SONG VARIATION IN A POPULATION OF INDIGO BUNTINGS[1]

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In a previous paper (Thompson, 1968) I described the general characteristics of the songs of several species of the genus *Passerina*. For a fuller understanding of a behavioral characteristic, just as in the case of a morphological feature, it is important to study the kind and amount of variation within a single population and, especially for behavior, within a single individual. This paper describes the song characteristics of the members of a single population of Indigo Buntings, *Passerina cyanea*. A paper now in preparation will describe song variation in individual Indigo Buntings.

Male Indigo Buntings sing three rather distinct types of song: advertising song (in the sense of Borror, 1961), a squeaky song in intensive territorial defense, and flight song. This paper deals only with advertising song. A typical Indigo Bunting advertising song is composed of a series of sounds, or song figures. The song in Figure 5A, for example, includes eight song figures of five different types. I define the term song figure (Thompson, 1968) as a sound or sounds that produce a single, complete, and distinct impression to the human ear and form a distinct unit of a song. A song figure may be composed of one or more continuous sounds or syllables. Each male Indigo Bunting usually sings a regular sequence of several different figures. Figures may occur singly in the song, or they may be repeated. In a typical advertising song repeated figures occur together. The fixed sequence of figures sung by each male is called a song pattern.

Methods

The population of Indigo Buntings on which this study is based lived in an area of roughly 3 square miles on and near the Edwin S. George Reserve near Pinckney, Michigan. The George Reserve itself covers an area of 2 square miles; additional areas just outside the reserve add approximately 1 square mile.

I tried to record a series of songs of every bird on the study area during June, July, and August of 1965 and June and July of 1967. As may be seen in Figures 6 and 7 I was not completely successful in either year, but the recording census of 1967, to my knowledge, was complete except for one singing male. All singing male Indigo Buntings were plotted on a map of the area. In 1965 the work was carried out in conjunction with other studies of bunting behavior and ecology and the territorial boundaries and movements of the individual birds were investigated thoroughly. Some of the birds in 1965 were color banded. The separate identities of neighboring males having the same song pattern were established by recording their songs when both were singing simultaneously on their own territories.

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All recordings were made with a Uher Report S tape recorder at 7½ inches per second. During 1965 at least 20 consecutive songs were recorded whenever possible, and some individuals were recorded on several different days. Because most Indigo Buntings sing one song pattern all day, day after day (Thompson, 1968), I recorded only 10 songs of each bird in 1967. Some buntings sing two slightly different song patterns, but usually alternately, so that a series of 10 songs will include both patterns.

Sound spectrograms were made of the longest song using a Kay Electric Company Sona-Graph, model 661-B at the high shape and wide band settings. Comparing the spectrograms of all the songs revealed that certain figures occurred in the songs of several individuals. Each distinguishable figure was traced in outline, transferred to drawing paper, and inked. This method has several advantages over using the original spectrograms (Thielcke, 1967). These distinguishable figures were then grouped according to similarity of shape to form a catalog of all the kinds of sounds produced in the songs of the Indigo Buntings in the George Reserve population.

Some figures show considerable variation within the population. The decision whether to call the variants one form or more than one is made according to the ease of assigning them consistently to one figure type or another. Some rather diverse, although clearly related figures are connected within the population by a series of intermediates that grade almost imperceptibly from one extreme form to another (Figure 3). This entire series is called a single figure type because of the arbitrariness of assigning the intermediate types to one end or the other. Figures that are similar, but that show consistently different form, are given different catalog numbers.

Results

Figures 1 and 2 illustrate the catalog of figures from the songs of the Indigo Buntings of the George Reserve in 1965 and 1967. I considered 98 different figures distinctive enough to be called separate. Figure 3 shows the variation in form of several figures as sung by different individuals. Table 1 presents the frequency of each figure type in the George Reserve Indigo Bunting populations of 1965 and 1967. The abundance of particular figures in the population varies considerably from year to year. Of the 98 figure types recorded in the two years 56 were recorded in both years, 22 were present only in 1967, and 20 only in 1965. The mean number of kinds of figures included in the songs of individual males in 1965 was 7.0, and in 1967, 5.6. For the 2 years combined the mean is 6.3 different figures per individual.

Figure 4 indicates the amount of sharing of various song figures from bird to bird in 1965 and 1967 combined. Some figures are widely distributed throughout the population, but most are present in only a few individuals. The modal number of individuals in whose songs a given figure type occurs is 4. The mean number of songs containing a given figure is 5.96.

