MARKOVIAN VERSUS RHOMBOIDAL PATTERNING IN THE SONG OF SWAINSON'S THRUSH

by

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(With 11 Figures)
(Acc. 20-XII-1976)

The organization of behaviour remains one of the prime concerns of ethologists with the songs of birds representing one area of particular interest. The songs are well suited to sequential analysis because they usually consist of discrete acoustic patterns rather analogous to phonemes in human speech. Instrumental analysis has now reached such sophistication that these can readily be studied visually in long sequences.

To date, certain models have been used to predict the sequential relationships of events in song in probabilistic terms. Of these, one has exploited the urn model of CANE (1961) showing that events are serially repeated such that the number of repetitions of each kind of event is relative to its probability. Repetitions of the same song type in series by Cardinals (*Cardinalis cardinalis*) (LEMON & CHATFIELD, 1971) fit this model to some extent, although the number of repetitions exceeds that expected by chance alone. Another probabilistic model employed is the Markov series wherein events of different kinds are predictable solely on the basis of immediately preceding events. Again in Cardinals, switches from one song type to another follow a first order Markov rule in being predictable solely on the basis of the immediately preceding event. Markov models have also been applied to song in other species such as Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) (LEMON & CHATFIELD, 1973) and Western Meadowlarks (*Sturnella magna*) (FALLS & KREBS, 1975).

A linear control model has been developed by TODT and his colleagues. Using European Blackbirds (*Turdus merula*) which tend to repeat immediately a song played to them if they have it in their repertoire, TODT (1975) has gathered evidence of three interacting factors: the input component from another bird or playback of a recording; the periodic component or probability of recurrence of a particular song; and the throttling component

1) Supported by NRC grants to R. E. LEMON.

which reduces the probability of the song being immediately repeated for some time after it has been sung.

These models recognize the discreteness of particular events of song and might be called atomistic. NELSON (1973) has suggested that such an approach is less satisfactory than one which recognizes more general patterns of organization, the so-called holistic approach of BOHM (1968).

In support of his contention he presented results from the songs of Swainson's thrushes (*Hylocichla ustulata*) and from these claims a "rhomboidal patterning" which is shared with human music and features of plant and animal morphology. This model asserts that within songs of this thrush successive sound patterns tend to fit a pentatonic scale with approximately equal logarithmic frequency intervals. The rhomboidal patterning results from interaction of the regular pentatonic intervals with the fact that different song types begin from different key notes.

In this paper we examine for ourselves the songs of the Swainson's Thrush. In so doing we do not find consistent rhomboidal patterning or pentatonic scales. Instead our thrushes exhibited so much individuality that we question whether such a holistic model contributes much to an understanding of song organization.

MATERIALS AND METHODS

We recorded songs of Swainson's thrushes from 10 individuals of which six gave sufficient samples for analysis of sequences of song events. All thrushes were resident in the Province of Quebec when recorded in July 1975 (Table I). Recordings were made by a Uher 4200 tape recorder at 19 and 9.5 cm per second using a Dan Gibson parabolic reflector and microphone.

TABLE I

A summary of the recordings from six Swainson's thrushes of this study

No.	Date recorded	Location	Songs recorded	Songs per bout	Song types
1	18/7/75	Matane, Québec	346	100, 78, 65, 54, 32, 10, 4, 3	5
2	18/7/75	Matane	57	42, 15	4
3	18/7/75	Matane	55	32, 12, 8, 5	4
4	6/7/75	Lac Carré	40	22, 9, 5, 2, 2	3
5	20/7/75	Percé	222	73, 34, 31, 39, 24, 16, 15	5
6	20/7/75	Percé	41	26, 10, 5	4

We analyzed the songs on a Ubiquitous Spectrum Analyzer (Federal Scientific, model UA-500) equipped with an Analyzer Averager (model UA-500-1), a three dimensional Automatic Display Generator (66-2A) and an Intensity Modulator (option 67). Displays were made on a Tektronix Oscilloscope (5103N) and recorded by a Grass Kymograph Camera (model C4N). Such instrumentation yields a continuous frequency analysis on

35 mm paper (Kodak Linagraph 1930), instead of isolated 2.4 second analyses made by the Kay Electric Sonagraph more commonly used. Playback of recordings was at one-quarter or one-eight speed. The method is that of HOPKINS, ROSETTO & LUTJEN (1974).

A Kay Electric Sonagraph (model 6061A) was used for detailed analysis of some patterns.

Frequency-amplitude analyses were also made with the Federal Ubiquitous Analyzer with the Averager. The resultant display on the oscilloscope (Fig. 6) shows peaks of most prominent frequencies which can then be measured by a cursor yielding digital readings accurate to the nearest 0.2% of the total analysis range, which in practice was 10,000 Hz.

Amplitude versus time oscillograms were made of all song types of one bird (Fig. 5) on the oscilloscope mentioned.

GENERAL DESCRIPTION OF SWAINSON'S THRUSH SONGS

The territorial songs of Swainson's thrushes are organized into groupings of small sound units or syllables. These groupings or songs last about two or more seconds in length, and are typically separated from each other by intervals of silence of about five seconds duration. Fig. 1 shows a frequency histogram of song and interval lenghts from three birds. Consecutive songs consist of different sequences of syllables, each sequence being called a song type of which each thrush had a repertoire of three to seven. Variations between songs of a single type are minor and do not make classification difficult.

Each song type consists of 5 to 7 kinds of syllables, one or two of which may be repeated, especially toward the end of the song. In Fig. 1, 2, 3 and 4,

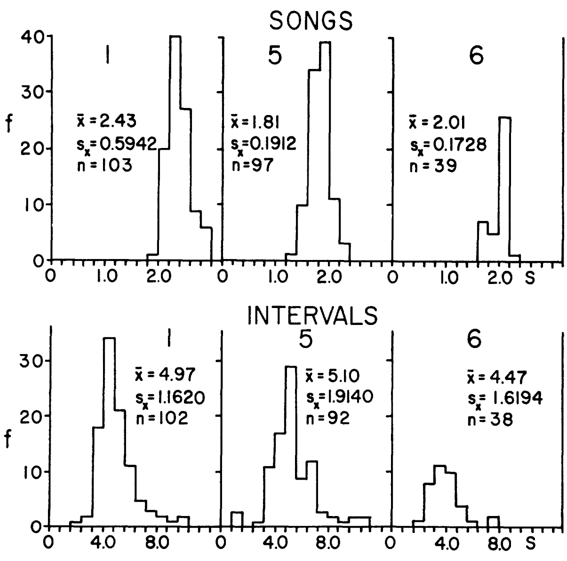

Fig. 1. Histograms of song durations and time intervals between successive songs of birds 1, 5, 6.

