



Vocal Repertoire in the Dhole *Cuon alpinus* (Carnivora, Canidae) in Captivity

I. A. Volodin, E. V. Volodina, and I. V. Isaeva

Moscow Zoo, Moscow, 123242 Russia

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Abstract—Three independent structural components form the dhole vocal repertoire: low tonal, high tonal, and pulsed. The repertoire was divided into three vocal classes and eleven call types based on the occurrence of these components. Two broadband signals with a pronounced pulsed pattern were referred to the pulsed vocal class. Two vocal types involving the high component within the band 6–9 kHz were assigned to the class with the component of high frequency. The other seven types with a distinct component of low frequency were positioned to the class of tonal signals. The vocal components differed by their contribution to the structural variability of the vocal repertoire as a whole. The high variability of the low tonal component results in a structural radiation to a few vocal types, whereas both high tonal and pulsed components follow the “one or zero” principle, i.e. a component is present or absent. The fact that different components may be produced simultaneously makes it possible to suppose that they arise from various vocal sources. A general scheme of structural transitions between different vocal types in the dhole has been developed on the basis of the structural analysis of signals and their relation to a certain situation.

The dhole is one of the most poorly studied representatives of the family Canidae. The number of this species in nature is steadily decreasing (Johnsingh, 1985). The last reliable records of the dhole in Russia fall on the beginning of the 1970s (Abramov and Pikunov, 1976). During the last 30–40 years the species disappeared in large areas of its former range in Tibet (G.B. Schaller, pers. comm.), in Altai and in Tuva (A.D. Poyarkov, pers. comm.). That is why any data on the biology and behavior of this endangered species, including those obtained in captivity, are very important.

The dhole shows very high acoustic activity both in nature and captivity (Sosnovskii, 1967; Davidar, 1973, 1975; Cohen, 1977, 1985; Johnsingh, 1982). However, at present there are hardly any studies on the vocal repertoire of dholes in nature. There are only sounds imitating descriptions of calls, which do not give any idea of their structural characters. The spectrographic analysis was used only in the study of individual variability of a single vocal type in the dhole in captivity (Durbin, 1998).

High acoustic activity in the dhole during a year considerably facilitates collecting of material and allows a researcher to consider this species as a suitable object for a whole number of bioacoustic studies. The description of the acoustic repertoire in the dhole in

captivity was the first step of these studies and the aim of the current work.

MATERIALS AND METHODS

The material was obtained from 9 dholes born in captivity. Eight animals were adults (elder than 1.5 years) with various experience of breeding; the ninth dhole was 9–10 month old. Four adult animals (two heterosexual pairs) were kept in the exposition of Moscow Zoo and five others (heterosexual pair and three), in the zoo brooder of Moscow Zoo (Volokolamsk District of Moscow Province). Both pairs were formed in the Zoo some years ago and each of them had delivered pups at least once. The pair in the zoo brooder was formed in the summer of 1998 from animals one and a half year old that had no experience of reproduction. The three some were early reproducing male and female united in November of 1998 and a young not related to them male, which was introduced to them on December 30, 1998 the day before the beginning of material collecting. Both in the Zoo and zoo brooder the animals were kept in the adjoining outdoor enclosures 20–30 m², divided by a wirenet, so that the partners of the neighboring groups were able to have contacts with each other.

The material was collected in the Zoo in the period from March till December of 1998 not rarer than once

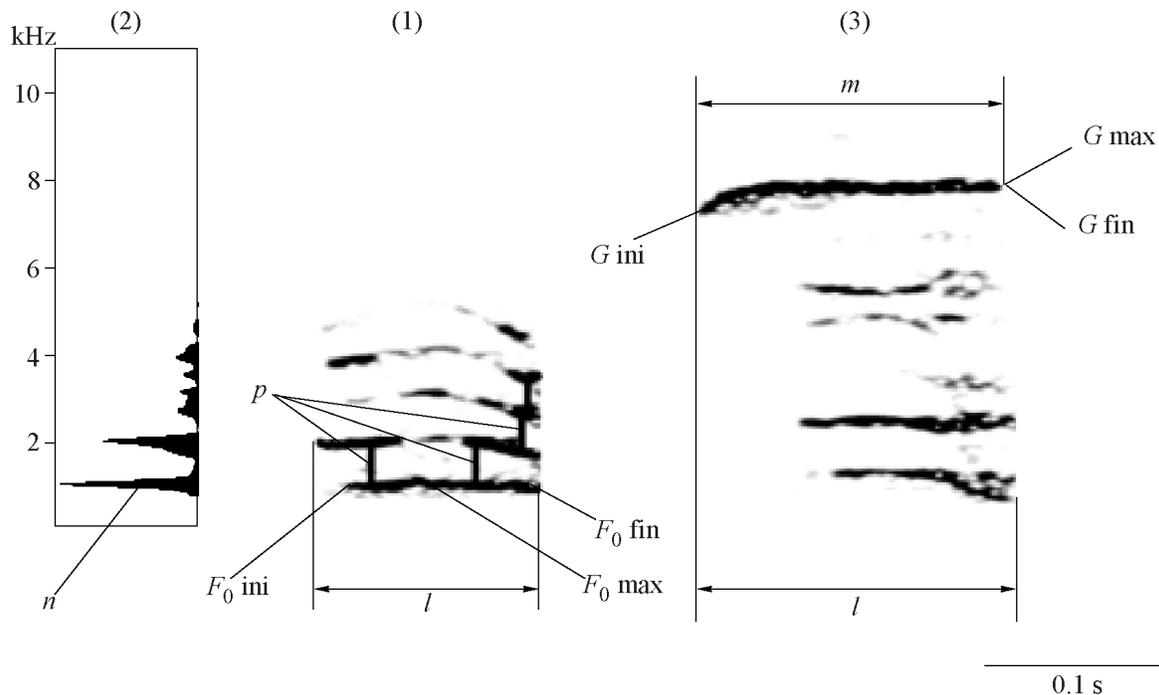


Fig. 1. The measured parameters in the tonal signals in the dhole. The spectrogram (1) and mean energy spectrum (2) of the tonal sound, spectrogram (3) of the tonal sound with a high frequency component are given. The following points of measures are given: F_0 ini, F_0 max, F_0 fin, respectively are initial, maximum and final values of the fundamental frequency; G ini, G max, G fin, initial, maximum and final values of the high frequency component respectively. The letters designate: l , the total duration of the sound; m , duration of the high frequency component; n , harmonics of dominate intensity (here F_0); p , the way of maximum energy during the sound production (here U-shaped).

in two weeks and in the zoo brooder from December, 31, 1998 till January 8, 1999 daily, during the light time of the day in the periods of the animals' activity. A video camera Panasonic-RX10 and a tape-recorder Reporter-5P with the microphone MKE-100 (frequency responses within 50–15000 Hz) were used for parallel recording of moving and acoustic behavior. The volume of records comprised 15 h for the Zoo and 8 h for the zoo brooder.

