in *amoena* plumage at Chadron. Figure 7 shows examples of song composition of birds of different plumage types.

Even in this zone of sympatry no intermediate song figures were discovered. Intermediacy between the species' songs did occur, but it was achieved

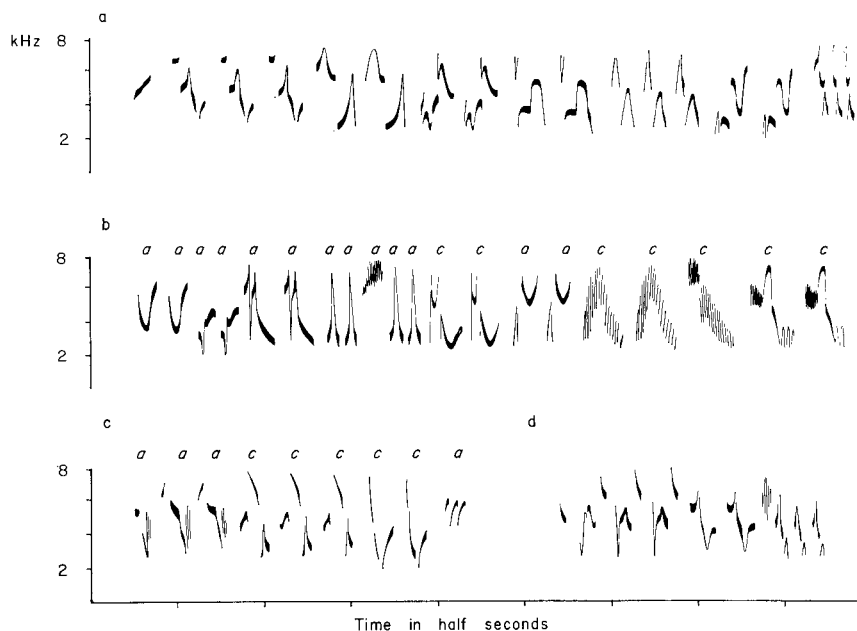


FIG. 7. Songs of some male buntings at Chadron, Nebraska. (a) Male in *P. cyanea* plumage (CU 34250) singing 100% *P. cyanea* song figures. (b) Male in *P. cyanea* plumage (CU 34252) singing both *P. cyanea* and *P. amoena* figures. Letters above figures indicate those from *cyanea* and *amoena* catalogs. (c) Male in *P. amoena* plumage (CU 34261) singing a mixture of *P. cyanea* and *P. amoena* figures. (d) Male in *P. amoena* plumage singing all *amoena* figures.

by an individual bird incorporating both pure *amoena* and pure *cyanea* figures into its territorial song.

*Repetition index.*—One feature of the songs of both species is the marked tendency for song figures to be repeated in pairs or even triplets (Thompson 1968, Emlen 1972). Table 2 presents the repetition index values obtained during our transect across the Plains. When these Plains data are lumped into “eastern,” “western,” and “Chadron” (sympatry) categories, no significant differences are apparent ( $\chi^2 = 2.85$ ). Closer examination of all the data, however, suggests a possible trend toward increased degree of repetition in the Plains.

*Frequency of buzzes.*—We defined a “buzz” as a song figure that contained a series of rapid frequency reversals. The ninth figure in song b of Fig. 7 is a good example.

Efforts to compare songs with respect to their “buzziness” are complicated by the fact that *P. cyanea* songs tend to be longer than *P. amoena* and also

TABLE 2  
 REPETITION INDICES FOR *PASSERINA* SONGS RECORDED AT DIFFERENT LOCATIONS

Species	Locality	Number of birds	Repetition index
<i>P. cyanea</i>	Eastern United States	62	1.77*
<i>P. cyanea</i>	Eastern Nebraska (allopatric zone)	31	1.86
All birds pooled	Chadron, Nebraska (sympatric zone)	21	2.10
<i>P. amoena</i>	Western Wyoming and central Colorado (allopatric zone)	17	2.00
<i>P. amoena</i>	Western United States and southwestern Canada	30	1.95

\* Pooled mean from Thompson's (1968) studies in Michigan and Emlen's (1972) studies in New York.

that the data were not normally distributed. We calculated the ratios of buzzes to non-buzzes and analyzed by chi-square tests. When the eastern and western samples are pooled and compared with the birds at Chadron there is a significant difference ( $\chi^2 = 7.63$ ,  $p < 0.05$ ) with the birds at Chadron showing a greater frequency of buzzes. No tendency for differential buzziness among the 3 phenetic categories at Chadron was distinguishable ( $\chi^2 = 2.49$ ,  $p > 0.05$ ).

*Temporal features of song.*—The spacing between successive song figures is somewhat different in Indigo and Lazuli buntings. The Indigo has a slower cadence to its song with a mean inter-figure interval of 0.09 sec. There is a further temporal subdivision of song structure with the interval between successive repetitions of similar figures being regularly and significantly shorter than the interval between dissimilar figures ( $p < 0.001$ ; factorial analysis of variance). This temporal organization is one of the most regular features of *P. cyanea* song (see Table 3, Emlen 1972).

Among Lazuli Buntings, the song cadence is significantly quicker with mean intervals between successive song figures of 0.05 sec (Thompson 1968). The differences in the intervals between identical and dissimilar figures are not significant in this species.

Along our transect, the recorded songs of Indigo Buntings from areas east of the Chadron sympatry zone were similar to their far eastern counterparts; similarly, the Lazuli Bunting songs from Colorado and Wyoming were basically similar to Lazuli songs from the far west (see Table 3).

TABLE 3  
TEMPORAL FEATURES OF *PASSERINA* SONG

Locality	Number of birds	Number of intervals analyzed	Mean interval (sec) between successive song figures		Standard error
			Dissimilar	Similar	
Eastern U. S. (Michigan & New York)	86		0.09	0.07	
Eastern Plains (Iowa and eastern Nebraska)	30	173 171	0.09	0.07	0.0026 0.0018
Chadron, Nebraska (all morphs pooled*)	20	124 136	0.07	0.05	0.0020 0.0018
Chadron Indigo morph	(4)			(0.069)	
Chadron intermediate morph	(2)			(0.056)	
Chadron Lazuli morph	(14)			(0.054)	
Western Plains (Colorado & Wyoming)	20	94 100	0.06	0.05	0.0022 0.0017
Western United States (California, Utah & British Columbia)	23		0.05	0.05	

\* Morphs described here are determined on the basis of plumage only.