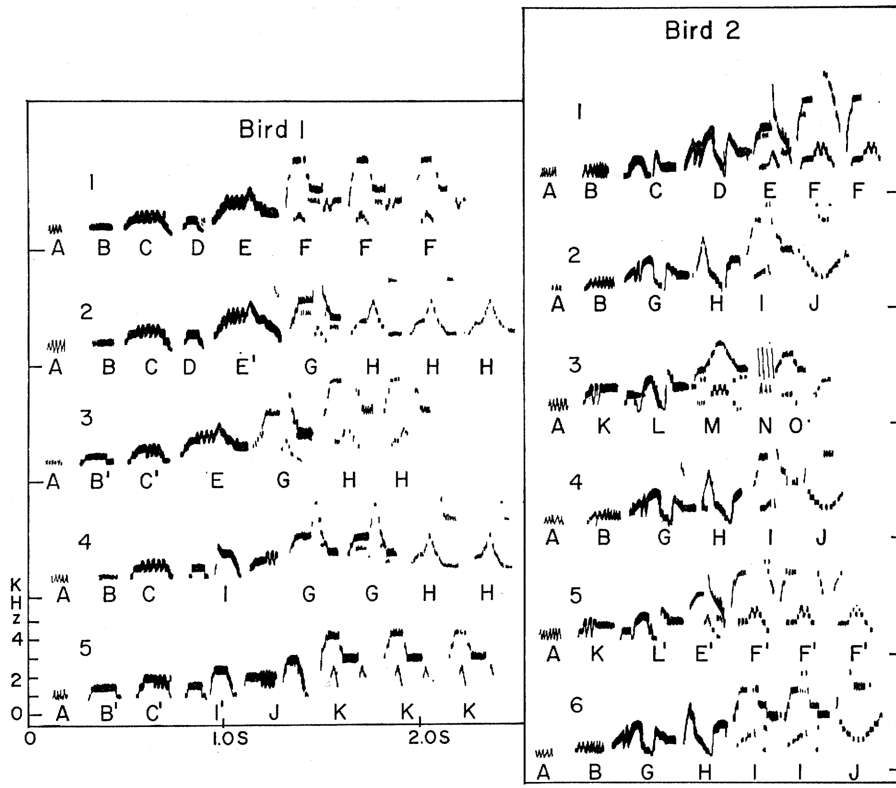

Fig. 2. The song types of birds 1 and 2 presented in the order of singing.
N.B.: C' left bottom row should read C".

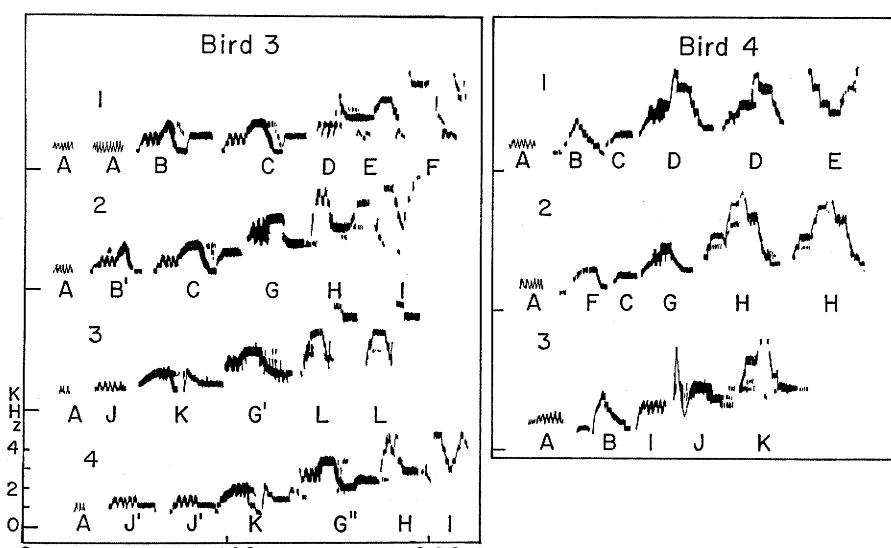

Fig. 3. The song types of birds 3 and 4 presented in the order of singing.

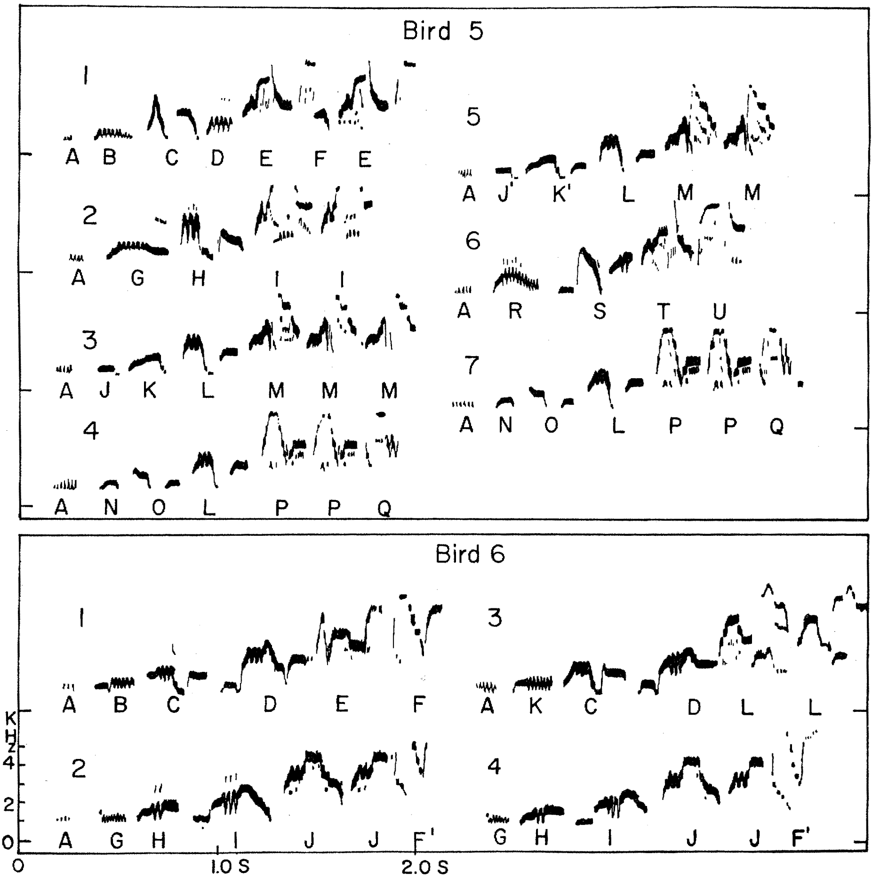

Fig. 4. The song types of birds 5 and 6 presented in the order of singing.

syllable types are labelled by letters. A syllable, as used here, refers to a unit producing a relatively continuous figure in the sonogram, separated from similar units by gaps, or periods of silence of about .05 sec. The term "syllable" is comparable to "primary pattern" used in the earlier study. The letters we applied to syllables hold only for the song types of any one bird; that is, syllable L in bird 3 has no relation to syllable L in birds 1, 2, or 4.