Only records of calls of high quality and known attribution were selected for the spectrographic analysis. The software Avisoft-SASLab Pro version 3.4e (© R. Specht) was used for the analysis of vocal repertoire. Sound analysis was carried out with sampling rate 22 kHz and for the high frequency signals also with the sampling rate 44 kHz. The following parameters were used for the computation of spectrograms: Hamming window; FFT-length 512 points; frame 50%; overlap 87.5%. Accordingly, the bandwidth of the frequency filter comprised 111 Hz, time resolution 2.9 ms, frequency—43 Hz. In total, 983 calls were analyzed.

The duration was measured in all calls and the presence of the noise component in the call spectrum was recorded. For the tonal calls the initial, maximum and final values of fundamental frequency (F_0) were measured, the number of harmonic of dominate intensity, occurrence of acoustic energy in the main frequency domain and the character of energy redistribution between harmonics (the maximum energy progress during the call) were recorded (Fig. 1). If in the spectrum of the call high frequency component (G) was present then, additionally, its duration and initial, maximum and final frequency values were measured. For the pulsed calls the mean value of the pulsation period was calculated according to five randomly selected periods between pulses. The depth of the frequency modulation was calculated as a residual between the maximum and minimum values of the fundamental frequency or a high frequency component.

The situation during vocalization was described by videotape recording for the vocalizing animal. The situation itself was referred to one of the seven groups: spontaneous vocalization—during everyday activity, without evident reasons; pacing—during the stereo-

Table 1. The main frequency-temporal parameters of various types of signals in dholes

| Signal type | $\frac{N}{n}$ | Parameters of the signal | | | | |
|--------------------------------------|-----------------|--------------------------|----------------|----------------|--|--------------|
| | | F_0 ini, kHz | F_0 max, kHz | F_0 fin, kHz | the depth of frequency modulation, kHz | duration, ms |
| Yap | $\frac{9}{449}$ | 0.768 | 0.906 | 0.781 | 0.174 | 85 |
| | | 0.139 | 0.156 | 0.152 | 0.100 | 38 |
| Whistle | $\frac{6}{58}$ | 0.813 | 0.994 | 0.841 | 0.216 | 181 |
| | | 0.157 | 0.169 | 0.175 | 0.125 | 84 |
| Bark | $\frac{7}{150}$ | 0.722 | 0.879 | 0.714 | 0.203 | 57 |
| | | 0.204 | 0.252 | 0.197 | 0.139 | 15 |
| Howl | $\frac{6}{33}$ | 0.718 | 0.801 | 0.670 | 0.162 | 804 |
| | | 0.333 | 0.315 | 0.278 | 0.130 | 748 |
| Squeal | $\frac{3}{54}$ | 1.548 | 1.826 | 1.606 | 0.321 | 80 |
| | | 0.291 | 0.270 | 0.307 | 0.217 | 46 |
| Scream | $\frac{2}{32}$ | 1.468 | 2.037 | 1.643 | 0.645 | 332 |
| | | 0.313 | 0.384 | 0.374 | 0.336 | 181 |
| Whine | $\frac{1}{32}$ | 1.314 | 1.408 | 1.171 | 0.247 | 493 |
| | | 0.199 | 0.221 | 0.220 | 0.149 | 270 |
| Yap-squeak (low frequency component) | $\frac{5}{44}$ | 0.965 | 1.010 | 0.712 | 0.300 | 61 |
| | | 0.166 | 0.197 | 0.141 | 0.182 | 29 |

The mean (above) and standard deviation (below) are given for every parameter. N , the number of individuals; n , the number of measured signals; F_0 , the fundamental frequency.

type moving along a certain route; interpair aggression, the context of the interaction was almost always aggressive; intrapair neutral interaction—in direct tactile contact or in call-over with the partner of its own pair; aggressive contact within the pair, the call of the initiator of aggression; aggressive contact within the pair, the call of the recipient of aggression; sexual interaction within the pair—the female's displays, mounts and copulation.

The statistical analysis of variables was carried out using non-parametric Mann-Whitney U -test and White t -test for the comparison of probabilities. Statistical analysis was performed using STATISTICA, version 5.0.

RESULTS

The Description of Acoustical Repertoire of the Dhole

Three independent structural components were revealed in the acoustic repertoire of dholes: low tonal, high tonal and rhythmic. The acoustic repertoire of

dholes was divided into three vocal classes and 11 call types based on the occurrence or absence of these structural components. Two types of broadband signals with a pronounced rhythmic pattern and composed of pulses rapidly following one another were referred to the class of calls with a rhythmic component. Two vocal types involving the high component within the band 6–9 kHz were referred to the class with a component of high frequency. The other seven types with distinct component of low frequency were grouped into a class of tonal signals. Onomatopoeic names were given to all types of signals.

The Class of Tonal Signals

This class included 7 types of signals consisting of only well pronounced, low frequency harmonic component. The fundamental frequency of signals of this class is usually well noticeable and lies within a range of 0.6–2.0 kHz. All types of tonal signals via intermediate forms may be represented as a graded continuum. The parameters of the tonal signals are given in Tables 1, 2, 3.

Table 2. The distribution of harmonics of dominate intensity in the signals of various types in dholes

| Signal type | Harmonics of dominate intensity | | | | | | Total |
|--------------------------------------|---------------------------------|-------|-------|-------|-------|-------|-------|
| | F_0 | F_1 | F_2 | F_3 | F_4 | F_5 | |
| Yap | 350 | 43 | 30 | 17 | 8 | 1 | 449 |
| | 78.0 | 9.6 | 6.7 | 3.8 | 1.8 | 0.2 | 100 |
| Whistle | 53 | 3 | 2 | 0 | 0 | 0 | 58 |
| | 91.4 | 5.2 | 3.4 | | | | 100 |
| Bark | 25 | 53 | 55 | 14 | 2 | 1 | 150 |
| | 16.7 | 35.3 | 36.7 | 9.3 | 1.3 | 0.7 | 100 |
| Howl | 21 | 7 | 4 | 1 | 0 | 0 | 33 |
| | 63.6 | 21.2 | 12.1 | 3.0 | | | 100 |
| Squeal | 28 | 26 | 0 | 0 | 0 | 0 | 54 |
| | 51.9 | 48.1 | | | | | 100 |
| Scream | 17 | 14 | 1 | 0 | 0 | 0 | 32 |
| | 53.1 | 43.8 | 3.1 | | | | 100 |
| Whine | 7 | 24 | 1 | 0 | 0 | 0 | 32 |
| | 21.9 | 75.0 | 3.1 | | | | 100 |
| Yap-squeak (low frequency component) | 37 | 3 | 1 | 0 | 0 | 0 | 41 |
| | 90.2 | 7.3 | 2.4 | | | | 100 |
| Gramble | 20 | 2 | 3 | 2 | 0 | 1 | 28 |
| | 71.4 | 7.1 | 10.7 | 7.1 | | 3.6 | 100 |

The absolute value (above) and percents (below) are given for every parameter. F_0 , the fundamental frequency; F_1 , F_2 , etc., harmonics of the fundamental frequency.

