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Vocal Repertoire of Cheetah *Acinonyx jubatus* (Carnivora, Felidae) in Captivity: Sound Structure and Search for Means of Assessing the State of Adult Animals

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Abstract—Vocalization is a rich potential source of information on the internal state of animals. This information is necessary for assessing the animal behavior and ensuring the most favorable conditions for holding and breeding animals in captivity. The sound indicators of animal's behavioral and physiological well-being can be applied without traumatic manipulations, which is especially important for such a rare and endangered species as the cheetah *(Acinonyx jubatus).* Bight types of sounds were distinguished and attributed to three classes: pulsed, tonal, and noisy. The classification proposed is discussed in relation to mechanisms for producing different kinds of sounds. A hypothetical diagram of the correlation between the sound structure and states of confidence/diffidence and aggressiveness/nonagressiveness in the cheetah is considered.

Establishing a correlation between the sound structure and internal state of animals during sound production is one of important issues both in theoretical and applied acoustics (Morton, 1977; Nikolskii, 1984; Hauser, 1996). It has been shown in numerous studies using various methods of independent monitoring of the internal state of animals that animal sounds bear the "honest" information on their emotions and motivations. For example, Weary and Fraser (1995a. 1995b) showed that the call structure of pigs *(Sus scrofa* L.) is changing depending on the extent of food deprivation and displeasing impact. Jurgens (1976a) presented reliable arguments indicating that the sound structure of the squirrel monkey *(Saimiri sciureus* L.) is related to subjective displeasing or pleasing feelings of these animals, and sounds of different structure are localized in different areas of vocal centers of the brain. Dessereau *et al.* (1995) found that structural characters of vocalization in humans also give true information on their internal state: stronger emotional tension is reflected in those sounds, in which the pauses are excessively long as related to frequency.

The field of application of vocal indicators of the internal state of animals and humans is potentially very wide. Such indicators, for example, are used in the lie detector, for the emergency stop of machines in response to cry, estimation of reproductive cycle stages of animals in zoos and farms (Smith *et al,* 1983; Lindburg, 1990; Huang *et al.,* 1994; Volodina and Volodin, 1996). At present, bioacoustic methods for estimating subjective states of animals and humans, such as, e.g., well-being, suffering, etc., attract special attention due to the development of legislation concerning humanistic keeping of animals at farms, laboratories, and zoos, and also in connection will medical programs (Broom and Johnson, 1993; Volodin and Volodina, 1997).

The sounds are convenient indicators of the internal state, because they can be easily recorded and analyzed. In addition, bioacoustic analysis does not require traumatic manipulations or immobilizing, which are necessary, e.g., in blood sampling. This is especially important in the work with rare, endangered species, when an investigator is strongly limited in possibilities of manipulating with animals. The cheetah *(Acinonyx jubatus* Schreber), the object of the current study, just belongs to this kind of species.

A description of the vocal repertoire is a necessary premise for the development of non-manipulating bioacoustic approach for estimation of the internal state. Despite the ample body of published data on the vocal behavior of cheetah (Adamson, 1969, 1972; Schaller, 1972; Kingdom, 1977; Movchan and Opakhova, 1981; Peters, 1981, 1983; Frazer Sissom *et al.,* 1991), the vocal repertoire of this species still has not been described satisfactorily, and the terminology for designation of sound types is rich in synonyms.

In this paper, I describe the vocal repertoire of adult cheetahs in captivity on the basis of structural charac-

ters of sounds, substantiate the proposed classification on the basis of published data on differences in the mechanisms of sound production for various types of sounds, discuss the question on discreteness and continuity of vocal flow and hypothetical relationship between the structure of sounds and state of confidence / diffidence / aggressiveness / non-aggressiveness in the cheetah.

MATERIAL AND METHODS

Sound recordings of 14 adult cheetahs (6 males and 8 females) with simultaneous commentary of situations accompanying the record have been done at the Moscow Zoo, and small part at the Bukhara goitred gazelle brooder (Uzbekistan) within the period from June 1984 till December 1992. All cheetahs were over three years old; one male and two females were bom at the Moscow Zoo, the rest were obtained through zoo commercial firms.

The sounds were recorded from a distance of 0.5 to 8 m, using a Reporter-5P tape recorder with tape transport velocity of 9.5 cm/s, with an MKE-2 or MKE-100 microphone within the frequency range between 50 and 15000 Hz. The number of analyzed sounds is given in the table.

The sound structure was analyzed using a Spektr-1 dynamic spectrograph (Russia), Kay Elemetric 7800 sonograph (USA) and Sono software (Biooptima, Russia). Spectrograms Spectr-1 were at frequencies in the range from 0.2 to 16 kHz; sonograms Kay, at 2, 4, or 8 kHz, depending on frequency-temporal characteristics of sounds, with 22.5, 45, and 90 Hz filters, respectively. The Sono sonograms were measured in the frequency range under 10 kHz with frequency resolution 109 Hz and temporal resolution 6.8 ms. The depth of frequency modulation was calculated as the difference between the main maximum and main minimum frequencies.

A statistical analysis of variables was carried out using Mann-Whitney criteria (Zar, 1984). The calculations used the method of "data summation", with variables for different individuals processed as independent events (Leger and Didrichsons, 1994). This method is appropriate when the intra-individual variability of variables exceeds their inter-individual variability, which was confirmed for the following parameters: frequency of pulsation of cries of churtling and growling, duration of churtling, growling and miaowing, and maximum frequency of miaowing (Volodina and Volodin. 1998).

RESULTS

The Description of Vocal Repertoire of Cheetah

Three types of sounds were distinguished in the repertoire of cheetah: sounds with internal pulsation (4 types), tonal sounds (3 types) and noisy sounds (1 type). The data on the structural characteristics of these sounds are given in the table. The sounds, in which characters of different structural types occur simultaneously, are determined as intermediate, and sounds, in which one structure successively changes another, as transitional.

