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BIPHONATION AS A PROMINENT FEATURE OF DHOLE *CUON ALPINUS* SOUNDS

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ABSTRACT

Spectrographic analysis showed that dholes produce sounds with two fundamental frequencies (components): the high-frequency and the low-frequency, which may occur simultaneously or separately. The fundamental frequency of the low-frequency component varied from 0.52 to 1.44 kHz, and that of the high-frequency component from 5.51 to 10.77 kHz. In calls where both the frequencies occurred simultaneously, they were not integer multiples of each other. They also had different frequency modulations and had additional combinative frequency bands. These are features of biphonation. Our data showed biphonation occurs in a lot of dhole calls (20 to 92% of the calls, depending on the individual (n=14); average occurrence 44.3%, n=1317 sounds). The occurrence of biphonation did not differ between sexes and ages; however, occurrence of the high component only was significantly higher in subadult animals, whereas the occurrence of the low component only was significantly higher in adults. Based on the sound structures, we discuss probable mechanisms of sound production for both the components in the dhole. For the low component, the normal vocal folds oscillation mechanism is suggested. For the high component, four possible mechanisms of sound production are discussed. We conclude that the vortex-shedding mechanism is the most probable.

Keywords: vocalisation, nonlinear phenomena, biphonation, vocal membrane, whistle, Canidae, dhole, *Cuon alpinus*

INTRODUCTION

Harmonic calls of terrestrial mammals are generated by aerodynamically driven vibrations of the vocal folds in the larynx. Typically, vibratory movement in the vocal folds produces signals whose frequency spectra include a few frequency bands, the lower of them representing a fundamental frequency (fO), that corresponds to

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the rate of vocal fold vibration. The higher frequency bands, or harmonics, are integer multiples of the fundamental frequency. This pattern is characterised by periodic vocal fold oscillations and may be named harmonic phonation (Shipley et al. 1991, Owren and Linker 1995, Wilden et al. 1998).

However, the vocal folds, together with the vocal tract column of air, can be considered as a system of coupled oscillators and constitute a nonlinear self-oscillating system (Herzel et al. 1995, Mergell and Herzel 1997). Changes in subglottal pressure, elongation asymmetry in vocal folds, air flow rate through glottis, stress-strain relations of vocal fold tissues and vocal fold collisions are responsible for the various nonlinear phenomena. Among these phenomena are: the appearance of frequency bands of 1/2 or 1/3 of fO (subharmonics), simultaneous occurrence of two independent fundamental frequencies (biphonations), abrupt transitions from one fO to another (frequency jumps) and broadband noise, interrupted by a periodic window (deterministic chaos) (Berry et al. 1996, Herzel and Reuter 1996, Riede et al. 1997, Wilden et al. 1998).

The biphonations may be recognised from spectrograms by: (1) frequency bands that are not integer multiples of a fundamental frequency; (2) differences in frequency modulations between some of frequency bands; (3) appearance of combined frequency bands, representing linear combinations of two independent frequencies. These combined frequencies may be calculated using the formula $nf + mg$, where f and g are two independent frequencies; n and m are integer numbers (Fletcher 1992, Wilden et al. 1998).

Biphonation may result from different modes of the production mechanism. One of them lies in asynchronous vibration patterns of the left and right vocal folds, supported by large subglottal pressure and vocal tract effects. This mechanism was studied in humans (e.g. Mergell and Herzel 1997, Tigges et al. 1997) and on excised larynges of domestic dogs (Berry et al. 1996). Also, specific extensions of vocal folds - vocal membranes, or vocal lips, may support and facilitate the generation of biphonation (Brown and Cannito 1995, Schön Ybarra 1995, Mergell et al. 1999, Riede et al. 2000b). Another possibility is represented by vortex-shedding at the glottal constriction inducing a whistle-like sound. Solomon et al. (1995) proposed such a mechanism for "whine sounds" produced in experiments with excised larynges in domestic dogs. This whistle-like sound may appear as a second frequency in biphonic sounds (Wilden et al. 1998). Other causes of biphonation may be the result of source-tract-coupling. "Vortex induced vibrations" of vocal folds resulting from interaction of vortices in the vocal tract with vocal resonances induces a periodic lifting force on the folds and can evoke an appearance of a second frequency (Herzel and Reuter 1996, 1997, Mergell and Herzel 1997).