Each male Indigo Bunting sings a characteristic sequence of song figures to make up a complete song pattern. The songs of many birds had figures in common, but they either contained some different figures or placed the shared figures in a different sequence, and so I did not consider the

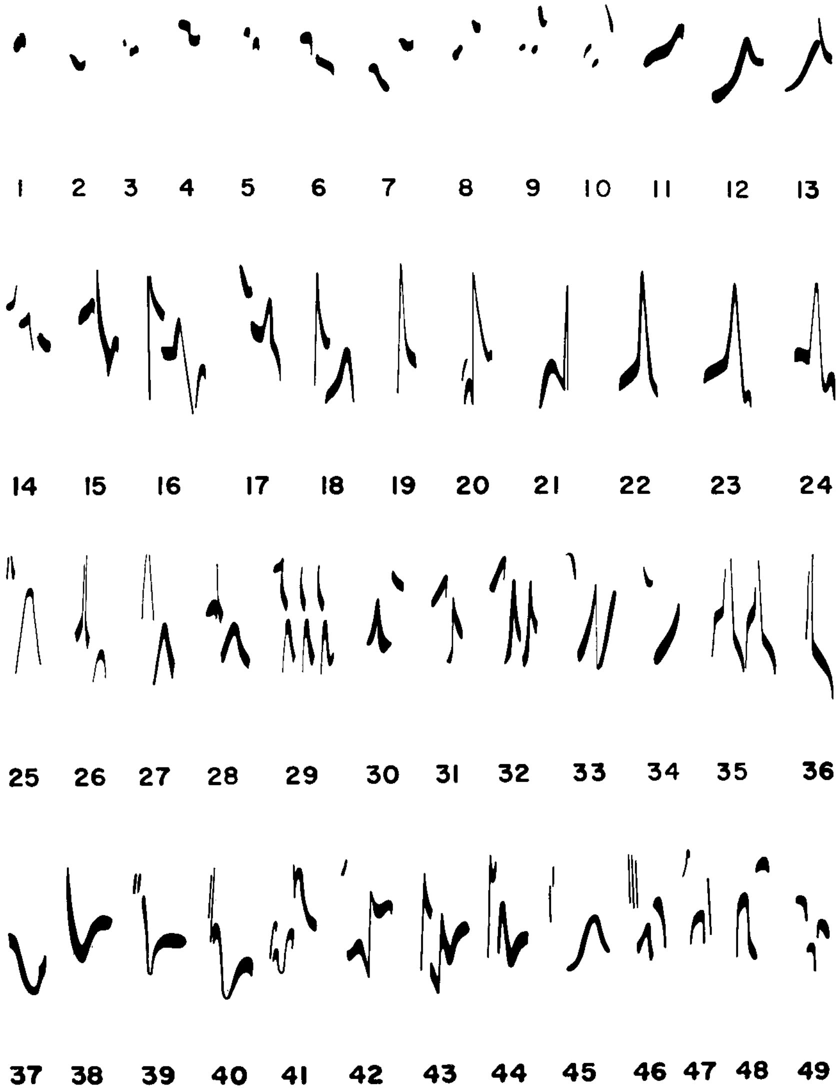

Figure 1. Song figures 1 through 49 of the Indigo Buntings of the George Reserve, Pinckney, Michigan, in 1965 and 1967.

song patterns to be the same. A few birds sang identical figures in the same sequence, and I considered them to have identical song patterns. In some instances one individual sang only the first part of the pattern of another bird, but those figures that were sung were identical in form and sequence to those of the second individual. Two song patterns of