The syllables and song types differed greatly even among the immediate neighbors, birds, 1, 2 and 3 at Matane. However certain overall similarities are apparent. The first syllable of each bird started with a short, low-pitched quiet trill of about .15 sec. duration and frequency of 1500-1900 Hz, with 6 to 9 modulations of amplituude and frequency (Fig. 2). Following this quiet introduction, a second short whistle typically follows. This may be slightly longer (.15-.20 sec.), higher pitched (2000-2300 Hz) and often with at least part of the syllable on one sustained pitch. Parts of this syllable also may be small glides (bird 1, syllable B′) or trills or both. This second syllable is usually somewhat louder. The third syllable in a song is quite variable, but usually reaches a higher pitch, and has a greater frequency range (from about 1500 to 3000 Hz). It is also somewhat longer (.25 sec. for syllable C, bird 1) and louder than the second (Fig. 5). If the second syllable is highly modulated, the third, fourth and fifth are usually even more so. The fourth syllable in a song is usually even higher pitched than the third (to about 4000 Hz). Often the fifth syllable is the highest but is somewhat quieter than the fourth. It

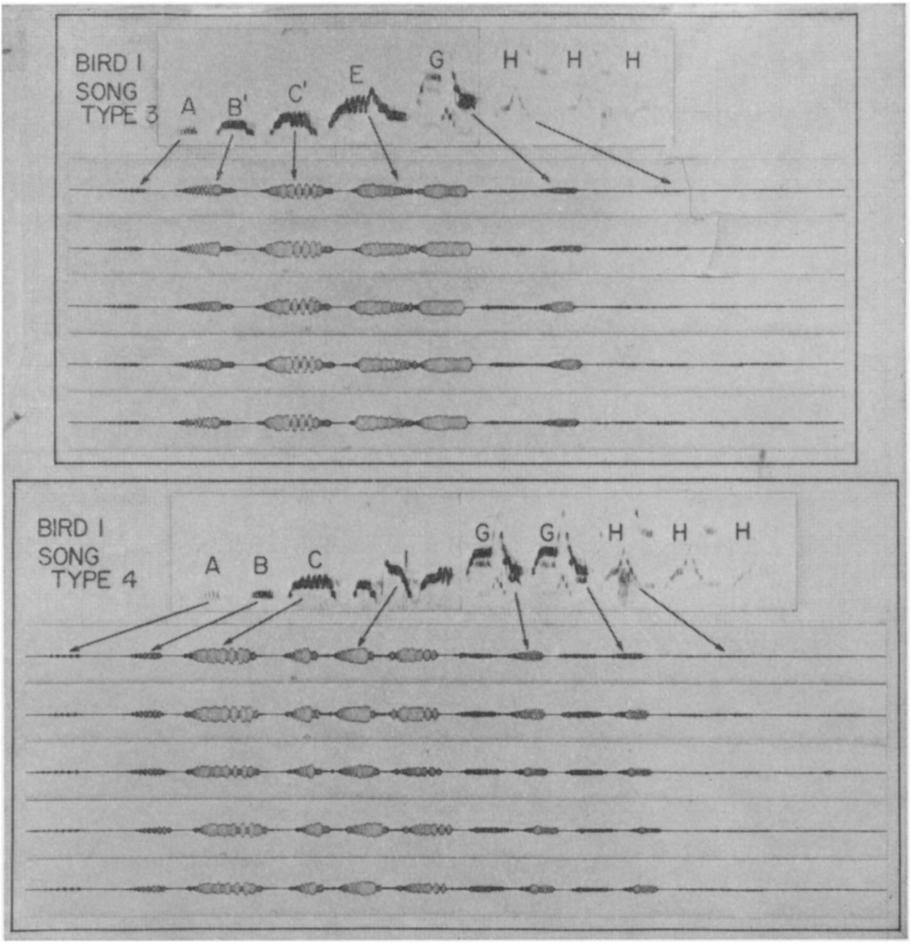

Fig. 5. Song types 3 and 4 of bird 1 shown as sonograms and in five amplitude tracings from the oscilloscope.

may be repeated once or twice, finishing the song, or may be followed by a very quiet, high-pitched terminal syllable. In individual songs the number and position of syllables varies somewhat from the generalized pattern presented above. For example song 2 of bird 1 contains a short low-pitched isolated syllable F near the end of the song separating two E syllables.

As Fig. 5 shows clearly the overall loudness of the song increases during the first four syllables, but decreases thereafter. In the second last or last syllable two voices become evident, the lower voice being softer than the upper; examples of this can be seen in several songs. The decrease in loudness at the end of the song may reflect the correlation of frequency and amplitude noted by GREENEWALT (1968); that is, frequency and amplitude first increase together but as frequency increases still further, amplitude decreases. It is possible that this applies especially to the upper voice but that the lower voice, whose frequency is not as high, is basically weak. In other words, the upper voice may be from the left side of the syrinx as in other song birds, and the lower, weaker voice from the right. Of course this is conjecture only.

SCALE RELATIONSHIPS

To the ear the songs are melodic and flutelike, with gradually rising overall pitch. We examined the frequency relationships of syllables relative to musical scales. To do so, we used a Ubiquitous Spectrum Analyser to produce frequency versus amplitude displays in which strongly emphasized frequencies stand out as peaks (Fig. 6). This process compresses the song over

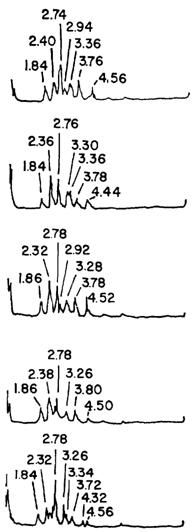

Fig. 6. Facsimiles of oscilloscope displays of amplitude versus frequency from five songs of song type 1 of bird 1. Peaks are labelled in KHz.

time so that frequency peaks cannot always be assigned with certainty to a syllable. However, since the successive syllables rise in pitch relative to each other, then successive peaks of amplitude tend to relate to the successive syllables. Therefore this method should relate generally to that used by NELSON who employed sound spectrograms. As a check we compared the peaks obtained from the Ubiquitous Analyzer with those obtained using narrow and wide band filters of the Kay Electric Sonagraph. This was done on song type 5 of bird 1 which seemed especially suitable because of the portions of sustained frequencies of some syllables. We got good agreement with narrow band analysis but not so with wide band, even when taking account of the suggestions of GREENEWALT (1968, p. 9).

