HOWLING AS A MEANS OF COMMUNICATION

IN TIMBER WOLVES (*Canis lupus*)

by

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I

INTRODUCTION

Many species of animals form social groups - from loose aggregations to strong tightly bound units. A group is considered social "when the members stay together as a result of their social responses to one another rather than by responses to other factors of the environment." (Etkin, 1964). "Responses to one another" implies communication. Communication "is now recognized as the mechanism by which all essential interactions between organisms are accomplished; a system of transmitters and receivers which intergrates organisms and coordinates their activities into functioning social groups or communities ...." (Borror, 1960).

Auditory communication is but one type of communication among animals (others are visual, tactile, and olfactory). Yet it is common, especially among terrestrial vertebrates. An understanding of auditory communication - its information content and signal value, is essential to an understanding of the behaviour of social species which vocalize.

How can we set about understanding an animal's language? There is a basic problem. The tools we must use to decode animal sounds are our human brain, our human ear, and our electronic gadgets. The tools any given species uses to decode intraspecfic sounds are its brain and its ear. Since we very imperfectly understand the sensory world of animals, we are at a great disadvantage.

Nevertheless, if we systematically classify an animal's sounds and attempt to relate the sounds to the conditions and environment of the sender, we might be able to find potential information content in the sound - units of sound that correspond to specific conditions. Then, if we can ascertain that a receiving animal can detect these sound units, and as a result alters its behaviour, we have demonstrated that potential information is actual information, and communication has taken place. This is the approach I have attempted in this study.

Besides the basic problem mentioned above, others are inherent in research of this type. Subtle behavioural changes that might indicate that potential information was comprehended are difficult to recognize, particularly with a wolf, where the observer's known presence often acts as a disturbance. The objective description and classification of sound units that might be carrying information can only be a trial and error technique. Mammalian studies are so few that nomenclature does not exist. Perhaps the biggest problem lies in the fact that captive animals provide the only source for detailed studies. Certainly this is true for the timber wolf where observation in the wild is rare. Wild animals put into captive conditions usually exhibit profound disruptions in normal behaviour (Schenkel, 1947). Animals captive all their lives lose the opportunity to learn in their natural environment.

These are the problems. Despite them, advances are being made, particularly in arthropod and bird acoustic behaviour studies. High quality tape recorders and the sound spectrograph for studying sound are mainly responsible for these advances.

Mammalian studies however, are few, partly because of the difficulties of keeping large animals in laboratory environments. The field that has received the most investigation in mammals is that of ultrasonics. Echolocation has been studied in two orders, the Chiroptera and Cetacea. Besides ultrasonic studies, sonic study has been made of the vocalizations of the Northern elephant seal (Bartholomew and Collias, 1962). Tembrock (1963) has made a general survey of the frequency range and types of sound for a large number of mammals, but this was not a detailed study of individual species. Behaviour studies of Primates have yielded parhaps the most information on vocalization in mammals, although detailed sound analysis has not been undertaken. Howler monkeys are believed to have "fifteen or twenty distinct and important vocal patterns in their repertoire." (Carpenter, 1934). Studies such as Carpenter's, and those by Altman (1959) and Bernstein (1964) have yielded information under wild conditions as to the function of different vocalizations and the behavioural responses of receiving animals. Studies by Schaller (1963) list twenty-one vocalizations of the mountain gorilla heard in the wild, along with the situation in which the sounds occurred, their probable functions and appraisal of the animal's emotions.

Types of Sound in the Canidae

The types of sounds of the fourteen genera (Cockrum, 1962) of the Family Canidae are the bark, whine, yelp, whimper, growl, and howl (Tembrock, 1963, Colby, 1965, Huxley and Koch, 1964). Barking is perhaps the most common sound form. A precise discussion of the occurrence of these types of sound cannot be undertaken since they have not received sufficient study. For example, Tembrock (1963) does not list whining, a sound form commonly heard and recorded during my investigations, for Canis lupus. Canis familiaris is not listed by him to whine or yelp, these both being common "dog sounds". Huxley and Koch (1964) say, "The wolves do not appear to have a true bark, given separately from howling." Although barking was rarely heard in captivity during my study, Dr. D. H. Pimlott (pers. comm.) taped wild wolf barking at Annie Bay, Algonquin Park, Ontario, in August 1962.

Also complicating a detailed discussion of sound forms is a lack of common nomenclature. Bleicher (1963) in studying dog vocalizations, reports "pup groan" and "grunt", sounds not mentioned elsewhere.

Because of these problems and since this study confined itself to one sound form, the howl, these other sound forms will not be discussed in detail.

Howling is reported for Canis lupus, C. latrans, C. familiaris, C. dingo, C. aureus, C. anthus, C. adustus, C. mesomalas (Tembrock, 1963), C. niger (Joslin, pers. comm.), Cuon alpinus, Chrysocyon jubatus, Nyctereutes procyonides (Colby, 1965). Tembrock (1963) states, "All data on these sound forms howling outside the species Canis (obvious error - should read genus Canis) are problematical. There are references to Vulpes vulpes L. and Alopex lagopus L., but the homology is most doubtful. Nyctereutes has a howl-like sound. Chrysocyon jubatus Desm. has a sound which has a certain similarity with howling, but which is unlikely to be homologous. Thus all definite findings are confined to Canis." He states that the barking "stanza" (series of barks) occurs in the place of howling and is homologous to howling in Alopex, Vulpes, and possibly other genera, satisfying his first criterion of homology, occurrence in similar circumstances. Also, they have structural similarities - the "last sound of the barking sequence may be drawn out" (in Vulpes), and, "the howling stanza of Canis has distinctly recognizable barking components," thus satisfying his second criterion of homology. He goes on to state, "The howling stanzas ... are derived from the barking stanzas."

Tembrock (1957) has made the only detailed study of vocalizations of an adult canid - Vulpes vulpes. He classified "about forty forms of sound (in roughly 28 groups)." (Tembrock, 1963). Since howling is not a sound form of Vulpes, this study is not directly related to mine, except in terms of the suggested homologous relation of barking and howling.

Scott and Fuller (1965) in their detailed book "Genetics and the Social Behavior of the Dog" confine their remarks on vocalization to that of pups. Their studies center around pup behaviour and so lend little to my study.

Therefore, as far as could be determined, no study of howling as a sound form has been undertaken, except that of an inventory nature by Tembrock.

Literature on Wolf Howling

Although specific sound studies have not involved wolves, there is a great deal of literature about wolf howling. Man has responded emotionally to the howl of the wolf for generations. Perhaps the sound of no other animal has captured our imagination as that of the wolf. Pioneer accounts of the settling of Canada invariably talk of wolves and their howling, describing howls with adjectives such as "terrifying" and "savage". Besides this historical writing, wolf howling is discussed in books designed to be scientifically accurate. Young and Goldman (1964) state that "the wolf utters five distinct vocal sounds." Two of these are howls - "... a loud, throaty howl, seemingly a call of loneliness. It is best heard in zoological parks where either the male or the female wolf is confined alone; and when a sudden loud noise such as the sound of a whistle, a clap of thunder, or the clang of a fire-bell causes the animal to give voice. This long lonesome-sounding howl is also uttered during the breeding season (Dec., Jan., and Feb.)." The second type of howl is "a loud, deep gutteral, though not harsh, howl, apparently the call of the chase, that generally is given by an adult male and is answered by other wolves on the hunt for food. It might be termed a call for assembling a group of wolves in the same vicinity. This gutteral howl may at times be followed by a loud bark or two similar to that of a Newfoundland dog." Young and Goldman go on to cite some quotations of an historical nature such as one by R. F. Kurtz. "Their speech is a howl, which varies according to the motive that actuates the beast. When the wolf is hungry or gets the scent of something he dares not tackle he sends forth a prolonged, dismal howl ...."

Since Young and Goldman present no supporting evidence for their generalizations on wolf howls except the opinions of others, their remarks cannot be considered as scientific evidence.

Huxley and Koch (1964) state, "The wolf produces two distinct kinds of howls. There is first the solo howl, which Mr. Koch believes is given by the leader of the pack." (My observations do not confirm this statement). "This is different in various ways from the howlings which go to make up a chorus." Unfortunately, he does not say in what ways these differ.

The remarks by Huxley and Koch were based on a limited study of wolf vocalizations. The emphasis of their work was on a general survey of a large number of animals. The observation that solo howling differs from chorus howling is interesting - one which I was not able to assess.

Crisler (1958), who observed wolves in the Arctic, states, "there are many howls - the happy social howl, the mourning howl, the wild deep hunting howl, the call howl. All are beautiful. The wolf's voice is pure except when the wolf is crushed by despair. The only set pattern is that of the mourning howl. The others vary but the meaning is clear. Mountain men in the old West gathered valuable clues about movements of Indians and wild animals from the changeful voices of the wolves."

In personal communication Crisler suggests that the hunting howl should have been "social howl at or near the start of the hunt since wolves are silent when hunting."

By living with wolves in natural surroundings, Crisler had a unique opportunity to observe acoustic behaviour. Unfortunately she is unable to describe the differences between the types of howls, and has no recordings (pers. comm.).

Ecological studies of wolves make reference to wolf vocalizations. Murie (1944) describes fourteen instances of vocalizations - howling or barking. No description of the sound is made. Pimlott (1961) discusses the "howling technique" used to locate wolves in ecology studies in Algonquin Park, Ontario. Both tape-recorded wolf howls and human howls were found to elicit howling by wild wolves enough times to make this technique valuable in locating wolves. It is from this research program, in which I participated, that the background planning of the present study originated. While conducting an "auditory census" of wolves and studying the summer movements of packs during the summers of 1960, 1961, 1962, and in discussions with Dr. Pimlott and other members of the research team, many questions and possibilities arose as to the ecological significance of wolf howling. It became obvious that basic questions needed answering before the potential of wolf howling as a communicatory mechanism could be assessed. This thesis attempts to answer some of them. In a final section, the possible ecological significance of the results of this study will be discussed.

Statement of Purpose

This study attempts to determine the communicatory function of wolf howling by intensive study of the howls of individual captive wolves. Specifically, the following questions were assessed:

1) How much individual variation exists in wolf howls?

2) Does variation in wolf howls correlate with the behaviour or situation the wolf is in and thus represent units of potential information?

3) What ability does a wolf have to distinguish sound variation?

4) What circumstances surround spontaneous howling (howling which was not elicited by auditory stimulation)?

5) What is the ecological significance of howling?

The assessments of each of these questions form the five major sections of this thesis.

II

MATERIALS AND METHODS

Three wolves (Canis lupus) were used in the study. All were male members of the subspecies lycaon (Young and Goldman, 1964), born wild, but captured when approximately one month of age. They have spent their life, with the exception of Wolf B, in the pens at the Wildlife Research Station, Algonquin Park, Ontario. Wolf B was allowed partial freedom up to the time he was two years old. The ages of the wolves in the spring of 1964 were; Wolf A - two years, Wolf B - four years, Wolf C - three years.

In order to record vocalizations of individual animals, a pen was constructed. Its dimensions were 16 feet x 8 feet x 8 feet high. It was made of chain link wire and angle iron, with a floor consisting of pine needles and shavings. A shelter house, food trough and water bucket were included within the pen.

In the summer of 1964, the pen was erected three and one half miles from the Wildlife Research Station. This afforded both physical and auditory isolation for experimentation. One wolf, Wolf A was housed at this location. In the summer of 1965 the pen was re-constructed one quarter mile away from the group pens at the Wildlife Research Station, affording visual isolation but not always auditory isolation. Three wolves were housed individually for short periods of time (two to three weeks) at this location - Wolf A, Wolf B and Wolf C. Wolf A was housed there for two different periods during the summer.

In 1964, tests were conducted and recordings made from a cabin approximately 70 feet from the pen. A window afforded a view of the pen, but due to its placement did not allow the wolf to see the observer. In 1965, experiments were conducted from a tent 50 feet from the pen.

Both summers work involved recording as many howls as possible. Recordings were made with a Uher 4000 Report-S tape recorder and microphone at 7½ inches per second. Sound analysis was made with a sound spectrograph (Missile Data-Reduction Spectrograph, Kay Electric Co., Pine Brook, N.J.).

Play-back tests during the summer of 1964 were conducted mostly at night, the usual time of wolf howling in wild conditions. In 1965, day work predominated after experimentation showed no difference between day or night results. Playback equipment in 1964 was the same Uher 4000 Report-S recorder and either its built-in monitor speaker or a 12 inch speaker in a wooden cabinet 13 inches x 14 inches x 10 inches. In 1965, in addition to these two systems, a custom built play-back machine (15 inches per second) with the 12 inch speaker was also used.

Spontaneous howling (with no known auditory stimulus) was recorded whenever possible.

All daytime recordings were accompanied by detailed notes of behaviour. Movie film (Bolex 16 mm. camera) was made to supplement notes.

Detailed methods will be discussed at the beginning of each section of this thesis.

III

DESCRIPTIVE ANALYSIS OF WOLF HOWLS

A major part of this study was an effort to ascertain the extent of individual variation in wolf howls by examining various features of the howls themselves. Tape recordings were made of as many howls as possible. Howls were elicited by auditory stimulation of the wolf or occurred spontaneously, with no known auditory stimulation. For the purposes of analysis, both types of howling, stimulated and spontaneous, were combined for each wolf.

The descriptive analysis of wolf howls falls into two separate sections; analysis of the sound fundamental, and analysis of sound harmonics.

Sound Fundamental

By definition, the fundamental is the lowest frequency in the sound produced by a vibrating string (Borror, 1960).

Howls were graphed by means of the sound spectrograph until the features to be studied could be recognized by ear. Slowing the howl down by playing the recorder at a reduced speed was found to be helpful. Since the number of howls in the collection was large, spectrographic analysis of each howl was not feasible due to the time required to make each graph. However, human auditory discrimination of the features studied was at least as accurate as sonographic analysis.[1]

Howls were divided into three parts - beginning (the first 0.5 seconds of the howl), ending (the last 0.5 seconds of the howl) and body (the howl between the beginning and ending).

Beginning. - Three types of beginnings were apparent - one in which the howl was initiated on a comparatively low note and broke upward abruptly to a high note (Plate III (h)), one which began on a high note and decreased gradually in pitch or remained at constant pitch (Plate VII (y)), and one which rose smoothly in pitch (Plate I (b)).

Table 1. - Type of Beginning of Howls

Wolf	Number of Howls	Break Upward (Percent)	Begins High (Percent)	Smooth Rise (Percent)
A	393	10.4	1.5	88.1
B	184	99.5	0.5	0
C	120	83.4	16.6	0

Each wolf showed a marked individual preference for type of beginning of howls (all three had a category into which at least 83% of their howls fell.) (Table 1). Of the howls of Wolf A, 88.1% were distinctive from all the

[1] When determining notes, auditory analysis was more accurate than spectrographic analysis due to the width of line and confidence limits on the frequency calibration of the machine. The accuracy of auditory analysis was confirmed by rechecking at random. Results fell within the range of values indicated by spectrographs.

howls of the other wolves, since he was the only wolf producing beginnings that rose smoothly in pitch. He began on a high note on six of his howls. Of these, three were initiated with his mouth closed, and the volume increased suddenly when his mouth opened. This also occurred twice in his howls that broke upward in pitch. This feature occurred only in the howls of this wolf.

Wolf B and Wolf C both showed a preference for beginnings that broke upward in pitch. In Wolf B, this type of beginning occurred in all but one howl. This one howl was immediately preceded by whining, and the whines broke into the howl.

Wolf C produced high beginnings in twenty howls. In three of these, his voice was hoarse as he began the howl. This hoarse quality which appeared as a diffuse blur on sonographs, occurred only in the howls of this wolf.

Ending. - Four types of endings were apparent - one which slurred rapidly downward in pitch so that the final note could not be ascertained by ear (Plate IV (p)), one which dropped less abruptly in pitch, enabling one to ascertain the final note (Plate VI (v)), one which rose in pitch (Plate VII (w)), and one which remained steady or continued the rate of decline of pitch displayed in the body of the howl immediately preceding it (Plate I (a)).

Table 2. - Type of Ending of Howls

Wolf	Number of Howls	Slur (Percent)	Drop (Percent)	Rise (Percent)	Steady (Percent)
A	391	19.3	7.7	.01	72.6
B	187	91.6	0	0.5	7.9
C	120	47.5	10.7	7.4	34.4

Table 2 shows that individual preferences for endings were not as marked as they were for beginnings, except in the case of Wolf B. Wolf A preferred an ending which remained steady, differing from the other two wolves. Individual preferences for Wolf B and Wolf C were similar. Wolf C showed a more even distribution of endings than the other two wolves.

A rise in pitch in the ending was the least common category for Wolves A and C, and was represented only once in the howls of Wolf B.

Body of the Howl.- Three characteristics involving change of pitch are obvious to the human ear in the body of howls. They are: a sudden drop in pitch (at least three semi-tones in 1/4 second or less) (Plate I (d)), a rise in pitch incorporating the highest note of the howl[2] (Plate I (b)), and a rise in pitch which does not reach the highest note of a howl (Plate II (g)). This latter feature gives a measure of the amount of "warble" in a howl.