Table 3. Redistribution of energy between harmonics of the fundamental frequency during the sound production in the signals of tonal type in dholes

| Signal type | Energy redistribution | | | | | | Total |
|-------------|-----------------------|------------|------------|-------------------|----------|--------------|-------|
| | absent | increasing | decreasing | inverted U-shaped | U-shaped | more complex | |
| Yap | 171 | 33 | 40 | 102 | 22 | 81 | 449 |
| | 38.1 | 7.3 | 8.9 | 22.7 | 4.9 | 18.0 | 100 |
| Whistle | 30 | 5 | 2 | 15 | 1 | 5 | 58 |
| | 51.7 | 8.6 | 3.4 | 25.9 | 1.7 | 8.6 | 100 |
| Bark | 45 | 14 | 17 | 25 | 12 | 37 | 150 |
| | 30.0 | 9.3 | 11.3 | 16.7 | 8.0 | 24.7 | 100 |
| Howl | 9 | 0 | 0 | 2 | 1 | 21 | 33 |
| | 27.3 | | | 6.1 | 3.0 | 63.6 | 100 |
| Squeal | 17 | 9 | 5 | 6 | 8 | 9 | 54 |
| | 31.5 | 16.7 | 9.3 | 11.1 | 14.8 | 16.7 | 100 |
| Scream | 3 | 5 | 2 | 4 | 0 | 18 | 32 |
| | 9.4 | 15.6 | 6.3 | 12.5 | | 56.3 | 100 |
| Whine | 10 | 1 | 4 | 3 | 1 | 13 | 32 |
| | 31.3 | 3.1 | 12.5 | 9.4 | 3.1 | 40.6 | 100 |

The absolute value (above) and percents (below) are given for every parameter.

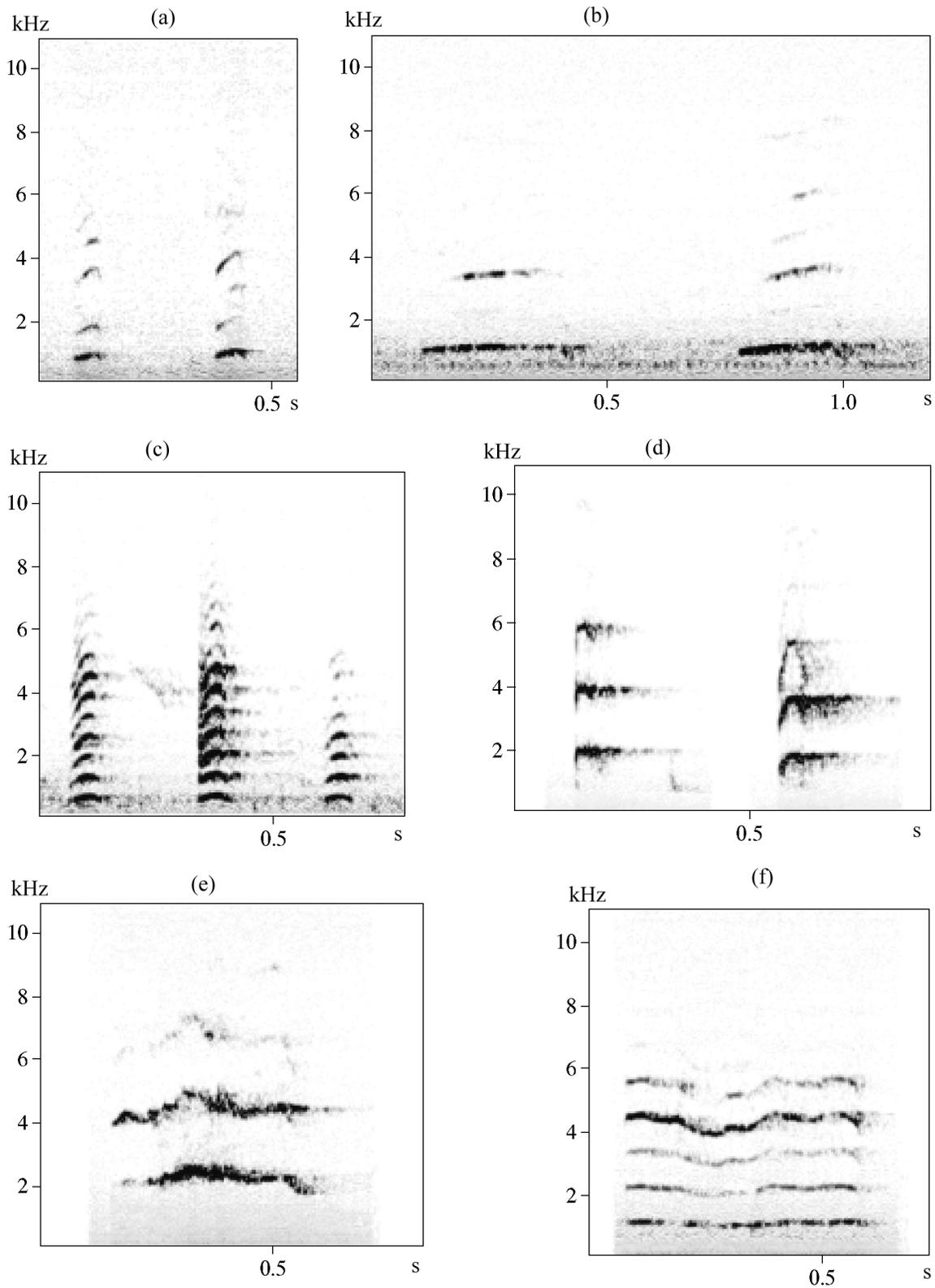


Fig. 2. The spectrograms of signals of tonal type in the dhole: (a) yap, (b) whistle, (c) bark, (d) squeal, (e) scream, (f) whine.

Yap (Fig. 2a). The maximum of the fundamental frequency of yap varies within 0.5–1–4 kHz, but usually does not exceed 1 kHz (Table 1). The fundamental frequency is pronounced in 98.2% of recorded signals. The fundamental frequency usually (in 78% of cases) is the harmonic bearing maximum energy of the signal. The dominate harmonics F_1 , F_2 and F_3 are (Table 2) significantly more rare. The characteristics of frequency modulation of yap is of an arch-like shape, the depth of frequency modulation may achieve 0.56 kHz, but usually does not exceed 0.2 kHz (Table 1). The duration varies within 23–540 ms. The great majority of analyzed blathers (98.7%) lack the noise component. In more than 60% of blathers the redistribution of maximum energy between harmonics during sound production was observed (Table 3).

Whistle (Fig. 2b) by the general pattern of frequency spectrum resembles yap, but differs by a number of structural features. The maximum of fundamental frequency and the depth of frequency modulation of whistles is somewhat larger than in blathers and the duration of the former is twice as long as that of the latter and comprises on the average 180 ms (maximum up to 650 ms) (Table 1). The fundamental frequency is pronounced in 96.5% of whistles. A characteristic feature of this type is energetic accentuation of the fundamental frequency (in more than 90% cases), which alongside with greater duration gives to the signal a specific sound (Table 2). The noise component in the whistle was not observed. The redistribution of energy between harmonics occurs rarer than in other types of tonal signals (less than in 50% of the cases), but usually has a rather complicate shape (Table 3).