In different examples of the same song type some variation in peaks occurred. We exploited only those peaks which were prominent in all of five examples analyzed of each song type. By so doing minor peaks were omitted. The result was 4 to 10 peaks for each song type, with the standard deviations of these peaks ranging from 10 to 70 Hz.

In order to confirm whether the successive intervals between peaks relate to pentatonic scales as suggested, it is convenient to convert the frequencies to logarithmic intervals such as are used for music (BACKUS, 1969, p. 292). We converted the frequency intervals to "cents", where numbers of cents $= 1200 \frac{\text{Log R}}{\text{Log 2}}$, R being the ratio of one frequency to another. As there are 1200 cents in an octave, an equal-tempered pentatonic scale would contain 240 cents between major notes. On our analysis of frequency peaks, then, we would expect intervals of roughly 240 cents.

Actually the lengths of the intervals tend to change within a song as well as from song to song (Fig. 7). The first intervals are much longer than the middle intervals, and often the last are also longer. While some of the middle intervals approximate to 240 cents, such as interval 4-5 in songs 1, 2 and 3 of bird 1, there is so much variation that any claim of conformity to a particular interval seems inappropriate. Further confirmation of the variation of intervals is seen in the histogram of Fig. 8. Even in the combined data of the proportion of intervals lie between 180 and 400 cents. Nor do these modes correspond to western musical scales, such as meantone, pythagorean, just and tempered, whose intervals cluster in multiples of 100 cents or so.

Some consistency is evident in particular intervals in different song types such as 2-3, 3-4 and 4-5 of bird 1, although the successive intervals differ from each other. This consistency results from the fact that different song types are exceedingly similar, as discussed below.

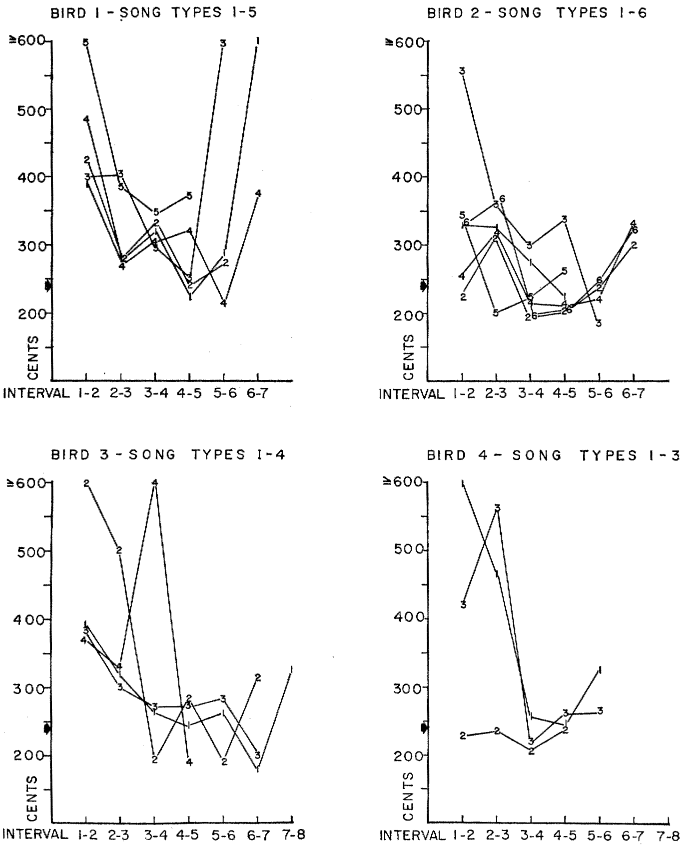

Fig. 7. Frequency intervals in cents in the different song types of birds 1, 2, 3 and 4. Intervals are designated between peaks such as 1-2. Arrows indicate 240 cents or pentatonic interval.

RECURRENCE OF THE SAME SYLLABLES IN DIFFERENT SONG TYPES

Syllables tend to be similar across song types of the same bird if found in the same ordinal position. It is difficult to know to what extent such similarities are a function of mere position within the song unless samples from a number of birds are used. The pattern of apparently identical syllables did not occur in precisely the same way among the birds we studied, but each bird used identical syllables in more than one song type. Similar syllables occurred in successive song types in some birds, while in others, intervening songs without such repetitions occurred. Sometimes different syllables followed both patterns of distribution. Following are examples from the six birds. For sake of clarity, we point out here the song types usually occur in fixed orders as presented in Figures 2, 3, 4.

Some syllables of bird 1 recurred in consecutive song types (Fig. 2). The first three syllables, A, B and C of each song type, were much alike from song to song. Syllable D appeared unconnected to E but was similar to the first part of I and I′, and it was unclear whether I and I′ might be separated into two syllables, the first of which could be labelled D; however, oscillograms such as those in Fig. 5 indicate continuity of both parts of I. Syllables K and F are also somewhat similar, especially in the upper voice. The repetition of a syllable in adjacent song types is shown by E, which appears in song types 1, 2, and 3, but not in 4 nor 5. Syllables G and H also cluster in the adjacent song types 2, 3, and 4.

Bird 2 had six song types, three of which were almost identical in form, if not pitch (song types 2, 4 and 6). The three differed consistently in their frequency peaks as shown by the frequency-amplitude analysis (Fig. 11). Syllables E and F both showed similarities to their counterparts in songs 1 and 5. Unlike the situation in bird 1, then, similar syllables did not follow in song types occurring serially, but instead in alternating song types.

Bird 3, which had four song types, had syllables which alternated and others which followed serially. Syllables B and C were in adjacent song types 1 and 2, and syllables J and K were in 3 and 4. However H and I alternated in 2 and 4, while G or a variant of G was found in 2, 3, and 4. Note also that this bird sang the first or second syllable of a song twice in song type 1.

Bird 4 had B syllables similar in songs 1 and 3 and C in 1 and 2. The first syllables were also similar in all songs, and D and H syllables are similar in song types 1 and 2.

Bird 5 from Percé had the largest number of song types, 7, but two pairs were almost identical in form (3 and 5, 4 and 7). Although the syllables appeared identical in these pairs, their absolute pitches in the second song types were all from 100 to 300 Hz higher. In bird 5, unlike in bird 1, similar syllables did not appear in consecutive song types, nor did the first three syllables of each song type resemble each other to the degree found in bird 1; however, syllables in the second position (B, G, J, N, and R) resembled each other slightly. The most shared was syllable L, found in both pairs of repeated song types.