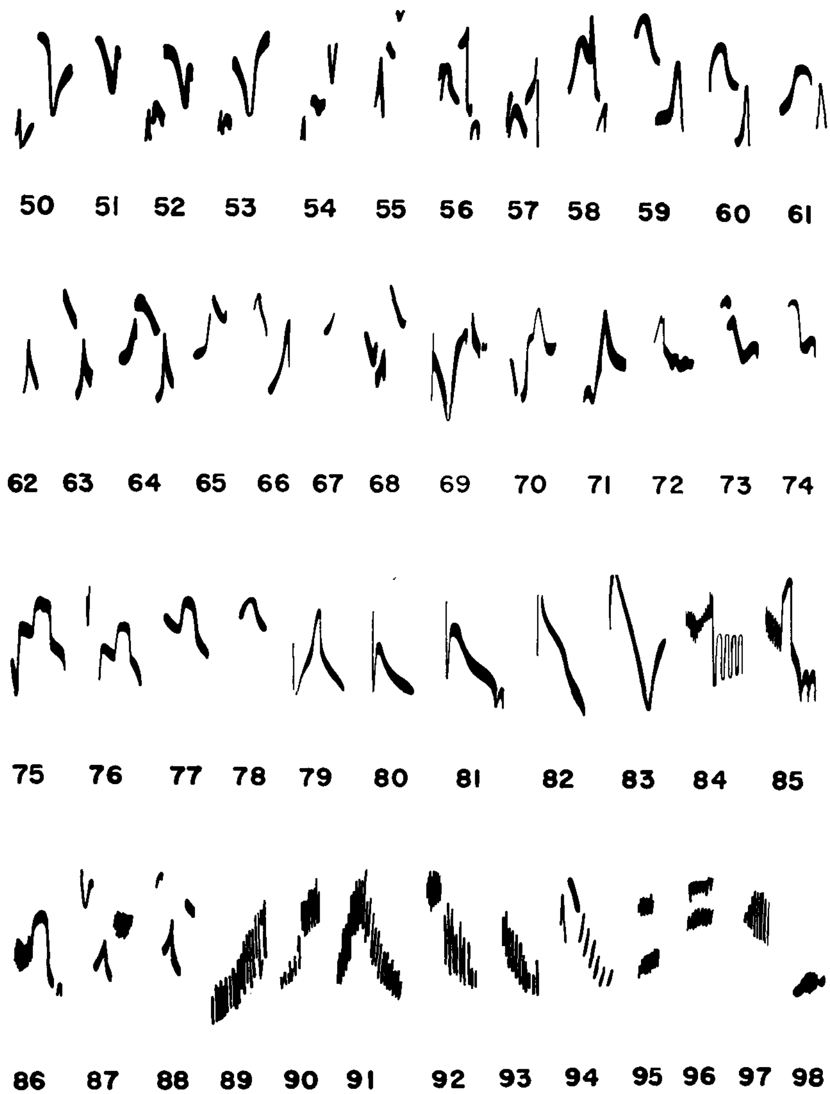

Figure 2. Song figures 50 through 98 of the Indigo Buntings of the George Reserve, Pinckney, Michigan, in 1965 and 1967.

this sort were considered to be the same for the purposes of this analysis. Figure 5 illustrates two such pairs of identical songs sung by neighboring males. Songs A and B were sung by one pair of neighbors, and songs C and D by another pair some distance away. Figure 6 illustrates the spatial distribution of song patterns in 1965.

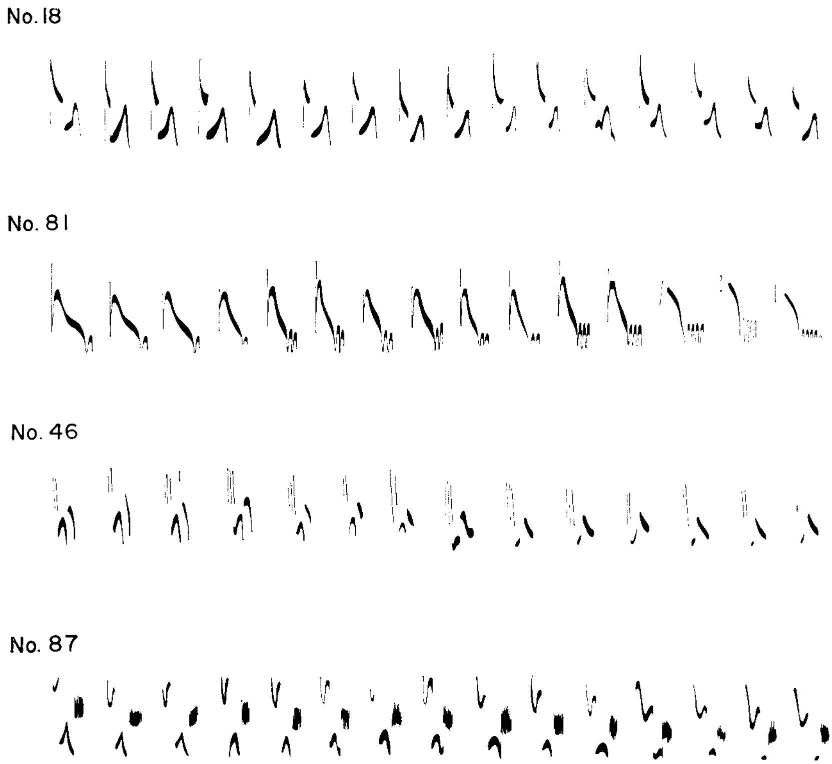

Figure 3. Examples of variation in form of figures sung by different individuals in the population.