Sounds with rhythmic pulsation. *Churtling* (Fig. 1). The following designations are used for sounds of this type in the English literature: "chirr" (Schaller, 1972), "pr-pr" (Adamson, 1969, 1972; Kingdom, 1977), "gargle" (Peters, 1984), "mixed voice and purr" (Frazer Sissom *et al.,* 1991), "churtling" (Asa *et al.,* 1992). The sound represents a series of 3-15 staccato pulses with total duration from 0.1 to 1.3 s. On the spectrogram the sound pulses look like stacks of formants with distribution resembling the arrangement of harmonics in tonal sounds. *Gurgling* (Fig. 1). The proposed term is a Russian equivalent of "prusten" applied by Peters (1978, 1983) to sounds of other cats, which spectrographically resemble these sounds of cheetahs. The gurgling is a sound in the form of a short series of 5-7 unequal sound pulses. repeated in a rapid irregular succession and partly fusing. The total duration of vocalization varied between 0.25 and 0.6 s. *Purring* (Frazer Sissom *et al.,* 1991) (Fig. 1). This is a regular sequence of equal sound pulses practically unlimited in duration due to the permanent production during both respiration phases (Frazer Sissom *et al.,* 1991). *Growling* (Schaller, 1972) (Fig. 2). The sound comprises a series of many similar pulses with total duration from 0.5 to 4.5 s, repeated with a period around 0.027 s or fusing in a noise vocalization, which can be observed within one vocalization.

Tonal sounds. *Miaowing* (Fig. 3). Peters (1978) applied this name to sounds of other cats, which spectrographically resemble these sounds of cheetahs. These are the sounds of total duration from 0.08 to 0.6 s, with varied type of frequency modulation: either arch-like, or with almost unpronounced modulation, or with two frequency peaks, and others. *Chirping* (Fig. 3). the following names are used for designation of sounds of this type in the English literature: "chirp" (Adamson, 1972; Schaller, 1972; Asa *et al.,* 1992), "explosive yelp" (Kingdom, 1977),

The structural characteristics of cheetah's sounds

Parameter	Sounds class							
	with internall pulsation				tonal			noisy
	sound type							
	churl ling	purring	growling	gurgling	miaowing	chirping	howling	hissing
Duration, s	0.62 ± 0,03 N = 100	Unlimited	2.60 ± 0.18 N = 92	0.37 ± 0.06 N = 6	0.32 ± 0.02 N = 52	0.30 ± 0.01 N = 10	1.30 ± 0.13 N = 10	0.55 ± 0.04 N = 20
Period between impulses, ms	54.44 ± 0.31 N = 737	42.64 ± 0.29 N = 221	27.49 ± 0.18 N = 693	Irregular	-	-	-	-
Basic initial frequency, kHz	-	-	-	-	0.72 ± 0.08 N = 45	1.19 ± 0.03 N = 33	0.24 ± 0.01 N = 9	-
Basic maximum frequency, kHz	-	-	-	-	1.09 ± 0.10 N = 60	1.19 ± 0.03 N = 33	0.38 ± 0.01 N = 9	-
Basic final frequency, kHz	-	-	-	-	0.70 ± 0.08 N = 45	0.68 ± 0.03 N = 31	0.27 ± 0.01 N = 9	-
Extent of fundamental frequency modulation, kHz	-	-	-	-	0.47 ± 0.06 N = 45	0.50 ± 0.04 N = 31	0.09 ± 0.01 N = 9	-
Overall frequency range, kHz	0.2-7	0.2-6	0.2-7	0.4-6	0.4-8	0.35-8	0.2-8	0.2-7

Mean, standard error, and sampling size are given in the table.

"stutter-barking" (Lindburg *et al.*, 1985). The chirping is a tonal sound with a drastically falling frequency. The total duration of this sound varies between 0.09 and 0.48 s. Sometimes also stepwise frequency modulation occurs. This type of modulation results from uneven energy distribution both between harmonics and during the cry. *Howling* (Fig. 3). Low frequency, drawling tonal sounds with duration 0.9 to 1.55 s, with a very poorly pronounced frequency modulation.

Noisy vocalization. *Hissing* (Fig. 2). These are sounds with duration of 0.6 to 1.0 s, with a noisy spectrum. The sound energy is distributed uniformly along the frequency range excluding narrow accented band from 0.2 to 0.95 kHz.

Transitional sounds (Fig. 4). The tonal sounds of such structure (miaowing or chirping) alternate with pulsating sound (churtling, growling, or gurgling) during one vocalization.

Intermediate sounds (Fig. 4). Intermediate forms between churtling and miaowing, howling and growling, and howling and miaowing, and miaowing and chirping have been found.

Statistical Differences in Measurements of Structural Parameters of Different Vocalization Types

In calls with sound pulsation, significant difference was found in periods between pulses of the following sound types (mean values and sampling sizes are given in table): purring-growling (Mann-Whitney test, $U = 2379.5$; $p < 0.01$); churtling-growling ($U = 7570$; $p < 0.01$); churtling-purring ($U = 15507$; $p < 0.01$). The duration of growling significantly exceeded that of churtling ($U = 260.5$; $p < 0.01$).