Biphonation was described for vocalisations both from healthy humans and voice patients (e.g. Keating and Buhr 1978, Herzel and Reuter 1996, 1997). In adult terrestrial mammalian vocalisation, biphonations are found in red deer *Cervus elaphus bactrianus* (Nikolskij 1975), Sykes's monkey *Cercopithecus albogularis* (Brown and Cannito 1995), chacma baboon *Papio cynocephalus ursinus* (Fischer et al. 2001), timber wolf *Canis lupus* (Nikolskij and Frommolt 1989, Frommolt 1999), domestic dog *Canis familiaris* (Solomon et al 1995, Riede et al. 2000b) and African wild dog *Lycaon pictus* (Wilden 1997, Wilden et al. 1998, Robbins 2000). Biphonations are also found in young animals of some species: Japanese macaque *Macaca fuscata* (Riede et al. 1997), marbled cat *Pardofelis marmorata* (Wilden et al. 1998), domestic cat *Felis catus* (Riede and Stolle-Malorny 1999), timber wolf (Coscia et al. 1991) and domestic dog (Wilden 1997). However, only in the African wild dog were biphonations described as highly regular events and they were found in all individuals of this species. For other species of mammals, including humans, biphonations were described as rare phenomena, especially characteristic of juveniles (whose vocal tract is developing), or of ill individuals (reviewed in Riede 2000).

The dhole *Cuon alpinus* is a canid, hunting in packs on large prey in mountains and bush and cooperatively raising the young of single breeding females (Cohen 1977, Johnsingh 1982, 1992, Karanth and Sunquist 1995, Venkataraman et al. 1995, Venkataraman 1998). Being extremely social, dholes possess a highly developed vocal communication system (Davidar 1975, Cohen 1977, 1985, Johnsingh 1982). However, until recently, sound recordings were not used for studying its sounds. Analysis with the unaided ear provided only onomatopoeic names for calls, without taking into account sound structures. Spectrographic analysis has been used for studying one particular dhole sound type, termed "Glockenlaut" in German (Wilden 1997) and, after Johnsingh (1982), "whistle" (Durbin 1998). Wilden (1997) also described the biphonic nature of the "Glockenlaut".

In our recent study we showed that the dhole vocal repertoire consists of three vocal classes with eleven call types (Volodin et al. 2001). Two broadband calls with a pulsed pattern were classed as pulsed signals. Seven calls, whose spectrum consisted of only low-frequency harmonic components, were classed as tonal signals. Two calls involving high-frequency components higher than 5 kHz were classed as the high-frequency component signals. One of these calls was a biphonic vocalisation, because both low and high-frequency components occurred simultaneously in the spectrum. Here we describe this phenomenon in the dhole and discuss its occurrence and possible mechanisms.

METHODS

Audio and video recordings of dhole vocal behaviour were made in outdoor enclosures in Moscow Zoo (Russia) from 8 adult (4 males and 4 females) and 6 subadult (4 males and 2 females) dholes. Ages and sexes of the study animals are given in Table 1. All the adults had bred and all the subadults were born in 1999 from two pairs (Bill - Barby and Vak - Viky). The dholes were kept in groups of 2 to 5 animals. All individuals from the same enclosure could be reliably identified by their coloration pattern. The group enclosures were separated by wire mesh, so, the groups could interact without direct contact.

The recordings were made with Sony WM-D6C recorder and MCE-100 undirectional electret microphone. Frequency responses of both components were 40-15,000 Hz. Distance to animals during the recordings varied from 2 to 8 m. The sounds were produced spontaneously without stimulation by the observers, who stood outside the enclosures.

In order to exclude influences of season and age, calls for quantitative analysis (100 per animal) were taken from recordings made during a restricted period between 2 November 1999 and 8 January 2000. All subadult animals in this period were between 8-10 month of age. Two adult males, who provided less than 100 calls per individual throughout the research period (Aik - 32 calls, Tom - 85 calls), were also included into analysis, so the total sample size comprised 1,317 sounds. The call samples were selected from sounds recorded in contexts of spontaneous activity, peaceful interactions between animals and during pacing. Other contexts of courting/sexual behaviour, solicitations by young to parents and aggressive behaviour occupies a small part of dholes' time budgets. These were related to enhanced excitement and may provide additional reasons for sound disorders because of extreme muscular tension and desynchronisation of vocal folds in comparison with the normal state. Thus we omitted from the analysis calls occurring in these contexts.

All spectrograms were calculated using Avisoft SASLab v. 3.4e software (R. Specht, Germany), which contains built-in anti-aliasing filters. The process used Fast Fourier Transform with 22 or 44 kHz sampling frequency, and 512 points and Hamming window. Spectrograms are presented with their corresponding time signals (oscillograms). The spectrograms are presented in their original form, i.e. no additional filters were applied and no parts of the spectrogram were deleted or redrawn.

