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'The bone is mine': affective and referential aspects of dog growls

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A number of species are considered to use functionally referential signals such as alarm calls or food-related vocalizations. However, this particular function of communicative interaction has not previously been found in canids. We provide the first experimental indication that domestic dogs, *Canis familiaris*, rely on context-dependent signals during interspecific agonistic encounters. We recorded several sequences of growls from dogs in three different contexts: during play, guarding a bone from another dog, and reacting to a threatening stranger. We analysed the acoustic structure of the growls and additionally performed playback tests in a seminatural food-guarding situation. We found that play growls differed acoustically from the other two (agonistic) types of growls, mainly in their fundamental frequencies and formant dispersions. Results of the playback experiment showed that food-guarding growls deterred other dogs from taking away a seemingly unattended bone more effectively than growls recorded in the threatening stranger situation. We ruled out an effect of the signaller's body weight on the subjects' responses. These results provide the first evidence of context specificity of agonistic vocalizations in the dog. We discuss the possible aspects of honesty and deception through acoustic modulation of growls.

Most of the commonly encountered acoustic signals are graded and carry information about the caller's inner state; accordingly, they are considered to be nonreferential (Hauser 1996). However, studies have shown that some of the graded vocalizations are also context specific (Fischer 1998; Rendall et al. 1999) and suggested that this latter class of vocalizations should be differentiated as functionally referential signals. According to this view, these call types have the potential to carry context-specific information, if the graded calls can be sorted along an axis of one or more acoustical parameters into several distinct subtypes with relatively little overlap, and these subtypes can be wedded to different behavioural contexts (Marler 1976). Moreover, the two or more differing calls should basically represent the same inner state. For example, a study on captive chimpanzees, *Pan troglodytes*, showed that two subtypes of food call, 'rough grunts', can be distinguished based on the quality of two discovered foods (Slocombe & Zuberbühler 2005a, b). One can hypothesize that a chimpanzee's inner states are similar when he/she finds either kind of food. Thus, when the animal produces different calls for the two types of food, the quality of the vocalizations might represent the quality of the food item, and not different inner states of the chimpanzee. The same principle may work for the alarm calls in several species, with some of the best known examples having been collected on vervet monkeys, *Chlorocebus aethiops* (e.g. Seyfarth & Cheney 1984, 2003). When the animals observe an approaching predator, their inner state ('fear') may be almost the same in each case, but they mark the possible threats with distinct vocalizations. Support for functionally referential signalling comes from various mammalian and bird species investigated in the context of antipredator behaviour (primates: e.g. Macedonia 1990; Zuberbühler et al. 1997; suricate, *Suricata suricatta*: Manser et al. 2002; prairie dog, *Cynomys* spp.: Slobodchikoff et al. 1986; chicken, *Gallus gallus*: Evans et al. 1993) and searching for food (rhesus monkey, *Macaca mulatta*: Hauser & Marler 1993; chicken: Evans & Evans 1999). This suggests that functionally referential signals may be more widespread among animals then previously thought.

Several studies have already shown that besides alarm and food calls, signals used in various social contexts may also be functionally referential (Rendall et al. 1999; Crockford & Boesch 2003). Slocombe & Zuberbühler (2005a, b) reported that chimpanzees use different subtypes of screams during agonistic encounters, one of which can be linked to the aggressor and the other to the victim.

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They suggest that these calls can function referentially because out of sight third-party individuals seem to use these signals to decide whether or not to interfere.

Until now, the vocal communication of large terrestrial carnivores has not been investigated from the aspect of functional referentiality, even though it is known that species of the Canidae family use different vocalizations in a wide range of social contexts (Cohen & Fox 1976; Tembrock 1976; Lehner 1978). In regard to vocalizations, the only domesticated member of this group, the dog, differs markedly from its closest relative, the wolf, *Canis lupus*, in the more frequent occurrence of barking as well as barking in more variable contexts (Cohen & Fox 1976). Recent studies show not only that dog barks are diverse, but also that acoustic subtypes of barks can be reliably linked to social contexts (Feddersen-Petersen 2000; Yin & McCowan 2004). Moreover, Pongrácz et al. (2005, 2006) found that human listeners are able to categorize dog barks correctly by the context, and that they can judge the assumed emotional state of the dog associated with the particular situation, for example whether the dogs were aggressive, fearful or playful. As humans can reliably recognize the context of dog barks, the possibility of referentiality of these signals also emerged. However, functional referentiality has been investigated in the case of communication mostly among conspecifics, with just two studies examining the role of barks in dog–dog communication. These studies show that dogs are able to differentiate barks originating from distinct social contexts (Maros et al. 2008) as well as between individuals (Molnár et al. 2009), but more detailed research has not been conducted on this topic.

While diverse kinds of barking seem to be predominantly a dog-specific vocalization, comparative vocal analysis in canids, including dogs, has so far found few interspecific differences in the function of growls (Cohen & Fox 1976; Tembrock 1976; Yeon 2007). The growls in both wolves and dogs are low-frequency broadband signals, which are uttered in sequences of variable duration interspersed by pauses (Riede & Fitch 1999). Observations have shown that wolves and dogs growl in three different situations: (1) offensive threatening in social conflict, (2) guarding food or (3) during social play (reviewed in Yeon 2007). From the work of Taylor et al. (2008) we know that defensive growls of dogs convey information about the size of the signaller: formant dispersion was positively correlated, and the fundamental frequency negatively correlated, with the body size (Riede & Fitch 1999; Taylor et al. 2008). Whether the growls can be interpreted as functionally referential signals however, is not clear. Our study is the first with the aim of testing the contextual specificity of these vocalizations of dogs.

Hauser (1998) suggested that calls could be described as functionally referential if they fulfil three criteria. (1) Do the signals displayed in different contexts have different acoustic structures? (2) Do prerecorded signals evoke different behavioural responses in a playback experiment? (3) Does the manipulation of the putative referent alter the signal production? We are aware that Hauser's criteria are lacking at least one important factor of referential communication: the identical inner state during the different kinds of vocalization. However, despite this shortcoming, his approach at least provides a framework for testing possibly referential signal forms. Accordingly, we first conducted an acoustical analysis of growls recorded from three different situations (two agonistic and one nonagonistic): (1) the subject dog guards his food from a strange conspecific (food-guarding growl, FG), (2) a strange human approaches the subject dog threateningly (threatening growl, TS) and (3) the subject dog plays a tug-of-war game with the owner (play growl, PL).

