

VOCALIZATIONS OF THE LAZULI BUNTING

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The Lazuli Bunting (*Passerina amoena*), the western representative of its genus in North America, ranges from British Columbia to Baja California, and from the Pacific coast to the Great Plains. It occupies dry, brushy canyon slopes and hillsides, but also inhabits riparian vegetation, especially in the Great Plains. Like its eastern counterpart, the Indigo Bunting (*P. cyanea*), it seems to prefer the interface between open fields and woodlands.

The genus *Passerina* is remarkable in the number of hybrid combinations known among its six generally recognized species. Indigo and Lazuli buntings overlap rather broadly in distribution, and their hybridization is well documented (Sibley and Short 1959, Emlen et al. 1975). Storer (1961) reported a hybrid between the Painted (*P. ciris*) and Varied (*P. versicolor*) buntings, and recently a hybrid between Indigo and Painted buntings was reported (Taylor 1974). Such extensive interbreeding suggests relatively recent speciation of the various forms. It also offers an unusual opportunity to study the behavioral characteristics of what seem to be very closely related, but morphologically quite distinct species.

General features of the songs of five of the species of buntings have been described elsewhere (Thompson 1968). In this paper I describe in more detail the vocalizations of the Lazuli Bunting and compare them to those of the Indigo Bunting.

METHODS

Field recordings and observations of Lazuli Buntings were made in the summer of 1963 at Logan, Utah, and the Hastings Reservation, Carmel Valley, California, and in the summer of 1969 at Chadron, Nebraska; Shoshoni, Wyoming; and Littleton and Boulder, Colorado. Recordings of several Lazuli Bunting songs were made available by the Library of Natural Sounds at Cornell University (CU), Ithaca, New York. Included was material from British Columbia (CU #3, R. C. Stein, July 1959), Pullman, Washington (CU #2, R. C. Stein, June 1958), Lucia, California (CU #6, C. A. Sutherland, June 1961), Big Sur, California (CU #7, C. A. Sutherland, June 1961), California (locality not stated; CU #11, W. R. Fish), Brigham City, Utah (CU #4, R. S. Little, June 1961), Austin, Texas (CU #5, R. C. Stein, April 1961), and Baja California (CU #1, L. I. Davis, July 1958). Young hatched and reared in the laboratory at Wayne State University by adult birds caught in California were also recorded. Tape recordings were made with a Transmagnemite tape recorder, model W612 EV, at 15 ips using an Electrovoice Slimair

microphone, and with a Uher 4000 Report-S tape recorder at 7½ ips using both a Uher microphone and a Shure 545 Unidyne III unidirectional, dynamic microphone. A 36 inch aluminum, parabolic reflector was used in making the 1963 recordings and a 24 inch reflector in subsequent field work. In the laboratory, a Uher microphone was placed about 20 cm above a nest to record nestling and adult female calls. Recordings of non-nesting adults and fledglings were made with the parabolic reflector and Uher microphone. Sound spectrograms were made on a Kay Electric Co. model 661 B Sona-Graph at wide band and H-S settings. Illustrations of the calls, except for the *eeee*, were made by tracing the original audiospectrograms. Actual audiospectrograms are used to illustrate the *eeee* call, subsong, and fully developed song. Measurements of calls were made directly from the audiospectrograms. Calls that extended above 8 kHz, such as the adult *chip* and *tink*, were measured on audiospectrograms made from tapes played at half speed.

As in the compilation of the Indigo Bunting song figure catalog (Thompson 1970) it was necessary to use a somewhat pragmatic approach to the problem of what should be considered one song figure type and what should be considered distinct forms. There was less variation in figure form in the Lazuli than in the Indigo buntings, probably because of the smaller sample size. There are more buzzes (figures such as 73-80 of the catalog, characterized by a rapid frequency modulation) in Lazuli song than in that of the Indigo. These were difficult to categorize, but I finally separated them on the basis of modulation rate, mean frequency and frequency range.

RESULTS

CALLS

Peep. I have not heard sounds from eggs of Lazuli Buntings. The first vocalization produced after hatching is the *peep*. Chicks probably are able to *peep* from the time of hatching, as are *P. cyanea*, but ordinarily do not do so if brooded and fed normally. By day 3 or 4 the chicks are more vocal and *peep* when fed. It is not clear whether they *peep* before or after being fed, or both. *Peeps* are heard while the female is standing on the rim of the nest, or after she has settled on the nestlings to brood. The nestlings rarely *peep* when the female is off the nest. The *peep* is given with decreasing frequency after day 5. One 7-day-old nestling gave a *peep* when being weighed. Some Indigo Buntings give occasional *peeps* until fledging, and this may be true of Lazuli Buntings, also.

The *peeps* recorded show a fairly consistent form (fig. 1a-d). All were given by nestlings 4 and 5 days old. The bottom frequency is