Table 3. - Drops in Pitch in the Body of Howls

Wolf	Number of Howls	No Drop (Percent)	One Drop (Percent)	Two Drops (Percent)
A	381	76.9	21.9	1.0
B	175	32.6	27.1	40.3
C	117	26.8	37.5	35.7

[2] The highest note was often found in the beginning 0.5 seconds of the howl, in which case the characteristic was lacking in the body. The location of the highest note creates a distinct difference to the human ear.

Most of the howls of Wolf A, (76.9%) did not have a sudden drop in pitch in their body (Table 3). This differed from Wolves B and C who each had a close to equal distribution of howls with no drop in pitch, one drop in pitch and two drops in pitch.

Table 4. - Rise in Pitch Incorporating the Highest Note of Howls

Wolf	Number of Howls	No Rise (Percent)	Rise (Percent)
A	381	13.0	87.0
B	175	90.1	9.9
C	117	100.0	0

Very marked preferences showed up related to rise in pitch incorporating the highest note of howls (Table 4). Once again, Wolf A showed a preference which differed from the other two wolves. The highest note of howls of Wolf C always occurred in the beginning 0.5 seconds of the howl rather than the body of the howl.

Table 5. - Rise in Pitch not Reaching the Highest Note of Howls

Wolf	Number of Howls	No Rise (Percent)	One Rise (Percent)	Two Rises (Percent)
A	381	91.5	8.5	0
B	175	97.2	2.2	0
C	117	66.9	26.8	6.3

As shown in Table 5, the preferences related to rise in pitch not reaching the highest note of howls was marked and similar for Wolves A and B (no rise), and less marked for Wolf C. Two rises in pitch were distinctive for Wolf C when they occurred (6.3%).

<u>Length of Howls</u>. - The three wolves all varied in respect to length of howls (Fig. 1). The length of howls of Wolf C had a greater range (11 seconds) than Wolf A (eight seconds) or Wolf B (six seconds).

Table 6. - Length of Howls

Wolf	Number of Howls	Mean	Confidence Limits on Mean (95%)	Standard Deviation
A	391	4.7	± 0.2	1.6
B	185	3.5	± 0.1	1.3
C	117	6.4	± 0.5	2.5

The average length, as a measure of central tendency, is most meaningful for Wolves A and B (Table 6). Both of these averages fall in the class adjacent to the model class. This is not true for Wolf C, whose mode was two classes away from the mean.

The standard deviation, as a measure of dispersion, reflects principally the greater variation in lengths in the howls of Wolf C than the other two wolves (Table 6). This difference is also evident on the histograms in Fig. 1.

The means of all three wolves showed a significant difference from each other (95% confidence level). Wolf C produced longer howls more

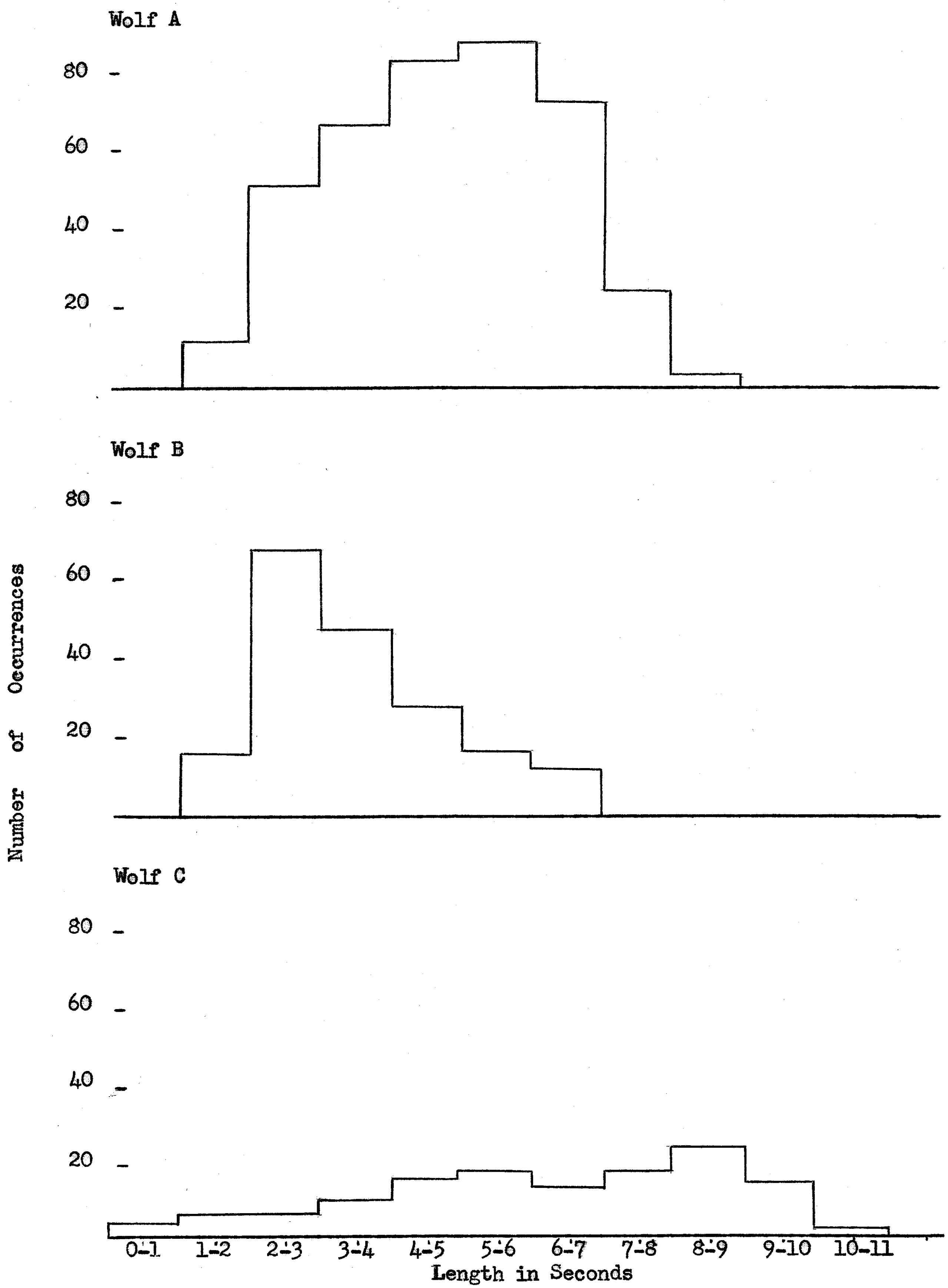

Fig. 1 - Distribution of Lengths of Howls
Number of howls were; Wolf A - 391; Wolf B - 185; Wolf C - 117

frequently than the other two wolves, and his model class was actually beyond the range of Wolf B and was represented only twice by Wolf A.

Highest Note of Howls. - The highest note of howls was determined by matching by ear to a chromatic scale pitch pipe. Data are presented in terms of semi-tones. The equally tempered scale, which is a close approximation of the chromatic scale, is made up of twelve semi-tones of equal difference to the human ear. In terms of cycles per second, this scale is a geometric progression. Equal intervals to our ear are therefore not equal values in terms of cycles per second. For example, the difference between F and F# above middle C represents a different number of cycles per second than the difference between F and F# below middle C. We hear these as equal intervals not as a function of cycles per second change. The assumption is made that wolves, being mammals, distinguish pitch change as we do - in terms of equal intervals rather than absolute changes in cycles per second. Therefore, each semi-tone in the equally tempered scale is assigned a number in arithmetic sequence (for high note analysis C#=1, D=2, D#=3, etc.), and mathematical analysis is carried out using these numbers. (Note that B and E have no corresponding B# or E#. However, the difference between B and C, and E and F are still one semi-tone, by definition of the equally tempered scale).

A sub letter "h" after a note will denote the octave beginning with C above middle C. (Middle C is 261.6 cycles per second).

Wolf A was quite variable in his high notes compared to Wolves B and C (Fig. 2). The range of high notes for Wolf A encompassed fourteen semi-tones - more than a full octave. The ranges for Wolves B and C were five semi-tones and eight semi-tones respectively (Fig. 2).

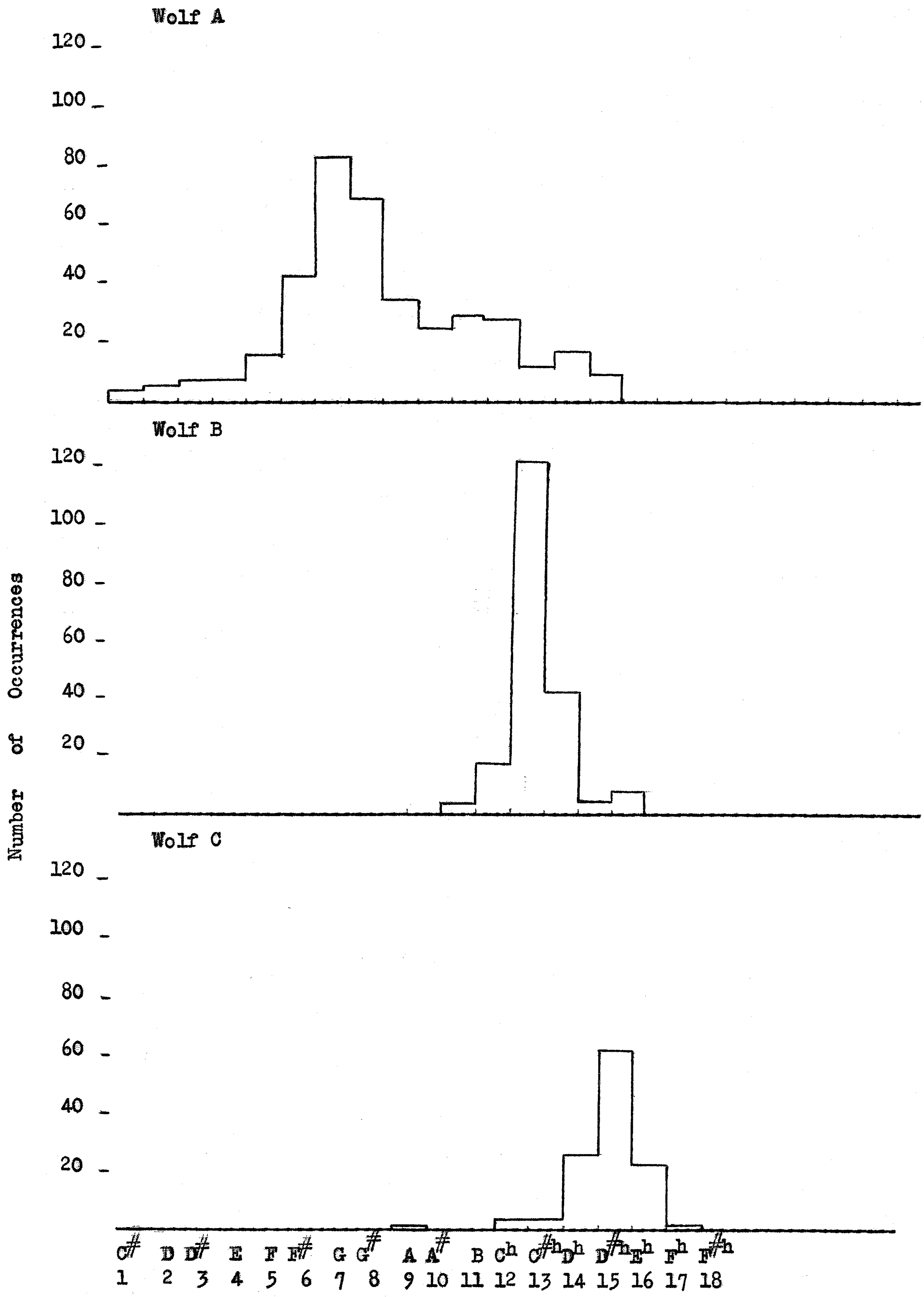

Fig. 2. - Distribution of Highest Note of Howls
Number of howls were; Wolf A - 392, Wolf B - 198, Wolf C - 119

Table 7. - Highest Note of Howls

Wolf	Number of Howls	Mean	Confidence Limits on Mean (95%)	Standard Deviation
A	392	8.7 (A)	$\pm$ 0.3	2.7 ($F^{\#}$ to B)
B	198	13.4 ($C^{\#h}$)	$\pm$ 0.04	0.3 (<1 semi-tone)
C	119	14.7 ($D^{\#h}$)	$\pm$ 0.3	1.0 (E^h to D^h)

The standard deviations (Table 7) for Wolves B and C also reflect the small amount of variation in highest note for these two animals. A large difference (half an octave) existed between the mean highest note of Wolves A and C (Table 7).

The means of highest notes of howls of all three wolves differed significantly at the 95% confidence level.

Lowest Note of Howls. - Each semi-tone was again assigned a number (D_L=1, $D^{\#}{}_L$=2, E_L=3, etc.). The sub letter "L" after the note denotes the octave below middle C.

No data exists for Wolf B due to his propensity to produce slurred endings (Table 2) making low note determination impossible.

Histograms in Fig. 3 show that a wide range of low notes existed for Wolf A (19 semi-tones), and a range of nine semi-tones existed for Wolf C.

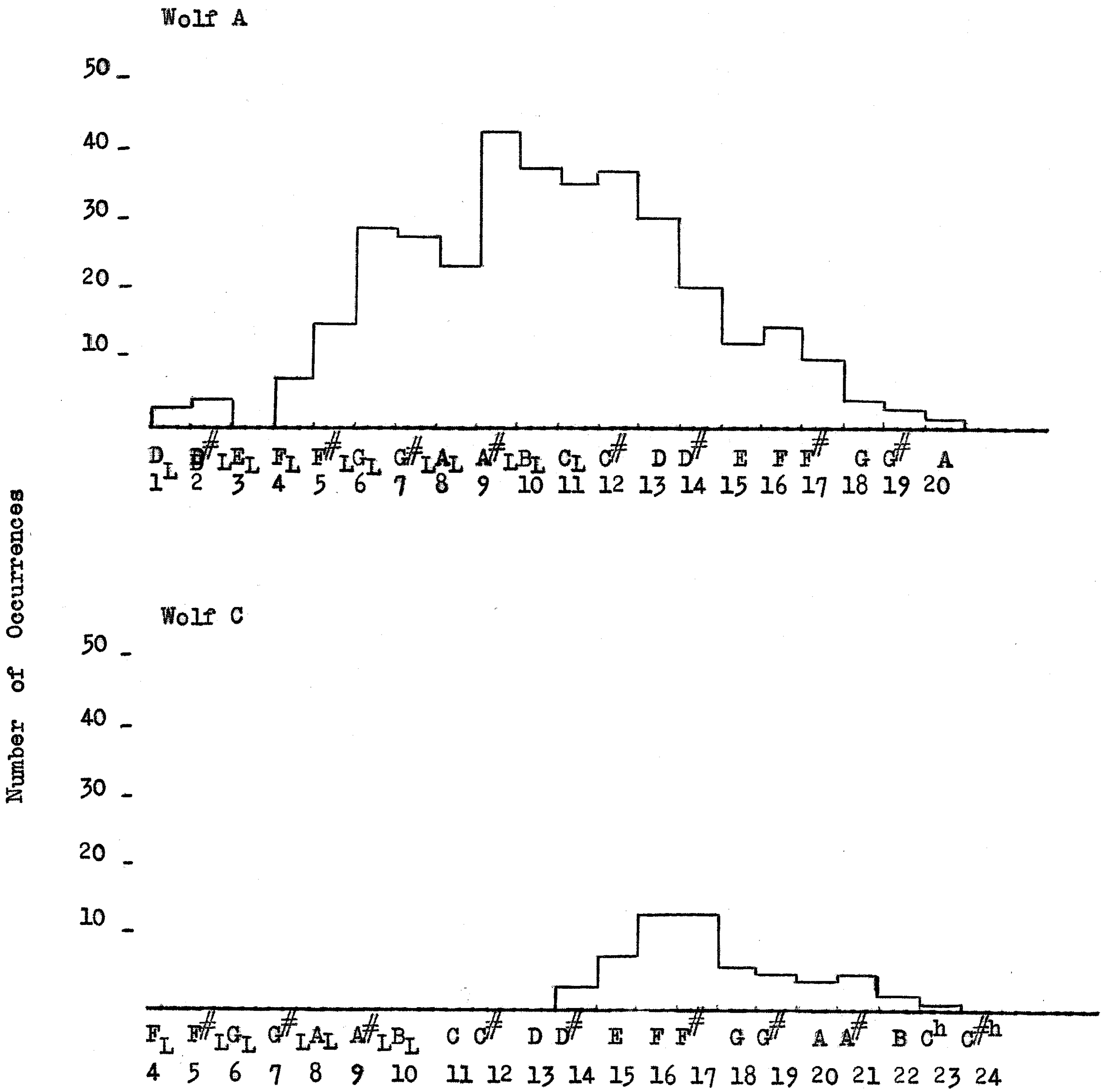

Fig. 3. - Distribution of Lowest Note of Howls
Number of howls were; Wolf A - 351, Wolf C - 62

Table 8. - Lowest Note of Howls

Wolf	Number of Howls	Mean	Confidence Limits on Mean (95%)	Standard Deviation
A	351	10.7 (C)	0.3	3.0 ($A^{\#}_{1}$ to $D^{\#}$)
C	62	17.4 ($F^{\#}$)	0.8	1.8 (F to $G^{\#}$)

The standard deviations (Table 8) of lowest notes for the two wolves also reflect a larger range for Wolf A than Wolf C. The mean of the lowest notes differed by more than half an octave (Table 8). This represented a statistically significant difference at the 95% confidence level.