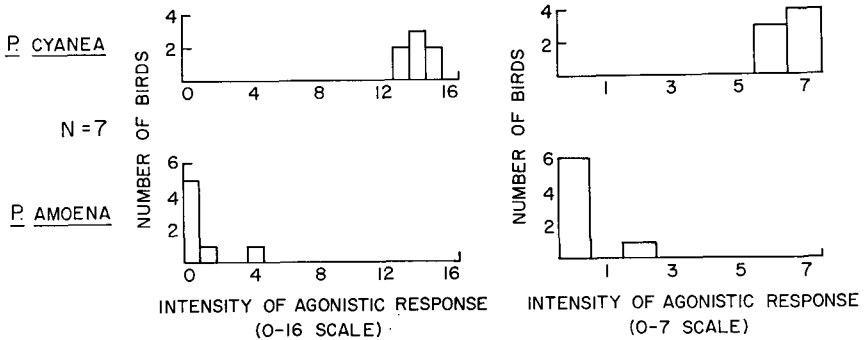


FIG. 8. Agonistic responses of territorial male Indigo Buntings at Niobrara, Nebraska, to playback of songs of Indigo Bunting (top) and Lazuli Bunting (bottom) song. Left: Responses measured on a 0-16 "Character Index" scale. Right: Responses measured on a 0-7 "maximum intensity" scale. Test songs used are those shown in Fig. 2.

At Chadron the temporal characteristics of song were intermediate. The mean intervals between similar and dissimilar successive song figures were 0.05 and 0.07 sec respectively. This trend toward intermediacy was due primarily to a shift toward faster cadence among *P. cyanea*. Although several individual *P. amoena* showed weak tendencies toward intermediacy, most did not and the mean values for temporal intervals were not statistically different from those of Lazuli Buntings recorded farther to the west. Hence the trend toward convergence was shown primarily by individuals of the less common species.

#### Behavioral Interactions

*Niobrara, Nebraska.*—We performed playback experiments to 7 territorial males here, all Indigo Buntings which had little, if any, contact with phenetic Lazuli Buntings. Each gave an intense agonistic response to the *P. cyanea* test song, but essentially ignored the *P. amoena* test song (Fig. 8). Only one bird (CU 34222) showed any interest in the Lazuli song, answering the playback with "long songs" and giving an occasional "chip" call (mild alarm). It ceased responding, however, and flew off while the test was still in progress.

These results are basically similar to ones obtained previously in areas of allopatry. Thompson (1969) found that *P. amoena* songs elicited only weak, if any, responses from male *P. cyanea* in southern Michigan although one Lazuli Bunting song was more stimulatory than were others. In New York, territorial Indigo Buntings showed no response when presented with the same Lazuli Bunting song shown in Fig. 2 (see Fig. 10 in Emlen 1972).

*Valentine, Nebraska.*—We recorded the songs of 18 birds, performed play-

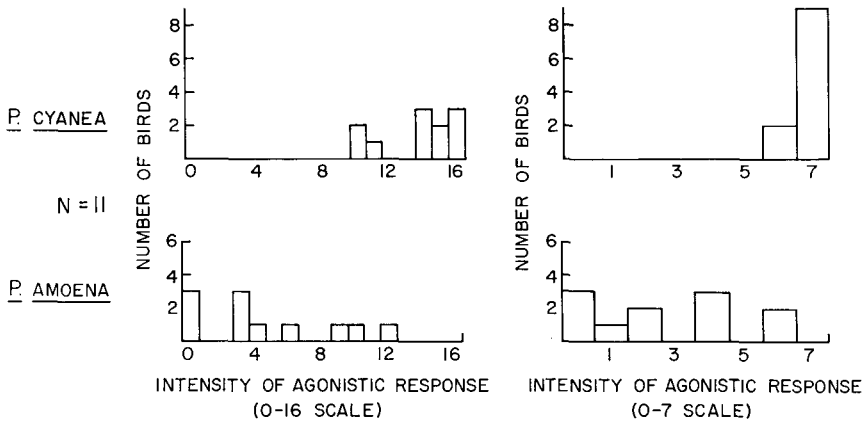


FIG. 9. Agonistic responses of territorial male *P. cyanea* at Valentine, Nebraska, to playback of songs of Indigo Bunting (top) and Lazuli Bunting (bottom).

back experiments to 11, and collected 18 specimens here. All were “pure” Indigo Buntings. Each individual gave a strong agonistic response to the *P. cyanea* test song (Fig. 9). Unlike the birds near Niobrara, these gave mixed responses to the *P. amoena* song. Three birds (CU 34229, 34237, 34238) showed no sign of song recognition, failing even to break their normal singing pattern when the playback was presented. Four others (CU 34224, 34227, 34228; 1 not collected) gave mild responses, ranging from increasing their rate of singing, to giving “alarm calls” and displays, to approaching the speaker and making display flights over it. The remaining 4 birds (CU 34225, 34226, 34235, 34236) showed strong responses involving numerous display flights, calls, modified singing behavior, and actual attacks on the speaker. In no instance, however, was a bird’s response to the Lazuli Bunting song so strong as it was to the Indigo song.

We interpret these findings to imply that some of the Valentine birds have had previous experience with Lazuli song types and have learned to recognize and to respond to *P. amoena* song as that of a competitor. Interestingly, they retained this responsiveness even though no phenetic *P. amoena* were seen or heard near Valentine.

*Chadron, Nebraska.*—Ten km south of Chadron, Nebraska, we encountered and collected buntings of both species plus a small number of intermediate individuals. We performed playback experiments to 10 territorial males and found that every bird, regardless of phenotype, gave a full agonistic response to *both* song types (Fig. 10). We next tested whether the birds responded any more strongly to one song type over the other. All birds (regardless of

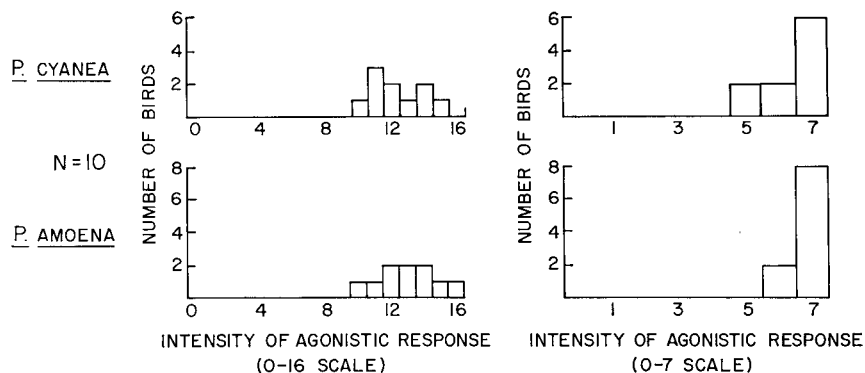


FIG. 10. Agonistic responses of territorial male buntings (both species plus intermediates) from Chadron, Nebraska, to playback of songs of *P. cyanea* (top) and *P. amoena* (bottom). See Table 4.

