

A CATALOG OF SONG SYLLABLES OF INDIGO AND LAZULI BUNTINGS¹

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Abstract. Tape recording of singing male Indigo Buntings (*Passerina cyanea*) and Lazuli Buntings (*P. amoena*) from allopatric populations produced catalogs of 127 indigo and 122 lazuli syllable types. These totals result from adding newly-described syllable types (29 indigo, 42 lazuli) to previous descriptions (Thompson 1970, 1976). While some syllable types are more variable than others, the overall variation is remarkably discontinuous and syllable types are usually easily recognized. The same syllable types occur and at similar frequencies of abundance in different populations and at different times. The patterns of commonness and rarity of syllable types fit a "broken-stick" distribution, a model developed to explain relative abundance of species in communities. Some syllable types are specialized in their position within songs, some are used virtually anywhere in the song, but many are intermediate in degree of specialization of position.

Together with results from other studies of bunting songs, our data suggest that the individual syllables in bunting songs can be considered memes, the cultural equivalent of genes. These syllable memes constitute the units of recombination from which whole-song variation is generated. A minor amount of variation is introduced by mutation of syllables. The syllable types are geographically widely distributed and may be considered species universal song elements, similar to findings in the songs in populations of Swamp Sparrows (*Melospiza georgiana*, Marler and Pickert 1984). The stability of syllables over space and time raises the possibility of a canalizing factor that guides the learning process in young buntings even during cross-species syllable acquisition.

Key words: Bunting song; geographic distribution; song; syllable types.

INTRODUCTION

The eastern-distributed Indigo Bunting (*Passerina cyanea*) and western-distributed Lazuli Bunting (*P. amoena*) are closely related species whose populations meet and hybridize in the Great Plains of North America (Short 1969, Rising 1983). They have received considerable attention from both systematists and behaviorists. The biology of their vocal communication behavior has been a popular target of research (Payne et al. 1981, Emlen 1971, Emlen et al. 1975, Shiovitz and Thompson 1970, Margoliash et al. 1991). Fundamental to these and other studies of vocal communication in the buntings have been catalogs of the vocal units, referred to as figures or syllables, that males use to compose their songs (Thompson 1970, 1976). In addition to species differences in syllables, there are also differences in temporal features of syllable delivery within songs (Emlen et al. 1975) but these are not treated here.

In previous work examining the geographic occurrence of these basic syllabic building blocks

of whole songs sung by buntings, a broad generalization emerged: virtually all across the species distribution the same basic lexicon of syllables is used to construct an enormous variety of songs (Shiovitz and Thompson 1970, Emlen 1971, Emlen et al. 1975, Thompson 1976). Ontogenetic studies (Rice and Thompson 1968, Payne 1981) revealed that buntings acquire their songs through cultural transmission. Field studies showed that each species can learn and produce the song syllables of the other (Emlen et al. 1975).

Our studies of the role of bunting songs in reproductive behavior have included the use of one species syllables in the song of the other species, the effects such sharing has on mating associations and territorial defense, and the ontogenetic process through which syllable production and perception are acquired (Baker and Baker 1990; Baker 1991; Boylan 1995; Baker and Boylan, unpubl. ms). During the course of our studies, we found it necessary to expand and update the original syllable catalogs of Thompson for several reasons. First, we found syllables in songs of males in overlap populations that were not in the published catalogs and therefore we

¹ Received 16 March 1995. Accepted 17 July 1995.

TABLE 1. Recording locations, dates and sample sizes of male Indigo and Lazuli buntings.

Location	Date	<i>n</i>	Species
Hawkeye Wildlife Refuge Corralville, Iowa	18 June 86	6	Indigo
Dudgeon Lake, Vinton, Iowa	29 June–1 July 91	13	Indigo
Wildcat Bluff, Urbana, Iowa	11 June 87	5	Indigo
Salt Creek Wilderness, Lincoln, Nebraska	10–12 July 88	19	Indigo
Fontanelle Forest, Neale Woods, Omaha, Nebraska	12–13 July 88	20	Indigo
Gateway, Colorado	27 May–3 June 86	10	Lazuli
Pocatello, Idaho	12–15 June 89	36	Lazuli
Pocatello, Idaho	*24–25 June 90	20	Lazuli

* Recorded in the laboratory.

could not attribute such syllables to one species or the other without recording additional allopatric populations. Additionally, much less work had been done on Lazuli populations than on Indigo populations in the development of the earlier syllable catalogs. Second, the illustrations in Thompson's catalogs have no frequency or time scales, are line drawings of actual sound spectrograms, and therefore are not always easily matched up with the component syllables of a newly-recorded song. Adding these features may make the catalogs more useful to others. Third, variation within a syllable type differs for different syllables; therefore while some highly stereotyped syllables are relatively easy to categorize, more variable syllable types sometimes present problems, and thus we found it necessary to apply an analytical method to resolve some syllable identities. Application of this method may be a first step in producing more objective classifications of song structures. Fourth, our recordings made in allopatric populations uncovered a number of new syllable types that were not in Thompson's published catalogs. Fifth, whereas our new data often support earlier conclusions, some of the earlier interpretations were not confirmed by our studies of bunting syllables. In some cases, these differences may be a consequence of our application of digital signal processing not available at the time of the earlier work. Finally, we use our recordings to examine the relative abundance patterns of syllables within and between populations and the use of syllable types in specific locations within whole songs.

