SONG VARIATION IN A POPULATION OF OREGON JUNCOS

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Besides its contribution to the study of vocal communication, the study of song variation in natural passerine populations is of basic importance for the analyses of comparative, genetic, and developmental aspects of song, just as the study of variation is important in comparative morphology. The song of the Oregon Junco (*Junco oreganus*) is found to be very suitable material for such analyses, and the developmental aspect has already been considered by Marler, Kreith, and Tamura (1962) and Konishi (1964). Furthermore, with additional reports on song variation we are beginning to see some possibility of objective comparisons and of generalizations about differences between species.

METHODS

Field recordings were made with a Magnemite 610-E tape recorder and an Altec 633-A microphone mounted in a parabolic reflector at a tape speed of 7½ inches per second. Sixty-two song types of 51 birds from 1962 and an additional 15 songs of 13 birds from Marler's collection of previous years, all collected in or near Berkeley, California, were used for analysis. The recordings were played back on a Wollensak T 1500 tape recorder and their audiospectrograms were made on a Kay Electric Company Sonagraph using the "high-shape" circuit and "wide band" filter settings. Measurements were made on the audiospectrograms with the clipboard designed by Marler and Isaac (1960*a*). The measurements of infer-song intervals were made on oscillograms prepared with a Sanborn single channel recorder 151-100A (Fish, 1953). Unless otherwise stated all the data on Chipping Sparrows (*Spizella passerina*), Brown Towhees (*Pipilo fuscus*), and Mexican Juncos (*Junco phaeonotus*), cited in the tables in this paper, are from Marler and Isaac (1960*a*, 1960*b* and 1961, respectively).

CHARACTERIZATION OF SONG

There are several ways of defining "song." These may be by function, by the form or morphology of the sounds, or by the underlying physiological mechanism. All can be acceptable in as far as they offer consistent approaches. The criterion most accessible to us is the morphology of sounds. So far in the description of bird songs a system of nomenclature analogous to that of human linguistics or music has been employed (Thielcke, 1961; Marler and Isaac, *op. cit.*). Recently Isaac and Marler (1963) have introduced a more objective method in dealing with the complicated song of the Mistle Thrush (*Turdus viscivorus*). The essence of their method is to recognize the different levels of temporal groupings of the most elementary units in a train of sounds by examining the frequency distribution of time intervals between those units. The same method was used in the present study.

Any continuous marking on an audiospectrogram will be called a "note," which is immediately recognizable as the most elementary and stable unit. It is repeated in the same form not only within each junco song but also from song to song. Notes are arranged to form a new unit which will be called a "syllable" by analogy, with linguistics. The syllable unit has a definite composition in terms of the types and number of notes. The average number of notes per syllable is 2.26 and the standard deviation is 0.77. The song of the Oregon Junco is composed of repetitions of the same syllable unit with constant intervals (fig. 1). Each song usually contains only one syllable type but in a very few cases (4 out of 77, see songs K and L in fig. 1), there are two syllable types within a song. Even in such a case, instead of two syllable types mixing up, they form separate parts of the song after the rule of repetitive alternations of the same syllable
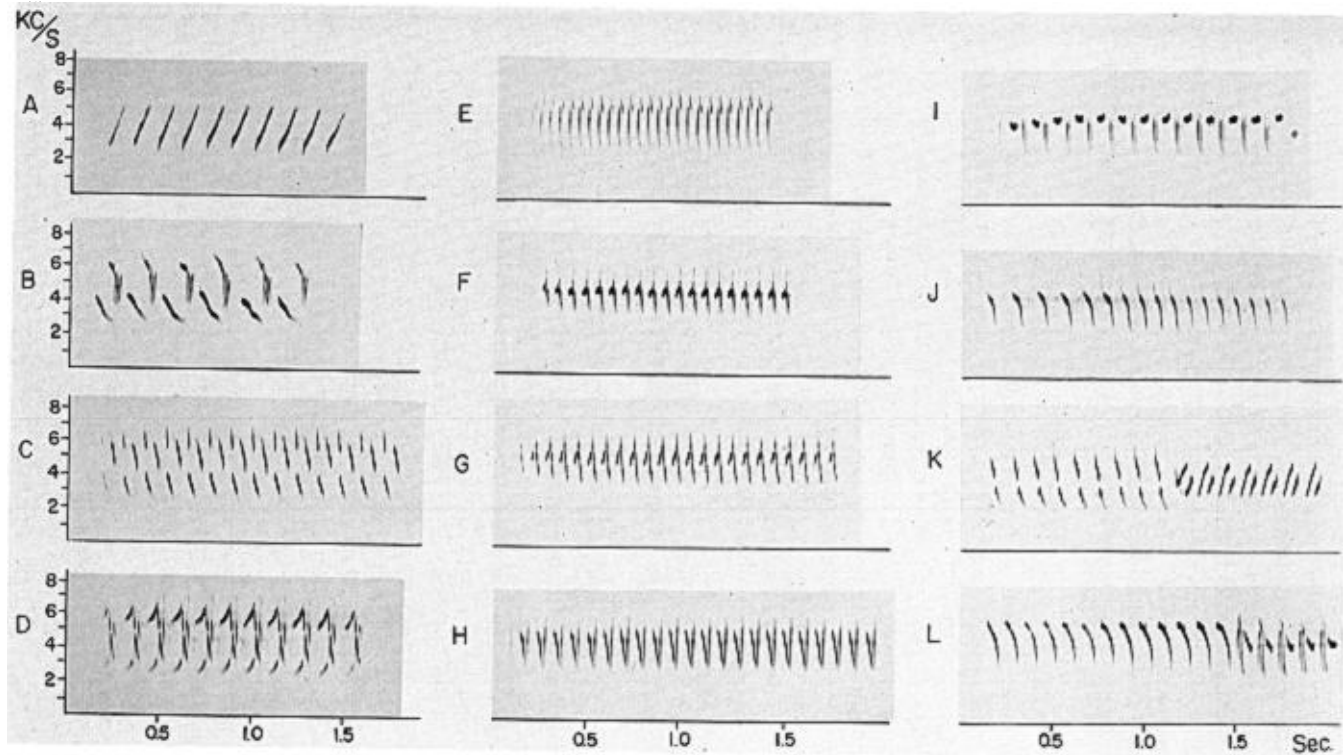
Fig. 1. Audiospectrograms of a selection of songs. Ordinate—frequency in kilocycles per second; abscissa—time in seconds. A, song containing one note per syllable; B, two notes per syllable; C, three notes per syllable; D, more than three notes per syllable; E–H, songs with a shorter syllable duration having greater number of syllables per second as compared with A–D, with a longer syllable duration; I, a rare song type in which inter-syllable and inter-note intervals are almost equal; J, an exceptional song in which syllable duration decreases progressively toward end of song; K and L, two-part songs with two syllable types within a song.