In 1965 five pairs of adjacent males (23.8 per cent of the 21 adjacent males whose songs were recorded) sang identical song patterns according to the criteria set forth above. In addition to these adjacent pairs of males, some other birds whose territories were not contiguous sang identical song patterns. The 38 males whose songs were recorded used 25 distinct song patterns. The songs of 23 additional males were not recorded, giving a total of 61 singing males on the study area.

Of the 46 territorial males present on the study area in 1967 the songs of 45 were recorded. Of 31 adjacent pairs of males 7 (22.6 per cent) had identical songs. Figure 7 plots the spatial distribution of song patterns in 1967. Song patterns that were sung by more than one individual in a given year or that persisted from 1965 through 1967 are designated by different patterns, labeled A through I for the 2 years.

Identical song patterns in a given year tend to be clumped. Pattern A of 1965, for example, is sung by two pairs of adjacent males, as well as

TABLE 1

FREQUENCY OF SONG FIGURES IN 1965 AND 1967

Figure no.	1965	1967	1965 and 1967	Figure no.	1965	1967	1965 and 1967
1	31	20	51	50	7	3	10
2	0	3	3	51	1	1	2
3	0	1	1	52	8	3	11
4	2	9	11	53	0	3	3
5	0	1	1	54	4	0	4
6	0	1	1	55	2	1	3
7	0	1	1	56	6	5	11
8	2	1	3	57	1	1	2
9	0	2	2	58	7	2	9
10	0	1	1	59	2	6	8
11	2	0	2	60	3	3	6
12	1	3	4	61	1	1	2
13	0	1	1	62	1	0	1
14	0	1	1	63	6	2	8
15	12	3	15	64	9	2	11
16	2	0	2	65	1	2	3
17	5	3	8	66	0	1	1
18	8	13	21	67	0	1	1
19	1	1	2	68	3	0	3
20	5	2	7	69	2	0	2
21	3	1	4	70	1	0	1
22	6	1	7	71	2	0	2
23	2	2	4	72	1	0	1
24	8	3	11	73	1	0	1
25	6	3	9	74	0	1	1
26	0	3	3	75	4	2	6
27	6	2	8	76	6	3	9
28	6	0	6	77	4	5	9
29	2	1	3	78	0	1	1
30	2	0	2	79	0	8	8
31	0	4	4	80	1	1	2
32	6	3	9	81	13	7	20
33	2	3	5	82	2	0	2
34	1	1	2	83	5	2	7
35	4	5	9	84	5	5	10
36	10	6	16	85	8	5	13
37	1	1	2	86	0	1	1
38	3	0	3	87	9	11	20
39	4	0	4	88	0	1	1
40	7	10	17	89	2	2	4
41	4	3	7	90	0	1	1
42	2	2	4	91	7	8	15
43	5	7	12	92	6	3	9
44	6	0	6	93	1	0	1
45	3	3	6	94	3	2	5
46	7	6	13	95	3	0	3
47	4	3	7	96	0	1	1
48	1	0	1	97	1	2	3
49	0	1	1	98	3	0	3

by three other males. This pattern is confined to one side of the study area. Other song patterns in both years tend to be limited to one small segment of the George Reserve. An exception is song pattern B, sung by birds with territories on opposite sides of the study area in 1965. Those