Second, we conducted a playback experiment in a seminatural situation. The playback experiment corresponded to the food-guarding situation. The aim of the experiment was to investigate whether growls recorded in the food-guarding situation have the potential to evoke the expected behaviour (retreat) from the receiver in the physical absence of the sender.

Third, in the same experiment we expected to see differences in the receiver's behaviour when hearing the threatening growl or the play growl in the food-guarding situation. We hypothesized that the food-guarding growl, which was recorded in a similar situation (food guarding), has the most deterrent effect on dogs, while the other two types (TS and PL) have no or only a weaker effect. The difference between the effects of the situation-specific growl (FG) and the two other types of growls (TS, PL) would indicate that the dogs' behaviour is influenced mainly by the context-specific information. Alternatively, if no difference was found between the effects of the three growl types, or if the two agonistic growls (FG and TS) had an equally strong deterrent effect, then the receiver's behaviour was probably mostly influenced by the affective content of the vocalization.

METHODS

Preparation of the Audio Files

Sound recording

We recorded growls of 20 adult dogs (for details see Table 1) in three different social contexts using a Sony Digital Audio Tape Walkman (type: TCD-D100) with a directional microphone (type: ECM-MS907). All growls were recorded in a silent, 5.5 $\times$ 4 m empty room. The contexts were as follows (presented in the order of recording, see also Fig. 1a–c).

Threatening stranger (TS; Fig. 1c). The dog was held on a leash by the owner who stayed behind the dog. The owner was not allowed to touch or talk to the dog. The experimenter crouched near the dog to keep the microphone as close as possible (15–30 cm). A stranger (25-year-old male) started to approach the dog, slowly and silently, while continually staring at the dog. If the dog did not pay attention to the stranger he tried to draw the dog's attention towards him with coughs or foot taps (see details in Vas et al. 2005). This slow approach was finished when approximately 10 growls were

Table 1
Name, breed and parameters of the subjects used for the sound recordings

Name	Breed	Sex	Age (years)	Weight (kg)	Height at withers (cm)	Type of growl recorded
Angel	Mudi	Female	7.0	13	44	FG, **TS**
Barka	Border collie	Male	2.5	19	56	TS, **PL**
Boskó	Magyar vizsla	Male	10.0	27	63	FG, PL
Bodza	Pumi	Female	2	18	48	**PL**
Chili	Mudi	Female	2.5	15	46	TS
Cooper	Border collie	Male	5.0	20	54	**TS**
Fecske	Mudi	Female	7.0	17	50	**FG**, **TS**, **PL**
Gréti	Schnauzer	Female	3.0	17	43	PL
Guru	Belgian shepherd	Male	2.5	29	64	**FG**
Jamile	Mongrel	Male	4.0	35	60	**FG**, **TS**, **PL**
Jenny	Mongrel	Female	3.0	25	55	TS, **PL**
Jóság	Mudi	Female	0.8	10	46	TS
Kevin	Mongrel	Male	5.5	32	61	FG, TS, PL
Kicsifeka	Mongrel	Male	3.0	18	30	TS
Kira	Mongrel	Female	4.5	12	45	FG
Linka	Mongrel	Female	5.0	34	64	**FG**, **TS**
Lucy	Border collie	Female	4.0	18	52	FG, TS, PL
Mio	Mongrel	Male	2.5	30	60	**FG**, **TS**, **PL**
Totó	West highland terrier	Male	4.0	10	35	TS, PL
Vacak	Pumi	Male	1.5	15	46	TS

Bold type indicates the growls used for sound playback.

Figure 1. The method of recording the growls in the three different contexts. (a) Food guarding (FG), (b) playing tug of war (PL) and (c) threatening stranger approaching (TS).

recorded, or just before the stranger reached the dog. After the recording, the stranger started to talk to the dog in a friendly manner and play with it.

Tug-of-war game (PL; Fig. 1b). The owner started to play with the dog using a rag, a ball or another dog toy. The experimenter stood near the dog to keep the microphone as close as possible (15–30 cm). The play was continued until approximately 10 growls were recorded.

Food guarding (FG; Fig. 1a). The dog was kept on a leash, and he/she was given a large, meaty bone. We waited until the dog started to chew on the bone. At that point an unfamiliar dog was led out to approach the chewing dog (both dogs were on a leash and controlled by their owners). The experimenter held the microphone as close as possible (15–30 cm). The unknown dog stayed and tried to reach the bone until approximately 10 growls were recorded. We took care that the situation did not escalate into a fight and none of the dogs were harmed.

Editing the playbacks

For editing the sound recordings, we used Adobe Audition 1.5 software (Adobe Systems Inc., San Jose, CA, U.S.A.). The entire recording of each dog was copied to the computer with 16 bit resolution and 44.1 kHz sampling rate for editing. The recorded sequence of growls was split into separate growls (average length $\pm$ SE: FG: 1.53 ± 0.2 s; TS: 1.36 ± 0.18 s; PL: 0.68 ± 0.09 s) from which we selected those with the least background noise. Then we made copies of each growl and normalized them (to -6 dB) for the acoustical analysis. After this, from the intact growls, we constructed different growl sequences (16.5 ± 7.8 s long) from four or five growls originating from the same situation and from the same dog. These sequences were saved as different files, and labelled with a number code, so the assistant who operated the playback device during the experiment did not know which type of growl he actually played back.