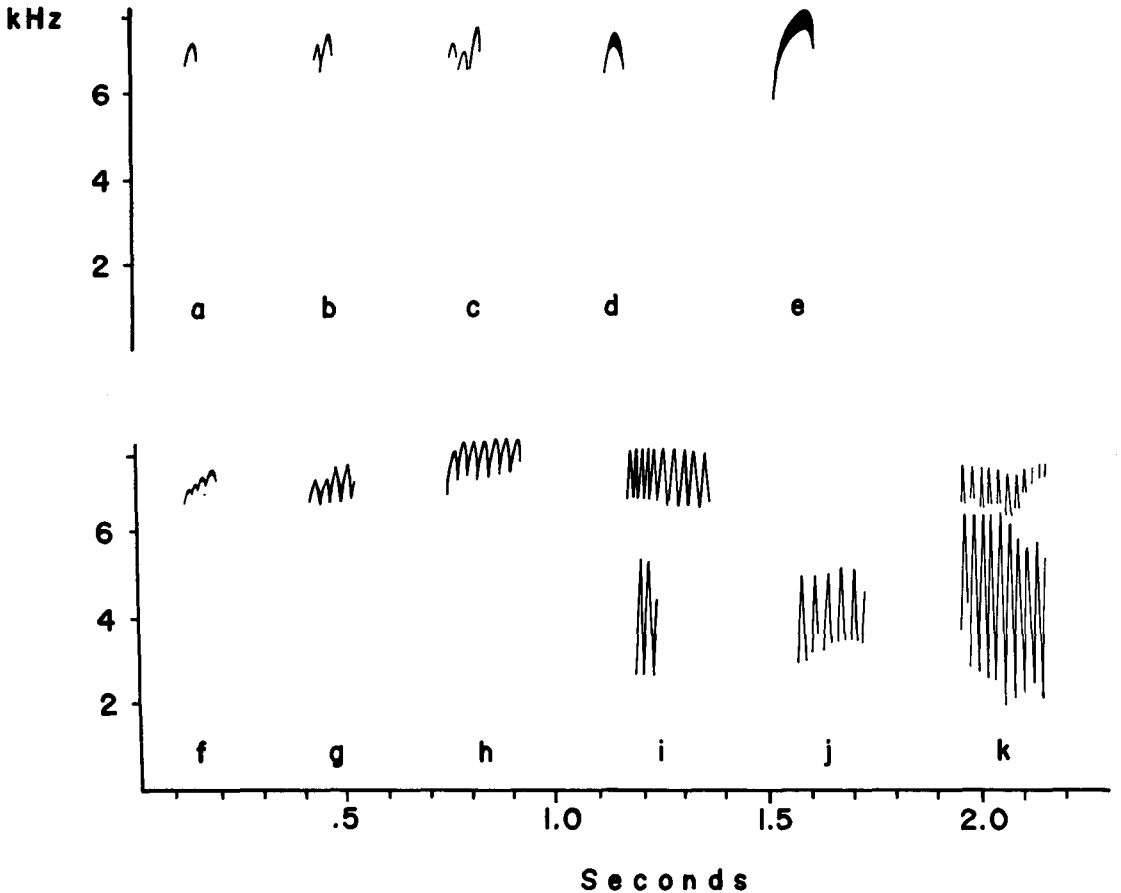


FIGURE 1. Audiospectrograms of Lazuli Bunting calls. a-e: *peeps* given by 4- (a-c) and 5- (d-e) day-old nestlings. f-j: *cheeps* given by 4- (f-g), 6- (h), 8- (i) and 9- (j) day-old nestlings. k: *sheep* of fledglings.

relatively stable at 6.3 kHz, but the top is quite variable with a mean of 7.2 kHz. The average duration is 0.02 sec. The Lazuli Bunting *peep* sounds similar to the corresponding call of the Indigo Bunting (Thompson and Rice 1970) and audiospectrograms indicate that it is of similar form.

Peeps may be given in groups, as in figures 1b-c, or singly, as in figures 1a, 1d. It is not clear whether the grouped calls are given by one or several nestlings. The form and arrangement of the groups remain remarkably consistent for several minutes and for numerous repetitions.

A somewhat different call that resembles the *peep* and may represent an extreme form of it is illustrated in figure 1e. It has a larger frequency range (5.7-7.9 kHz) and time spread ($\bar{x} = 0.10$ sec) than the more characteristic form of the *peep*. Two of these calls were recorded on day 5 from a group of nestlings that also produced the more usual *peeps*. Circumstances seemed to the observer to be no different from usual.

Cheep. The *cheep* appears about day 4 and is given along with the *peep* call. Very shortly it replaces the *peep* as the feeding call, persisting as long as the young are fed by their parents. The *cheep* is an extremely variable call (figs. 1f-j). Ontogenetic change in form occurs from day 4 to day 8 (Table 1) involving an increase in duration. Slight increases in amplitude and rate of modulation occur, but the mean frequency remains more or less the same. In the Indigo Bunting (Thompson and Rice 1970) both amplitude and rate of modulation of the *cheep* call increase much more than in the Lazuli Bunting. Whether this is a real difference between the two species or just a reflection of small sample size, especially in the Lazuli Bunting, I do not know.

On day 8 the *cheep* begins to show an upper component of about the same form and frequency as the single *cheeps*, and a lower component from 2.5 to 5.5 kHz (fig. 1i). Because I have so few clear examples of this two-part call, I have not included their measurements in table 1. In the Indigo Bunting (Thompson

TABLE 1. Variation in the *cheep* call with age.

	No.	\bar{x} (Range)
4 days		
Duration (sec.)	17	0.12 (0.03- 0.17)
\bar{x} freq. (kHz)	17	6.75 (6.1 - 7.5)
Deviation (kHz)	17	0.52 (0.4 - 0.7)
Modulation rate (kHz)	17	39.0 (28.6 -57.1)
5 days		
Duration	19	0.12 (0.05- 0.19)
\bar{x} freq.	19	6.75 (6.1 - 7.3)
Deviation	17	0.5 (0.3 - 0.7)
Modulation rate	16	45.0 (25.0 -50.0)
6 days		
Duration	13	0.19 (0.16- 0.20)
\bar{x} freq.	13	7.45 (5.7 - 7.9)
Deviation	13	0.8 (0.5 - 0.9)
Modulation rate	13	41.1 (35.0 -44.4)
7 days		
Duration	7	0.21 (0.17- 0.29)
\bar{x} freq.	8	7.20 (7.0 - 7.8)
Deviation	8	0.8 (0.5 - 1.0)
Modulation rate	7	42.2 (36.8 -50.0)
8 days		
Duration	7	0.18 (14 -21)
\bar{x} freq.	8	7.1 (6.6 - 7.7)
Deviation	7	0.7 (0.6 - 0.8)
Modulation rate	7	47.3 (44.4 -50.0)
9 days		
Duration	5	0.21 (0.15- 0.20)
\bar{x} freq.	6	6.6 (6.1 - 7.3)
Deviation	7	0.74 (0.5 - 1.0)
Modulation rate	5	47.7 (37.5 -53.0)

and Rice 1970) these two-part calls appear on day 5 and persist into the period of juvenile dependence on adults for food. A few examples recorded in the field from birds about 9 days old lack the upper component (fig. 1j). In all other respects these calls seem similar to those composed of both upper and lower components. They seem to be generated by separate, independently operating sources as has been described for other songbirds (Greenewalt 1968). The upper component is not a harmonic of the lower; its frequency characteristics are not those of a harmonic of the lower part, and the modulation rate, inflection points, and duration of the components do not always coincide.

Sheep. Older nestlings and fledglings beg from adults with a loud, insistent *sheep* call (fig. 1k) that seems to be a slight modification of the *cheep*. The lower component is emphasized, and the amplitude of modulation is increased. The modulation rate is about the same as that of the 8-day *cheep*. The female parent gives a similar sounding call while leading fledglings from one place to another.

Churr. Typically, 9- to 10-day-old nestling Lazuli Buntings crouch at the approach of a hand, then suddenly flutter from the nest giving vigorous *churr* calls (fig. 2b) when touched. The *churr* is rather similar to the *cheep* in basic structure but is lower in pitch. The mean frequency is only 3.3 kHz modulated at 58.4 Hz and with a deviation of 0.73 kHz from the mean frequency. The *churr* has an upper component, apparently the first overtone of the fundamental frequency as it does follow the pattern of the fundamental closely and is at the proper frequency for an overtone.