Fundamental initial frequencies in tonal calls significantly differed in the following sound types: chirping-miaowing ($U = 88$; $p < 0.01$); chirping-howling ($U = 0$; $p < 0.01$), miaowing-howling ($U = 15$, $p < 0.01$). Chirping and miaowing significantly differed in fundamental maximum frequency ($U = 516.5$; $p < 0.01$). Chirping and howling ($U = 0$; $p < 0.01$), as well as miaowing and howling ($U = 8$; $p < 0.01$) were significantly different in fundamental final frequency, whereas chirping and miaowing were not. Chirping and howling ($U = 0$; $p < 0.01$) and miaowing and howling ($U = 15$; $p < 0.01$) significantly differed in depth of modulation of fundamental frequency; chirp-

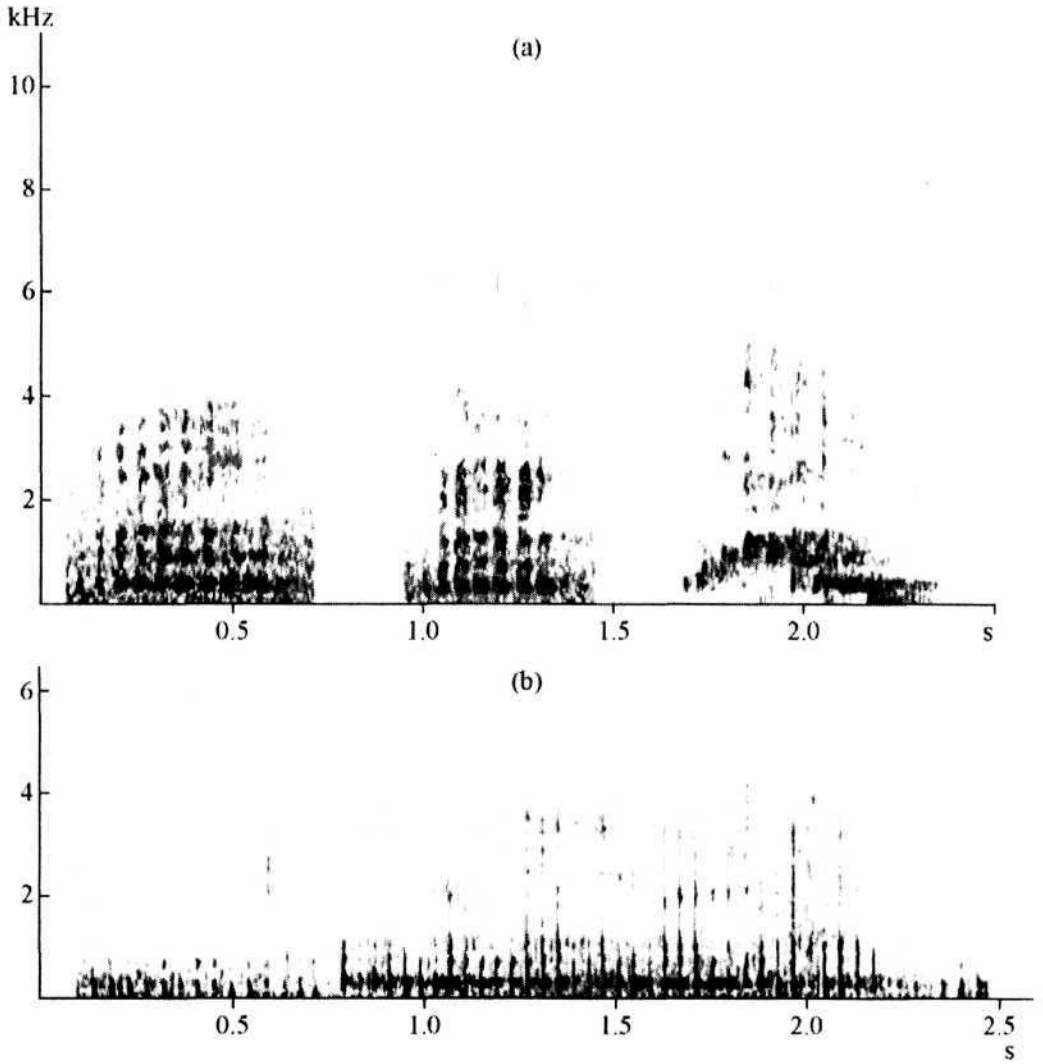

Fig. 1. Sonograms of the cheetah's sounds with rhythmic pulsation; (a) churtling of female (at the left), churtling of male (at the center), and gurgling of male (at the right); (b) purring of female.

ing and miaowing did not significantly differ in that parameter. Howling and chirping ($U = 0$; $p < 0.01$) and howling and miaowing ($U = 0$; $p < 0.01$) significantly differed in duration, while the difference between chirping and miaowing was statistically insignificant.

DISCUSSION

Mechanisms of Sound Production in Cheetah

At least three different mechanisms are operative in sound production in cheetah. For example, Frazer Sissom *et al.* (1991) showed in a paper devoted to sound production in cheetahs, pumas, and domestic cats that tonal sounds in the cat family are produced by means of phonation, and purring, by means of vibration. In phonation, the sound is generated by aerodynamically started vibration of vocal chords in the larynx. The purring is produced by mechanic activation of laryngeal muscles that cause periodical connection of vocal chord in the larynx. Purring is produced during the whole respiratory cycle, and phonations, almost always only with expiration. According to the measurements of these authors, the frequency of pulsation in cheetah purring is 26 Hz in the phase of expiration and 21 Hz in inhalation. These values are similar to the data we obtained (23.7 Hz) calculating summarized measurements for both respiratory phases.

According to data of the same authors (in their paper churtling is called "mixed voice and purring"), the churtling is produced in simultaneous operation of both mechanisms, phonation and vibration. The harmonic structure of formant arrangement in churtling that I indicated, is likely to be accounted for by this fact. This is not surprising, so far as complex,