and interval units. While adjoining syllable units are always separated along the time axis, the notes within a syllable can be separated from one another along the time axis and/or along the frequency axis on the audiospectrograph.

Of 77 songs, 66 (86 per cent) have syllables containing more than one note type, and in 46 of these the notes are separated from one another along the frequency axis only; in other words, here the notes form a tight cluster within the syllable unit. In the remaining 13 songs, the notes within the syllable unit are separated from one another along the time axis. This might be thought to make the distinction between the syllable and note units difficult. However, they are clearly distinguishable from each other even in these thirteen cases, because the interval separating the notes within a
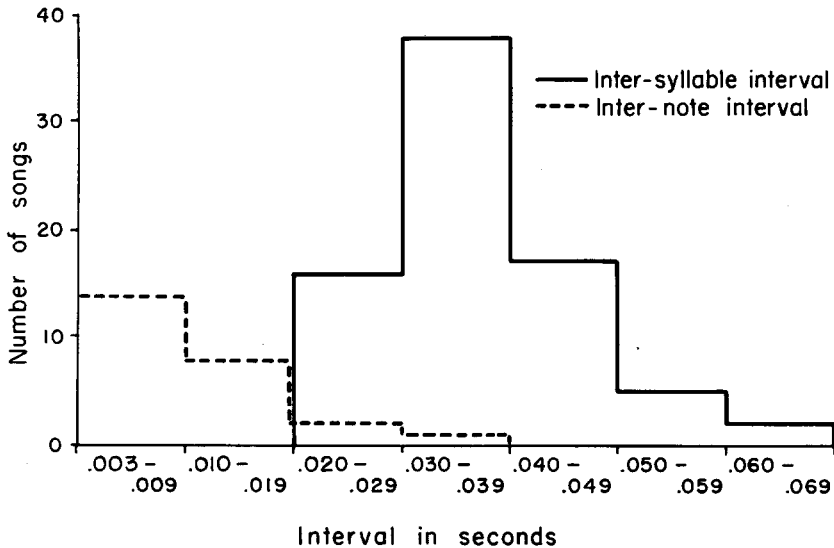

Fig. 2. Frequency distributions of inter-syllable and inter-note intervals. Each of 77 song types used here contributes to the sample inter-note intervals within one syllable and the inter-syllable intervals.

syllable is always shorter than the interval between two adjoining syllable units. Two exceptions to this rule were found (see song I, fig. 1). This rule holds only within a song, since different songs have different ratios between the inter-note and inter-syllable intervals. Hence, the sample comprising all the inter-note intervals within a syllable and an inter-syllable interval from each of 77 songs has a bimodal distribution with an overlapping zone between the two modes, one of which represents the inter-note interval and the other the inter-syllable interval (fig. 2).

In is interesting to note that in those songs (11 out of 77) in which the syllable unit contains only one note, the interval between notes has the size of the inter-syllable interval. This supports the treatment of such note units as syllables.

In contrast with the songs of many other birds in which there are levels of temporal grouping within the song higher than the syllable level, such as phrases and trills, the second level of temporal grouping in the Oregon Junco is the song itself. It can be recognized immediately as a unit of temporal grouping when we compare the range of the intervals between songs (2.0–7.0 seconds) with that of inter-syllable intervals (0.020–0.060 seconds). This indicates that a certain number of syllables forms a unit of temporal grouping, which we call a song.

