A COMPARATIVE STUDY OF "ADVERTISING SONG" IN THE *HYLOCICHLA* THRUSHES

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It has recently become possible to describe the sound patterns of animals objectively because of the development of recording and sound spectrographic analysis. Bird sounds can now be recorded on magnetic tape with light-weight portable equipment, with a self-contained power supply, operated by one man.

The early method of analysis, microscopic measurement of sound film tracks (Brand, 1938) has been superseded by the sound spectrograph. The application of this latter method to bird sound analysis was first suggested by Koenig *et al.* (1946) and was restated by Bailey (1950). For a recent description of the method see also Borror and Reese (1953). The following study explores further the use of the sound spectrograph for the comparison and description of the vocal utterances of the five species of *Hylocichla*, all found in eastern North America.

The spectrograms show the actual distribution of frequency in time for an individual pattern, in this case the apparently complete "advertising song," *sensu* Lack (1943), which functions to attract females and repel males of the same species when uttered by a territorial male. The term "sound pattern" has been applied to the generalized pattern derived from all the "individual patterns" of a given type analyzed. It can also be applied to any discrete vocal utterance, such as call note, alarm note, "advertising song," etc.

Sound spectrograms of the "advertising song" patterns of several individuals of each of the five species of *Hylocichla* were made for measurement and visual comparison. These analyses are from recordings made in widespread localities, although often more than one recording of a species, or of more than one species, were made at the same locality. The recordings studied were either field recordings in the collection at Cornell University or disc recordings published by Kellogg and Allen (1941, 1955), J. and N. Stillwell (1953), and Gunn (1954).

The descriptions of the sound patterns for each of the five species follow:

Wood Thrush (*Hylocichla mustelina*).—The following recordings were used in the analyses, with the number of individual patterns of "advertising song" analyzed indicated in parentheses:

June 24, 1948, Mt. Pisgah, Saranac Lake, New York (7)
June 28, 1951, Cornell University, Ithaca, New York (12)

June 18, 1952, Ithaca, New York (9)
May 16, 1951, Ithaca, New York (13)
June 5, 1953, Swallow Falls State Park, Maryland (8)
(recorded by J. and N. Stillwell)

The sound pattern of the Wood Thrush can be divided into three sections, major divisions distinct as to frequency or complexity. The first is a series of introductory notes of lower sound intensity than the middle section. There are from two to four individual notes (average three) about 0.1 second apart. Two variations, illustrated in Plate 21, Figures 1-A and 1-B, were observed.

The middle section is loudest and is the part by which people usually recognize the sound pattern of the species. In the 49 individual patterns of the five birds studied, 21 different phrases, groups of notes which are observed as a unit, were noted. The variations were found both within an individual series of one bird and between those of different birds. Some individual patterns included two phrases, the second being more complex, as illustrated in Plate 21, Figures 1-C and 1-D. Some phrases were common to a number of individuals, but the combination of these phrases was different in individual birds.