The motivation for the *churr* seems to be fear, and the call accompanies flight from the frightening object. The motivation for the similar *cheep* seems on the other hand to be one of comfort. We have the interesting situation, as was pointed out by Thompson and Rice (1970) for the Indigo Bunting, of calls that are similar in structure apparently having very different motivational bases. The *churr* of *P. amoena* is similar to that of *P. cyanea* but is modulated at a slower rate (58.4 vs. 80.0 Hz).

Cheet. This is typically an adult location call or mild alarm call. It often is given by territorial males in response to intruders, and by nonbreeding birds feeding in flocks. Structurally (fig. 2a) the call is similar to the *cheep*. The three *cheets* in my recorded sample have a mean frequency of 7.0 kHz, with a deviation of ± 1.1 kHz, a mean duration of 0.14 sec, and a modulation rate of 63.1 Hz. It very closely resembles the *cheet* of the Indigo Bunting (Thompson and Rice 1970), although the *cheet* of the Lazuli Bunting has a somewhat higher mean frequency (6.0 kHz in *cyanea*) and a slower modulation rate (80 Hz in *cyanea*). Emlen (1967) recorded a very similar call during migratory restlessness of caged Indigo Buntings. It is likely that Lazuli Buntings use the call in this context as well.

Chip. Adults, fledglings and sometimes nestlings give *chips* in response to disturbing situations. The structure of the call does not change as motivation increases, but the rate of calling may increase considerably. The *chips* of fledglings and nestlings (figs. 2c-e) are slightly different from those of the adults (figs. 2f-g). The nestling *chip* (fig. 2c) represents little more than a spike extending from 2.0 to 6.1 kHz with a duration of 0.03 sec. The fledgling call (fig. 2d) is similar but lacks the descending arm of the spike. The ascending arm, the tip of the spike, including the beginning of the downward arm (fig. 2e), and the lower part of the overtone, are the same. The mean duration of this call is 0.025 sec.

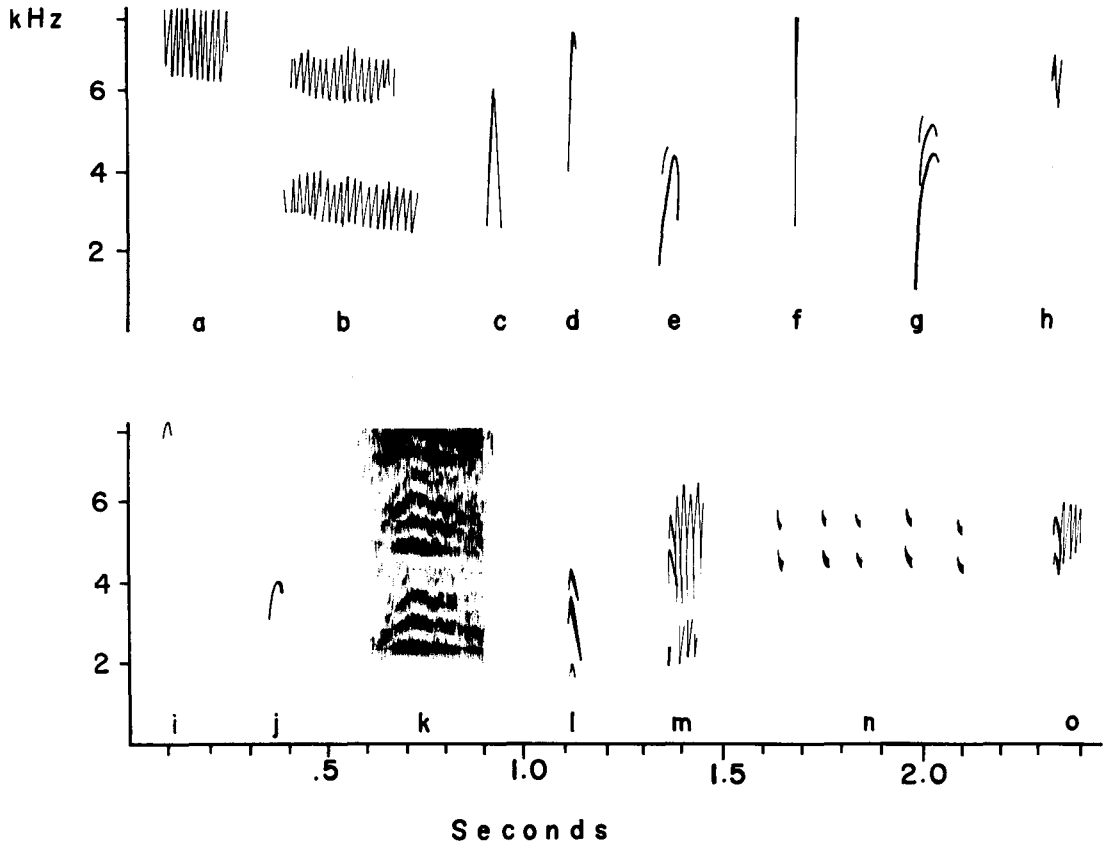


FIGURE 2. Audiospectrograms of Lazuli Bunting calls. a: *cheet* of adult. b: *churr*. c-e: nestling *chips* at full (c-d) and half speed (e). f-g: adult *chip* at full (f) and half speed (g). h: *chip*-like call of nestling shortly before leaving nest. i-j: adult *tink* at full (i) and half speed (j). k: *eeee*. l: *took*. m: *cheek*. n: *ti-ti-ti-ti*. o: *tseep*.

The *chip* is the call most frequently used by adults, but it does not have the clear structure of the call of younger birds. An audiospectrogram made of the call played at full speed (fig. 2f) shows a frequency range of from 2 to more than 8 kHz. One made from a call played at half speed (fig. 2g) shows two formants at the top at 8.6 and 9.6 kHz. The formant at 9.6 cannot represent an overtone of the lower one. It would appear, then, that two separate vibratory portions of the syrinx are responsible for the production of this call in the adult. The duration of the adult *chip* is 0.025 sec.

Figure 2h shows an example of several rather different-sounding fledgling calls resembling the *chip*. These calls are higher-pitched than the usual fledgling *chip* because the lower portion of the spike is missing. This call may represent a transition to the adult *tink* which it resembles in general form and in narrow frequency range.

Tink. Lazuli Buntings, like Indigo Buntings, give *tink* calls in response to more intense disturbance than that eliciting the *chip*.

