



# BRILL

---

An Experimental Analysis of the Parameters of Bird Song Eliciting Species Recognition

Author(s): Stephen T. Emlen

Source: *Behaviour*, Vol. 41, No. 1/2 (1972), pp. 130-171

Published by: [BRILL](#)

Stable URL: <http://www.jstor.org/stable/4533433>

Accessed: 04/09/2013 13:45

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at  
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



BRILL is collaborating with JSTOR to digitize, preserve and extend access to *Behaviour*.

<http://www.jstor.org>

AN EXPERIMENTAL ANALYSIS OF THE PARAMETERS OF  
BIRD SONG ELICITING SPECIES RECOGNITION

bv

STEPHEN T. EMLEN <sup>1)</sup>

(Section of Neurobiology and Behavior, Division of Biological Sciences,  
Cornell University, Ithaca, N.Y., U.S.A.)

(With 19 Figures)  
(Rec. 5-IV-1971)

CONTENTS

Introduction . . . . .	130
Methods . . . . .	132
Scales of responsiveness . . . . .	133
The Indigo Bunting and its song . . . . .	137
Results . . . . .	140
Species recognition . . . . .	140
Syntactical information . . . . .	142
Temporal information . . . . .	145
Figure morphology . . . . .	147
Discussion . . . . .	151
Ontogeny . . . . .	152
Individual recognition . . . . .	153
Motivation . . . . .	155
Comparison with other species . . . . .	156
Summary . . . . .	164
References . . . . .	165
Zusammenfassung . . . . .	166

INTRODUCTION

One of the central questions in the study of animal communication concerns the encodement of information in different types of signals. During the past few decades, biologists have devoted considerable effort to this problem and much has been learned about the types of messages transmitted between members of a species as well as between groups of sympatric species. An overwhelming preponderance of these studies, however, has dealt solely with cases of visual communication. Few attempts have been made to study

1) This work was supported by an NIH health science advancement award to Cornell University. D. Mock, B. Miller, and B. Sorrie offered valuable assistance in the field and V. Engelhard and the Cornell Laboratory of Ornithology allowed use of some of their acoustical equipment. R. C. Capranica, J. B. Falls, M. Ficken and H. C. Howland offered helpful suggestions on the manuscript.

the information content of acoustical signals. This paper represents one such attempt.

Many types of information are conveyed by the singing behavior of birds. These may include the singer's species; sex; and, frequently, individual identity; his territorial and reproductive status; and his probability of responding aggressively or sexually to a potential recipient. For each kind of information, there must exist some optimal signal form for its conveyance. There is good reason to believe that these optima will be different for the different messages carried in bird song. For example, due to the differential attenuation, reflection, and absorption of sounds of different frequencies, the ideal physical characteristics for signals that function in long distance territorial advertisement might be quite different from those of signals used over shorter distances, as in the maintenance of pair bonds (KONISHI, 1970). Similarly, if a message requires the precise localization of the emitter, this places certain structural constraints on the form of the acoustical signal that otherwise might not be present (MARLER, 1957).

Comparable statements can be made concerning the degree of variability in bird song. Experimental studies have confirmed that several species of birds can recognize individual conspecifics on the basis of voice (WEEDEN & FALLS, 1959; TINBERGEN, 1960; TSCHANZ, 1968; BEER, 1969; FALLS, 1969; EVANS, 1970; MUNDINGER, 1970; STEVENSON *et al.*, 1970; EMLER, 1971). This requires that the song or repertoire of songs of any one bird be distinctive from the songs of other members of the population. In other words, if one function of bird vocalization is to allow individual identification, then the detailed structure of song must be a highly variable trait within a population. On the other hand, songs are species specific traits that commonly function in species recognition. To minimize the chances of species misidentification, songs should be highly stereotyped and unvarying throughout a population. Thus we see a direct conflict between those attributes favorable for species recognition on the one hand and individual recognition on the other.

As we consider additional messages transmitted by song, each with its own optimum signal structure, the situation becomes even more complex. With all of these different, often conflicting, selection pressures operating on acoustical signals, we may ask how the different messages have been encoded simultaneously in the structure of a single bird song. One hypothesis, first proposed by MARLER (1960), suggested a segregation of information within a vocalization, different components or parameters of the signal conveying different types of information. The problem thus becomes one of decoding the information content of a bird song.

## METHODS

The species selected for intensive study was the Indigo Bunting, *Passerina cyanea*, a bird of open forest-edges that breeds throughout much of the eastern United States. The males are highly vocal, singing throughout the day for most of the breeding season. Each individual male has a vocal repertoire consisting of one principal song type that remains constant from year to year (THOMPSON, 1968), and previous experiments have indicated the use of song as a means of both species and individual recognition among males (EMLEN, 1971).

The procedure followed in these studies was to perform playback experiments of normal and artificially modified songs during June and July, after territorial boundaries were firmly established. The level of agonistic response of the male territory holder was used as a bioassay of the effectiveness of the experimental song in allowing species recognition. Underlying this approach is the assumption that the strength of the territorial response is proportional to the amount of species-specific information contained within the experimental song. In other words, as those parameters allowing species recognition are removed, the experimental song will become less recognizable as that of a conspecific, and the level of response to it will decrease.

Care must be taken, however, in the interpretation of full agonistic responses to modified songs. This need not imply that the parameter altered does not play a role in the behavioral context under question. Rather, due to possible redundancy in information content, one can only conclude that the modified parameter is not *essential* in the species recognition process.

Tape recordings were made of the songs of buntings that resided outside of the study area. This precaution was taken to rule out the possibility of the experimental birds having had prior experience with and, thus, being habituated to these "control" songs. All recordings were made with a Uher 4000-Report L tape recorder at a speed of  $7\frac{1}{2}$  i.p.s., using a Sennheiser NK 404 condenser microphone mounted in a 24-inch parabolic reflector. "Experimental" tapes were made by modifying the "control" songs in various ways, including the splicing and reorganizing of note sequences, the shortening or lengthening or inter-note intervals, *etc.* First, bunting songs were re-recorded at a speed of 15 inches per second. These tapes then were edited using a pair of Ampex Model 350 studio recorders and a pair of headphones. By turning the tape manually, it was possible to locate the precise onset or termination of a sound source on the tape with an accuracy of plus or minus  $\frac{1}{8}$  inch (corresponding to a temporal accuracy of 0.008 seconds). After completion of all splicing modifications, the tape was re-recorded at  $7\frac{1}{2}$  inches per second. Playback tapes then were made in which the test song

was repeated at 12 second intervals, a typical singing rate for this species.

The responsiveness of each experimental bird was compared when exposed to the playback of a "control" and an "experimental" (= modified) song. Playbacks were conducted using the Uher 4000-Report L tape recorder, a Nagra DH portable amplifier and an Atlas WT-2 speaker connected to the amplifier by 35 m of cord. In practice the speaker was placed on the ground, directed upward, near the known center of a territory or adjacent to one of the principal song perches within the territory. The observer then would retreat and conceal himself behind available vegetation. At no time were visual decoys used in this study.

In order to minimize variance due to extraneous factors such as differences in responsiveness at different stages in the reproductive cycle, or inter-individual differences in the quality of response, each experimental bird was exposed to playback of only two songs, one the control and the other an artificially modified version of the control. The sequence of presentation was randomized.

Preliminary experiments indicated that buntings habituate rapidly to repeated song playback (EMLEN, unpublished). Consequently, a period of two days was allowed between successive tests to minimize this effect. Attempts were made to conduct the two tests for each individual bird at the same time of day. All results were compared by paired statistical analyses (see below).

I initiated experiments only when the territorial male was known to be in the vicinity of the speaker. The tape recorder was turned on and the song allowed to play for a period of three minutes measured from the time the test bird made its first response to the playback. If no immediate response occurred, playback was continued for a total of six minutes. If the bunting still had not responded, the experiment was terminated.

If the bird did respond, detailed notes were taken of its behavior during the three minutes of playback plus a period of six minutes immediately following playback. The behavioral responses noted appeared identical to the agonistic behaviors observed in male-male encounters in the field as well as to interactions noted in captive aviary buntings. All components of the agonistic repertoire, including different call notes and threat posturings, were observed.

### Scales of responsiveness.

I recorded agonistic behavior according to two pre-determined scales of responsiveness. The first evaluates the *maximum* intensity of the response on a scale ranging from 0, implying no reaction, to a value of 7. This type of weighted scale has enjoyed widespread use among ornithologists (LANYON,

1963; STEIN, 1963; GILL & LANYON, 1964; TRETZEL, 1965; BREMOND, 1967, 1968a, b; THOMPSON, 1969). However, I feel that it suffers from two serious drawbacks. The first is that only one piece of information is used in evaluating the strength of a bird's response—the one posture or display that is presumed to represent the highest intensity of aggressive motivation. All other behaviors are excluded from consideration as in any quantitative information referring to the frequency of occurrence of different displays.

My second objection refers to the degree of subjectivity with which intensity scales are derived. Before presuming to understand the motivational states underlying specific postures or displays, it is necessary to understand thoroughly the full agonistic repertoire of the species being considered. To avoid circularity, the information used to derive the intensity scale must be gathered *independently* from the playback experiments that are themselves to be evaluated according to this scale.

In deriving an intensity of response scale for the Indigo Bunting, I made heavy use of data obtained from captive birds. Motion picture analysis of encounters between known dominant and subordinant individuals allowed an accurate correlation to be made between specific postures and presumed motivational states. Pilot playback experiments in the field also were conducted solely for the purpose of constructing this intensity scale. One interesting finding was that a bird consistently could be made to change his response from a full attack to submission by increasing the volume of the playback. This is in agreement with DILGER's (1956) observations on *Hylocichlid* thrushes and has prompted me to place the full submissive posture at the top of the scale, indicative of the most intensive stimulus situation. The full scale includes eight categories of response and is presented in Table 1.

One may wish to debate the relative merits of placing attack *vs* submission as the top rank in such a behavioral scale. In fact, most previous authors have failed to consider submissive displays at all in their analyses of responsiveness. I feel that this is due primarily to a lack of familiarity with the complete behavioral repertoire of the species in question.

It should be obvious from the above that maximum intensity scales are subject to differing interpretations and evaluations. In order to minimize this subjective weighting of behavior and to make better use of the full range of behaviors elicited by playback, I devised a second type of scale for evaluating the effectiveness of a song in evoking territorial behavior. The approach is analogous to the hybrid index scales employed in taxonomic studies (see SIBLEY, 1954; SIBLEY & SHORT, 1959). I divided the agonistic repertoire of the Indigo Bunting into eight categories. These correspond to the behaviors used in the previous scale with one exception—the change in

TABLE 1

*Behavioral scale used in evaluating the maximum intensity of agonistic response to playback*

- 0 = no change in behavior resulting from song playback
- 1 = increased rate of singing, songs frequently lengthened by the addition of terminal notes
- 2 = "alarm", erect posture (body plumage sleeked, head held high, crest raised, tail raised and flicked from side to side); usually accompanied by a short, harsh, "chip", call note
- 3 = approach (to within 3 meters of loud speaker)
- 4 = flights ( $N > 2$ ) over the loud speaker
- 5 = "attack" (hopping on the loud speaker, wings held erect over the back, body plumage sleeked); frequently accompanied by a long harsh call note
- 6 = quiver posture (plumage ruffled, wings held out, drooped, and quivered rapidly; body orientation rotated slowly from side to side); frequently accompanied by a soft repetitive twittering call note. This posture is believed to represent an ambivalent motivational state in which both escape and attack tendencies are present
- 7 = "submission", indicated by a fluffed posture (plumage fluffed, head retracted, bird immobile); frequently accompanied by a high frequency "tseep" call note

singing behavior is subdivided into two components. Each of these eight components is scored separately on a rank scale of 0, 1 or 2 according to its frequency of occurrence. The quantitative values corresponding to these ranks are presented in Table 2. These were determined empirically from the pilot playback tests, such that a value of 1 indicates a moderate, and 2 an intense, response for each behavior type. These eight values then are summed to give a quasi-quantitative 0 to 16 scale. Although still non-linear, this scale takes into account the full spectrum of agonistic behaviors, thereby minimizing the subjective weighting of one posture or call note over another.