Bird 6 had four song types. In his sequency syllables C and D occurred in alternate songs as did H and I. Songs 2 and 4 were essentially identical with slight differences in the third and fourth syllables differentiating the two. Song types 1 and 3 also contained similar syllables in the third and fourth position, and the final very soft syllable was similar in 1, 2, and 4.

SYLLABLE SEQUENCES

NELSON noted in at least one Swainson's thrush that syllables or "primary patterns" tended to repeat in the different song types in consecutive pairs or "recombination units". We have just shown that the same syllable can occur in different song types and hence can be associated with quite different syllables. So the syllables seem the basic units, not pairs of them. Further evidence of the absence of recombination units is seen in the sequences of syllables in our birds with the most song types, birds 1, 2 and 5, and with NELSON's thrush for comparison as shown in Table 2. The pairs of syllables of his example are underlined.

TABLE 2

Sequences of syllables in thrushes 1, 2 and 5 and NELSON's thrush 1, showing the assumed pairing or recombination units in the last example

Bird 1 (Matane)

1. A B C D E F F F
2. A B C D E′ G H H H
3. A B′ C′ E G H H
4. A B C I G G H H
5. A B′ C″ I′ J K K K

Bird 2 (Matane)

1. A B C D E F F
2. A B G H I J
3. A K L M N O
4. A B G H I J
5. A K L′ E′ F′ F′ F′
6. A B G H I I J

Bird 5 (Percé)

1. A B C D E F E
2. A G H I I
3. A J K L M M M
4. A N O L P P Q
5. A J′ K′ L M M
6. A R S T U
7. A N O L P P Q

Nelson's

1. A B C D′ E′ F′ L
2. A B C D′ I J′ J
3. A B C D E F L′
4. A B C D E″ F″
5. A B G H′ D″ K L
6. A B G H I′ J J

His recognition of pairs seems quite arbitrary, for repeated sequences of 3, 4, 5, or 6 syllables also occur in different song types. In our thrushes, bird 1 showed the most pairing but again the recognition of such is arbitrary. For example AB always occur together, but C occurs twice with D and I, and once with E. Pairing in birds 2 and 5 is less obvious, and in bird 5 occurs only in the nearly identical song types 3,5 and 4,7.

Instead of pairs of syllables, again it seems better to consider the syllables themselves as the units of organization, with the proviso that they are not entirely interchangeable within songs although they may occur in appropriate ordinal positions in different songs.

We might have shown overall sequences of syllables of a bird in a single flow diagram in order to show choice points or switches. However, since the sequences of both syllables and song types are fixed, the idea of choice points is also rather misleading.

VARIATIONS IN SYLLABLES WITHIN THE SAME SONG TYPE

Variations in the numbers of syllables, their forms and sequences, occurred within song types of all birds studied. The most common variation was in the number of repeated terminal syllables. Without going into detail, these terminal syllables were repeated from one to three times for each song type in bird 1.

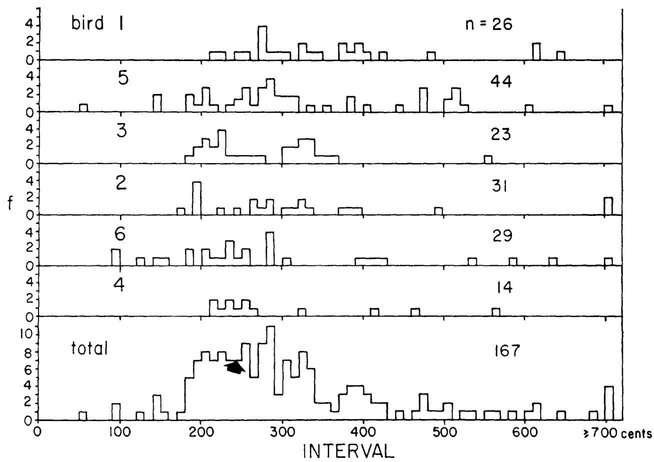

Fig. 8. Histogram of frequency intervals from all song types of each bird and all birds combined.

Other variations involved changes in the sequential order of the syllables or changes in their forms. These variations often occurred together and were considered in detail only in bird 1.

The instances of syllable variation of this bird from 333 songs are listed in Table 3. These fall into four major categories: 1) lengthening the syllable by placing an interval of silence within it (1 instance); 2) omitting part of the syllable without affecting the following sequence (3 instances); 3) shortening the syllable by omitting part and then repeating it in total (6 instances); and 4) interjecting a syllable sung earlier in the sequence (1 instance).

Variations in category (3) are interesting because they suggest the bird has done something comparable to stuttering in our speech. Alternatively he may be aware of a sudden omission of part of the song and has corrected for