Bark (Fig. 2c). The shortest among all types of tonal signals in dholes; the duration do not exceed 100 ms (Table 1). The maximum of the fundamental frequency varies within 0.4–1.5 kHz (Table 1). The fundamental frequency was pronounced in 96% of recorded calls. Unlike yap and whistle the maximum of energy in the barks usually bear the first and the second harmonics but not the fundamental frequency (Table 2). The characteristics of frequency modulation of signals of this type has a well pronounced shape of the inverted U. The mean depth of the frequency modulation is 0.2 kHz, but it may achieve 0.67 kHz (Table 1). The bark is usually produced with a very high intensity, which may result in the appearance of noisy components in the spectra of this type of signals

(in 10% of the analyzed barks). The redistribution of energy between the harmonics was not observed only in 30% of barks. (Table 3). Despite small duration, complex forms of energy redistribution with more than one extreme were commonly observed in the barks.

Howling (Fig. 3a). The longest among all types of tonal signals. The duration of howling may achieve 3 s, however, usually it does not exceed 1 s (Table 1). The fundamental frequency is, as a rule, low (minimum 0.26 kHz); the mean value of the fundamental frequency is the least among all types of tonal signals (Table 1). Frequency modulation is poorly pronounced, usually only at the beginning of the signal. The fundamental frequency, usually, occurs in the spectrum (in 94% of the cases). Most often the dominate harmonics is the fundamental frequency, rarer it is F_1 , and even still rarer, F_2 (Table 2). Similar to bark, the occurrence of noisy components in the spectra of signals is typical of howling (in 9% of howls). This can also be related to high intensity of signals of this type. The great duration of howls allows the energy to be redistributed in a complex way between harmonics during sound production, repeatedly increasing and decreasing the frequency of maximum intensity (Table 3).

Squeal (Fig. 2d). A rather short, deeply modulated signal, the fundamental frequency of which is twice as great as in blather and may achieve 2.2 kHz (Table 1). The way of frequency modulation is like inverted an U or arch-like. The fundamental frequency was well pronounced in all the recorded sounds. Both the fundamental frequency and the first harmonics of the signal can bear the maximum energy with an equal probability (Table 2). The shrieks usually are produced with a high intensity, however signal spectra lack the noisy components. In 68% of the analyzed shrieks various forms of energy redistribution between harmonics were observed (Table 3).

Scream (Fig. 2e). Similar to squeal, the high values of the fundamental frequency are typical of the scream (up to 2.5 kHz) (Table 1). However, unlike the squeal, the scream manifests itself as a long signal with a complex form of frequency modulation, which forms several peaks and falls during its duration. The depth of the frequency modulation of the scream is the largest among all the tonal signals and may exceed 1 kHz. The fundamental frequency was pronounced in all the signals analyzed. The maximum energy of the signal similar to the squeal is either concentrated on the fundamental frequency or on the first harmonics (Table 2).

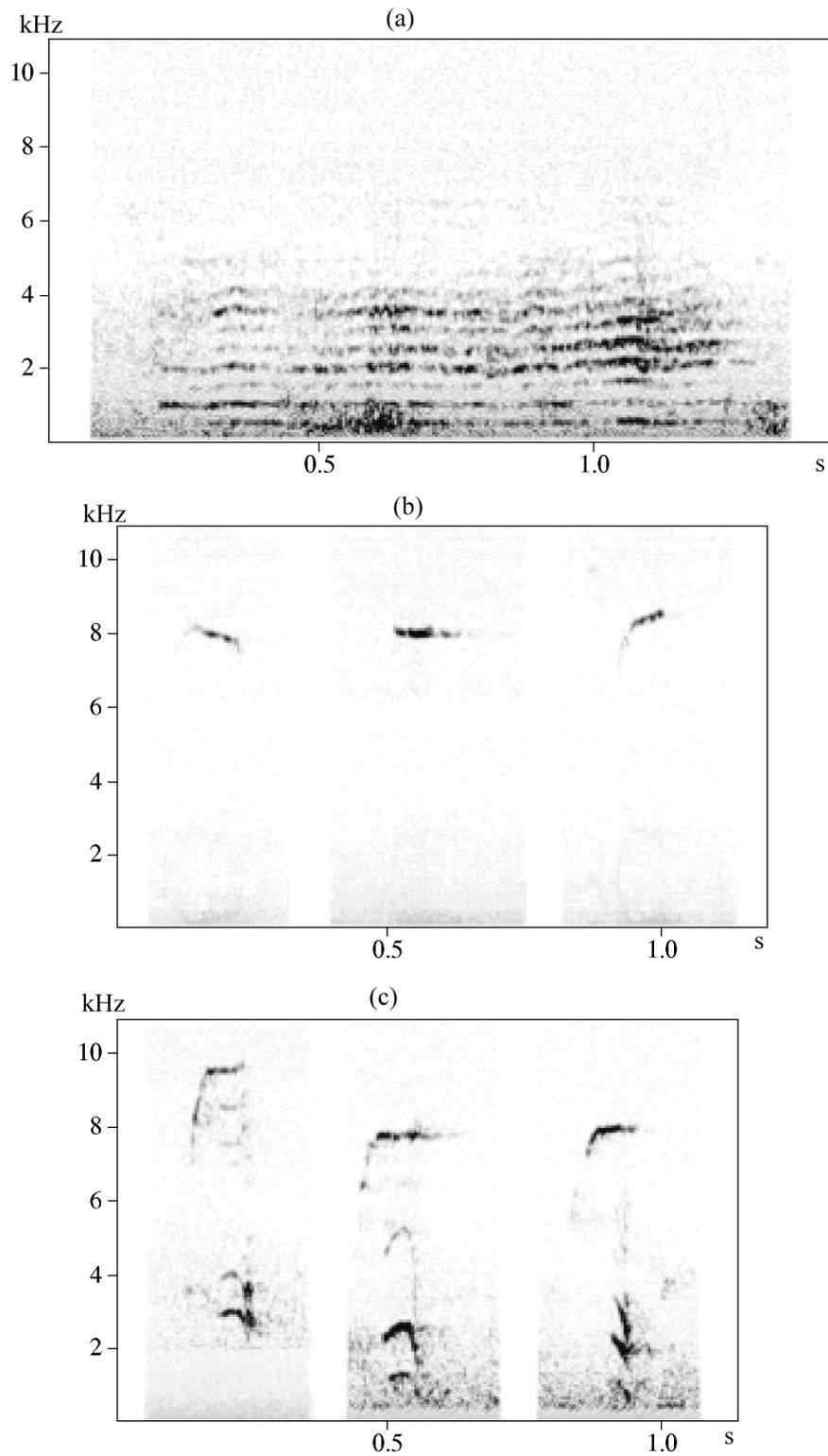


Fig. 3. The spectrograms of tonal type and signal types with a high frequency component in the dhole: (a) howl, (b) squeak, (c) yap-squeak.

