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CUES TO ORIENTATION OF A CALLER TO A LISTENER IN BIPHONIC AND NON-BIPHONIC CLOSE RANGE CONTACT CALLS IN THE DHOLE (*CUON ALPINUS*)

ORIENTACIJA RDEČIH VOLKOV (*CUON ALPINUS*), KI SE OGLAŠAJO PROTI CILJNIM ŽIVALIM Z BIFONSKIM IN NEBIFONSKIM KONTAKTNIM KLICEM V BLIŽNJEM OBMOČJU

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ABSTRACT

Cues to orientation of a caller to a listener in biphonic and non-biphonic close range contact calls in the Dhole (*Cuon alpinus*)

Dholes produce two call types with wide frequency ranges, potentially providing cues to orientation of a caller to a listener because of different distribution for the higher and lower frequencies. One call type is biphonic (yap-squeak), the second one (yap) includes only one fundamental with its harmonics. Here we compare the abilities the biphonic and non-biphonic, but rich in harmonics call types to encode orientation of a caller to a listener. We recorded calls and movements from three male Dholes, running singly forward and back in their identical enclosures and subdivided the recorded calls into two groups: produced toward a microphone in sector ±45°, and produced away from a microphone in sector 135-225°. For each call, within 20.3 ms time segment taken in a call centre, we calculated the amplitude ratio of sum of amplitudes higher 5 kHz to sum of amplitudes lower 5 kHz. For the pooled sample of yaps and yap-squeaks, the amplitude ratio was significantly higher for "toward" than for "from" call group. For yaps and yap-squeaks separately the results were similar. Also, Dhole showed interindividual differences both in preference of a particular call type and in reliability of cues to orientation. Overall, both biphonic yap-squeaks and non-biphonic yaps bored cues to orientation. We discuss, that the increased occurrence of biphonic yap-squeaks in the Dhole may be conditioned by their additional function as individual markers, lacking in non-biphonic yaps.

KEY WORDS: Vocal communication, nonlinear phenomena, individuality, amplitude ratio.

IZVLEČEK

Orientacija rdečih volkov (*Cuon alpinus*), ki se oglašajo proti ciljnim živalim z bifonskim in nebifonskim kontaktnim klicem v bližnjem območju

Rdeči volkovi oddajajo dva tipa glasov s širokim frekvenčnim območjem, ki morda vsebujeta informacijo o orientaciji kličočega volka proti sprejemniku klicev, glede na različno distribucijo višjih in nižjih frekvenc. En tip glasu je bifoničen (lajež-cvilež), drugi (lajež) pa vsebuje le osnovno frekvenco z njenimi višjimi harmoničnimi komponentami. V raziskavi smo proučevali lastnosti bifoničnih in nebifoničnih glasov z ozirom na sposobnost prenosa informacije o smeri kličoče živali proti poslušalcu. Snemali smo glasove in gibanje treh rdečih volkov ki so tekali tja in nazaj v svojih sicer identičnih ogradah in smo razdelili glasove na na dve skupini: tiste, ki smo jih posneli med gibanjem proti mikrofonu v sektorju ±45° in druge, ki smo jih posneli med gibanjem stran od mikrofona v sektorju 135-225°. Za vsak klic v časovnem okviru 20,3 ms v sredini klica smo izmerili amplitudno razmerje med vsoto amplitud nad 5 kHz proti vsoti amplitud pod 5 kHz. Po združevanju teh podatkov za lajež in lajež-cvilež smo ugotovili, da je bilo amplitudno razmerje pri klicih, posnetih med gibanjem živali proti mikrofonu signifikantno višje kot med gibanjem od mikrofona. Rezultata za oba tipa oglašanja sta bila podobna. Rdeči volkovi so kazali tudi precejšnje individualne razlike za oglašanje z enim ali drugim tipom klica in v komponentah, ki nosijo informacijo o orientaciji. Oba tipa glasov nosita tako orientacijo. Zato v članku razpravljajo avtorji o možnosti, da je pogostejše pojavljanje bifoničnega oglašanja pogojeno z dodatno funkcijo individualne prepoznavnosti, česar ne omogoča nebifoničen lajež.

Ključne besede: zvočna komunikacija, nelinearni pojavi, individualnost, amplitudno razmerje.