From the observations of distinguishing features, and the large amount of "individuality" in howls caused by marked preferences which differed between wolves, it can be concluded that the potential for individual recognition is quite great.

Classification of Howls - Repertoire

A number of characteristics of wolf howls for each of three animals have been discussed, each treated singly. When each characteristic appears in a howl, it is only one of the total characteristics that make up the howl.

Classifications can be made of sounds by integrating into groups any number of single characteristics. An attempt has been made in this section to produce a classification of some use in the field. The three characteristics of the body of howls (sudden drop in pitch, rise in pitch incorporating the highest note of the howl, and rise in pitch not reaching the highest note of the howl) are very distinctive to humans, and are easily recognized from a distance. These were chosen as the basis for the repertoires that will be discussed.

Sudden drop in pitch was considered most important since it occurred in at least thirty percent of the howls of each wolf. Its presence was used to create different howl "types". The other two characteristics were used to create "sub-types". A spectrograph for each sub-type for each wolf is provided in Plates I to VII[3].

Table 9 shows that the repertoire of Wolf A consisted of seven different howls. The majority of his howls were of sub-type 1R (rise in pitch incorporating the highest note of the howl and no drops in pitch). This sub-type, together with sub-type 2R (rise in pitch incorporating the highest note of the howl and one drop in pitch) and sub-type 1 (no drops or rises) made up most of the howls (88.8%) of Wolf A.

The repertoire of Wolf B consisted of six different howls. The largest category was sub-type 3, with two drops and no rises, followed by sub-type 2 (one drop and no rises) and sub-type 1 (no drops or rises). These three sub-types made up most of the howls (87.8%) of Wolf B.

The repertoire of Wolf C consisted of nine different howls. Besides having the greatest variety in his repertoire, Wolf C did not show strong preferences for specific sub-types (25% was the largest percentage for one sub-type). Sub-type 1 (no drops or rises), sub-type 1Rr (both types of rises and no drops) and sub-type 2 (one drop and no rises) were represented almost equally.

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[3]A tape recording of the sub-types, in the order of their presentation in Plates I to VII is deposited in the sound library of Dr. J. B. Falls at the University of Toronto, Department of Zoology.

Table 9. - Classification of Howls According to Body Characteristics

Category	Wolf A (Percent)	Wolf B (Percent)	Wolf C (Percent)
Type 1[1]			
Sub-type 1	10.1	20.4	25.0
Sub-type 1R[2]	62.0	7.7	
Sub-type 1Rr[3]	4.0		
Type 2[4]			
Sub-type 2	2.7	27.1	21.2
Sub-type 2R	16.7		
Sub-type 2Rr	3.5		
Sub-type 2r			11.6
Sub-type 2rr			4.5
Type 3[5]			
Sub-type 3		40.3	20.6
Sub-type 3R		2.2	
Sub-type 3Rr	1.1		
Sub-type $3r_1$[6]			9.8
Sub-type $3r_2$[7]			3.6
Sub-type 3rr			1.8
Type 4[8]			
Sub-type 4r		2.2	1.8

Sample sizes were: Wolf A - 378 howls; Wolf B - 175; Wolf C - 112.

1 Type 1 has no sudden drop in pitch

2 R = rise in pitch in body of howl incorporating highest note in howl.

3 r = rise in pitch in the body not reaching the highest note of the howl.

4 Type 2 has one sudden drop in pitch.

5 Type 3 has two sudden drops in pitch.

6 Arranged in time as d (sudden drop in pitch), d, r.

7 Arranged in time as d,r,d.

8 Type 4 has three sudden drops in pitch.

Sound Harmonics

Three quotations provide the acoustic "theory" necessary for this section.

"Sound waves are initiated by the vibration of strings, air columns, drum-like structures, or various three-dimentional bodies. When a violin string vibrates, the entire string vibrates with frequencies that are integral multiples of the vibration frequency of the whole string. The lowest frequency produced by this vibrating string is the fundamental; the higher frequencies are called harmonics. The vibration of strings and air columns generally produce harmonics ...." (Borror, 1960).

"Vibrations of the vocal chords produce a fundamental and numerous harmonically related overtones (harmonics)." (Fletcher, 1953).

"When these waves (fundamental and harmonics) pass through the throat, the mouth, and the nasal cavities, those frequencies near the resonant frequencies of these cavities are radiated into the air very much magnified, the amount depending upon the damping constant of the cavity." (Fletcher, 1953).

The quality of sound is determined by the number and relative intensity of the harmonics. Humans recognize each other by means of sound quality, as well as the way various elements of the language are spoken. Are there characteristics of sound quality that are distinctive for individual wolves?

A sample of 25 howls was analyzed for harmonic content for each of the three wolves. Sonographs were made using a frequency scale of 50-5000 cycles per second in order to see on one graph all harmonics. The relative intensity of harmonics was assessed by the relative width and darkness of lines. Only lower harmonics could be related to each other

- higher ones were generally too weak to make comparisons.

The first harmonic is considered to be twice the pitch of the fundamental, the second harmonic three times the fundamental, etc.

The 25 howls in each sample were randomly picked from the total collection for each wolf. In each sample were howls given spontaneously and howls given in response to auditory stimulation. Also represented were howls given when the wolves were lying, standing and pacing, and howls that were recorded when the microphone was located at approximately 18 feet and 120 feet from the pen[4]. Harmonic content was not altered by these variables, so the data were combined for the analysis.

Wolf A

First harmonic. - The fundamental of six of Wolf A's howls exceeded G# in pitch. In two of these, the first harmonic increased in intensity when the fundamental rose above G#, two showed a decrease in intensity and two remained at approximately the same intensity . When the fundamental was below G# in pitch the first harmonic was uniformly strong.

Second harmonic. - The second harmonic also showed variation in intensity with pitch, but of a more constant nature. When the fundamental was above G#, the second harmonic was weak. As the fundamental dropped from G# to F# there was an increase in intensity, and at F# and below, a further increase in intensity.

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[4]When microphone was 120 feet from the pen, howls that dropped suddenly in pitch exhibited a carry-over of the original note, seen on spectrographs as a continuing line. This was believed to be the effect of reverberation off vegetation.

Relative Intensity of First and Second harmonics. - When the fundamental was above G#, the first harmonic was always stronger than the second. When the fundamental was between G# and F#, there was variation in relative intensity, and below F# the second harmonic was stronger than the first. All howls in the sample had notes below F# so all showed the low range relationship. Only six howls had notes above G#, showing the reverse (Plate VIII (a)).

Higher harmonics. - The third harmonic was much weaker than the first or second harmonics in 20 of the howls. It existed throughout almost the total length of all but two howls. The fourth and fifth harmonics, weaker still, existed throughout almost the total length of fifteen howls. A sixth harmonic showed up as a partial slight trace in eighteen howls, four of these showing a slight eighth harmonic also. One howl showed traces of a ninth harmonic and one a twelfth.

Wolf B

First harmonic. - Wolf B expressed a strong first harmonic in 16 of his 25 howls; it was somewhat weaker in the rest. In 17 of the howls the strength of this harmonic was reduced considerably when the fundamental fell below G# (all howls in this sample crossed G#) (Plate VIII (b)). In the remaining eight cases, the first harmonic stayed at approximately the same intensity throughout its pitch range.

Second harmonic. - The second harmonic remained very weak and approximately of equal intensity over its whole range for seven of the 25 howls, became markedly stronger when the fundamental fell below G# in 13 of the howls (Plate VIII (b)), and petered out when the fundamental fell below G# in one of the howls. An additional four howls could not be assessed due to reverberation, previously mentioned.

<u>Relative Intensity of First and Second harmonics</u>. - When the fundamental was below $G^{\#}$, 12 howls showed the first and second harmonics approximately equal in intensity, eight showed the second harmonic stronger than the first (Plate VIII (b)), and five could not be determined due to reverberation.

When the fundamental was above $G^{\#}$ the first and second harmonics were of approximately equal intensity in four howls, and the first harmonic was stronger than the second in 21 howls (Plate VIII (b)).

<u>Higher harmonics</u>. - Ten howls had a partial, weak third harmonic. Six had a very weak fourth harmonic, and two a weak fifth. The almost non-existence of harmonics above the second contrasted with Wolf A. These weak higher harmonics seemed to occur with the highest notes of the fundamental of the howl, being generally absent in the range $G^{\#}$ and below.

<u>Wolf C</u>

<u>First harmonic</u>. - The fundamental of all howls in the sample reached high notes of either D^h, $D^{\#h}$, or E^h. The first harmonic became weak when the fundamental was D^h or above in all howls in the sample. When the fundamental dropped below B, the second harmonic underwent a sudden increase in intensity down to the level of approximately $F^{\#}$ where it appeared to weaken slightly (Plate VIII (c)).

<u>Second harmonic</u>. - The second harmonic was very weak with only one exception, down to a pitch level of the fundamental of approximately $F^{\#}$ where it increased in intensity (Plate VIII (c)).

<u>Relative Intensity of First and Second harmonics</u>. - When the fundamental was above approximately $F^{\#}$ the intensity of the second harmonic was negligible. At $F^{\#}$ and below, in eight cases the second harmonic was more intense than the first. In 11 cases at $F^{\#}$ and below the harmonics were

comparable in intensity, and in the remaining five cases the relation was masked by the reverberation effect of the vegetation.

Higher harmonics. - Sixteen howls showed a partial trace of a weak third harmonic, six showed a fourth harmonic and four a fifth harmonic, all very weak.

Comparison of Harmonics Between Wolves

First harmonic. - Some of the howls of all three wolves showed a decrease in the intensity of the first harmonic at low pitches - Wolf A decreasing at the pitch level of the fundamental of $G^{\#}$ in two of the six howls that crossed this level, Wolf B decreasing at $G^{\#}$ in 17 of the 25 howls that crossed this level, and Wolf C decreasing at $F^{\#}$ in all his howls.

Wolf C's first harmonic could be distinguished from those of the other two wolves by a sudden increase in intensity when the pitch of the fundamental was between B and $F^{\#}$. Also a decrease in intensity from D^{h} upward was characteristic, not being shown by Wolf B . Wolf A did not reach this high level in his howls. These two features are diagnostic for all the howls of Wolf C.

Second harmonic. - Some of the howls of all three wolves showed a strengthening of the second harmonic as the fundamental decreased in pitch, Wolf A in all his howls as the fundamental crossed $G^{\#}$ to $F^{\#}$, Wolf B in 13 of his howls as the fundamental crossed $G^{\#}$, and Wolf C in all his howls as the fundamental crossed $F^{\#}$. Wolves A and C could be distinguished on the basis of strength of this harmonic between $G^{\#}$ and $F^{\#}$, the harmonic always being more intense for Wolf A than Wolf C somewhere within this three note range. Wolves A and B could not be distinguished in this range. The variation in the second harmonic in Wolf B made it non-diagnostic.

Relative Intensity of First and Second harmonics. - All three wolves showed some howls which had a stronger second than first harmonic at low pitches - true for all howls of Wolf A when the fundamental was below $F^{\#}$, seven howls of Wolf B when the fundamental was below $G^{\#}$, and eight howls of Wolf C when the fundamental was below $F^{\#}$. In the remainder of the howls of Wolves B and C, the two harmonics showed approximately equal intensities at low pitches.

The high pitch ranges of some howls of all three wolves had a stronger first harmonic than second - true for all six howls of Wolf A when the fundamental exceeded $G^{\#}$, 21 of the 25 howls of Wolf B when the fundamental exceeded $G^{\#}$, and all the howls of Wolf C when the fundamental was $F^{\#}$ and above. The remainder of the howls of Wolf B showed approximately equal intensities when the fundamental was above $G^{\#}$.

Higher Harmonics. - Wolf A was much richer in harmonics above the second than the other two wolves, having up to a twelfth harmonic in one howl. These high harmonics were diagnostic for all his howls. Both Wolf B and Wolf C produced only weak third, fourth and fifth harmonics at the most.

Summary and Discussion

From this analysis it is possible to formulate a definition of a wolf howl. A wolf howl is a continuous sound of approximately half a second to 11 seconds in length. It consists of a fundamental frequency which may be between 150 and 780 cycles per second, and up to 12 harmonically related overtones. Most of the time it is changing smoothly or remaining at a constant pitch. It may change direction of pitch as many as four or five times. Its total intensity remains approximately constant throughout.

This is a general definition of a wolf howl, encompassing the large amount of variation that existed in the howls of the wolves studied. There were more specific similarities related to harmonics. Generally the first harmonic decreased in intensity at low pitches (occurred in 44 of the 56 howls). A narrow range of pitch (G# to F#) was the point at which the change of intensity occurred in all three wolves.

Similarly, the second harmonic generally increased in intensity at low pitches (occurred in 44 of 56 howls). The same narrow pitch range (G# to F#) was the point in howls of all three wolves at which the change of intensity occurred.

The relative intensity of first and second harmonics also showed general agreement; among the three wolves, the second harmonic was stronger than the first at low pitches (in 40 of the 75 howls) and the reverse was true at high pitches (in 52 of the 75 howls). All the remaining howls showed approximately equal intensity of the first and second harmonics.

That these patterns of harmonic intensity did not occur in every howl of each wolf is not surprising, since a number of variables can affect harmonic content.

1) Harmonic content will vary as total intensity. This is because resonance within the cavities of the head will change as sound energy changes.
2) Harmonic content will vary with the pitch of the fundamental, both due to different vibration frequencies of the vocal chords and different resonances.
3) Harmonic content will vary with the position of the mouth and associated structures. "The mouth with its associated

vocal cavities is an adjustable resonator; by varying the position of the jaws, cheeks, tongue, lips and other parts, this resonator can be tuned to reinforce one or two different frequencies." (Miller, 1937).

Although a sample size of three wolves is too few upon which to base a firm statement, the similarities in harmonic structure of howls may demonstrate characteristics of wolf howls in general.

The analysis of the fundamental frequency of wolf howls showed that vocal characteristics varied considerably within the howls of individual wolves. With only one exception (rise in pitch in the body of the howl incorporating the highest note of the howl for Wolf C) no one animal produced any one characteristic in all his howls. In other words, the possibility of variation existed for each wolf in almost all categories which were studied (beginning and ending of howls, and pitch changes in the body of howls). The potential, in terms of coding information, is apparent, since the requirement of ability to vary sound is met.

Despite the ability to vary howls, strong individual preferences existed for most wolves for specific types of beginning, ending, and features of the body of the howl. In all but one case (rise in pitch not reaching the highest note of the howl - all usually left this characteristic out of howls), these preferences were not the same for all three wolves, indicating the amount of "individuality" in the howls of each wolf. Similarly, the analysis of the grouping of characteristics of the body of howls demonstrated "individuality" - the most common groupings were different for each animal. "Individuality" was further shown by the average length, highest notes and lowest notes of howls, all which differed significantly between wolves.

Although all howls of any one wolf did not show a unique feature, unique features did occur in some howls of individuals. These were:

Wolf A - beginning with mouth closed (1.3% of howls)

- beginning low and rising (88.1% of howls)
- highest note lower than A (34.0% of howls)
- lowest note D or below (27.0% of howls)

Wolf B - none

Wolf C - hoarse beginning (2.5% of howls)

- howls with two rises in pitch not reaching the highest note of the howl (6.3% of howls)
- howls 9 to 11 seconds in length (13.7% of howls)
- highest note $F^{\#h}$ (1.7% of howls)
- lowest note $A^{\#}$ or higher (19.4% of howls)

The analysis of the overtones of wolf howls demonstrated that features existed in harmonics that were unique to all howls of an individual in two cases. These features were:

Wolf A - richly endowed with harmonics above the second harmonic

Wolf C - sharp increase in intensity of the first harmonic when the fundamental was between B and $F^{\#}$

- decrease in intensity of the first harmonic when the fundamental was D^{h} or higher

Therefore, on the basis of differences in sound quality potential individual recognition of individual wolves by another wolf is possible from any one howl if a wolf has the ability to distinguish harmonic differences. If characteristics of the fundamental only are distinguishable, the potential for individual recognition is still very great.

IV

POTENTIAL INFORMATION IN WOLF HOWLS

The fundamental of howls of individual wolves shows a great deal of variation, as seen in the previous section. If the variations are random they are of no inherent value in communication. However, if these variations are associated with some feature of the animal's behaviour or environment, they have potential value as conveyors of information.

In this section, the results of a detailed study made to determine whether any of the variations in howls were associated with behaviour patterns or with the environment of the howling animal are discussed. This search was for sound units that could be classed as having potential information content.

Relationship Between Characteristics of Howls and Behaviour

Four broad categories of behaviour were chosen with the aim of discovering whether or not characteristics of howls were in some way related to the posture or movement of the howling wolf. There were apparently four levels of activity:

I - lying

II - standing or walking slowly, tail in a relaxed position, head sometimes down.

III - pacing back and forth, tail in a relaxed position, head above horizontal.

IV - pacing rapidly back and forth, tail twitched as wolf paces and carried high (often above the horizontal), head above the horizontal.