Acoustical analysis

Acoustical measurements were done with Praat 5.0.34 acoustical analysis software (Boersma & Weenik 1996). Praat macro scripts (see Supplementary Material) were used to extract the following parameters: growl duration (L), fundamental frequency (F0: cross-correlation method, 125 ms time window, 20–2000 Hz frequency range), formant frequencies (F1–5: burg method, 25 ms time window, maximum frequency 6000 Hz, maximum five formants), formant dispersion (dF: calculated as given by Riede & Fitch 1999), standard deviation of formant dispersion (SDF: calculated as given by Riede & Fitch 1999), and harmonic to noise ratio (HNR: cross-correlation method, 10 ms timestep, minimum pitch 75 Hz). The fundamental and formant frequencies were checked visually. We calculated these parameters for each growl sample of the 20 subjects, and for further analysis we used the mean of the parameters of the growls originating from the same dog and from the same situation.

Experiments

Subjects

Subjects were 41 adult pet dogs recruited from the databases of the Clever Dog Lab (http://www.nc.univie.ac.at/index.php?id=14571) in Vienna and the Family Dog Project in Budapest (http://kutyaetologia.elte.hu/). We used subjects from different breeds and ages (minimum 1 year old). For detailed information see Table 2. Five subjects had to be excluded from the experiment because they did not show any interest in the bone.

Experimental set-up

The playbacks were conducted in silent rooms measuring 3.6 × 14 m (Vienna) and 3 × 6 m (Budapest; Fig. 2). The set-up was basically the same in the two rooms. We placed a dog cage covered with a blanket in the room and hid a speaker system in the cage. In Vienna we used a 3.1 speaker system (type: Medion sound system), whereas in Budapest a Genius type speaker pair, with Technics amplifiers (type SE-A909S and SU-C909U) was used. We placed a fresh, cooked calf bone (20–25 cm long, approximately. 0.5 kg) on the floor, at 20 cm from the cage. We used each bone only once, because of hygienic concerns and to avoid the possible effect the smell of an earlier subject's saliva may have.

During the experiment, the owner was alone with the dog in the room, while the experimenter and an assistant who operated the playbacks stayed in the adjacent room watching and recording the events in the experimental room through a webcam connected to a computer outside the room. In Vienna, to record the subjects' behaviour we used a camera (type: JVC HDD camcorder GZ MG20E) fixed on a tripod and placed in the posterior third of the room. For the live observation we used a webcam (type: Creative Live! Cam, Vista IM) fixed on the anterior wall of the room, at 1.9 m height. In Budapest, we used a quad camera system both for recording and for the live observation. The live picture was recorded on the computer with VirtualDub software (www.virtualdub.org). The same computer was also used to play back the sound sequence with Adobe Audition 1.5 software.

Table 2
Name, breed, parameters and the growls played back to the subjects in the experiment

Name	Breed	Sex	Age (years)	Weight (kg)	Height at withers (cm)	Type of growl heard
Angel	Mudi	Female	7.0	13	44	LinkaFG
Barnabás	Mongrel	Male	1.0	27	60	FecskeTS
Bastian	Border collie	Male	2.0	25	55	MioFG
Benji	Collie	Male	5.0	23	63	BarkaPL
Benji	Mongrel	Male	10.0	30	66	BodzaPL
Berci	Mongrel	Male	4.0	31	67	BodzaPL
Bertl	Australian shepherd	Male	5.0	26	60	MioPL
Boris	Mongrel	Male	6.0	30	62	CooperTS
Chilli	Mudi	Female	2.5	15	46	LinkaTS
Cooper	Border collie	Male	5.0	20	54	JamilPL
Cora	Staffordshire terrier	Female	2.5	26	53	FecskeFG
Diron	Belgian shepherd	Male	2.0	24	62	LinkaFG
Füli	Mongrel	Male	5.0	10	42	FecskeTS
Grimbusz	Belgian shepherd	Male	1.5	28	64	FecskeFG
Guiness	Border collie	Female	3.5	17	41	JamilFG
Guru	Belgian shepherd	Male	2.5	29	64	MioTS
Hanga	Mongrel	Female	1.5	20	59	FecskePL
Jamile	Mongrel	Male	4.0	35	60	MioFG
Jana	Mongrel	Female	2.0	22	62	CooperTS
Jeffi	Mongrel	Female	11.5	21	53	FecskePL
Jersey	Border collie	Female	1.5	14	47	LinkaTS
Kira	Mongrel	Female	4.5	12	45	JennyPL
Kutyácska	Mongrel	Female	12.0	12	23	GuruFG
Kyra	Mongrel	Female	12.0	24	55	JamilTS
Lidi	Mongrel	Female	10.0	23	55	AngelTS
Lili	Collie	Female	6.0	21	57	BarkaPL
Lujza	Mongrel	Female	11.0	35	45	AngelTS
Morzsi	Mongrel	Female	11.0	12	42	GuruFG
Rainbow	Border collie	Male	1.0	14	46	KevinFG
Sue	Mongrel	Female	6.0	15	50	MioTS
Summer	Border collie	Female	3.0	16	45	JamilTS
Swennie	Border collie	Female	3.5	17	41	KevinFG
Szöszke	Poodle	Female	1.0	6.5	43	JennyPL
Tódor	Mongrel	Male	5	15	37	JamilFG
Vito	Australian shepherd	Male	1	29	56	MioPL
Zsivány	Magyar vizsla	Male	4.0	28	61	JamilPL

Procedure

Each dog participated in only one experimental trial, because in a pilot study we found a very strong order effect when we conducted a within-subject design, even if there were several days between two tests with the same dog. In the experimental trial, the subjects heard a growl recorded from one of the three social contexts: TS, PL or FG. Dogs were randomly assigned to one of the three experimental groups and 12 dogs were tested in each group. Growl sequences for the playback experiments were chosen randomly from the pool of sound recordings from the 20 dogs. In sum, 11 dogs' growls were used for playbacks (see Tables 1 and 2).

Growls from the same dog in the same context were played back to no more than two subjects and even these growls consisted of different sequences. Thus, we used six dogs' growls in each group. Therefore, no two subjects heard exactly the same sequence. Moreover, we measured the sound pressure level of each sequence prior to the experiment, and corrected the volume manually, so that the playback's volume did not differ between the experimental groups (TS: mean ± SE = 72.9 ± 1.1 dB, $N = 12$; PL: 73.9 ± 1.7 dB, $N = 12$; FG: 72.9 ± 0.6 dB, $N = 12$; Kruskal–Wallis test: $\chi^2_2 = 1.414$, $P = 0.493$).