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INTRODUCTION

Biphonation is the nonlinear phenomenon that is evident from appearance of two independent fundamental frequencies in a call spectrum (HERZEL & REUTER 1996, WILDEN et al. 1998, FITCH et al. 2002). The biphonic calls have been found in many terrestrial mammals, especially in primates (BROWN & CANNITO 1995, FISCHER et al. 2001, BROWN et al. 2003) and in canids (NIKOL'SKII & FROMMOLT 1989, SOLOMON et al. 1995, WILDEN 1997, FROMMOLT 1999, RIEDE et al. 2000, VOLODIN et al. 2001, 2005, VOLODINA et al. 2006). In most canids, biphonic calls occur as irregular events and not in all individuals, however in the African Wild Dog (*Lycaon pictus*) and in the Dhole (*Cuon alpinus*) the biphonic calls have been found in all studied individuals and made up respectively 60% and 44% of vocal emissions, attending close range affiliative interactions (WILDEN et al. 1998, VOLODIN & VOLODINA 2002).

Dholes produce close range contact calls of three types: the low-frequency yap, with fundamental frequency of 0.5 to 1.4 kHz, the high-frequency squeak, with fundamental frequency of 5.5 to 10.8 kHz, and the biphonic yap-squeak, representing combination of these two calls (VOLODIN et al. 2001, VOLODIN & VOLODINA 2002). These types differ in their potential to encode individuality: the biphonic yap-squeaks provided better cues to individuality than the high-frequency squeaks, whereas the low-frequency yap lacked these cues at all (VOLODINA et al. 2006). The occurrence of biphonic calls (yap-squeaks) among contact calls varied in 14 individual Dholes from 20 to 92%, and was not related significantly to age, sex or litter membership (VOLODIN & VOLODINA 2002).

The question arises, why the biphonic calls appear so regularly, and what may be their function in the Dhole. One explanation is that the wide frequency range with the high and the low frequencies lying far apart from each other, provides cues to directionality for the account of difference in distribution and propagation ability for the higher and the lower frequencies (WILEY & RICHARDS 1978, OWINGS & MORTON 1998). For canids, this effect was experimentally confirmed for the domestic dog (*Canis familiaris*) (FROMMOLT & GEBLER 2004).

This idea was also supported by Miller's findings that the faster damping of the higher frequency provides information on orientation of a caller to a listener in the Killer Whale (*Orcinus orca*) (MILLER 2002). In the killer whale, only the biphonic calls bearing two independent frequencies, lying far apart from each other, showed a potential to encode the orientation. The calls, consisting only the low fundamental frequency with its harmonics did not provided such information (MILLER 2002). However, the non-biphonic call pattern was also reported as providing cues to orientation of a caller to a listener. Thus, in the Hawaiian Spinner Dolphin (*Stenella longirostris*) the non-biphonic high-frequency calls, rich in harmonic structure, showed the ability to encode orientation only for the account of different transmission pattern of the fundamental frequency and higher harmonics (LAMMERS & AU 2003).

The contact calls in the Dhole consist both the call patterns, that may potentially provide cues to the orientation of a caller to a listener: the non-biphonic yap, rich in harmonic structure, and the biphonic yap-squeak, including two independent frequencies, widely spaced from each other over the frequency range. Here we test a hypothesis that the biphonic yap-squeak provides better estimation of orientation of a caller in comparison with the non-biphonic yap, consisting singly the low fundamental frequency with its harmonics.

MATERIAL AND METHODS

Our objects were three adult male Dholes housed singly in neighbouring identical outdoor enclosures 4x8 m in Volokolamsk Moscow Zoo Breeding Centre (Russia). Each enclosure had wire-mesh walls and roof, with one meter high brick wall by perimeter. Each of Dholes run forward and back over their enclosures, using stereotype routes and called to each other through the wire mesh. Recordings were made within short time period from 15 to 25 January 2004.

The sound recordings were made with a SONY WM-D6C recorder and Tesla-AMD-411N cardioid dynamic microphone. Frequency responses of both systems were 40-12000 Hz. The animal movements during the calling were registered with camera Sony-TRV-65E. During the recording sessions, the camera and the audio operators were standing close to each other. Distance to animals during the recordings varied from 1.5 to 8 m. The calls were produced spontaneously without stimulation from observers.