Lying was a resting position, although at a sound, a wolf often became more attentive with ears forward. If a person or vehicle appeared or some strange noise began, the usual reaction was to stand and look in the direction of the disturbance or begin to walk slowly. There was some individual variation in behaviour. Some animals had become conditioned to disturbances, and during periods of the day when disturbances were common, often showed no interest. However, at night, or after long periods of being left alone, disturbance evoked interest and a higher level of activity. If the disturbance became more severe, the animal usually began to pace back and forth. When the disturbance was past, pacing continued for a few minutes, and then the wolf reversed the foregoing sequence of behaviour.

Wolves may pace for hours without stopping, even when left alone. Both Wolf A and Wolf B commonly did this. Whether this was a long-lived, relatively high activity level in some way linked with captivity, or reflected an inherited propensity to "travel" was not resolved.

Schenkel's (1947) study in which he described the "expressive function of the tail" suggested the use of the tail position as a criterion for the behaviour classes. According to Schenkel, high carriage was associated with "self-confidence", while the normal position occurred in situations "without social pressure".

Whenever possible, the behaviour exhibited by the animal was noted when howls were recorded.

Each characteristic of these recorded howls (type of beginning, type of ending, pitch changes in the body of the howl, highest note, lowest note and length) was individually tested for each wolf to see if any relationship existed between it and the four behaviour classes. When howls were given in a rapid series, with no movement between them, behaviour for each howl was considered to be the behaviour immediately prior to the first howl.[5] If any change in behaviour took place between howls, the following howls were considered to be associated with the changed behaviour.

All statistical tests in this section were X^2 tests based on contingency tables.

Wolf A

Type of beginning, type of ending, rise in pitch incorporating the highest note of the howl, highest note, lowest note and length were all tested to see if, at or beyond the 95% confidence level, any of them showed an association with behaviour. About 85 howls were used in these tests, the number varying because some partial howls in the collection showed some but not all characteristics. The small numbers necessitated grouping behaviour class I (lying) with II (walking slowly), and III (pacing with tail down) with IV (pacing with tail up). The ranges of highest notes, lowest notes and lengths were each divided into two categories for purposes of analysis. Both a sudden drop in pitch in the body of the howl and a rise in pitch in the body of the howl which did not reach the highest note of the howl were produced too infrequently by this wolf to be examined statistically.

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[5] Usually, when howls were given in rapid succession, the wolf remained stationary. The observation that the behaviour exhibited after a series of howls was complete was almost always the same as the behaviour immediately prior to the series, led to the categorization of all howls in a series as the same as the first howl of the series.

None of the characteristics tested showed a significant relationship with the behaviour classes for Wolf A.

Wolf B

Tests for this wolf were based on approximately 150 howls.

Several of the characteristics of this wolf's howls showed no significant relationship with the behaviour observed. This was the case with type of endings, highest note of the howl (range broken into two classes) and length of howls (two classes used). No tests were run for beginnings, since howls of this wolf broke upward in pitch on all but one occasion, for rise in pitch not reaching the highest note of the howl, since only 2.2% of this wolf's howls had this characteristic, or for lowest note of howls, since this animal usually slurred his endings making accurate measurement impossible. For those characteristics which were significantly related to behaviour, data are presented below.

Sudden Drops in Pitch in the Body of Howls. - This characteristic was related to the behaviour classes of the howling wolf. Table 10 shows that howls lacking drops in pitch were associated more commonly than expected with pacing, while howls with one or two drops occur more often than expected when the wolf was lying or walking slowly.

Table 10. - Relationship Between Sudden Drops in Pitch in the Body of Howls and Behaviour for Wolf A

Howl Character	Behaviour Class[1]	Number of Occasions Observed	Expected	Contribution to X^2
No drop	I & II	8	20.8	7.89
No drop	III	20	12.2	4.98
No drop	IV	12	7.0	3.38
One drop	I & II	28	20.2	3.00
One drop	III	5	11.9	4.00
One drop	IV	6	6.9	.12
Two drops	I & II	32	27.0	.93
Two drops	III	15	15.9	.05
Two drops	IV	5	9.1	1.87
			Total value X^2 =	26.22
			Tabular value X^2 .001 =	18.46

[1] I - lying, II - walking slowly, III - pacing with tail down, IV - pacing with tail up

Rise in Pitch Incorporating the Highest Note of the Howl. - The presence or absence of this characteristic was related to the behaviour of the howling wolf. Table 11 shows that howls lacking a rise in pitch incorporating the highest note of the howl occurred more than expected when the wolf was lying or walking slowly and correspondingly, howls with this rise occurred fewer times than expected when the wolf was lying or walking slowly.

Table 11. - Relationship Between Rise in Pitch Incorporating the Highest Note of the Howl and Behaviour for Wolf B

Howl Character	Behaviour Class[1]	Number of Occasions		Contribution to X^2 [2]
		Observed	Expected	
Rise	I & II	1	6.2	3.56
Rise	III & IV	69	63.8	.35
No Rise	I & II	11	5.8	3.81
No Rise	III & IV	55	60.2	.37
			Total value X^2 =	8.09
			Tabular value X^2 .01 =	6.64

[1] I - lying, II - walking slowly, III - pacing with tail down, IV - pacing with tail up

[2] Yates Correction Factor for small numbers was used

Wolf C

Tests for this wolf were based on 37 to 64 howls.

Type of beginning, type of ending, rise in pitch not reaching the highest note of the howl, highest note, lowest note and length, all were not significantly related to the observed behaviour. Rise in pitch incorporating the highest note of the howl was never produced by Wolf C.

The only characteristic of this animal's howls that was related to behaviour was sudden drops in pitch in the body of howls (Table 12). Howls with two drops in pitch occurred more frequently than expected when Wolf C was pacing.

Table 12. - Relationship Between Sudden Drops in Pitch in the Body of Howls and Behaviour for Wolf C

Howl Character	Behaviour Class[1]	Number of Occasions Observed	Expected	Contribution to X^2
No drop	I & II	17	14.9	.29
No drop	III & IV	7	9.1	.49
One drop	I & II	15	12.4	.55
One drop	III & IV	5	7.6	.89
Two drops	I & II	4	8.7	2.53
Two drops	III & IV	10	5.3	4.16
			Total value X^2 =	8.90
			Tabular value X^2 .01 =	7.82

[1] I - lying, II - walking slowly, III - pacing with tail down
IV - pacing with tail up

Relationship Between Characteristics of Howls and Whether Howling was Spontaneous or Stimulated

Recorded howls were divided into two categories - spontaneous and stimulated - to see whether or not howl characteristics were in some way related to these different environmental circumstances and therefore potential carriers of information of this type. Howls were classed as stimulated if they occurred within five minutes after the wolf heard an auditory stimulus.[6] After that, howls were classified as spontaneous, i.e. preceeded by no known auditory stimulation. The principal auditory stimuli used were the simulated wolf howls of my wife for Wolf A, and my simulated wolf howls for Wolf B. In addition, tape recorded wolf howls and frequency notes were also used. Responses to all auditory stimuli were grouped together for each wolf regardless of the specific stimulus involved.

Each howl characteristic (type of beginning, type of ending, pitch changes in the body of the howl, highest note, lowest note and length) was individually tested for each wolf to see if any relationship existed between it and the two situations in which howling occurred.

Wolf C rarely howled in response to auditory stimulation and so is not included in this analysis.

<u>Wolf A</u>

Analyses for this wolf were based on 352 to 393 howls.

The presence or absence of two characteristics, sudden drops in pitch in the body of howls, and rise in pitch not reaching the highest note of howls were not related to whether howling was spontaneous or stimulated. For those characteristics which were significantly related to whether howling was spontaneous or stimulated, data are presented below.

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[6] This time interval was chosen since most replies came either during the test sequence or within a minute after. If the wolf was silent for five minutes it was almost always silent for a much longer period of time.

<u>Beginning</u>. - The different types of beginnings of howls were related to whether howling was spontaneous or stimulated (Table 13).

Table 13. - Relationship Between Type of Beginning of Howls and Whether Howling was Spontaneous or Stimulated for Wolf A

Type of Beginning	Howling Situation	Number of Occasions Observed	Number of Occasions Expected	Contribution to X^2
Smooth	Spontaneous	140	149.8	.64
Break up	Spontaneous	23	13.2	7.26
Smooth	Stimulated	200	190.2	.50
Break up	Stimulated	7	16.8	5.71
			Total value X^2 =	14.11
			Tabular value X^2 .001 =	10.83

Although smooth beginnings occurred most of the time, beginnings that broke upward in pitch occurred more than expected when howling was spontaneous.

<u>Ending</u>. - The different types of endings of howls were related to whether howling was spontaneous or stimulated. Table 14 shows that more slurred endings than expected occurred when howling was spontaneous. There was a slight tendency for smooth endings to occur more than expected with stimulated howling.

Table 14. - Relationship Between Type of Ending of Howls and whether Howling was Spontaneous or Stimulated for Wolf A

Type of Ending	Howling Situation	Number of Occasions Observed	Number of Occasions Expected	Contribution to X^2
Smooth	Spontaneous	109	124.1	1.84
Slur	Spontaneous	49	36.2	4.53
Drop	Spontaneous	15	12.7	.42
Smooth	Stimulated	166	150.9	1.52
Slur	Stimulated	31	44.8	3.74
Drop	Stimulated	13	15.3	.35
			Total value X^2 =	12.40
			Tabular value X^2 .01 =	5.99

Table 15. - Relationship Between Rise in Pitch Incorporating the Highest Note of the Howl and whether Howling was Spontaneous or Stimulated for Wolf A

Howl Character	Howling Situation	Number of Occasions Observed	Number of Occasions Expected	Contribution to X^2
No Rise	Spontaneous	33	21.6	6.02
Rise	Spontaneous	132	143.4	.91
No Rise	Stimulated	17	28.4	4.58
Rise	Stimulated	199	187.6	.69
			Total value X^2 =	12.20
			Tabular value X^2 .001 =	10.83

Rise in Pitch Incorporating the Highest Note of the Howl. - The presence or absence of this characteristic was found to be related to whether howling was spontaneous or stimulated (Table 15). Although howls with such rises were in the majority, howls without rises tended to occur more often than expected in spontaneous howls, and less often than expected in stimulated howls.

Highest Note of Howls. - Three ranges of highest notes (low, middle and high) were related to whether howling was spontaneous or stimulated (Table 16). Highest notes of howls fell into the high range more than expected when howling was spontaneous. There was also a slight tendency for highest notes of howls to fall into the middle range when howling was stimulated.

Table 16. - Relationship Between Highest Note of Howls and whether Howling was Spontaneous or Stimulated for Wolf A

Range of Highest Note	Howling Situation	Number of Occasions Observed	Number of Occasions Expected	Contribution to X^2
Low	Spontaneous	18	16.1	0.22
Middle	Spontaneous	96	111.6	2.19
High	Spontaneous	55	41.3	4.53
Low	Stimulated	19	20.9	0.17
Middle	Stimulated	161	145.4	1.67
High	Stimulated	40	53.7	3.49
			Total value X^2 =	12.27
			Tabular value X^2 .01 =	9.21

Lowest Note of Howls. - Two ranges of lowest notes (low and high) were related to whether howling was spontaneous or stimulated (Table 17).

Table 17. - Relationship Between Lowest Note of Howls and Whether Howling was Spontaneous or Stimulated for Wolf A

Range of Lowest Note	Howling Situation	Number of Occasions		Contribution to X^2
		Observed	Expected	
Low	Spontaneous	51	70.4	5.35
High	Spontaneous	82	62.6	6.00
Low	Stimulated	135	115.6	3.26
High	Stimulated	84	103.4	3.64
			Total value X^2 =	18.25
			Tabular value X^2 .001 =	10.83

High range lowest notes occurred more than expected when howling was spontaneous, and correspondingly low range lowest notes occurred more than expected when howling was stimulated.

Length of Howls. - Two ranges of lengths of howls (short and long) were related to whether howling was spontaneous or stimulated. As can be seen in Table 18, short howls occurred more than expected when howling was spontaneous, and correspondingly long howls occurred more than expected with stimulated howling.

Table 18. - Relationship Between Length of Howls and Whether Howling was Spontaneous or Stimulated for Wolf A

Range of Lengths	Howling Situation	Number of Occasions Observed	Number of Occasions Expected	Contribution to X^2
Short	Spontaneous	106	91.4	2.33
Long	Spontaneous	63	77.6	2.75
Short	Stimulated	106	121.6	1.78
Long	Stimulated	117	102.4	2.08
			Total value X^2 =	8.94
			Tabular value X^2 .01 =	6.64

Wolf B

Tests with Wolf B were based on 175 to 196 howls.

Several characteristics in the howls of this wolf were not significantly related to whether howling was spontaneous or stimulated. This was the case with type of ending, rise in pitch incorporating the highest note of the howl and length of howls (range broken into three classes). No tests were run for beginnings, since howls of this wolf broke upward in pitch on all but one occasion, for rise in pitch not reaching the highest note of the howl, since only 2.2% of this wolf's howls had this characteristic, or for lowest note of howls, since this animal usually slurred his endings making accurate measurement impossible. Two characteristics were related to whether howling was spontaneous or stimulated.

Sudden Drops in Pitch in the Body of Howls. - This characteristic was related to whether howling was spontaneous or stimulated. As can be seen in Table 19, one drop in pitch occurred more than expected when howling

Table 19. - Relationship Between Sudden Drops in Pitch in the Body of Howls and Whether Howling was Spontaneous or Stimulated for Wolf B

Howl Character	Howling Situation	Number of Occasions Observed	Number of Occasions Expected	Contribution to X^2
No drop	Spontaneous	18	23.6	1.33
One drop	Spontaneous	32	22.2	4.32
Two drops	Spontaneous	31	35.2	.50
No drop	Stimulated	33	27.4	1.15
One drop	Stimulated	16	25.8	3.72
Two drops	Stimulated	45	40.8	.43
			Total value X^2 =	11.45
			Tabular value X^2 .01 =	9.21

was spontaneous. There was a slight tendency for howls without drops to occur when howling was stimulated.

Highest Note of Howls. - The ranges of the highest notes (low and high) were related to whether howling was spontaneous or stimulated. Table 20 shows that high range highest notes occurred more than expected when howling was spontaneous, and correspondingly low range highest notes occurred more than expected when howling was stimulated.

Table 20. - Relationship Between Highest Note of Howls and Whether Howling was Spontaneous or Stimulated for Wolf B

Range of Highest Notes	Howling Situation	Number of Occasions Observed	Number of Occasions Expected	Contribution to X^2
Low	Spontaneous	43	62.7	6.19
High	Spontaneous	43	23.3	16.60
Low	Stimulated	100	80.3	4.85
High	Stimulated	10	29.7	13.10
			Total value X^2 =	40.74
			Tabular value X^2 .001 =	10.83

Summary and Discussion

Characteristics of howls of three wolves were tested to see if there was any association between them and posture or movement of the howling wolf. As can be seen in Table 21, three relationships involving two characteristics (sudden drops in pitch in the body of howls, and rise in pitch incorporating the highest note of the howl) were found. Sudden drops in pitch in the body of howls did not show the same relationship with behaviour for both Wolf B and Wolf C. With Wolf B, howls lacking drops in pitch were associated more commonly than expected with pacing, whereas the reverse was true with Wolf C.

Table 21. - Relationships Between Characteristics of Howls and Behaviour for Wolves A, B and C

Howl Characteristic	Wolf A	Wolf B	Wolf C
Beginning	NR[1]	No test	NR
Ending	NR	NR	NR
Body			
Sudden drop	No test	R[2]	R
Rise incorporating highest note	NR	R	No test
Rise not reaching highest note	No test	No test	NR
Highest note	NR	NR	NR
Lowest note	NR	No test	NR
Length	NR	NR	NR

[1] NR = no relationship
[2] R = relationship

Characteristics of howls were tested to see if there was any association between them and whether howling was spontaneous or stimulated. As can be seen in Table 22, eight relationships involving seven characteristics were found. Only one of these, highest note, occurred in both wolves. In both cases, the highest notes of howls fell into the high range more than expected when howling was spontaneous.

Communication can take place on two levels - universal and individual. Communication that is universal (occurring within the species in general) requires a symbolism that is the same throughout the species. Characteristics of howls that showed the same significant relationship

Table 22. - Relationship Between Characteristics of Howls and Whether Howling was Spontaneous or Stimulated for Wolves

Howl Characteristic	Wolf A	Wolf B
Beginning	R[1]	No test
Ending	R	NR[2]
Body		
Sudden Drop	NR	R
Rise incorporating highest note	R	NR
Rise not reaching highest note	NR	No test
Highest Note	R	R
Lowest Note	R	No test
Length	R	NR

[1] R = relationship
[2] NR = no relationship

with either behaviour or whether howling was spontaneous or stimulated in all the wolves studied are the only ones of potential value in universal communication. One characteristic, highest note of howls, showed a significant relationship with spontaneous or stimulated howling in both Wolf A and Wolf B (no data existed for Wolf C). This significant relationship was primarily due to a greater number of high range highest notes than expected when howls were given spontaneously, in both wolves. This characteristic, satisfying the tenet of uniformity at least among two individuals, may have potential value in communication among wolves in general.