METHODS

Songs of territorial males were recorded in the field at a number of locations (Table 1) that were outside the zone of overlap and hybridization of

these two species. Additionally, we recorded 20 males in the laboratory that had been captured in an allopatric population. Thus, our syllable catalogs are constructed of song elements from allopatric populations. In addition to observations made during tape recording, many more hours were spent in these populations during playback studies (Baker 1991) and/or trapping of birds for laboratory experiments (Baker and Baker 1988, 1990). No male of the alternative species was seen in these populations during this research.

Tape recordings in the field were made with a Uher 4200 Report Stereo IC and Uher microphone mounted in a 60 cm parabolic reflector. Tape speed was 9.5 cm/sec using Ampex 641 audio tape. Laboratory recordings were made with a Sony TCM 5000 recorder, Sennheiser microphone and cassette tape. Sonagrams were created with a Kay Elemetrics DSP Sona-Graph (model 5500) and gray scale printer (model 5510). Spectrographic analysis settings on the Sona-Graph were flat shaping, 300 Hz transform, Hamming window, and no averaging.

In examining the sonagrams, we found that in the majority of cases our two independent judgments agreed on which of the published syllable categories matched our samples, and upon verification with W. L. Thompson found agreement with his judgment as well. In some cases, the two of us assigned a syllable to different categories, and in one case we both disagreed with Dr. Thompson's assignment. In such cases, we used the correlation function in Canary (Canary Software 1.1, Cornell Laboratory of Ornithology) to resolve the disagreement. This correlation function produces a sequence of correlation coefficients between two sound spectrograms, the maximum value of which (*R*) was used as an index of syllable similarity (Baker 1993). We also

used correlational statistics from Canary to illustrate degrees of variability in syllable categories.

RESULTS

From our sonographic analyses, we identified 99 different Indigo Bunting and 97 different Lazuli Bunting syllables (Figs. 1 and 2). In addition to the syllables identified previously by Thompson (1970, 1976), we also found 29 new Indigo and 42 new Lazuli syllables.

Some syllable types were more variable than others. We recognized this subjectively as we carried out the process of comparing our recordings with Thompson's catalogs and discovered that some syllables were easily assigned to particular categories whereas others required more examination before assignment to categories. To illustrate the range of variability, we identified one stereotyped and one variable syllable type for each species (Fig. 3) and used them for correlational analyses, which give quantitative measures of this variation. If our subjective impressions of the degree of variability are accurate, the average of pairwise correlations among a set of syllables from a variable syllable type should be smaller than that from a set of syllables representing a stereotyped syllable type. For both species, the correlation values averaged smaller for the variable syllable type compared to the more stereotyped syllable type (Lazuli stereotyped, mean $R = 0.80$; variable, mean $R = 0.67$; $P = 0.03$, $n = 6$ intercorrelations among four examples; Indigo stereotyped, mean $R = 0.79$; variable, mean $R = 0.59$; $P = 0.01$, $n = 6$ intercorrelations among four examples; Mann-Whitney U -test, Siegel 1956).

We also applied correlation analyses to resolve problematic syllable types. For example, after comparing representative syllables we identified Lazuli syllable type L-81 (Fig. 2) as distinctly different from L-30 and thus designated it as a new syllable type not found in Thompson's sample (1976). In examining our data, however, Thompson felt that our L-81 was indeed his L-30. We therefore performed correlational analyses and found a high correlation coefficient among L-81 examples (mean $R = 0.73$) and among L-30 examples (mean $R = 0.78$) but low values for L-81 vs. L-30 (mean $R = 0.53$). Moreover, the set of correlation coefficients within syllable types did not overlap with the set of coefficients cal-

culated between syllable types. Thus, we retained category L-81 as a new type of syllable.

A similar problem arose in which we initially assigned syllable renditions to a single syllable type that we subsequently realized was two different syllable types. This realization occurred after collecting all the representative syllables, from different birds, in a category and then subjectively recognizing two groups with no intermediates. We used correlation analyses to test our hypothesis of two syllable types. An example of such a case is represented by Indigo syllables I-25 and I-127 (Fig. 4), renditions of which were initially all placed in I-25. Correlation values fell into two non-overlapping groups, the group that retained the designation of I-25 (mean $R = 0.81$, $n = 6$ values) and a second group we designated I-127 (mean $R = 0.67$, $n = 6$ values). All these values were larger than those calculated between categories (mean $R = 0.51$, $n = 16$ values), justifying the subdivision into two syllable types.

A further question about syllable type boundaries arose when considering comparisons between the syllable catalogs of the two bunting species. Thompson (1976) recognized that Lazuli and Indigo catalogs appear to have some syllables in common, concluding that about 20% of the syllables of the two species were shared. Thompson (1976) presented no examples of which syllables of the two species he considered to be held in common, but supplied us with a list of these syllable types. Prior to obtaining the list, our experience suggested that overlap in the catalogs of the two species was quite small. One case of cross-species similarity that we identified in our recordings was that of Lazuli L-57 compared to Indigo I-83. Upon calculating the correlations within and between species, however, we found that the correlations within species were significantly greater than those between species (within, mean $R = 0.73$, $n = 6$ values; between, mean $R = 0.55$, $n = 9$ values; $P = 0.013$, two-tailed Mann-Whitney U -test). Thompson (pers. comm.) identified 19 pairs of syllables, one member of each pair from Indigo and one from Lazuli, that he judged to be shared between species. We used two of these pairs for which we had adequate data for conducting statistical comparisons. We had recordings of at least four males from each species that sang these syllables. For the remaining list of paired syllables from the two species, we had only one or two examples,