This type of analysis is feasible because the motivation of the experimental bird changes rapidly during the nine minutes that its behavior is being recorded. A typical temporal pattern of response would be the following: upon first hearing the playback, the bird flies to the vicinity of the speaker and makes numerous short flights back and forth above it. Interspersed between these flights, the bird either attacks the speaker or adopts the "quiver" posture. As the song playback continues, however, the bird shifts into the "fluffed" submissive posture, ceasing the flights and remaining immobile, emitting soft, high frequency "tseep" call notes for the remaining duration of the playback. Once playback has ceased, the bird re-initiates short flights over the speaker and adopts the sleeked, erect posture, frequently flicking his tail and emitting loud, staccato "chip" call notes. By the time the observation period is ending, the bird has usually ceased all postu-

TABLE 2

*"Hybrid Index" scale for evaluating levels of agonistic response elicited by song playback (For details of postures, see Table 1)*

<i>Behavioral Category</i>	<i>Rank Score</i>
Singing rate	<p>0 — Singing in 3 minutes immediately post-playback is a normal rate (not exceeding 18 songs per 3 minute period).</p> <p>1 — Rate increased: <math>18 &lt; N &lt; 21</math> songs per 3 minutes.</p> <p>2 — Rate greatly increased: <math>N &gt; 21</math> songs for 5 minute period.</p>
Song quality	<p>0 — No change.</p> <p>1 — Song lengthened by the addition of at least 3 figures.</p> <p>2 — Song lengthened and delivered at a soft (barely audible) intensity; high-pitched "squeak" notes occasionally added.</p>
"Alarm", Erect posture (usually accompanied by "chip" call note)	<p>0 — Rare.</p> <p>1 — Infrequent; <math>2 &lt; N &lt; 10</math> "chip" notes.</p> <p>2 — Frequent; <math>N &gt; 10</math> "chip" notes.</p>
Approach (to within 3 meters of loud speaker)	<p>0 — Never approaches.</p> <p>1 — Approaches, but not during first 60 seconds of playback.</p> <p>2 — Approaches within first minute of playback.</p>
Flights over loud speaker	<p>0 — <math>0 &lt; N &lt; 2</math></p> <p>1 — <math>3 &lt; N &lt; 10</math></p> <p>2 — <math>N &gt; 10</math></p>
"Attack" on speaker itself	<p>0 — Not present.</p> <p>1 — <math>1 &lt; N &lt; 4</math> attacks.</p> <p>2 — <math>N &gt; 4</math></p>
Quiver posture (usually accompanied by soft, repetitive twittering call note)	<p>0 — Not present.</p> <p>1 — Infrequent; <math>2 &lt; N &lt; 5</math> quiver bouts observed.</p> <p>2 — Common; <math>N &gt; 5</math> quiver bouts.</p>
"Fluffed" posture (usually accompanied by "tseep" call note)	<p>0 — Rare; <math>N &lt; 5</math> "tseep" notes.</p> <p>1 — Posture infrequent; <math>6 &lt; N &lt; 25</math> "tseep" call notes.</p> <p>2 — Posture common; <math>N &gt; 25</math> "tseep" notes.</p>



rings, retreated some distance from the speaker, and has begun singing songs that are not only longer than the typical songs but are emitted at a greater repetition rate. It is this utilization by the bird of a large part of its behavioral repertoire that permits usage of this hybrid-index scale.

In this study, data were analyzed and will be presented according to both scales. Results were compared by a paired statistical test. Since responsiveness was measured on ordinal scales, parametric statistical tests are inappropriate. All comparisons were made by the non-parametric Wilcoxon Matched-Pairs Sign-Rank Test (SIEGEL, 1956). Since the sign of the difference between experimental and control songs could be predicted in advance (modified songs being expected to elicit weaker responses than normal, control songs) this was treated as a one-tailed test in assigning significance levels.

Throughout this paper, data will be presented in histogram form. The actual paired values for tests with specific birds are included in the appendices.

### The Indigo Bunting and its song.

The advertisement song of the male Indigo Bunting has been described in detail by THOMPSON (1968). It consists of a series of high-pitched notes, commonly given in pairs and uttered with a characteristic rhythm. On closer examination, each note or "figure" (adopting THOMPSON's terminology) is seen to be a highly complex sound consisting of from one to five single utterances, called syllables, placed so closely together that to the human ear they appear as one continuous sound (see Figure 1). The detailed structure

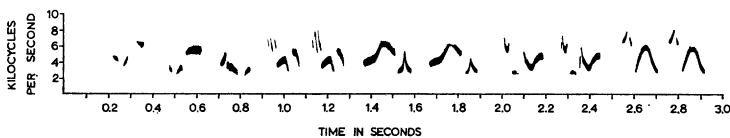


Fig. 1. Territorial song of a male Indigo Bunting.

of these figures is usually repeated twice with great precision giving rise to the "pairing of notes" characteristic so commonly mentioned in ornithological field guides. As stated by THOMPSON (*ibid.*) each figure has a narrow frequency range in any one instant, but varies rapidly in pitch, so that a very wide frequency range may be covered by a single figure. The changes in frequency pattern occur too rapidly to be resolved by the human ear; rather they impart a slurred or harsh quality to an otherwise musical song (BORROR, 1961; THOMPSON, *ibid.*).

Each individual male bunting has a territorial repertoire consisting of one principal song type. When birds do alter their songs, they usually either

omit the terminal figure or figures (during midday or when singing is interrupted by bouts of preening or foraging) or add figures to the end of the typical song (when stimulated by the presence of another bird or song playback). Thus each bird has a relatively constant signature that is clearly recognizable to a human observer. Playback experiments (EMLÉN, 1971) confirm this individual recognition ability among the bird's neighbors as well.

In contrast, the songs of different members within a population are markedly different. THOMPSON (1970) made a detailed study of song variation in Indigo Buntings in southern Michigan. He found that although a small number of song figures were widespread throughout the population, most were present in the songs of only a few individuals. Additionally, the arrangement of these figures into a full song generally was unique to the individual. Thus instances in which two males shared the identical song pattern were uncommon.

An analysis of the songs of 36 Indigo Buntings residing in the vicinity of Ithaca, New York yielded comparable results. I have observed only one instance of two males sharing the identical song. Interestingly, most of the specific song figures found in the Ithaca population have morphologically similar counterparts in the published sonograms from southern Michigan. Recently SHIOVITZ & THOMPSON (1970) reported an analogous finding for bunting songs recorded in Kentucky, Michigan and New York. The significance of this very high degree of geographic similarity in song is not yet fully understood.

In view of the degree of variability of songs of different members of a population, a quantitative analysis was performed on different song parameters in an attempt to identify those components showing maximum constancy. Audiospectograms were made of songs of 36 Ithaca birds. Since there is almost no variation in the consecutive songs of a given individual (THOMPSON, 1968; EMLÉN, personal observation), one song from each bird was selected for analysis.

Audiospectograms were made using a Kay Electric Company Model 685 Missilizer. Two spectograms were made of each song, one at wide band setting for temporal analysis and one at narrow band-width for frequency analysis. Measurements then were made of song length, number of figures per song, duration of each figure, length of the inter-figure interval, pairing index, frequency range, *etc.* The mean values as well as the standard deviations for a number of these measurements are given in Table 3. However, it is not the absolute magnitude of variation but the magnitude relative to the mean that is important in sensory discrimination. Thus the coefficient of variation ( $V$ ), defined as the ratio of standard deviation  $\times 100$  divided

by the mean, is co-listed in Table 3. (A more complete discussion of this ratio is provided by HUTCHISON *et al.*, 1968.) A glance at this table indicates that the song parameters showing the greatest constancy throughout the population include the frequency envelope, the pairing or repetition index (defined as the number of figures in a song divided by the number of types of figures) and the duration of both figures and inter-figure intervals. Additionally, certain features of figure morphology were widespread throughout the population; these will be discussed in detail in a later section.

TABLE 3

*Quantitative treatment of song parameters of Indigo Buntings from Ithaca, New York*

	Mean	Standard deviation	Sample size	Variability (s/ $\bar{x}$ X 100)
<b>"Syntax" Features</b>				
Pairing index (the number of figures in a song divided by the number of types of figures)	1.88	0.39	36	21%
Number of figures per song (excluding introductory note)	8.86	3.60	36	41%
Number of kinds of figures per song	4.83	1.93	36	40%
Number of syllables per song	23.80	10.57	36	44%
Number of kinds of syllables per song	11.14	4.20	36	38%
<b>Temporal Features</b>				
Song length (in seconds)	2.31	0.84	35	37%
Figure length (in centiseconds = 1/100 second)	18.16	7.83	288	24%
Inter-figure interval (in centiseconds)	9.93	2.88	262	29%
Interval between members of a pair of alike figures (in centiseconds)	7.89	1.85	125	23%
Interval between dissimilar figures (in centiseconds)	10.04	2.29	137	23%
<b>Frequency Features</b>				
Highest Frequency (kHz)	7.34	3.31	36	45%
Lowest Frequency (kHz)	2.45	0.29	36	12%
Frequency range covered/song (kHz)	5.10	0.70	36	14%
<b>Figure Morphology</b>				
Frequency range covered/ individual song figure (kHz)	4.15	0.96	296	23%
Number of elements per figure	2.91	2.38	356	82%

# RESULTS

## SPECIES RECOGNITION

I conducted a preliminary series of experiments to test the species recognition properties of Indigo Bunting song. This was done in two ways. First, responses of Indigo Buntings were noted to playback of songs of other species that, to the human ear, sounded similar to bunting vocalizations. In New York, two species satisfy this requirement, the common Goldfinch (*Spinus tristis*) and the Yellow Warbler (*Dendroica petechia*). Song variability is quite extensive in each of these species. Consequently, while most of their songs are easily identifiable as such, some cause considerable confusion even among experienced ornithologists. An attempt was made to select such an intermediate song type for playback experiments (see Figure 2).

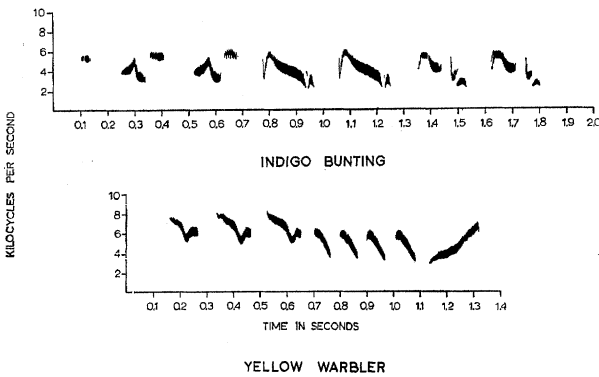


Fig. 2. Songs of Indigo Bunting (top) and Yellow Warbler (bottom) used in species recognition experiment.