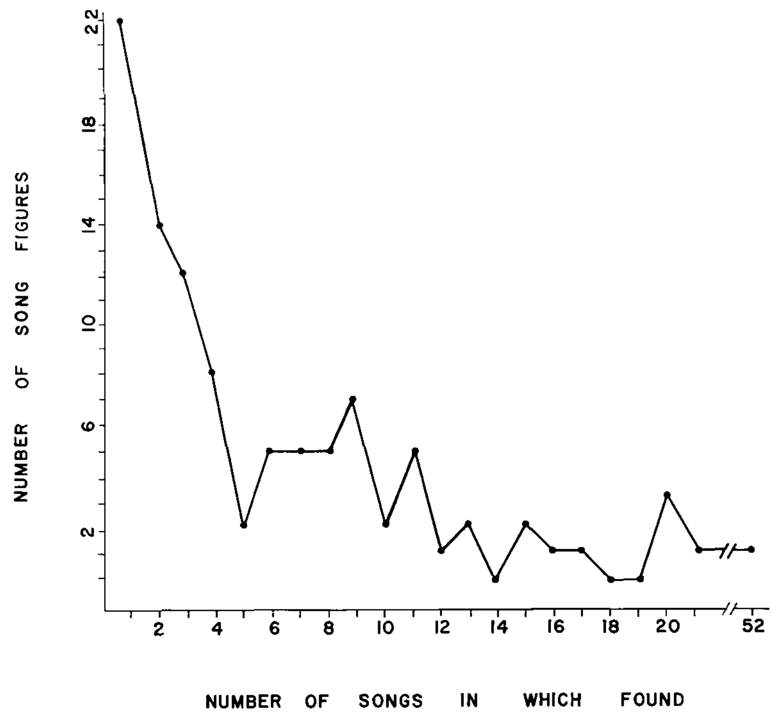

Figure 4. Frequency of occurrence of song figures in the Indigo Bunting populations of 1965 and 1967.

1965 patterns that persisted into 1967, A, C, D, and E, occurred in the same parts of the study area both years. No song patterns from 1965, aside from these patterns sung by more than one bird in that year, survived intact into 1967.

DISCUSSION

Few bird species whose songs are composed of a variety of figure types show so extensive an overlap in song figures from one individual to another within a single population as does the Indigo Bunting. Lemon (1965), who describes song figure overlap of this sort in a population of Cardinals (*Richmondena cardinalis*) in southern Ontario, found a much smaller number of figure types from individual to individual. Most Cardinals in the population sang all the figure types; each Cardinal also sang several different song patterns.

Some species of birds such as the Carolina Wren, *Thryothorus ludovicianus* (Borror, 1956), Ovenbird, *Seiurus aurocapillus* (Weeden and Falls, 1959), and Yellowthroat, *Geothlypis trichas* (Borror, 1967) differ

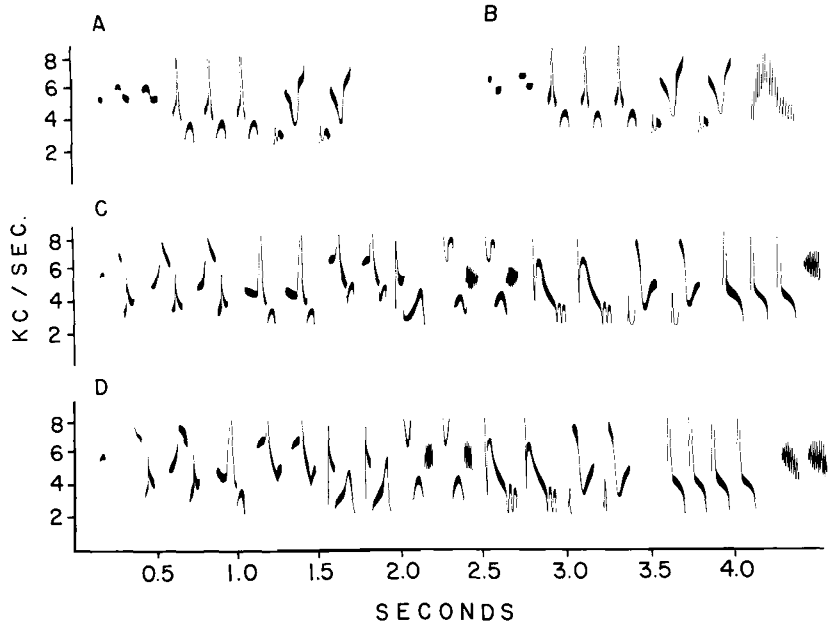

Figure 5. Two pairs of identical song patterns sung by neighboring males.

from individual to individual in the form of the figures that comprise the song. In the Chipping Sparrow, *Spizella passerina* (Marler and Isaac, 1960a; Borror, 1966), Oregon Junco, *Junco oreganus* (Konishi, 1964), and Brown Towhee, *Pipilo fuscus* (Marler and Isaac, 1960b), different individuals may sing different figure types, but a given song usually consists of a series of repetitions of a single figure type. Individual Oregon Juncos and Brown Towhees possess several distinct song types, each consisting of repetition of a different figure type. The Song Sparrow, *Melospiza melodia* (Nice, 1937; Borror, 1961, 1965; Mulligan, 1963), includes several figure types in each song pattern, and, further, has a variety of song patterns. Although some neighboring individuals may share song patterns, most birds in a given population sing distinctive song patterns. At the other extreme Marler and Tamura (1964) describe song variation in several populations of White-crowned Sparrows, *Zonotrichia albicollis*. In this species each male in a given population sings a song pattern composed of several different figure types, but a pattern that is almost identical to the song patterns sung by all the other males in the population.