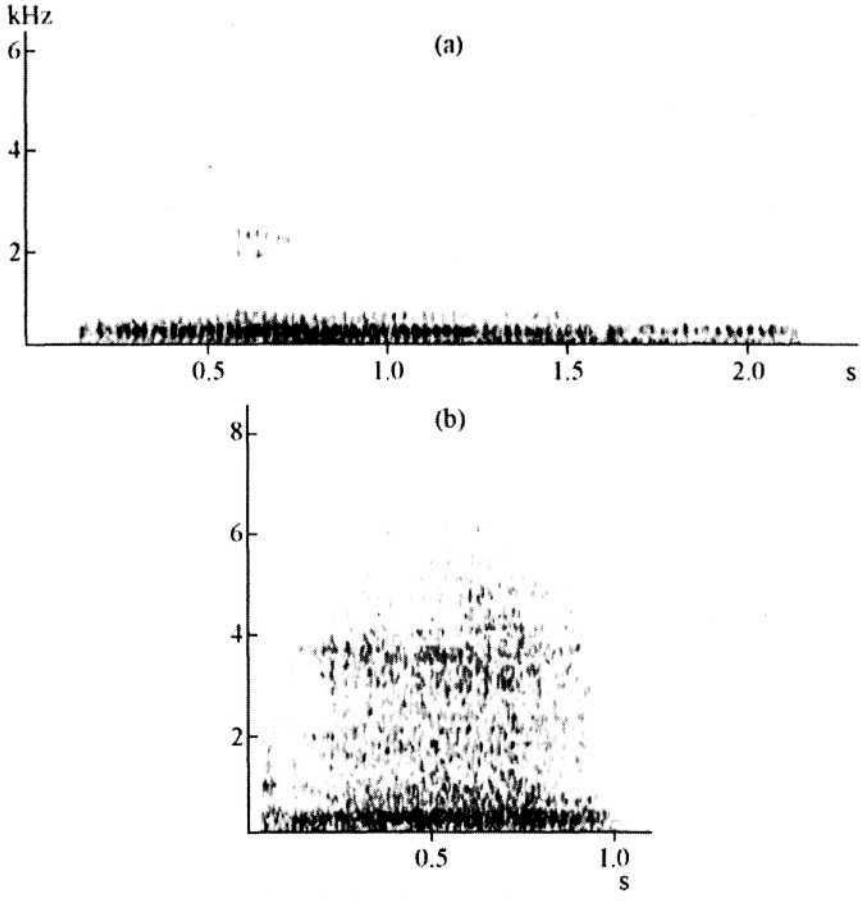

Fig. 2. Sonograms of cheetah's sounds with rhythmic pulsations and noisy sounds: (a) growling of male; (b) hissing of female.

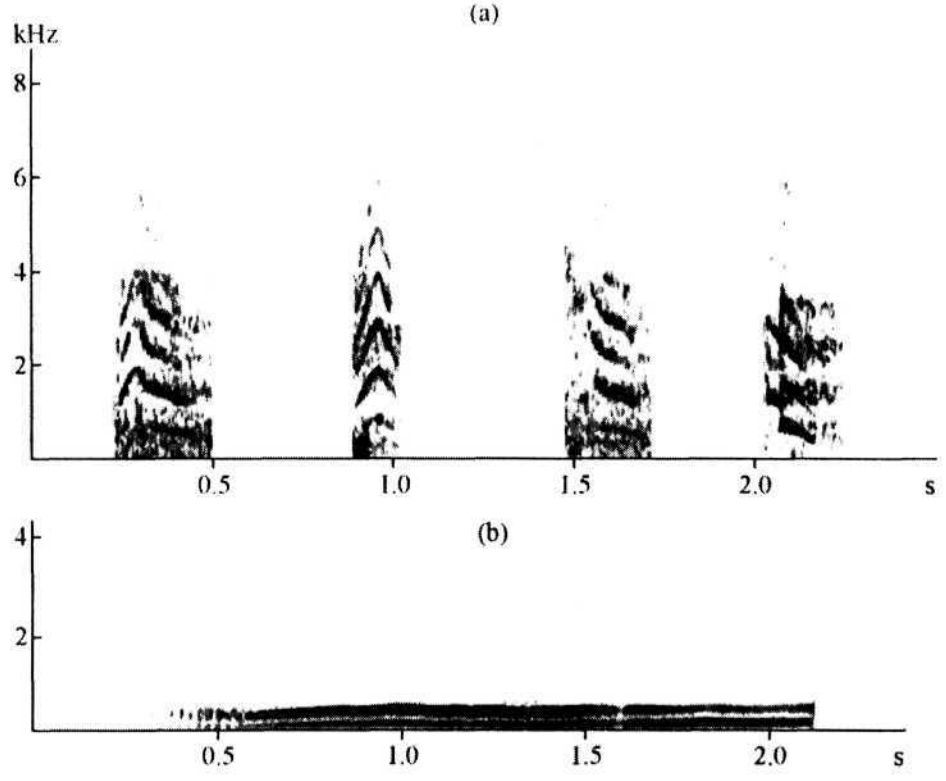

Fig. 3. Sonograms of tonal sounds of cheetah: (a) male miaowing (two at the left), male chirping (two at the right); (b) male howling.