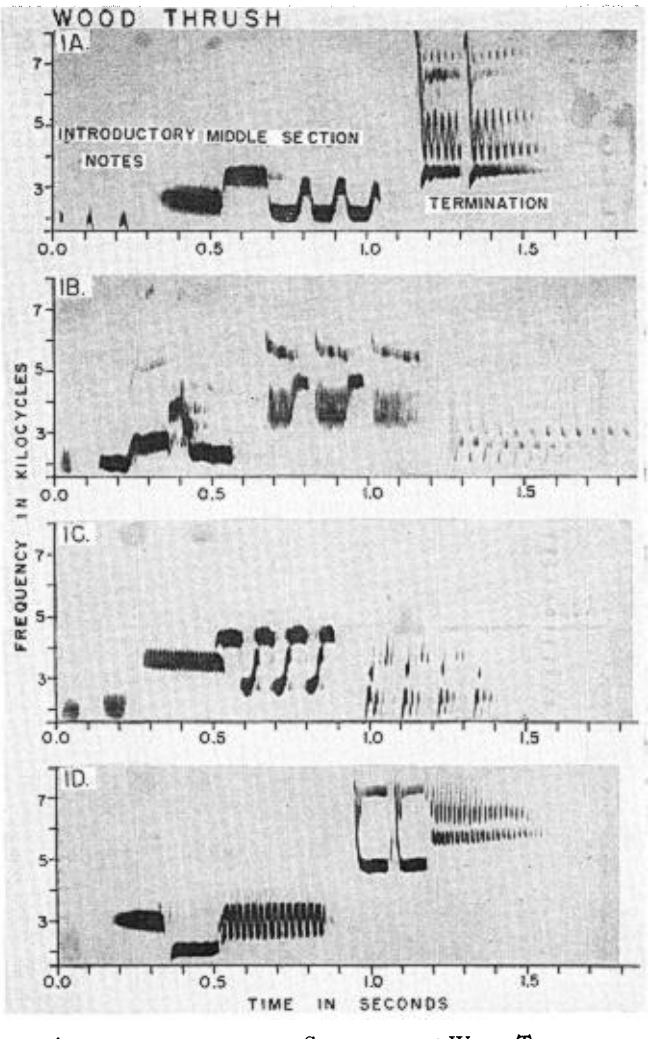
The terminal section, regularly the most complex part of the individual pattern, is characterized by having the highest average frequency of any section, and as being repetitious. At close range it frequently sounds buzzy or sometimes like a series of rapid clicks. Twenty-four variations were observed among the individual patterns studied.

In the termination, two notes are often sounded simultaneously. These notes are not harmonics, i. e. integral multiples of a fundamental frequency, and could not have been generated by the equipment. Plate 21, Figure 1-A, shows a lowest sustained note with a series of notes of higher frequency being alternated simultaneously.

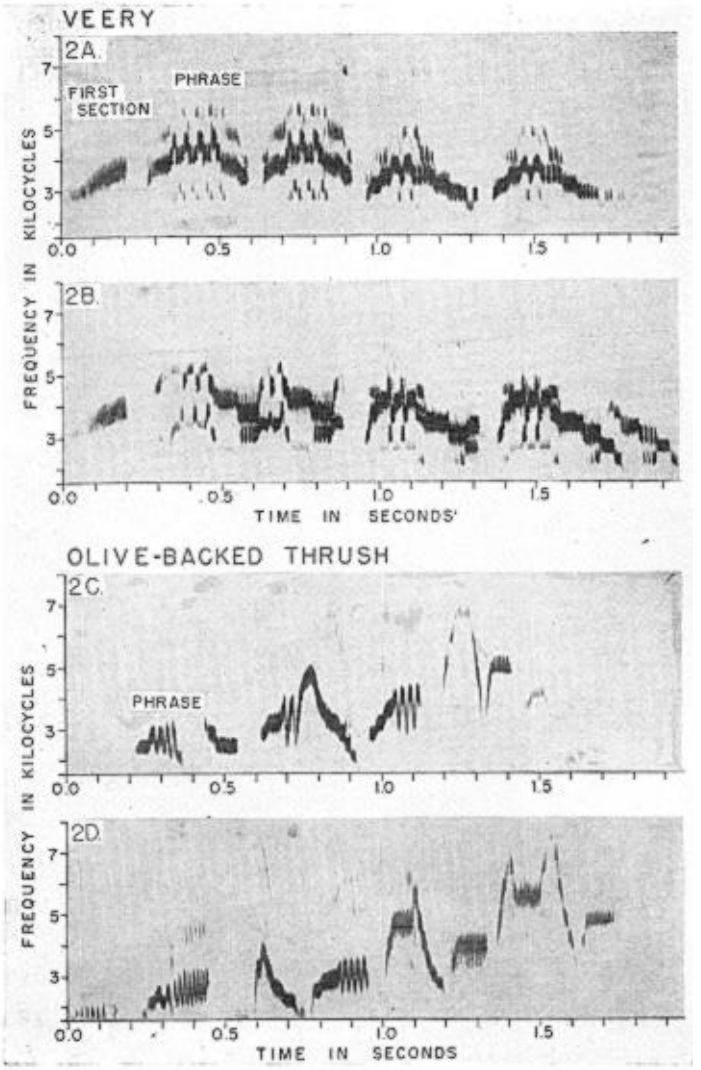
In some individual patterns a fourth section was observed, but this was regularly very similar to a phrase of the second section.