Table 4. The main frequency-temporal parameters of signal types with a high frequency component in dholes

| Signal type | $\frac{N}{n}$ | Parameters of the signal | | | | | |
|-------------|----------------|--------------------------|--------------|--------------|--|---|---------------------------------|
| | | G ini, kHz | G max, kHz | G fin, kHz | The depth of frequency modulation, kHz | Duration of high frequency component, s | Total duration of the signal, s |
| Squeak | $\frac{8}{80}$ | 7.723 | 8.685 | 8.372 | 0.974 | 0.091 | 0.091 |
| | | 1.095 | 1.004 | 1.125 | 0.661 | 0.033 | 0.033 |
| Yap-squeak | $\frac{5}{44}$ | 7.921 | 8.743 | 8.472 | 0.852 | 0.097 | 0.120 |
| | | 1.012 | 1.032 | 1.159 | 0.557 | 0.038 | 0.026 |

The mean value (above) and standard deviation (below) are given for every parameter. N , the number of individuals; n , the number of measured signals; G , the frequency of high frequency component.

The intensity of wails is rather considerable, yet, the noisy component occurred only in one of the recorded signals. The energy redistribution between harmonics during the sound production is more typical of wails than of shrieks. Therewith, usually this redistribution has a complex character (Table 3).

Whine (Fig. 2f) is a monotonous, long signal with a relatively high fundamental frequency (Table 1). Duration of the signals may exceed 1 s, but, on average, is lower than 0.5 s. The frequency modulation is poorly pronounced, usually a small increase in the frequency occurs at the beginning of the signal, then it stays at one level for a long time and an insignificant decrease is observed at the end of the signal. The mean value of the fundamental frequency maximum is 1.4 kHz. According to this parameter the whine is placed between the yap, whistle, bark and howling, on the one hand, and squeal and scream, on the other. In the signal's spectrum the fundamental frequency always occurs. The first harmonics is most energetically pronounced (Table 2). All the cries we analyzed were free of the noisy component. The energy redistribution between the harmonics could be absent or have complex shape with several peaks and falls with equal probability (Table 3).

The Class of Signals with a High Frequency Component

Two signal types were placed in this class. Their typical feature is the appearance in the frequency spectrum of a high frequency component within the band 6–9 kHz. One of the signals of that class had both high frequency and low frequency tonal component in its spectrum.

Squeak (Fig. 3b) is a high frequency slightly modulated signal of low intensity. The signal is represented by a single frequency band. The frequency of the signal is very high, the maximum may achieve 10 kHz (Table 4). Analysis of squeak within the frequency window up to 22 kHz did not reveal any superposed harmonics. Frequency modulation is pronounced only at the beginning and the end of the signal. The duration of squeak does not exceed 200 ms, the spectrum lacks noisy components.

Yap-squeak (Fig. 3c)—a signal of an intermediate (complex) structure (Volodin and Volodina, 1997). In this signal high frequency (squeak) and low frequency (yap) components produced simultaneously are distinct. Therewith, the high frequency component is not the harmonic of the fundamental frequency of the low frequency component. A high frequency component usually precedes a low frequency one, which appears somewhat later. At the moment of the end of the signal both components may occur in its spectrum or only one low frequency component. Thus, yap-squeak usually starts with squeak and ends with yap that is why this type of signals received such a name. The main frequency-temporal parameters of the high frequency component of yap-squeak and squeak are very similar (Table 4). In its structure the low frequency component of yap-squeak is similar to slightly modified signals of tonal types (yap, whistle and bark). The maximum of the fundamental frequency of the low frequency component varies within 0.7–1.7 kHz (Table 1). The maximum energy in 90% of cases is concentrated at the fundamental frequency (Table 2). The frequency usually decreases considerably from the beginning to the end of the low frequency component, therefore the depth of frequency modulation is rather

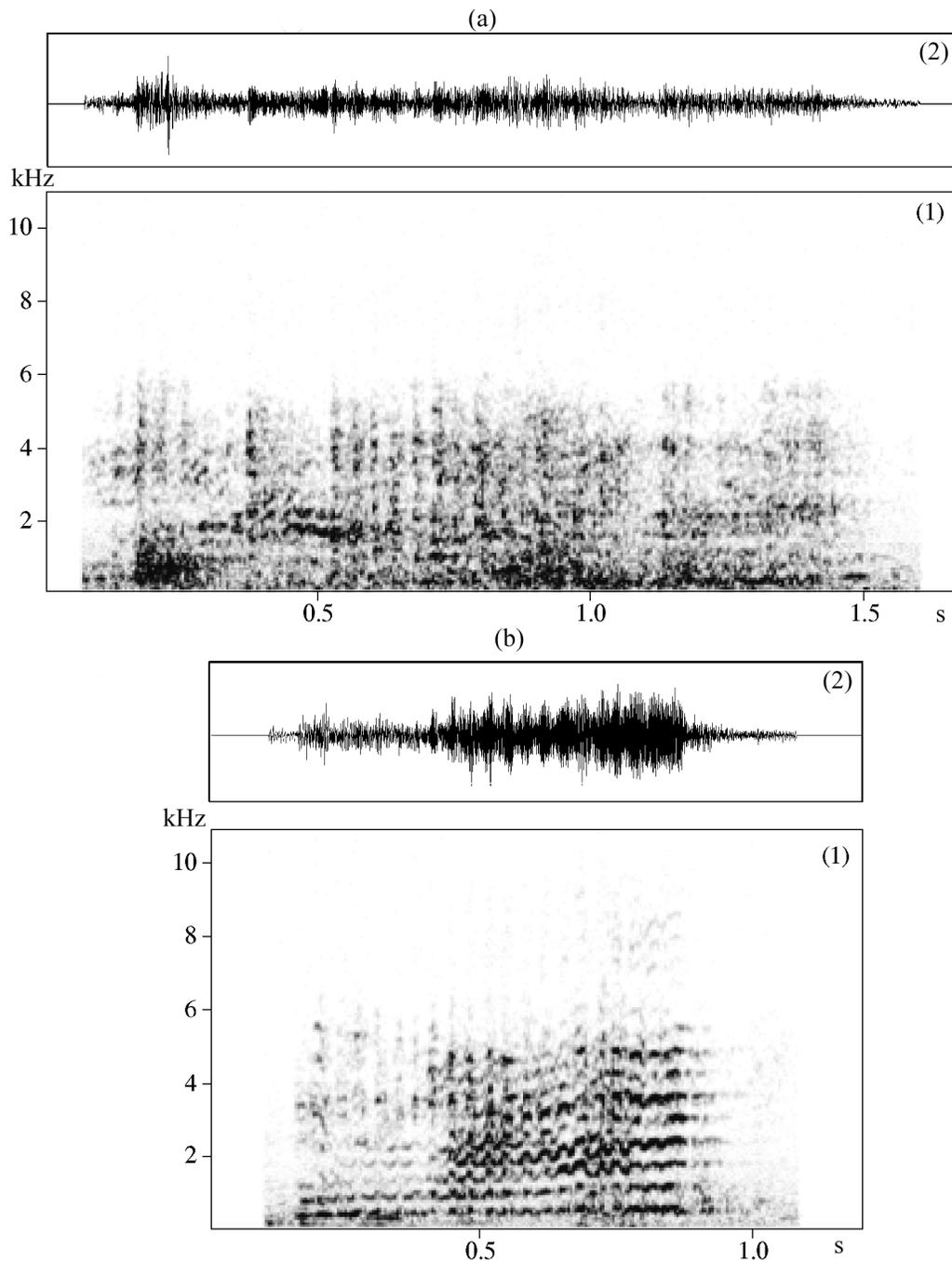


Fig. 4. The spectrograms (1) and wave forms (2) of signal types with a rhythmic component in the dhole: (a) staccato, (b) gramble.

high. The mean value of duration of the yap-squeak as a whole comprises 120.0 ± 3.9 ms, of high frequency and low frequency components—97 ms and 61 ms respectively (Tables 1, 4).