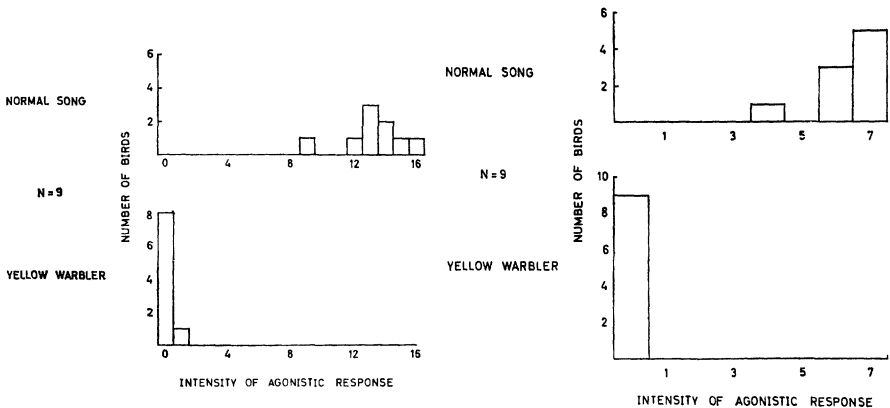


Fig. 3a and b. Agonistic responses of territorial male buntings to playback of songs of Indigo Bunting and Yellow Warbler (see Appendix 1). a) Responses measured on a 0-16 "Hybrid-Index" scale. b) Responses as measured on a 0-7 "maximum intensity" scale. (See text for explanations.)

Figures 3a and 3b demonstrate that territorial male buntings clearly distinguish the song of a conspecific from that of the Yellow Warbler; using either index of responsiveness, the Yellow Warbler song evoked predominantly zero responses. Completely analogous results were obtained with playbacks of Goldfinch vocalizations.

The Lazuli Bunting, *Passerina amoena*, is an extremely closely related species that breeds in the western portion of the United States. The songs of these two species are quite similar in a number of syntactical and morphological details but are quite dissimilar in temporal patterning. Playback of Lazuli songs (Cornell Laboratory of Ornithology cut number 11, tape recorded in central California) likewise failed to elicit any response from New York Indigo Buntings (Figures 4a and 4b). These results are especially interesting in view of the fact that the two buntings are known to hybridize in their zone of sympatry in the Great Plains (SIBLEY & SHORT, 1959). Similar weak responses were obtained when Lazuli songs were played to Indigo Buntings in Michigan (THOMPSON, 1969).

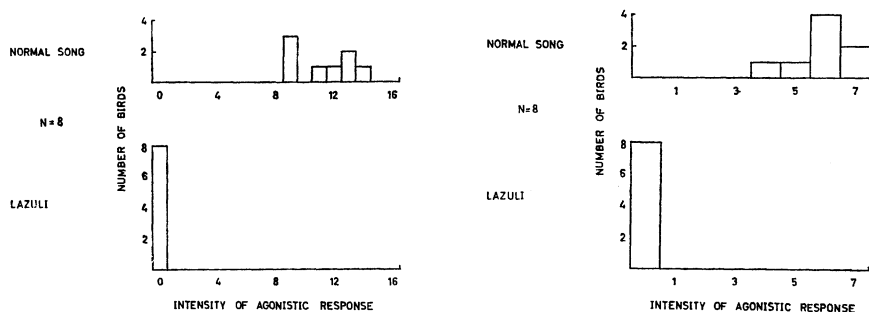


Fig. 4a and b. Agonistic responses to playback of songs of Indigo Bunting (*Passerina cyanea*) and Lazuli Bunting (*P. amoena*). (See Appendix 2.)

A second series of experiments tested the responses of male goldfinches and yellow warblers to the playback of Indigo Bunting songs. In no case was any aggressive response observed (sample sizes of six and eight birds respectively).

Conversely, during the course of this study (including EMLEN, 1971) 16 different Indigo Bunting songs have been used in experimental tests. Taken together these songs exhibit much of the variability described in Table 3, yet each one elicited immediate and full responses on the part of male territory holders.

It thus appears that the advertisement song of the Indigo Bunting is clearly functional in the process of species recognition.

In attempting to determine which song features are of importance in the process of species identification, one logical starting point is to examine features shared by most members of the population—in other words those parameters having the lowest ratio of standard deviation/mean in Table 3. The results obtained when such parameters are artificially modified are described below under the headings of syntactical information, temporal information, and figure morphology.

### SYNTACTICAL INFORMATION

This term, adopted from BREMOND (1967, 1968a), refers to information conveyed by the arrangement or ordering of figures within the song. The most noticeable syntax feature of Indigo Bunting vocalization is the high repetition index indicative of a tendency to repeat individual figures as pairs within a song. In the Ithaca population, 73 percent of the figures are paired (Figure 5). Not only is this characteristic often used by ornithol-

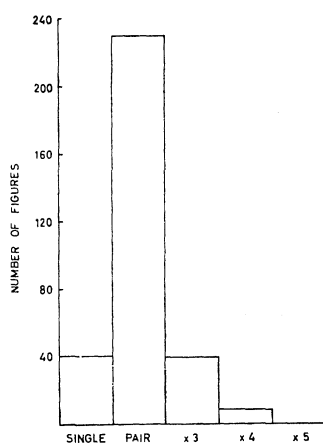


Fig. 5. Frequency of occurrence of note-figures given as single, paired, triplet and quadruplet units in the Ithaca, New York population of Indigo Buntings ( $N = 36$  birds).

ogists for identifying this species, it is also one of the most constant statistical features of the song as revealed in Table 3 ( $V = 21\%$ ).

To test the importance of this feature, an experimental tape was made in which the figures from a normal song were artificially “unpaired”. If we assign numbers to different figure types, the normal song in Figure 6 can be written 1 1 2 3 3 4 4 5 5 6 6, whereas the rearranged song would be 1 2 3 4 5 6 1 3 4 5 6. All features of the song other than syntactical arrangement are maintained intact. The figures are merely respliced in a new order. Playback of this song elicited full agonistic responses on the part of territorial male

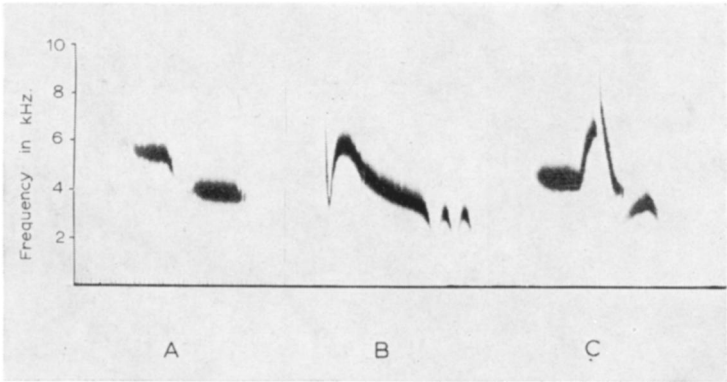


Fig. 9. Song Figures selected as “building blocks” for construction of artificial bunting songs.

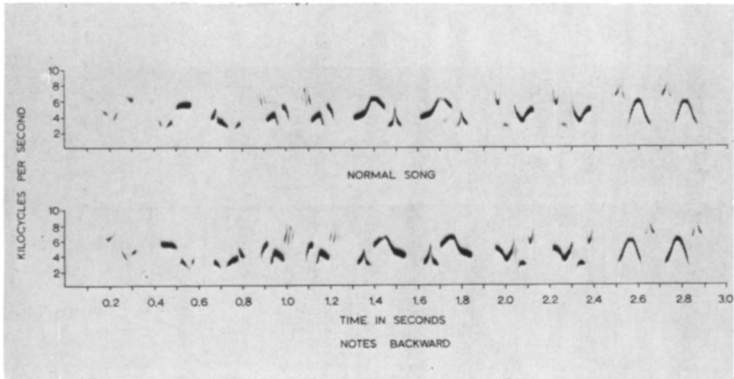


Fig. 13. Control Indigo Bunting song (top) and experimentally modified song in which each figure is reversed (bottom).

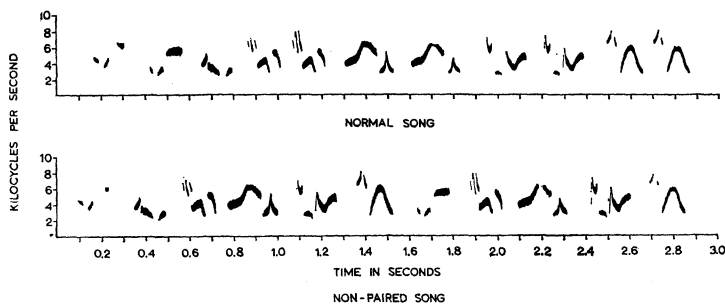


Fig. 6. Control Indigo Bunting song (top) and experimentally modified song in which repeated figures were re-spliced into a "non-paired" sequence (bottom).

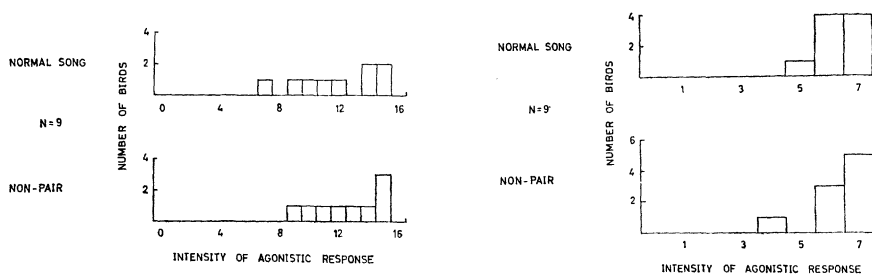


Fig. 7a and b. Agonistic responses to playback of normal and experimentally modified ("non-paired") bunting song. (See Appendix 3).

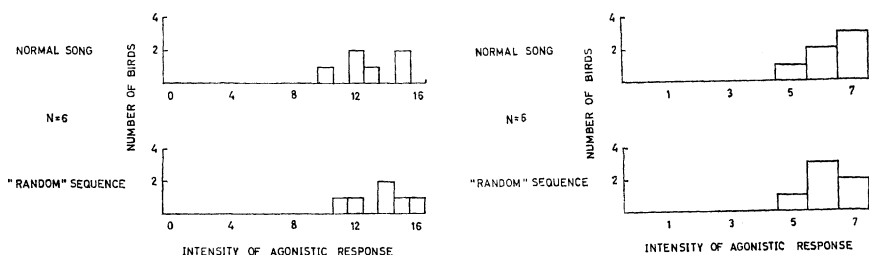


Fig. 8a and b. Agonistic responses to playback of normal and experimentally modified (figures rearranged into a "random" sequence) songs. (See Appendix 4.)

buntings that were statistically indistinguishable from responses to the normal, unmodified song (Figures 7a, b; Appendix 3).

A similar result was obtained when a second, shorter bunting song was rearranged in a similar manner. This song consisted of an introductory note followed by six figures that could be written 1 1 2 2 3 3 (an audiospectrogram of the song is shown in Figure 11). After a "random" unpairing of figures, the new arrangement was 3 1 2 1 3 2. No differential behavior on the part of the buntings is evident in the responses to this song although the sample size



of six birds is insufficient for statistical analysis (Figures 8a, b; Appendix 4).

Although I have never encountered an Indigo Bunting song in which the majority of the figures were not paired, the above results indicate that this feature is not essential for auditory recognition in this species. The results do not necessarily imply that the syntactical arrangement of figures is without importance in this context. But they do show that sufficient redundancy is present so that the removal of such information in no way decreases the effectiveness of song recognition by conspecifics.

It is possible that each type of figure in a bunting song contains some minimal amount of specific information and that a syntactical summation of several figures is necessary for recognition to occur. Songs of this species contain an average of nine figures per song (Table 3; see also THOMPSON, 1968) representing, on the average, five different figure types. An artificial song was constructed using only two figures as building blocks (arbitrarily called A and B, and shown in Figure 9). These figures were alternated to produce a song of average length (nine figures) that could be written A B A B A B A B A. Care was taken to insure that the time span between figures matched the mean value for the Ithaca population (0.1 seconds). Since this experimental song was synthesized by selecting one figure from each of two pre-existing vocalizations, there was no "proper" control for this playback series. I therefore selected the long song depicted in Figure 1 containing eleven figures of five types to serve as the control. The results, shown in Figures 10a and b and Appendix 5, indicate a strong response to the experimental tape even though it contained 60 percent fewer figure types than the control. Statistical tests of significance could not be run on these data as the sample size ( $N = 5$ ) is too small for the Wilcoxon Sign Rank Test.