At the beginning of a trial, the owner entered the experimental room with the dog on a leash. First, the owner was instructed to lead the dog around the room to let it get acquainted with the room and to discover the bone. The dog was allowed to sniff at the bone only from a distance of about 20 cm, but was not allowed to touch it. After the dog sniffed at the bone, the owner was told to lead his/her dog 3 m away from the dog cage and stay there. After a knocking signal from the experimenter, the owner released the dog from the leash. The owner was instructed to refrain from talking, touching or looking at the dog. The experimenter and the assistant observed the dog on the monitor, which was connected to the camera. If the dog did not approach the bone within 2 min, the trial was stopped and the dog was excluded from the analysis.

If the subject approached the bone within 5 cm (in essence, just before it could reach it) the assistant started to play back the assigned growl sequence. If the dog left the bone (withdrew its nose more than 5 cm from the bone) the playback of the sequence was stopped after the actual growl was over. If the dog did not approach the bone again within the next 90 s, the trial was terminated. If the dog approached the bone again, the experimenter continued to play back the growl sequence. If the dog did not leave the bone, the whole sequence was played back a maximum of three times, and if the dog was still chewing the bone, the trial was terminated. If the dog took the bone and moved more than 20 cm from the cage, the trial was also terminated. If the dog left, but went back to the bone repeatedly, the trial was continued and the growls

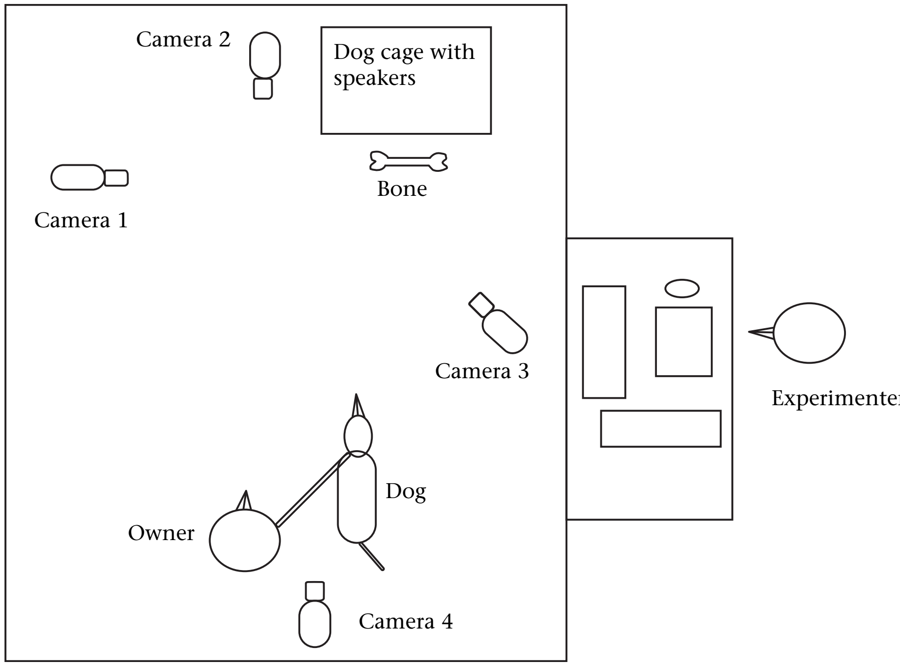

Figure 2. Sketch of the experimental set-up (not drawn to scale).

were played back each time the dog approached the bone. The trial was finished if the dog left the bone unattended for more than 90 s, or started to chew on the bone in front of the cage, or took the bone away from the cage.

Behaviour analyses

The behaviour analyses and coding were conducted with Solomon Coder beta 080510 software (developed by András Péter, at ELTE TTK Department of Ethology, Budapest). Each trial was divided into two parts for the analysis: first, the pretest phase, which started with the closing of the door after the owner had entered the room with the dog and ended when the dog was released from the leash; then, the test phase started with the release of the dog and ended when the experimenter entered the room to stop the experiment.

The frequency (making contact with the bone, leaving the bone) and the duration (licking, chewing, taking the bone away from its original location) of the dogs' bone-oriented behaviour were recorded and analysed. The following behavioural elements were used for the analysis: (1) contact with the bone: the dog touches the bone with his/her nose or mouth; (2) licking the bone: the dog repeatedly touches the bone with his/her tongue; (3) chewing the bone: the dog takes the bone into his/her mouth and chews it without taking it more than 20 cm from its original position; (4) taking the bone away: the dog grabs the bone with his/her mouth and carries it more than 20 cm from its original position; (5) leaving the bone: the dog steps away at least with his/her two front legs from the bone, and his/her head moves more than 50 cm from the bone.

During the analysis we measured the following variables: (1) latency of the second contact with the bone (the maximum latency was 90 s, see above); (2) latency of leaving the bone for the last time (latencies were measured from the first contact with the bone, the maximum was defined as 180 s according to the maximum duration of the trials: time elapsed from the first contact to the end of the trial); (3) frequency of contacts with the bone (number of contacts divided by the total time elapsed from the first contact to the end of the test trial); (4) percentage of time spent handling the bone (total duration of licking and chewing the bone divided by the total time from the first contact to the end of the test trial).

Statistical analyses

All the statistical analyses were conducted in SPSS 15 (SPSS Inc., Chicago, IL, U.S.A.).