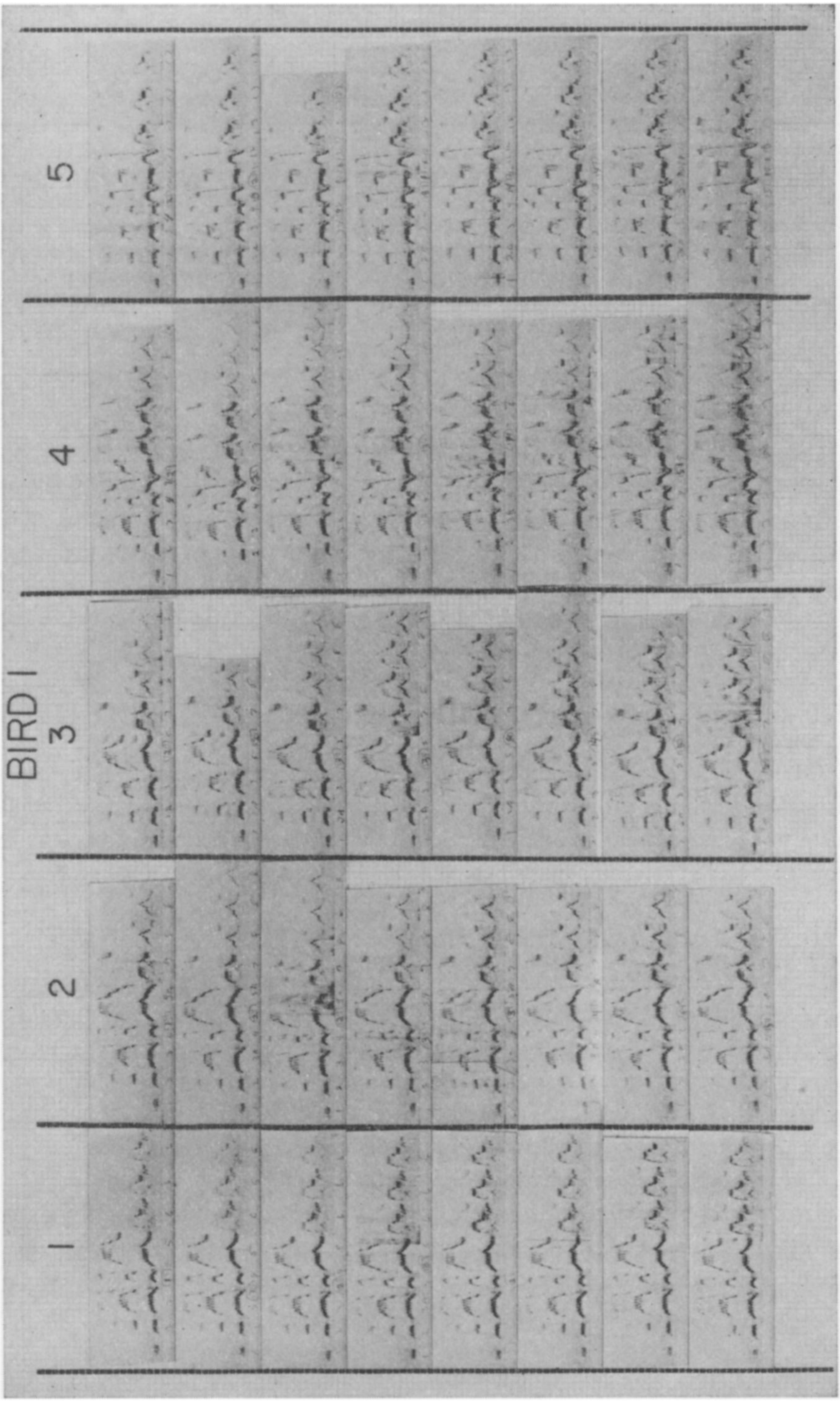

Fig. 9. Forty consecutive songs of bird 1, reading from top left to right, showing the fixed linear order of song types 1 through 5.

TABLE 3

Sequential variations of syllables within song types of bird 1

Example	*Expected*	*Observed*
1. *Syllables lengthened.*		
Song type 5	AB'C"I'JKKK	AB'C"*I'*[a])JKKK
2. *Syllables shortened.*		
Song type 3	AB'C'EGHH	AB'C'EG/H[b])H
Song type 4	ABCIGGHH	ABCI/GGHHH
Song type 5	AB'C"I'JKKK	AB'C"I'J/KKK
3. *Shortened syllable with complete syllable repeated.*		
Song type 1	ABCDEFFF	ABC/C[c])DEFFF
	"	ABCDE/DEFF
	"	ABCDE/E/FFF
Song type 3	AB'C'EGHH	AB'C'E/EGHH
Song type 4	ABCIGGHH	ABCI/IGGH (×2)
4. *One syllable shortened, another inserted.*		
Song type 5	AB'C"I'JKKK	AB'C'I'J/I'KKK

[a] *I'* means I' syllable lengthened.
[b] G/H means syllable G shortened with normal H following immediately.
[c] C/C means first syllable C shortened and second sung in entirety.

it by starting again with the first part of the syllable. We note, however, that in the second category omissions are not always corected.

Of course, we are assuming that these variants are a kind of error or deviation from the proper pattern. If they were to occur regurlarly we would have to consider them as alternative syllables or sequences of syllables as we now recognize between song types.

SEQUENCES OF SONG TYPES AND "ERRORS" OF SUCH

The sequence of song types sung by each thrush proved to be a fixed linear order which may be considered a perfect first order Markov sequence. The use of the term "linear order" recognizes differences in nearly identical song types such as 4 and 7 in bird 5, which were distinguished only by means of frequency-amplitude displays. Thrush 1 sang the fixed order in our entire sample of 346 songs recorded from him (Fig. 9).

Occasional variations in the fixed order of song types occurred in some individuals, however, and are quite instructive. Bird 5 showed several variations. His usual order of song types was 1, 2, 3, 4, 5, 6, 7. In 222 songs yielding about 30 chains of 1 through 7, eight variants occurred (Table 4). In six cases a single song type was omitted, song type 4 twice, and song

TABLE 4

Errors in the sequences of song types of bird 5-Percé

Expected	*Observed*	*Frequency*
1 2 3 4 5 6 7	1 2 3 5 6 7	X 2
„	1 2 3 6 7	X 2
„	1 2 3 4 5 6	X 4

type 7 four times. These two song types are almost identical (Fig. 4). In two other cases, song types 4 and 5 were omitted, the bird jumping immediately from 3 to 6. Again in this, 4 and 5 have near duplicates, that of 5 being 3 (Fig. 4). It is tempting to speculate that this bird's variations in order may be related on the one hand to its greater number of song types, and on the other by the similarity of the two pairs of songs in its repertoire. It is as if the near-duplicates confused the bird into assuming he had already sung the particular song type in question and he therefore skipped on to a later point in the series as in the sequence 1, 2, 3, 6, 7. Perhaps in part because of smaller sample sizes, we found no convincing variations in the sequences of our other birds, even though birds 2 and 6 also had song types which were essentially duplicates.

Such "errors" in sequence in song types, especially by bird 5 but also in the sequences of syllables such as described in bird 1 in the previous section, indicate that the birds monitor their song output. Some errors seem akin to those called Spoonerisms in our speech, particularly when one transposes the positions of particular phonemes.

A further implication of such errors is mentioned later.

During the recordings singing by other individuals sometimes occurred in the background, but with no apparent effect on the sequences of song types. In one instance a neighbor of bird 1 at Matane came within 25 feet of this bird and both uttered calls as well as songs. The vocalizations of bird 1 were recorded throughout this episode as well as immediately before and after. As noted above, no change in the song type sequence occurred. However the intervals between individual songs were about 1 sec shorter (3.93 ± 0.98 sec, $n = 43$) than those sung before or after (4.83 ± 1.16 sec, $n = 86$) ($t = 4.36$, d.f. 126, $p < .001$).

RHOMBOIDAL PATTERNING OF SEQUENCES

Following his claim that intervals fit a pentatonic scale, NELSON estimated a keynote frequency of this scale from the second syllable in each song type. He then related the sequence of song types to their relative keynotes. For example, his sequence was 2, 4, 6, 3, 5, 1, ... He then designated the first song as 0 and then listed the successive songs by their differences from the original song type, the sequence thereby becoming 0 + 2 + 4 + 1 + 3 — 1. Graphically this forms a rhomboid similar to the idealized up-2 down-3 pattern shown in Fig. 10A. He gives five examples from different species purporting to show this kind of pattern, one from his Swainson's thrush shown here in Fig. 10B.