The Class of Signals with a Rhythmic Component

Two broadband signals with a well pronounced rhythmic structure, consisting of a number of pulses

rapidly following one another were included in this class. One of the signals of this class in its spectrum also has a low frequency tonal component.

Staccato (Fig. 4a) is a broadband pulsing sound, which one hears as a noisy, rattling breathe out. The main energy of the signal is concentrated within the band 2 kHz. The duration fluctuates from 220 to 1460 ms (Table 5). The period between individual pulses comprises, on the average, 40 ms and varies

Table 5. The main frequency-temporal parameters of signal types with a rhythmic component in dholes

| Signal type | $\frac{N}{n}$ | Parameters of the signal | | | |
|-------------|----------------|--------------------------|--|-------------|----------------------------|
| | | F_0 max, kHz | the depth of frequency modulation, kHz | duration, s | the period of pulsation, s |
| Staccato | $\frac{5}{23}$ | – | – | 0.722 | 0.040 |
| | | | | 0.394 | 0.008 |
| Gramble | $\frac{7}{28}$ | 0.587 | 0.096 | 0.887 | 0.042 |
| | | 0.232 | 0.090 | 0.605 | 0.019 |

The mean value (above) and standard deviation (below) are given for every parameter. N , the number of individuals; n , the number of measured signals; F_0 , fundamental frequency.

Table 6. Pairwise comparison of duration and fundamental frequency maximum (F_0) in tonal types of signals in dholes by the Mann-Whitney U -test

| | Signal type | Duration | | | | | | |
|--------------|-------------|----------|---------|------|------|--------|--------|-------|
| | | yap | whistle | bark | howl | squeal | scream | whine |
| F_0 max | Yap | | +++ | +++ | +++ | + | +++ | +++ |
| | Whistle | +++ | | +++ | +++ | +++ | +++ | +++ |
| | Bark | ++ | +++ | | +++ | ++ | +++ | +++ |
| | Howl | +++ | +++ | + | | +++ | ++ | ins |
| | Squeal | +++ | +++ | +++ | +++ | | +++ | +++ |
| | Scream | +++ | +++ | +++ | +++ | +++ | | + |
| | Whine | +++ | +++ | +++ | +++ | +++ | +++ | |

Significance of differences: +++, with $p < 0.001$; ++, with $p < 0.01$; +, with $p < 0.05$; ins, the differences are non-significant.

Table 7. The pairwise comparison of initial and final values of the fundamental frequency (F_0) in tonal types of signals in dholes by the Mann-Whitney U -test

| | Signal type | F_0 fin | | | | | | |
|--------------|-------------|-----------|---------|------|------|--------|--------|-------|
| | | yap | whistle | bark | howl | squeal | scream | whine |
| F_0 ini | Yap | | +++ | +++ | +++ | +++ | +++ | +++ |
| | Whistle | ++ | | +++ | +++ | +++ | +++ | +++ |
| | Bark | +++ | +++ | | + | +++ | +++ | +++ |
| | Howl | ++ | + | ins | | +++ | +++ | +++ |
| | Squeal | +++ | +++ | +++ | +++ | | ins | +++ |
| | Scream | +++ | + | +++ | +++ | ins | | +++ |
| | Whine | +++ | +++ | +++ | +++ | +++ | + | |

For designations, see Table 6.

from 13 to 53 ms. The noisy component occurs in all recorded signals of this type.

Gramble (Fig. 4b) is a signal of intermediate structure between staccato and tonal signal similar to a howl. In gramble the tonal component superimposes

the rhythmic one, as a result, this signal sounds much more sonorous than a staccato one and one hears it as sonorous growling. In most gramble (96% of those analyzed) the fundamental frequency of the signal could be distinguished. It fluctuates between 0.3 and

Table 8. Comparison of frequency-temporal parameters of low frequency component of the yap-squeak and signals of the tonal type in dholes by the Mann-Whitney *U*-test

| Signal type | Low frequency component of the yap-squeak | | | | |
|-------------|---|-----------|-----------|-----------------------------------|----------|
| | F_0 ini | F_0 max | F_0 fin | the depth of frequency modulation | duration |
| Yap | +++ | +++ | ++ | +++ | +++ |
| Whistle | +++ | ins | +++ | ++ | +++ |
| Bark | +++ | +++ | ins | +++ | ins |
| Howl | +++ | +++ | ins | +++ | +++ |
| Squeal | +++ | +++ | +++ | ins | ins |
| Scream | +++ | +++ | +++ | +++ | +++ |
| Whine | +++ | +++ | +++ | ins | +++ |

For designations, see Table 6.

Table 9. Occurrence of various signal types in dholes in different situations

| Signal type | Situations | | | | | | | Total |
|---------------------|------------|-------|-------|-------|-----|-------|--------|-------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | |
| Yap | 196 | 56 | 47 | 134 | 1 | 5 | 10 | 449 |
| | 43.7* | 12.5* | 10.5 | 29.8* | 0.2 | 1.1 | 2.2 | 100 |
| Whistle | 13 | 1 | 19 | 22 | 0 | 2 | 1 | 58 |
| | 22.4 | 1.7 | 32.8 | 37.9* | | 3.4 | 1.7 | 100 |
| Bark | 1 | 0 | 140 | 0 | 4 | 5 | 0 | 150 |
| | 0.7 | | 93.3* | | 2.7 | 3.3 | | 100 |
| Howl | 0 | 0 | 27 | 5 | 1 | 0 | 0 | 33 |
| | | | 81.8* | 15.2 | 3.0 | | | 100 |
| Squeal | 0 | 0 | 1 | 0 | 1 | 48 | 4 | 54 |
| | | | 1.9 | | 1.9 | 88.9* | 7.4 | 100 |
| Scream | 0 | 0 | 0 | 0 | 1 | 24 | 7 | 32 |
| | | | | | 3.1 | 75.0* | 21.9* | 100 |
| Whine | 0 | 0 | 0 | 0 | 0 | 0 | 32 | 32 |
| | | | | | | | 100.0* | 100 |
| Squeak | 41 | 7 | 0 | 22 | 0 | 8 | 2 | 80 |
| | 51.3* | 8.8 | | 27.5 | | 10.0 | 2.5 | 100 |
| Yap-squeak | 31 | 1 | 1 | 10 | 0 | 1 | 0 | 44 |
| | 70.5* | 2.3 | 2.3 | 22.7 | | 2.3 | | 100 |
| Staccato | 0 | 0 | 20 | 0 | 1 | 0 | 2 | 23 |
| | | | 87.0* | | 4.3 | | 8.7 | 100 |
| Gramble | 1 | 0 | 24 | 2 | 0 | 0 | 1 | 28 |
| | 3.6 | | 85.7* | 7.1 | | | 3.6 | 100 |
| Total | 283 | 65 | 279 | 195 | 9 | 93 | 59 | 983 |
| Random distribution | 28.8 | 6.6 | 28.4 | 19.8 | 0.9 | 9.5 | 6.0 | 100 |

Situations: 1, everyday activity; 2, pacing; 3, interpair aggression; 4, intrapair neutral interactions; 5, intrapair aggression, initiator; 6, intrapair aggression, recipient; 7, sexual interactions. The absolute number of signals (above) and percents (below) are given for every situation.