Table 3
Comparison of the acoustical parameters of the three types of growls

Acoustical parameters	FG		TS		PL		$F_{2;18}$	*P*	FG vs TS	FG vs PL	TS vs PL
	Mean	SD	Mean	SD	Mean	SD					
Length (s)	1.53	0.21	1.36	0.18	0.68	0.09	**4.103**	**0.04**	0.782	**0.008**	**0.021**
Fundamental frequency (Hz)	178.38	51.13	149.95	49.69	506.07	114.09	**4.355**	**0.034**	0.96	**0.017**	**0.004**
Formant 1 (Hz)	631.77	61.3	561.22	33.38	886.06	51.02					
Formant 2 (Hz)	1933.6	100.21	1813.9	52.74	1838.4	53.98					
Formant 3 (Hz)	3235.7	71.06	3101.9	77.46	2971.4	57.56					
Formant 4 (Hz)	4526.2	47.74	4402.7	56.23	4258.5	81.41					
Formant 5 (Hz)	5380.1	18.03	5346.9	15.71	5304	23.75					
Formant dispersion (Hz)	1187.3	15.87	1196.8	8.4	1104.5	17.24	**9.638**	**0.002**	0.871	**0.001**	**<0.0001**
SD of formants (Hz)	333.96	25.05	314.18	25.28	292.02	33.42	0.339	0.718			
Harmonic to noise ratio	3.64	0.88	2.82	0.63	1.88	0.54	1.489	0.259			

Bold type indicates significant differences. Statistics: mixed-effects model with Tukey post hoc test.

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The acoustic parameters of the three groups were compared with linear mixed-effects models (fixed factor: type of growl; random factor: subject) and Tukey honestly significant difference, HSD, post hoc tests ($P < 0.05$).

Before the main analysis we examined the possible effect of the different test locations (Student's *t* tests: latency of second contact with the bone: $t_{34} = -0.450$, $P = 0.656$; latency of leaving the bone for the last time: $t_{34} = 0.763$, $P = 0.451$; contact frequency: $t_{34} = 0.86$, $P = 0.396$; percentage of time spent handling the bone: $t_{34} = 0.791$, $P = 0.435$). Since none of the behaviour elements were significantly different, we pooled the subjects from Vienna and Budapest for further analysis. Since none of the behavioural data met the criteria for homogeneity of variance and some groups did not show normal distributions, we used a Kruskal–Wallis test with a Bonferroni post hoc test ($P < 0.05$). Tests were all two tailed.

RESULTS

Acoustical Analysis

The comparison of the growls from 20 dogs showed marked differences in the acoustical parameters of growl duration, fundamental frequency and formant dispersion (mixed-effects models: L: $F_{2,18} = 4.103$, $P = 0.04$; F0: $F_{2,18} = 4.355$, $P = 0.034$; dF: $F_{2,18} = 9.638$, $P = 0.002$). Post hoc tests showed that FG and TS growls did not differ from each other. However, we found significant differences between PL and FG growls in all parameters as well as between PL and TS growls (for detailed parameters see Table 3).

These results show that play growls were at least half as short, as well as higher pitched, than the other two, agonistic growl types. Also, the play growls had a lower formant dispersion. This shows that the average frequency step between the formants was shorter in the play growls; in other words, the play growls' formant frequencies were relatively lower (Fig. 3).

The average height at withers and weight of the dogs whose growls were used for analysis did not differ significantly between the three groups (mixed-effects model: height: $F_{2,14} = 0.906$, $P = 0.426$; weight: $F_{2,14} = 0.906$, $P = 0.426$).

Behavioural Analysis

To investigate whether the three experimental groups differed in regard to their behaviour after hearing the growls, we analysed several parameters.

Individual responses

After hearing the growl for the first time, 11 of 12 dogs in the FG group withdrew from the bone within 15 s, whereas only two of the 12 dogs from the TS group and four of the 12 dogs in the PL group withdrew within 15 s. Seven dogs from the FG group did not approach the bone again within the next 90 s, while only one in the TS and one in the PL group stayed permanently away from