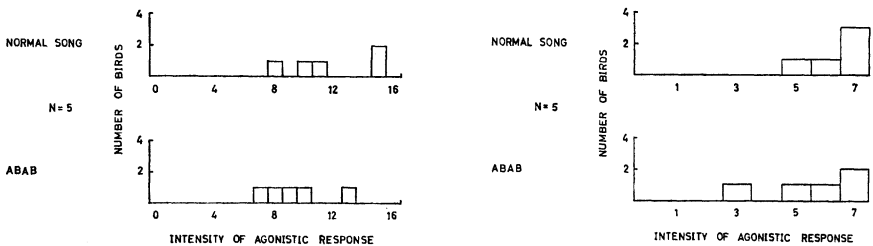


Fig. 10a and b. Agonistic responses to playback of a normal song (see Figure 1) and an artificially constructed song A B A B A B A B. (See Appendix 5.)

Additional evidence against the summation hypothesis is obtained from field observations during playback of normal, unmodified songs. Male bun-

tings frequently leave their song perches and fly directly toward the speaker during the playback of the very first song in the experiment. A search through my field notes reveals 16 instances where the territorial male initiated flight before the fourth figure of the first song had been broadcast. This gives one the distinct impression that acoustical recognition occurred almost immediately and that a very small number of figure types were sufficient for this recognition.

In summary, the syntactical arrangement of different figures in a song is not essential for species recognition in the Indigo Bunting.

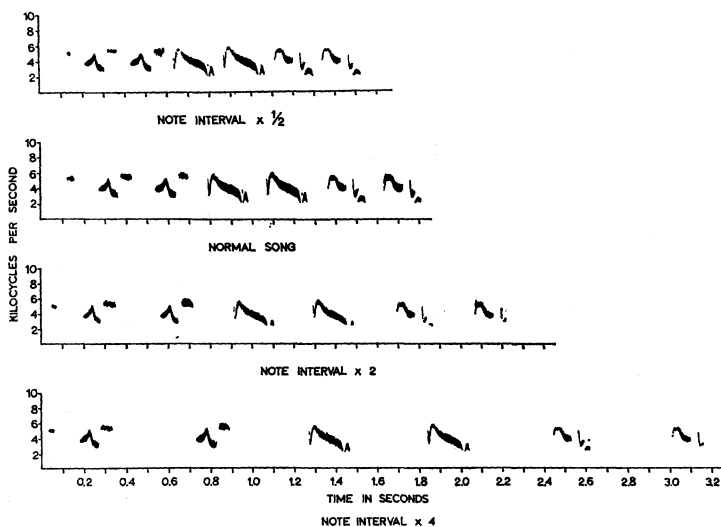


Fig. 11. Temporally altered Indigo Bunting songs in which the inter-figure interval has been shortened by one-half and lengthened by factors of two and four.

### TEMPORAL INFORMATION

A glance at Table 3 reveals that certain temporal characteristics are among the most constant parameters in Indigo Bunting song. Although song length varies widely from individual to individual, the rate of repetition of figures is quite constant and imparts the characteristic rhythm to the song of this species. A more detailed analysis indicates that both the length of the figures themselves and the interval between successive figures show low coefficients of variation (24% and 29% respectively). The rhythm is even more predictable than these V values suggest since the average interval between similar figures (between members of a pair) is somewhat less than the interval between unlike figures. When this is taken into account, the coefficients of variation for the two classes of inter-figure intervals drops to 23%.

To test the possible importance of temporal information in song recognition,

I constructed experimental tapes in which the interval between figures was modified by removing or adding sections of blank tape. This allowed the cadence of the song to be altered without any concomitant change in pitch. The normal song selected for this test consisted of an introductory note followed by six figures comprising three pairs. It should be stressed that the individual figures were not modified in any way; neither was their sequential arrangement within the song (see Figure 11).

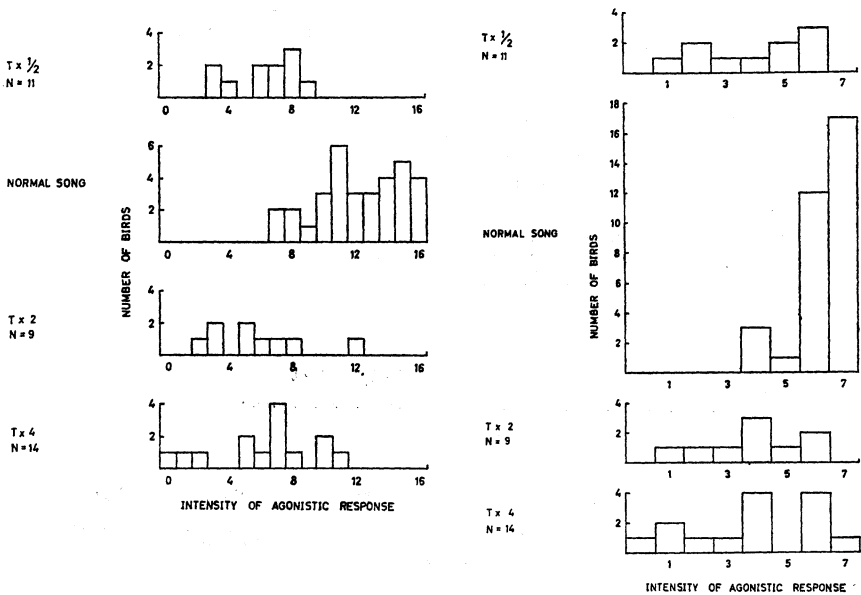


Fig. 12a and b. Agonistic responses to playback of normal and temporally altered bunting songs. (See Appendix 6.)

To avoid the possibility of habituation to playback, each bird was exposed to only one of the temporally altered songs in addition to its normal counterpart. This series of tests therefore required a considerable sample size of birds and the pooled results from 34 male buntings are presented in Figures 12a and b and Appendix 6. The results demonstrate a significant reduction in agonistic response to each of the three temporally altered songs. The unaltered tape elicited the full repertoire of attack, threat, and, in most instances, submissive behavior while the experimental tapes aroused only mild alarm, approach, and a small amount of threat posturing.

The rhythmic character of Indigo Bunting song thus emerges as one important parameter in the species recognition process. However, a comparison of Figure 12 with the zero responses elicited by playback of other species' songs (Figures 3 and 4) indicates that temporal patterning is not

the only critical song feature. Sufficient information remained in the experimental songs, presumably within the structure of the figures themselves, to cause the male buntings to respond weakly to this artificial intruder.

The length of the figures themselves is a second important contributor to the rhythmic cadence of Indigo Bunting song. As mentioned previously, figure length was a highly constant parameter in the local population. However, since it was difficult to modify this parameter without simultaneously altering the detailed structure of the figure itself, I did not conduct tests of its possible importance.

Total song length is a more variable parameter within this population and, as expected, it did not appear to play a role in the recognition process. The two principal songs used as "controls" in this study differed markedly in total length (see Figures I and II), yet responses to the two were statistically indistinguishable ( $p > .1$ ).

#### FIGURE MORPHOLOGY

Detailed quantitative studies of the morphology of Indigo Bunting song figures have been conducted at both the intra- and inter-population levels (THOMPSON, 1970; SHIOVITZ & THOMPSON, 1970). A complete catalog of all figures occurring in a population in southern Michigan has been published (THOMPSON, *ibid.*). This catalog can be applied directly to the Ithaca population since an analysis of the songs of 36 individual males reveals that 92 percent of song figures are shared between the two populations; only eight percent of the Ithaca figures do not have exact counterparts in the Michigan songs (EMLEN, in press). Upon studying the THOMPSON song catalog, one is struck by the tremendous variability in figure types. They are composed of anywhere from one to five subunits (average = 3), called syllables, that range from short, staccato clicks to long drawn out trills. In fact, it is difficult to find any reliable feature that is shared by the majority of figures.

But, with the exception of the simple, single syllable figures that frequently introduce a song (as in Figure II), almost all figures have a harsh or slurred quality. This is caused by rapid rises and falls in frequency, changes too rapid to be followed by the human ear. The average frequency span included in an entire bunting song is 5.1 kHz (see Table 3). Yet the average single figure covers 4.15 kHz, fully 81 percent of the range of an entire song. Additionally, most Indigo Bunting notes contain abrupt reversals of frequency change, a rising frequency changing abruptly into a dropping one, or *vice versa*. Such changes usually occur within a single syllable of a compound figure giving rise to "V" or inverted "V" figure shapes. In the Ithaca sample of 36 songs, 96 percent of the figure types contained at least one such reversal.

I conducted two series of experiments in an attempt to determine whether these figure characteristics contained vital recognition information for other buntings. First, the song shown in Figure 1 was modified again, this time by “reversing” each figure within the song (Figure 13). The song was not merely played backwards; rather each figure remained in its proper syntactical position and only the figure morphology was reversed. The arrangement of figures, the pairing of figures, and the temporal relationships between figures all remained unchanged. However, the detailed arrangements of syllables within each figure now was altered, as was the frequency pattern within these syllables. For example, looking in detail at the fourth figure of the song in Figure 13, we might write the sequence of syllables as A<sub>1</sub> A<sub>2</sub> A<sub>3</sub> B C. In the reversed song, this figure becomes C B A<sub>3</sub> A<sub>2</sub> A<sub>1</sub>. Similarly, while the frequency pattern of syllable C originated at a frequency of approximately 5.5 kHz and dropped precipitously to around 3 kHz, in the reversed song it begins at 3 kHz and rises abruptly to 5.5 kHz. If detailed patterns of frequency change or syntactical arrangement of syllables within figures were parameters carrying essential species’ specific information, then territorial male birds should show a decreased response to playback of this modified song. The general harsh quality imposed by large-scale, rapid fluctuations in frequency, however, is retained in the “reversed” song. Consequently, if this (or some other) general feature of bunting figures is important in species recognition, no difference in response would be expected for the two tapes.

The results of playbacks to nine territorial male buntings are shown in Figures 14a and b and Appendix 7. Although the overall level of responsiveness in both tests was somewhat lower than expected (probably due to the experiments being conducted late in the season, on birds raising second broods), no statistical difference occurred in the responsiveness to the two song types.

A second series of experiments involved constructing new songs from building blocks of carefully selected figure types. For this purpose, I devised a song consisting of two figures, one (A) containing very little in the way of rapid frequency changes, while the other (B) was more typical in this respect. The responses to playback of a composite song of these note types already have been described (Figure 10, Appendix 5). Additional experiments now were run in which the experimental song consisted of eight repetitions of a single figure spliced together to assure normal temporal patterning. The song A A A A A A A A failed to elicit a significant response, with four of six birds giving no response whatsoever and the remaining individuals merely increasing their singing rate, and showing mild alarm, respectively.

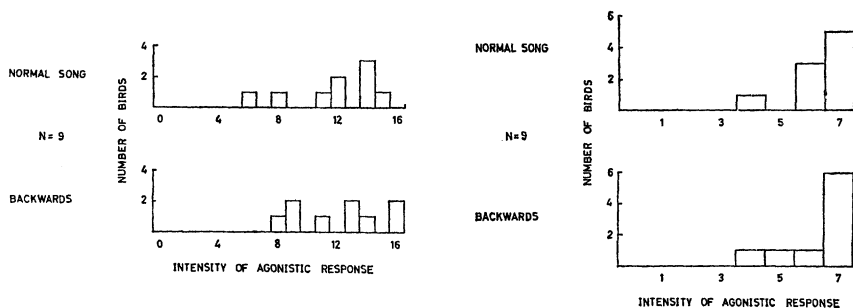


Fig. 14a and b. Agonistic responses to playback of normal and "backward" songs. (See Appendix 7.)