THE DEGREE OF STEREOTYPY IN SONG

In order to demonstrate the stability of the song unit, several measurements were made on eight selected song types. Songs which are morphologically different from one another are here referred to as different types whether they come from one bird or from more than one bird; for example, 58A and 58B in table 1 are two different song types recorded from bird no. 58. A sample of 20 consecutively recorded songs was taken of each type. Six measurements which can roughly characterize a song were obtained. The syllable and the inter-syllable interval in the middle of each song were chosen for measurement. The degree of variation for each parameter is expressed by the coefficient of variation which is $V = s \times 100/X$, where s is the standard deviation and X the sample mean. For comparison the averages (V) of V values for each parameter are presented. One observes that a pair of types with minimum and maximum V values for one parameter does not necessarily show the same trend in other parameters. Even two parts of a song (56 first parts and 56 second) may differ from each other in the degree of variation. By comparing the V values within each song type one finds that, with some exceptions, the least variable parameter is the minimum frequency and the second least variable parameter is the maximum frequency. The difference in the degree of variation between the minimum and maximum frequencies is partly due to the effect of amplitude variation on the higher frequency range, as pointed out by Marler and Isaac (1960a) for the song of the Chipping Sparrow.

TABLE 1

VARIATION IN SIX PARAMETERS IN A SAMPLE OF TWENTY SONGS FROM EACH OF EIGHT SONG TYPES

Song type	58A	58B	47	30	44C
No. syllables	14.2±0.88	15.5±0.69	12.4±1.24	22.0±1.26	15.9±0.95
	(6.19)	(4.45)	(10.00)	(5.72)	(5.97)
Song duration	1.72±.074	1.44±.065	1.64±.170	1.92±.101	1.54±.094
(seconds)	(4.30)	(4.51)	(10.40)	(5.26)	(6.10)
Interval between	.023±.0019	.032±.0017	.038±.0061	.035±.0032	.029±.0016
syllables	(8.26)	(5.31)	(16.10)	(9.14)	(5.52)
(seconds)					
Syllable duration	.099±.0018	.064±.0014	.098±.0053	.053±.0031	.072±.0016
(seconds)	(.182)	(2.19)	(5.41)	(5.85)	(2.22)
Max. frequency	6.85±.045	5.66±0.31	6.53±.061	6.35±0.37	6.64±0.15
(kc./sec.)	(0.66)	(5.48)	(0.93)	(5.82)	(2.26)
Min. frequency	2.67±.080	2.47±.0019	2.58±.052	2.97±.067	3.49±0.12
(kc./sec.)	(2.99)	(0.08)	(2.02)	(2.26)	(3.44)

Song type	56 1st	56 2nd	53B	V	Brown Towhee	Chipping Sparrow
No. syllables	13.0±0.92	4.5±1.10	9.80±0.62	7.98	10.2±2.1	3.65±0.45
	(0.12)	(24.40)	(6.32)		(20.60)	(12.30)
Song duration	1.35±.129	0.48±.110	1.26±.087	8.74	1.49±0.19	55.1±6.7
(seconds)	(9.56)	(22.90)	(6.90)		(12.80)	(12.20)
Interval between	.049±.0047	.029±.0043	.029±.0016	9.28	not available	
syllables	(9.59)	(14.80)	(5.51)			
(seconds)						
Syllable duration	.058±.0046	.086±.0039	.107±.0024	4.02	.116±.025	.0433±.0012
(seconds)	(7.93)	(4.53)	(2.24)		(21.50)	(2.77)
Max. frequency	5.85±0.25	5.25±0.11	6.18±0.14	2.97	5.86±0.86	5.98±0.27
(kc./sec.)	(4.27)	(2.09)	(2.27)		(14.70)	(4.52)
Min. frequency	2.24±.093	3.07±.039	2.55±0.13	2.66	1.84±0.35	2.43±0.14
(kc./sec.)	(4.15)	(1.27)	(5.10)		(19.00)	(5.76)

Pairs of figures are sample means of standard deviations. Figures in parentheses are $V = s \times 100 \div X$ or coefficients of variation. V: row average of V values. 56 1st and 2nd are two parts of one song treated as separate songs.

The degrees of variation in the number of syllables and song duration are obviously very close in all cases. For comparison, data on a Chipping Sparrow and a Brown Towhee are added to table 1. In the Brown Towhee the coefficient of variation is distinctly larger for all the parameters, supporting the subjective impression that its song is much less stereotyped than those of the other two species, even within an individual.

SONG VARIATION WITHIN A POPULATION

Variability in measurable characters.—For the data presented here a sample of 77 song types was used, and one song of each type was taken for the measurements of the six parameters as described in the previous section. From the averages of the coefficients of variation (V) in table 1, we already have some idea as to the variability of song within a population. In table 2, the distribution of the values of the coefficients of variation for the whole sample of songs of the Oregon Junco shows a very similar trend. For example, the minimum frequency is the least variable parameter, and the maximum frequency is again the second least variable. The inter-syllable interval varies significantly less than the syllable duration (also see fig. 8A).