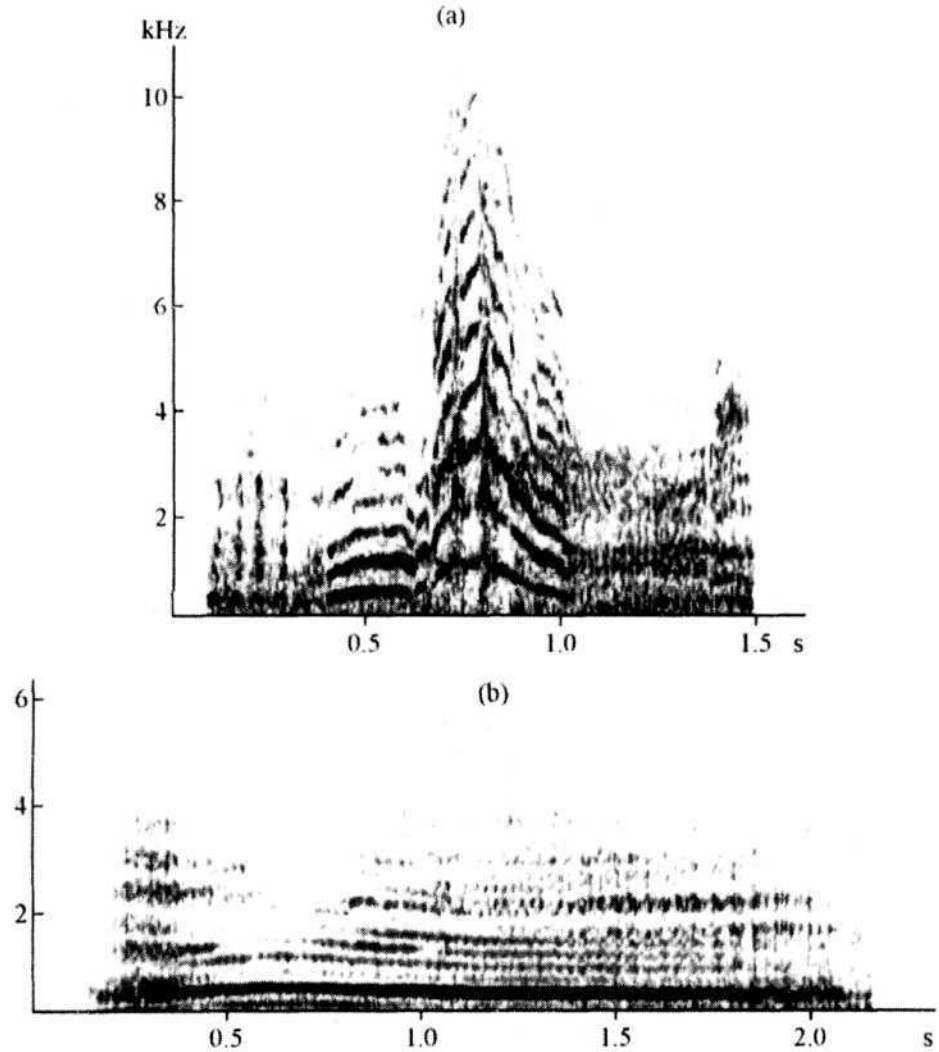

Fig. 4, Sonograms of transient and intermediate sounds of cheetah: (a) sound of transient structure from churtling to miaowing and further to growling of male; (b) sound of intermediate structure between howling and growling of male.

"double" mechanism of sound production of these calls sounds as interrupted tonal signal (Frazer Sissom *et al.*, 1991).

In hissing, vocal chords apparently do not. take part in sound production, and (he air flow from lungs goes through a narrow fissure at the exit of the vocal tract, similarly to the mechanism of hissing sounds in human speech.

Is the Vocal Repertoire of Cheetah a Continuum of Structural Forms or a Set of Discrete Types?

This problem arises again and again in respect to the vocal repertoire of any mammal (for example, see Nikolskii, 1984; Hauser, 1996) and, apparently, we should give affirmative answer to both questions, at least for the cheetah.

The matter is that mostly all sounds produced by the vocal tract of mammal may somehow be embodied in a graduated system, which is a continuous series of structural transitions. For example, in the vocal repertoire of cheetah, continuum of changing forms from sounds with evident pulsation to almost tonal ones may be observed. Thus, the range of vocal forms produced by cheetahs represents the gradual system, where extreme points of continuum, miaowing and churtling, are connected by a number of intermediate forms. In this system, the "sound type" is determined as some part of this continuum.

However, there are serious arguments in favor of regarding the vocal repertoire of cheetah as a set of discrete types. As follows from the preceding part of the paper, sound production of different types is based on different mechanisms, which may operate separately or simultaneously, but are strictly coordinated (as in sounds belonging to churtling type). Probably, owing to the failures in breathing at anxiety or excite-

ment, discrepancies in the work of these mechanisms may take place, producing sounds of "intermediate" structure, which obscure the existing boundaries between types. However, in most cases there are no doubts to what type could be referred each certain sound. Thus, the vocal repertoire of the cheetah falls under the definition of Marler's "gradual repertoire" (Marler, 1975; Green and Marler, 1979), continual at the level of sound producing and discrete at the level of perception.

The morphological basis of such a structure of the vocal repertoire in mammals was discovered in the work of Jurgens and Ploog (1970), where the relation of different sound types produced by the squirrel monkey to different brain regions was shown, pointing to discrete vocal types at the level of brain structures. These data confirm the possibility of discretion in perception, when the animal may perceive some range of vocal forms as related to some type, and forms lying outside that range, to a neighboring type. A similar mechanism occurs in perception of vowels by humans (V.N. Sorokin, private communication).

Correlation of Sound Structure and Confidence Diffidence State in Cheetah

Hypothetical scheme of relations between vocal structural types of cheetah and emotional states of confidence and diffidence is shown in Fig. 5. This scheme is based first of all on the estimation of differences in use by cheetah of tonal vocalizations and vocalizations with inner sound pulsation, depending on their role in socially asymmetrical situations.

Following Schaller (1972), I can confirm that cheetahs use as an attractive call two structurally different vocalizations: churtling (with sound pulsation) and miaowing/chirping (with tonal structure). What is the reason for two different vocalizations with the same function? Analysis of differences in the character of using these sounds may help to answer this question. In a previous work (Volodina, 1997), it was shown that in socially asymmetrical situations, such as male-female mating behavior and mother-cub relations, the number of produced churtlings and miaowing/chirpings is related to the social role of an animal. During mating, both partners produce churtling and chirping, but churtling significantly prevails in male, and chirping in female. In relations between mother and cub, by contrast, the fraction of churtlings is higher in females and chirpings/miaowings prevail in cubs.

Thus, the fraction of tonal sounds and churtlings is related to asymmetry in social interrelations in the cheetah. Inasmuch as social asymmetry of relations is determined by differences in subjective emotional state of animals, it is possible to presume that these structurally different, but functionally similar sounds bear different emotional loads. These differences can be characterized as individual power or weakness of one animal in comparison with another, or as its confidence or diffidence. Using the terms "confidence" and "diffidence" here, I mean predictability and uncertainty of the nearest events and proper action of animals (Sapolsky, 1990). For example, of two interacting animals, the more confident would be the one for whom the nearest events and its proper actions are more predictable. It is logical to presume that, in most cases, more confident would be the stronger animal, since it determines the course of current events to a greater extent, as compared with the weak one. Hence, tonal sounds reflect relative weakness and diffidence of an animal in socially asymmetrical situations.