Often a series of *chips* will give way to *tink* calls as a bird becomes more disturbed. In the Indigo Bunting this call is given in response to overhead predators, which probably is true for the Lazuli Buntings also, although I have not noted it in that context. The call (fig. 2i) ranges in frequency from about 7.6 to 8.4 kHz, with a duration of 0.01 sec. Details of its structure are clearer in the audiospectrogram made at half speed (fig. 2j). Because of its high pitch and narrow frequency range, the source of the *tink* is difficult to locate, even though the call does not begin and end gradually as is typical of overhead predator alarm calls (Marler 1957).

Eeee. A hand-held Lazuli Bunting often gives a loud *eeee* call, which seems to denote distress. This variable call is quite different structurally from all other bunting calls. It represents several sustained fundamental tones and their overtones. In fig. 2k the fundamental remains around 2.4 kHz. Immediately above this is another at about 3.0 and a third at about 3.6 kHz. Above these first three bands are several more, also strongly empha-

sized. Here again the animal is producing at least two separate fundamental sounds. The mean duration of the call is 0.21 sec. Typically it is given in groups of two to five calls which may be of different lengths. Data suggest a correlation between number of calls in the series and intensity of distress.

Tooks and *cheeks*. A female Lazuli Bunting arriving at the nest with food may give a soft feeding call if the nestlings do not gape immediately. At first she gives a soft *took* (fig. 2l), a chevron-shaped call usually of two emphasized fundamentals. The total call ranges usually from 2.02 to 4.6 kHz with a mean duration of 0.034 sec. It usually is given in groups of two to six, the calls within groups being 0.39 sec apart on the average, but single *tooks* are given occasionally. In captivity, with food readily available close to the nest, the female often returns with food before the chicks are hungry. In this circumstance she calls frequently and the *tooks* give way to buzzy *cheeks* (fig. 2m). *Cheeks* may be given in series with *tooks*, or by themselves. They seem to imply a stronger motivation to feed than the *took* call, or perhaps just a frustrated feeding tendency. The interval between *cheeks* averages 0.37 sec.

I have not heard *tooks* or *cheeks* under natural conditions, possibly because the calls are too soft to carry any distance from the nest. Also, the interval between successive visits to the nest in the wild usually is sufficiently long for at least one nestling to be hungry, and the parent seldom is frustrated in her effort to feed the young.

Cheeks resemble *cheeps* in general form but usually begin with a *took*-like chevron-shaped call. The *cheek* seems to be a prolonged *took* with a rapidly modulated ending. The mean frequency of the modulated portion is 5.4 kHz, with a deviation of ± 1.7 kHz and a modulation rate of 61.4 Hz compared with 47.7 for the 9-day-old *cheep* and 63.1 for the adult *cheet*. In most *cheeks* a lower component, apparently a harmonic, is evident. In some it is almost equal to the upper part in intensity, but it never is as clear in structural detail.

Ti-ti-ti-ti. During nest construction, often while carrying nesting material, the female solicits the male to copulate. As she assumes the typical tail-up posture, she gives a series of *ti* calls (fig. 2n). The structure of this call is very similar to that of the Indigo Bunting *ti-ti-ti-ti*. I have only two poor laboratory recordings of it, and therefore no measure of the range of structural variation. The number of *tis* in a series varies with the motivation of the female, although the structure remains

essentially the same. The call slurs downward with upper and lower components beginning at about 4.5 and 5.5 and ending at 4.3 and 5.7 kHz. Each *ti* lasts about 0.02 sec.

Tseep. As a male flies toward a female to copulate, he usually gives a *tseep* call (fig. 2o). It consists of a double chevron-shaped introduction followed by an upslurred buzz. The chevrons average 4.3 and 7.2 kHz. The mean duration of the entire call is 0.09 sec.; the modulation rate of the buzz is 74.0 Hz. The *tseep* shows a striking structural resemblance to the *cheek* of the female. Both begin with chevron-shaped bands of similar frequency and end in a frequency-modulated sound of similar duration. The modulation rate is similar, but the deviation is less in the *tseep*. The upper limits of the calls are similar, but roughly the lower half of the *cheek* call is missing from the *tseep*. I have heard *cheek* calls only from females attempting to feed young, and *tseep* calls only from males attempting to copulate.

SONG CHARACTERISTICS

Subsong. A hand-reared Lazuli Bunting first began to sing subsong at 29 days. Subsong differs from the territorial song in having an irregular frequency variation and erratic rhythm. Subsong represents almost continuous vocalization, but with no two figures exactly alike (fig. 3a). Figures vary more in duration and spacing than do the figures of crystallized song, as Thorpe (1961) mentioned for the Chaffinch (*Fringilla coelebs*). The subsong of Lazuli Buntings, however, may be loud, unlike Chaffinch subsong.

Typically subsong ceases in caged yearling birds during the winter, then begins again early the following spring. It is likely that migrating birds of the year sing subsong en route from the wintering to the breeding grounds, as Indigo Buntings seem to do. I have not heard subsong from birds known to have a crystallized song. They apparently do not pass through a subsong phase in the course of development of breeding condition each year. I have not followed the transition from subsong to full song in the Lazuli Bunting in detail, but it probably follows the same course as in the Indigo Bunting (Rice and Thompson 1968).

Song. I have described the general features of the Lazuli Bunting song elsewhere (Thompson 1968). Generally, it resembles Indigo Bunting song in being composed of figures of rather wide frequency spread ($\bar{x} = 3.70$ kHz) evenly spaced in groups (fig. 3b). Similar figures are not closer to each other than they are to unlike figures (see Emlen et al. 1975).