TABLE 2

INTER-SPECIES COMPARISON OF SONG VARIATIONS WITHIN A SPECIES POPULATION

Species	Oregon Junco	Mexican Junco	Brown Towhee	White-crowned Sparrow
No. syllables	14.1±4.38 (31.10)	10.1±2.9* (28.70)	10.4±4.5 (43.30)	10.2±1.08* (10.50)
Song duration (seconds)	1.49±.203 (13.60)	1.63±0.29 (17.80)	1.52±0.31 (20.40)	1.1±0.20 (18.20)
Interval between syllables (seconds)	.036±.0092 (25.60)	....	....	....
Syllable duration (seconds)	.080±.0293 (36.60)	.138±.077 (55.80)	.101±.057 (56.40)	....
Max. frequency (kc./sec.)	6.53±.648 (9.90)	6.39±0.51 (8.0)	6.50±0.71 (10.90)	6.78±.054 (8.0)
Min. frequency (kc./sec.)	2.98±.120 (4.0)	2.09±0.25 (12.0)	1.84±0.35 (19.0)	2.36±0.20 (8.50)
Frequency spread (kc./sec.)	3.52±.659 (18.80)	4.30±0.58 (13.50)	4.01±0.92 (22.90)	....
Sample size in songs	77	67	61	26

* Including syllables and phrases.

With the addition of data on the Mexican Junco, the Brown Towhee and the White-crowned Sparrow, *Zonotrichia leucophrys* (Marler and Tamura, 1962), we can now compare the degrees of song variation between species populations. By comparing the coefficients of variation, we find that the syllable duration is the most variable parameter for all the species for which this information is available. The maximum and minimum frequencies are the two least variable parameters for all four species. For all the parameters the Brown Towhee has larger values of the coefficients of variation, demonstrating that song variation in a population of this species is greatest among the species compared here.

However, it must be remembered that any statement regarding song variation is framed only in terms of those criteria selected for measurement. There are other properties that characterize a song and some of them may be more important than those chosen above. For instance, what we see here cannot support our observation that in

a population of White-crowned Sparrows song variation is extremely small, even though few would doubt the truth of this statement when confronted with audiospectrograms of their songs. This gap in our experience is largely due to the difficulty of quantifying some properties in bird songs. In particular there is as yet no way of expressing the form of a note numerically so that a quantitative comparison between notes is possible.
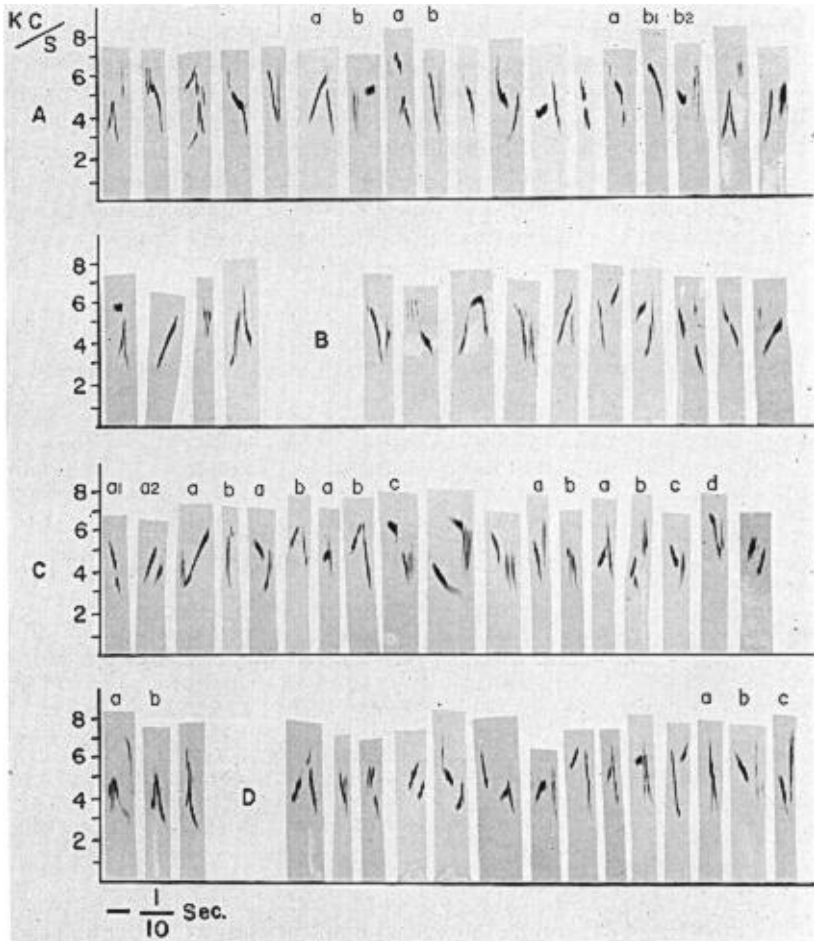

Fig. 3. Catalogue of 67 syllable types from four different localities. The presence of more than one song type per individual bird is shown as a, b, and so on. Two syllable types contained in one song, as in the case of two-part songs, are indicated as a 1, a 2, and so on.

Diversity in the forms of syllables and notes.—Syllable and note forms were compared qualitatively by displaying side by side the syllable types extracted from each song type (fig. 3). It may be seen that there is no sharing of a syllable type among different birds. In the figure, A, B, C, and D represent subpopulations from four different localities in and near Berkeley. The maximum distance between the different subpopulations was about two miles. Within one subpopulation the birds were generally within hearing distance, sharing their territorial borders. There appear to be no local differences in the

TABLE 3

DISTRIBUTION OF FOUR GENERAL CATEGORIES OF NOTE TYPES IN FOUR DIFFERENT SUBPOPULATIONS

		Subpopulations			
Note types	A	B	C	D	Total
1	6 (8.2)	5 (3.8)	8 (8.7)	7 (5.2)	26
2	14 (13.4)	6 (6.4)	15 (14.5)	8 (8.7)	43
3	6 (6.3)	3 (2.9)	7 (6.7)	4 (4.1)	20
4	14 (12.2)	5 (5.7)	13 (13.1)	7 (7.8)	39
Total	40	19	43	26	128

Figures in parentheses are expected frequencies, assuming a random distribution. Figures outside parentheses are observed frequencies.