phenotype) were pooled in this test but the hypothesis of significant differences in response was rejected ( $p > .1$ , Wilcoxon Sign-Rank Test). A second hypothesis states that birds of a particular phenotype should respond most strongly to the playback of the song appropriate to that phenotype (i.e., *amoena* phenotype to *amoena* song). No such tendency to respond more strongly to "conspecific" song was observed and this hypothesis also was rejected ( $p > 0.1$ ).

In the last section, we reported that birds at Chadron frequently sang songs including varying numbers of "pure" song figures from both *Passerina* species. In some instances a bird sang a song consisting entirely or primarily of heterospecific song figures. If we arbitrarily categorize individuals whose songs contain 25–75% figures of the heterospecific type as "intermediate" and those with greater than 75% "inappropriate" figures as examples of "song interchange," we can ask whether birds respond more strongly, not to their own plumage type, but to their own song type. This hypothesis is also rejected ( $p > .1$ ), indicating that buntings at Chadron respond equally to either song.

Other observations of the birds at Chadron nicely complement the results of the playback experiments. The density of buntings was high and they were in the peak of breeding with males singing vigorously and defending territorial boundaries. These borders were defended equally against both species with the result that suitable habitat was subdivided into a series of non-overlapping, interspecific territories. Figure 11 depicts the territory locations at one study site 10 km S Chadron. Of 8 birds mapped, 6 were collected representing 3 "pure" Lazuli Buntings (CU 34254, 34256, and 34259, occupying territories F, G, and J on the map), 1 "pure" Indigo Bunting (CU 34252,

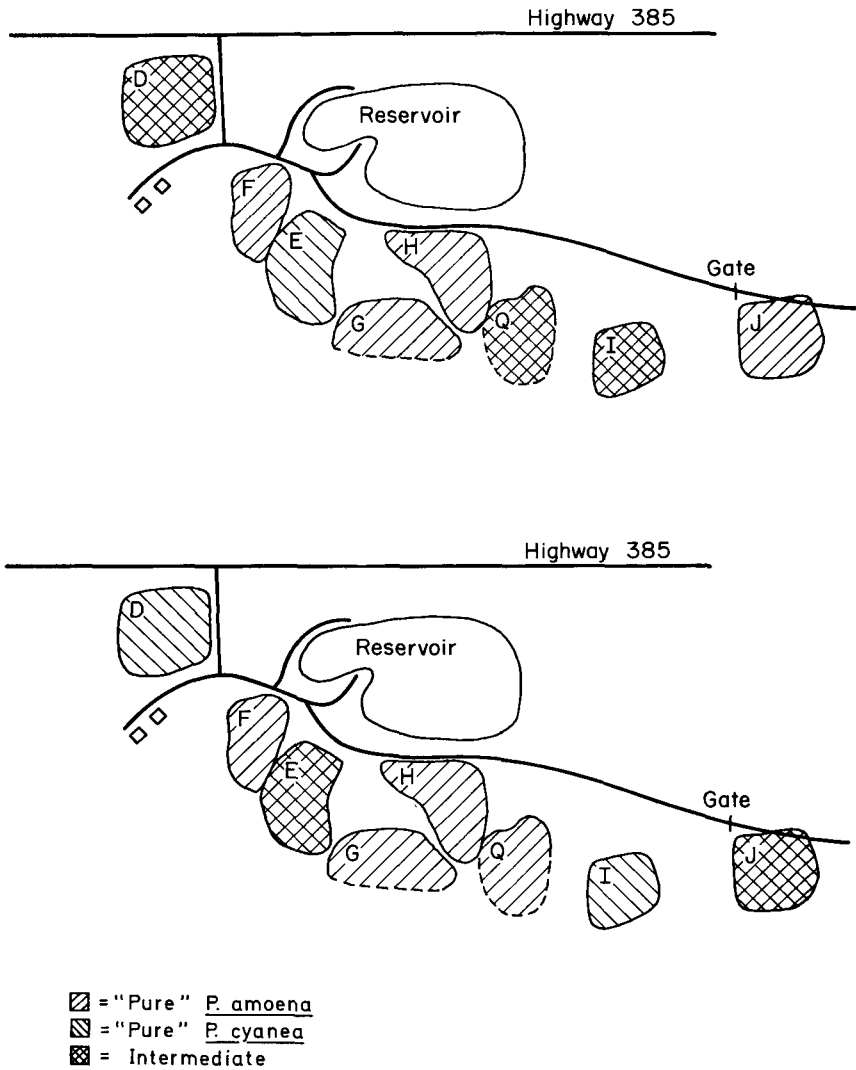


FIG. 11. Map of territorial boundaries of *P. cyanea*, *P. amoena*, and intermediates from 10 km S Chadron, Nebraska. Top: Territory owners identified on the basis of plumage. Bottom: Territory holders identified on the basis of their song. (See text).

occupying territory E), and 2 intermediates (CU 34251 and 34257; territories D and I). Two additional birds were observed but not collected; these were tentatively identified by plumage characters as being another Lazuli Bunting (on territory H), and an intermediate (territory Q). Several of

these birds sang either heterospecific (as defined above on the basis of figure types) or intermediate songs. Thus E appeared to be *P. cyanea* yet sang an intermediate song, whereas J appeared to be *P. amoena*, but had a 100% *P. cyanea* song. The 2 known phenetic intermediates both sang predominantly Indigo-like songs, whereas the presumed intermediate (on territory Q) had a Lazuli-like song. Figure 11, which maps these territories in terms both of phenotype and of song type, shows the mosaic assortment of interspecific territories.