We selected total 16 continuous record sessions from 7 to 20 minutes in duration; 5 to 6 per animal. The recorded calls were digitized with sampling frequency 22.05 kHz using Avisoft SASLab Pro v.4.3 (© R. Specht) with build-in anti-aliasing filter. Orientation of animals to microphone was checked from video records. According to video, the calls were subdivided into two groups: "toward" (produced when moving toward a microphone in sector ±45° to the microphone axis) and "from" (produced when moving away from a microphone in sector 135-225° to the microphone axis) (Fig. 1). Calls recorded under other angles, noisy or superimposed by other calls, were excluded from analysis. Totally, we analysed 1130 calls: 800 "toward" (542 yaps and 258 yap-squeaks) and 330 calls "from" (298 yaps and 32 yap-squeaks).

The spectrographic analysis was made with Avisoft SASLab Pro v.4.3. After high-pass filtration 500 Hz we measured a mean amplitude spectrum for a 20.3 ms time fragment taken within a centre of each call (FFT 256, frame 50%, overlap 93.75%, Hamming window), that provided call amplitude spectra with 128 successive bands with a frequency step 86.13 Hz. We accepted the sum of values for 53 bands below 5 kHz (from 516.8 to 4995.7 Hz) as the sum of amplitudes in the lower frequency range (Al), and the sum of values for 69 bands above 5 kHz (from 5081.8 to 10938.9 Hz) - as sum of amplitudes in the higher frequency range (Ah) (Fig. 2). For each call, we counted the amplitude ratio Ah/Al.

For statistical analyses we used nonparametric Wilcoxon matched pairs *T*-test and Mann-Whitney *U*-test. All the analyses were made in STATISTICA, version 6.0 (StatSoft, Inc).

RESULTS

At first, we estimated the received results over all the 16 recording sessions for all the three Dholes in total. We compared Ah/Al ratios between “toward” and “from” call groups within each of the 16 recording sessions with Wilcoxon matched pairs test. This test allows to exclude the influence of additional factors (such as individuality, the session recording conditions, etc.), as soon as it compares calls, differing only in one variable, in our case, calls produced “toward” or “from” a microphone. For yaps and yap-squeaks taken together, the ratio Ah/Al was significantly higher for "toward" call group than for "from" call group (Wilcoxon matched pairs test, n=16, T=19, p<0.05). For yaps and yap-squeaks taken separately, the results were similar: in both the cases, Ah/Al was significantly higher for "toward" call group than for "from" call group (Wilcoxon matched pairs test, n=15, T=13, p<0.01, and n=9, T=0, p<0.01 respectively).

Further, we estimated the received results for each of the Dholes separately (Fig. 3). Two of three Dholes called mainly yaps, whereas the number of yap-squeaks from these animals was not enough for analysis. For yaps, only one of these two animals showed higher Ah/Al ratio for "toward" call group than for "from" call group (Mann-Whitney U-test, n_1=90, n_2=105, U=2690, p<0.001), whereas the second one showed almost coinciding values (Mann-Whitney U-test, n_1=240, n_2=143, U=16854, p=0.77). The third Dhole called both yaps and yap-squeaks, and for both call types the Ah/Al ratio was significantly higher for "toward" call group (Mann-Whitney U-test, n_1=212, n_2=50, U=3291, p<0.001 for yaps, and n_1=219, n_2=26, U=1831, p<0.01 for yap-squeaks). Thus, the Dholes showed great interindividual differences both in preference of a particular call type and in reliability of encoding orientation.

DISCUSSION

Thus, both biphonic yap-squeaks and non-biphonic yaps can encode an orientation of a caller to a listener in the Dhole. The second high frequency was not obligate to encode orientation in the Dhole, however, it was "actively involved" into this process when it was presented in contact calls. Therefore, a hypothesis that the biphonic yap-squeak provides better estimation of orientation of a caller in comparison with the non-biphonic yap, should be declined.