Communication on the individual level may occur between animals that learn to recognize individual traits in animals with whom they are associated. In this regard, all relationships found in this section (Tables 21 and 22) represent cases of potential conveyance of information to other individuals that have had the opportunity to learn that the specific associations exist.

V

AUDITORY DISCRIMINATION

To establish that a communicatory system is in operation, something must be learned about the ability of the receiver. This was studied by stimulus-response experimentation.

Methods

In 1964, Wolf A was physically and audibly isolated from his pen mates. Each night, stimulus tapes were played to the wolf. Tests involving single howls as stimuli were given in a sequence of six howls spaced approximately 15 seconds apart. Other tests were played for approximately one minute. Tests were discontinued as soon as a reply was elicited if it occurred before the end of the sixth stimulus howl or the one minute period. Any howling by the experimental animal up to five minutes after the end of the test stimulus was recorded as a response to that stimulus. Howling after five minutes was classed as spontaneous - having no relation to the previous test stimulus. Later in the summer a second test stimulus was often played after five minutes if the first test was not answered. This allowed more tests to be played to the wolf. Normally, however, tests followed each other after a time interval of 30 minutes. This was true in all cases where the first test had elicited a response.[7]

Testing began at dark and ran through most of the night. This time was chosen as a result of observations of wild wolves which indicated that night was the normal period of howling. Each night's program of stimuli was randomly picked.

Experimentation took place over a period of three months - June, July and August. It was hoped that the large number of times each test was played over a long period of time would randomize the effects of any short term variable that might bias results, such as weather, presence of a wild wolf in the area, etc.

In the summer of 1965, Wolf A was isolated physically from his pen mates on two occasions, and two other adult males, Wolf B and Wolf C also underwent periods of isolation. Stimulus-response tests were again conducted. The same experimental technique was used as in 1964 except tests were mostly run in the daytime. Observations indicated that time of day did not affect results.[8] Day testing allowed behavioural observations to be made.

The data in this section will deal with howling "occasions", defined for Wolf A as a series of howls with breaks between individual howls of not more than 15 seconds. One "response" is therefore equivalent to one

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7 This time interval was chosen as the result of experience with wild wolves and the wolves at the Wildlife Research Station. If a wolf responded it was usually difficult to get a second response within approximately 15 minutes, illustrating a waning of readiness to respond. After that, however, eliciting of response was again usually possible, indicating that the effect of the first stimulation had worn off.

8 Some tests were run at night and no difference in results was observed.

howling "occasion". The definition does not apply to Wolves B or C due to the large range of time lengths observed between howls. A single response for them is any howl or howls, regardless of grouping or number, given within five minutes after stimulation.

Experiments with Recorded Sounds of Wolves

Table 23. - Vocal Responses[1] to Recorded Sounds of Wolves

Stimulus	Times Played	Total Responses	Percent Responses
Wolf B	32	2	6.3
Known single Wolf 1[2]	59	2	3.4
Known single Wolf 2	57	3	5.3
Unknown single[3]	49	3	6.1
Pups	45	0	0
Wolf Barking	41	2	4.8
Chorus of captives howling	13	0	0

1 Total responses by howling by Wolves A, B and C
2 Single howls of a previous fellow captive at the Research Station.
3 Single howls of a wild wolf with which the experimental animals had had no previous association.

Wolf sounds as stimuli were played to the three wolves a total of 296 times. As Table 23 shows, they rarely elicited a response. No individual wolf had a percentage response to any one test stimulus of more than 10%.

When housed with their normal pen mates at the Research Station, these three wolves all howled readily to loud sounds. They were all easily stimulated to howl by the seven test tapes just discussed. These general observations at the Research Station made the lack of responses when in isolation unexpected. Three explanations are possible:

1. Some distortion was caused by the recording or reproducing system that masked any significance that stimulus tapes might have held. In view of the response by the wolves to these same tapes at the Research Station, this reason is not sufficient by itself, but the possibility of a partial contribution will be presented later.
2. The physical surroundings of the experimental pen, including isolation from other wolves for the first time in their lives affected the wolves in such a way that these tests were not stimulatory.
3. In the absence of other stimuli, none of the stimulus tapes held any significance that would induce the wolves to howl.

From the results of these particular experiments, these possibilities cannot be fully assessed. Further mention will be made of them in the discussions of results using other stimulus sounds.

Experiments with Human Howls

In 75 test situations when I attempted to stimulate a wolf howl, Wolf A answered 10 times (13.3%). In 147 tests when my wife howled, he answered 103 times (70.0%). Table 24 shows that there was a general increase in response as the summer progressed.

This increase in response to my wife's howl when no increase in responsiveness to the other tests occurred, can be attributed to either a gradually changing relationship with my wife or a gradual learning that the howls my wife gave were her's. Tests were given out of sight of the

Table 24. - Weekly Vocal Responses of Wolf A to My Wife's Live Howl

Date	No. of Sequences	No. of Responses	Percent Responses
July 1-7	15	5	33
July 8-14	18	7	39
July 15-21	28	21	75
July 22-28	15	10	67
July 29-August 4	23	17	74
August 5-11	18	16	89
August 12-18	13	13	100
August 19-26	17	14	82

animal so recognition of my wife's howl was on the basis of sound alone. Since the wolf's behaviour throughout the summer towards my wife was essentially the same, there is evidence for the second possibility - a gradual learning process. His behaviour towards my wife was friendly and subordinate, according to the following description by Schenkel (1947): "Liberal swinging of the tail in a sideways manner (wagging) with a free movement signifies friendly relations.... Individuals of low status frequently conduct these swinging motions with tightly pulled in tail and movements of the whole hindquarters. Deeply subordinate wolves... curve their legs, duck their heads, curve the tail base downward ("pull in"), do not raise the back hairs and do not growl."

Wolf A's behaviour towards me was one of fear - pacing rapidly as far away from me as possible. Only occasionally would he approach me, and then only when my wife was present.

These data suggest that the relationship of the receiver to the stimulator is an important factor affecting vocal response by the receiver. This may also have been true for tests with recorded wolf sounds. Wolf A had no relationship with the wolves he heard on the test tapes during the period of the experiments.

The human-wolf relationship could not be established in 1965 with Wolf A or the other two wolves. The period of isolation was not as long or as complete.

Experiments with Frequency Notes

Experiments with frequency notes were carried out to see if the discrimination between my howl and my wife's howl was on the basis of pitch or harmonics. Four different sound sources were used to make four tapes each of a steady note of 500 cycles per second (c.p.s.) and a steady note of 400 c.p.s. They were my wife holding the note, me holding the note, Mr. D. Robinson (assistant of Dr. Falls) holding the note, and a pure tone (no harmonics) produced by audio oscillator.

Discrimination, if it occurred, between the 500 c.p.s. notes on the one hand, and the 400 c.p.s. notes on the other hand, must be on the basis of harmonics since pitch was the same.

These tests were played in random order to Wolf A from July 23 until the end of August, 1964.

Table 25 shows that for each stimulus there is a smaller percentage response at 400 c.p.s. than 500 c.p.s. This suggests that pitch played some role in eliciting response. My wife's normal howls to which the animal usually responded, passed through the 500 c.p.s. range but not the 400 c.p.s. range. My normal howls to which this wolf rarely responded,

Table 25. - Vocal Responses of Wolf A to Recorded Frequency Notes

Stimulus	Times Played	No. of Responses	Percent Responses
500 c.p.s.[1]			
My Wife	22	7	32
Me	10	1	10
Robinson	6	2	33
Pure tone	16	2	13
400 c.p.s.			
My Wife	12	1	8
Me	2	0	0
Robinson	1	0	0
Pure tone	12	1	8

[1] c.p.s. = cycles per second

went through the 400 c.p.s. range but not the 500 c.p.s. range. It is possible, although not fully demonstrated, that Wolf A associated the higher range with my wife, and the lower range with me, and accordingly, responded more to howls in the higher range regardless of source.

However, Wolf A answered my 500 c.p.s. note only once in 10 tests (10%) - a much lower percentage response than to my wife's 500 c.p.s. note (31.8%). This fact suggests that the wolf was able to distinguish between my wife's howls and mine even when the pitch of the fundamental was the same.

Thus, it appeared that both pitch and harmonics played a part in affecting response to the frequency note tests. The possibility exists that both these factors, since they appeared to be recognizable by the wolf, played a part in the auditory discrimination of my wife's howls from my howls.

Experiments with Recorded Versus Live Human Howls

On August 8, 1964, a recording was made of my wife's howl, hereafter called "tape X". This recording was made in the cabin. Immediately after it was made, Wolf A responded. During the rest of the summer this tape was played as were the other tapes, through the Uher monitor speaker, on 11 occasions. It was answered only twice (18%). During this period, Wolf A's responses to my wife's live howl were much greater, occurring in all but four of 43 tests (93%).

The same tape was played through an external amplifier and a 12 inch speaker in a wooden box on 14 occasions. It was never answered.

To demonstrate how striking this pattern was, the following is the sequence of tests and responses to them for the evening and night of August 23, 1964.

Time	Test	Response
22.50	My Wife	Reply
23.20	Recording-Uher	No reply
23.50	My Wife	Reply
00.20	Recording-Uher	No reply
00.50	My Wife	Reply
01.20	Recording-box speaker	No reply
01.50	Recording-box speaker	No reply
01.55	My Wife	Reply

On what basis was this discrimination taking place? On October 30, 1965, conditions similar to those at the cabin were simulated at the Wildlife Research Station and a second Uher was used to record the three tests (my wife's live howl, tape X played through the Uher monitor speaker, and tape X played through the box speaker), at the same distance Wolf A had been from the sound source at the cabin. Plate IX (a, b and c) shows sonographs of these three sounds respectively (the first 4.8 seconds of each).

Comparing tape X played through the Uher monitor speaker (Plate IX (b)) with the live howl (Plate IX (a)), there are two distinct differences.

1. Through the Uher monitor speaker the fundamental is accompanied by two lines, one slightly above and one slightly below, during part of the howl. This distortion is audible, and sounds like a slightly lower note superimposing itself on the fundamental. The live howl does not show this.

2. Through the Uher monitor speaker during most of the howl, the second harmonic exceeds the first in intensity. The reverse is true of the live howl.

Comparing the howl played through the box speaker (Plate IX (c)) with the live howl (Plate IX (a)), essentially the same differences exist.

Total intensity can be measured by means of an "amplitude display" accessory to the Missilizer. Amplitude displays were made for the three howls on Plate IX. Fluctuation of intensity with time was observed to be quite great in all three howls. However, in general, the intensity of the live howl was greater than the other two. The intensity through the box speaker was only slightly less than that of the live howl (indistinguishable to human ears). The intensity through the Uher monitor speaker was the least (noticeably less than the other two sound sources to human ears).

Two additional recordings of my wife at the Research Station, and three recordings of her made in a "sound isolation room" at the University of Toronto, and tape X itself all showed the same acoustic properties as shown on Plate IX (a) (no distortion around the fundamental, the first harmonic stronger than the second and high intensity).

Similarly one additional recording of tape X played through the Uher monitor speaker at the Research Station, two more in the sound isolation room, and one re-recording of another live howl of my wife's in the sound isolation room all showed the same acoustics as shown on Plate IX (b) - distortion around the fundamental, stronger second than first harmonic and reduced intensity.

These additional howls provided evidence of the uniformity of acoustic characteristics of the live howls and of howls broadcast through the Uher monitor speaker, in two very different acoustic situations - open air at the Research Station and a sound room at the University of Toronto. There is little doubt that the characteristics would have been the same at the cabin where conditions were similar to those at the Research Station.

Therefore, it is concluded that Wolf A distinguished my wife's recorded howls from her live howls on the basis of any one or all of three acoustic differences - distortion around the fundamental of the sound, difference in relative intensity of the first two harmonics, and difference in intensity. Since the same howl showed these differences between its live properties and play-back properties, play-back apparatus was the source of the variation that the wolf distinguished.

Record and reproduction may have similarly affected sound quality of the recorded wolf sounds used in experiments, and be responsible for the lack of response to them. This, however, is unconfirmed.

The results presented demonstrate the ability of the wolf to distinguish subtle differences in sound. This implies that features of both the fundamental and harmonics previously discussed may be recognizable, and adds to the possibility that individual recognition and conveyance of information may take place through howling.

Summary

Wolves A, B and C responded fewer times than expected to recorded sounds of wolves. Two possible reasons gained support in tests with other sounds - distortion by the sound reproduction systems - tapes held no significance for the wolf.

Wolf A responded considerably more often to my wife's live howl than to mine. The wolf's behaviour towards each of us differed. It was possible that relationship between the wolf and the individual producing the sound affected willingness to respond.

Wolf A responded more often to 500 cycles per second notes than to 400 cycles per second notes. This suggested that pitch was recognizable by the wolf. It was further observed that my 500 c.p.s. note elicited much fewer responses than my wife's 500 c.p.s. note. This suggested that harmonics were also recognizable by the wolf. Pitch and harmonics may also have been the basis for Wolf A's distinguishing my wife's howl from my howl.

Wolf A responded much more frequently to my wife's live howl than to a recording of her howl played through a speaker. Three acoustic properties were found in recorded howls that differed from live howls - distortion around the fundamental, reversal of relative strength of the first two harmonics and lower total intensity. One or all of these differences provided the basis for discrimination of live from recorded human howls. The possibility that individual recognition and conveyance of information may take place through howls is strengthened, since it has been demonstrated that the animal can detect subtleties in sounds.

VI

CIRCUMSTANCES IN WHICH SPONTANEOUS HOWLING OCCURRED

By definition, spontaneous howling is howling given with no known auditory stimulation. As defined, it must occur more than five minutes after an auditory stimulus. A large percentage of the howls discussed in this thesis fall under this definition. It is therefore of value to examine the circumstances surrounding their occurrence.

Results in 1964

In 1964, the total amount of time Wolf A was isolated from his pen mates could be divided into three categories. These were:

1. Hours when either my wife or I was present in the cabin near the wolf pen.
2. Hours when the wolf was left entirely alone, or was presumed to be alone.
3. Hours following our arrival back in the area of the pen after an absence.

Arbitrary time limits must be set to separate certain of these categories. Category 3 is separated from Category 1 by being defined as 15 hours immediately following a return to the pen area after an absence of at least five hours. These 15 hour periods are therefore not included in Category 1.

Rate per hour of spontaneous howling "occasions"[9] was calculated for each category. The number of hours in Category 1 was an estimate. Category 2 was restricted to hours that we were still actually within hearing only and therefore could note when howling occurred.

Table 26. - Spontaneous Howling as it Relates to Environmental Circumstances

Environmental Circumstances Category	No. of Hours	No. of Howling Occasions	Howling Occasions Per Hour
1	1200 ≁	11	0.009
2	20	68	3.4
3	400	78	0.19

1 My wife or I present in pen area
2 Wolf left alone
3 My wife or I in pen area after an absence

Table 26 shows that the rate of howling varied enormously depending on environmental circumstances. The highest rate occurred while the wolf was left alone, demonstrating the effect of isolation. A medium rate occurred while we were in the area of the pen but had been absent immediately before. The lowest rate occurred while the wolf was not in

9 "occasion" was previously defined as a series of howls given in rapid succession with no more than 15 seconds between individual howls.

isolation,[10] or had not been in the previous 15 hours. The medium rate in category 2 may have been the result of a carry-over effect from isolation.

The onset of howling in category 2 - howling when left alone showed variation as the summer progressed. Because of its location it was necessary to walk by the pen when leaving the area. Early in the summer, this event was usually followed by at least 12 hours during which we were away and the wolf was left alone. Before July 23, we were out of hearing of the wolf within five to 10 minutes after leaving in all instances except one, and so did not hear howling if it did occur. In the one instance, Wolf A gave two sets of howls (occasions), the first one seven minutes after our departure and the second one ten minutes later.

After July 23, we tested the effect of isolation by walking by the pen and down the trail out of sight but staying within hearing. This test was attempted 10 times, each on a different day. Every time, our departure was followed by howling. The time lapse between our departure and the first howling occasion varied from three to 50 minutes, with an average of 19 minutes. The length of our absence varied from 20 minutes to three hours. Whether we were away a short or long time, spontaneous howling occasions occurred every five to 30 minutes until we returned.

Walking by the pen in the opposite direction produced somewhat different results. Before July 23, my wife and I arrived together six

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[10] Most of the hours we were in the area of the pen were spent in the cabin, approximately 70 feet from the pen. It is assumed that the wolf usually knew we were present. Although it was doubtful if he could hear our talking, noises such as clatter of pans were doubtless often heard. The fact that he looked in the direction of the cabin when such noises occurred, confirmed this.

times following an absence of at least 12 hours. Four of these were followed by howling within an hour after arrival (67%). After July 23, arrival at the pen and subsequent disappearance to the cabin was never followed by howling during the first hour back in the cabin.

These results suggest that our movement by the pen when leaving the area either itself was stimulatory, or Wolf A learned that this action led to isolation. If the latter was true, the action marked the beginning of a period of isolation and therefore the onset of increased howling.

Movement in the opposite direction - by the pen and out of sight to the cabin had the same effect early in the summer as movement by the pen when leaving, suggesting that the significance of the two directions in terms of isolation was not realized. The change in effect on howling that movement to the cabin had later in the summer suggests that Wolf A learned that this did not result in isolation.