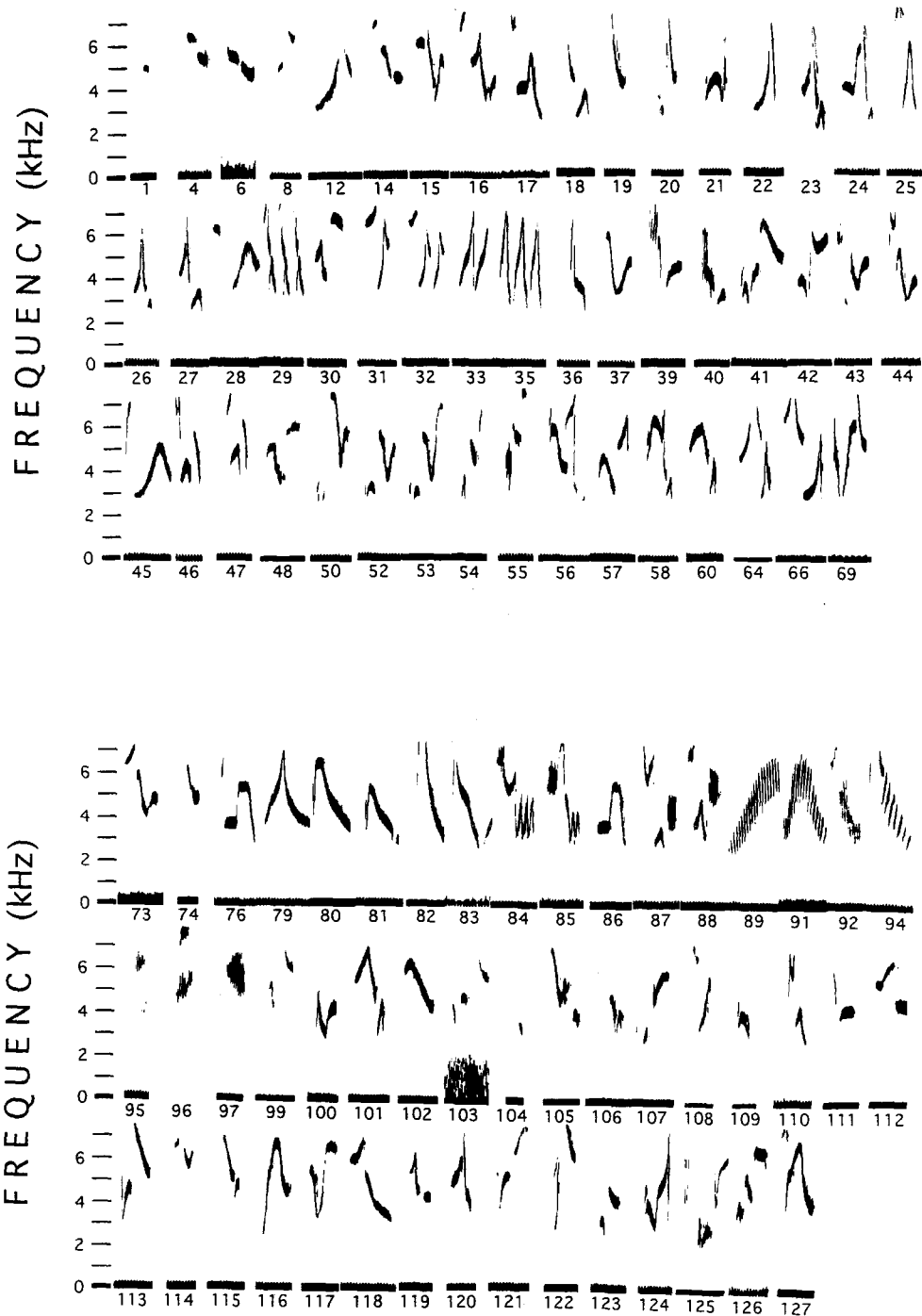


FIGURE 1. Catalog of Indigo Bunting syllables recorded in allopatric populations. Numbers below syllables 1-97 correspond to the catalog of Thompson (1970). Missing numbers indicate that we did not have in our recordings the syllables illustrated by Thompson. Syllables 99-127 are new syllables not recorded by Thompson (1970).