Although from previous studies parts of the individual patterns were known to be above 8000 cps., these parts were either of very short duration or were overtones and consequently were not used in these analyses. For recordings at normal speed, the sound spectrograph used has a high-frequency limit of 8000 cps.

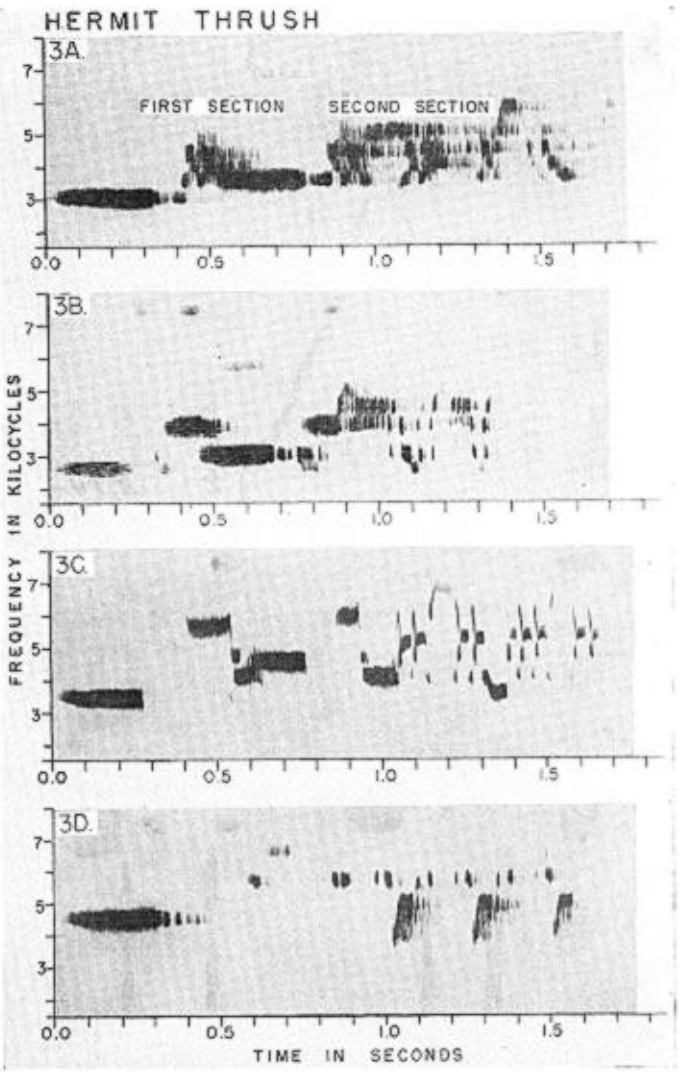
The time intervals and extreme frequencies for each of the three sections of the pattern, with the fundamental frequency averages rounded to the nearest 100 cps., are as follows (number of individual patterns measured in parentheses):