Results in 1965

In 1965, isolation, as mentioned, was not as complete. Wolf A was isolated physically from the other wolves on two occasions. During his first period of isolation, of 12 days, he was heard to give spontaneous howls on 45 occasions. Of the 45 spontaneous occasions, 13 were given while we were absent from the general area of the pen. Due to the much increased occurrence of our going to and leaving the pen, the effect of our movement is not clear. Five of these 13 occasions occurred within five minutes of our movement past the pen.

The remaining 32 occasions took place while we were in the tent. Two possible explanations for these howls are offered. One, when we were in the tent, the wolf was unaware of our presence, and two, isolation of eight to 12 hours the night before was showing its carry-over effect. Data are insufficient for either assertion.

During his second period of isolation, of five days, Wolf A was heard to howl spontaneously on 19 occasions. These all occurred while we were absent.

Quantitative data do not exist for Wolves B or C regarding situations involving spontaneous howling. This was because howling "occasions" usually did not exist as discrete entities. Qualitative rather than quantitative data were collected. However, both wolves howled spontaneously a great deal while we were absent from the experimental area - so much so that with them, as well as with Wolf A, the technique for recording howls necessitated not being discovered while recording.

Thus, observations of Wolf A in the summer of 1965 provided more evidence that spontaneous howling was stimulated by isolation. The effect of isolation was not as great as in 1964, presumably because isolation was not as complete. General observations of Wolf B and Wolf C also indicated that isolation had a pronounced stimulatory effect on spontaneous howling.

Discussion

Scott and Bronson (1964) studied the effects of isolation on "distress vocalizations" of puppies, concluding that since "puppies appear to be lonely and afraid when isolated in a strange situation" it is this emotional state that is causal to their distress vocalizations in isolation. They go on to say that distress vocalization due to isolation wanes at approximately 10 weeks of age. However, it is a common observation that adult dogs will vocalize when shut up alone. It is not a large step to go from Scott and Bronson's observations of puppies and what we know of adult dogs to these observations of adult wolves. Wolpy (pers. comm.) states that adult wolves in a zoological garden in Chicago, howl if shut off from the rest of the pack.

Scott and Bronson (1964) state, "Many of the behaviour patterns of the two species (man and dog) are mutually comprehensible, and puppies develop with their human masters a social relationship that is in many ways comparable to the human parent-child relationship." A human-wolf relationship appeared to have formed in 1964 between Wolf A and my wife. This explains how a human might be the animal causing a wolf to feel isolated or otherwise.

Vocalization as a result of isolation seems logical in an adaptive sense. Scott and Bronson (1964) state, "Isolation in the puppy produces an emotion which is uncomfortable and which is immediately relieved by the presence of other animals. A young animal would be expected to learn quickly that in order to avoid such emotions he must do as the others do, and this could lead to a very strong habit of roaming in packs, whether canine or human. This may suggest that the emotional response to isolation may function as a general motivational basis for maintaining social contact."

In personal communication, Crisler says, "loneliness - provided there is no fear - may touch off a solitary wolf's night howl." This differs from Scott and Bronson's statement in regard to fear.

Humans tend to presume that loneliness and fear accompany isolation. This may be true, However, due to the dangers involved in assigning specific human emotions to animals, the safest conclusion is that an emotion is engendered by isolation, one manifestation of which is howling.

VII

ECOLOGICAL SIGNIFICANCE OF HOWLING

Wolves are highly developed socially (Schenkel, 1947, Etkin, 1964), forming groups which occupy fairly distinct territories (Meech, 1962). In order to function as a group, interaction among individuals is necessary. Interaction involves communication. Wolves communicate at close range by facial expression, tail position, body posture, scent, touch (Schenkel, 1947) and vocalization. Obvious close range vocal communication observed with captive wolves at the Wildlife Research Station included whining, snarling and low bark (in defense of pup). Also observed by many writers is the so-called social or group howling, a common phenomenon of the Wildlife Research Station captives, and heard many times during field studies in which the writer took part.

The food and hunting habits of wolves require members of a social unit to be separated at times. Single wolves were often heard and occasionally seen in the field studies mentioned above. Meech (1962) on Isle Royale describes a wolf trailing behind a pack a number of times during aerial surveys. The author observed a single wolf which rarely joined the other three adults and four pups of its social unit on Baffin Island in August, 1965. When separated, visual (in forested regions especially) or tactile means of communication are eliminated, as well as low volume vocal communication. Scent still exists - instead of body "besnuffling" (Schenkel, 1947), urination is probably a common method of communication, as it appears to be in dogs. It seems a natural adaptation for an animal, socially developed, forced to be separated from members of its social unit, and in all of its habitats rarely having to fear discovery of its location by another species (no predator), to have evolved a form of vocal communication functional over long distances. This thesis has explored the possible refinements of this type of communication.

Besides group howling, ecological studies have demonstrated that an unusual disturbance elicits howling. Of 14 instances of barking and howling cited by Murie (1944), eight occurred when the wolves were disturbed by Murie's presence. On two occasions, while the author was near a den on Baffin Island, wolves barked and howled from a distance of a few hundred yards. In August 1962, Dr. Pimlott recorded barking, then barking changing to howling from an adult wolf observing him at close range in Algonquin Park (pers. comm.). This type of howling - disturbance howling, has not entered into my study. Qualitatively, like chorus howling, its characteristics are not known.

The third broad class of howling is isolation howling, with which this thesis has dealt. Evidence was presented in the section entitled "Circumstances in which Spontaneous Howling Occurred" on the propensity of a wolf to howl when separated from the members of its social unit (in this case, humans). It was suggested that vocalization in isolation is a manifestation of an internal state, by both my studies and those quoted in the discussion of spontaneous howling. This internal state could conceivably come about while an animal is separated in the wild from its associates, and thereby be the cause of spontaneous single howling. Such howling may impart information. The common features of both the fundamental and harmonics may identify the source of the sound as a wolf. Information on the location of the wolf may be provided. Dogs are able to detect the location of a sound source with great accuracy (Katz, 1961). Murie (1944), cites examples in which howling brought other pack members to the single howling animal. The author, Dr. Pimlott and Mr. Joslin have experienced a number of occasions when wolves came to their human howls or recorded wolf howls during the field studies in Algonquin Park.

By imparting information on location, pack members may stay in contact with one another. Vocal territory advertisement, as is believed to exist in howler monkeys (Carpenter, 1954), may also take place.

Wolves commonly howl in response to the howls of other wolves, a fact upon which much of this research was based. This trait allows for two way communication.

It has been demonstrated in this thesis that unique features exist in the howls of individual wolves. Harmonic characteristics were found that would distinguish individuals on the basis of any one howl. This fact means that wolf howls may provide a basis for individual recognition. The ability of a wolf to detect subtleties in sound indicates that reception of this information is possible. The significance of individual recognition from howls is obvious in both location of specific individuals and efficient territory advertisement.

Characteristics of howls were found to be related to the behaviour of the howling wolf and circumstances surrounding howling. This fact, again coupled with the ability of a wolf to detect subtle differences in sound, suggests that specific information about the howling animal may be communicated.

In the lives of wild wolves, often forced to be separated from members of their social unit, a form of long distance communication stimulated by isolation is of positive value. If, as suggested in this thesis, this long distance communication identifies the species, functions in the location of animals, territory advertisement, individual recognition, and provides information on the behaviour, internal state, environment or some combination of these, it is of great value in coordinating the social activities of wolves.

SUMMARY

A study was made of the howls of three individually housed, captive timber wolves to assess the potential of howling as a communicatory mechanism. Five questions were posed:

1) How much individual variation exists in wolf howls?

2) Does variation in wolf howls correlate with the behaviour or situation the wolf is in and thus represent units of potential information?

3) What ability does a wolf have to distinguish sound variation?

4) What circumstances surround spontaneous howling (howling which was not elicited by auditory stimulation)?

5) What is the ecological significance of howling?

To answer question one, recorded howls of the three wolves were subjected to auditory and spectrographic analysis. The following information was obtained.

a) A howl could be defined as a continuous sound of approximately half a second to 11 seconds in length. It consists of a fundamental frequency which may be between 150 and 780 cycles per second, and up to 12 harmonically related overtones. Most of the time it is changing smoothly or remaining at a constant pitch. It may change direction of pitch as many as four or five times. Its total intensity remains approximately constant throughout.

b) Similarities existed in the strength of harmonics of a majority of howls. These were a decrease in intensity of the first harmonic at low pitches, and an increase in intensity of the second harmonic at low pitches. In all three wolves these changes in intensity of harmonics took place across the narrow pitch range of the fundamental of G# to F#.

c) Variations in the fundamental occurred between howls of the same individual with respect to beginning, ending, pitch changes in the body of howls, highest note, lowest note and length. This variation provides for potential coding of information.

d) Comparing the howls of the three wolves, a high degree of "individuality" was observed. Individual preferences occurred for type of beginning, type of ending and pitch changes in the body of howls. Individual preferences were also apparent for types of howls (based on combinations of characteristics). Averages of highest notes, lowest notes and lengths differed significantly among the three animals. Unique features occurred in the fundamental of many of the howls of two of the wolves. Unique features occurred in the harmonics of all of the howls of two of the wolves. Thus, howls of different individuals were at least potentially recognizable by other wolves.

To answer question two (Does variation in wolf howls correlate with the behaviour or situation the wolf is in and thus represent units of potential information?), an attempt was made to relate characteristics of howls to behaviour (posture and movement). The presence or absence of two characteristics (sudden drops in pitch in the body of howls, and rise in pitch incorporating the highest note of howls) was found to be related to whether the wolf was lying, walking slowly or pacing. The first characteristic was related to behaviour in two of the three wolves, but the nature of the relationship was different.

An attempt was also made to relate the characteristics of howls of two wolves to whether the wolf howled spontaneously or as a result of auditory stimulation. Seven characteristics (type of beginning, type of ending, sudden drops in pitch in the body of howls, rise in pitch incorporating the highest note of howls, highest note, lowest note and length) were found to be related to whether howling was spontaneous or stimulated. Only one of these characteristics, highest note, showed the same relationship in both wolves.

Thus, little basis was discovered for a universal system of communicating information of a behavioural or environmental nature. However, information did exist in howls of potential value in communication on an individual level (between wolves familiar with each other and therefore able to recognize any significance howl characteristics may have in the other individual).

The third question (What ability does a wolf have to distinguish sound variation?), was studied by stimulus-response experimentation.

a) Tests using tape recordings of wolf sounds as stimuli were responded to vocally only 4% of the time.

b) Tests involving live (non-recorded) simulated wolf howls by humans were responded to in different amounts depending on the human involved. (These experiments were carried out on one wolf only). My wife's howl elicited 70% response whereas my howl elicited 13% response. The behaviour of the experimental wolf towards us differed greatly.

c) Five hundred cycles per second (c.p.s.) frequency notes were responded to more often (22%) than 400 c.p.s. notes (7%), suggesting that pitch of the fundamental was distinguished. (My wife's simulated wolf howl fell in the 500 c.p.s. range whereas my howl fell in the 400 c.p.s. range). My wife holding a 500 c.p.s. note was answered more commonly (32%) than me holding the same note (10%) indicating that harmonic differences were distinguished. It was concluded that both pitch and harmonics could have been responsible for the wolf's differentiation of my wife's howl from mine.

d) Response was more common to my wife's live (non-recorded) howl (93%

during the period of this experimentation) than to a recording of her howl played through either of two speakers (8%). Three fairly subtle acoustic properties were found in played back howls that differed from live howls. These were: slight distortion of the fundamental, reversal of the relative strength of the first two harmonics, slightly lower total intensity. It was concluded that the wolf was able to detect these differences. This ability adds to the possibility that individual recognition and conveyance of information may take place through howls.

In assessing the fourth question (What circumstances surround spontaneous howling?), it was found that spontaneous howling was much more common when the experimental wolf was in isolation (or presumed isolation) from other wolves and humans. The suggestion made by other workers that vocalization in isolation is the result of an emotional state linked with isolation appeared feasible in view of the results.

As to the fifth question, related to the ecological significance of howling, in the lives of wild wolves, often forced to be separated from members of their social unit, a form of long distance communication stimulated by isolation is of positive value. If, as suggested in this thesis, this long distance communication identifies the species, functions in the location of animals, territory advertisement, individual recognition, and provides information on the behaviour, internal state, environment or some combination of these, it is of great value in coordinating the social activities of wolves.

PLATES

Plate I

Represented are sonographs of four howls (a, b, c, d) of Wolf A.

The lowest line in each case is the fundamental frequency.

Higher lines are harmonics.

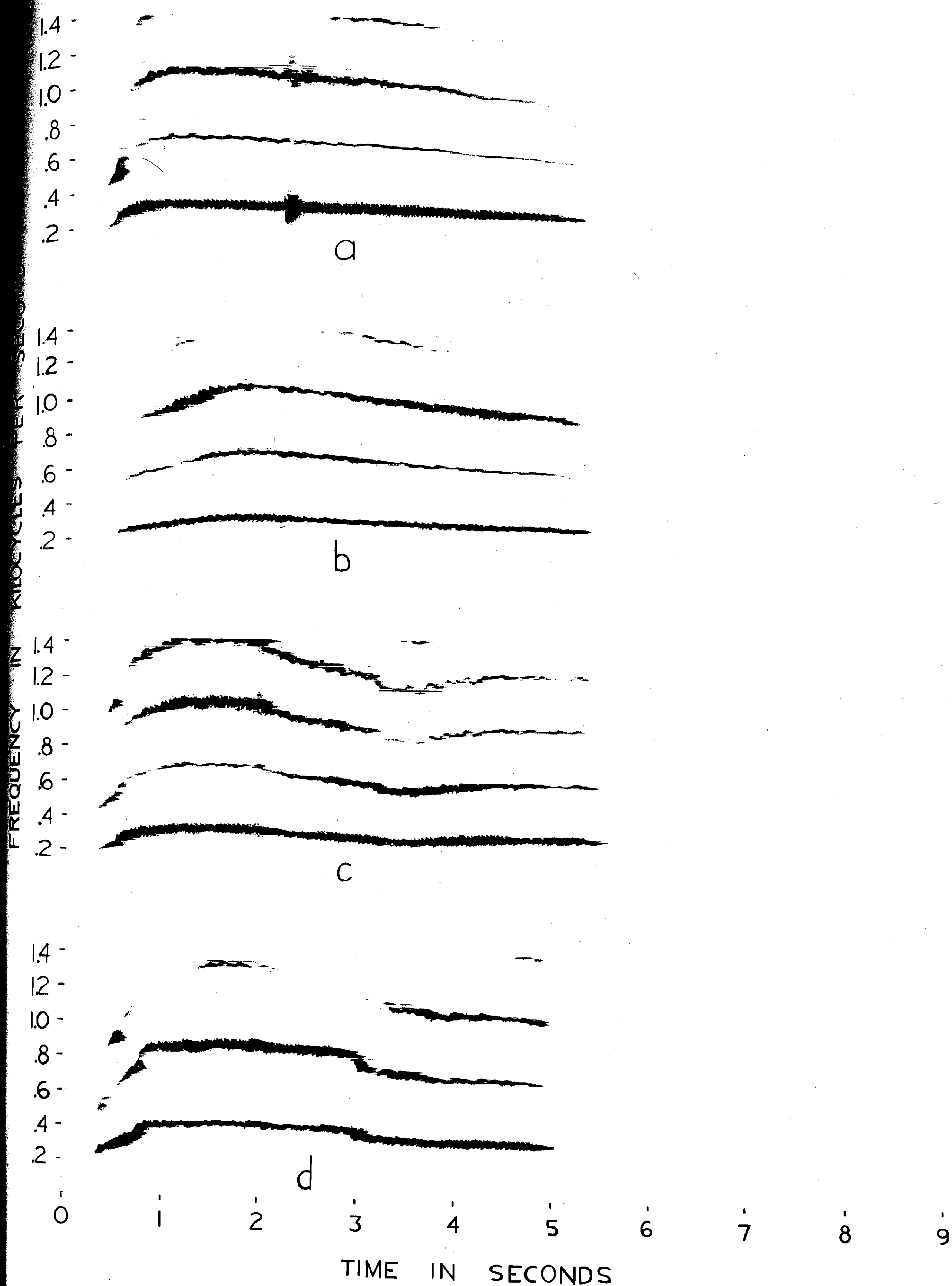
Sub-types are on the basis of pitch changes in the body of howls. The body of the howl is all the howl except the first 0.5 seconds and last 0.5 seconds.

a is sub-type 1 (no drops in pitch or rises in pitch in the body of the howl)

b is sub-type 1R (rise in pitch incorporating highest note of the howl, no drops)

c is sub-type 1Rr (rise in pitch incorporating highest note of the howl, rise in pitch not reaching the highest note)

d is sub-type 2 (one drop in pitch, no rises)