The number and spatial distribution of identical song patterns on the George Reserve could provide some insight into the time of learning the song pattern that a male Indigo Bunting retains throughout his life. Pre-

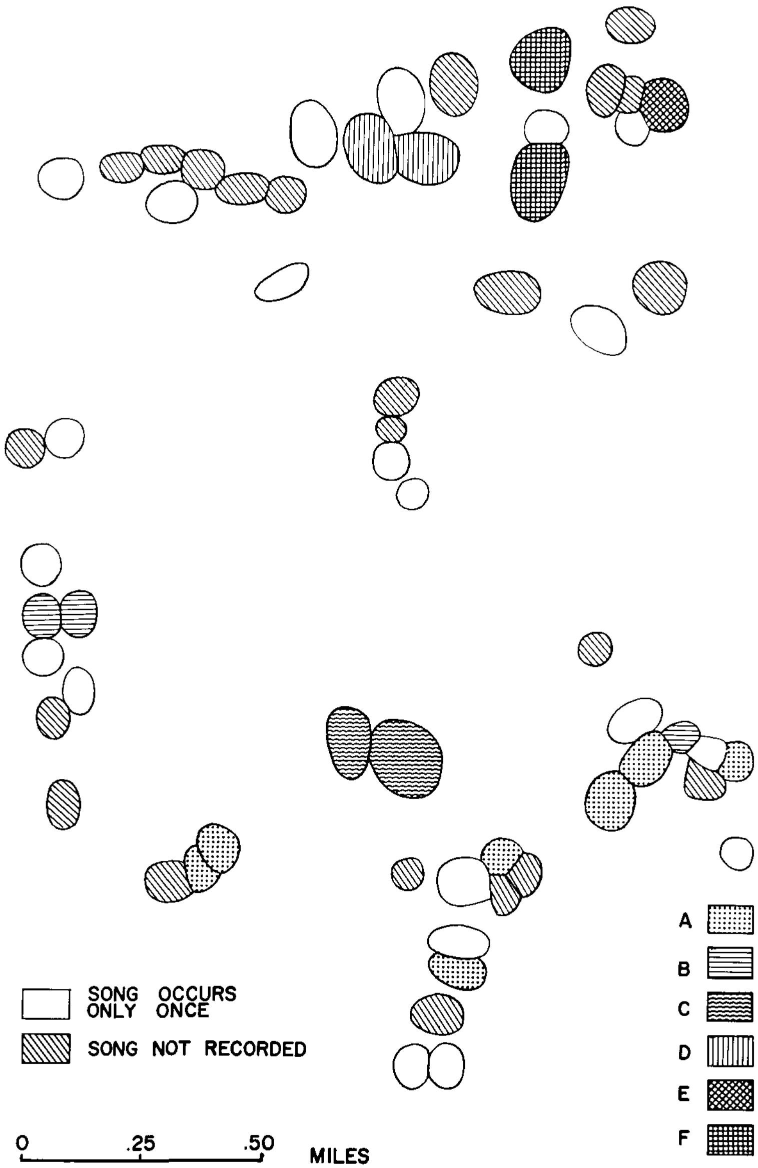

Figure 6. The spatial distribution of song patterns in 1965. Patterns A through F represent different song patterns that were sung by more than one individual in 1965 or that persisted into 1967.