* The observed values of occurrence significantly exceed the random ones ($p < 0.01$).

1.5 kHz (Table 5). Such considerable borders in the spread in values of the fundamental frequency result from both by variability between individual signals and frequency modulation during the signal, the depth of which may achieve 0.39 kHz. The maximum energy in 71% of cases is concentrated on the fundamental frequency of the signal (Table 2). The average duration of grumble do not exceed 0.9 s, varying within considerable limits—from 0.2 to 2.4 s. The mean values of periods of pulsation of grumble and staccato are practically consistent (Table 5). Unlike staccato only in 68% of grumble the noisy filling of signal spectrum was revealed.

Statistical Comparison of Various Signal Type Parameters

The results of pairwise comparison of the main frequency-temporal parameters of the tonal signals are given in Tables 6 and 7. It can be seen that the differences were significant between all types of tonal signals.

The pairwise comparison of the main frequency-temporal parameters of squeak and high frequency component of yap-squeak (duration of high frequency component, initial, maximum and final frequencies) according to the Mann-Whitney *U*-test, on the contrary, did not show significant differences anywhere. The differences between staccato and grumble, analogous, in duration and frequency of pulsation also do not exceed the threshold of significance.

The comparison of the tonal type signal parameters and low frequency component of yap-squeak showed that the latter did not differ significantly from some tonal types in a number of parameters (Table 8). However, grumble and howling (the closest to the grumble type of tonal signals by structural parameters) differed significantly in all parameters ($p < 0.05$, Mann-Whitney *U*-test) except duration.

The Relation of Signals of Various Types to a Certain Situation

The absolute and percent values of occurrence of signals of various types in seven different situations and the results of comparison between the observed and random values according to the White *t*-test are given in Table 9. The distribution of the general sample of signals according to certain situations was adopted as a random one.

The signals of various types are specifically related to the certain situations. During their everyday activity dholes produce yap, squeak and yap-squeak significantly higher than randomly. Yap is also typical for pacing. Bark, howling, staccato and grumble are related to the situation of an interpair conflict. Peaceful interaction between the partners of one pair is followed by yap and whistle, during aggressive intrapair contacts the recipient of aggression produces shrieks and yells. For sexual interactions yells and cries are typical. It is interesting that except yap and scream all other types of signals occur significantly more frequently than at random level only in a single certain situation.

DISCUSSION

During our study we did not discover in dholes long distant vocal demonstrations analogous to the howl of gray wolves (*Canis lupus*), coyotes (*Canis latrans*) and jackals (*Canis aureus*) or to the territorial bark of arctic foxes (*Alopex lagopus*). Very high intensity and specific functions are typical of such demonstrations. It allows researchers to consider these demonstrations as consolidating or territorial (Lehner, 1978; Naumov *et al.*, 1981; Nikolsky and Poyarkov, 1981; Ovsyanikov *et al.*, 1985; Nikolsky and Frommolt, 1989). The loudest vocalizations of dholes in captivity were recorded during aggressive conflicts and during exciting before the feeding (bark, howling, grumble, shrieks, scream). However, these vocalizations were considerably less intensive than the howling of gray wolves and coyotes in the neighboring cages, which dholes never joined. The other researchers also showed that dholes in the zoos did not join either choir howling of wolves or malamutes (*Canis familiaris*) (Cohen, 1985), or the howling of coyotes (Sosnovskii, 1967). The distant acoustic demonstration in dholes in nature also has not been recorded (Cohen, 1977; John-sigh, 1982; A.B. Venkataraman, pers. comm.). Such vocalizations do not seem to be typical of this species, despite its gregarious mode of life.

Considerable differences in the variation of three structural components are typical of the vocal repertoire of the dhole. The main parameters of the rhythmic and high frequency components are practically stable in all the signals where they occur. The contribution of these components to the structural variation of the repertoire as a whole is displayed according to "one or zero" principle, i.e. either the component is present or absent. This explains the small amount of

signals included in the class with rhythmic and high frequency components, as far as they allow only two variants of variability, occurring either alone or in combination with the tonal low frequency component.

The parameters of the low frequency tonal component, on the opposite, show a high degree of variability, which results in the appearance of intermediate forms. At the same time, the tonal types of signals differ significantly from one another by fundamental frequency time parameters (Tables 6, 7). Such pronounced differences in a whole group of parameters allow us to consider the tonal signals as discrete types as Marler understood them (Marler, 1975; Nikolsky, 1984; Hauser, 1996). Thus, the variation of low frequency tonal component is displayed not according to the principle “one or zero” but as a radiation of structural forms, which results in the appearance of a great number of signals types.

Thus, in the vocal repertoire of the dhole two rigid and one variable vocal components occur independently. The fact that different components may be produced simultaneously testify to the fact that they are generated by different mechanisms of sound production.

Phonation. Phonation or voice, the source of which is glottis of the larynx, is responsible for most tonal sounds produced by mammals. The vocal folds, extended across the glottis, vibrate and periodically approach each other when air is blasted through the glottis with an effort. The frequency of vocal folds fluctuation corresponds to the fundamental frequency of the sound produced and its spectral characteristics are formed as the result of the interaction of the sound wave and the vocal tract (Shipley *et al.*, 1991; Owren and Linker, 1995). The low frequency vocal component in the sounds of dholes has just such a spectrum.

The periodical collapse of the soft structures of the vocal tract, appears to occur by the production of a rhythmic component in the dhole. Such collapse may take place both in the larynx (as it was shown for the felines—see Frazer Sissom *et al.*, 1991) and in the upper parts of the vocal tract with the intensive blast of air through its narrowing, similar to the production of the rolling sound “r-r-r” in humans. In particular, the necessary occurrence of the noisy component in the spectrum of staccato of the dhole points to this. The simultaneous action of both mechanisms, phonation and collapse, seem to be displayed when dholes

produce grumble, in which the rhythmic component is superimposed on the howl-like tonal component. This results in the appearance of rhythmic “breaks” in the continuous spectrum of howling (see Fig. 4b). The possibility of combination of the vocal and rhythmic components was shown for the sounds of felines (Frazer Sissom *et al.*, 1991; Volodina, 2000).

The vocal lips and vorticity as the possible mechanisms of producing the high frequency component. Characteristic features of some sounds in dholes allow us to suppose that they possess an additional vocal source. These features are expressed in the simultaneous appearance of signals of low and high frequency components in the spectrum that have an independent character of frequency modulation (Fig. 3c). Such complex signals were also described for other species of terrestrial mammals: the red deer (*Cervus elaphus bactrianus*) (Nikolsky, 1975), gray wolves (Nikolsky and Frommolt, 1989; Coscia *et al.*, 1991; Frommolt, 1999), hunting dogs (*Lycaon pictus*) (Wilden *et al.*, 1998) and blue monkeys (*Cercopithecus albogularis*) (Brown and Cannito, 1995).