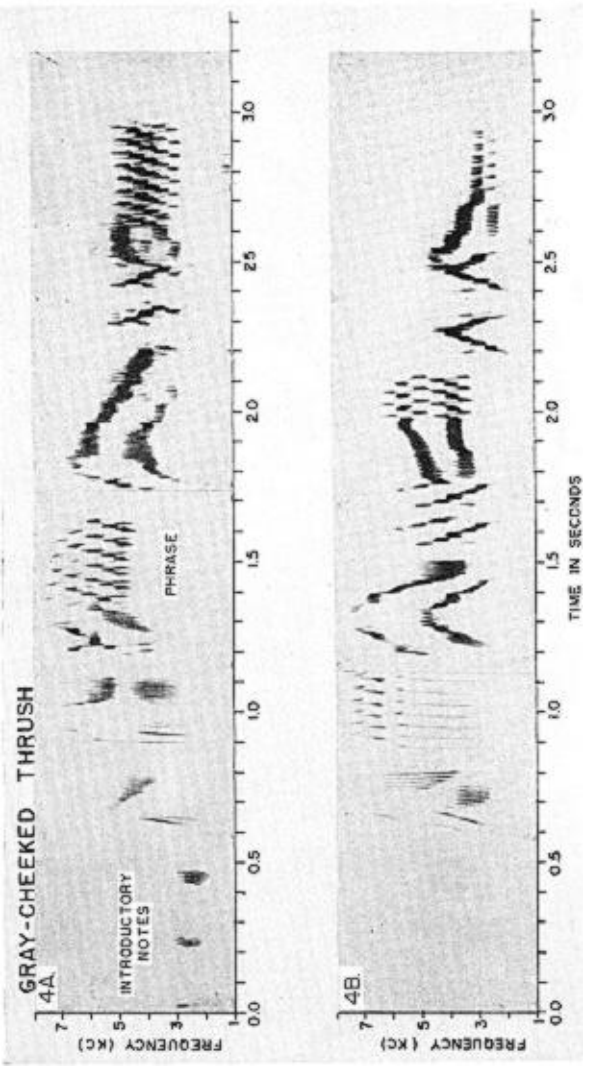
AUDIOSPECTROGRAPHS OF SONGS OF THE WOOD THRUSH



AUDIOSPECTROGRAPHS OF SONGS OF THE VEERY AND THE OLIVE-BACKED THRUSH



AUDIOSPECTROGRAPHS OF SONGS OF THE HERMIT THRUSH



AUDIOSPECTROGRAPHS OF SONGS OF THE GRAY-CHEEKED THRUSH

	Time interval (sec.)	*Highest frequency (cps.)*	*Lowest frequency (cps.)*
Introductory notes	0.21 (27)	1900 (40)**	
Middle	0.60 (49)	3600 (49)	2000 (49)
Termination	0.53 (48)	6800 (46)	3600 (46)
Total	1.56 (30)*		

* Total includes time interval between sections.

** Only the average frequency of the introductory notes was measured.

Veery—(*Hylocichla fuscescens*).—The following recordings were used in these analyses:

June 6, 1953, Sturgeon Point, Victoria Co., Ontario (5)
(recorded by W. W. H. Gunn)
June 23, 1949, Ashland, Wisconsin (5)
May 31, 1951, Ithaca, New York (5)
June 31, 1951, Ithaca, New York (5)
June 7, 1953, Swallow Falls State Park, Maryland (5)
(recorded by J. and N. Stillwell)

The "advertising song" of the Veery has two sections. The first of these is a long note, increasing in frequency (see Plate 22, Figures 2-A and 2-B).

The second section is composed of a series of phrases of essentially similar composition. Each phrase has a rising series of notes, then a series of short notes at different frequencies and arranged in a complex manner, and an ending with notes similar to the beginning, but decreasing in frequency.

Two shorter patterns, similar in general composition to the basic phrase, and uttered simultaneously with it, one each at a higher and a lower frequency, always were observed.

We recognize the species by a decrease in frequency in the "advertising song," which is easily observed in the spectrograms. Measurements of each of the phrases also suggest an increase in the length of each successive one. The following table gives the time interval

	Time interval	*Initial frequency*	*Highest frequency*	*Terminal frequency*
First section	0.24 (25)	2700 (24)	4300 (25)	
Second section				
Phrase I	0.34 (25)	3800 (25)	5300 (25)	3000 (25)
II	0.34 (25)	3400 (22)	5100 (25)	2900 (24)
III	0.36 (25)	2600 (21)	4200 (24)	2400 (24)
IV	0.46 (17)	2600 (17)	4400 (17)	2200 (17)
V	0.34 (4)	2300 (2)	4000 (4)	2100 (2)
VI	0.52 (1)	2400 (1)	4300 (1)	2300 (1)
Total	1.84 (25)			

and frequencies (averaged to the nearest 100 cps.) for each of the various sections and phrases.