Transitional vocalizations in cheetah, where the tonal component is replaced by an interval of sound pulsation or vice versa, allow researcher to observe how exogenous circumstances affecting an animal cause change in its state and respectively the sound structure. For example, female disturbed by the observer during the play with cubs changes churtling for churtling with a tonal component (Volodina, 1997). Emotional states, to which transitional sounds correspond, may apparently be determined as marginal, ambivalent, conflict or rapidly changing. It is possible also to presume that transitional sounds correspond to some "mixed" states.

Purring in cheetah is related to comfort, friendly behavior in pleased, relaxed animals under calm conditions, where behavior of animals is quite predictable both for observer and, apparently, for themselves. Therefore, interior state of purring cheetahs may be interpreted as confident. There are published data confirming that the interior state experienced by mammals producing sounds of such structure as purring is subjectively pleasant for them, and tonal sounds of such structure as chirping, unpleasant. For example, in the experiments of Jurgens (1976a, 1976b), squirrel monkey switched off electrical stimulation, when electrodes were implanted to those brain regions which control chirping and did not switch off stimulation, if the electrodes were implanted in regions controlling purring. In addition, it is known that localization of, at least, centers of growling and hissing in the brain co-

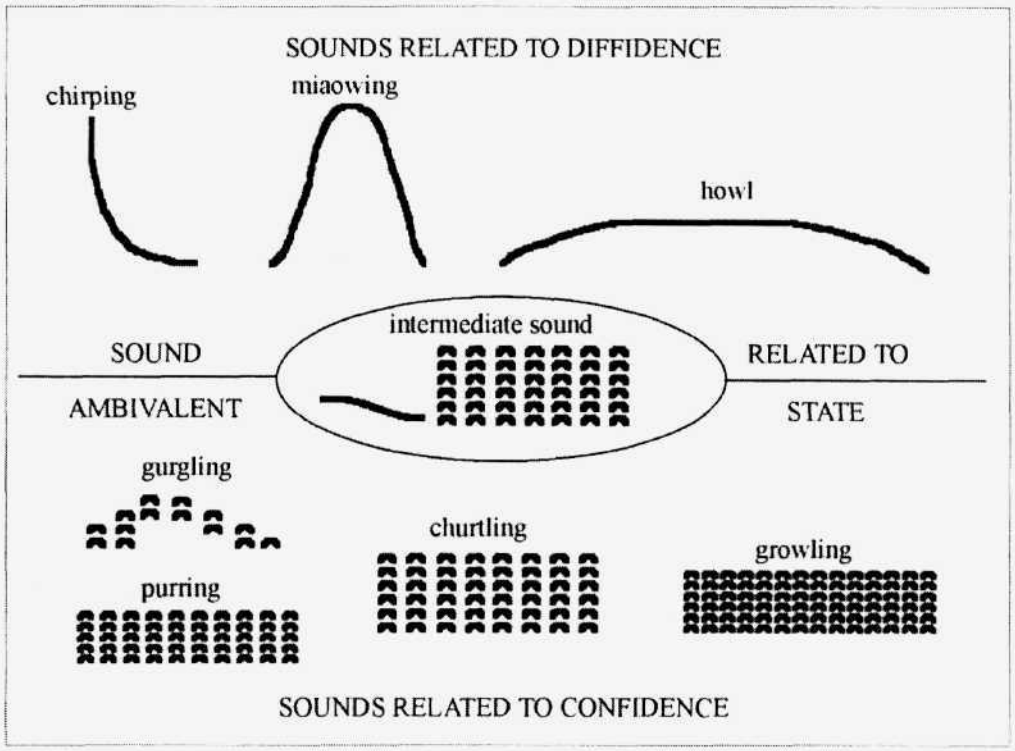

Fig. 5. Scheme of interrelationships between the sound structure and emotional state of confidence and diffidence in cheetah.

incides in cat family and squirrel monkey (Jurgens and Ploog, 1970).

Gurgling accompanies friendly meetings in familiar environment between well-acquainted cheetahs of the same or different sex after their short parting irrespective of sexual activity. Such circumstances are quite predictable for both animals, so this sound type with rhythmic pulsation is also related to emotional state of confidence.

Growling and howl is rather difficult to interpret in terms of confidence and diffidence. Functionally, cheetah howl is apparently related to asserting by a host of its claims to the territory and is produced during different kinds of intrusions or threats of intrusions (such as introduction of female into the group of females-residents, introduction of a male into the territory of females in heat, or approaching of people to a cheetah kept on a large enclosed territory in the Bukhara brooder). In such situations, the animal, on the one hand, was confident in its rights, but there occurred some uncertainty in the course of events. Having this in mind, I tentatively put the howl among the "diffident" vocalizations on the scheme below.

During growling cheetah threatens, at a short distance from the object of threat. In producing this vocalization, the probability of running away is low (see also Jurgens, 1976a), i.e. it means that predictability of animal's behavior is high both for itself and the others. In a number of cases, when records of responses of cheetah's cubs to approach of an attendant and to taking them were made, the following sequence of change in types of vocalizations was observed as the distance was decreasing: aggressive demonstration with hissing and paw hit was changed by growl and then by miaowing. That is why it could be suggested that a more confident animal produces growling, while a less confident, miaowing.