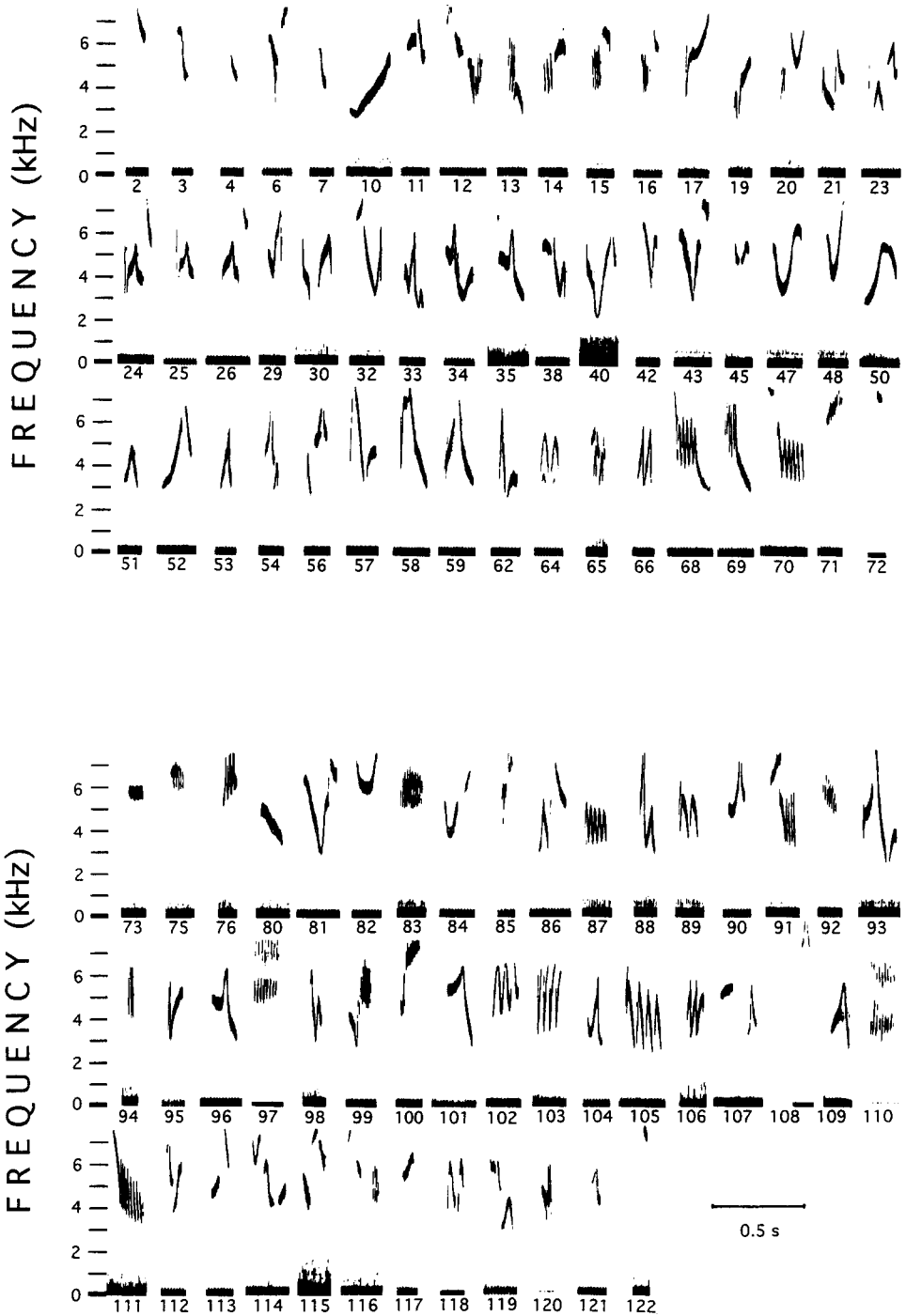


FIGURE 2. Catalog of Lazuli Bunting syllables recorded in allopatric populations. Numbers below syllables 1-80 correspond to the catalog of Thompson (1976). Missing numbers indicate that we did not have in our recordings the syllables illustrated by Thompson. Syllables 81-122 are new syllables not recorded by Thompson (1976).

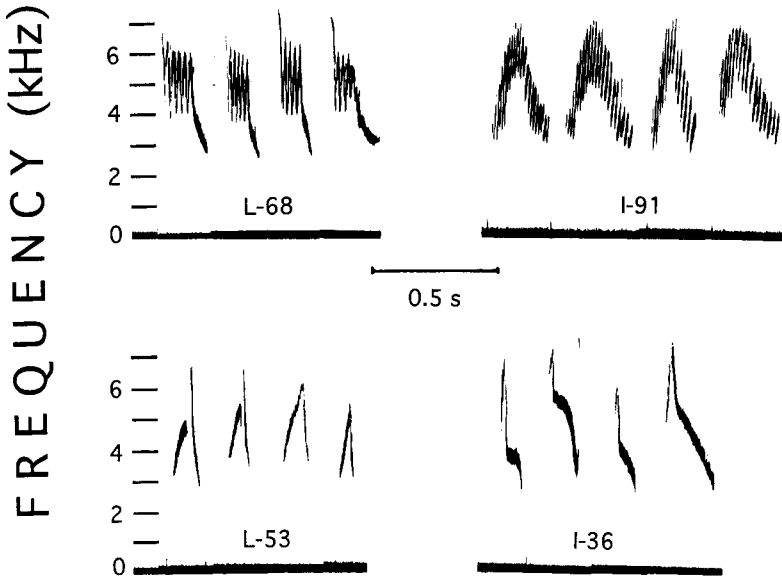


FIGURE 3. Examples of stereotyped syllables L-68 (Lazuli) and I-91 (Indigo) and variable syllables L-53 (Lazuli) and I-36 (Indigo).

insufficient for statistical comparisons. We calculated correlation coefficients for the samples representing the pair of syllables I-24 and L-33, hypothesized to be shared between species, and found the correlations within species to be significantly greater than those between species (within, mean $R = 0.74$, $n = 12$ values; between, mean $R = 0.56$, $n = 16$ values; $P = 0.0001$, two-tailed Mann-Whitney U -test). A similar result came from comparing I-17 and L-35 (within, mean $R = 0.72$, $n = 12$ values; between, mean $R = 0.61$, $n = 16$ values; $P = 0.0003$, two-tailed Mann-Whitney U -test). Even though some syllable types of the two species appear similar, we found no statistical support for the hypothesis that the two species share a large portion of their syllable repertoires.