The presented data provide first evidence concerning possibility to encode caller-to-listener orientation in calls of terrestrial mammals. Earlier, similar results were reported only for marine mammals – for biphonic calls of killer whales and harmonically rich non-biphonic calls of the Hawaiian spinner dolphin (Miller 2002, Lammers & Au 2003). The possibility of estimation of orientation of a caller to a listener comes from physical frameworks, suggesting that high frequencies, propagated in the environment, attenuate much more strongly, than low frequencies. Besides, the higher frequencies distribute by narrower beam in comparison with the lower ones, which distribute nearly omnidirectionally (Wiley & Richards 1978, Owings & Morton 1998, Naguib & Wiley 2001). For domestic dogs, Frommolt & Gebler (2004) showed experimentally, that frequency below 1 kHz damped equally both forward and back to the mouth of barking dog. On the other hand, frequencies higher 1 kHz damped less in forward direction to the mouth in comparison with direction back to the mouth (Frommolt & Gebler 2004). Together, these effects result in the higher high-to-low amplitude ratio for the animal, calling toward a listener in comparison with the high-to-low amplitude ratio for the animal, calling from the same distance, but turned away from a listener (MILLER 2002).

However, such estimation of orientation is possible only with calls consisting energy both in the lower and in the higher parts of a spectrum, that is, calls should be compound signals, containing both "directional" and "non-directional" components, named "mixed directionality" by LARSEN and DABELSTEEN (1990). Both our data on the Dhole and the reported data on the Hawaiian spinner dolphin (LAMMERS & AU 2003) suggest that the fundamental with well-expressed harmonic structure is already sufficient for coding orientation of a caller to a listener. However, the amplitude of higher-ordered harmonics decreases about 6-12 dB per octave (TITZE 1994, OWREN & BERNACKI 1998), so, theoretically, there are two possibilities to enforce cues to orientation in calls. The first one – the use of biphonic calls with widely spaced fundamentals, as in the killer whale (MILLER 2002) and in the Dhole in the presented study. The second one – the vocal tract filtration of middle harmonics in calls consisting only one fundamental, resulting in enforcement of presentation of the higher order harmonics in a spectrum. Probably, this second possibility was realized in contact calls of Bush Dogs (*Speothos venaticus*) (our unpublished data).

The presented data on cues to orientation in the Dhole calls highlight the probable role of contact biphonic calls in communication of this species. The Dhole is pack-living canid, communally hunting on large prey and inhabiting areas with complex relief in mountains and in locations with dense vegetation; with primary breeding by a dominant pair and with other group members functioning as helpers, and with very low intrapack aggression (COHEN 1977, JOHNSINGH 1982, KARANTH & SUNQUIST 1995, VENKATARAMAN et al. 1995, VENKATARAMAN 1998, LUDWIG & LUDWIG 2000). In the previous study, we showed that the biphonic yap-squeaks provide significantly better individual discrimination in comparison with non-biphonic yaps and squeaks occurring as separate vocalisations. Moreover, the yaps lacked cues encoding individuality at all (VOLODINA et al. 2006). At the same time, the squeak lacks cues to orientation of a caller, because the high-frequency narrow-band calls are the most difficult to locate (MARLER 1955, KLUMP & SHALTER 1984). Namely the combination of two frequencies into a biphonic yap-squeak provides simultaneously cues both to individuality and to orientation of a caller to a listener. This peculiarity of biphonic calls in the Dhole may be used for the delicate coordination of movements within a pack in conditions of poor visibility and high social density, and is explaining the very high occurrence of biphonic calls in this species, in comparison with other canids (excluding the African Wild Dog) and other mammals as the whole.

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REFERENCES

BROWN, C.H. & CANNITO, M.P., 1995: Modes of vocal variation in Sykes's monkey (*Cercopithecus albogularis*) squeals.- *J. Comp. Psychol.*, 109, 398-415.

BROWN C.H., ALIPOUR F., BERRY D.A. & MONTEQUIN D., 2003: Laryngeal biomechanics and vocal communication in the squirrel monkey (*Saimiri boliviensis*).- *J. Acoust. Soc. Am.*, 113, 2114-2126.

COHEN, J.A., 1977: A review of biology of the dhole or Asiatic wild dog (*Cuon alpinus* Pallas).- *Animal Regulat. Studies*, 1, 141-158.

FISCHER, J., HAMMERSCHMIDT, K., CHENEY, D.L. & SEYFARTH, R.M., 2001: Acoustic features of female chacma baboon barks.- *Ethology*, 107, 33-54.

FITCH, W.T., NEUBAUER, J. & HERZEL, H., 2002: Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production.- *Anim. Behav.*, 63, 407-418.