In order to exclude the probabilities of possible artefacts (Wilden et al. 1998, Frommolt 1999) we made a preliminary sound analysis. The observed biphonation effect was not a result of aliasing, which can occur if signal frequencies are above one half of the sampling frequency. The observed spectral structures were the same whether or not a 10 kHz low-pass filter was used. The effect was also not specific to certain acoustic equipment, because control recordings on other tape recorders and microphones showed similar spectral pictures. Analysis of call production by video allowed us to discount the suggestion that this was a result of simultaneous sound production by a few animals. The observed sound patterns could not be a result of reverberation. Overloading (clipping) effects were also excluded, as suggested by corresponding oscillograms. So, the biphonation was a product of the animals' sound production system and not of acoustic equipment or recording effects.

RESULTS

We found two independent vocal components in the tonal sounds of dholes. The previous study (Volodin et al. 2001) showed that the fundamental frequency (f0) of the low-frequency component varied from 0.52 to 1.44 kHz (mean±SE = 0.91±0.16 kHz, n=449), and that of the high-frequency component (g0) from 5.51 to 10.77 kHz (mean±SE

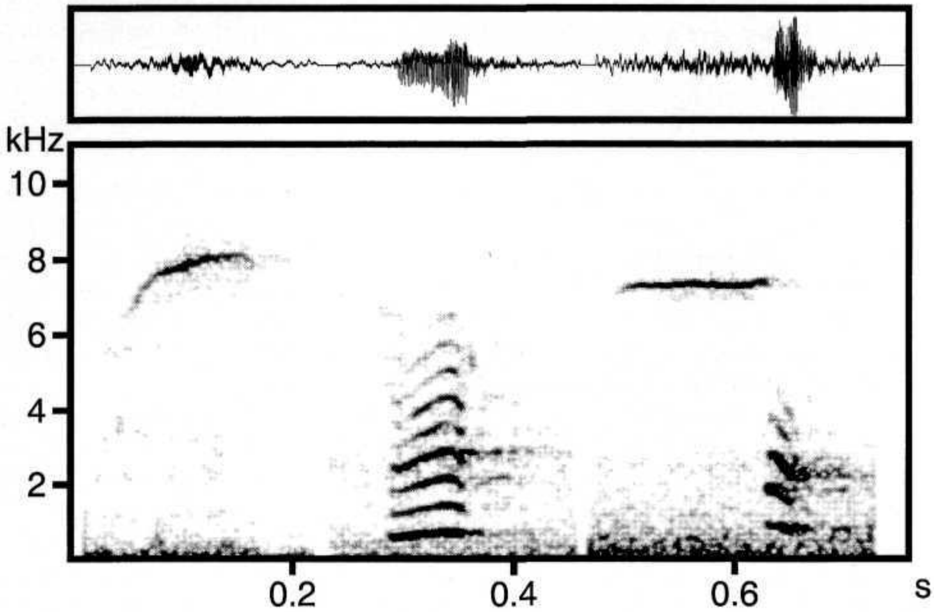

Figure 1. The left call is the high-frequency component which appears as an independent vocalisation. The middle call is the low-frequency component, appearing as an independent vocalisation. In the right call the low-frequency component follows immediately after the high-frequency component, representing a frequency jump from the high to the low component.