Border encounters involving aerial chases, displays, or in one instance, prolonged combat, were observed between 8 "pairs" of territorial males (Table 4). Two cases involved 2 "pure" Lazuli Buntings in which both visual and acoustical cues could be considered "conspecifically appropriate." Five encounters featured rivals with inappropriate or intermediate visual cues but appropriate song types. The remaining instance was a "pure" Lazuli-"pure" Indigo encounter in which neither visual nor auditory stimuli were conspecifically appropriate. This latter was the most intense aggressive interaction any of us have witnessed among *Passerina*. Bird CU 34250 intruded into 34249's territory and was routinely chased back. However, 34250 turned back (presumably near the territory border) and engaged 34249 in actual physical combat. The 2 birds met breast-to-breast and appeared to grapple with the legs while remaining almost stationary in the air. After a brief period they tumbled to the ground and remained there a meter or so apart. They then resumed the conflict, took to the air and leg-grappled while they hovered or slightly ascended. This was repeated 4 times before the birds separated, each returning to its own territory. Table 4 reveals that border encounters were most frequently observed between neighbors with "appropriate" songs, regardless of visual phenotype. The overall mosaic pattern of interspecific territories, however, and the aggressive fight described above attest that Chadron territorial males are able to recognize and respond to other buntings irrespective of plumage or song characteristics.

Similar isolated instances of interspecific territorial behavior between Indigo and Lazuli buntings have been reported from Utah by Wells (1958) and Whitmore (in press).

We made a special attempt to record male-female behavior, to locate nests, and to collect females at the study areas near Chadron. We succeeded in collecting the mates of 5 males and made visual identifications of 2 others (Table 5). All proved to be phenotypically *P. amoena*. (The visual assessments of the uncollected birds were based on the presence of white wing bars and the lack of striped breast appearance.)

The male members of the pairs include 5 *P. amoena*, 1 *P. cyanea*, and 1

TABLE 4  
MORPHOLOGICAL AND SONG CHARACTERISTICS OF MALE *PASSERINA* OBSERVED IN TERRITORIAL BORDER ENCOUNTERS AT CHADRON, NEBRASKA

Male 1			Male 2			Appropriateness of cues	
Bird	Morph type	Song type	Bird	Morph type	Song type	Acous-tical	Visual
CU 34248	a <sup>1</sup>	a	CU 34249	a	a	+	+
Not collected (H) <sup>2</sup>	a <sup>3</sup>	a <sup>4</sup>	CU 34256 (G)	a	a	+	+
Not collected (H)	a <sup>3</sup>	a <sup>4</sup>	Not collected (Q)	a-c <sup>3,5</sup>	a <sup>4</sup>	+	±
CU 34261	a	c <sup>4</sup>	CU 34262	c	c <sup>4</sup>	+	—
CU 34264	c	a	Not collected (M)	a <sup>3</sup>	a <sup>4</sup>	+	—
CU 34264	c	a	Not collected (O)	a <sup>3</sup>	a <sup>4</sup>	+	—
CU 34254 (F)	a	a	CU 34252 (E)	c	a-c <sup>3,5</sup> (65% a)	±	—
CU 34249	a	a	CU 34250	c	c	—	—

<sup>1</sup> a = *amoena*, c = *cyanea*.

<sup>2</sup> Letters in parentheses refer to territory locations in Fig. 11.

<sup>3</sup> Identification based on plumage alone.

<sup>4</sup> Song based on field notes alone (song not tape recorded).

<sup>5</sup> a-c = intermediate.

intermediate. Birds CU 34252 and 34253 are a mixed pair; examination of the female revealed the presence of large follicles suggesting that she was egg-laying or in early incubation. The pair CU 34257-34258 is also of interest: the male is intermediate in plumage and by PCA while his mate is a typical *P. amoena*. Our behavioral notes and ovary examination show this pair also to be in the early egg-laying stage.

Song playback experiments test the abilities of *males* to discriminate between conspecific and heterospecific songs. But they reveal nothing about *female* responsiveness. Since female discrimination and preference could be crucial for species segregation, it is informative to examine the data in Table 5 more closely. The sample sizes are small, but of the 7 Lazuli females, 5 were mated with males that were also visually Lazuli Buntings. When the males are partitioned on the basis of song types, only 3 females were mated

TABLE 5  
COMPOSITION OF MATED PAIRS FROM CHADRON, NEBRASKA, WITH NOTES ON THEIR  
NESTING BEHAVIOR

Identification	Male			Female		Stage of breeding cycle
	Age	Morph type	Song type	Identification	Morph type	
CU 34254	Adult <sup>1</sup>	a <sup>2</sup>	a	CU 34255	a	4 advanced fledglings
CU 34256	Adult	a	a	Not collected	a <sup>3</sup>	Advanced nestlings (female seen several times with food)
Not collected		a <sup>3</sup>	a <sup>4</sup>	Not collected	a <sup>3</sup>	Unknown
CU 34261	Adult	a	c <sup>4</sup>	CU 34263	a	Advanced nestlings plus 1 cowbird egg (nestlings collected)
CU 34259	Adult	a	c	CU 34260	a	2 advanced young (almost ready to fledge)
CU 34252	Adult	c	a-c <sup>5</sup> (65% a)	CU 34253	a	Early incubation (ovary with large follicles)
CU 34257	Adult	a-c <sup>5</sup>	c	CU 34258	a	Nest building or egg- laying (ovary with enlarging follicles)

<sup>1</sup> Second year or older.

<sup>2</sup> a = *amoena*, c = *cyanea*.

<sup>3</sup> Identification based on plumage alone.

<sup>4</sup> Song based on field notes alone.

<sup>5</sup> a-c = intermediate.

to *P. amoena* types, the remaining males having intermediate or predominantly *P. cyanea* songs.

If we assume that individuals expressing "appropriate" behavioral signals for mate selection spend less time in pair formation and courtship, we would predict that such pairs would be at a more advanced stage in the breeding cycle than pairs consisting of birds possessing less optimal or inappropriate stimuli. Table 5 shows that 4 pairs had advanced nestlings or fledged young; in each case the male was of the appropriate visual phenotype while in only 2 of the 4 instances did the male sing a "conspecific" song. The remaining 2 pairs were in the early incubation or egg-laying stages. In one, the male sang an intermediate song, but was of the opposite visual phenotype; in the other, the male was of intermediate plumage and sang a heterospecific song.

Admittedly any statement drawn from these small samples must be regarded as speculative, but the data suggest that female Lazuli Buntings may rely more heavily on visual than upon acoustical cues in mate selection, at least in zones of sympatry.

*Little Bordeaux Creek, Nebraska.*—We spent only one afternoon at Little Bordeaux Creek, 10 km ESE of Chadron, but several findings lead us to believe that Little Bordeaux Creek was fundamentally different from the other Chadron study area and might have been a less optimal, overflow, area for *Passerina*. We observed 5 male and 2 female buntings, collecting 3 males and both females.