The morphological basis of the production of complex sounds is yet not quite clear. In the blue monkeys a small specific morphological structure, “vocal lips” was found on the vocal folds. The participation in the production of independent high frequency components for these lips has been proved (Brown and Cannito, 1995; Schön Ybarra, 1995). Similar morphological structures have been also found in domestic dogs, hybrids between wolves and dogs and spotted hyenas (*Crocuta crocuta*) (Riede *et al.*, 2000a, 2000b). In dholes high frequency spectral components may be also produced due to the functioning of similar morphological structures.

An other possible mechanism of high frequency component production may be the vorticity of the air flow that originates with the compression of the glottis (Wilden *et al.*, 1998). In this case a typical sound whose character is a single frequency band on the spectrogram without any superimposed harmonics may appear. The squeak of the dhole has just such a spectrum (Fig. 3b). A similar mechanism of sound production was described for some high frequency calls of domestic dogs (Solomon *et al.*, 1995).

In mutual production of low and high frequency components in dholes the combined frequencies that look like spectral bands located above and below the high frequency component (Fig. 3c, the left spectro-

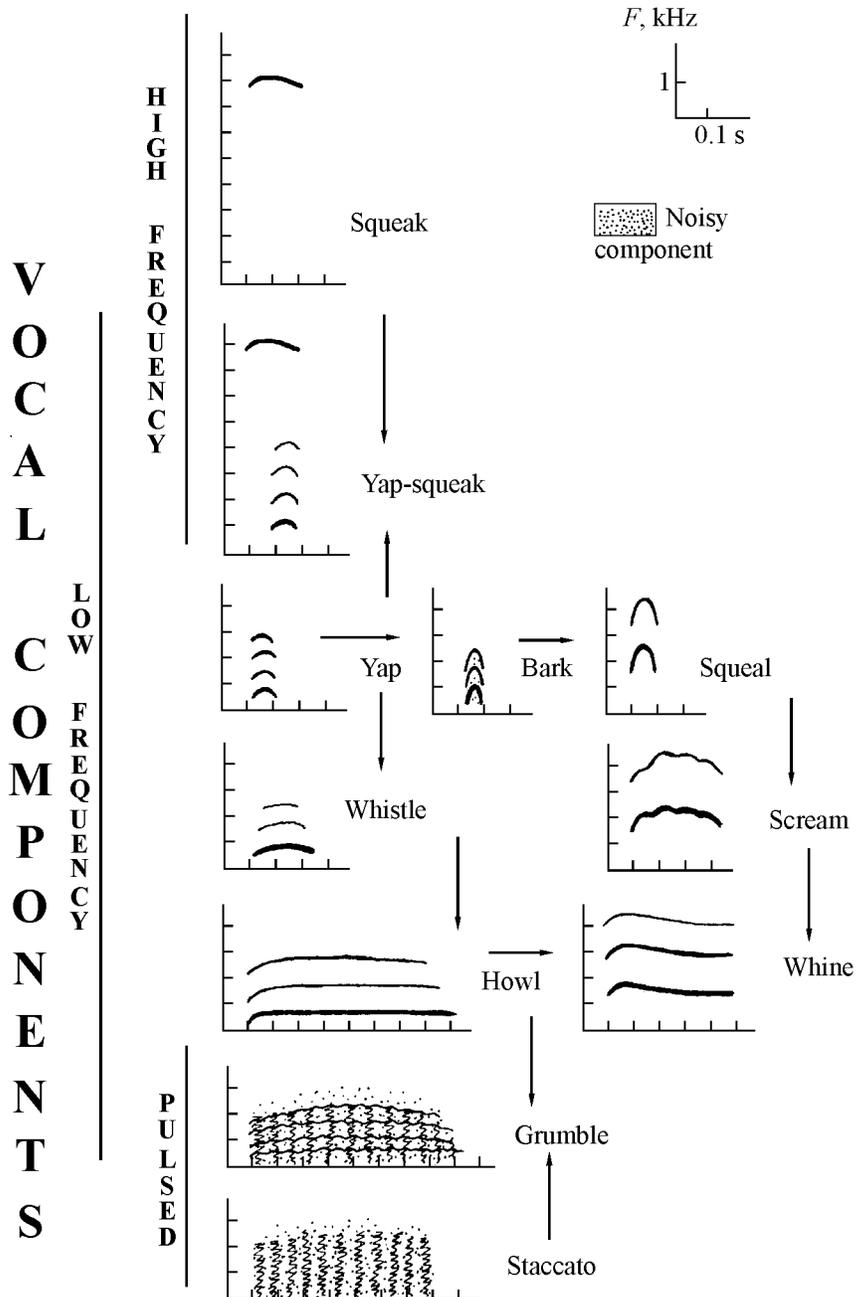


Fig. 5. The general scheme of structural transitions between various types of signals in the dhole. The arrows show the possible way of development of types of sounds with different structure on the basis of three vocal components.

gram) appeared. The values of these frequencies were equal to the sum or the residual of fundamental frequencies of high and low frequency components. A similar phenomenon was described for the complex sounds of the gray wolf (Frommolt, 1999), hunting dogs and the marbled cat (*Felis marmorata*) (Wilden *et al.*, 1998).

The analysis of relation between signals and a certain situation showed that nine from 11 types of signals in dholes occur significantly more frequently than randomly only in one certain situation (Table 9). As for the two remaining types, one of them, scream, was produced either by the young male when intra-group aggression was directed at him or by the female of the

group of three animals during sexual interactions, i.e. in this case also a certain type and a certain situation were related but at the individual level. Only one type of signals in dholes, yap, did not show a rigid relation to a certain situation.

This allows us to make two conclusions. First, all types of signals in dholes, except yap, show a high degree of situational isolation from one another. The signals of similar structure (squeak and yap-squeak, staccato and gramble) are related to the same situation. Such rigid relation between structure and behavioral context may testify to a high degree of ritualizing of dholes' sounds and acquisition by some signal types of "demonstrative" functions (Hinde, 1970).

Second, the situational "universality" of yap may point to a special place, which this type of signal occupies in the vocal repertoire of dholes. All types of tonal signals, except yap, possess one or two definite structural "labels" (whistle—accentuation of the fundamental frequency; howling—the great duration; scream—special form of frequency modulation and so on), which allow us to classify them accurately. Although the parameters of yap lie within certain limits, they vary widely from signal to signal even within a series of calls of one animal. This allows us to distinguish yap as a peculiar "archetype" of the tonal vocalizations of the dhole, which served as the basis for the origin of a whole diversity of signals of that class.

The considerations given above allowed us to build the general scheme of structural transitions between various types of signals in the dhole (Fig. 5). With certain allowances all tonal types of signals via intermediate forms could be derived from yap. Two independent vocal components (high frequency and rhythmic ones) bring additional variation into the repertoire of this species, each forming one "pure" and one complex type of signals.

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