Upon completion of the descriptive syllable catalogs of the two species, we addressed additional issues concerning the use of syllable types in the organization of songs within and between populations. First, we asked how are the component syllables used to construct whole songs of individuals? Are all the syllable types used with the same probability or are some syllable types more commonly used than others? We found considerable variability in the frequency with which the birds used the syllables in the construction of songs. We examined 483 Indigo

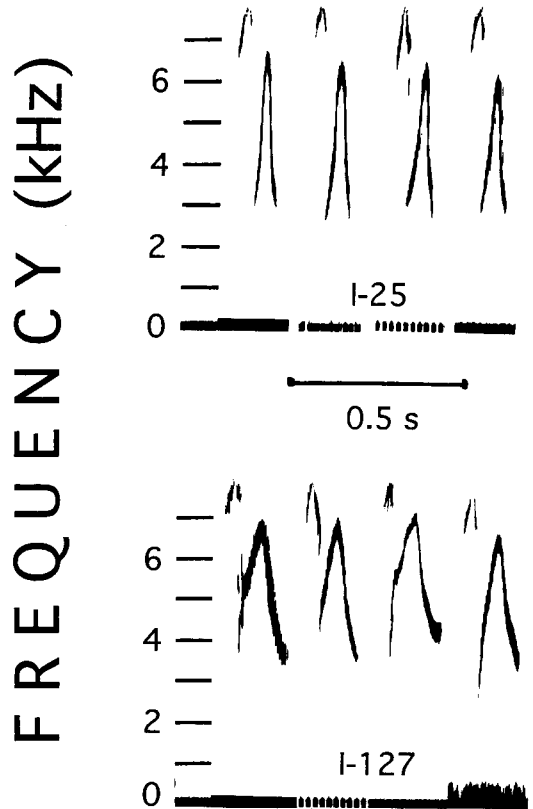


FIGURE 4. Examples of Indigo syllable I-25 and a similar but distinct new syllable I-127.

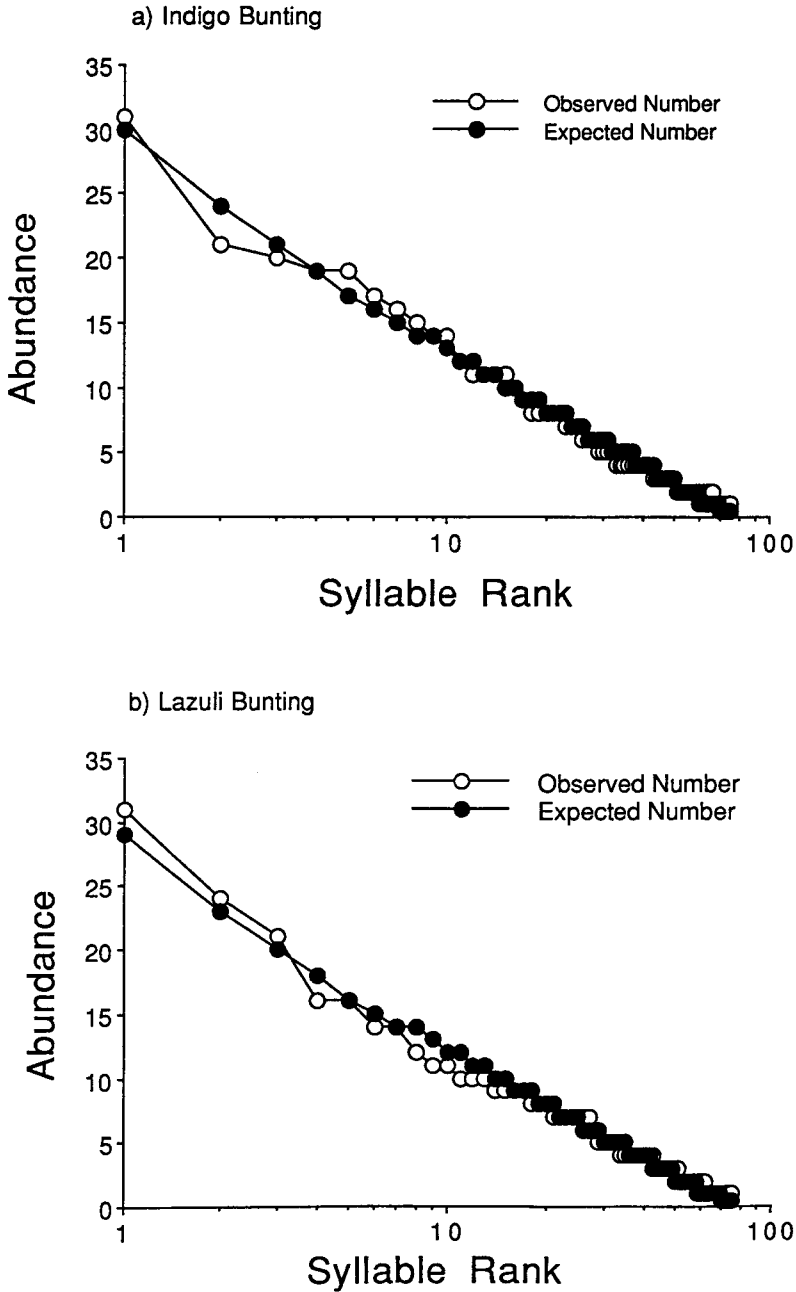


FIGURE 5. Observed and expected (see text) frequency of syllable use by (a) Indigo Buntings ($n = 63$), and (b) Lazuli Buntings ($n = 66$). Abundance was measured as the number of males that included at least one repetition of the syllable in their songs.

syllables and 443 Lazuli syllables and found some types to be abundant and some rare (Fig. 5). The relative abundance of syllables within each species was well-described by the broken-stick mod-

el developed by ecologists to describe the patterns of commonness and rarity of animal species in communities (MacArthur 1957, 1960). Expected and observed syllable abundances for