All 3 males collected were 1st-year birds whereas all 12 males collected from 10 km S Chadron were in their second breeding season, or older.

Although no quantitative playback experiments were performed here, both Indigo and Lazuli songs were played in attempts to lure birds in for collecting. The buntings seemed to respond, but frequently 2 or more males would be called in. This resulted in numerous chases, and we surmised that either territorial boundaries had not yet stabilized, or non-territorial (presumably unmated) males were present.

Finally, both females collected were in early stages of reproduction. One had not yet developed an incubation patch and had a granular ovary; the other had an incubation patch but had not yet laid (largest follicle = 4 mm). On the basis of this small sample, pair formation and breeding seemed retarded compared with the other Chadron study sites.

These findings, coupled with our subjective impression of sub-optimal bunting habitat along the Little Bordeaux, lead us to speculate that this sample might represent individuals that were unable to establish territories or obtain mates in other areas. In this regard, it is especially interesting that a high percentage of the birds collected here showed signs of intermediate morphology. One of the females (CU 34246) was "misidentified" by DFA, 2 of the males (34242, 34243) were outside the reference clusters on DFA (Figs. 5 and 6), and the third male (34245) may be intermediate by PCA (Fig. 3; bird "O"). The remaining female (34244) seemed intermediate by plumage, yet clustered with *P. amoena* in both DFA and PCA.

*Shoshoni, Wyoming.*—Glendo, Wyoming is west of any area of sympatry found by Sibley and Short. We had expected this to be our final study site and although we located several apparent Lazuli Buntings here, the first bird we called in with playback was an obvious intermediate which, though not collected, appeared similar to CU 34257, and had a short, *P. cyanea*-sounding song.

Consequently, our study ended north of Shoshoni where we did find an



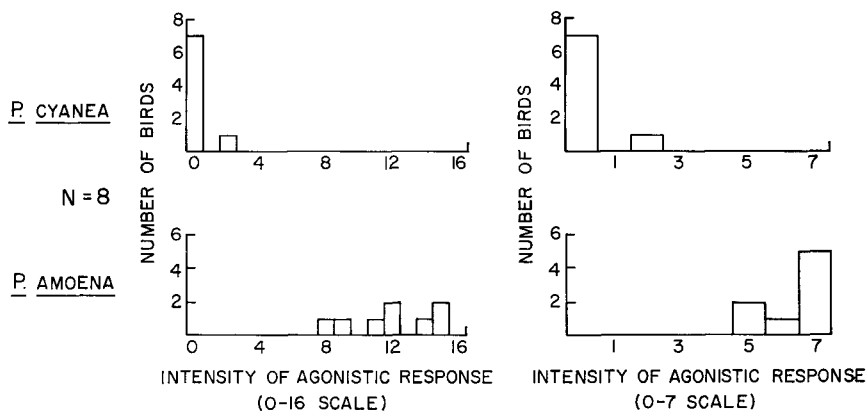


FIG. 12. Agonistic responses of territorial male Lazuli Buntings at Shoshoni, Wyoming, to playback of *P. cyanea* (top) and *P. amoena* (bottom) songs.

allopatric population of Lazuli Buntings. The 6 males collected here were phenetically *P. amoena* as were the 11 songs recorded. We performed playback experiments to 8 males whose territories were strung out almost linearly along a narrow creek bed. The results provide an exact converse to the Indigo Buntings from Niobrara: each male responded strongly to playback of the *P. amoena* song, but failed to respond to *P. cyanea* song (Fig. 12).

In summary, birds of both species from populations outside the zone of possible sympatry clearly distinguish between Indigo and Lazuli songs and respond only to that of the conspecific. Within areas of contact, song response parameters are broadened to encompass both song types and either will elicit the full repertoire of agonistic behaviors.

## DISCUSSION

### *Morphological Variation*

All of our data from PCA, DFA, and simple visual assessment of plumage suggest the same conclusions: (1) Individuals intermediate in size and plumage between Indigo and Lazuli buntings occur in the Plains. (2) These are restricted to a few areas where both "typical" species also occur and thus are presumed to be hybrids. (3) These hybrids are uncommon, comprising only 6 or 7% of the specimens. (4) There is no evidence to suggest introgression. All but the few specimens from the Plains mentioned in this paper fall within the range of variation of eastern and western stocks. This additionally suggests that geographic variation in size within Lazuli and Indigo buntings must be slight, although they differ from each other. (5) The

Indigo Bunting appears to be extending its range westward at the expense of the Lazuli Bunting. Both the change in species composition at Chadron and Valentine between 1955 and the present study, and the occurrence of intermediate forms and *P. cyanea* song influence as far west as Glendo, Wyoming suggest this.

The lack of correspondence between the individuals intermediate in size and color (and song, for that matter) is interesting. Inasmuch as a small percent of the reference specimens for DFA are "misidentified," it is conceivable that intermediates identified by this program are inappropriately so characterized. However, the fact that 5 of the 6 male hybrids identified by DFA are from the zone of distributional overlap in Nebraska (4 are from Little Bordeaux Creek; 1 is from Valentine, 1955), and the sixth is an extralimital specimen of a "Lazuli" taken from southwestern Kansas, where Indigo Buntings occur regularly in low density (Rising 1974), leaves random error an unlikely and unconvincing explanation. Rather, this suggests independent assortment between mensural and color features. In short the number of birds identified as intermediate by any analysis stressing any one correlated set of features is low, but only specimens from sympatric populations were found to be intermediate by any of our criteria.

#### *Song Variation*

Buntings from the eastern and western edges of the Plains sang songs that were indistinguishable from reference song types recorded in Michigan and New York (Indigo) or Texas and California (Lazuli). But in the zone of sympatry several song modifications were evident: (1) The tendency to repeat song figures in pairs, triplets, or more was highest at Chadron. (2) Figures with a "buzzy" quality were more prevalent at Chadron. We have no adequate explanation for these trends but raise the possibility the "buzziness," as well as repetition of song figures, might somehow be adaptive for transmission of information in the dry, windy, Plains environment. (3) The cadence of Indigo song is significantly slower than Lazuli, as a result of a longer average interval between successive song figures. At Chadron, the mean values for inter-figure spacings were intermediate between typical eastern (Indigo) and western (Lazuli) values primarily as a result of cadence shifts among Indigo Buntings. (4) The individual song figures recorded from birds at Chadron were no different from those sung by buntings elsewhere in North America. Almost every figure had a structural counterpart in the catalogs of *Passerina* song figures drawn from allopatric populations of either *P. cyanea* or *P. amoena*. The remarkable finding is that an individual male would include in its song, figures from *either* or *both* the Indigo and the Lazuli catalogs, singing them "perfectly" regardless of his morpho-

logical phenotype. The percentage of "appropriate" figures varied between individuals, ranging from 100% correct to cases of complete song interchange.