FREQUENCY IN KILOCYCLES PER SECOND
1.4
1.2
1.0
.8
.6
.4
.2
a
b
c
d
0 1 2 3 4 5 6 7 8 9
TIME IN SECONDS

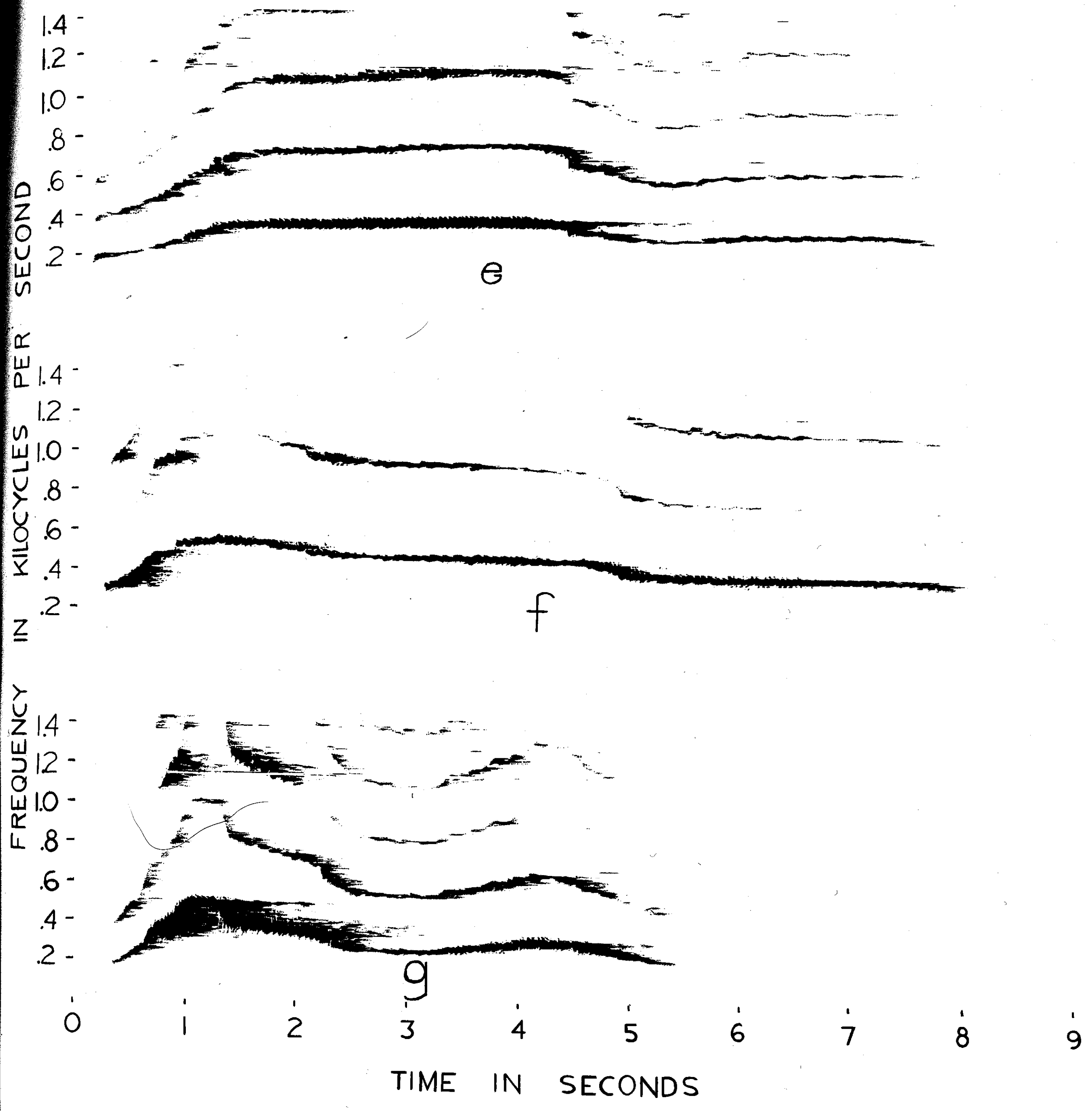
Plate II

Represented are three howls of Wolf A

e is sub-type 2R (one drop in pitch, rise in pitch incorporating the highest note of the howl)

f is sub-type 2Rr (one drop in pitch, rise incorporating the highest note of the howl, one rise not reaching the highest note of the howl)

g is sub-type 3Rr (two drops in pitch, one rise incorporating the highest note of the howl, one rise not reaching the highest note of the howl)



FREQUENCY IN KILOCYCLES PER SECOND
1.4
1.2
1.0
.8
.6
.4
.2
e
f
g
0
1
2
3
4
5
6
7
8
9
TIME IN SECONDS

Represented are five howls of Wolf B

h is sub-type 1 (no drops in pitch, no rises)

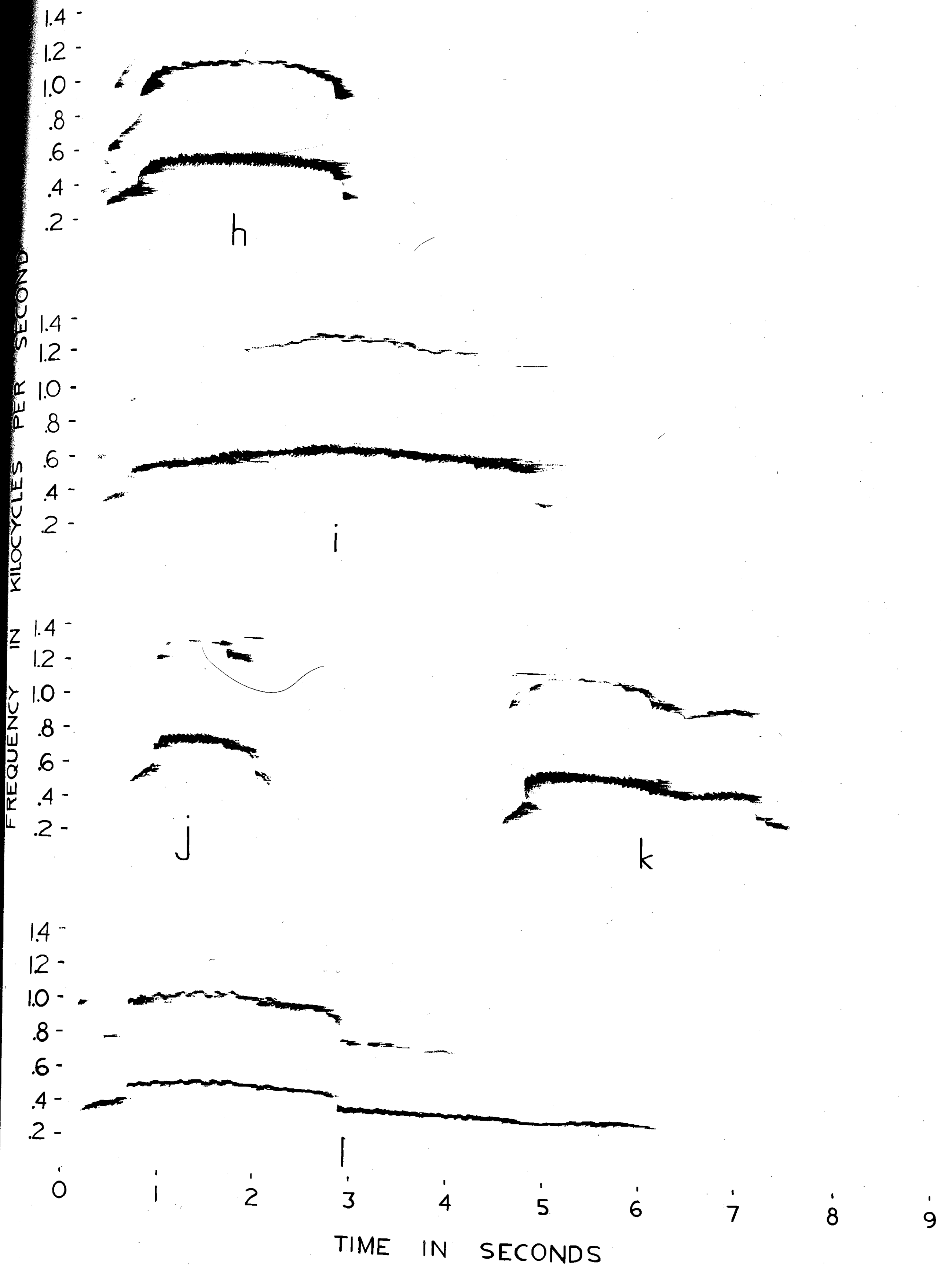
i is sub-type 1R (rise in pitch incorporating the highest note of the howl, no drops)

j is sub-type 2 (one drop in pitch, no rises)

k is sub-type 2 (one drop in pitch, no rises)

l is sub-type 2 (one drop in pitch, no rises)

(j, k and l represent variations in total lengths of three howls in the same sub-type).



FREQUENCY IN KILOCYCLES PER SECOND
1.4
1.2
1.0
.8
.6
.4
.2
h
i
j
k
l
0
1
2
3
4
5
6
7
8
9
TIME IN SECONDS

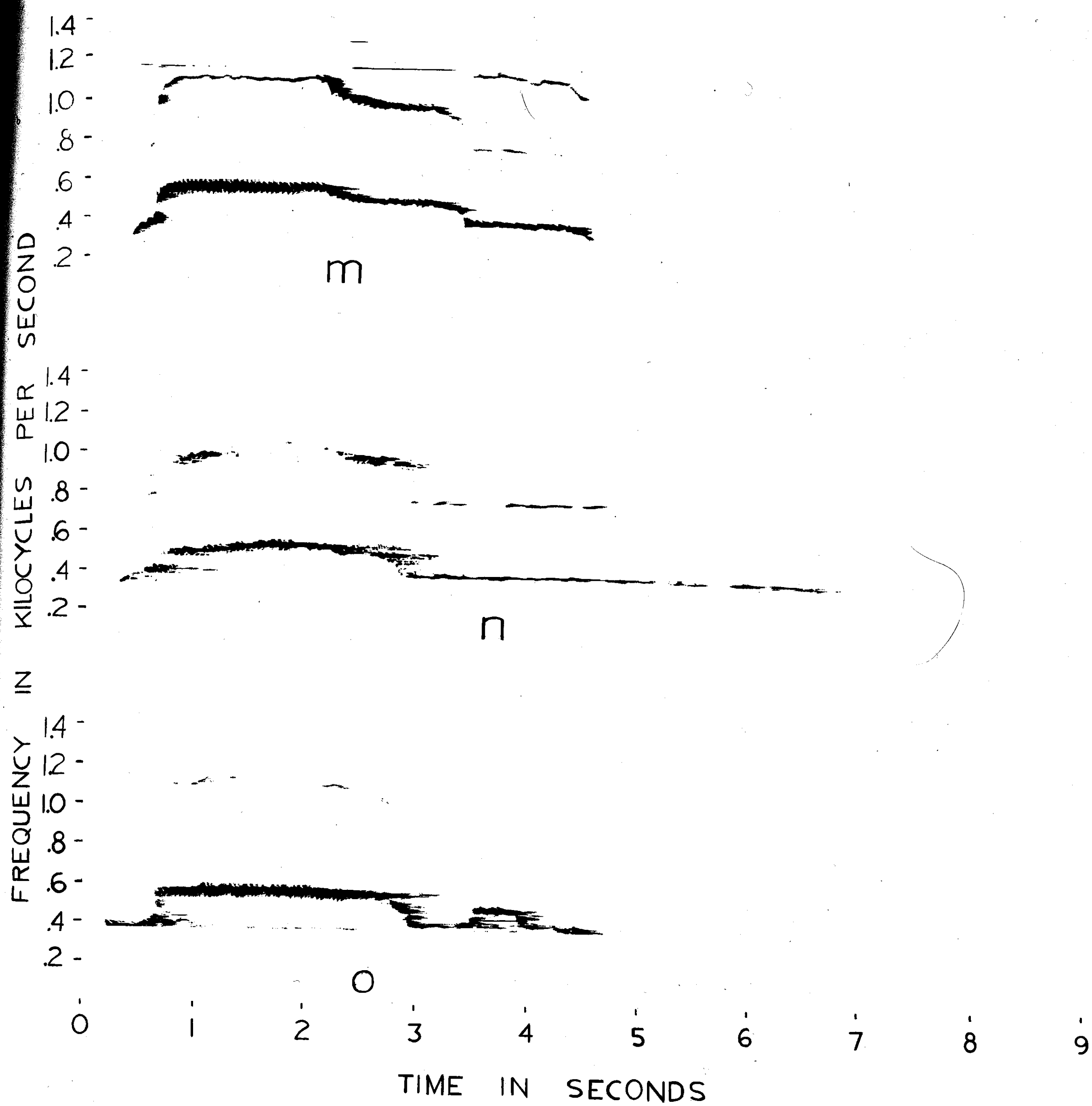
Plate IV

Represented are three howls of Wolf B

m is sub-type 3 (two drops in pitch, no rises)

n is sub-type 3R (two drops in pitch, rise in pitch incorporating the highest note of the howl)

o is sub-type 4r (three drops in pitch, one rise in pitch not reaching the highest note of the howl)



FREQUENCY IN KILOCYCLES PER SECOND
1.4
1.2
1.0
.8
.6
.4
.2
m
n
o
0
1
2
3
4
5
6
7
8
9
TIME IN SECONDS

Plate V

Represented are four howls of Wolf C

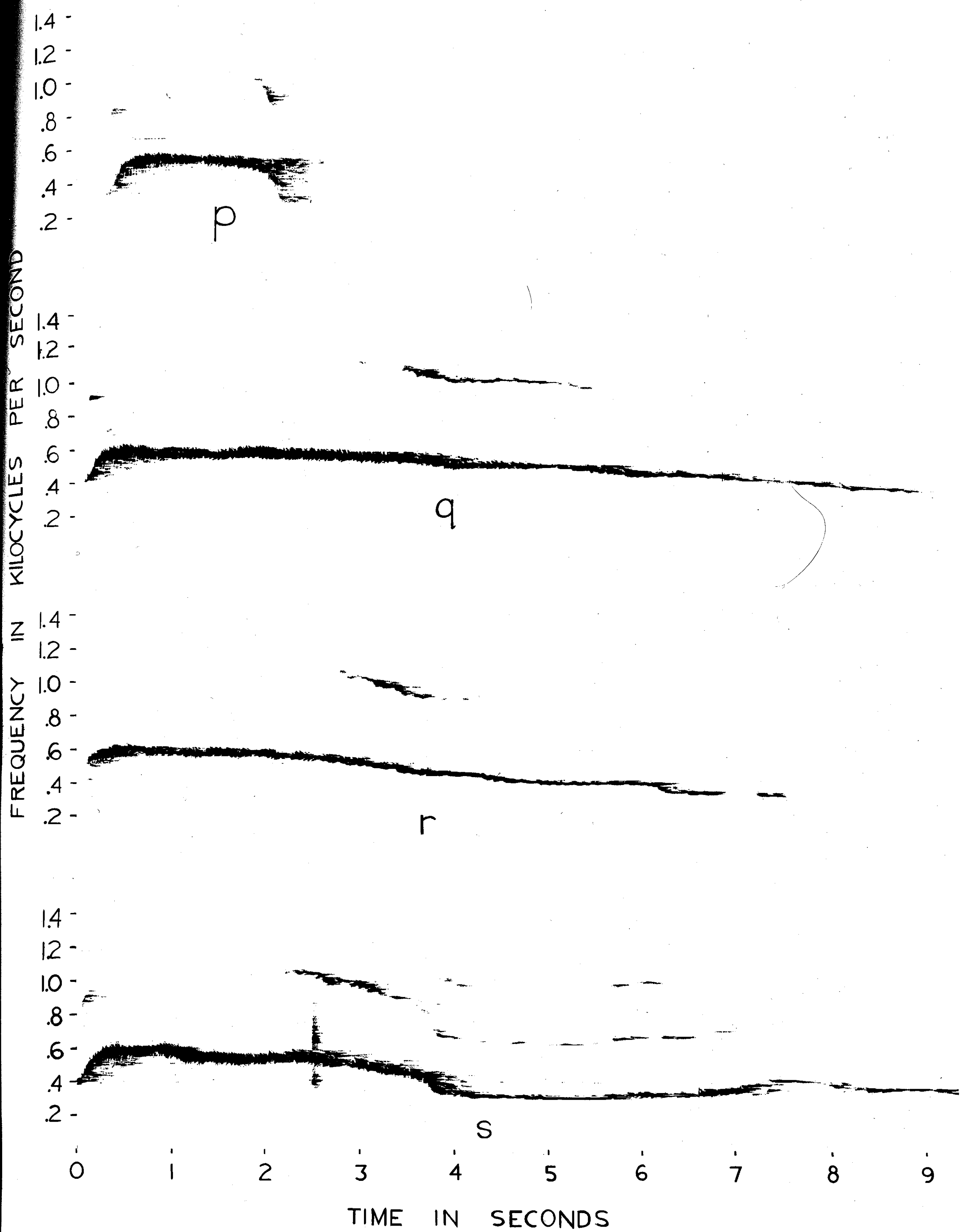
p is sub-type 1 (no drops in pitch, no rises)

q is sub-type 1 (no drops in pitch, no rises)

r is sub-type 2 (one drop in pitch, no rises)

s is sub-type 2r (one drop in pitch, one rise not reaching the highest note of the howl)

(p and q represent a variation in total length of two howls in the same sub-type).