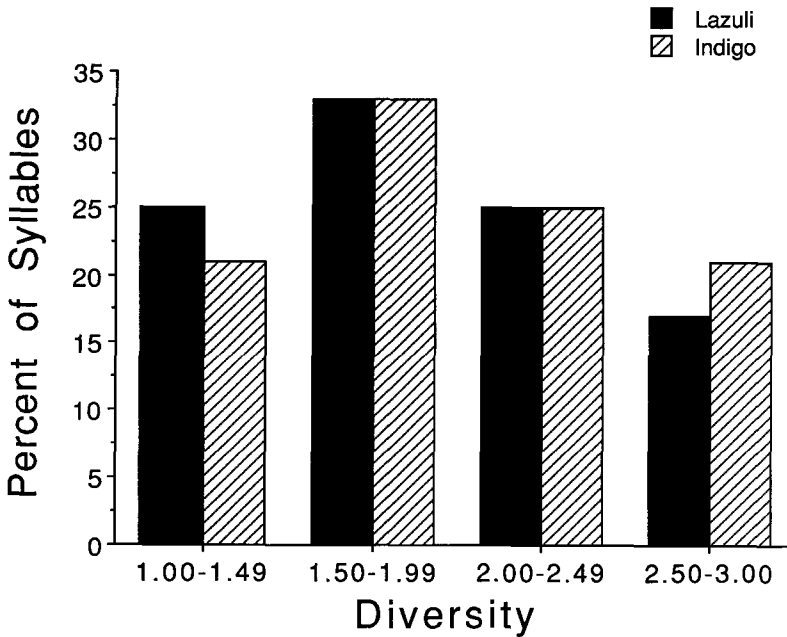


FIGURE 6. Degree of specialization with which syllable types are used in the songs of Indigo and Lazuli Buntings. Low values of diversity indicate syllable types that tend to be used in only one segment of the songs and are rarely found in other locations. High diversity values imply broad use of the syllables throughout the songs. Calculations are derived from the 49 most commonly occurring types of Indigo syllables and the 51 most commonly occurring types of Lazuli syllables.

Lazuli and Indigo Buntings were not significantly different (chi-squared test, Lazuli = 25.9, Indigo = 27.9, both $P_s > 0.995$, Sokal and Rohlf 1981).

Second, we examined the position of syllable types within songs. Are syllables taken randomly from the catalog to form a sequence of components in the whole song or are certain syllables specialized for use in certain portions of the song? To address this question, all songs that had at least three syllable types were divided into three equal segments: beginning, middle and end. Each syllable type was then examined for its location in these three segments over all songs that contained that syllable type. To be included in the analysis, a syllable type had to occur at least three times in the total sample so that it would be possible for it to occur in each of the three segments of the songs. The number of occurrences of each syllable type in the three segments was used to calculate an index of diversity (B, Levins 1968: 43). This diversity value was calculated by the formula:

$$B = 1/\sum p_i^2$$

in which p_i = proportion of occurrences of the

syllable in the i -th segment (beginning, middle, end) of the songs. In this application, B-diversity ranges from a low of 1.0 to a maximum of 3.0 and provides a simple description of the location-specialization of each syllable. Syllables that are restricted in their spatial occurrence in the whole song have low B values, whereas syllables that occur about equally often in all three portions of the songs have high B values.

In Indigo and Lazuli Buntings, roughly equal proportions of the total syllable repertoire are spread over the diversity spectrum (Fig. 6). Approximately 20–25% of the syllables are narrowly restricted in use to certain locations in the songs, about 33% are somewhat more spread over the songs, about 25% are yet more widely distributed, and about 15–20% are fairly evenly distributed in occurrence over the entire song. Overall, the distributions of B values between the two species did not differ significantly (Mann-Whitney U -test, two-tailed, $P = 0.33$, $n = 49$ Indigo, 51 Lazuli). Considering the narrowly-restricted category of syllables ($B = 1.0$ – 1.49) and both species together, 20 of 23 syllable types were narrowly restricted to the first one-third of the song,

one was restricted to the middle of the song and two to the last segment of the song.

Finally, we asked how the geographic patterns of syllable occurrence in our samples compared to those described previously. Studies of both Indigo Buntings (Shiovitz and Thompson 1970, Emlen 1971) and Lazuli Buntings (Thompson 1976) found syllable types to be stable in form and widely distributed over the species' ranges. Overlap values calculated in these previous studies within populations over time and between geographic locations ranged from 90–100% for Indigo Buntings and 59–63% for Lazuli Buntings. Our recordings revealed a somewhat similar pattern. In our Indigo Bunting samples from Iowa ($n = 24$), Lincoln, Nebraska ($n = 19$) and Omaha, Nebraska ($n = 20$) we found overlap with Thompson's (1970) Michigan samples (1965 & 1967) of 76, 85 and 83%, respectively. Thompson's (1976) Lazuli Bunting catalog is derived from a number of populations. Therefore, we pooled our Lazuli samples for an overall comparison with Thompson's (1976) sample. The overlap of 70% suggests, as Thompson observed, that syllable types of Lazuli Buntings may be slightly less widely represented in populations than are syllable types of Indigo Buntings.

Having supported the findings of stable syllable morphology and geographically widespread use of the same syllable types that were first described by Thompson (1970, 1976), we asked to what extent the frequency of use of each syllable type in our samples of Lazuli and Indigo syllables correlated with his results. For both our Lazuli and Indigo samples, the frequencies of occurrence of syllable types were significantly correlated with those in Thompson's samples (Lazuli: $R = 0.69$, $df = 78$, $P < 0.01$; Indigo: $R = 0.46$, $df = 96$, $P < 0.01$; product-moment correlation coefficient, Sokal and Rohlf 1981).