The most common number of phrases observed in the second section was four, with a range from three to six. Three of the individuals had four phrases in each individual pattern, and one had a single pattern with three. The fifth Veery had double-peaked phrases in each of its individual patterns. A pattern from this individual is illustrated in Plate 22, Figure 2-B. For frequency measurements each peak was considered to be in a separate phrase.

Even considering the peculiar patterns exhibited by this last Veery, the species probably has less variation in sound pattern than any of the other *Hylocichla* thrushes. Spectrograms from birds recorded at Ithaca were almost identical; those from the Maryland recording show only minor variation. The most frequently observed variations are in the terminal phrase, which in each individual bird seems to have a characteristic form.

Hermit Thrush—(*Hylocichla guttata*).—The recording data for the five individuals studied is as follows:

June 20, 1951, Bay Pond, New York (8)
June 29, 1953, Whiteface Mountain, New York (5)
(recorded by J. and N. Stillwell)
June 17, 1951, Elk Lake, New York (5)
June 18, 1951, Elk Lake, New York (5)
June 11, 1953, Lake Pocono, Pennsylvania (5)
(recorded by J. and N. Stillwell)

Like the Veery and the Olive-backed Thrush, the sound pattern of the Hermit Thrush does not have a series of introductory notes. The sound pattern appears more variable than those of the other four species. To many people the pattern strongly suggests that of a Wood Thrush.

Aurally, the individual patterns of a Hermit Thrush may be divided into two categories on the basis of average frequency. Extreme examples are easy to distinguish, but intermediate forms, which occur quite regularly, present problems and make less apparent the distinctness of the extreme types. On the Stillwell (1953) recording, examples of both extremes are pointed out in the vocal commentary.

The sound pattern has two sections. The first contains some sustained notes in a pattern suggesting the middle section of the Wood Thrush song, to which it might well be homologous.

In this section there are frequently short time intervals without sound, as there are in the middle section of that Wood Thrush in-

dividual pattern which has two phrases. However, a time interval is sometimes absent between the two sections of the Hermit Thrush pattern. Plate 23, Figure 3-A, illustrates a series of short notes within the first section which is also found in the second section. Both sections have about the same time interval.

The second section is more complex and variable than the first and is in many ways similar to the terminal section of the Wood Thrush pattern. Plate 23, Figures 3-B, C, and D, shows some of the variation in individual patterns.

The spectrograms from individual birds are very different from one another. Two birds show distinct notes in the second section of their patterns, while the other three recordings show blurred notes. Each of the birds showed a wide frequency range in both sections of the sound pattern.

The averages derived from the 28 individual patterns analyzed from the five individuals follow:

	First section	*Second section*	*Total*
Time interval	0.76 sec.	0.77 sec.	1.59 sec.*
Low frequency	2700 cps.	2900 cps.	
High frequency	4900 cps.	5700 cps.	

* Includes time interval between sections.

Olive-backed Thrush (*Hylocichla ustulata*).—The spectrograms studied were made from the following recordings:

July 25, 1953, Bonaventure Island, Quebec (5)
June 22, 1948, Mount Washington, New Hampshire (5)
June 23, 1949, Bay Pond, New York (5)
June 17, 1951, Elk Lake, New York (5)
July 5, 1953, Whiteface Mountain, New York (5)
(recorded by J. and N. Stillwell)

Aurally the sound pattern of the Olive-backed Thrush is characterized by an increase of frequency. The spectrograms show that the sound pattern is not divisible into major sections, as are those of the other four species, but has instead a series of short phrases with an alternation of relatively higher and lower frequencies. A comparison of the lower or higher phrases, when studied in sequence, always shows a relative frequency increase, with the highest frequency near the end of the sound pattern.