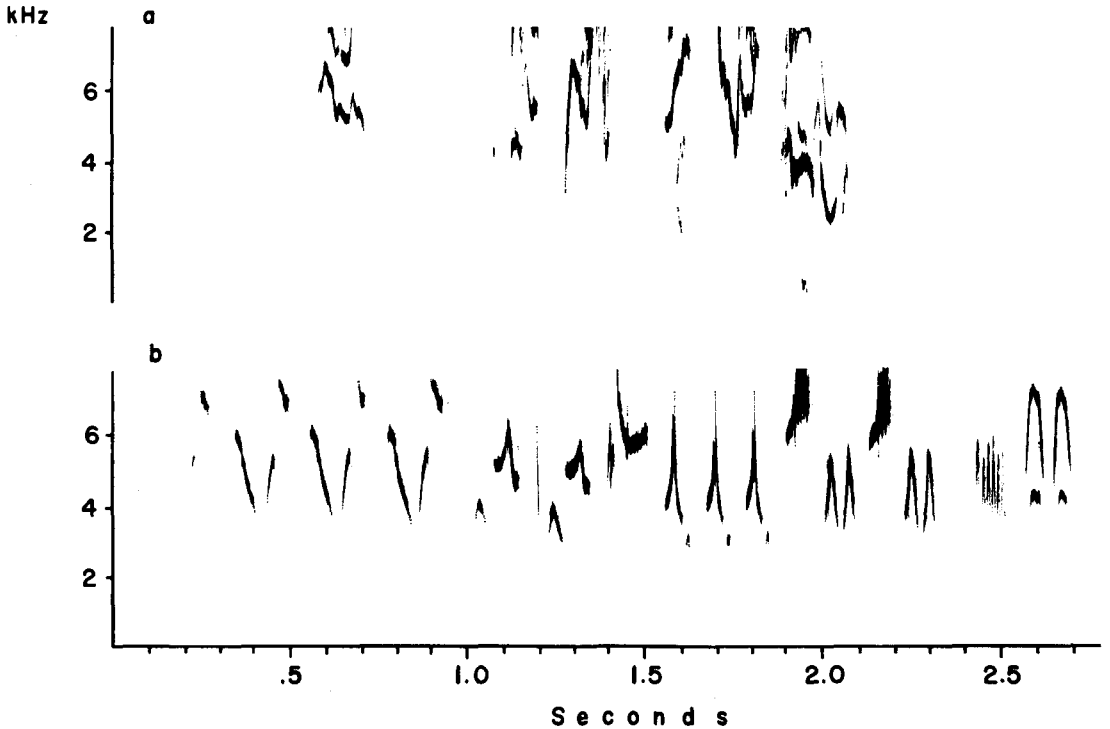


FIGURE 3. a. Lazuli Bunting subsong. b. crystallized song.

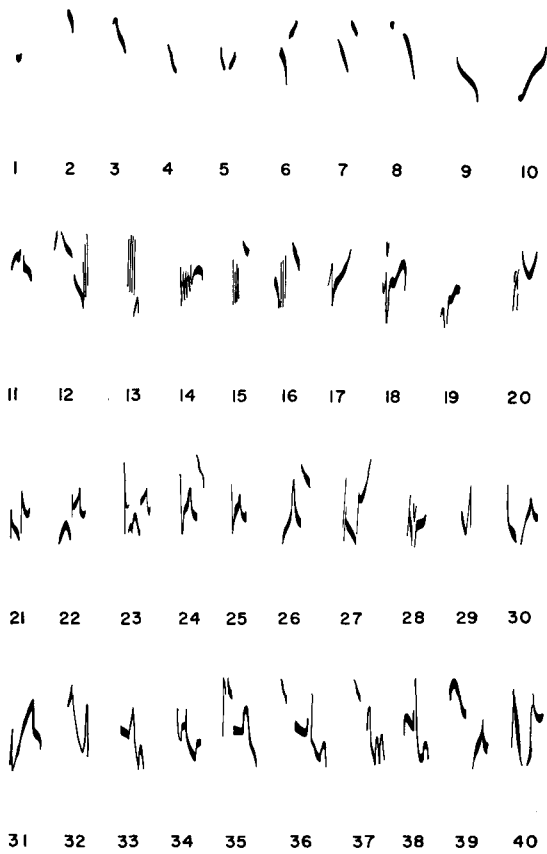
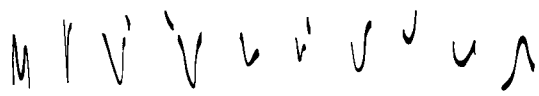
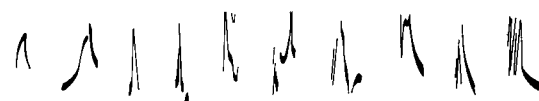


FIGURE 4. Song figure catalog of Lazuli Bunting (figs. 1-40).

Like the Indigo Bunting (Thompson 1970), Lazuli Buntings over most, or perhaps all of their range, sing songs composed of a few kinds of song figures (figs. 4, 5). For the present analysis of song figures I used songs of 44 birds outside the zone of sympatry in seven western states, and songs of 14 birds within the zone of sympatry of Indigo and Lazuli buntings in Nebraska. Eighty song figures are known for the species in the parts of its range that have been sampled. Table 2 shows the distribution of Lazuli figures in western North America. All populations sampled extensively to date overlap considerably in their use of the known figures. The only exceptions are songs from Austin, Texas and Baja California, which differed in all respects; knowing nothing of the individuals recorded, I have not included them in this analysis. They may represent aberrant, crystallized songs of isolated individuals, late stages of subsong of young males, or local dialects. Austin, Texas is well outside the normal range of *amoena*, and the individual recorded probably was an isolated bird. With the possible exception of the Baja California sample there is no evidence of song dialects, such as have been demonstrated in the White-crowned Sparrow (*Zonotrichia leucophrys*) in coastal California (Marler and Tamura 1964).



41 42 43 44 45 46 47 48 49 50



51 52 53 54 55 56 57 58 59 60



61 62 63 64 65 66 67 68 69 70



71 72 73 74 75 76 77 78 79 80

FIGURE 5. Song figure catalog of Lazuli Bunting (figs. 41-80).

TABLE 2. Distribution of *P. amoena* song figures in western North America.¹

Fig. no.	Br. Col. (1) ²	Wash. (1)	Cal. (13)	Utah (10)	Wyo. (14)	Col. (6)	Neb. (13)	No. states in which fig. re- corded
1			1					1
2			1					1
3				2				1
4			1	1			1	3
5				2				1
6			1					1
7				1				1
8			1					1
9							1	1
10				1	1		1	3
11			1				2	2
12				1			1	2
13					1			1
14			4	2	2	2	1	5
15						2		1
16		1	3			1	2	4
17			1		4			2
18			1					1
19				1	2		1	3
20	1			1	1		3	4
21			2	1	1		3	4
22			2	3		1		3
23					1			1

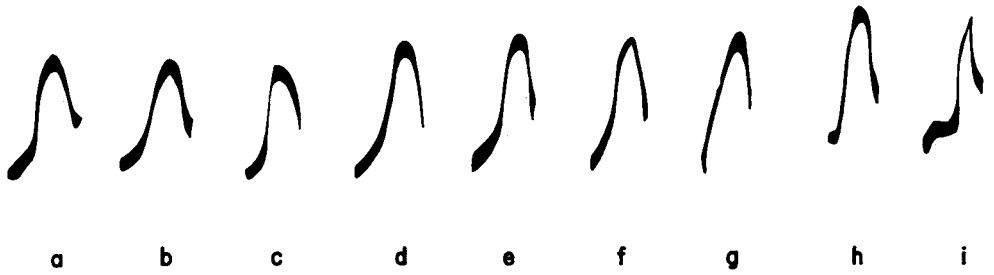
TABLE 2. Continued.