DISCUSSION

GENERAL CONCLUSIONS

Our analyses of the songs recorded from allopatric Indigo and Lazuli Buntings demonstrated the following (1) Both species have a similarly-sized set of syllable types (Indigo = 127, Lazuli = 122) from which songs are constructed. (2) Geographically, these same syllables are spread widely, perhaps occurring in virtually all populations throughout the species ranges. (3) As indicated by the number of males whose songs

contain the syllable type, some syllables are very common whereas other are very rare. (4) In two collections of Lazuli Bunting syllables and two of Indigo Bunting syllables from different locations made at different times, the abundances of the syllables were significantly correlated between samples within species, indicating widespread and stable agreement on the relative popularity (success) of individual syllables. (5) The patterns of commonness and rarity of syllables do not differ from those expected under the "broken stick" model of non-overlapping niches, a model developed to explain species abundance patterns in animal communities. (6) Some syllables are highly specialized in their location of use in whole song construction (usually restricted to the first part of the song), others are used with equal likelihood throughout the song, but many are intermediate in location-specificity. (7) The technique of cross-correlating sound spectrograms (e.g., Canary software) is useful for conducting comparative studies of vocal signals.

REPertoire SIZE

The similarity in size of the pool of syllable types for the two species may at first be unsurprising given that these are closely-related species. If allopatric populations of these two species share only about 20 syllables in common, as Thompson (1976) estimated, or fewer as our analyses suggest, the implication is that the remaining hundred odd syllables in each species arose independently since the presumed isolation and divergence in the Pleistocene (Mengel 1970). It is unknown whether these remaining syllables are modifications of earlier versions (also possibly shared by the two species) that came about through a series of minor cultural mutations or if they are novel new syllables invented since divergence and therefore represent a net increase in the meme pool. It is interesting, however, that a large and similar number of variants has arisen in both species. Perhaps this indicates a similar rate of mutations and extinctions of syllable types in the two species, a consequence of similar song learning programs during ontogeny.

UNIVERSAL SYLLABLE TYPES

The general pattern of "universal" elements (syllable types) found from population to population in the buntings is reminiscent of the pattern described for the Swamp Sparrow, *Melospiza georgiana* (Marler and Pickert 1984). In the latter

species, the song is composed of a single repeated syllable. The set of syllables differs from population to population, but the individual notes constituting the syllables form a set of species-wide universal elements. These same notes are used as the basic building blocks from which all populations construct their locally distinct set of syllables. Thus, there is a parallel in the way the individual notes of Swamp Sparrows and syllables of buntings are used as the species-wide building blocks of song variation. Other cases in the literature are also suggestive of such species universals: songs and syllables of the Wood Thrush (*Hylocichla mustelina*; Whitney and Miller 1987; Whitney 1989, 1992) and to some extent the Northern Cardinal (*Cardinalis cardinalis*; Lemon 1966) as well as certain calls of Black-capped Chickadees (*Parus atricapillus*; Ficken and Weise 1984, 1990; Hailman et al. 1985, 1987) may also follow this pattern.

ABUNDANCE PATTERN OF SYLLABLE TYPES

Patterns of commonness and rarity of syllables have seldom been described in the literature. There are no particular theories that attempt to explain the observed unevenness of these distributions. Our data on both Indigo and Lazuli Buntings, showing correlated syllable abundances in samples from different locations taken several years apart, indicate higher rates of annual survival of these syllables and begs for an explanation for the consistency. Because in allopatric populations these vocal units are learned from conspecifics, we therefore are led to inquire why some seem to be more popular than others? Are some syllables more common because they have a higher valence to an individual in the process of learning song, perhaps easier to memorize and reproduce? Do these syllables match most closely the perceptual properties of the auditory receptor system (Dooling 1982)? Do these more frequent syllables belong to older or dominant males that act as models, which younger males copy (Payne 1983)? This latter explanation does not readily explain why different populations tend to have the same common syllable types. As in the attempts to explain patterns of gene frequencies among populations, frequencies of syllables can be affected by founder events, random extinction caused by meme drift, immigration and local (social) selection, variables whose values are largely unknown for these bunting species. In contrast to our findings, a pre-

vious analysis on the Indigo Bunting (Emlen 1971) suggested that a syllable's abundance varies among different populations and supports random fluctuations in syllable abundances, perhaps analogous to random walk of neutral alleles.

SYLLABLE CONSTANCY

In a single population of Indigo Buntings in Michigan, sampled from 1965 to 1980, whole-song types had a half-life of about 4–8 years (Payne et al. 1981). Changes in a song tradition occurred when a single syllable was substituted, deleted or added during the copying of one bird by another. Thus, although the population of whole songs sung by all the males in the study area evolved enormously over the 15 year period, the building block syllable population probably changed little in terms of types present. Although the frequency distribution of syllable types in the early and later song samples was not described, our correlations between two Lazuli and between two Indigo samples of syllables suggest that relative abundance of syllable types should be similar over the 15 year period.

Moreover, when geographically disjunct populations of Indigo Buntings are examined for song similarity, there is little or no matching of whole songs, even though 50% or more of the individuals within a population match at least one other bird's song (Payne et al. 1981). Thus, syllable repertoires of different populations are very similar but the ordering of syllables into whole songs is very different.