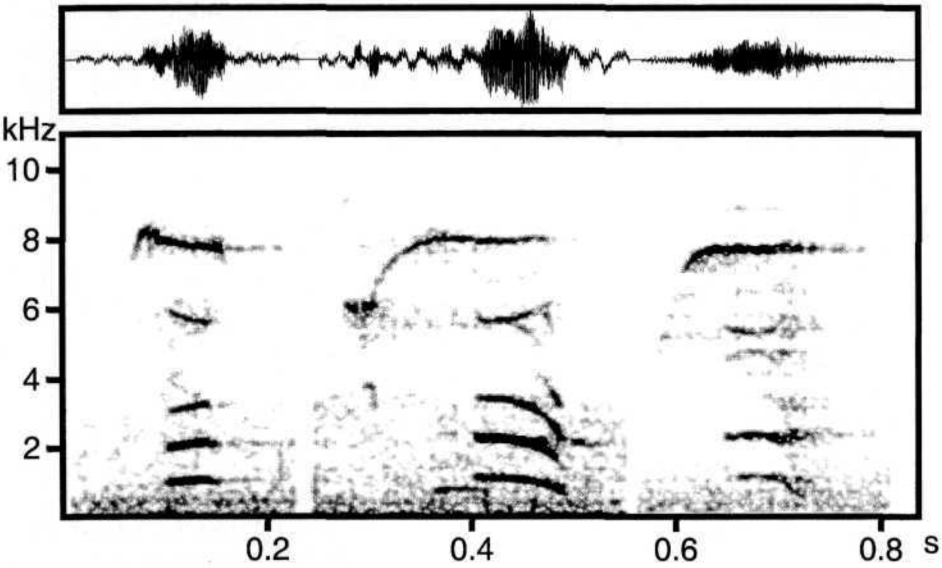

Figure 2. Three biphonic calls from different animals where both high-frequency and low-frequency components occur simultaneously. The fundamental frequency of the low-frequency component f0 ~ 1 kHz, with a few higher harmonics. The fundamental frequency of the high-frequency component g0 ~ 8 kHz. In all three calls the g component starts earlier and is longer than the f. The differences in frequency modulation between the components suggest their independent production.

- 8.69±1.0 kHz, n=80). These components occurred as independent vocalisations, or with the low component following immediately after the high one, representing a frequency jump from the high to the low component (Figure 1). The components could also be produced simultaneously. This kind of production represented biphonation, with independent characteristics of frequency modulations of the high and the low frequency components. The biphonic calls show different patterns. In one of them, a call begins with the high component and the low component starts later, sometimes continuing after the high component stops (Figure 2). In these calls, the durations of the high component are always longer than those of the low component. In another call pattern, both components start simultaneously and their durations are nearly equal (Figure 3). However, we never found sounds where the low component starts before the high component.

Ratios of the g0 and f0 frequencies of calls, presented in Figures 2 and 3, suggest that g0 is not a harmonic of f0. In Figure 2, in the left call the ratio of g0/f0 is 7881/1034 Hz = 7.62 (in 10 ms segment centred at 0.111 s); in the middle call the ratio of g0/f0 is 8010/1077 Hz = 7.44 (in 10 ms segment centred at 0.455 s); in the right call the ratio of g0/

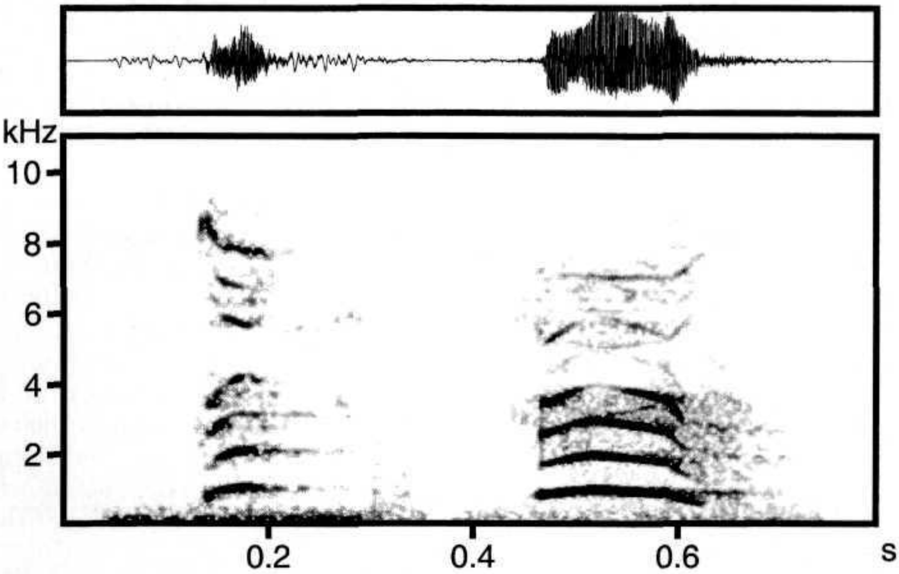

Figure 3. Two biphonic calls from different animals where both high-frequency and low-frequency components occur simultaneously. The fundamental frequency of the low-frequency component f0 ~ 1 kHz, with a few higher harmonics. The fundamental frequency of the high-frequency component g0 ~ 8 kHz in the left call and g0 ~ 7 kHz in the right call. In these calls both the components start simultaneously, and are of similar durations. The differences in characteristics of frequency modulation between the components suggest their independent production. The artificial sound prolongation, especially evident on the left call, is a result of reverberation.