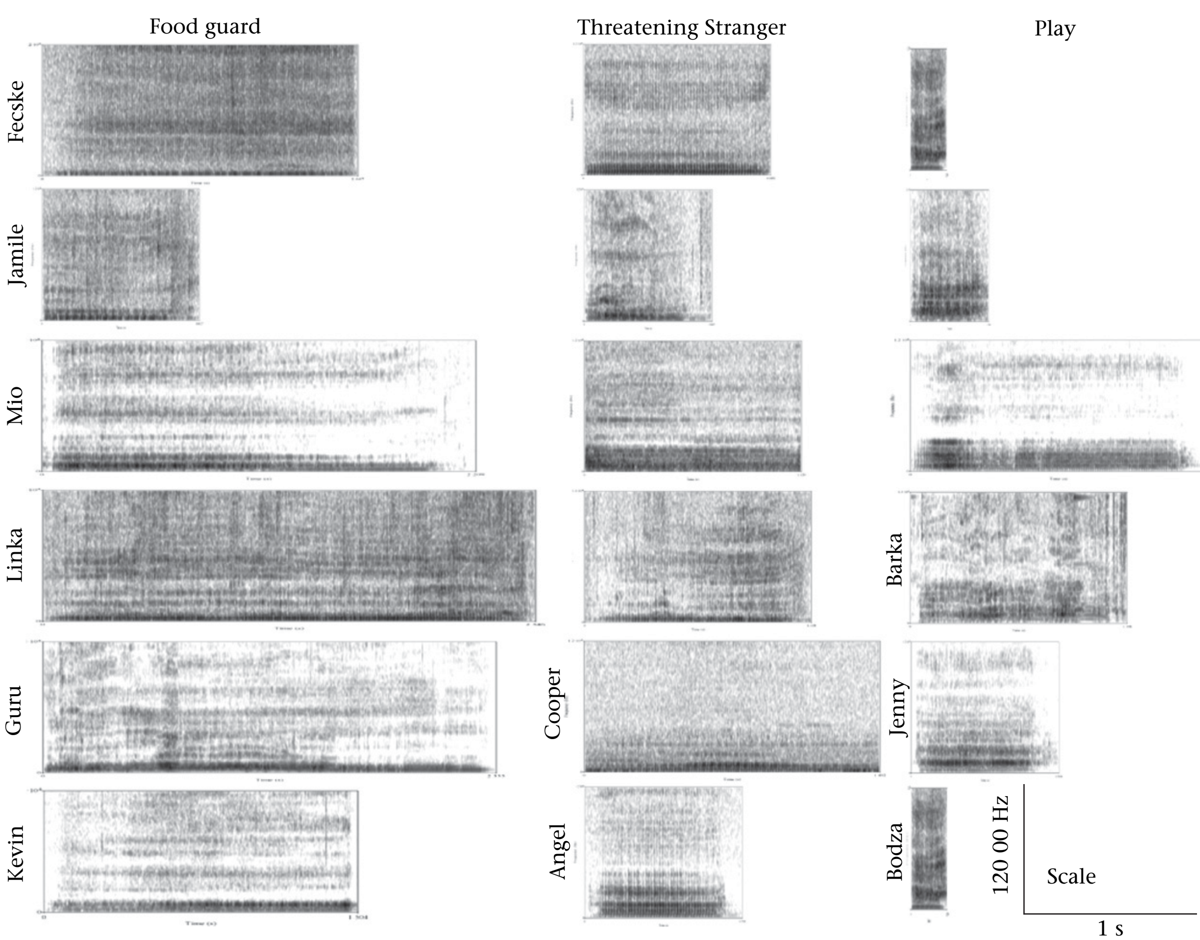

Figure 3. Spectrogram examples of growls recorded in the three different social contexts (food guarding, threatening stranger, play) from the 11 individuals used for sound playback (dogs' names given on *Y* axes).

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Table 4
Number of dogs that showed different bone-directed behaviours after one or more contacts with the bone

Number of contacts and bone-directed behaviour	Number of dogs in groups		
	Food guard	Threatening stranger	Play
One contact, leave	7	1	1
One contact, eat	0	0	0
One contact, take	0	2	0
More contacts, leave	2	1	4
More contacts, eat	1	3	4
More contacts, take	2	5	3

the bone. Table 4 shows the distribution of individual responses of the dogs in the three groups. Most of the dogs in the FG group left the bone, and only one ate it, but in the TS group most of the dogs took the bone away, or ate it, suggesting that FG growls had a stronger deterrent effect on the behaviour of dogs than TS growls. In contrast, in the PL group more dogs left the bone than in the TS group, showing that these growls evoked ambivalent responses from the dogs.

Latencies of contact with and withdrawal from the bone

We found significant differences between the groups in the latencies of approaching the bone after being scared away the first time by the playback (Kruskal–Wallis test: $\chi^2_2 = 11.34$, $P = 0.003$). The Bonferroni post hoc test revealed that dogs in the FG group approached the bone significantly later than the dogs in the other two groups (FG versus TS: $P = 0.008$; FG versus PL: $P = 0.006$). There was no significant difference between the TS and PL groups ($P = 1.0$; Table 5).

The latencies of leaving the bone for the last time also differed in the three groups (Kruskal–Wallis test: $\chi^2_2 = 10.098$, $P = 0.006$). The post hoc tests showed that latencies of leaving the bone for the last time were shortest in the FG group (FG versus TS: $P = 0.002$; FG versus PL: $P = 0.032$), and there was no difference between the latencies of the TS and PL groups ($P = 0.887$; Table 5).

Durations and frequencies

There were no significant differences between the groups either in the frequency of contact with the bone (Kruskal–Wallis test: $\chi^2_2 = 4.704$, $P = 0.095$) or in the total percentage of dogs handling the bone (Kruskal–Wallis test: $\chi^2_2 = 4.33$, $P = 0.115$; Table 5).

Effect of playback duration

We compared the relative playback durations (length of growl playbacks divided by the numbers of contacts in a given trial). We did not find a significant difference between the groups (Kruskal–Wallis test: $\chi^2_2 = 5.818$, $P = 0.06$). Therefore the variability of playback lengths could have had only a minimal effect on the dogs' behaviour.

Effect of dog size

We also tested whether the differences between the body sizes of the growling dogs caused the behavioural differences between the experimental groups. Thus we made three groups according to the weight of the growling dogs (small: 13–20 kg, $N = 5$, mean $\pm$ SE $= 17.28 \pm 0.56$ kg; medium size: 29–30 kg, $N = 3$, 29.6 ± 0.16 kg; large: 32–35 kg, $N = 3$, 34.16 ± 0.32 kg), and we compared the behaviour of these groups with Kruskal–Wallis tests. There were no significant differences (latency of the second contact: $\chi^2_2 = 5.394$, $P = 0.07$; latency of leaving the bone for the last time: $\chi^2_2 = 2.764$, $P = 0.251$; frequency of contact with the bone: $\chi^2_2 = 1.994$, $P = 0.369$; percentage of time spent handling the bone: $\chi^2_2 = 1.584$, $P = 0.453$); hence we can reject the alternative hypothesis that the bigger dogs' growls had a stronger effect than those of the smaller ones.

DISCUSSION

Our results show that (1) the growls recorded in agonistic and nonagonistic contexts have different acoustical characteristics, and (2) food-guarding growls (FG) have a significantly stronger deterrent effect on other dogs in a food competition situation than growls recorded from a threatening (TS) or play context (PL).

Acoustical Analyses

The two most important findings of our acoustical analysis were the differences between the fundamental frequencies and the formant dispersions of the play growls and the two agonistic growls. We found that play growls on average had a higher fundamental frequency and lower formant dispersion than the growls originating from the two agonistic contexts. According to Taylor et al. (2008), growls with lower fundamental frequencies usually belong to larger dogs, so the deeper pitched growls in the agonistic situations (FG and TS growls) could indicate that the individual dogs appear 'bigger' with regard to body size than the same dogs giving a play growl. However, according to Riede & Fitch (1999), in our case the formant dispersion would indicate just the opposite, namely that when a dog is producing a play growl, he/she would indicate that it is 'bigger' than during production of an agonistic growl. Fitch & Reby (2001) reported that some mammals are able to modify their vocal tract to change the acoustic pattern of their vocalizations (and see Fitch 2000). Fitch's (2000) cineradiographic observations also showed that a dog's vocal tract is highly modifiable, which can serve as anatomical background for the diverse vocalizational potential of dogs. We hypothesize that dogs may also modify their growls, and thus can use growling to communicate either aggressive intention in an agonistic situation or the lack of this during play. Additionally, the tension and position of the vocal folds can be modified affecting the fundamental frequency, and pulling back the lips with open mouth shortens the vocal tract and increases formant dispersion. By lowering their larynx, or vocalizing with lips closed on the side of the mouth and open at the frontal part, dogs can 'lengthen' their vocal tract and decrease the formant dispersion (Fitch 2000). This can explain why play growls have lower formant dispersion, because in the