FROMMOLT, K.-H., 1999: Sidebands - facts and artefacts.- *Bioacoustics*, 10, 219-224.

FROMMOLT, K.-H. & GEBLER, A., 2004: Directionality of dog vocalizations.- *J. Acoust. Soc. Am.*, 116, 561-565.

HERZEL, H. & REUTER, R., 1996: Biphonation in voice signals.- In: KATZ, R.A., FRISON, T.W., KADKE, J.B. & BULSARA, A.R. (Eds.): *Nonlinear, Chaotic, and Advanced Signal Processing.*- Methods for Engineers and Scientists, Woodbury: American Institute of Physics, pp. 644-657.

JOHNSINGH, A.J.T., 1982: Reproductive and social behaviour of the dhole, *Cuon alpinus* (Canidae).- *J. Zool.*, 198, 443-463.

KARANTH K.U. & SUNQUIST M.E., 1995: Prey selection by tiger, leopard and dhole in tropical forests.- *J. Anim. Ecol.*, 64, 439-450.

KLUMP, G.M. & SHALHER, M.D., 1984: Acoustic behaviour of birds and mammals in the predator context.- *Z. Tierpsychol.*, 66, 189-226.

LAMMERS, M.O. & AU, W.W.L., 2003: Directionality in the whistles of Hawaiian spinner dolphins (*Stenella longirostris*): a signal feature to cue direction of movement?- *Marine Mam. Sci.*, 19, 249-264.

LARSEN, O.N. & DABELSTEEN, T., 1990: Directionality of blackbird vocalization. Implications for vocal communication and its further study.- *Ornis Scand.*, 21, 37-45.

LUDWIG, W. & LUDWIG, C., 2000: Beobachtungen zur sozialen Organisation eines Rudels Rothunde (*Cuon alpinus*) im Zoo Dresden.- *Zool. Garten N.F.*, 70, 39-59.

MARLER, P., 1955: Characteristics of some animal calls.- *Nature*, 176, 6-8.

MILLER, P.J.O., 2002: Mixed-directionality of killer wale stereotyped calls: a direction of movement cue?- *Behav. Ecol. Sociobiol.*, 52, 262-270.

NAGUIB, M. & WILEY, H., 2001: Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication.- *Anim. Behav.*, 62, 825-837.

NIKOL'SKII, A.A. & FROMMOLT, K.-H., 1989: Vocal activity in the timber wolf.- Moscow: Moscow State Univ. Press. [In Russian].

OWINGS, D.H. & MORTON, E.S., 1998: Animal vocal communication: a new approach.- Cambridge: Cambridge Univ. Press.

OWREN, M.J. & BERNACKI, R.H., 1998: Applying linear predictive coding (LPC) to frequency-spectrum analysis of animal acoustic signals.- In: HOPP, S.L., OWREN, M.J. & EVANS, C.S. (Eds.): *Animal Acoustic Communication*.- Berlin: Springer-Verlag, pp. 129-162.

RIEDE, T., HERZEL, H., MEHWALD, D., SEIDNER, W., TRUMLER, E., TEMBROCK, G. & BÖHME, G., 2000: Nonlinear phenomena and their anatomical basis in the natural howling of a female dog-wolf breed.- *J. Acoust. Soc. Am.*, 108, 1435-1442.

SOLOMON, N.P., LUSCHEI, E. & KANG, L., 1995: Fundamental frequency and tracheal pressure during three types of vocalizations elicited from anaesthetized dogs.- *J. Voice*, 9, 403-412.

TITZE, I.R., 1994: Principles of voice production.- Prentice Hall: Englewood Cliffs.

VENKATARAMAN, A.B., 1998: Male-biased adult sex-ratios and their significance for cooperative breeding in dhole, *Cuon alpinus*, packs.- *Ethology*, 104, 671-684.

VENKATARAMAN A.B., ARUMUGAM R. & SUKUMAR R., 1995: The foraging ecology of dhole (*Cuon alpinus*) in Mudumalai-Sanctuary, southern India.- *J. Zool.*, 237, 543-561.

VOLODIN, I.A. & VOLODINA, E.V., 2002: Biphonation as a prominent feature of the dhole *Cuon alpinus* sounds.- *Bioacoustics*, 13, 105-120.