No introductory notes are indicated on the spectrograms, or are noticeable on critical listening to the recordings. These phrases

seem like simplified versions of those of the Gray-cheeked Thrush and vary in number from three to ten (average seven).

Each individual tended to repeat phrases, but such similarity was not observed among individuals. The three New York recordings, unlike the others, each show alternations of two individual patterns. The six patterns (two each from three individual birds) are all different. Plate 22, Figure 2-D, shows a pattern from the Elk Lake recording.

Individual patterns of the Quebec recording all have essentially the same beginning, but with some addition and modification of phrases. The endings of the patterns are all different, two of them having echo-like, weak final phrases. The New Hampshire recording, a pattern of which is illustrated in Plate 22, Figure 2-C, has three different beginnings and three different endings, but no entire sound pattern was repeated among those analyzed.

Because of the large number of different phrases observed, the variety of ways in which they were combined, and the small number of representatives of each different phrase in the analyses made, no detailed frequency analysis of individual phrases was calculated. The following average figures, however, were derived from all the individual patterns:

Total time interval	1.62 sec.
Lowest frequency	1600 cps.
Highest frequency	6500 cps.

There are no sustained notes of the type found in the Wood and Hermit thrushes. There is also no indication of two notes being produced simultaneously, other than harmonics.

Gray-cheeked Thrush (*Hylocichla minima*).—Recordings of only four individual Gray-cheeked Thrushes were available for this study:

June 17, 1953, La Tabatière, Quebec (6)
June 29, 1953, Mount Mansfield, Vermont (5)
July 9, 1953, Mount Mansfield, Vermont (5)
(recorded by J. and N. Stillwell)
June 29, 1954, Fort Churchill, Manitoba (7)

The pattern of the Gray-cheeked Thrush is in many ways the most complex of the five species studied and is, on the average, the longest. Aurally it suggests that of a Veery with some added elements at the end. The commonly recognized call notes of the two species also sound very much alike, but no spectrograms of these were made.

The first section of the Gray-cheeked Thrush sound pattern is a series of introductory notes, which are all at one frequency in an individual pattern and are very similar to the introductory notes of the Wood Thrush. Although they were not observed in most of the spectrograms, this omission may have been owing in some cases to the fact that they were too weak to be picked up by the recording or analyzing equipment.

The second section of the sound pattern is composed of a series of complex phrases. There was a tendency for different birds to use some similar phrases, and to use them in a similar order within the section.

Each individual bird seemed to use a characteristic ending, except for one pattern of one bird. In contrast to this individuality, the first phrases tended to be similar among the various individuals. Figures 4-A and 4-B on Plate 24 illustrate sound patterns from the June 29, Mount Mansfield recording and the Fort Churchill recording, respectively. Some of the phrases show the complex arrangement of short notes, with more than one note being sounded simultaneously. Some phrases are repeated two or three times in an individual pattern. In several cases very similar phrases were observed in the spectrograms from individual patterns of both the Olive-backed and Gray-cheeked thrushes.

Individual birds repeated individual patterns regularly, although not in succession.

The highest frequency for almost all of the individual patterns was above 8000 cps. The endings of the terminal phrases varied from 2000 to 6000 cps. but were much less variable for any individual bird. The two recordings from Mount Mansfield, with almost the same terminal phrase, have different frequency ranges for the last part: one 3900–6300 cps., the other 2700–5300 cps. (averages from five observations each).

The average individual pattern length, exclusive of introductory notes, was 2.14 seconds. The number of individual introductory notes varied from zero to four, with 0.1 to 0.2 seconds between notes. The frequency range of these notes was 2600 to 3600 cps., although the range for an individual bird was not more than 200 cps.

The individual birds whose patterns were analyzed show a remarkable similarity of phrases among individuals. However, because of the complex arrangements of phrases, the songs of these individuals were distinct.