Fig. no.	Br. Col. (1) ²	Wash. (1)	Cal. (13)	Utah (10)	Wyo. (14)	Col. (6)	Neb. (13)	No. states in which fig. re- corded
24					3	1	2	3
25					1			1
26				1				2
27					2		1	1
28				2				1
29			1		1			2
30			1	2		1		3
31			1				1	2
32			2		4			2
33			3	4	1		2	4
34					2			1
35			2		3			2
36					1			1
37						1		1
38				1		2	1	3
39				1				1
40		1						1
41						1		1
42				3	1		1	3
43				1	1	2	2	4
44	1							1
45			2	1	1			3
46						1		1
47		1	1	3	2		3	5
48							1	1
49					1			1
50			3	2	5	2		4
51						1	1	2
52			1		1	1	1	4
53			2	1	1	2	1	5
54	1					1	1	3
55			3	2	2	1		4
56		1	2	3	3	2		5
57			1				1	2
58				3				1
59				2				1
60			1				1	2
61					2		2	2
62				3	4	1	1	4
63	1				1	1		3
64			3	5	6	2	3	5
65			2	2		1		3
66	1	1	4	5	2	2	5	7
67			1	3	2	2		4
68		1	2	3	2		1	5
69						1		1
70				2				1
71	1						1	2
72			2	1	1			3
73		1	3	2	1	1	3	6
74				3	2	1	2	4
75			7	8	2	1	5	5
76		1	3	6	3		2	5
77			1	1	6			3
78			1					1
79						2		1
80						2		1

¹Geographic designations represent clusters of localities sampled. Grouped localities are close enough so that contact may occur between individuals. Distances between localities from state to state are much greater.

²Numbers in parentheses are sample sizes.

No. 50



No. 56

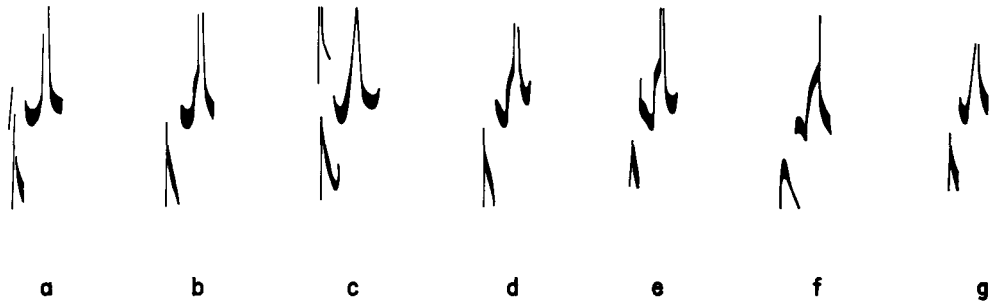


FIGURE 6. Variation in song figure form. Figure No. 50: a, b, c, h recorded in Shoshoni, Wyo. (a, c, one individual); d. Boulder, Colo.; e. Littleton, Colo.; f. Carmel Valley, Calif.; g. Walker, Calif.; i. Brigham City, Utah. Figure No. 56: a-b. Shoshoni, Wyo.; c. Truckee, Calif.; d. Lucia, Calif.; e. Logan, Utah; f. Carmel Valley, Calif.; g. Littleton, Colo.

Work with the Indigo Bunting (Shiovitz and Thompson 1970) has shown that a sample size of 38 to 54 or more individuals is necessary to include all of the song figure types in a population. In figure 8 I have plotted the cumulative number of figure types for the three largest samples of Lazuli Buntings. The curves follow essentially the same slope as for Indigo Bunting song, but because of the smaller samples, they do not level off. The slopes for the Wyoming and California samples are about the same, but the slope for the Utah sample is steeper (fig. 8), which indicates more new figures per song. This can mean either that figures overlap less from song to song, or that there are more figures per song. A comparison of song characteristics of these three populations (table 3) shows that the steepness of the Utah curve is due primarily to a larger number of figures per song.

TABLE 3. Comparison of song characteristics of three populations of Lazuli Buntings.

	Wyoming	California	Utah
No. birds	14	12	10
No. figures	84	72	83
Figures/bird	6.0	6.0	8.3
No. figure types	41	39	41
Overlap ¹	48.80%	54.16%	49.39%

¹ Among individuals of each population.

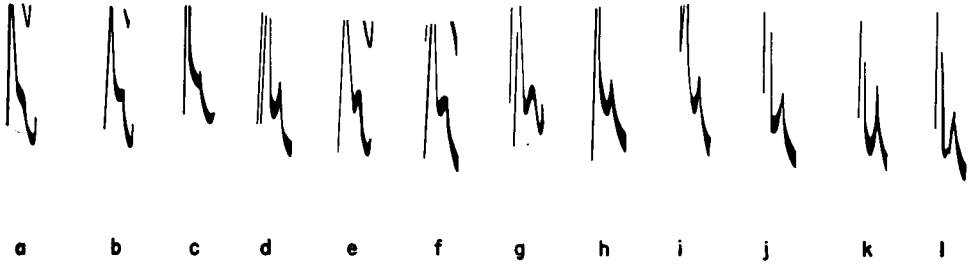
Shiovitz and Thompson (1970) found overlap values (% of figures from one sample also found in the other) of 91.2% for Indigo Bunting populations in Kentucky and Michigan, and Emlen (1971) found a value of 92% for populations in New York and Michigan. California and Utah Lazuli samples overlap by 61.53 and 63.41%, respectively, with the Wyoming sample, and by 58.97% with each other. The samples from British Columbia and Washington are too small for meaningful comparisons. The sample from Nebraska is complicated by the mixture of Indigo and Lazuli song figures in songs from Chadron (Emlen et al. 1975), so overlap values were not calculated.

Song figure shape may be remarkably consistent (fig. 6:50, 56) throughout the range of the species or considerably variable in form (fig. 7:14, 55) even within a single population.

DISCUSSION

The form of most of the commonly used calls of *Passerina cyanea* and *P. amoena* is essentially identical. Differences may be due in part to the incomplete sampling. I have no record of the occurrence in the Lazuli Bunting of the *aaaa* call that is given by aggressive juvenile Indigo Buntings and by adult female Indigo Buntings on the nest (Thompson and Rice

No. 55



No. 14



FIGURE 7. Variation in song figure form. Figure No. 55: a, b, g, l. Shoshoni, Wyo. (a, b, g one individual); c, i. Logan, Utah; d. Littleton, Colo.; e-f. Calif.; h. Boulder, Colo.; j. Lucia, Calif.; k. Pullman, Wash. Figure 14: a, b, g, h. Shoshoni, Wyo. (all one individual); c, d. Carmel Valley, Calif.; e. Lucia, Calif.; f, j. Littleton, Colo.; i. Logan, Utah.