TABLE 4

VARIATION IN SYLLABLE DURATION AND INTER-SYLLABLE INTERVAL WITHIN A SONG

				SYLLABLE			
	1st	2nd	3rd	4th	5th	6th	7th
Syllable duration (seconds)	.099±.0031	.105±.0037	.105±.0022	.106±.0021	.105±.0027	.104±.0024	.106±.0023
Interval between syllables (seconds)	.0300±.0024	.0281±.0021	.0287±.0019	.0286±.0013	.0306±.0018	.0317±.0021	.0328±.0021

Song 53B, sample size 19 consecutively recorded songs.

form of syllables or notes and no noticeable homogeneity within subpopulations, in striking contrast to the situation in the White-crowned Sparrow.

While there is diversity in syllables, most of the component notes of different syllables can be classified into a few general categories of frequency-time patterns such as are shown in figure 4. Table 3, which is based on the sample of syllables shown in figure 3, shows the frequency distribution of note forms according to the above criteria in different subpopulations. An X^2 test reveals no significant difference ($p < 0.01$) in the distribution of these four categories of notes in four different subpopulations, thus reinforcing the impression that there is no sign of "dialects" in Oregon Junco song.

Fig. 4. Five general categories of note types.

SOME PRINCIPLES IN THE STRUCTURAL ORGANIZATION OF SONG

It is of interest to examine what sort of relationship exists among the different parameters in the structural organization of song. Since syllable duration and inter-syllable interval remain relatively constant during the course of a song (table 4), the total duration of a song can be expressed as follows: $S = N \times t_s + (N - 1) \times t_i$ where S is song duration, N the number of syllables, t_s syllable duration and t_i inter-syllable interval. We see that the duration of a song depends on all these variables. Now, there is a positive correlation ($r = +0.916$) between song duration and the num-
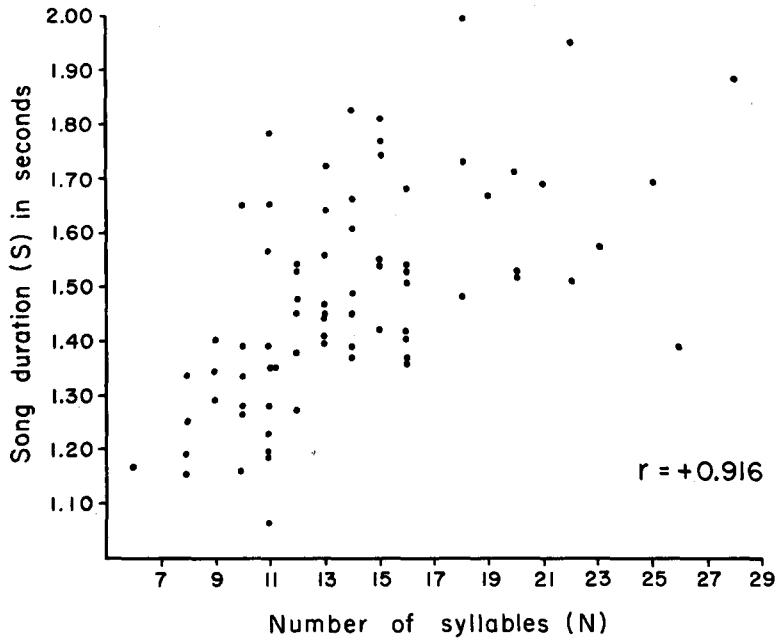
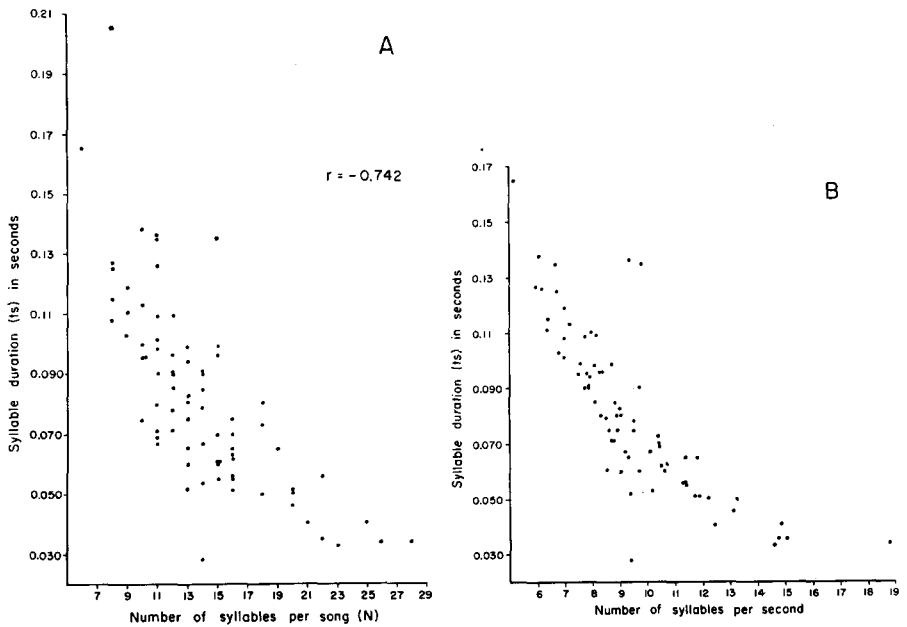Fig. 5. Relation between the number of syllables and song duration.