VOLODIN, I.A., VOLODINA, E.V. & FILATOVA, O.A., 2005: Structural peculiarities, occurrence and functional significance of nonlinear phenomena in calls of terrestrial mammals.- *Journal General Biology*, 66, 346-362 [In Russian].

VOLODIN, I.A., VOLODINA, E.V. & ISAEVA, I.V., 2001: Vocal repertoire in the dhole *Cuon alpinus* (Carnivora, Canidae) in captivity.- *Zoologicheskii Journal*, 80, 1252-1267. [in Russian, translated into English in *Entomological Review*, 2001, 81, suppl. 2, S346-S361].

VOLODINA, E.V., VOLODIN, I.A., ISAEVA, I.V. & UNCK, C., 2006: Biphonation may function to enhance individual recognition in the dhole, *Cuon alpinus*.- *Ethology*, 112, 815-825.

WILDEN, I., 1997: Phonetische Variabilität in der Lautgebung Afrikanischer Wildhunde *(Lycaon pictus)* und deren frühe Ontogenese.- Aachen: Shaker Verlag.

WILDEN, I., HERZEL, H., PETERS, G. & TEMBROCK, G., 1998: Subharmonics, biphonation, and deterministic chaos in mammal vocalization.- *Bioacoustics*, 9, 171-196.

WILEY, R.H. & RICHARDS, D.B., 1978: Physical constraints on acoustic communication in the atmosphere: implication for the evolution of animal vocalizations.- *Behav. Ecol. Sociobiol.*, 3, 69-94.

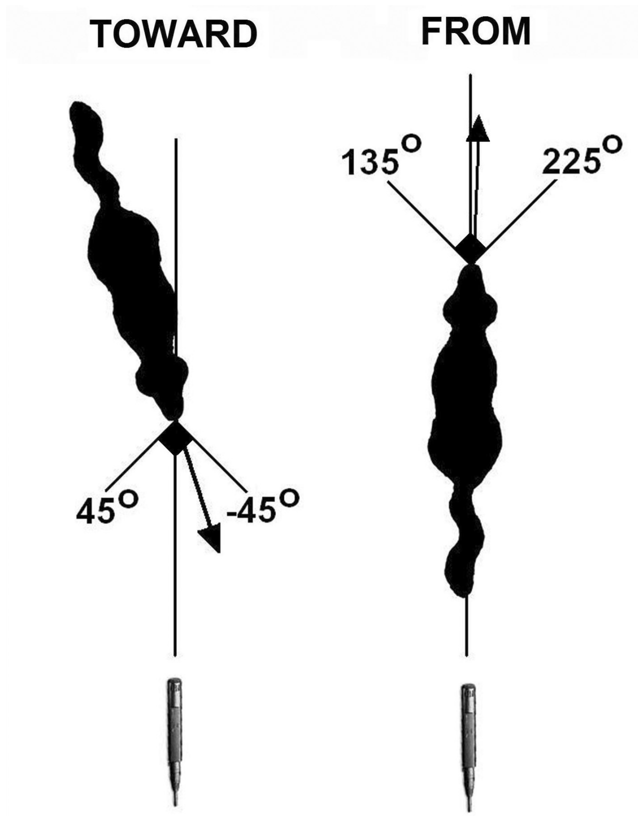

Figure 1: The selection of calls for analysis depending on orientation of a Dhole (*Cuon alpinus*) to a microphone: "toward" call group – calls produced in sector ±45° to the microphone axis; "from" call group – calls produced in sector 135-225° to the microphone axis.