Table 5
Behaviour elements observed in the playback experiment

	Food guard				Threatening stranger				Play			
	Mean	Median	Interquartiles	SD	Mean	Median	Interquartiles	SD	Mean	Median	Interquartiles	SD
Latency of second contact with bone	57	90	23.18/90	35.86	161.2	6.38	2.75/15.81	32.99	131.81	4.12	2.06/10.68	33.19
Latency of leaving bone for last time	65.08	8	0.75/155.18	77.89	20.16	180	180/180	51.63	18.68	180	52.12/180	70.88
Contact frequency	0.32	0.01	0.01/0.05	0.05	0.06	0.05	0.04/0.09	0.03	0.04	0.04	0.01/0.06	0.03
Percentage time spent handling bone	13.55	0.78	0/32.77	23.64	33.96	26.94	8.55/63.51	30.29	28	23.35	2.26/48.41	26.83

Statistics: Kruskal–Wallis test with Bonferroni post hoc tests.

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tug-of-war game the dogs held the toys in their mouths and growled with closed teeth, which also lengthens the vocal tract.

We did not find any significant difference between the HNR of the three growl types. HNR refers to the noisiness of the sounds (Riede et al. 2005) and it was one of the main variables that discriminated aggressive and nonaggressive barks for human listeners (Pongrácz et al. 2006). This phenomenon might be attributed to the fact that barking represents an unusually diverse cluster of vocalizations, which gained new functions in dogs rather recently during domestication (Feddersen-Petersen 2000), while growls are used in a narrower range of contexts.

Our sample of growls in its present form and size is not suitable for a detailed acoustical analysis (for example permuted discriminant function analysis, see Mundry & Sommer 2007), which could prove the existence of distinct growl types in the different contexts. However, in light of the results of the playback tests, it is clear that the acoustic differences between the growls were noticeable enough to elicit different (and context-specific) responses from the dogs.

Playback Experiments

Dogs avoided the bone mostly when they heard FG growls, while the PL and TS growls were less effective deterrents. If the dogs had reacted differently only in the case of the PL growls then the different inner states of the signaller (play versus defensive aggression) could explain the differences in their behaviour. However, the results of the playback experiment suggest that the dogs clearly differentiated the FG and TS growls. If we assume that the growling dogs were in similar inner states in the two agonistic (FG and TS) situations, then the effect of FG growls could be interpreted in the functionally referential framework. These results are also in agreement with Hauser's (1998) arguments (see above), because the contextually most relevant vocalization had the largest effect on the behaviour of dogs. PL and TS growls remained ineffective as deterrents, because the subjects probably did not process them as contextually appropriate.

An alternative hypothesis regarding functionally referential communication is the possible existence of different inner states behind the different signals (Owren & Rendall 1997). In our case it would mean that dogs have markedly different inner states in the FG and TS contexts, and these are reflected directly in the acoustic structure of the different vocalizations. Our acoustic analysis somewhat contradicts this hypothesis, because we found only subtle or no differences between the TS and FG growls when analysing the wide range of the well-established acoustic parameters (Riede & Fitch 1999; Pongrácz et al. 2006; Taylor et al. 2008). One would expect more distinct signals if the context were less important than the signals' acoustic structure. However, we cannot exclude the possibility that dogs differentiate TS and FG growls by attending to other more subtle acoustical features, which we did not measure in this study. One possible difference could be that the dogs always growled at the threatening human with a closed mouth, while during defence of their food they often showed their teeth and pulled back their lips.

We should note that these conceptual problems could apply to many earlier studies on functionally referential calls. For example, compare the present results with the study by Slocombe & Zuberbühler (2005b) which presents the most similar behavioural situation to the present one. In both cases signallers (dogs and chimpanzees) produced vocalizations in social contexts (dogs: defensive aggression; chimpanzees: aggression/defence in an agonistic scenario). If we examine carefully the situations in both cases, we could argue that it is more likely that dogs in their two agonistic contexts should have more similar inner states than the chimpanzees in which it is more likely that the 'aggressor' chimpanzee is in a different inner state to the 'victim' (see Introduction). Furthermore, social referents, such as 'victim' or 'aggressor', or in this study the different subtypes of dogs that show defensive aggression, are may be less clear-cut examples of functionally referential communication (compared to 'predator class' for example), as it is difficult to know how 'external' the referent really is to the individuals involved.

In summary, there were strong differences between the reactions to the two agonistic growl types, when only one of them was appropriate in the given context. Based on the approach of Hauser (1998) and Seyfarth & Cheney (2007), it would be possible to assume that dog growls are functionally referential. However, we should also take into consideration simpler explanations. For instance, studies like that of Fischer (1998) showed that slight acoustic differences between particular calls are enough for Barbary macaques, *Macaca sylvanus*, to associate them with different meanings. It is highly possible that many of the subject dogs learned earlier how a food-guarding or a threatened dog growls, and the possible consequences of these growls; hence they showed appropriate behaviour, independently from the intentionality of the signaller. Unfortunately, subtle differences between inner states of dogs during various agonistic situations are difficult to measure, as are communicative intentions, so whether growls are referential or not will remain a somewhat philosophical question. In the future more emphasis should be laid on more detailed acoustical analysis of the differences between similar, but relevant signals, such as FG and TS growls.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2010.01.005.

References

Boersma, P. & Weenik, D. 1996. Praat: a system for doing phonetics by computer. www.praat.org.

Cohen, J. A. & Fox, M. W. 1976. Vocalization in wild canids and possible effects of domestication. *Behavioural Processes*, **1**, 77–92.

Crockford, C. & Boesch, C. 2003. Context-specific calls in wild chimpanzees, *Pan troglodytes verus*: analysis of barks. *Animal Behaviour*, **66**, 115–125.