We found no evidence for vocal character displacement in the area of sympatry. Rather, 2 song features showed an increased frequency in both species (repetition index and occurrence of buzzes) whereas 2 other features appeared to be "intermediate" between the parental songs (intervals between figures and actual figure types). Interestingly, "intermediacy" was shown in precisely those parameters experimentally demonstrated to be of extreme importance for male-male recognition in a previous study by Emlen (1972). Our results thus are consistent with Cody's (1969) hypothesis that among species that derive significant benefit from interspecific territoriality, selection will favor convergence of auditory and/or visual stimuli that promote interspecific recognition. This convergence has the effect of facilitating heterospecific spacing. Such convergence is far from complete in the buntings and "intermediacy" of song figures refers to intermediate percentages of *P. cyanea* and *P. amoena* figures, not to intermediate figure structure. Furthermore, figure shape and temporal spacing can be dissociated so that many birds of both species sang *P. cyanea* figures, but sang them with something like *P. amoena* spacing.

#### *Interspecific Territoriality and Responsiveness to Heterospecific Song*

Both Indigo and Lazuli buntings from populations outside the area of sympatry clearly distinguished between conspecific and heterospecific song and responded only to the former. At Chadron, in the area of overlap, all birds apparently failed to discriminate between the test songs: they maintained mutually exclusive interspecific territories and responded aggressively to intrusion by any other bunting, regardless of its plumage or song type. At Valentine, just east of the present zone of contact, the birds (all *P. cyanea*) gave mixed responses to *P. amoena* song. Some individuals discriminated between the songs; others gave mild to strong responses to the heterospecific song.

We propose that an individual bunting's behavior, upon hearing a heterospecific song, is determined by its prior behavioral experience with birds of the opposite species or song type. For example, if a bunting interacted with another bird of conspecific plumage but which sang an intermediate or heterospecific song, it could come to associate a wide range of song types with conspecific competitors and would respond accordingly in future encounters. A similar, although converse, experience could lead to the recognition of and defense against the heterospecific or intermediate plumage type.

In areas of sympatry, such interactions between birds of different plumage types or song types presumably are quite common. In fact, at Chadron, only

33% of the males proved to be both visually and (appropriately) vocally "pure." But how could Indigo Buntings from Valentine have had contact or interacted with Lazuli Buntings? We suggest 2 possibilities. First, some *P. amoena* might have been present in the area but not located by us. The habitat becomes more xeric farther away from the river and Lazulis frequently inhabit more arid habitats than Indigos (Wauer 1969); hence a few *P. amoena* may have been in these areas. Also, Sibley and Short (1959) found evidence of Lazuli Buntings at Valentine in 1955. Thus some of our Indigo Buntings may have encountered Lazulis earlier in the breeding season, prior to settling on a permanent territory.

The common tendency for 1st-year passerine birds to settle and breed some distance from their natal site (Nice 1937, Lack 1946) suggests a second explanation for the heterogeneous responses of the Valentine birds. Those individuals showing strong recognition of Lazuli Bunting song may represent birds reared in areas farther to the west where Indigo-Lazuli interactions are more frequent. This tendency for 1st-year *P. cyanea* to wander has been documented in Michigan by Thompson (1972), who found colormarked adult buntings returning to his study area over a 4 to 5 year period, but did not recover any birds marked as nestlings or fledglings.

Not all the birds that reacted to Lazuli Bunting song were second year males, however. Of four 1-year-old birds tested, 2 (CU 34236, 34226) responded, one of them giving the strongest Valentine response to *P. amoena* song. Unless these birds had encountered Lazuli Buntings at Valentine during their brief period of mobility prior to territory establishment, we must assume that they learned to recognize Lazuli Bunting song the previous year—during the summer and autumn of their hatching. If true, this would imply that song recognition occurs at a time prior to the development of singing behavior or to the initiation of territorial or aggressive responses to song.

Both Rice and Thompson (1968) and Emlen (unpublished observations) believe that the critical period for song learning in *P. cyanea* occurs not in the summer and autumn of hatching, but in the following spring. This raises the intriguing possibility of the existence of 2 separate processes in the ontogeny of bunting song: one associated with learning song *utterances* and another with song *recognition*.

Gill and Murray (1972) have suggested a similar behavioral model (based on a bird's individual experience) to explain a very different pattern of responsiveness to interspecific song in the genus *Vermivora*. Blue-winged (*V. pinus*) and Golden-winged warblers (*V. chrysoptera*) from allopatric populations frequently fail to distinguish between their Type I songs. But in southern Michigan, in an area of sympatry, Gill and Murray found that

discrimination was improved; Blue-wings ceased responding to heterospecific songs. They hypothesized that the 2 species' songs were extremely similar and interspecific responses were the result of misidentification. But where one species encounters the other, individuals have the opportunity to associate in appropriate plumage cues with heterospecific song. These individuals should then become more discriminating, limiting their responsiveness to song types associated with birds of conspecific plumage.

The 2 species of *Vermivora* are morphologically distinct and Gill and Murray (1972) found no evidence of direct ecological competition or of interspecific territoriality.

We did not collect any information concerning the degree of ecological separation between Indigo and Lazuli buntings. Rather, we assume that the presence of strongly defended, interspecific territories implies either that ecological divergence is minimal or that divergence normally present in other parts of their ranges cannot be expressed within the restricted bands of riparian habitat available along the rivers crossing the Plains.

Murray (1971) suggested that interspecific territoriality is usually maladaptive and results from one or both species misidentifying or failing to discriminate the other. Although "misidentification" occurs among male buntings at the zone of sympatry, we believe that this "misidentification" is adaptive in promoting the establishment and maintenance of interspecific territories. In effect, we hypothesize that sympatric buntings "learn" to misidentify congeners as a result of individual behavioral experiences. This argument is based on the assumption that the extra energy expended in defending a territory against heterospecific or intermediate phenotypes is less than the energy that would be lost through the mutual sharing of territories.