Fig. 6. A, relation between the number of syllables and syllable duration; B, relation between the number of syllables per second and syllable duration.

ber of syllables (fig. 5). The regression coefficients are $b_{SN} = 0.026$, which indicates the amount by which S increases for unit increase in N, and $b_{NS} = 32.4$, indicating the amount by which N increases for unit increase in S. While song duration is rather uniform in a population of Oregon Juncos (1.40 ± 0.203 and the coefficient of variation $V = 13.6$), the number of syllables varies more widely ($V = 31.1$). Given that there is a positive correlation between these two variables, how is such constancy in song duration maintained? One might rather expect a similar degree of variation in both of these variables, as found within a sample of one song type. However, there are two more variables contributing to song duration. Remembering that syllable duration is far more variable than the interval, we may plot t_s against N (fig. 6A).

It is clear from the figure that there is a negative correlation ($r = -0.75$, $b_{t_s N} = -0.0049$ and $b_{N t_s} = -112$) between t_s and N. Now, $b_{SN} = 0.026$ seconds; the amount by which song duration increases for unit increase in N, namely the integer 1, is only 1.7 per cent of the average song duration of 1.49 seconds. On the other hand, $b_{t_s N} = -0.0049$ seconds, which is the amount by which syllable duration decreases for unit increase in the number of syllables, and is 6.1 per cent of the average syllable duration of 0.080 seconds. Hence, for unit increase in the number of syllables, song duration is not only less affected than syllable duration but also is negatively correlated with the number of syllables. The above relationship must hold for the entire length of a song. The total number of syllables divided by song duration gives the number of syllables per second. When we plot syllable duration against this number, we obtain a much
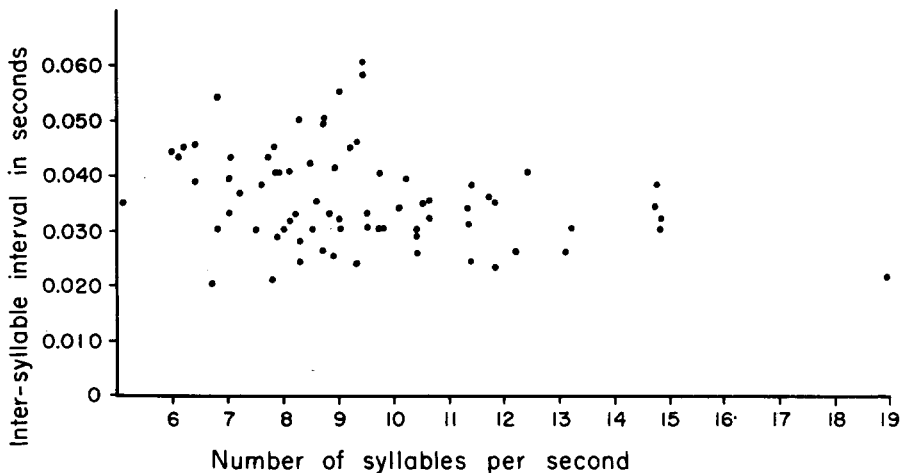

Fig. 7. Relation between the number of syllables per second and the inter-syllable interval.

better linear relationship ($r = -0.81$). And in this case the regression coefficient $b_{t_s N/s}$ is 12 per cent of the average syllable duration of 0.080 (fig. 6B). In this connection, Song J of figure 1 is very instructive, for its syllable duration decreases progressively during the course of the song and parallel with this the rate of syllable delivery increases (there is no change in inter-syllable interval, however!).

The remaining variable that affects song duration is the inter-syllable interval. Judging from its variance, which is much smaller than that in syllable duration, it does not seem likely that it has a relationship with N, the number of syllables, similar to

that between t_s and N. Figures 7 and 8A indicate that the t_i is independent of either the number of syllables per second or t_s, respectively.

Hence, we can conclude that the relative constancy in song duration within a population, in the face of wide differences in the number of syllables, is achieved only by varying the syllable duration. This also explains why this parameter has such a high variability in a population. It is interesting to note that this compensatory phenomenon was found in the songs of Mexican Juncos and Brown Towhees, in populations of which the syllable duration is again the most highly variable character. Furthermore, the relationship holds only for the "trill" part of their songs, the trill being the rapid repetition of one structural unit corresponding with the song of Oregon Juncos. According to the data presented by Borror (1959) on the song of Chipping Sparrows, the same relationship may hold there between syllable duration and the number of syllables. It seems that this correlation may be one of the rules governing the structural organization of trill type songs.