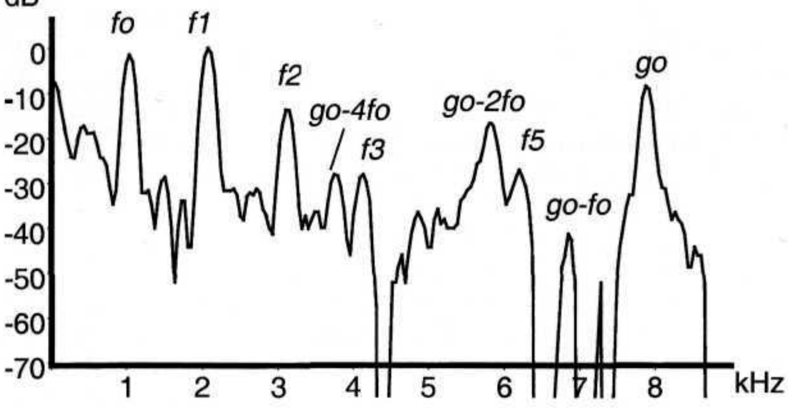

Figure 4. Power spectrum of 10 ms time segment (from 0.106 till 0.116 s) in the left call in Figure 2. First peak represents f0, the last peak g0. The other peaks represent harmonics of f0 or linear combinations of f0 and g0.

f0 is 7709/1206 Hz = 6.39 (in 10 ms segment centred at 0.680 s). In Figure 3, in the left call the ratio of g0/f0 is 7795/1034 Hz = 7.54 (in 10 ms segment centred at 0.175 s); in the right call the ratio of g0/f0 is 7063/904 Hz = 7.81 (in 10 ms segment centred at 0.570 s). Thus, all ratios of g0/f0 are not the integer values expected in harmonic relations.

In many cases when the g0 value was not the integer multiple of f0, combined frequency bands occurred, representing linear combinations of the two independent frequencies. For example, Figure 4 shows the power spectrum of a 10 ms time segment (from 0.106 to 0.116 s) in the left call in Figure 2. The value of the first peak, that represents f0, is 1034 Hz; the value of the last peak, representing g0, is 7881 Hz. The other peaks on Figure 4 represent harmonics of f0 or linear combinations of f0 and g0. Table 1 shows measured values of power peaks and predictions of these peaks for given values of f0 and g0. The high degree of coincidence between the pairs of figures suggests that some peaks indeed are linear combinations of two independent frequencies.

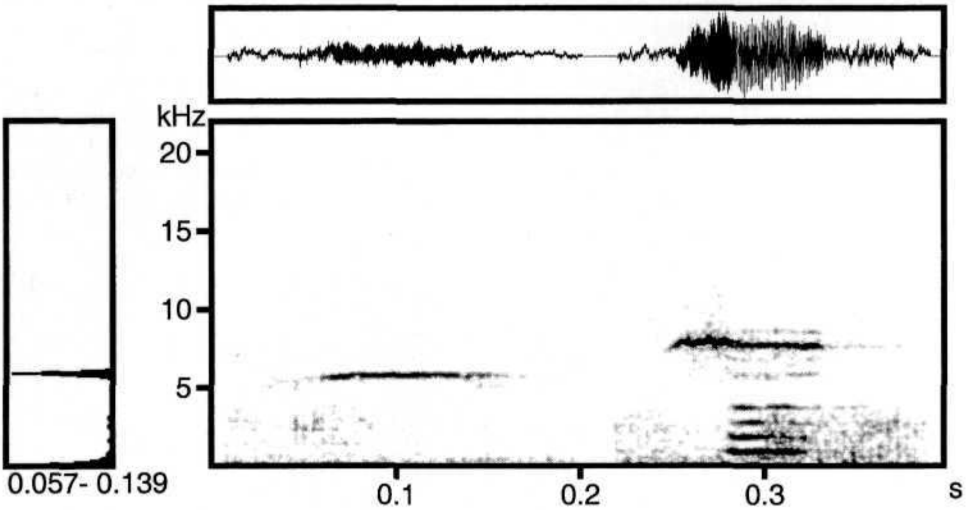

Figure 5. Sound digitised from sampling frequency 44 kHz. The left call represents the high-frequency component that appears separately as an independent vocalisation. The right call represents the biphonic sound, where both high-frequency and low-frequency components occur simultaneously. The absence of higher harmonics in the high-frequency component are evident from the spectrograms of both the calls, in contrast to the apparently harmonic pattern of the low-frequency component. The mean power spectrum of the left call (on the time interval from 57 to 139 ms) also shows a single energy peak in the area of about 6 kHz and absence of any energy in the higher frequency band.

TABLE 1

Measured and predicted values of peaks from power spectrum presented in Figure 4. f0 = fundamental of low-frequency component; g0 = fundamental of high-frequency component.