No individuals showed any tendency to approach the sound source (Figures 15a and b and Appendix 8).

The response to song type B B B B B B B was much more variable. One individual failed to give any response; three others responded strongly, attacking the speaker and adopting the "quiver" posture believed to represent an ambivalent motivational state in which both escape and attack tendencies are present. The remaining males responded at intermediate levels (Figures 16a, b; Appendix 9). Unfortunately, only five of these birds were exposed to normal, control, songs. The sample size is thus too small for statistical analysis. However, the results certainly suggest that the song composed of "B" notes elicited a much stronger response than that built from "A" figures. This would seem to indicate that figure B contained more properties allowing species identification than figure A.

One final experiment of this sort was conducted using a third figure, which I will call C. Again, the test song was constructed by splicing eight identical figures together with the proper inter-figure spacing. I selected figure C, also shown in Figure 9, to represent an extreme case in containing a rapid, large-scale frequency change. As seen in Figure 17 and Appendix

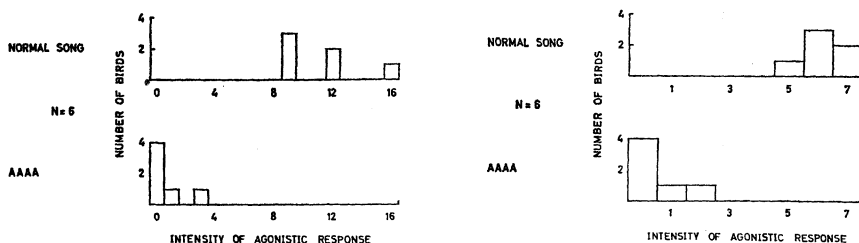


Fig. 15a and b. Agonistic responses to playback of a normal song and an artificially constructed song, A A A A A A A. (See Figure 9 and Appendix 8.)

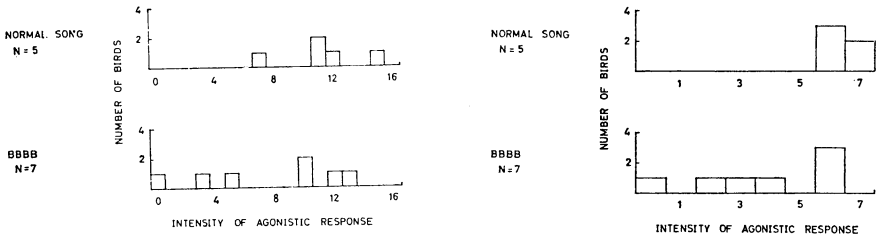


Fig. 16a and b. Agonistic responses to playback of a normal song and an artificially constructed song, B B B B B B B B. (See Fig. 9 and Appendix 9.)

10, the responses to this song were very comparable to the previously constructed song, B B B B B B B B. Although most birds definitely responded to the song, the intensity of their agonistic behavior varied greatly.

These results are difficult to interpret. Some structural feature of bunting song figures seems to be essential for imparting species distinctiveness to the vocalization. Since song figures are extremely variable within a population, we are probably dealing with several generalizable note features. The search for such constant features suggests an importance of rapid and reversed frequency changes; empirical evidence from two series of experiments at least is consistent with this hypothesis.

The morphology of Indigo and Lazuli Bunting song figures is extremely similar. The latter cover a comparable frequency spread and show analogous, abrupt changes in pitch (THOMPSON, 1968). But the notes of *amoena* are significantly shorter in duration, are slightly higher in frequency, and are uttered in more rapid succession than those of *cyanea*. A final experiment was conducted in which a Lazuli song was modified by lengthening the inter-figure intervals to correspond to the mean value appropriate for Indigo song. In this way I hoped to test whether Lazuli song figures were sufficiently similar to elicit a response from *cyanea* males. A positive result would imply that the principal barrier to inter-species recognition was due to temporal

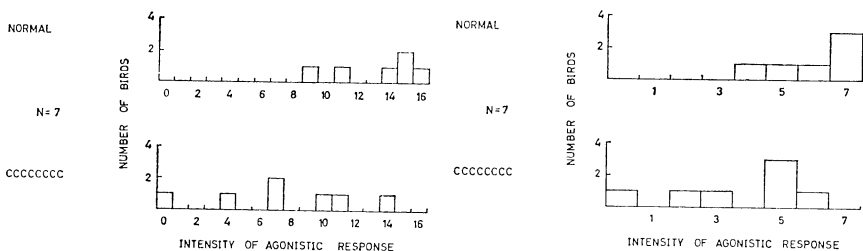


Fig. 17a and b. Agonistic responses to playback of a normal song and an artificially constructed song, C C C C C C C C. (See Fig. 9 and Appendix 10.)

differences in the two species' songs. As seen in Figure 18 (and Appendix 11), however, this test song was completely ineffective in inducing agonistic responses. This suggests that the "generalized" Indigo Bunting figure must fall within rather strict frequency and/or temporal limits.

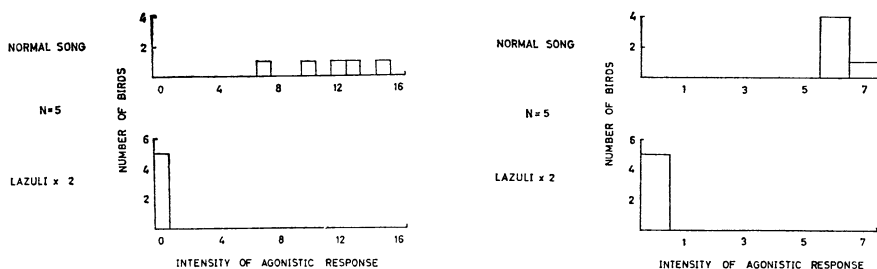


Fig. 18a and b. Agonistic responses to playback of a normal Indigo Bunting song and a Lazuli Bunting song in which the inter-figure intervals have been doubled. (See Appendix 11.)

Unfortunately, the technique of building experimental songs from actual bunting vocalizations is a weak one and rapidly approaches the point of diminishing returns. Alternate hypotheses concerning the essential features of song are possible that also would be consistent with the available experimental data.

For future studies, I recommend the use of artificially generated sounds in the construction of experimental tapes. I attempted to make synthetic songs of this type with the equipment available at the Cornell Laboratory of Ornithology and at New York's Haskins Laboratory. Neither attempt resulted in the production of anything remotely duplicating an Indigo Bunting's song. However, new synthesizing techniques are becoming available and this approach offers great possibilities for future work. Instead of progressively removing pieces of information from a normal song, one can construct a synthetic vocalization containing only those features hypothesized to be of importance in the context under examination.

## DISCUSSION

For an Indigo Bunting song to be recognizable to a conspecific, it must consist of a series of figures possessing a characteristic quality and repeated in a characteristic temporal rhythm. Although the exact nature of this figure quality remains unclear, it is hypothesized to be dependent upon a spectral structure that is narrow at any one instant in time, yet which rises and falls extremely rapidly in frequency during its short duration. I assume that the



frequency range of an effective song would have to fall within the 2.5 to 7.3 kHz range typical of the species, although experimental confirmation of this was not attempted. The ordering of single utterances (or syllables) within figures, and the syntactical arrangement of figures within a song are not essential features for conspecific recognition.

A glance at Table 3 indicates that the most constant features of bunting song do, in fact, correspond to those empirically demonstrated to be of importance in species recognition. The more variable parameters, including song length, the number of figures or figure types within a song, the number and arrangement of syllables within figures, and the details of figure morphology, do not appear critical for species identification among male buntings.

However, this correlation is far from absolute. While all the key parameters for song recognition will probably turn out to be among those with low standard deviation/mean values, the converse is not true. Not all of the constant features are essential for recognition by conspecifics. The syntactical arrangement of song figures into pairs provides a clear example. Thus, one should be extremely cautious about predicting the functional significance of specific song parameters solely on the basis of a statistical analysis of variability.

### ONTOGENY

I had further expected to be able to predict which song features would be of importance in playback experiments by studying the ontogenetic development of singing behavior. It seemed logical that those features developing in the absence of outside acoustical input would represent the most stable, and hence most reliable, recognition characteristics.

When Indigo Buntings taken as early nestlings (two to six days old) are reared in acoustic isolation from adult conspecifics, they develop songs which are abnormal in several respects. These songs "... are longer than those of wild birds, have about the same number of figures per song, but fewer kinds of figures per song, and a longer interval between songs. The frequency envelope is narrower and lower. The general characteristics of figure shape, spacing and repetition of figures, frequency range, and even the interval between songs, however, are all close to those of free-living birds" (RICE & THOMPSON, 1968, p. 469). Individual figures often contain rapid and reversed changes in frequency imparting the typical slurred or harsh quality to the human ear; however, the detailed figure structures do *not* match up with counterparts in wild adult buntings (RICE & THOMPSON, 1968; EMLEN, unpublished observation). Although these findings suggest a partial correlation between key features of isolate and playback songs, many aspects of isolate

songs are highly variable. This is especially true for temporal traits where the durations of individual figures and the intervals between figures often greatly exceed those found in normal adult bunting songs (EMLEN, unpublished observation).

One additional constant, yet "non-essential", trait of bunting song is the high repetition index. Birds reared in acoustic isolation tend to repeat figures to an even greater degree than wild birds, and triplet and quadruplet figures are not uncommon.

It thus appears that predicting the functional significance of different song parameters on the basis of "genetic templates" (KONISHI, 1965), is likewise a partial solution at best.

### INDIVIDUAL RECOGNITION

The results of this study suggest that male Indigo Buntings rely heavily upon selective feature extraction in recognizing the songs of conspecifics; the birds respond to only a small number of the acoustical cues potentially available in the sound source. This leaves a large reservoir of information unused, information that, theoretically, could provide raw material for the conveyance of other messages with differing or opposing acoustical requirements.

Territorial male buntings are able to distinguish between, and respond differentially to, the songs of familiar (neighbor) and unfamiliar (stranger) individuals (EMLEN, 1971). Although experiments aimed at elucidating the acoustical basis of this individual recognition are still underway, it seems plausible that details of figure morphology will prove to be of importance in this context. Each individual bird has a constant song type consisting of a series of specific figures arranged in a specific order. Individuals are distinguishable to a human observer on this basis and it seems a reasonable first hypothesis to expect the same on the part of the birds. While some general features of note morphology could convey specific distinctiveness, these features might be satisfied by a variety of figure types and differences in figure fine structure could provide the variability essential for individual distinctiveness.

The ordering of figures within a song also merits consideration in this context. While a high repetition index is a constant feature of Indigo Bunting songs, the actual sequence of paired and unpaired notes within songs is not. Among the Ithaca buntings, the majority of song figures were paired (73 percent) but some figures occurred singly (13 percent) and rarely a figure was uttered as a triplet (12 percent) or quadruplet (2 percent; see Figure 5). A song composed of seven figures, three pairs ("2") and a single ("1"),

could be arranged in the following four ways: 1 2 2 2, 2 1 2 2, 2 2 1 2, or 2 2 2 1. As stated previously, each bird sings one song type, so this arrangement is constant and characteristic for the individual. Might this provide an additional source of information allowing individual recognition?