For forms that are extremely similar ecologically, or which may not have had sufficient opportunity to diverge ecologically (for a variety of possible reasons), a responsiveness to both Indigo and Lazuli song clearly would be adaptive in promoting interspecific territoriality and thus minimizing ecological competition or interference. The tendency for the songs of such birds to show "convergence" in precisely those song parameters known to play a role in male-male recognition would further enhance heterospecific identification by minimizing the information loss inherent in using a conspecific song in interspecific communication.

If females are unable to discriminate between Indigo and Lazuli song types, this could lead to increased hybridization at the zones of sympatry. This possibly is one explanation for the hybrid birds and mixed pairs we observed. The relative rarity of these mis-matchings, however, suggests that females additionally use other cues in the mate selection process.

TABLE 6

FREQUENCY OF MALE TYPES IN THE POPULATION 10 KM S CHADRON COMPARED TO THE TYPES MATED TO *P. AMOENA* FEMALES

	Plumage types		
	<i>amoena</i>	<i>cyanea</i>	intermediate
Frequency in male population:	64% (14/22)	23% (5/22)	13% (3/22)
Frequency of mated males:	71% (5/7)	14% (1/7)	14% (1/7)
	Singing types		
	<i>amoena</i>	<i>cyanea</i>	intermediate
Frequency in male population:	60% (12/20)	20% (4/20)	20% (4/20)
Frequency of mated males:	43% (3/7)	43% (3/7)	14% (1/7)

#### *Pair Formation and the Success of Intermediates*

Studies of behavior of females and of the success of mixed pairs are crucial to an understanding of the present and future interactions of *Passerina* in the Plains. In regions where only one species occurs regularly, behavioral selection may well be against an immigrant individual that exhibits an "odd" plumage or song. Thus, there may be effective segregation of the species in regions where one is uncommon. But what occurs in areas where both forms are common? How accurate is the female-male recognition and what are the consequences of "inappropriate" pairing?

Unfortunately, our samples are too small to perform statistical tests to answer the first question. At Chadron (excluding Little Bordeaux Creek), 64% of the males in the population were morphologically *P. amoena* as compared with 71% of those males mated to *P. amoena* females (Table 6). Alternatively, 60% of the male population sang *P. amoena* song types (defined on the basis of > 75% appropriate song figures) as compared with 43% of the males mated to *P. amoena* females (Table 6). Females thus are pairing with the appropriate visual phenotype slightly more often, and with the appropriate singing type less often, than would be expected on the basis of a purely random selection of mates.

Data from several indirect sources suggest that mixed pairs and hybrids may be at a selective disadvantage. First, hybrid individuals are uncommon. Second, our analyses revealed practically no evidence of introgression. Third, our behavioral and ecological notes from the Little Bordeaux Creek area suggest that this is a sub-optimal area, populated by 1st-year male buntings that are considerably retarded in territory development and breeding behavior.

Four of the 5 birds collected there proved to be intermediate by either PCA or DFA and the fifth seemed intermediate in plumage. Finally, both the mis-matched pair and the hybrid pair from Chadron were delayed in their breeding when compared to the 4 "pure" pairings.

If mixed pairings are disadvantageous, natural selection should favor accurate female-male selection. Data in Tables 5 and 6 suggest that females at Chadron may rely more heavily on visual than upon auditory information in selecting mates. If true, this would be advantageous since in *Passerina*, morphology is a better indicator of genotype than song and there can be no selection for accurate female-male selection unless the cues used have a genetic basis. Details of song are learned and, where both species are in close contact, cases of intermediate song and song interchange are frequent.

For use in territorial advertisement, however, song is the more nearly optimal cue. Acoustical advertisement carries over greater distances and penetrates through concealing vegetation, thus freeing the male from having to physically patrol his territory, making his visual appearance known to would-be intruders. Song also enables a male to indicate his awareness of an intruder and to issue a mild threat, without actually flying to the location of the intrusion. In many instances, this is sufficient to repel the trespasser. Such subtle use of acoustical information can result in considerable energetic savings. The equal responsiveness of both species to both song types at Chadron, and the tendency toward intermediacy in some song features support the view that song is a principal advertisement cue for male-male interactions among these sympatric populations of *Passerina*.

#### *Evolutionary Status of Passerina in the Plains*

The ranges of Indigo and Lazuli buntings in the Plains seem to be in a dynamic state. In Nebraska the Indigo Bunting has apparently displaced the Lazuli Bunting westward, perhaps as much as 215 km in 15 years (1955-1969). Interestingly, a comparable modification of range may have been made by the eastern and northern Baltimore Oriole (*Icterus galbula*) at the expense of its geographic complement, Bullock's Oriole (*I. galbula*) in the northern Plains (Rising 1973). The east-facing and west-facing ranges of *P. amoena* and *P. cyanea* may well be "sharpened" by the presence of the congener. An "odd bird" will rarely find a mate. Nevertheless, the combination of variables that variously gives the adaptive edge to either *P. amoena* or *P. cyanea* probably shifts subtly, and the changes in the ranges of the birds are sequelae of these changes. If we assume that adult buntings return to previous breeding sites with high fidelity, this rapid change in range suggests that first-year dispersal distances of these birds must be large. This would have some

important implications: stochastic phenomena, such as the random fixation of a song- or morph-type, are unlikely. An abrupt or limited zone of sympatry thus would appear to be stable and dynamically maintained by natural selection (Endler 1973).

Thus, the evolution of the *Passerina* in the Great Plains need not be in a transitional stage. If hybrid individuals have reduced fitness, as would seem to be the case, it is probable that genetic divergence between the forms has progressed beyond the point of probable return. Genetic convergence in the future, therefore, seems unlikely.

#### SUMMARY

In the summer of 1969 we studied the morphology and behavior of the Indigo Bunting (*P. cyanea*) and the Lazuli Bunting (*P. amoena*) along a transect across the Great Plains. We concentrated on studying singing, territoriality, and mating behavior of known individuals that were later collected for morphological examination. Our hope was that this integrative approach would lead to a better understanding of the breeding biology of *Passerina* at their zone of contact.

An examination of 274 specimens showed that most individuals from the Plains fall within the normal ranges of eastern (*P. cyanea*) or western (*P. amoena*) reference populations as defined by either principal components analysis or discriminant functions analysis. Only 6 to 7% of the specimens showed signs of intermediacy (hybridization) and there was little evidence of introgression.

Intermediate specimens as well as both phenotypes were encountered near Chadron, Nebraska. Comparisons of the species compositions collected by us and by Sibley and Short (1959) indicate a rapid westward shift in the range of *P. cyanea* and, correspondingly, in the location of the area of sympatry.