Peaks (Hz)	f0	f1	f2	g0-4f0	f3	g0-2f0	f5	g0-f0	g0
Measured	1034	2067	3101	3747	4134	5814	6202	6848	7881
Predicted	1034	2068	3102	3745	4136	5813	6204	6847	7881

Generally, the high component was represented by a single frequency band without higher harmonics (Figure 5). Rarely we noted a g1 harmonic of extremely low energy. In contrast the low component represented a typical tonal sound with well-expressed harmonics varying in energy content (Volodin et al. 2001).

Figure 6 shows the occurrence of four different call patterns (low component only, high component only, biphonation and frequency jump) among all 14 dholes. The average occurrence of biphonation was 44.3%. The high-frequency component was present in 67.6% of studied calls and the low-frequency component in 80.4% of calls.

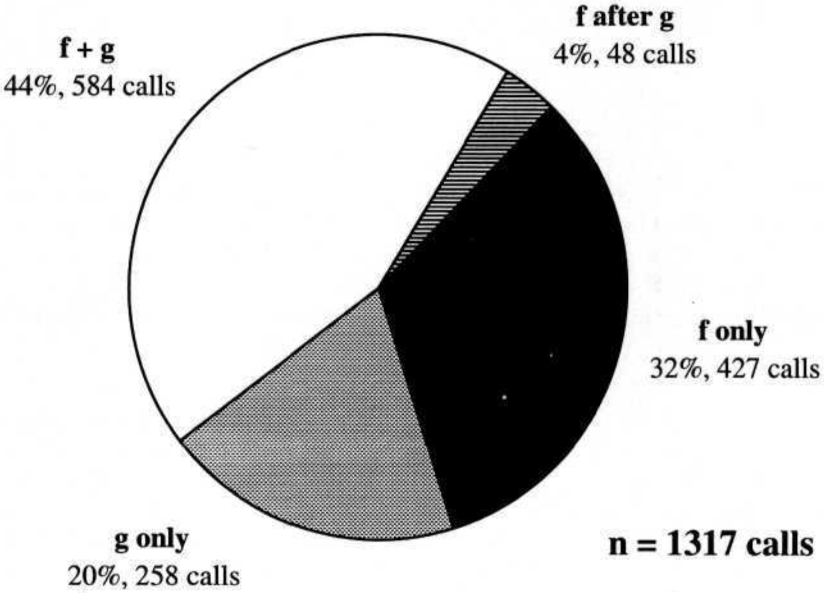

Figure 6. Average occurrence of low component only (f only), high component only (g only), biphonation (f + g) and frequency jump (f after g) in all 14 individuals.

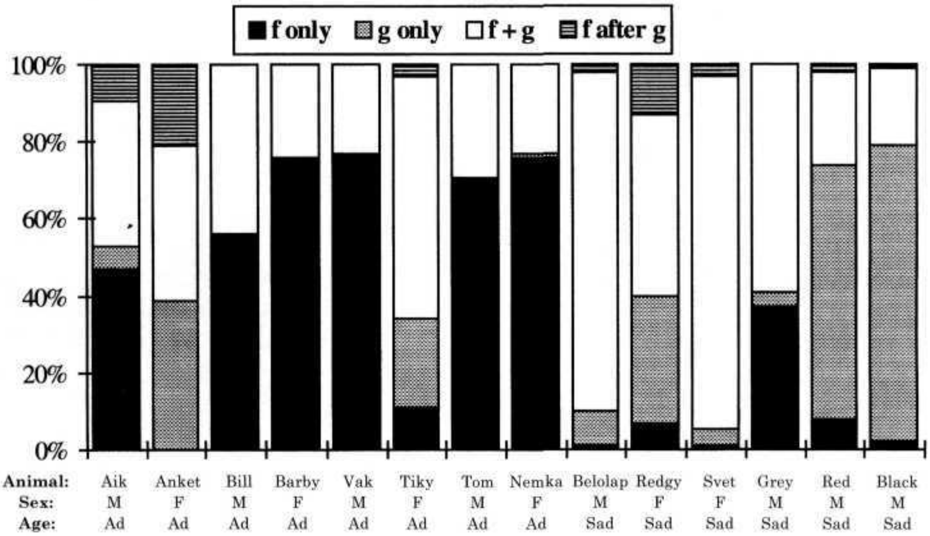

Figure 7. Occurrence of low component only (f only), high component only (g only), biphonation (f + g) and frequency jump (f after g) in each of 14 dhole individuals.