Tamers-practitioners are well informed on the relation of growling to confidence in animals. Boris Eder, a famous tamer of large cats, applied, in order to establish the dominance of the tamer over the animal, painful actions while aggressive grin and spurts of animal were accompanied by growling. The asymmetry was considered to be established when the animal ceased to growl and only grinned. Just at this moment all painful actions should be canceled, otherwise there is high probability to suppress the animal to such degree that it becomes unsuitable for further training (K.T. Sulimov, private communication). Cheetah male Oman was the victim of such an inadequate work of

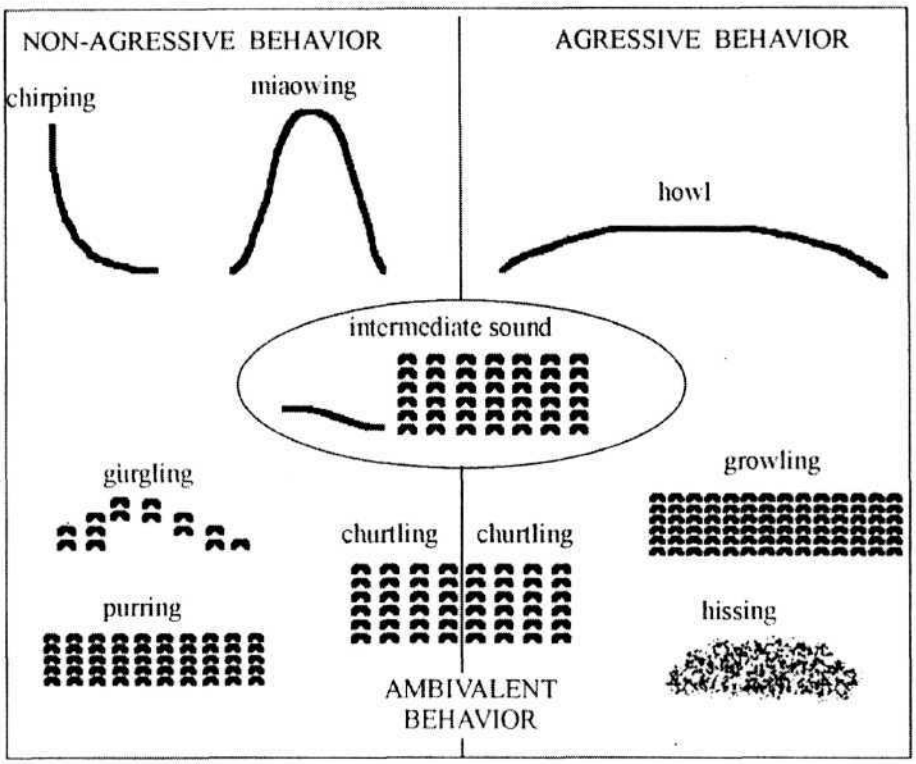

Fig. 6. The scheme of interrelationship between the sound structure and aggressive and non-aggressive behavior of cheetah.

circus tamers. Even in semi-free conditions of goitred gazelle brooder it was not able to maintain necessary level of social asymmetry in relations with a female, and as a result was not fit for reproduction. Though it had howl in its vocal repertoire, vocalizations with rhythmic pulsation were absent.

It follows from the aforesaid that sounds with rhythmic pulsation apparently express greater confidence of animal than tonal sounds.

Relation of Sound Structure to Aggressive Behavior of Cheetah

The scheme of relations between the structural types of vocalizations in cheetah and aggressive and non-aggressive behavior is shown in Fig. 6. The term "aggressive behavior" is used here in the sense of animal's readiness to attack or actively defense itself; the term "non-aggressive behavior" embraces friendly and appeasing forms of behavior.

Both growling and hissing are produced by cheetahs at impossibility to avoid close contact in infringement of individual distance and are followed by threatening poses. Therefore, both these vocalizations were referred to aggressive, and, apparently, functionally they duplicate each other. Hissing also frequently follows growling in vocal sequences that accompany angry demonstration with powerful hit of paw against ground.

Howling is also accompanied by aggressive behavioral demonstrations and was given by hosts of territories, which was usually associated with low probability of running away. For example, when a female was introduced in the group of females-residents, one of the resident females howled and the introduced one miaowed. This vocalization was also defined as aggressive.

Purring, gurgling, miaowing, and chirping were never recorded in relation with aggressive behavior.

Churtling, as a rule, is not accompanied by open aggressive demonstrations; therefore, this vocalization may be regarded as non-aggressive. Anyway, I marked churtling in relation to behavior of defensive threat in one tame female in contacts with males of its group; however, this female displayed a number of deviations in behavior, and, most likely, such a behavior was untypical. Therewith, churtling is often used by cheetah's cubs in play, when it can be interpreted as an expression of fighting spirit or indignation. Kingdom (1977) gives an example of aggressive behavior of cheetah in nature, accompanied by vocal demonstra-

lion typical of mating behavior in cheetah: "An interesting interaction between two males in Kidepo National Park was seen by Ross (pers. comm.). A solitary adult male ... was approached by a second male, which announced its arrival with yaps [miaowing, according to my terminology] interspersed with purring. ... Suddenly he started to run ... charged the first cheetah and struck him with his forepaw. He than moved off into the dusk, still yapping and purring." Perhaps, in this case the demonstration of sexual behavior was combined with aggression addressed to potential sexual competitor.

In view of the aforesaid, it is possible to state that, on the whole, there is no explicit relation between structural characters of sounds and aggressive behavior of cheetah. These data only partly confirm motivational-structural rules of Morton (1977).