In areas of allopatry in the Plains, the songs recorded from *Passerina* were indistinguishable from those of their counterparts recorded far to the east or west. At Chadron, however, birds of both species sang songs incorporating figures from both song types. For example, *P. amoena* songs ranged from 100% "appropriate" (100% *P. amoena* figures), through intermediates, to cases of complete song interchange (100% *P. cyanea* figures). Temporal parameters of song also tended to converge toward intermediate values at Chadron, especially among the less common species (*P. cyanea*).

Behavioral playback experiments showed that territorial male *P. cyanea* from the eastern Plains (Niobrara) respond agonistically only to songs of conspecifics; *P. amoena* songs are ignored. Conversely, *P. amoena* from the western Plains (Shoshoni) respond fully to playback of *P. amoena* song but fail to recognize the song of the congener. At Chadron, however, both species as well as intermediates give full agonistic responses to either song type. We hypothesize that buntings learn to respond to heterospecific song as a result of individual encounters and experiences.

Territorial behavior observed at Chadron complemented these findings. The birds were interspecifically territorial, with both species as well as intermediates defending territorial boundaries against all other *Passerina*.

An analysis of mated pairs at Chadron suggested that most females were mated to appropriate males and that inappropriate pairings (defined morphologically) were delayed in their breeding compared to normal pairings. We speculate that females rely, at least



in part, on visual cues in mate selection; such a strategy clearly would be advantageous since morphology is a good predictor of genotype whereas song (which is learned and often "inappropriate" at Chadron) is not.

Four lines of evidence suggest that mis-matings, where they occur, are selectively disadvantageous: (1) the small number of intermediate individuals and minimal introgression found, (2) the rarity of mixed-mated pairs, (3) the temporal retardation of breeding of such pairs, and (4) the occurrence of a high percentage of both first-year males and intermediate phenotypes at one particular study site that was judged on the basis of vegetation to be sub-optimal.

*We conclude:* (1) That massive convergence and introgression is not occurring among the *Passerina* of the Great Plains. (2) The species appear to have diverged to a point where hybrids and mixed-pairs are at a selective disadvantage. (3) The 2 forms minimize possible ecological competition through the maintenance of non-overlapping, interspecific territories. Both the changes in singing behavior and the increased responsiveness to congeneric song noted in the area of sympatry are seen as adaptations that promote recognition of, and aid in the defense of, these territories against heterospecifics.

#### ACKNOWLEDGMENTS

This work was supported in part by an NIH health science advancement award to S. T. Emlen and Cornell University. The manuscript has profited from comments and criticisms by N. J. Demong, D. Forsythe, D. Husnel, J. C. Rice, T. L. Rising, S. A. Rohwer, R. C. Rybczynski, V. H. Schaefer, and F. W. Schueler. Computing was carried out at the Univ. of Toronto Computing Center. We are especially grateful to W. C. Dilger for painting the frontispiece and to the George M. Sutton fund for financing its reproduction.

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APPENDIX 1  
CHARACTER INDEX SCORES FOR MALE *PASSERINA*

Region	Index score	Description
Head	0	forehead cobalt blue, as in <i>cyanea</i>
	1	forehead intermediate
	2	forehead turquoise blue, as in <i>amoena</i>
Rump	0	cobalt, as in <i>cyanea</i>
	1	turquoise, as in <i>amoena</i>
Wing bars	0	absent, as in <i>cyanea</i>
	1	reduced
	2	present, middle covert ca. 5 mm white, as in <i>amoena</i>
Abdomen	0	cobalt, as in <i>cyanea</i> , or with a few white feathers
	1	mottled
	2	white, or light buffy-brown, as in <i>amoena</i>
Breast band	0	cobalt, as in <i>cyanea</i>
	1	mixed (rusty and blue, or white and blue)
	2	bright rusty, as in <i>amoena</i>
Throat	0	cobalt, as in <i>cyanea</i>
	1	intermediate
	2	turquoise, as in <i>amoena</i>

APPENDIX 2  
CHARACTER INDEX SCORES FOR FEMALE *PASSERINA*

Region	Index score	Description
Throat and breast	0	throat whitish; breast light gray-brown, and conspicuously but faintly streaked; breast rarely with blue, as in <i>cyanea</i>
	1	light tawny or cinnamon brown; breast unstreaked or only faintly so, as in <i>amoena</i>
Wing bars	0	lesser secondary coverts indigo bluish; middle coverts edged with light buffy brown; greater faintly buffy edged, as in <i>cyanea</i>
	1	lesser coverts light blue-green; middle coverts edged with pale white or cinnamon; greater coverts buffy brown, as in <i>amoena</i>
Back and rump	0	generally unicolored, olive-brown, faintly streaked; rump can be bluish, as in <i>cyanea</i>
	1	back light brown, with faint streaks; rump grayish-blue and unstreaked, as in <i>amoena</i>

## APPENDIX 3

## CHARACTER PROJECTIONS COMPUTED FOR PRINCIPAL COMPONENTS ANALYSIS

Sex	Character	Projections	
		Component 1	Component 2
Male	Crown Color	0.3544	0.0706
	Back "	0.3556	0.0534
	Breast "	0.3553	0.0760
	Belly "	0.3529	0.0661
	Rump "	0.3357	0.0685
	Under Tail		
	Covert Color	0.3544	0.0714
	Wing Length	0.3057	-0.2651
	Tail "	0.3031	-0.2224
	Tarsus "	0.0501	-0.6408
	Culmen "	-0.2663	-0.1733
	" Width	0.0129	-0.6417
	Female	Throat Color	0.4489
Wing Bar Color		0.4380	-0.0101
Back Color		0.4315	-0.0944
Wing Length		0.4020	0.2664
Tail "		0.4172	0.1677
Tarsus "		0.0594	0.6653
Culmen "		-0.2812	0.4112
" Width		-0.0474	0.5248

## APPENDIX 4

DISCRIMINANT WEIGHTS COMPUTED FOR THE 5 CHARACTERS MEASURED ON MALE AND FEMALE *PASSERINA*

Sex	Character	Discriminant weight
Male	Wing Length	-1.522007
	Tail "	-1.477634
	Tarsus "	4.058525
	Culmen "	6.514037
	Culmen Width	-1.201126
Female	Wing Length	-2.315963
	Tail "	-1.868002
	Tarsus "	8.098619
	Culmen "	6.085967
	Culmen Width	-1.173168