1970). It is not given frequently by Indigo Buntings, and I may simply have missed hearing it from Lazuli Buntings. On the other hand, the *took* and *cheek* calls of the female parent are known only from the Lazuli Bunting. These calls were recorded frequently from a female that devoted much more care and attention to feeding young than any other birds in the laboratory. Indigo females in the laboratory are rather poor parents in my experience, which may explain my failure to hear the call. Nestlings in the wild seldom need urging to eat, and so this is probably a rare call under natural conditions. The *sheep* call has been tape recorded only for the Lazuli Bunting, but I have heard similar sounding calls from Indigo fledglings. Whether or not it should be listed as distinct from the *cheep* to which it is so clearly related and from which it seems to develop is questionable. Recordings indicate that the Lazuli *peep* is a less distinctive and a less variable call than the Indigo *peep*, but this almost certainly is due to my more extensive tape recording of the calls of nestlings in various stages of hunger. As mentioned before, the one successful brood of Lazuli Buntings was fed so regularly by their mother that they seldom called until they began *cheeping* at four days.

The forms of the adult *chip*, *cheet*, *eeee* and *tink* are essentially identical in structural detail in both species. These are generally alarm calls, and except for the *cheet* and *tink* sound

much like similar calls of a variety of bird species. This similarity is adaptively advantageous to all the species concerned because it warns others nearby of potential danger

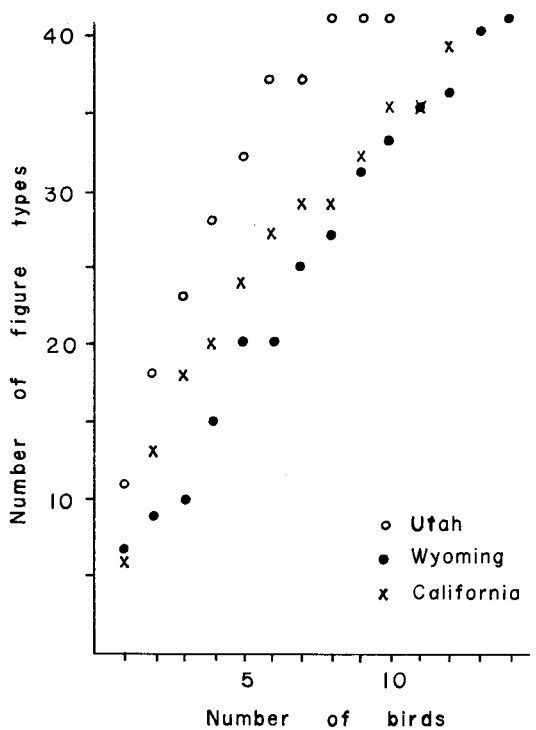


FIGURE 8. Cumulative plot of the number of song types as a function of numbers of birds sampled from three localities in western North America.

(Marler 1957). Aside from this mutually advantageous convergence of alarm calls, warning or alarm calls might be expected to be less subject to rapid evolutionary change than calls directly related to reproduction. In most groups of closely related species, reproductive behavior tends to be distinctive and critical for species recognition (Tinbergen 1960). Thus it is especially remarkable that the soliciting and male precopulatory calls are essentially identical in the Indigo and Lazuli buntings. Hinde (1955, 1956), however, pointed out that displays that occur in the early stages of pair formation or courtship in the cardueline finches are more distinctive for each species than those occurring later, after pair formation has occurred. Johnsgard (1965) noted a similar phenomenon in ducks.

In comparison with the Indigo Bunting, the most distinctive vocalization of the Lazuli Bunting is its song. Thus, like the carduelines and anatids, the buntings (*Passerina*) display their most distinctive species-specific characteristics (vocalization in combination with plumage pattern) in the early stages of pair formation. Territorial male Indigo Buntings do not respond to playbacks of Lazuli songs within their territory (Thompson 1969), indicating their ability to distinguish Indigo and Lazuli songs. Presumably female buntings also differentiate upon arriving at the breeding grounds. In the zone of overlap between Indigo and Lazuli buntings, however, song distinctiveness of the two forms breaks down (Emlen et al. 1975). Birds in Lazuli plumage may sing songs approaching the Indigo type or songs that are intermediate between the two, as well as songs appropriate to their plumage. Birds of either plumage respond equally to either song type, and territories are defended against birds of both plumage characteristics. Nevertheless, hybrid pairs seem to occur less frequently than conspecific pairs, and it appears that some sort of species recognition factors operate, even if incompletely. Because of the mixture of song characteristics throughout the population in the area of sympatry and the similarity of calls, the acoustic communication system may be less useful as a means of species recognition than plumage characteristics. This is an example of a more plastic, learned behavior (song) serving to break down barriers to interbreeding rather than to enhance them by means of character displacement (Marler and Hamilton 1966).

The significance of the difference in song figure overlap percentages for different populations of Lazuli Buntings as compared to

those of Indigo Buntings is not clear. It may simply reflect the smaller samples of Lazulis as compared to those of Indigos. The plots of cumulative figure types in the Lazuli Bunting (fig. 8) indicate that the slopes had not reached the asymptote, and thus that all the figure types in the population had not been obtained. Samples of Indigo populations in Michigan and Kentucky were larger, and the slopes of the cumulative plots did level off (Shiovitz and Thompson 1970). Another possible, but less likely explanation is that the populations of Lazuli Buntings are more isolated because of the more patchy habitat in which they are found and therefore have developed divergent song characteristics. I plan to test this hypothesis with more extensive sampling of Lazuli populations.

The science of glottochronology traces the temporal relationships of human languages (Farb 1968). From documented instances of language divergence in basic vocabulary over time, fairly reliable information on the rate of change of human language has been derived. Because human languages are structurally similar, comparisons of vocabulary offer a fairly straightforward approach to the problem. The same sort of information should be obtainable for animal communication systems if the difficulty of comparing systems can be overcome.

Lazuli and Indigo bunting songs with their closely similar organization and limited number of song figures represent a situation roughly paralleling human language. A comparison of the Indigo and Lazuli catalogs reveals 19 figures common to both. Thus, 23.75% of the Lazuli repertoire duplicates that of the Indigo, and 19.38% of the Indigo that of the Lazuli. Roughly 80% of the figures of the two forms have diverged. It generally is assumed (Sibley and Short 1959) that the Indigo and Lazuli buntings diverged following the isolation of populations of a previously continuous form by Pleistocene glaciation and subsequent climatic changes. Mengel (1964) explained the evolution of several groups of North American warblers in this way. It is impossible to determine which glacial advance divided the bunting ancestor into eastern and western populations, but the date of the last advance, the Wisconsin, gives an estimate of the minimum time involved. Dating the peak of Wisconsin glacial advance at 18,000 years ago (Dreimanis and Goldthwait 1973) gives a rate of song figure change of roughly 4.4% per 1,000 years. This compares with a 19% loss in human vocabulary per 1,000 years.