There are several problems with these manipulations. The first is the assumption of a pentatonic scale or at least some ordered scalar relationships between frequency peaks. We have already shown the difficulty in verifying such a claim.

Even assuming the validity of some scalar regularity, there are difficulties in recognizing a keynote which to us implies some sustained frequency. The second syllables in some birds fit this demand, but in some the second syllables or indeed most syllables are so rapidly modulated that no sustained portions are evident. Our birds 4 and 5 show clear examples of these rapid modulations. Syllable A is often unsuitable also because it is quiet and is usually poorly recorded.

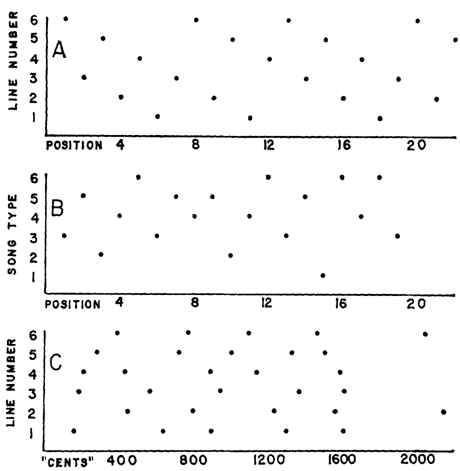

Fig. 10. Three distributions of points related to the rhomboidal model. a) A simple "up-2, down-3" model showing perfect rhomboidal patterning. b) Song types ranked according to frequency of keynote from NELSON's main thrush from his Fig. 4C. c) Distribution formed by selecting pseudo-random numbers from a Hewlett-Packard Calculator.

A third point concerns the definition of rhomboidal patterning. In such patterning one expects to see sequences of data on lines at equal angles to on axis. But in practice it is unclear how much deviation should be permitted in the alignments of the points. We make no attempt to consider this matter theoretically here. Instead we have arranged the frequency peaks of the

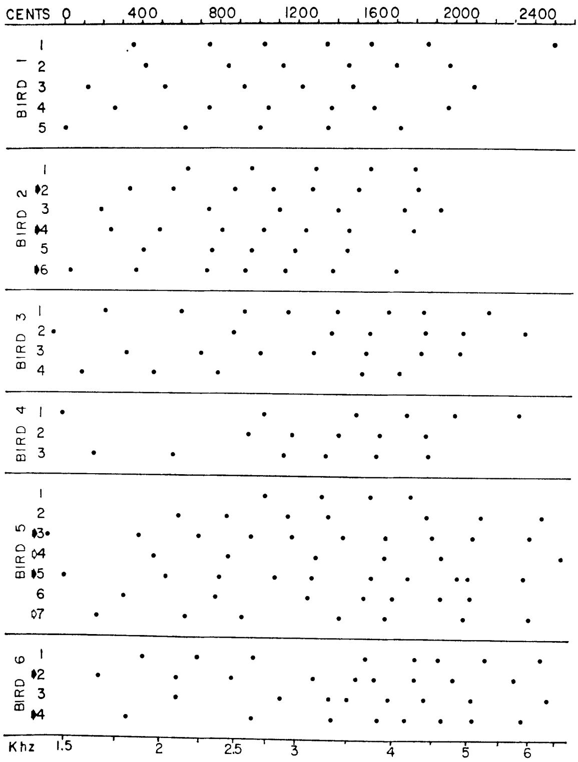

Fig. 11. The peak frequencies given in KiloHertz and in cents from an arbitrary 1.5 KHz origin. Songs with nearly identical sequences of syllables are designated by arrows.

successive song types for each of our birds and presented them in the order of their singing in Fig. 11. In spite of the lack of recognizable scale intervals, some patterning is still evident. However the lines of points bear no consistent relationships to a vertical axis. It is worth noting that if intervals are picked in a manner approaching randomness, provided they lie within certain limits, diagonal patterning may still be perceived. Fig. 10C shows such a display. Points were derived by obtaining pseudo-random numbers ranging from 0 to 1 from an HP-65 calculator, program ST 1-08, and then multiplying them by 450 and then adding 150. This yields intervals in the range of 150 to 600, about the range in cents of intervals shown in Fig. 11.

Considerable regularity in diagonal patterning can result from two or more songs in the repertoire which are much more similar than others. In NELSON'S bird, three of the six songs were similar, and the rhomboidal model does little more than emphasize it.

Such diagonal patterning as is evident in our birds 1 and 2 is also highly dependent on the similarity of some of the song types. To be explicit, song types 1, 2 and 3 of bird 1 are especially similar in the first four or five syllables (Fig. 2). What diagonal patterning is seen in the distributions of the frequency peaks as shown in Fig. 11 is particularly so between these three song types. The reader may convince himself of this point by connecting the peaks with lines. However there are no simple scale relationships between the successive intervals within a given song. This fact can be seen more clearly in Fig. 7. Here, in the similar song types 1, 2 and 3, comparable intervals, such as 2-3, 3-4, and 4-5, are nearly equal although they differ noticeably in succession within a song. The same can be said for song types 2, 4 and 6 in bird 2.

Although similar song types might reflect holistic control of entire songs as opposed to sequences of smaller units, two points oppose this view. First, were all intervals equal between successive syllables, then each syllable could be shifted upward in a holistic manner; but in the songs of bird 1 and 2, the intervals are not equal. Instead, the shift of each syllable is correlated with the shift of the syllable preceding it, leading to a first order Markov sequence.

The second point against the holistic model is that errors in the sequences of syllables also indicate the importance of syllables as the basic units of song organization. This is particularly so since errors tend to cluster around similar or identical syllables which might provide confusing choice points in Markov sequences.

DISCUSSION

In several respects the results from our study of Swainson's thrushes agree with those found by NELSON (1972). We both interpret the songs to be organized around small units which we call syllables, although we found no pairing of successive syllables into "recombination units". Within a song the successive syllables usually become higher in frequency; they appear to be based in many if not all cases on increasingly complex patterns of modulation of syllables sung previously in the song; and nearly identical syllables or sequences of them appear in different song types. In short we agree on certain of the basic features of song in this species.

In spite of this there are important disagreements. One concerns the claim that frequencies of successive syllables fit a pentatonic scale with a recognizable keynote. The successive frequency intervals tend to shorten, as noted by NELSON, but we find the variation of even the shortest intervals so great that the pentatonic interval is approached only in overall averages of a few intervals in some birds (Fig. 7). Nor did we find the intervals to fit any commonly used western musical scale other than pentatonic.