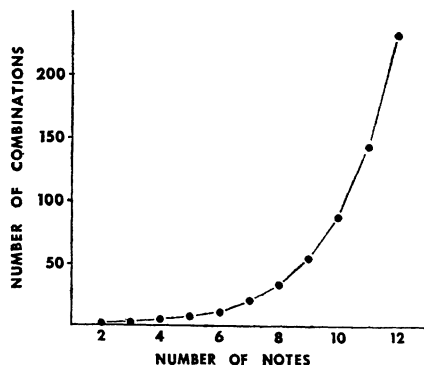


Fig. 19. The number of unique "repetition sequences" plotted as a function of the number of figures in a song. (See text for full explanation.)

When this "repetition sequence" was investigated among the 36 Ithaca birds, only three instances were found where two individuals shared the same sequence. Thus a human observer could identify almost all the males individually without relying upon figure structure at all. The redundancy of information provided by such a second, independent, source of individual distinctiveness could greatly reduce the likelihood of misidentification.

The number of possible "repetition sequences" is given by the formulae:

$$\sum_{N=0}^{N-1/2} \frac{(N-P)!}{P! (N-2P)!} \quad \text{where } N \text{ is an odd number}$$

and

$$\sum_{N=0}^{N/2} \frac{(N-P)!}{P! (N-2P)!} \quad \text{where } N \text{ is even;}$$

where  $N$  is the number of figures and  $P$ , the number of pairs. (This simple model ignores triplets and quadruplets. The number of possible permutations increases greatly when these are considered.) The curve in Figure 19 shows that the number of different possible sequences rises rapidly as a function of the number of figures in the song. For the mean Indigo Bunting song length of nine notes, the number of permutations approximates 60, a number exceeding the population size of male buntings in the Ithaca study area.

Whether this feature of syntax is of any importance for individual recogni-

tion is unknown. It is directly testable, however, since it leads to the prediction that the song of a neighbor, rearranged using the identical song figures but in a new sequence should be treated as that of a strange intruder and should elicit an increased agonistic response.

### MOTIVATION

Some features of Indigo Bunting song are highly variable, not only between individuals within a population, but within the repertoire of a single individual. As mentioned previously, the principal change involves the addition of figures to the end of the song (during encounters with other males, or in response to acoustical playback) and the omission of terminal figures during periods of low intensity singing in the mid-afternoon. A second type of change consists of singing the same song but at a much reduced volume. At times, this "soft song" is barely audible at a distance of eight meters and one gets the impression that the high frequencies are being accentuated. Thirdly, a bunting may add high frequency "squeak" notes to his normal song, interspersing these between successive pairs of normal figures.

Each of these three types of change normally occurs in response to the same stimulus situation. Consequently, they often occur in combination, "soft songs" and long songs frequently containing squeak notes, "soft songs" usually being longer than "normal", *etc.* As mentioned previously, a male bunting goes through a fairly ordered sequence of agonistic behaviors in response to song playback. Following an initial attack phase, it adopts the "quiver" and/or "fluff" postures. Displays and call notes are frequent at this stage, but singing almost never occurs. When playback ceases, the bird shifts to the "erect" posture in which the head is stretched high, the crest erected and the body plumage sleeked. The tail is flicked from side to side and the bird gives sharp "chip" alarm notes; but, again, singing is rare. It is not until this point in the temporal sequence of response, as the erect posture ceases, that singing begins. In the majority of cases (76 percent) the first songs are both soft and long. Squeak notes are also most common at this time although they only occurred in 32 percent of the birds tested. As singing continues, the songs increase to normal volume while maintaining their extra length (98 percent of birds). By the end of the recording session, six minutes after the termination of playback, many birds (42 percent) had returned to singing songs of normal volume and normal length. Many birds increased their singing rate (by decreasing the interval between successive songs) and this tendency continued for as much as fifteen minutes post-playback.

The regularity of these changes suggests that they are determined largely

by differences in the motivational state of the individual singer. As a first approximation, I would hypothesize that the graded series of song deliveries is related to the intensity of an escape tendency. Thus singing does not occur in submissive birds ("fluff" posture), soft song appears correlated with a conflict or ambivalent motivational state, long song occurs when the escape tendency is weak, and a heightened singing rate is representative of a heightened attack tendency. Support for this hypothesis would require quantitative probabilities of the occurrence of different types of agonistic behavior following the singing of such modified songs; to date, this type of data has not been obtained.

The implication from this discussion is that those aspects of bunting song that are variable within an individual seem to represent differences in the motivational state of the singer and thus convey information about the probability of occurrence of successive behaviors. The species and individual identification messages remain unchanged. This is in agreement with the findings of FALLS (1969) in White-throated Sparrows.

#### COMPARISON WITH OTHER SPECIES

Although the use of playbacks of experimentally modified songs is a recent tool in the study of information content of avian vocalizations, it is interesting to compare the results of the current study with those obtained from other species. To date four other species have been investigated in sufficient detail to warrant consideration here. These are the Ovenbird, *Seiurus aurocapillus* (WEEDEN & FALLS, 1959; FALLS, 1963), the White-throated Sparrow, *Zonotrichia albicollis* (FALLS, 1963, 1969), the Wood Lark, *Lullula arborea* (TRETZEL, 1965), and the European Robin, *Erithacus rubecula* (BRÉMOND, 1967, 1968b). Taken together, these five species represent four families of passerine birds that reside in a wide variety of habitat types.

Following the example of FALLS (1969), I have extracted the results from these studies and have re-presented them in a common format in Tables 4 through 8. Song parameters have been categorized as "phrase" features (the term phrase replacing figure, note, or motif from the original studies), temporal features, and syntactical, or arrangement, features. The constancy of each such feature in terms of species or individual variation, as well as the experimental conclusions regarding function, is recorded by appropriate pluses and minuses.

With so few species having been studied, it would be premature to hypothesize specific correlations between types of parameters conveying species identification information and specific ecological or behavioral factors. However, it can be seen that in each of the five species, only a fraction of

TABLE 4

*Summary of information on structure and function of Indigo Bunting song*

	Typical of Species	Species Recognition Function	Present in Hand-raised Birds	Stereotyped in Individual	Individual Recognition Function	Variable in Individual	Strength of Motivation Function
Indigo Bunting <i>Passerina cyanea</i>							
<i>"Phrase" Features:</i>							
"quality" (slurred)	+	+	±				
frequency range	+	+	+				
detailed phrase morphology				+	+		
<i>Temporal Features:</i>							
Phrase length	+	+	±				
inter-phrase interval	+	+	±				
song length						+	+
singing rate						+	+
<i>"Syntax" Features:</i>							
phrases paired	+	—	+				
specific pairing sequence				+	?		

the potentially available song features are essential for conspecific recognition.

A more detailed look at Table 5 reveals that the song parameters important for identification in the Ovenbird are remarkably similar to those serving the same function in the Indigo Bunting. Thus FALLS (1963) determined that for an Ovenbird song to elicit a full territorial response from a conspecific male, it had to contain phrases of a characteristic structure repeated according to a specific temporal rhythm. Altering the general structure of the individual phrase (in particular, rearranging the three elements comprising each phrase) or modifying the time intervals between phrases caused a marked reduction in male response. On the other hand, details of phrase structure (particularly the first element within each phrase) and the syntactical arrangement of phrases within the song proved non-essential in this context. This is especially interesting since a constant feature of Ovenbird song is the crescendo arrangement of phrases, each being sung with a volume exceeding its predecessor. As with the Indigo Bunting, field ornithologists

have come to rely upon acoustical identification markers that are different from those used by the birds themselves.

TABLE 5

*Summary of information on structure and function in the song of the Ovenbird, Seiurus aurocapillus. Based on FALLS, 1963*

	Typical of Species	Species Recognition Function	Present in Hand-raised Birds	Stereotyped in Individual	Individual Recognition Function	Variable in Individual	Strength of Motivation Function
Ovenbird							
<i>Seiurus aurocapillus</i>							
"Phrase" Features:							
discrete elements	+	+					
(order & structure)							
detailed element structure				+	?		
frequency range	+	?					
Temporal Features:							
phrase length	+	?	—				
inter-phrase interval	+	+					
phrase length	?	?					
singing rate						+	+
"Syntax" Features:							
element arrangement	+	+					
(within a phrase)							
loudness pattern	+	—					
(crescendo)							

The work of FALLS (1963; 1969) with White-throated Sparrows suggests a completely different set of parameters functioning for species recognition. While temporal patterning remains important (neither note length nor the interval between notes can be modified greatly without producing reduced responses), the dominant factor is the quality of the notes themselves. These must be unvarying pure tones lying within a prescribed frequency range. Varying the pitch or adding harmonics reduces the effectiveness of the artificial song. The presence of notes of two different frequencies

TABLE 6

Summary of information on structure and function of song in the White-throated Sparrow, *Zonotrichia albicollis*. Based on WEEDEN & FALLS, 1959; FALLS 1963, 1969

	Typical of Species	Species Recognition Function	Present in Hand-raised Birds	Stereotyped in Individual	Individual Recognition Function	Variable in Individual	Strength of Motivation Function
White-throated Sparrow <i>Zonotrichia albicollis</i>							
"Note" Features:							
"quality" (long, pure tones)	+	+	+				
frequency range	+	+	+				
absolute frequency				+	+		
Temporal Features:							
note length	±	±	±				
inter-note interval	+	+	+				
song length							
singing rate						+	+
"Syntax" Features:							
frequency change	+	+	+				
details of freq. change				+	+		
triplets	+	—	—				
loudness pattern				+	?		

further enhances the effectiveness of the song although the direction of change of pitch is of little significance. On the basis of additional experiments, BROOKS & FALLS (in FALLS, 1969) suggest that absolute pitch and pattern of pitch change within the song are important in the process of individual recognition.

Studies by THORNEYCROFT (unpublished; cited in FALLS, 1969) demonstrate that song features present in hand-reared, acoustically isolated, sparrows coincide roughly with the features serving a species recognition function.

Not all constant features of White-throated Sparrow song, however, are essential in the identification process. The last notes in the territorial song normally are triplets, consisting of three similar elements spaced closely



together. Yet the triplets can be replaced by a single pure tone with no resulting decrease in effectiveness.

TABLE 7

Summary of information on structure and function of song in the Wood Lark, *Lullula arborea*. Based on TRETZEL, 1965

	Typical of Species	Species Recognition Function	Present in Hand-raised Birds	Stereotyped in Individual	Individual Recognition Function	Variable in Individual	Strength of Motivation Function
Wood Lark <i>Lullula arborea</i>							
“Phrase” (Motif) Features:							
discrete elements	+	+					
(Vorlaut & Hauptlaut)							
“quality” (harmonics)	+	+					
detailed phrase structure						+	?
frequency range	+	+					
Temporal Features:							
phrase length	?	±					
inter-phrase interval	?	—					
song length						+	+
singing rate						+	+
“Syntax” Features:							
repetitive phrases	+	+					
frequency pattern	+	—					
(decrease during song)							
temporal pattern	+	—					
(speed up during song)							

In the Wood Lark, once again, different parameters are functional in giving the song its species specificity. Experiments by TRETZEL (1965) point to phrase structure (each phrase consisting of two discrete elements, a higher pitched “vorlaut” followed by a lower “hauptlaut”) and tonal quality (the presence of characteristic harmonics) as being key song parameters. Although quantitative data are not presented, TRETZEL (*ibid.*) states that the songs of Wood Larks exhibit two characteristic syntactical features: (1) the

pitch of individual phrases decreases throughout the song and (2) the interval between successive phrases decreases. Rearranging the notes of a song to violate these syntactical rules does not cause a decrease in the response of conspecific males.