The frequency characteristic is another aspect in the structural organization of song. As mentioned earlier the maximum frequency is more variable than the minimum.
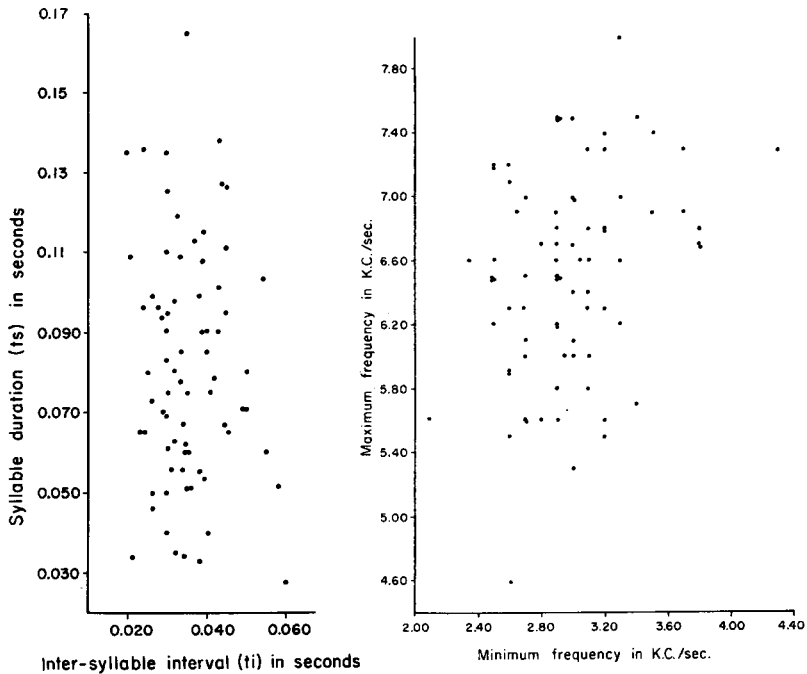

Fig. 8. Left, relation between inter-syllable interval and syllable duration; right, relation
     between maximum and minimum frequencies.

Figure 8B indicates that there is a linear correlation (correlation coefficient $r = +0.96$) between them. The regression coefficients are $b_{min.max.} = 0.178$ (kc./sec.), which is the amount by which the minimum frequency increases for unit increase in the maximum frequency, and $b_{max.min.} = 5.18$ (kc./sec.), the amount by which the maximum frequency increases for unit increase in the minimum frequency. Therefore, their linear relationship is asymmetrical, as predicted from the significant differences in the degree of variation between the two frequency measurements.

TABLE 5

VARIATION IN INTER-SONG INTERVALS

Song	$X \pm s$ (seconds)	V	Sample size	Song	$X \pm s$ (seconds)	V	Sample size
37	3.81±.866	22.7	23	43	4.40±1.19	27.0	18
44C	5.92±1.63	27.5	24	57	5.08±.729	14.4	23
56	6.51±.685	10.5	31	46	7.02±.159	22.6	17
47	5.04±1.35	26.7	23	55A	2.73±.531	35.9	15
*60	4.70±.938	20.0	18	55B	2.05±0.33	14.5	53
*60	4.95±1.32	26.9	28	58	6.79±1.59	23.4	48
42	5.52±1.32	23.9	32				

* Denotes the same song type recorded on two different days.

SHORT-TERM PATTERN IN SINGING

The pattern of singing in many passerine species is characterized by its periodicity, both short-term and long-term. Although the frequency distribution of inter-song intervals was not studied over very long periods, it appears that there are two size classes in the intervals between consecutive songs: songs are delivered in clusters within which the inter-song interval is quite constant (table 5); however, the interval between these clusters is, on the average, longer than the inter-song interval within a cluster. Such a cluster will be called a "bout." This pattern of singing is clearly exhibited when a bird has more than one song type. The great majority of birds with more than one song type delivered different song types in separate bouts producing a pattern such as AAAAAAA BBBBBBBBBBBBBB. In the Oregon Junco a bout often contains a great number of songs. This explains in part why so few birds in the sample (10 out of 66) had more than one song type, the length of one bout usually exceeding the recording time and patience available to the observer.

As seen in table 5, the inter-song interval varies widely from individual to individual. We do not know the cause of such a wide variation. However, it is possible that the inter-song interval varies in relation to song duration in order to maintain a relative constancy in the rate of singing expressed as the number of songs per second. This possibility was tested with two birds which happened to have more than one type of song. Birds no. 58 and no. 55 had two song types which differed in their average durations. As these birds switched from A to B type during short recording periods, they also changed the average inter-song intervals; table 6 shows the results. There seems to be an inverse relationship between song duration and inter-song interval. Its consequence is to maintain the number of songs per second relatively constant, implying that variation in song duration is compensated for in some degree by variation in the interval between songs. It is not known whether this relationship holds in general. Nor is it known whether it is true at all times with these individuals. It may only apply when

TABLE 6

RELATION BETWEEN SONG DURATION AND INTER-SONG INTERVAL

Song type	Average song duration	Average interval	No. songs per second	Sample size No. songs
55A	1.82	2.05	0.306	54
55B	1.26	2.73	0.228	15
58A	1.68	6.41	0.128	27
58B	1.46	6.95	0.123	23

Differences between the means for 55A and B, and for 58A and B were shown by t-tests to be highly significant.

birds are singing at their maximum delivery rate. However, if this is true in general, it is an interesting contrast to what we have found in the internal structure of the song, where variation in syllable duration was not compensated for by change in inter-syllable interval.