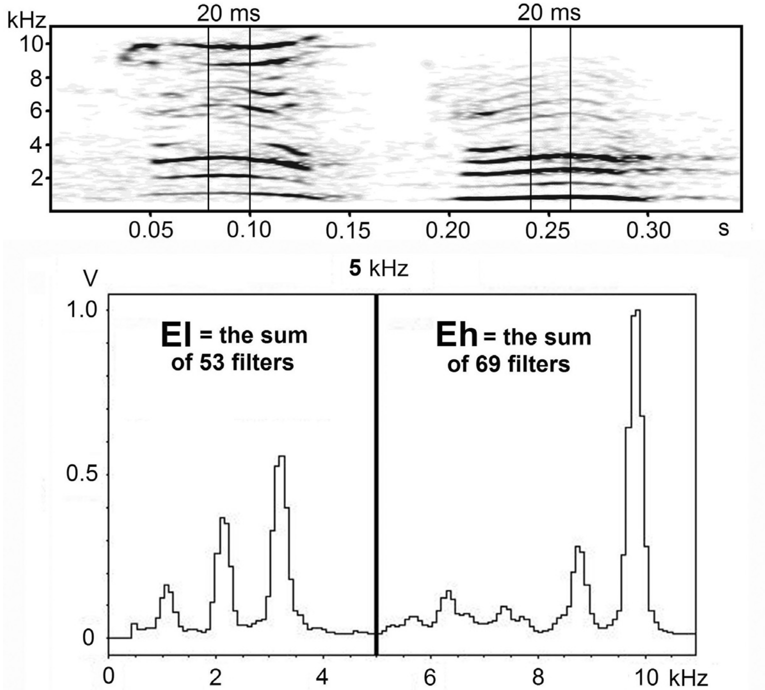

Figure 2: The measurement of amplitude ratio of sum of amplitudes higher 5 kHz to sum of amplitudes lower 5 kHz (Ah/Al) in the Dhole calls (*Cuon alpinus*). Above: selection of 20.3 ms time fragment within a call centre in the yap-squeak (left) and in the yap (right). Below: mean amplitude spectrum of 20.3 ms time fragment for the yap-squeak from above; the part left to the vertical bar shows the sum of amplitudes for 53 bands below 5 kHz (Al), the part right to the vertical bar shows the sum of amplitudes for 69 bands above 5 kHz (Ah).

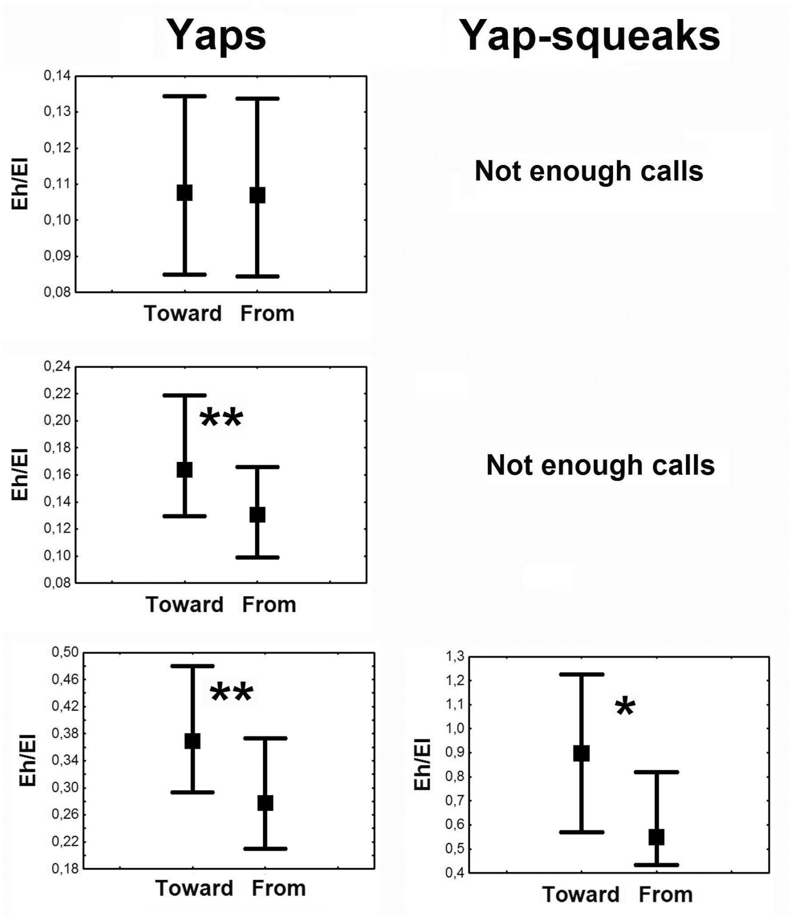

Figure 3: Comparison of Ah/Al ratio between "toward" and "from" call groups for three individual Dholes (*Cuon alpinus*) for two call types. The points represent medians, vertical lines – quartiles. * - $p<0.01$; ** - $p<0.001$, Mann-Whitney *U*-test.