TABLE 8

Summary of information on structure and function of song in the European Robin, *Erithacus rubecula*. Based on Brémond, 1967, 1968a, 1968b

	Typical of Species	Species Recognition Function	Present in Hand-raised Birds	Stereotyped in Individual	Individual Recognition Function	Variable in Individual	Strength of Motivation Function
European Robin <i>Erithacus rubecula</i>							
“Phrase” (Motif) Features:							
repetitive elements	+	+					
detailed element structure						+	+
frequency range	+	+					
detailed frequencies						+	+
Temporal Features:							
inter-element interval	—	—					
phrase length	+	—					
inter-phrase interval	—	—					
song length						+	+
singing rate						+	+
“Syntax” Features:							
alternation of high and low freq. phrases	+	+					
all phrases different	+	+					

Lastly, BRÉMOND (1967, 1968b) has demonstrated that in the European Robin species recognition is based primarily upon just those features shown to be unimportant in the Wood Lark. In the Robin, the song consists of a series of phrases, or motifs, each constructed from a series of repetitive elements. All phrases within a song are different from one another and they are arranged in an alternating sequence of high and low frequencies. These

syntactical features turn out to be those essential in eliciting aggressive behavior from territorial males. Temporal features are highly variable within populations and appear to play little role in the recognition context.

In keeping with the results from Indigo Buntings and White-throated sparrows, BRÉMOND (1968b) found that song characteristics that were intra-individually variable were related to motivational states and did not convey species identification information.

The results from these different studies are not directly comparable since different playback techniques were involved and different measures of responsiveness employed. Nevertheless, some generalizations do appear. For each of the five species, only a small number of song parameters proved critical for species recognition. These features were always from among the most constant and unvarying in the species repertoire. This high degree of feature extraction implies either that a large number of song parameters function in the conveyance of other (non-identification) messages and/or that a high degree of redundancy of information content is common in passerine vocalizations. The redundancy hypothesis is supported by finding that in each species studied, highly stereotyped song traits occurred that were demonstrated to be *non-essential* for identification by conspecifics.

On the other hand, many other song features, also non-essential for imparting species distinctiveness, were variable in the population or within the repertoire of individuals. These features presumably transmit different messages and, hence, have been shaped by different selective pressures. This is partially consistent with MARLER's (1960) hypothesis of a segregation of information among different components of bird song.

While only a few vocal parameters are essential for the identification of each species, the five species studied yield a fairly complete spectrum of parameter-types fulfilling this function. The harmonic quality of individual phrases in the Wood Lark, the syntactical arrangement of elements within individual phrases in the Ovenbird, the temporal separation of phrases in the Indigo Bunting, and the order of arrangement of different phrases in the European Robin—each conveys species identity to other males. One would like to be able to predict, on the basis of ecological and behavioral information, the physical structure of the acoustical cues that would function optimally in this regard. This is not possible at present, but several considerations deserve mention.

Many different messages are conveyed by bird song. The great majority of these are meaningful only to individuals of the same species as the singer. Consequently, unless a song is identifiable as belonging to a conspecific, the additional messages may be without meaning. This implies that song para-

meters utilized for species recognition should be among those most clearly distinguishable from the background sound environment, even at distances at the extreme edge of audibility. The distances involved are dictated largely by the population dispersion pattern and social organization of the animal in question. Thus a species that is widely spaced yet maintains auditory contact with neighbors might be expected to employ low frequency sounds since the rate of attenuation is much lower than at higher frequencies. The need for accurate localizability also will influence the structure of the vocalizations as discussed at length by MARLER (1957). Alternatively, a highly gregarious species that maintains close contact with fellow flock-members would have fewer restrictions placed on its vocal repertoire. The need for long-distance contact and localizability are reduced, and many communicative functions can be served best by visual signals. In Estrildine finches, for example, IMMELMANN (1968) reports that acoustical cues are of minor importance in species recognition and most vocalizations are soft, high in frequency and rich in harmonics, a feature that would only be functional over short distances since the different frequencies would attenuate at different rates (KONISHI, 1970).

The vegetative structure of the birds' environment also must be of extreme importance in the evolution of acoustical signals. Although this area of investigation has received little attention, it is probable that the need for maximum penetratability has had a strong selective influence on vocalizations. The density and the size of the vegetative obstacles should affect both the intensity and the frequency of the signals. In keeping with this, the FICKENS (1962) report that warblers (family Parulidae) that forage in the tops of trees have higher pitched songs than do related species that forage on the forest floor. They interpret these findings in terms of greater possible sound reflection and absorption of short wave-length sounds from the denser vegetation near the forest floor.

As more studies of this nature are conducted, more detailed predictions should emerge. Certain song parameters may prove optimal for long distance penetration through conifer forests, other parameters for the crowns of deciduous trees, *etc.* Among species that reside in areas of deciduous forest, it is even conceivable that those species that establish territories before the leaves have emerged will have evolved signals with a different structure than species that commence breeding activities at a later date.

A third factor to be considered in the evolution of acoustical recognition parameters is the nature of the sound environment itself. The existence of sympatric species with similar vocal signals will influence the details of song structure as well as the level of complexity necessary to achieve specific

distinctiveness. This has been discussed in detail by MARLER (1960) and his co-workers.

Song structure obviously represents a weighted compromise between numerous selective forces. The possibility of using ecological and behavioral information to predict not only the types of information conveyed in bird vocalizations but also the parameters involved in this conveyance represents an exciting challenge for future investigations.

The need for additional, comparative studies in this area is obvious. Such investigations not only could provide us with information on acoustical signals *per se* but might form a much-needed link between the ethologist in the field and the neurophysiologist in the laboratory. The determination of the types of acoustical cues used by the birds themselves might suggest optimal types of stimuli to be employed in neurological decoding experiments. Such combined efforts should lead to an increased understanding of the general processes of acoustical stimulus filtering.

#### SUMMARY

During the summers of 1967 1968 and 1969, I studied the acoustical communication system of the Indigo Bunting (*Passerina cyanea*) by means of playback experiments. Attention was directed to deciphering those properties of territorial song used in species identification.

I tested the importance of different song parameters by exposing birds to recordings of normal and artificially modified vocalizations. The level of agonistic response exhibited by male territory holders was used as a bioassay of the effectiveness of the experimental song in allowing species recognition. The results indicate the following:

- 1) Syntactical features of song (the arrangement or order of notes (= figures) within the song) are not essential recognition cues.
- 2) Altering the rhythmic cadence of the song by lengthening or shortening the intervals between successive notes causes a marked reduction in male responsiveness.
- 3) The structure or morphology of the individual notes is also important in song identification. I hypothesize that notes must have a particular acoustical quality characterized by their covering a wide frequency range (mean = 4 kHz) in a short time interval (mean length = 0.18 seconds) and by their containing abrupt changes and reversals of pitch. A wide diversity of bunting note-types fit this description, and differences in details of their fine structure probably provide the variability necessary for permitting individual identification.
- 4) Only a small number of the acoustical cues potentially available are critical for species recognition. This high degree of feature extraction suggests that a) considerable redundancy is present in bunting song and, b) a large number of song parameters function in the conveyance of other (non-identification) messages.

When these results are compared with data from other species of passerines (the Ovenbird, *Seiurus aurocapillus*, White-throated Sparrow, *Zonotrichia albicollis*, Wood Lark, *Lullula arborea*, and European Robin, *Erithacus rubecula*) several generalizations emerge:

- 1) In all five species, recognition depends upon song features that are among the most constant and unvarying in the species repertoire.

2) Song characteristics that are constant in the repertoire of an individual bird but variable within a population are unimportant in species identification but often function in allowing recognition of specific individuals.

3) Those aspects of territorial song that are variable within an individual's repertoire often convey information about the motivational state of the singer.

While only a few vocal parameters are essential for identification in each of these species, the parameters serving this function cover the entire spectrum of morphological, temporal and syntactical features. One would like to be able to predict optimal physical structures for acoustical signals that convey recognition information. At present, too few studies have been conducted to make this possible. However, several speculations are advanced concerning the importance of behavioral and ecological factors such as population dispersion pattern, social organization, habitat structure, and the background sound environment.

## REFERENCES

- BEER, C. G. (1969). Laughing gull chicks: Recognition of their parents' voices. — *Science* 166, p. 1030-1032.
- BORROR, D. J. (1961). Songs of finches (Fringillidae) of eastern North America. — *Ohio J. Science* 61, p. 161-174.
- BRÉMOND, J.-C. (1967). Reconnaissance de schémas reactogènes liés à l'information contenue dans le chant territorial du Rouge-gorge (*Erithacus rubecula*). — *Proc. XIV Internatl. Ornithol. Congress, Oxford*, p. 217-229.
- (1968a). Valeur spécifique de la syntaxe dans le signal de défense territoriale du Troglodyte (*Troglodytes troglodytes*). — *Behaviour* 30, p. 66-75.
- (1968b). Recherches sur la sémantique et les éléments vecteurs d'information dans les signaux acoustiques du Rouge-gorge (*Erithacus rubecula*). — *La Terre et la Vie* 2, p. 109-220.
- DILGER, W. C. (1956). Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. — *Auk* 73, p. 313-353.
- EMLÉN, S. T. (1971). The role of song in individual recognition in the Indigo Bunting. — *Zschr. Tierpsychol.* 28, p. 241-246.
- EVANS, R. M. (1970). Parental recognition and the "mew call in Black-billed Gulls (*Larus bulleri*). — *Auk* 87, p. 503-513.
- FALLS, J. B. (1963). Properties of bird song eliciting responses from territorial males. — *Proc. XIII Internatl. Ornithol. Congress*, p. 259-271.
- (1969). Functions of territorial song in the White-throated Sparrow. — In: HINDE, R. A. (Ed), *Bird Vocalizations*, Cambridge University Press, p. 207-232.
- FICKEN, M. S. & FICKEN, R. W. (1962). The comparative ethology of the wood warblers: a review. — *The Living Bird* (Cornell Laboratory of Ornithology) 1, p. 103-122.
- GILL, F. B. & LANYON, W. E. (1964). Experiments on species discrimination in Blue-winged Warblers. — *Auk* 81, p. 53-64.
- HUTCHINSON, R. E., STEVENSON, J. G. & THORPE, W. H. (1968). The basis for individual recognition by voice in the Sandwich Tern (*Sterna sandvicensis*). — *Behaviour* 32, p. 150-157.
- IMMELMANN, K. (1968). Zur biologischen Bedeutung des Estrildidengesanges — *J. Ornithologie* 109, p. 284-299.
- KONISHI, M. (1965). The role of auditory feedback in the control of vocalization in the White-crowned Sparrow. — *Zschr. Tierpsychol.* 22, p. 770-783.
- (1970). Evolution of design features in the coding of species-specificity. — *American Zool.* 10, p. 67-72.
- LANYON, W. E. (1963). Experiments on species discrimination in *Myiarchus* Flycatchers. — *Amer. Museum Novitates* 2126, p. 1-16.