In another study, we also found no simple relationship to scale of western music in the songs of White-throated Sparrows (*Zonotrichia albicollis*) (DOBSON & LEMON, 1977) which is a species noted for sustained pure whistles. African Shrikes (THORPE, 1972) show a preference for a particular interval which could be claimed to fit more than one western musical scale. It is possible that the fairly constant interval of the shrikes is the closest obtainable while still avoiding dissonance. The shrikes differ from White-throats and Swainson's thrushes and many other birds by singing duets in which sounds of both parties may be emitted at the same time. With such synchrony, dissonance is possible if the sounds have certain frequency relationships.

Since we question the existence of a regular scale in the songs, the validity of the keynote is also doubtful. A keynote by definition must have prescribed consistent relationship to other notes or syllables. Further, the syllables of most songs lack portions of sustained frequency so that in a practical sense it is also difficult to select appropriate frequencies for measure. Many of the second or B syllables selected by NELSON as the keynote cover a wide range of frequencies in our birds.

In addition to the absence of both a regular scalar relationship between syllables and a recognizable keynote, we found little evidence of rhomboidal patterning in successive songs. We have noted, however, that any regularity of intervals yields a regularity of pattern usually seen as a diagonal arrangement of points (Fig. 10). Diagonal patterning obviously becomes even more apparent if one orders data on the basis of keynote frequencies alone, as NELSON did in his Fig. 2. Since the regularity of sequential patterning in a diagonal or rhomboidal form is an outcome of regularity of sucessive frequency intervals, the rhomboidal patterning does not seem a significant phenomenon in itself. FALLS & KREBS (1975) also failed to find rhomboidal patterning in the Western Meadowlark (*Sturnella neglecta*), one of the species also claimed by NELSON to show it.

Instead of the rhomboidal nature of sequences, we feel that they relate more to the Markov model. The fixed orders of syllables within songs and of successive song types can be handled by the Markov model and might be considered a special case of first order transitions with probabilities of 1.0. Admittedly high Markov orders become absurdly difficult to analyze and other approaches may have to be used.

The sequences of events in our study were quite fixed even when two birds sang in proximity. It is possible, however, that some variation in sequences occurs as in Blackbirds (TODT, 1975) and, as suggested by NELSON, in the Swainson's thrush. Therefore the linear control model also has advantages for some purposes over the Markov model and, of course, over the rhomboidal model also.

The songs of Swainson's thrushes are a mixture of characteristics of the individual bird and of the species. We have seen how all the songs tend to progress upward in frequency with increasingly complex modulations. At the same time the songs of immediate neighbors show little detail in common, as judged by a very small sample. It may be this lack of conformity in the repertoire which prevents influences of singing thrushes on each other's sequences of song events; mutual influences are evident in many species, including another thrush, the European Blackbird. It appears that the songs develop through improvisation somewhat in a fashion comparable to the occurrence of drift described in a number of other species (LEMON, 1975). NELSON also offers some interesting speculations as to how this may occur.

Identical syllables can occur in different song types and even entire sequences of nearly identical syllables can occur in different song types. So modulations in successive syllables are not always based on the immediately preceding events although this no doubt has an influence on where the particular syllables will occur.

We have noted that sequential errors sometimes occur much in the manner somewhat comparable to "Spoonerisms" in human speech. Such errors reinforce the importance of the Markov model. In singing a bird apparently monitors his output continuously and is able to correct errors which may arise because of confusion of syllable types.

SUMMARY

1. This paper examines a claim of NELSON (1973) of rhomboidal patterning in the songs of Swainson's Thrushes reflecting supposed holistic control of the sequences.

2. The subjects were six Swainson's Thrushes recorded in the wild in Québec. Samples from the six birds ranged from 40 to 346 songs.

3. We used a Ubiquitous Spectrum Analyzer, and Sonagraph to produce frequency-time displays, and the former to produce also amplitude-frequency spectra.

4. The songs consist of 5 to 7 consecutive syllables given in fixed sequence, except for occasional errors. Each bird had 3 to 7 song types, or particular sequences of syllables, also sung in fixed order.

5. Similar syllables may occur in different songs of individual birds. No convincing evidence of "recombination units" of syllable pairs was found.

6. Evidence essential to support the claim of rhomboidal pattern was found wanting. In particular a) the frequencies (pitches) of successive syllables do not fit a pentatonic scale; b) the validity of a keynote is doubted; c) the definition of rhomboidal patterning is so vague that even pseudorandom numbers yield results similar to those claimed for the thrushes.

7. Alternatively the Markovian model of sequences of events appears more suited to the songs of Swainson's Thrushes, based on the evidence of sequences of syllables and songs, and errors in these sequences.

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ZUSAMMENFASSUNG

1. Diese Abhandlung untersucht eine Angabe von NELSON (73) über ein rhomboidales Muster in den Gesängen der Swainson's Drosseln (*Hylocichla ustulata*), das heisst, dass eine holistische Kontrolle der Reihenfolgen stattfinden soll.

2. Die Subjekte waren sechs wilde Swainson's Drosseln, deren Gesang in der Umgebung von Quebec aufgenommen wurde. 40 bis 346 Gesänge pro Tier konnten fixiert werden.

3. Ein Breitspektrum-Analysierapparat und ein Sonograph wurden benutzt, um die Frequenz-Zeit-Entfaltung hervorzubringen; der Analysierapparat wurde ebenfalls angewandt um die Amplituden-Frequenz-Spektra zu produzieren.

4. Die Gesänge bestanden aus 5 bis 7 aufeinanderfolgenden Silben, die in bestimmter Reihenfolge gegeben wurden, mit Ausnahme gelegentlicher Fehler. Jeder Vogel hatte 3 bis 7 Gesangsarten oder bestimmte Reihenfolgen von Silben, die auch in bestimmter Ordnung gesungen wurden.

5. Gleichartige Silben können in verschiedenen Gesängen individueller Vögel vorkommen.

6. Wesentliche Beweise, um die Angabe von rhomboidalen Mustern zu unterstützen, wurden nicht gefunden. Genauer: a) die Frequenzen (Tonhöhen) der aufeinanderfolgenden Silben passen nicht in eine pentatonische Tonfolge; b) Die Anwendung einer bestimmten Tonart wird bezweifelt; c) die Definition der rhomboidalen Muster ist so unklar, dass sogar pseudo-wahllose Zahlen ähnliche Resultate ergeben als jene, die für die Drosseln angegeben wurden.

7. Auf Basis des Beweismaterials von Silbenreihenfolgen und Gesangordnung, mit Irrtümern in diesen Reihenfolgen scheint die Alternative des Markovschen Modelles der Reihenfolgen von Ereignissen mehr auf die Gesänge der Swainson's Drosseln zu passen.