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REFERENCES

1. Adamson, J.. *The Spotted Sphinx,* London: Collins and Havill, 1969.
2. Adamson, J., *Pippa's Challenge,* London: Collins and Havill, 1972.
3. Asa, C.H., Junge, R.E., Bircher, J.S., Noble, G.A.. Sarri, K.J., and Plotka, E.D., Assessing Reproductive Cycles and Pregnancy in Cheetahs *(Acinonyx jubatus)* by Vaginal Cytology, *Zoo Biol.,* 1992, vol. 11, pp. 139-151.
4. Broom, D.M. and Johnson, K.G., *Stress and Animal Welfare,* London: Chapman and Hall, 1993.
5. Dessereau. B., Olson, C, and Thomson, N.S., Human Cries as Honest Signals, *ASAB Summer Meeting "Behavioural Mechanism and Evolution*", Leiden, 1995.
6. Frazer Sissom, D.E., Rice, S.D.A., and Peters, G., How Cats Purr, *J. Zool.,* 1991, vol. 223, pp. 67-78.
7. Green, S. and Marler, P., The Analysis of Animal Communication, *Social Behaviour and Communication. Handbook of Behavioral Neurobiology,* Marler, P. and Vandenbergh, J., Eds., New York: Plenum, 1979, vol. 3, pp. 73-158.
8. Hauser, M.D., *The Evolution of Communication,* Cambridge: MIT. 1996.
9. Huang, B., Lu, H., Yu, Ch., and Liu, M., Oestrus and Copulatory Behavior of Rearing Xinjang-Mongolia Beaver, Acta *Theriol. Sin.,* 1994, vol. 14, pp. 260-264.
10. Jürgens, U., Positive and Negative Reinforcing Properlies of Electrically Elicitable Vocalizations in the Squirrel Monkey, *Brain Stimulation Reward,* Wanquier, A. and Rolls, E.T., Eds., Amsterdam, 1976a.
11. Jurgens, U., Reinforcing Concomitants of Electrically Elicited Vocalizations, *Exp. Brain Res.,* 1976b, vol. 26, pp. 203-214.
12. Jurgens, U. and Ploog, D., Cerebral Representation of Vocalization in Squirrel Monkey, *Exp. Brain Res.,* vol. 10, pp. 532-554.
13. Kingdom. J., Cheetah. *East African Mammals. An Atlas of Evolution in Africa,* vol. 3, part A (Carnivores). London: Academic, 1977.
14. Leger, D.W. and Didrichsons, I.A., An Assessment of Data Pooling and Some Alternatives, *Animal Behav.,* 1994, vol. 48, pp. 823-832.
15. Lindburg, D., Proceptive Calling by Female Lion-tailed Macaques, *Zoo Biol.,* 1990, vol. 9, pp. 437-446.
16. Lindburg, D., Millard, S., and Lasley B., Induced Estrus in the Cheetah, *AAZPA Ann. Proc,* 1985, pp. 560-562.
17. Marler, P., On the Origin of Speech from Animal Sounds, *The Role of Speech in Language,* Kavanagh, J.F. and Cutting, J., Eds., Cambridge: MIT, 1975. pp. 11-37.
18. Morton, E.S., On the Occurrence and Significance of Motivation—Structural Rules in Some Bird and Mammal Sounds, *Amer. Natur.,* 1977, vol. 111, pp. 855-869.
19. Movchan, V.N. and Opakhova, V.R., The Studies of Acoustic Signalization in the Cat Family (Felidae) in Conditions of the Zoo. *Zool. Zh.,* vol. 60, pp. 601-608.
20. Nikolskii, A.A., *Zvukovye signaly mlekopitayushchikh v evolyutsionnom protsesse* (Acoustic Signals of Mammals in the Evolutionary Process), Moscow: Nauka, 1984.
21. Peters, G., Vergleichende Untersuchung zur Lautgebund einiger Feliden (Mammalia, Felidae), *Zeit. Zool., Spixiana Suppl. 1,* 1978, pp.-283.
22. Peters, G., Das Schnurren der Katzen (Felidae), *Saugetierkundliche Mitteil,* 1981. vol. 40, pp. 30-37.
23. Peters, G., Beobachtungen zur Lautgebungsverhalten des Karakal, *Caracal caracal* (Schreber, 1776) (Mammalia, Carnivora, Felidae), *Bonner Zool. Beitrage,* 1983. vol. 34, pp. 107-127.
24. Peters, G., On the Structure of Friendly Close Range Vocalizations in Terrestrial Carnivores (Mammalia: Carnivora: Fissipedia), *Zeit. Sauget.,* 1984, vol. 49, pp. 157-182.
25. Sapolsky, R.M., Adrenocortical Function, Social Rank, and Personality Among Wild Baboons, *Biol. Psychiatry,* 1990, vol. 28, pp. 862-878.

26. Schaller, C, *The Serengeti Lion,* Chicago: Chicago Univ., 1972.
27. Smith. H.J., Neuman, J.D., Bernhards, D., and Symmes, D., Effects of Reproductive State on Vocalizations in Squirrel Monkeys (*Saimiri sciureus). Folia Primatol.,* 1983, vol. 40, pp. 233-246.
28. Volodin, I.A. and Volodina, E.V., Stress, Adaptive Behavior and Animal's Welfare in Captivity, *Nauchn. Issled. v Zool. Parkakh,* Moscow, 1997, no. 9, pp. 56-94.
29. Volodina, E.V., Vocalization as Emotional Indicator in Cheetah *Acinonyx jubatus* in Captivity, *Nauchn. Issled. v Zool. Parkakh,* Moscow, 1997, no. 9, pp. 149-162.
30. Volodina, E.V. and Volodin, I.A., Vocalizations Accompanying Reproductive Behavior in Rare Cat Family Species (Felidae), *Nauchn. Issled. v Zool. Parkakh,* Moscow, 1996, no. 6, pp. 142-184.
31. Volodina, E.V. and Volodin, I.A., Summation of Data in Analysis of Sounds Produced by Cheetah in Captivity. *Nauchn. Issled. v Zool. Parkakh,* Moscow, 1998, no. 10, pp. 262-264.
32. Weary, D. M. and Eraser, D., Calling by Domestic Piglets:Reliable Signals of Needs? *Anim. Behav.,* 1995a, vol. 50, pp. 1047-1055.
33. Weary, D. M. and Fraser, D., Signalling Need—Costly Signals and Animal Welfare Assessment, *Appl. Anim. Behav. Sci.,* 1995b, vol. 44, pp. 159-169.
34. Zar, J.H., *Biostatistical Analysis,* Englewood Cliffs, New-Jersey: Printaise Hall Inc.