- MARLER, P. (1957). Specific distinctiveness in the communication signals of birds. — Behaviour 11, p. 13-39.
- (1960). Bird songs and mate selection. — In: LANYON, W. E. & TAVOLGA, W. (Eds), Animal Sounds and Communication. A.I.B.S. Washington, D. C., p. 348-367.
- MUNDINGER, P. C. (1970). Vocal imitation and individual recognition in finch calls. — Science 168, p. 480-482.
- RICE, J. O. & THOMPSON, W. L. (1968). Song development in the Indigo Bunting. — Animal Behaviour 16, p. 462-469.
- SHIOVITZ, K. A. & THOMPSON, W. L. (1970). Geographic variation in song composition of the Indigo Bunting, *Passerina cyanea*. — Animal Behaviour 18, p. 151-158.
- SIBLEY, C. G. (1954). Hybridization in the Red-eyed Towhees of Mexico. — Evolution 8, p. 252-290.
- & SHORT JR., L. L. (1959). Hybridization in the buntings (*Passerina*) of the Great Plains. — Auk 76, p. 443-463.
- SIEGEL, S. (1956). — Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York, 312 p.
- STEIN, R. C. (1963). Isolating mechanisms between populations of Traill's Flycatchers. — Proc. Amer. Philosophical Soc. 107, p. 21-50.
- STEVENSON, J. G., HUTCHISON, R. E., HUTCHISON, J. B., BERTRAM, B. C. R. & THORPE, W. H. (1970). Individual recognition by auditory cues in the Common Tern (*Sterna hirundo*). — Nature 226, p. 562-563.
- THOMPSON, W. L. (1968). The songs of five species of *Passerina*. — Behaviour 31, p. 261-287.
- (1969). Song recognition by territorial male buntings (*Passerina*). — Animal Behaviour 17, p. 658-663.
- (1970). Song variation in a population of Indigo Buntings. — Auk 87, p. 58-71.
- TINBERGEN, N. (1960). — The Herring Gull's World. Basic Books, New York, 255 p.
- TRETZEL, E. (1965). Artkennzeichnende und reaktionsauslösende Komponenten im Gesang der Heideleerche (*Lullula arborea*). — Verhandlungen Deutsch. Zool. Ges. in Jena, 1965, p. 367-380.
- TSCHANZ, B. (1968). Trottellumen. Die Entstehung der persönlichen Beziehung zwischen Jungvögeln und Eltern. — Zschr. Tierpsychol., Beiheft 4, p. 1-103.
- WEEDEN, J. S. & FALLS, J. B. (1959). Differential responses of male ovenbirds to recorded songs of neighboring and more distant individuals. — Auk 76, p. 343-351.

## ZUSAMMENFASSUNG

In den Sommern von 1967, 1968 und 1969 untersuchte ich die Lautverständigung der Indigo-Ammer (*Passerina cyanea*). Mit Hilfe von Tonbandaufnahmen, die den Tieren vorgespielt wurden, untersuchte ich vor allem jene Bestandteile des Reviergesangs, die das Erkennen der eigenen Art ermöglichen.

Hierzu spielte ich den Tieren nicht nur normale Gesänge vor, sondern auch künstlich abgeänderte. Der Grad kämpferischer Aktivität, den die dargebotenen Gesänge bei revierbesitzenden Männchen auslösten, diente als „natürlicher“ Maßstab dafür, wie „artgemäß“ sie jeweils wirkten. Die Ergebnisse waren:

1. Die „Syntax“ des Gesanges (Zusammensetzung und Reihenfolge der Töne = Themen) ist für die Arterkennung unwesentlich.
2. Ändert man den Gesangsrhythmus, indem man die Intervalle zwischen einzelnen Tönen verlängert oder kürzt, so reagieren die Männchen deutlich schwächer.
3. Die Tonstruktur der Einzeltöne ist für die Arterkennung ebenfalls wichtig. Ich kam zu der Annahme, daß die Töne eine eigenartige Klangqualität besitzen müssen, indem sie (a) einen weiten Frequenzbereich enthalten (im Mittel 4 kHz) und nur



sehr kurze Dauer haben (durchschnittlich nur 0,18 sec.); außerdem ändern sie sich abrupt in der Tonhöhe, oft von einem Extrem zum anderen. Selbst verschiedenste, von den Ammern produzierte Töne entsprechen dieser Beschreibung. Die feineren Unterschiede der Tonstruktur liefern wahrscheinlich dabei jenes Ausmaß an Variabilität, welches den Tieren ermöglicht, sich individuell zu erkennen.

4. Nur eine kleine Zahl von allen vorhandenen Gesangsmerkmalen sind für die Artenkennung wesentlich. Dies bedeutet (a) daß der Ammer-Gesang erhebliche Redundanz enthält und (b) viele Merkmale anderen Informationszwecken als dem der Artenkennung dienen.

Wenn man diese Ergebnisse mit dem vergleicht, was von anderen Singvogelarten bekannt ist (z.B. Töpfervogel *Seiurus aurocapillus*, Weißkehlsperring *Zonotrichia albicollis*, Baumlerche *Lullula arborea* und Rotkehlchen *Erithacus rubecula*), ergeben sich einige Gemeinsamkeiten:

1. Bei allen 5 Arten hängt das Erkennen der eigenen Art von solchen Gesangsmerkmalen ab, die regelmäßig im Repertoire aller Individuen vorkommen und geringste Schwankungsbreiten aufweisen.
2. Gesangselemente, die geringe individuelle bei größerer inter-individueller Variabilität aufweisen, dienen weniger dem Art-, oft jedoch dem Individualerkennen.
3. Anteile des Reviergesangs, welche das Einzeltier in unterschiedlichen Abwandlungen ausführt, lassen die jeweilige Stimmungslage des Sängers erkennen.

Obwohl bei jeder Art nur einige wenige Lautmerkmale für das Erkennen der eigenen Art wesentlich sind, können alle nur möglichen Merkmale von Gestalt (Melodie), Zeitmaß und Zuordnung im Dienst dieser Funktion stehen. Es wäre schön, wenn man die optimale Struktur akustischer Signale, die das Erkennen vermitteln, vorhersagen könnte. Gegenwärtig jedoch haben wir dafür zu wenige, gute Untersuchungen.

Immerhin sind aber einige Vermutungen möglich hinsichtlich der Einflüsse von Verhaltenseigentümlichkeiten und ökologischen Bedingungen wie Verteilung der Individuen innerhalb der Population, Sozialstruktur, Art des Lebensraumes und allgemeiner Geräusch-hintergrund im Wohngebiet.

## APPENDIX 1

Agonistic responses of territorial male buntings to playback of songs of Indigo Buntings and Yellow Warblers). (See Figures 3a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Indigo Bunting	Yellow Warbler	Indigo Bunting	Yellow Warbler
1	7	0	13	1
2	6	0	13	0
3	6	0	13	0
4	7	0	14	0
5	7	0	15	0
6	4	0	9	0
7	7	0	12	0
8	6	0	16	0
9	7	0	14	0

Significance

by Wilcoxon

Signed Rank Test

$p < .005$

$p < .005$



## APPENDIX 2

Agonistic responses to playback of songs of Indigo and Lazuli Buntings.  
(See Figures 4a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Indigo Bunting	Lazuli Bunting	Indigo Bunting	Lazuli Bunting
1	5	0	11	0
2	7	0	13	0
3	6	0	9	0
4	6	0	12	0
5	4	0	9	0
6	7	0	13	0
7	6	0	9	0
8	6	0	14	0

Significance

by Wilcoxon

Signed Rank Test

$p = .005$

$p = .005$

## APPENDIX 3

Agonistic responses of buntings to playback of normal and experimentally modified (non-pair) song. (See Figures 7a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Control	Non-Pair	Control	Non-Pair
1	7	7	15	15
2	6	6	11	11
3	7	7	14	15
4	6	4	7	9
5	5	6	9	12
6	6	7	10	10
7	6	6	14	15
8	7	7	12	13
9	7	7	15	14

Significance

by Wilcoxon

Signed Rank Test

Sample size insufficient  
for statistical analysis  
(due to "ties").

$p > .1$

## APPENDIX 4

Agonistic response to playback of normal and experimentally modified  
(figures rearranged into a "random" sequence) songs. (See Figures 8a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	"Random" Sequence	Normal	"Random" Sequence
1	6	6	12	12
2	7	6	13	14
3	5	5	10	11
4	7	7	15	15
5	7	6	15	14
6	6	7	12	16

Significance by

Wilcoxon Signed-Rank Test

Sample sizes insufficient for  
statistical analysis (due to "ties").

## APPENDIX 5

Agonistic responses to playback of a normal bunting song (shown in Figure 1) and an artificial song constructed from "building blocks" A and B.

(See Figures 9 and 10a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	A B A B A B A B	Normal	A B A B A B A B
1	5	3	8	7
2	7	5	15	8
3	7	7	15	7
4	7	6	10	9
5	6	7	11	13

Sample size insufficient for statistical analysis.

## APPENDIX 6

Agonistic responses to playback of normal and temporally altered songs.

(See Figures 11 and 12a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	Tx 1/2	Normal	Tx 1/2
1	7	5	14	9
2	—	6	—	8
3	5	4	10	6
4	7	6	11	8
5	—	2	—	6
6	7	6	15	8
7	6	3	7	4
8	6	1	7	3
9	7	2	13	3
10	6	6	10	7
11	6	5	8	7

Significance

by Wilcoxon

Signed Rank Test

$p < .005$

$p < .005$

## APPENDIX 6

Continued

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	Tx 2	Normal	Tx 2
1	—	3	—	5
2	6	4	10	5
3	6	4	11	8
4	4	1	11	3
5	7	6	16	12
6	7	4	14	7
7	7	6	12	6
8	7	2	16	3
9	6	5	11	2

Significance

by Wilcoxon

Signed Rank Test

$p .005$

$p .005$

## APPENDIX 6

Continued

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	Tx 4	Normal	Tx 4
1	—	4	—	8
2	6	6	12	7
3	4	0	13	0
4	7	4	12	7
5	7	6	16	10
6	—	6	—	11
7	4	2	8	5
8	7	7	15	10
9	7	4	9	5
10	6	6	16	7
11	7	4	14	6
12	6	1	11	2
13	6	1	15	1
14	7	3	13	7

Significance

by Wilcoxon

Signed Rank Test

 $p < .005$  $p < .005$ 

## APPENDIX 7

Agonistic responses to playback of normal and "backward" bunting songs.  
(See Figures 13 and 14a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	"Backward"	Normal	"Backward"
1	7	7	14	16
2	7	7	14	16
3	7	6	14	11
4	6	7	11	14
5	7	7	12	13
6	6	5	8	8
7	4	7	6	9
8	6	4	15	13
9	7	7	12	9

Significance

by Wilcoxon

Signed Rank Test

Sample size insufficient  
for statistical analysis  
(due to "ties").

 $p > .1$ 

## APPENDIX 8

Agonistic responses to playback of a normal bunting song and an artificial song  
constructed from "building block". A. (See Figures 9 and 15a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	A A A A A A A A	Normal	A A A A A A A A
1	5	0	9	0
2	7	2	12	3
3	6	0	12	0
4	6	0	9	0
5	6	0	9	0
6	7	1	16	1

Significance

by Wilcoxon

Signed Rank Test

 $p = .025$  $p = .025$

## APPENDIX 9

Agonistic responses to playback of a normal bunting song and an artificial song constructed from "building block" B.  
(See Figures 9 and 16a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	B B B B B B B B	Normal	B B B B B B B B
1	—	2	—	3
2	6	6	7	13
3	6	6	11	10
4	7	3	15	5
5	6	0	12	0
6	—	6	—	12
7	7	4	11	10

Sample size insufficient for statistical analysis.

## APPENDIX 10

Agonistic responses to playback of a normal bunting song and an artificial song constructed from "building block" C. (See Figures 9 and 17a and b.)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	C C C C C C C C	Normal	C C C C C C C C
1	5	2	11	7
2	7	6	15	7
3	7	5	16	14
4	6	5	14	11
5	4	0	9	0
6	—	5	—	10
7	7	3	15	4

Significance by Wilcoxon

Signed Rank Test  $p = .025$

$p = .025$

## APPENDIX 11

Agonistic responses to playback of a normal Indigo Bunting song and a modified Lazuli song (in which the inter-figure intervals were lengthened by a factor of 2).  
(See Figures 18a and b)

Bird	0-7 Intensity Scale		0-16 "Hybrid-Index" Scale	
	Normal	Lazuli $\times 2$	Normal	Lazuli $\times 2$
1	12	0	6	0
2	13	0	6	0
3	7	0	6	0
4	15	0	7	0
5	10	0	6	0

Sample size insufficient for statistical analysis.