Analysis of occurrence of four different call patterns in 8 adult and 6 subadult dholes showed that biphonation occurs in all the animals (Figure 7). Individuals show noticeable differences in occurrence of this phenomenon, ranging from 20% (Black) to 92% (Svet). The relative usage of the low and high components was age-dependent but not sex-dependent. The low component occurred significantly more in adults (K-W ANOVA; H = 4.84, *p* = 0.03), whereas the high component occurred significantly more in subadults (K-W ANOVA; H = 3.84, *p* = 0.05). Differences in the appearance of biphonation and frequency jump were non-significant between ages (K-W ANOVA; H = 1.21, *p* = 0.27 and H = 0.65, *p* = 0.42 respectively). A similar comparison between sexes did not show significant differences (K-W ANOVA; low component only: H = 0.34, *p* = 0.56; high component only: H = 0.07, *p* = 0.79; biphonation: H = 0.60, *p* = 0.44; frequency jump: H = 1.81, *p* = 0.18). A comparison of the occurrence of different call patterns between sexes among 8 adults (4 males, 4 females), also did not show significant differences (K-W ANOVA; low component only: H = 0.34, *p* = 0.56; high component only: H = 1.92, *p* = 0.17; biphonation: H = 0.02, *p* = 0.88; frequency jump: H = 0.44, *p* = 0.51). Also, membership of a certain litter (Belolap, Redgy, Svet and Grey, Red - Black) did not influence the occurrence of biphonation or any other certain call structure (K-W ANOVA; low component only: H = 2.40, *p* = 0.12; high component only: H = 0.78, *p* = 0.38; biphonation: H = 2.33, *p* = 0.13; frequency jump: H = 3.14, *p* = 0.08).

DISCUSSION

All the dholes produced a high proportion of biphonic sounds. These sounds were not pathological, unlike those shown for some ill individuals in humans, Japanese macaque, and domestic cat (Herzel and Reuter 1996, Riede et al. 1997, Riede and Stolle-Malorny 1999). All analysed dhole sounds were recorded under conditions of everyday routine events in the Zoo, excluding aggressive or stressful situations. All animals were healthy, in a good physical state, and performed all normal age- and season-related behavioural activities. None of the animals showed fear or fearfulness to Zoo visitors. So, we can conclude that biphonations represent an inherent characteristic of the dhole vocal repertoire that gives a peculiar quality to many calls in this species.

High rates of vocal activity are a characteristic feature in the dhole behaviour, both in the wild and in captivity (Davidar 1975, Cohen 1977, 1985, Johnsingh 1982, Durbin 1998). All the authors mention the "whistling" sounds; however, only the last researcher made spectrographic analysis of these sounds. Cohen (1977) reported that dholes hunting in packs in dense cover maintain constant intra-pack acoustic contact by "whistling"; this may be important for the pack cohesion. Johnsingh (1982) mentioned that the dholes use a "repeated whistle" to maintain contact during and after hunting, when a pack is scattered. Hunters in India accurately imitated the sounds by blowing across the opening of an empty shotgun cartridge in order to call up dholes to be shot (Cohen 1977). "Whistling hunters" was the name given to dholes by Fox (1984) for their peculiar calls.

Based on our recent analysis of the dhole vocal repertoire (Volodin et al. 2001), we suggest that the "whistling quality" of the dhole sounds is due to presence of the high-frequency component in these sounds. We suppose that the presence in the dhole vocal repertoire of sounds consisting of the high-frequency component, both separately and together with the low-frequency component (biphonic), allows reliable short-distance acoustic communication. A high-frequency signal is hard to locate and easily dispersible, however, it is perfectly audible because its frequency exceeds that of background noise (Nikolskij 1992). Analysing our tape recordings, we regularly faced the problem that the low-frequency components of the dhole sounds were swamped by the background noise (cars, human voices, other animal sounds, etc.), while the high-frequency components could be accurately distinguished from the spectra.

From another perspective, the resistance to noise that is inherent to the high-frequency component may be used for individual identification of a caller. This idea is suggested by Durbin's (1998) research of individual differences in biphonic (as revealed in his figures) dhole sounds. "The frequency of the highest emphasised (visible) harmonic" was among three most important discriminatory parameters in stepwise discriminate procedure (Durbin 1998). We think that this parameter corresponds to the high-component fundamental frequency. Our unpublished data also support this hypothesis: based on their spectral pattern about half of dhole biphonic sounds may be visually identified as calls of a certain individual.