Evans, C. S. & Evans, L. 1999. Chicken food calls are functionally referential. *Animal Behaviour*, **58**, 307–319.

Evans, C. S., Evans, L. & Marler, P. 1993. On the meaning of alarm calls: functional reference in an avian vocal system. *Animal Behaviour*, **46**, 23–28.

Feddersen-Petersen, D. U. 2000. Vocalization of European wolves (*Canis lupus lupus l.*) and various dog breeds (*Canis lupus f. familiaris*). *Archiv für Tierzucht, Dummerstorf*, **43**, 387–397.

Fischer, J. 1998. Barbary macaques categorize shrill barks into two call types. *Animal Behaviour*, **55**, 799–807.

Fitch, W. T. 2000. The phonetic potential of nonhuman vocal tracts: comparative cineradiographic observations of vocalizing animals. *Phonetica*, **57**, 205–218.

Fitch, W. T. & Reby, D. 2001. The descended larynx is not uniquely human. *Proceedings of the Royal Society B*, **268**, 1669–1675.

Hauser, M. D. 1996. *The Evolution of Communication*. Cambridge, Massachusetts: MIT Press.

Hauser, M. D. 1998. Functional referents and acoustic similarity: field playback experiments with rhesus monkeys. *Animal Behaviour*, **55**, 1647–1658.

Hauser, M. D. & Marler, P. 1993. Food associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors influencing call production. *Behavioral Ecology*, **4**, 194–205.

Lehner, P. N. 1978. Coyote vocalizations: a lexicon and comparisons with other canids. *Animal Behaviour*, **26**, 712–722.

Macedonia, J. M. 1990. What is communicated in the antipredator calls of lemurs? Evidence from playback experiments with ringtailed and ruffed lemurs. *Ethology*, **86**, 177–190.

Manser, M. B., Seyfarth, R. M. & Cheney, D. L. 2002. Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*, **6**, 55–57.

Marler, P. 1976. Social organisation, communication and graded signals: the chimpanzee and the gorilla. In: *Growing Points in Ethology* (Ed. by P. P. Bateson & R. A. Hinde), pp. 239–280. Cambridge: Cambridge University Press.

Maros, K., Pongrácz, P., Bárdos, G., Molnár, C., Faragó, T. & Miklósi, Á 2008. Dogs can discriminate barks from different situations. *Applied Animal Behaviour Science*, **114**, 159–167.

Molnár, C., Pongrácz, P., Faragó, T., Dóka, A. & Miklósi, Á 2009. Dogs discriminate between barks: the effect of context and identity of the caller. *Behavioural Processes*, **82**, 198–201.

Mundry, R. & Sommer, C. 2007. Discriminant function analysis with non-independent data: consequences and an alternative. *Animal Behaviour*, **74**, 965–976.

Owren, M. J. & Rendall, D. 1997. An affect-conditioning model of nonhuman primate vocal signaling. In: *Perspectives in Ethology: Vol. 12. Communication* (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 299–346. New York: Plenum.

Pongrácz, P., Molnár, C., Miklósi, Á & Csányi, V. 2005. Human listeners are able to classify dog (*Canis familiaris*) barks recorded in different situations. *Journal of Comparative Psychology*, **119**, 136–144.

Pongrácz, P., Molnár, C. & Miklósi, Á 2006. Acoustic parameters of dog barks carry emotional information for humans. *Applied Animal Behaviour Science*, **100**, 228–240.

Rendall, D., Seyfarth, R. M., Cheney, D. L. & Owren, M. J. 1999. The meaning and function of grunt variants in baboons. *Animal Behaviour*, **57**, 583–592.

Riede, T. & Fitch, W. T. 1999. Vocal tract length and acoustics of vocalization in the domestic dog (*Canis familiaris*). *Journal of Experimental Biology*, **202**, 2859–2867.

Riede, T., Mitchell, B. R., Tokuda, I. & Owren, M. J. 2005. Characterizing noise in nonhuman vocalizations: acoustic analysis and human perception of barks by coyotes and dogs. *Journal of the Acoustical Society of America*, **118**, 514–522.

Seyfarth, R. M. & Cheney, D. L. 1984. The acoustic features of vervet monkey grunts. *Journal of the Acoustical Society of America*, **75**, 1623–1628.

Seyfarth, R. M. & Cheney, D. L. 2003. Signalers and receivers in animal communication. *Annual Review of Psychology*, **54**, 145–173.

Seyfarth, R. M. & Cheney, D. L. 2007. *Baboon Metaphysics: the Evolution of a Social Mind*. Chicago: University of Chicago Press.

Slobodchikoff, C. N., Fischer, C. & Shapiro, J. 1986. Predator-specific alarm calls of prairie dogs. *American Zoologist*, **26**, 557.

Slocombe, K. E. & Zuberbühler, K. 2005a. Functionally referential communication in a chimpanzee. *Current Biology*, **15**, 1779–1784.

Slocombe, K. E. & Zuberbühler, K. 2005b. Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *Journal of Comparative Psychology*, **119**, 67–77.

Taylor, A. M., Reby, D. & McComb, K. 2008. Human listeners attend to size information in domestic dog growls. *Journal of the Acoustical Society of America*, **123**, 2903–2909.

Tembrock, G. 1976. Canid vocalizations. *Behavioural Processes*, **1**, 57–75.

Vas, J., Topál, J., Gácsi, M., Miklósi, Á & Csányi, V. 2005. A friend or an enemy? Dogs' reaction to an unfamiliar person showing behavioural cues of threat and friendliness at different times. *Applied Animal Behaviour Science*, **94**, 99–115.

Yeon, S. C. 2007. The vocal communication of canines. *Journal of Veterinary Behavior*, **2**, 141–144.

Yin, S. & McCowan, B. 2004. Barking in domestic dogs: context specificity and individual identification. *Animal Behaviour*, **68**, 343–355.

Zuberbühler, K., Noë, R. & Seyfarth, R. M. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. *Animal Behaviour*, **53**, 589–604.

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