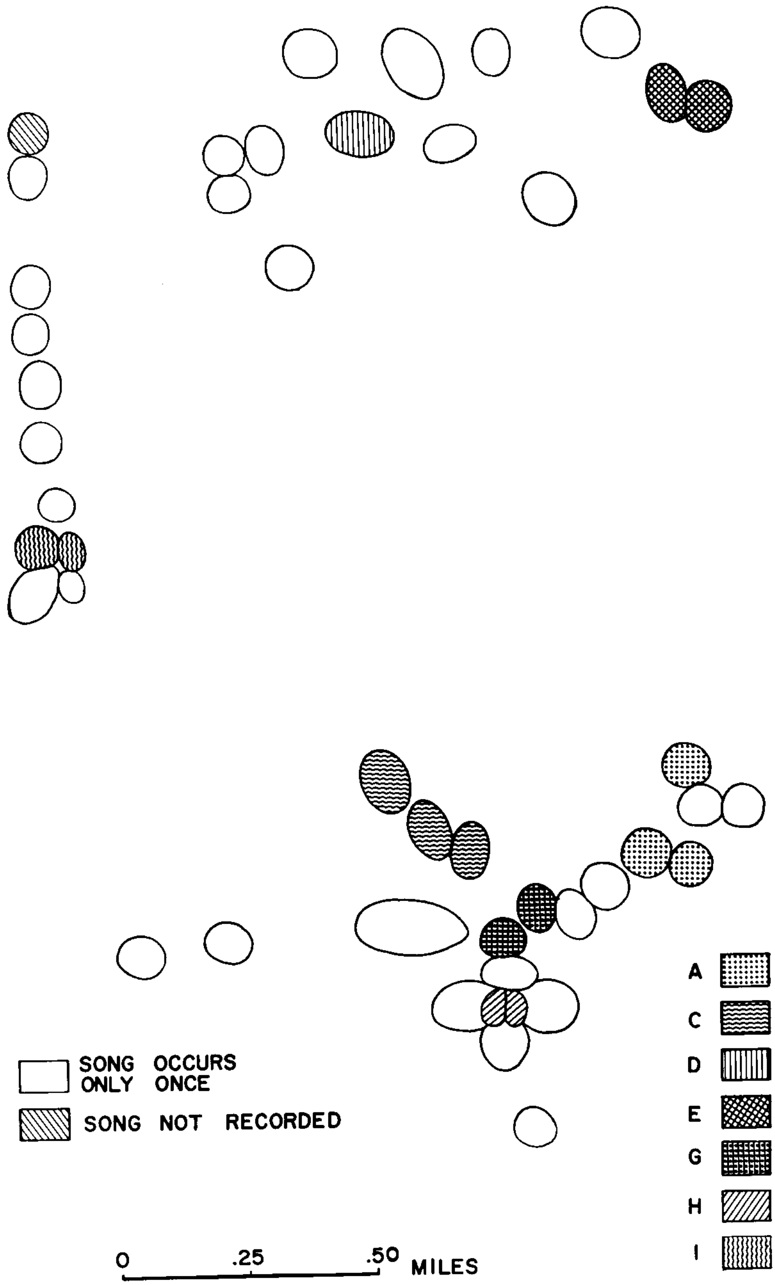

Figure 7. The spatial distribution of song patterns in 1967.

vious work (Rice and Thompson, 1968) has clearly demonstrated that the detailed structure of the song is learned after the young leave the nest. Learning could take place in the summer and early fall while the fledglings and independent juveniles remain in the general vicinity of the nest. In this way they would most likely learn the pattern of their father's song, or of the songs of neighboring males. For birds hatched late in the season this may not be possible, because singing stops almost completely before the clutches of some late-nesters hatch.

A second possibility might be for the song to be learned on the wintering grounds, but Walter P. Nickell (pers. comm.), who has banded Indigo Buntings extensively in Central America, assures me that Indigo Buntings do not sing on their wintering grounds or during migration through Central America northward. Observations of migrating Indigo Buntings in southeastern Michigan and in southern Texas in the spring also suggest that the birds do little singing before they actually begin to settle on a territory.

Still a third possibility is that the definitive song develops in the spring when a male hatched the previous summer begins to establish a territory. When his subsong, typical of birds just settling down in the spring, begins to crystallize into definitive song, he will tend to duplicate the song of a neighboring male he sings against. This idea is supported by observations of two males singing against each other in the spring of 1967. The birds sang identical songs and flew back and forth attempting to drive each other away. Eventually both birds left the area, but this was a clear example of the behavior of two males attempting to set up territorial boundaries early in the nesting season. The distribution of identical song patterns in clumps seems to support this idea. Both in 1965 and 1967 most identical patterns are found in the songs of neighboring males. An alternative explanation for this is that the returning first-year males may tend to settle near their hatching place, which could put them next to their father or the neighbor from whom they learned the song pattern the year before. Unfortunately no data are available on where first-year Indigo Buntings establish their territories in relation to their hatching sites, so we can only speculate on this question.