We can propose, on the basis of propagation characteristics, that the high component aids contact over short distances in conditions of dense vegetation. In this case, the precise location of a neighbour is not so important as detecting its presence. Thus, the distinctiveness of the high component against the background noise is in perfect correspondence with this function. Breaking contact with a pack evokes the use of another call pattern (whistle), with accented f0 of the low component (Johnsingh 1982, Durbin 1998, Volodin et al. 2001). This call type, produced in series, should increase noticeably the propagation ability of these calls (Nikolskij 1992). Therefore, the high and low components may serve as alternative tools for communication depending on the distance between individuals.

We found that the high component occurs more often in young dholes. This fact may result from age-related anatomical peculiarities in the vocal tract and poorer vocal control in young animals (e.g. Herzel and Reuter 1997, Wilden et al. 1998). However, the higher proportion of high frequency components only found in young individuals could be also a signal of subordinate status, because the young are always subordinate to the adults. However, our other data contradicts this hypothesis: because adult male and female dholes did not differ in their call patterns, whereas adult breeding females are subordinate to adult males (Johnsingh 1982, Venkataraman 1998, Ludwig and Ludwig 2000). The reason maybe reflects a prevalence of certain emotions in young animals in comparison to adults. This is perhaps related to unsure anxiety in the young (e.g. Volodina 2000) although not with fear. We never observed production of the high component in frightened dholes. Fear in the dhole correlates with silence or with squeals or screams, which are tonal harmonic sounds with very high fundamentals (Volodin et al. 2001).

What is the most probable production mechanism for biphonation in the dhole? The low-frequency component undoubtedly represents the result of normal vocal fold oscillations (Shipley et al. 1991, Owren and Linker 1995). When produced alone, the low-frequency component represents a normal tonal sound, whose fundamental frequency has well-expressed harmonics.

From the number of possible production mechanisms for biphonation in the dhole, the asynchronous pattern of vocal fold vibrations and source-tract-coupling are less probable, because with these mechanisms both fundamentals have harmonics (Berry et al. 1996, Herzel and Reuter 1996, 1997, Mergell and Herzel 1997). In the dhole the high component, as a rule, lacks clearly visible harmonics.

Vocal membranes - specific extensions of vocal folds - also may support and facilitate the generation of biphonation (Brown and Cannito 1995, Mergell et al. 1999). The relation between the presence of vocal membranes and occurrence of biphonation was reported by Riede et al. (2000b). Vocal membranes were recently found in a few canid species: domestic dogs, dog-wolf hybrids and spotted hyenas *Crocuta crocuta*, but not in every individual of the studied species (Riede et al. 2000a). However, the morphology of the dhole vocal folds is not yet studied and there is no evidence of the occurrence of vocal membranes in this species. Our results show that without exception all our dholes could produce both the high-frequency component and the biphonic sounds. We suggest that if a further study showed that the vocal membranes do not appear in every individual dhole, the hypothesis concerning the exclusive role of the vocal membranes in production of the high component should be rejected. Another argument against a vocal membranes based mechanism in this species comes from differences in the spectra of biphonic sounds between dholes and species in which both vocal membranes and the presence of biphonic sounds were suggested (Brown and Cannito 1995, Riede et al. 2000b). The difference between the dhole and Syke's monkey or dog-wolf hybrid biphonation is that the two independent fundamental frequencies in the dhole differ by a few kiloHertz, while in the other species the difference between the two fundamentals is only a few hundred Hertz.

A final possible mechanism for the production of a second high fundamental frequency in biphonic sounds is vortex-shedding at the glottal constriction, inducing "true whistle"-like sounds, as was presumed for domestic dogs (Solomon et al. 1995) and other canids (Wilden et al. 1998). A characteristic feature of the "true whistle" is the absence of harmonics and the high-frequency component found in dhole sounds fits this pattern. The appearance of the high component separately from the low one and the absence of harmonics in the high component favour the vortex-shedding as the likely production mechanism. However, other mechanisms of biphonation production also cannot be excluded without further investigations.

It is interesting that among the terrestrial mammals, biphonation occurs primarily in the family Canidae. These sounds have been reported from timber wolves, domestic dogs, dog-wolf hybrid, African wild dogs and now also for the dhole. Furthermore, the biphonic sounds structures differ in the dog-wolf hybrid, on the one hand, and in the timber wolf, African wild dog and dhole, on the other hand. More intriguing is the discovery, in some representatives of this family, of specific morphological structures on the free edges of the vocal folds — the vocal membranes. It is possible that extensive studies of vocal anatomy and vocal production will reveal in the future multiple modes for the biphonation production mechanisms in canids.

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