TABLE 4. Message categories used in vertebrate communication (from Smith 1969) and corresponding displays of Lazuli Buntings.

Message categories	Bunting displays
Identification	
Species	all calls, song
Individual	all calls (?), song
Sex	<i>ti-ti-ti-ti</i> , <i>tseep</i> , <i>took</i> , <i>cheek</i> , song
Maturity	<i>ti-ti-ti-ti</i> , <i>tseep</i> , <i>took</i> , <i>cheek</i> , song
Probability	non-vocal display (?)
General set	<i>cheet</i> (?)
Locomotion	non-vocal display
Attack	non-vocal display
Escape	<i>chip</i> , <i>tink</i>
Nonagonistic subset	<i>chip</i> , <i>tink</i>
Association	<i>cheet</i>
Bond-limited subset	<i>took</i> , <i>cheek</i> , <i>cheet</i> , <i>sheep</i>
Play	song (?)
Copulation	<i>ti-ti-ti-ti</i> , <i>tseep</i>
Frustration	<i>eeee</i> , <i>chip</i> , <i>tink</i> , <i>cheek</i>

There are reasons to suppose that the rate of song change may vary according to the selective pressures imposed by general sound milieu, and by overlap with closely related forms (Marler 1957). Until more data on rate of song change are available from a variety of birds, we cannot reach any conclusions regarding the constancy of change in bird song. The rate of change of human language, however, seems to be quite constant (Farb 1968). If it should prove to be so in birds, then we will have a new tool for analyzing the time at which closely related forms diverged, and thus for helping to determine phylogenetic relationships.

Smith (1969) attempted to categorize the messages used in vertebrate communication based primarily on his own work with flycatchers. In table 4 I list the Lazuli Bunting displays that seem to fit his categories. In some cases non-vocal displays of the buntings (e.g., *tail flicking* and *head-forward* displays) convey the message, and I have so indicated in the table.

Smith (1969) suggested that many species of vertebrates use their limited number of displays in a variety of contexts and that the specific information communicated depends on a combination of display and context. It is apparent from table 4 that Lazuli Bunting calls occur in such a wide variety of Smith's message sets that they seem very ambiguous. This may be due to my difficulty in understanding his categories or in interpreting the behavior of one group of animals in terms of the rather different behavior of another. Assuming, however, that I have understood and interpreted correctly, it seems to me that a sys-

tem depending so heavily on context to convey meaning would not be very efficient. The evolution of displays in animal communication has moved toward making the message less ambiguous to the receiver (Morris 1957). It seems likely that each bunting call may depend somewhat on context for precise meaning (message), but that the messages transmitted by each are fewer than suggested by Smith.

In addition Smith omitted some categories that seem important for the buntings. Because song characteristics are species-specific and yet vary usually from bird to bird, song conveys information on species and individual. Because only adult males sing, it also conveys information on sex and maturity. Song is most characteristic of adult males *on territory*; birds off their territories seldom sing. Territorial status is therefore another important message category. Unmated male Indigo Buntings sing much more frequently than mated males (Thompson 1972) and presumably the same is true of Lazuli Buntings. Frequency of singing therefore indicates the stage in the nesting cycle of a particular individual.

The communication system of these buntings does not fit into the Smith system comfortably, but this is not really surprising in view of the different life styles, evolutionary histories, and ecological adaptations of tyrannid flycatchers and cardinaline finches. The lack of fit emphasizes the need for refinement of the message category classification in order to reflect the broadest possible range of animal communication systems.

The Lazuli calls raise the same interesting question as those of the Indigo regarding the relationship between call structure and motivation. Intuitively one might assume that morphologically similar calls would have similar motivations and would communicate related messages. This does not seem to be so in the buntings. Nearly all of the rather similarly-shaped buzzy sounds seem to convey different messages. The *cheep* and the *sheep* are both related to hunger, but the former is given by the nestling being fed, while the *sheep* is given by fledglings calling for food from an absent parent. *Churr*, an alarm call, *cheet*, a location call, and *tseep*, the male precopulatory call, all have different messages and presumably different motivational bases. If they can be related to a single motivational system, it probably is some form of discomfort. The *peep*, *chip*, *tink*, *ti-ti-ti-ti*, *took*, and *eeee* calls show less morphological consistency, but as was shown for the Indigo Bunting, seem to be

structurally related to the *peep*. Here again the variety of contexts in which the various calls are given suggests no clear unifying motivational basis.

What does a comparison of Lazuli and Indigo bunting vocalizations tell us about the systematic status of the two forms? Unfortunately, not much. The close similarity of the system of calls supports the assumption that the two forms are very closely related and have not undergone extensive behavioral evolution during their time of separation. The song differences, although recognizable by birds outside the zone of overlap, are not extensive and break down in areas of sympatry. Nevertheless, until additional information from other sources is available it seems best to follow Short's (1969) recommendation that the two be considered separate species.

SUMMARY

The system of calls employed by Lazuli Buntings is essentially the same as that used by Indigo Buntings. Adults utter seven clearly distinguishable calls, while nestlings and fledglings produce sounds that change from day to day.

Lazuli Bunting songs throughout the species' range, like those of the Indigo Bunting are made up of varying combinations of a limited set of song figures. About 80 different figures were found in songs of 44 individuals outside the range of overlap in seven western states, and 14 individuals from areas of sympatry in Nebraska. Roughly 76% of the Lazuli figures are distinctive from those of the Indigo. Assuming that the Indigo and Lazuli buntings diverged as a result of the last Pleistocene glaciation, 4.4% of the Indigo and Lazuli song figures have changed per 1,000 years, compared with 19% loss in human vocabulary per 1,000 years.

Overlap of figures between different populations is generally less than for populations of Indigo Buntings. This may reflect smaller samples of Lazuli Bunting songs, or may represent a higher degree of isolation among the Lazuli populations.

The Lazuli Bunting vocalization system is discussed in terms of Smith's (1969) analysis of the messages of vertebrate communication. Lazuli Bunting calls suggest questions concerning the relationship between call structure and motivation. A variety of calls of rather similar general structure seem to convey very different information, reflecting different motivational bases.

Lazuli and Indigo bunting vocalizations are

very similar, indicating close relationship between the two forms. Moreover, the song differences are not extensive and tend to break down in the area of sympatry. At the present time, nevertheless, it seems best to consider the Indigo and Lazuli buntings separate species.

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This is contribution no. 335 of the Department of Biology, Wayne State University.

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