DISCUSSION

Each of the five species of *Hylocichla* has a general sound pattern which is distinct in many ways. Certain characteristics of these patterns may be found in more than one species.

The Wood Thrush song usually has a three-section pattern: the introductory notes, a middle section with sustained notes, and a termination usually at a distinctly higher frequency and having more complex frequency distribution.

The sound pattern of the Hermit Thrush has two sections, the first of which, like the middle section of the Wood Thrush pattern, regularly has long, sustained notes. The second section is more complex and often at higher average frequency, as is the terminal section of the Wood Thrush pattern. It frequently contains short notes in a repetitive arrangement at more than two frequencies. Introductory notes are lacking.

The Veery also has a two-section sound pattern. The first is a rising note, and the second is a series of phrases essentially similar to one another. This second section has a complex arrangement of short notes in each phrase. There is an average frequency decrease in the successive phrases.

The Olive-backed Thrush has a one-section sound pattern composed of a series of phrases of increasing frequency. The notes are relatively simple and pure. As in the Hermit Thrush and Veery, there are no introductory notes.

Similarly, the Gray-cheeked Thrush may appear to have a one-section sound pattern, since the introductory notes are often weak or absent. The remainder of the sound pattern is a series of phrases. There is no distinct general frequency trend, although there is some evidence for a high frequency peak in the middle of the pattern. The sound pattern of this species is the most complex of those studied. The phrases in some instances show a similarity to some at the beginning of the Olive-backed Thrush sound pattern. In some parts of the pattern, short notes at more than one frequency were observed.

With the exception of the Wood Thrush and Hermit Thrush, sympatric species have distinct contrasts in sound pattern. The Wood Thrush, which has a breeding range overlapping to some extent all of the other species except the Gray-cheeked Thrush, has characteristic sustained notes. The breeding range of the Hermit Thrush overlaps to some extent those of the other species except the Gray-cheeked Thrush. Its sound pattern is especially similar to that of the Wood Thrush. The pattern of the Olive-backed

Thrush contrasts in its relative simplicity to that of the Gray-cheeked Thrush and in frequency increase to that of the Veery. Certain phrases of both the Gray-cheeked and Olive-backed thrushes are very similar in pattern.

Sound patterns of species allopatric during the breeding season show some similar characteristics. This is true of the Veery and Gray-cheeked Thrush in sound quality, and of the Wood Thrush and Gray-cheeked Thrush in introductory notes. The apparently anomalous situation of the Wood and Hermit thrushes might be explained by the recent range extension northward of the former species into part of the range of the latter.

It is also suggested that species which have ranges overlapping the largest number of closely related species have sound patterns distinctive in different characteristics. In contrast to the other *Hylocichla* species the Wood Thrush has a three-section sound pattern with quite audible introductory notes. The Olive-backed Thrush has a relatively simple pattern of frequency distribution and a definite frequency increase. The Veery has a distinct frequency decrease and repetition of similar phrases.

Because all of the sound patterns analyzed were of "advertising songs," they were similar in function. These sounds have the same physical origin also. In order to be considered homologous, the songs must, by definition, be similar in structure. The following similar sections of patterns are from allopatric or recently sympatric species: the introductory notes of the Wood and Gray-cheeked thrushes; the middle section and termination of the Wood Thrush's song and the first and second sections of the song of the Hermit Thrush, respectively. The following, probably also homologous, have developed modifications in sound structure which appear to have resulted from selective pressures because of sympatry: the second section of the Wood Thrush's song and the first sections of the songs of the Veery and Hermit Thrush; the first section of the Hermit Thrush's and Veery's songs; and the second sections of the songs of the Hermit Thrush, Veery, and Gray-cheeked Thrush to the complete song of the Olive-backed Thrush.

The preceding analyses of sound patterns indicate the greatest similarity of component parts between the Wood Thrush and Hermit Thrush and between the Olive-backed and Gray-cheeked thrushes. The sound pattern of the Veery appears more closely related to that of the former pair.

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