FREQUENCY IN KILOCYCLES PER SECOND
1.4
1.2
1.0
.8
.6
.4
.2
p
q
r
s
0
1
2
3
4
5
6
7
8
9
TIME IN SECONDS

Plate VI

Represented are three howls of Wolf C

t is sub-type 2rr (one drop in pitch, two rises not reaching the highest note of the howl)

u is sub-type 3 (two drops in pitch, no rises)

v is sub-type $3r_1$ (two drops in pitch, one rise not reaching the highest note of the howl)

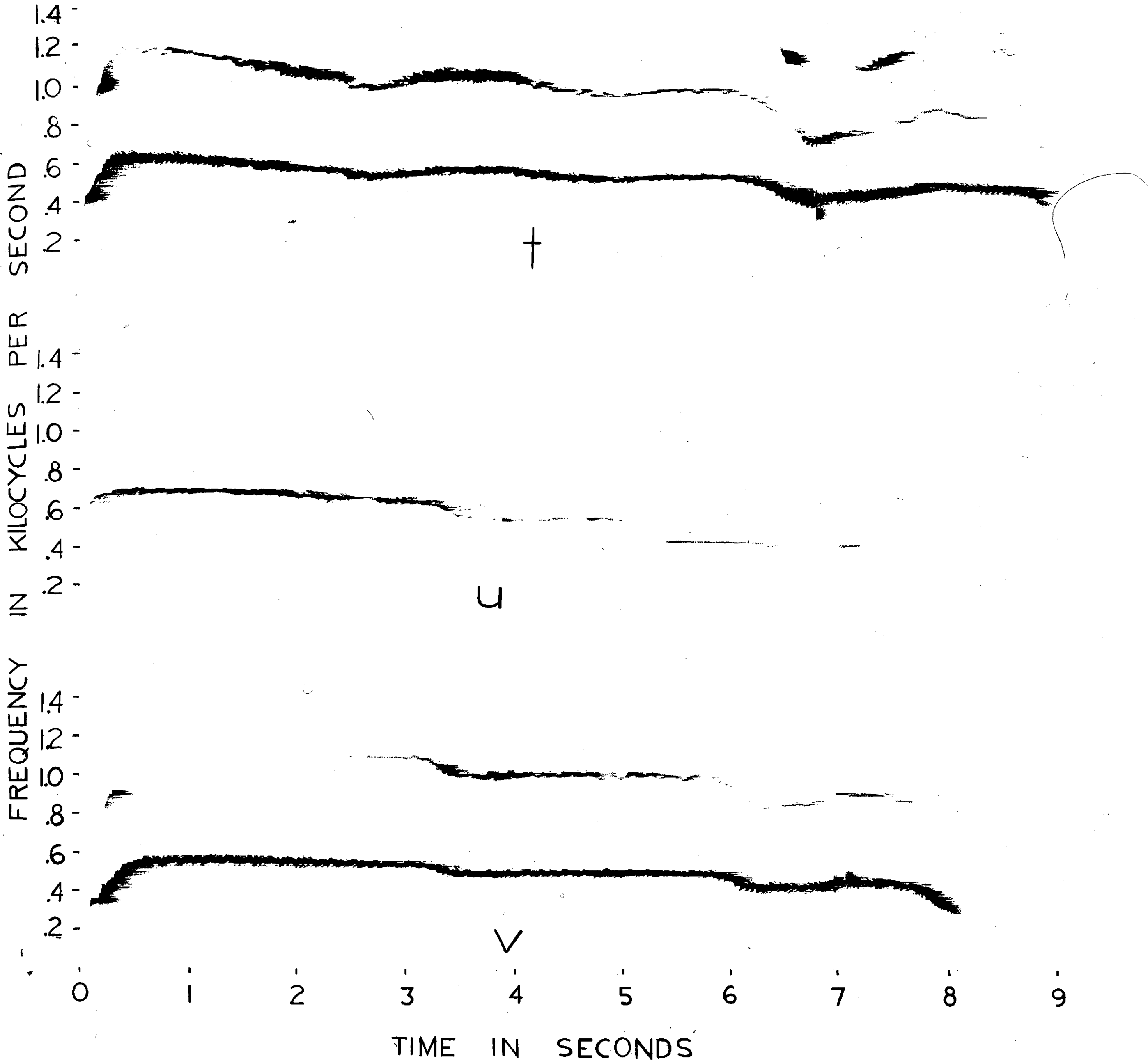

FREQUENCY IN KILOCYCLES PER SECOND
1.4
1.2
1.0
.8
.6
.4
.2
†
u
V
0
1
2
3
4
5
6
7
8
9
TIME IN SECONDS

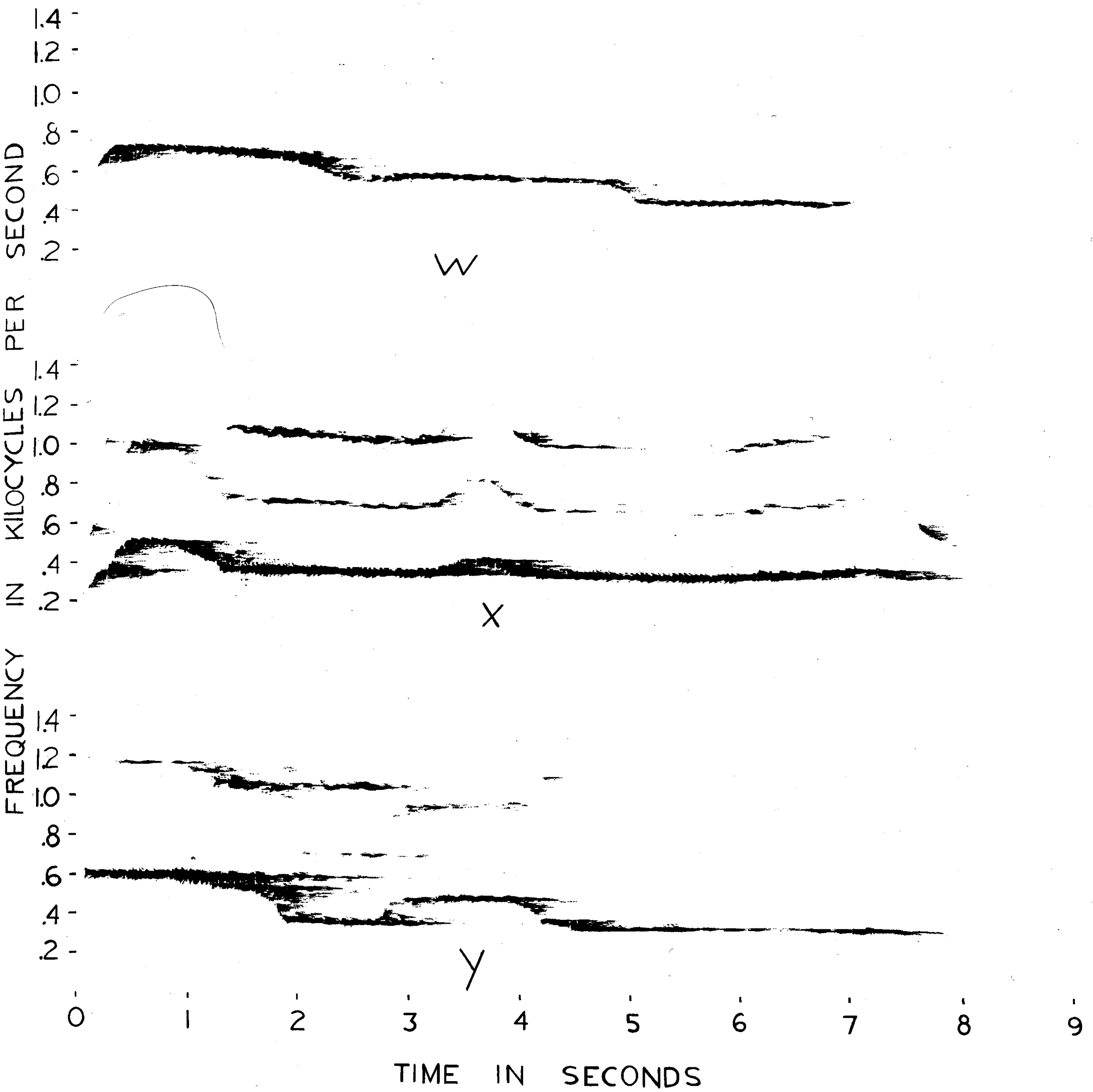
Plate VII

Represented are three howls of Wolf C.

w is sub-type $3r_2$ (two drops in pitch, one rise not reaching the highest note of the howl)

x is sub-type 3rr (two drops in pitch, two rises not reaching the highest note of the howl)

y is sub-type 4r (three drops in pitch, one rise not reaching the highest note of the howl)



FREQUENCY IN KILOCYCLES PER SECOND
1.4
1.2
1.0
.8
.6
.4
.2
W
X
Y
0
1
2
3
4
5
6
7
8
9
TIME IN SECONDS

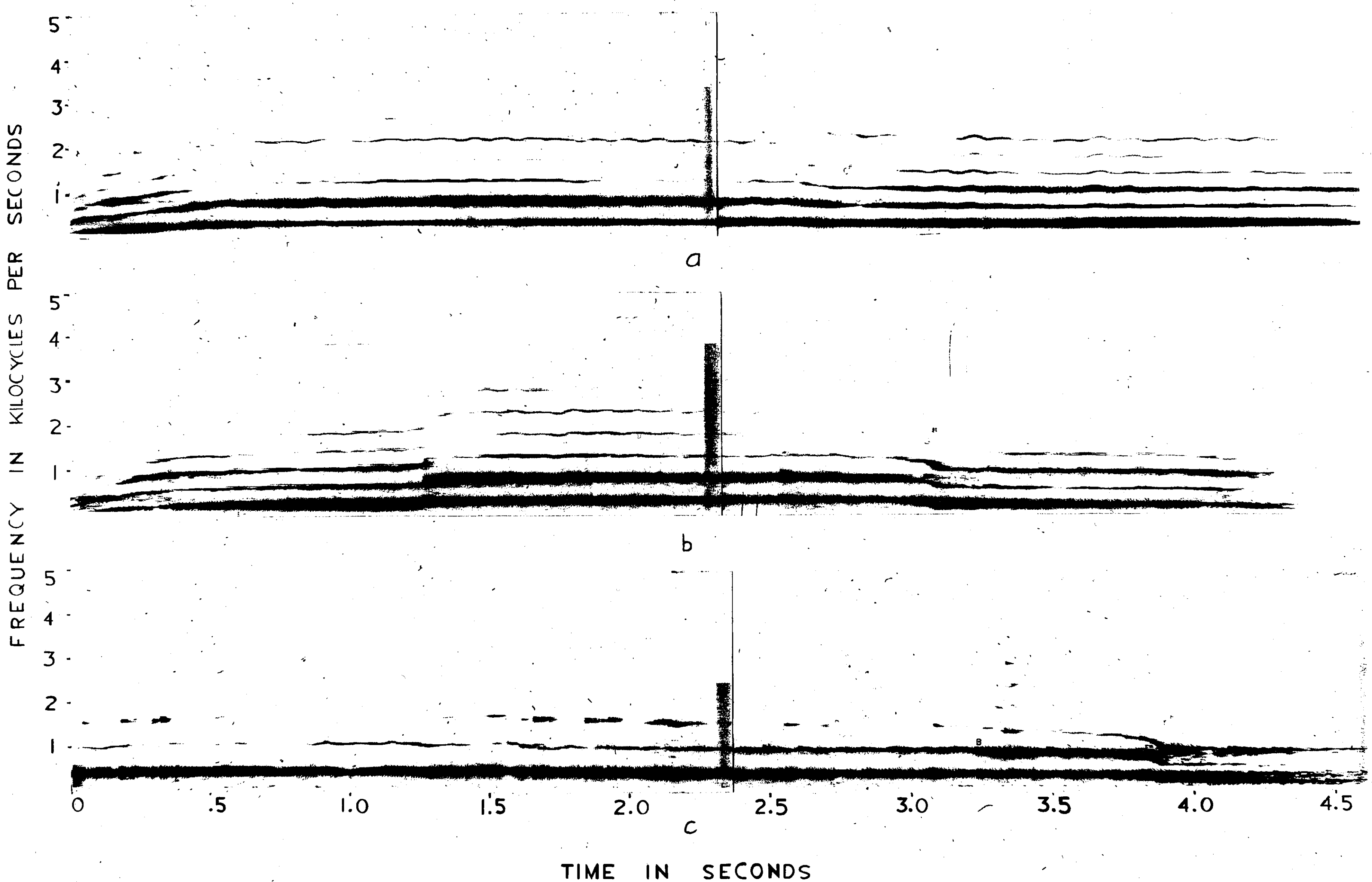
Plate VIII

Represented is the first 4.8 seconds of three howls, one each from wolves A,B,and C.

a is Wolf A

b is Wolf B

c is Wolf C



FREQUENCY IN KILOCYCLES PER SECONDS
5
4
3
2
1
a
b
c
0
.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
TIME IN SECONDS

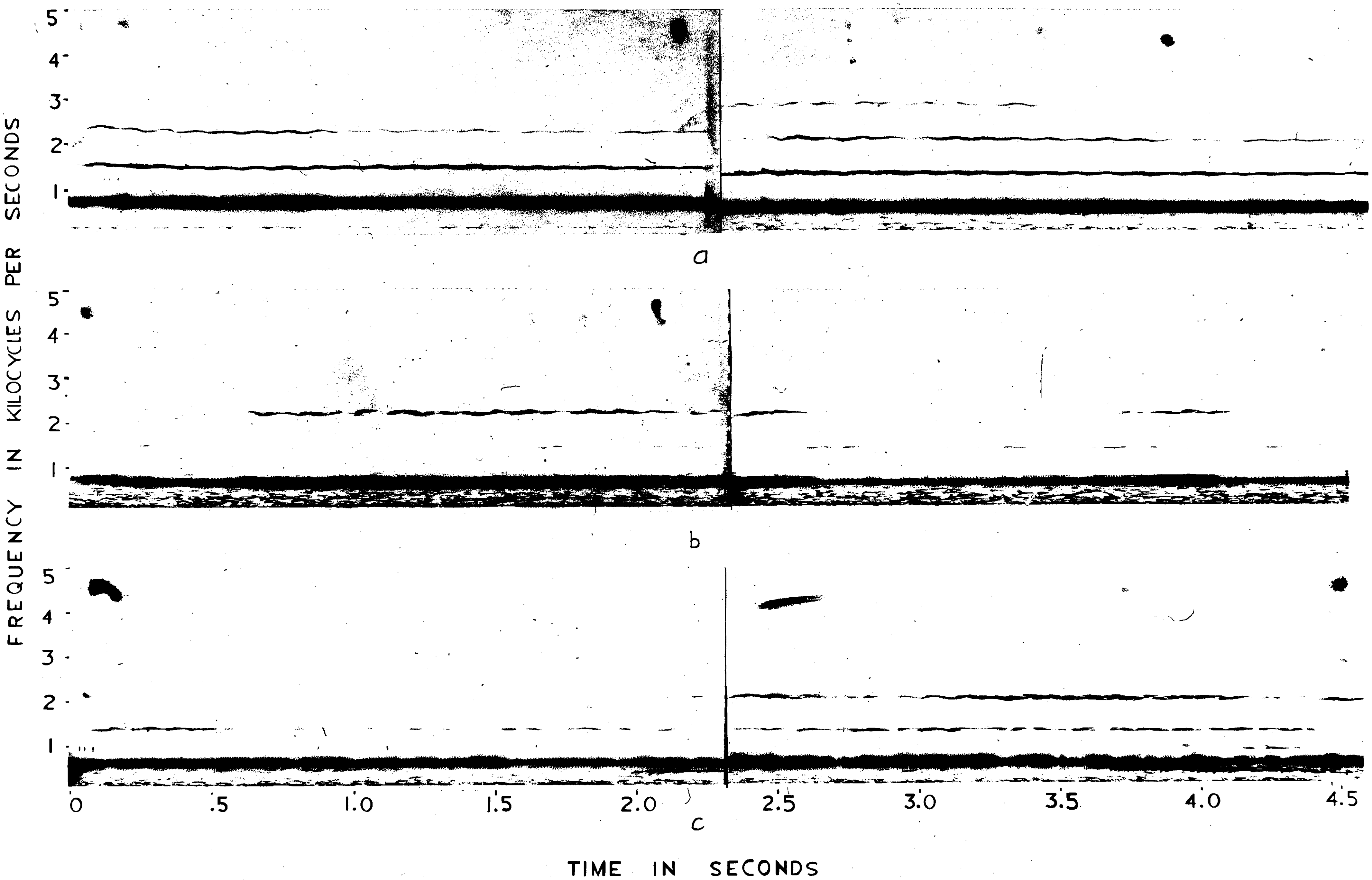
Plate IX

Represented is the first 4.8 seconds of a simulated wolf howl by the author's wife.

a is howl as it appeared on the original tape

b is a re-recording of the howl played through a Uher monitor speaker

c is a re-recording of the howl played through a 12" speaker in a box enclosure



FREQUENCY IN KILOCYCLES PER SECONDS
5
4
3
2
1
a
b
c
0
.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
TIME IN SECONDS

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