A related case has been described in the Chaffinch (*Fringilla coelebs*). Colonization of the Chatham Islands by birds from New Zealand probably occurred around 1900. Eighteen of 20 syllable types currently sung by Chatham birds have been found in the New Zealand source populations (Baker and Jenkins 1987). Calculations we can make from another study on a Chaffinch population in England over an 18 year period (Ince et al. 1980) give a population half-life of whole songs to be between 10–14 years. Thus, in Chatham Island Chaffinches we would expect essentially no whole songs to have survived to the present, whereas the syllable types have survived relatively unchanged for about 85 years.

BROKEN STICK MODEL

The distributions of relative abundance of syllable types sung by the buntings are described quite well by the broken-stick model. This model

was developed on an ecological assumption of a resource continuum that is broken into random lengths, each length representing the abundance of a different species in the community (MacArthur 1957, 1960). Thus, the model assumes competition and non-overlapping niches. For bunting syllables, the fit to the broken stick model indicates that the number of representatives of a syllable type in the community pool of syllables is a random variable. The analog of ecological resource space and competition in the case of song syllables would be the brain space within which the ability of each syllable type to compete is a random variable. The ecological analogy would view this brain environment as containing n non-overlapping niches of random size and this leads to the broken-stick distribution. Given the general correlation between song repertoire size and size of a song control nucleus (HVC) in the brain (DeVoogd et al. 1993), the assumption of limited brain space seems realistic. In what sense can syllable types be thought of as competing for brain space?

Consider a simplified example. Assume the syllable pool consists of 100 different types (analogous to species) and consider a population of 100 males that each sing one song. The average number of syllable types per song in six populations of Indigo Buntings is approximately seven (Shiovitz and Thompson 1970). Therefore, this hypothetical population of 100 males collectively sings about 700 syllables, which represents the limit of brain space available in the local culture. Within this finite space, the relative abundances of the various syllable types are described by the broken-stick model. Thus, an increase in the abundance of any one or more syllable types must be accompanied by a decrease in abundance of others. Is there evidence for syllable competition during song ontogeny?

Margoliash et al. (1991), studying Indigo Buntings, found that as a crystallized song structure is being developed during song learning, there is overproduction of syllables with attrition of some as the final song structure emerges. In our laboratory, studies of song development in hand-raised Lazuli Bunting nestlings (Boylan 1995) also found overproduction and winnowing of syllables as song is crystallized. This process of selective attrition during development may be the point at which the competition among kinds of syllables occurs and produces the broken stick distribution of abundances. When adult Indigo

Buntings change their crystallized song, they do so by modifying syllable types they already sing into new syllable types (Margoliash et al. 1994). For every new syllable type the male sings, one old syllable type is eliminated.

CULTURAL EVOLUTION OF SONG

To consider the process involved in cultural evolution of songs, we can now address the question of the units of transmission across generations. By analogy, the meme (Dawkins 1976) is the unit of cultural transmission corresponding to the gene in biological transmission (Lynch et al. 1989, Lynch and Baker 1993). One way to define the gene is as the unit of recombination, or recon. We suggest that the unit of recombination in buntings is the syllable. Thus, an appropriate definition of meme for buntings is the "recon," which is the syllable. After the first breeding season, an individual male bunting usually retains the same song. Mechanistically, then, recombinations of syllables taken from the population meme pool to form a new whole song is accomplished through song learning by males during and before their first breeding season. We found, as did Shiovitz (1975), that most of the syllable types were unrestricted in their locus within songs, but we also found a set of syllable types that tend to be restricted to the first part of the song. Therefore, there are rules of meme recombination that disallow certain syntactical arrangements. We also may consider the individual notes making up multi-note syllables of bunting songs to be the units of mutation, and they are the cultural equivalent of the "muton" definition of the gene, or the smallest unit capable of mutational change. In these birds, it appears that even though cases of such mutation do occur in elements of syllables they do not cause such massive reorganization of the songs in a population as do the recombinations. As in population genetics, mutation events in songs seem a smaller agent of change compared to changes brought about by recombination.

These observations raise the question of whether there may be canalizing factors in the learning-transmission process that serve to maintain syllable types as recognizable units, perhaps disallowing certain mutations of notes. Otherwise, it would seem that syllable morphology would become so variable that recognizable categories would not exist. In Swamp Sparrows, the syllable is most likely the unit

transmitted from teacher to pupil (Marler and Pickert 1984). Their work supports the idea of a filtering process that allows only a certain set of constrained acoustical features to serve as a learning model. Studies like these on swamp sparrows have not been done on buntings.

In conclusion, cultural transmission of song in Indigo and Lazuli Buntings is based upon sets of universal syllables that are distributed widely among populations, and from which whole songs are composed. These units of cross-generation transmission can be remarkably stable in their phonological features, both in space and time. The syllable recons may be the most appropriate units from which we can construct a basic theory of the cultural evolution of sound signals in birds.

ACKNOWLEDGMENTS

We thank Ann E. M. Baker, Mark Mantych, Eric Stone and Andy Thompson for their help with tape recording bunting songs. Tom and Angie Reisser provided housing and hospitality in Iowa. Field work in Idaho was made possible by James Hayden, Idaho Fish and Game Department. Comparison of our syllable catalog with previous recordings would have been impossible without the cooperation of W. L. Thompson. Comments and advice on the manuscript were kindly provided by W. L. Thompson, L. L. Payne, S. T. Emlen and two anonymous reviewers. Fernando Nottebohm supplied some additional insight on the correlation between the volume of HVC and repertoire size. Birds were captured under USFW permit (PRT-694924) and maintained under supervision of the Animal Care and Use Committee, Colorado State University. Financial support was by a grant from the National Science Foundation to MCB (BNS-87-06526) and by a National Science Foundation Predoctoral Fellowship to JTB.

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