Although little concrete evidence favors a choice between alternatives one and three, I consider the third possibility the most likely. For one thing it seems unlikely that returning first-year birds should be able to settle so consistently right next to the male from whom they learned their song the previous fall. We would expect a higher number of identical songs to be separated by a few other patterns, indicating that the returning birds of the year had settled near their natal site, but had not been able to establish a territory immediately adjacent to it. On the other hand, a bird learning its song during this first spring would logically be expected to learn from an immediate neighbor. Also against the first possibility are the birds hatched too late in the season to hear their species' song. They must have some opportunity to learn an appropriate song, and spring seems the most likely time. Some experimental evidence supports this third explanation. Thorpe (1961) reports that Chaffinches (*Fringilla coelebs*) reared in captivity learned the details of their songs from hearing other birds sing during their first spring.

All the information currently available suggests that the first-year males arrive on their general nesting area with an imprinted or innate sense of the general rhythmic pattern and frequency envelope of the song (Rice and Thompson, 1968). As they attempt to establish a territory and compete with other birds whose song is already developed, they copy the song of the neighbor. When they sing against neighbors having different songs, parts of both may be combined. The song patterns recorded in 1967 show some evidence of this. Theoretically the number of pairs of identical songs should equal or exceed the number of first-year males in the population. Again, information concerning the number of first-year males in Indigo Bunting populations is inadequate. Banding records of Indigo Buntings at the George Reserve suggest that about 33 per cent of the males are first-year birds. Nice (1937) found that the percentage of first-year birds in populations of Song Sparrows in Ohio ranged from 30 to 52.1 per cent. Lack (1943) found about 30 per cent first-year birds in populations of the European Robin in Britain. Not all first-year birds are successful in competing against other males, and some are forced out of the territory they originally settled and where they developed their song pattern. This helps explain why fewer neighbors sing identical songs than we might expect. The figures of 23.8 and 22.6 per cent for 1965 and 1967 respectively seem to substantiate this hypothesis.

We might assume that birds returning to the same area a second year, by tending to settle in the same territories they occupied the year before, would cause these clumped song patterns to persist. Although banding records at the George Reserve indicate that some individuals return to the same area year after year, other evidence suggests that adult birds tend to choose optimal habitat, while some first-year birds, generally arriving and setting up territories later than older birds, have to settle in habitats only marginal to the species' nesting or feeding requirements. These birds will tend to settle elsewhere in subsequent years. This movement to more suitable habitat, as well as the population turnover, may explain why persistent clusters of identical song patterns are so few.

The great variety of song patterns and song figures within the population must certainly enhance individual recognition. Experimental studies of the response of territorial birds to familiar and unfamiliar songs of the same species (Weeden and Falls, 1959) suggest that wild birds recognize individual songs. The human ear can distinguish many Indigo Bunting songs readily, mostly by differences in the rhythmic characteristics of the different song patterns. The detailed frequency structure of each figure is not clearly evident to the human ear, but it very likely is to birds. Pumphrey (1961) and Thorpe (1963) suggest that the avian ear can distinguish sounds at a rate about 10 times faster than the human ear. It should, therefore, be as easy for a bird to distinguish the detailed sound patterns of two different song figures as it is for us to distinguish them visually on a sound spectrogram. For this individual recognition to be effective, it would seem essential that a shuffling of the song patterns take place to reduce the likelihood that identical patterns will occur together. The various dispersal mechanisms discussed above assume great importance to the species, not only for the most efficient utilization of the environment for nesting and rearing young, but also for the most efficient means of communication among individuals. The relatively few instances of identical song patterns that do persist would not greatly reduce the possibility of recognizing individuals, as seldom are more than two individuals involved in a given cluster of identical songs, and the spatial separation of the territories helps to resolve this difficulty to some degree.

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SUMMARY

Sound spectrograms of the songs of 82 male Indigo Buntings in the summers of 1965 and 1967 at the Edwin S. George Reserve in southeastern Michigan revealed that the songs of most individuals were different. The songs consist of different arrangements of 98 sound figures that were widely distributed throughout the population. The average number of kinds of figures per song was 6.3. Of the total 98 figure types 57.1 per cent were recorded in both years, 20.4 per cent in 1965 only, and 22.4 per cent in 1967 only. Some figures were widespread throughout the population, but most appeared in only a few individuals. The mean number of songs containing a given figure was 5.96. Of the adjacent males recorded in the 2 years, 23.1 per cent sang identical song patterns. The implications of this type of distribution for the learning of song and for individual recognition are discussed.

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