DISCUSSION

A morphological study of song in a natural population can provide basic information as to the variability of several properties of song. If the song is used for species recognition, there are some predictions that we can make. The value of a communication signal for species recognition can be judged only in relation to other signals belonging to the same sensory modality in the environment of a species. Thus the most important condition for the song of a species which is to be used in species recognition is that it should differ from the songs of other species living in the same area in at least one property—a property that must also be relatively constant in the species population. As demonstrated in this study, there are several variable properties in junco song. Less variable parameters in junco song such as inter-syllable interval and frequency range have the potentiality, singly or in combination, to be used in species recognition. However, from the morphological study of song variation alone, it is impossible to find out which of these is actually employed in species recognition.

Recent studies by Falls (1963) on properties responsible for species recognition in the songs of Ovenbirds (*Seiurus aurocapillus*) and White-throated Sparrows (*Zonotrichia albicollis*) re-emphasize the value of the morphological study of song variation in natural populations. In the Ovenbird the temporal pattern and phrase structure of its song are very important in species recognition whereas the pattern of change in loudness within a song is not important, even though this property is quite constant in a population. In the White-throated Sparrow the properties that are less variable in the natural population, such as the intervals between notes, are the most important in species recognition and "for some properties the permissible limits of variation (as tested by artificial modification) correspond closely with the known ranges of natural variation," as was found with note length and frequency range. It is remarkable to find that those properties found to be relatively constant in the Oregon Junco are also relatively constant in the White-throated Sparrow and actually proved to be important in species recognition in that species. Another important point found by Falls is that the song conveys information for species recognition not by a single constant property, as occurs in some orthoptera (Walker, 1957), but by a combination of properties. Addition to the number of variables in a sound signal increases the amount of information that it can carry. Combinations of different parameters of sound can provide an enormous number of signal patterns, although in practice there must be physiological limits on the production and perception of these patterns. This combining system of signal coding permits the presence of a great number of species in the environment and also the use of sound to serve a great number of functions. The system of signal coding also allows a gradual change in the signal spectrum of a species environment instead of a drastic all or nothing change. The introduction of each new member into a given signal environment will require an adjustment in the use of signals. However, it is unlikely that a signal can take any form demanded by the signal environment, because of the dependency relationships between different properties of song which were discussed earlier.

As Falls (1963) found in the song of White-throated Sparrows, the various properties employed in species recognition are not equally significant, some being more important than others. Marler (1960) points out a paradoxical relationship between the uniformity in song necessary for species recognition and the diversity needed for individual recognition. The very fact that the less variable properties of songs are those

which are especially important in species recognition, permits the development of variability in other properties which can then serve other functions such as individual recognition. The reality of individual recognition by song has been demonstrated by Weeden and Falls (1959) with the Ovenbird.

In this discussion there is another important issue that has not been considered. The variation in the properties of song as discussed above is meaningful in actual communication, for instance in individual recognition, only if the animal concerned is capable of registering it. If we consider what is known of avian auditory physiology, the power of frequency resolution in song birds and parakeets is reported to be 0.3 per cent, as determined by a behavioral method (Knecht, 1939). If this value holds for the Oregon Junco, the birds can easily detect a departure from the average by one standard deviation unit in either the maximum or minimum frequency (9.9 per cent and 4 per cent, respectively). As to the power of time resolution there are no direct measurements, but Schwartzkopff (1958) states that because of considerable damping of sound waves transmitted throungh the columella onto the tegumentum, the basilar membrane can change its pattern of movement within a very short time. He ascribes to this the ability of some birds (parakets, in this case), in contrast with mammals and owls, to resolve very rapid phasic sound signals, such as we have described in songs of Oregon Juncos.

Although there is usually good agreement between the results of physiological and behavioral investigations, the latter give the final answer about the function of sense organs in an intact animal. Paradoxically, the behavioral method does not prove that a lack of sensory discrimination is due to the incapability of sensory organs. Therefore, both aspects must be studied in order to reach a definite conclusion. On the other hand, studies such as those done by Falls (1963), especially when they are combined with the morphological studies of the songs of natural populations, can establish the direct functional significance of the various properties of song, which will lead us to a better understanding of the evolution of avian song.

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SUMMARY

Variation in syllable shape and in six measurable properties of the songs of a population of Oregon Juncos (*Junco oreganus*) was studied. An attempt was made to describe different structural units in a song as different levels of temporal grouping of the most elementary units, notes. These in turn form a new unit, a "syllable." The song is composed of repetitions of the same syllable with constant intervals. Within the sample of 77 songs, the minimum and maximum frequencies are the two least variable measures. Syllable duration is most variable. The number of syllables in a song and song duration have a positive correlation and yet vary to different degrees. This is due to the tendency to maintain song duration relatively constant by varying syllable duration in an inverse relation to the number of syllables per song or per second. This phenomenon is also found in Brown Towhees and Mexican Juncos and is perhaps one of the rules in the structural organization of songs consisting of rapid repetitions of one structural unit. The inter-syllable interval varies little and is independent of either the number of syllables per second or syllable duration. The maximum and minimum frequencies have a linear correlation. The forms of syllables and notes are characteristic of indi-

viduals. There is no sharing of note or syllable forms between individuals. The forms of notes as classified into four general categories show a homogeneous distribution in four subpopulations. Finally some problems on the communicatory significance of uniformity and diversity in songs are discussed.

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