

On the structure of friendly close range vocalizations in terrestrial carnivores (Mammalia: Carnivora: Fissipedia)

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Abstract

Sound spectrographic analyses were made of friendly close range vocalizations of species of all families of terrestrial carnivores (Canidae, Felidae, Hyaenidae, Mustelidae, Procyonidae, Ursidae, Viverridae), and their structural characteristics are described. A review of these vocal forms mentioned in the literature is given. Their function generally is appeasement, reassurance, greeting, coaxing and probably maintaining contact at close range; their functions largely correspond in the various families. They are heard most frequently in ♀♀ with young, in ♂♂ and/or ♀♀ during courtship and mating, and in adults and juveniles during friendly close contact. With few exceptions these vocal forms have a fairly uniform structural pattern of which two variations occur. It is highly probable that the majority of these sounds evolved independently in the various families and in some cases even within the same family. Friendly close range calls with similar structural characteristics are known in other mammalian orders. Possible ultimate causes for their convergent phylogenetic development are discussed.

Introduction

Several investigations into the vocal repertoire of mammals have shown that vocal forms with a corresponding function in different species, genera and occasionally even higher taxa sometimes reveal a fairly uniform basic structure (e.g. Artiodactyla, Perissodactyla: KILEY 1972; Canidae: TEMBROCK 1976a, b; Caviomorpha: EISENBERG 1974; Cercopithecidae: STRUHSACKER 1970, GAUTIER and GAUTIER 1977; Felidae: PETERS 1978a; Marsupialia: EISENBERG et al. 1975; Mustelidae: GOSSOW 1970; Sciuridae: EMMONS 1978; Viverridae: WEMMER 1977). The phylogenetic origin of these structural similarities is often difficult to establish (cf. GOSSOW 1970; EISENBERG 1974; EISENBERG et al. 1975).

General developmental tendencies of the structure of vocal forms resulting from their function have been discussed by various authors (e.g. MARLER 1955, 1957, 1967; TEMBROCK 1959, 1971, 1977; COLLIAS 1960; MORTON 1977, 1982; GOULD 1983). Strong selective influences are exerted by physical factors connected with the need for optimum broadcast of the vocal signal and/or location of the vocalizing individual in the specific conditions of the species' natural habitat or to avoid long-range broadcast and/or location of the sender. The structure of some species' vocalizations or of animal vocalization in general has been discussed under these aspects (e.g. MARLER 1959; CHAPPUIS 1971; MORTON 1975; MARTEN and MARLER 1977; MARTEN et al. 1977; WASER 1977; WASER and WASER 1977; WILEY and RICHARDS 1978; GISH and MORTON 1981; BROWN 1982; WASER 1982; WILEY and RICHARDS 1982).

In an investigation of a friendly close range vocalization of the Polar bear (*Ursus maritimus*) they call chuffing, WEMMER et al. (1976) express the opinion that structurally and functionally similar sounds are produced by other carnivores and probably by further orders of placentals and by the marsupials. The authors mention calls of other bear species and some mustelids and viverrids without giving further details.

The present publication thoroughly examines the occurrence of functionally and structurally equivalent friendly close range vocalizations in the various families of the terrestrial Carnivora, lines out their common basic structural pattern and discusses what factors in evolution could have led to the development of structural similarities in these vocalizations.

Materials and methods

The vocal forms described in this paper were selected according to two criteria: 1. function and 2. structure. As regards function, all the vocalizations listed may be designated as sounds for appeasement, reassurance, greeting, coaxing and/or maintaining contact at close range. They are heard most frequently in ♀♀ with young, from ♂♂ and/or ♀♀ during courtship and mating and in juveniles and adults during friendly close contact. According to the structural pattern represented by ursid chuffing only those friendly close range calls were considered that are sounds of low to at most medium intensity, exhibit some kind of rhythmical amplitude fluctuation and are relatively short; vocal forms deviating from this structural scheme are not listed. This is also true of a vocalization like purring in the Felidae and Viverridae (PETERS 1981) and similar, more or less continuous sounds like the nursing sound of the Ursidae.

This investigation is based on the sonographic analyses of relevant vocalizations from all families of the terrestrial Carnivora and on a survey of such vocal forms mentioned in the literature. The latter, however, have been taken into account only if sonagrams or oscillograms are figured in the respective publication(s), or if the general description of the behavioural context and of the vocalization's structure enable it to be attributed fairly safely to the group of vocal forms dealt with here. The choice of species included in this paper reflects the stage so far reached in collecting tape recordings and observations and the extent of relevant information published, and should not be taken as an indication whether or not such vocalizations occur in the vocal repertoire of species not mentioned here. The taxonomy of the species listed basically follows EWER (1973).

Details on friendly close range calls drawn from the literature are summarized in a table for each family, giving the source(s) of the original information. Publications cited that present structural details of vocalizations are marked with an asterisk (*). Within each table those species of a family that have the same type of vocalization are listed together. The terms used for them and their structural characterization are those given by the authors cited. Identical terms for vocal forms in the same or in different species used by the same or by different authors do not necessarily imply that these calls are identical or structurally similar. Conversely different names do not purport automatically that the relevant vocal forms differ in structure or are not phylogenetically related. Several of the publications listed in the tables make no express statement as to the occurrence and uniform structure of these vocal forms in adults of both sexes and in juveniles. Thus, where in a table the sound is listed for several species combined and is detailed to be present in juveniles and adult ♂♂ and ♀♀, this is not generally fully established in each species, but it seems fairly safe to assume that all species listed together agree in this respect. Where a publication cited in the tables provides equivocal information on a criterion listed this is marked with a question-mark (?). Gaps in the tables represent lack of relevant data in the literature.

Statements that vocalizations are functionally equivalent are made irrespective of their structural similarities or differences and their phylogenetic origin. The problem of homology in mammalian vocalization has been discussed by GOSSOW (1970), EISENBERG (1974), EISENBERG et al. (1975) and PETERS (1978a). A hypothesis that vocal forms are homologous is only put forward under the presuppositions detailed in the last publication cited.

The tape recordings were done with a portable tape recorder UHER 4200 Report Stereo at 19 cm per s tape speed and a microphone SENNHEISER MD 421-2, a few with a SENNHEISER MKH 805. Some of the recordings provided by colleagues were made with different equipment and at another tape speed. Sonographic analyses were done with a VOICEPRINT Model 4691A in shaping flat, normal and filter WB (300 Hz). Temporal and frequency parameters were taken from the sonagrams with the help of a calibrated overlay grid. Repetition rates were calculated according to method B given by SCOVILLE and GOTTLIEB (1978). For nearly all species listed the sample size is small. Therefore no standard mathematical treatment of data (means, SD) is presented. Due to multiple steps of reproduction the sonagrams figured show fewer details and less temporal and frequency resolution than the originals.

Results

In the following, for each family of the terrestrial Carnivora (in alphabetical order) a tabulated survey of the relevant vocal forms mentioned in the literature will be given first, in each case followed by a description of those friendly close range sounds for which

Table 1
Friendly close range vocalizations in the Canidae

Species	Vocalization	Observed in ad. ♂ ad. ♀ juv.	Behavioural context(s)	Function(s)	Call structure	References	Comments
<i>Canis lupus</i> , <i>C. lupus</i> f. familiaris, <i>C. mesomelas</i> , <i>C. aureus</i> , <i>C. latrans</i> , <i>Vulpes vulpes</i> , <i>V. chama</i> , <i>V. corsac</i> , <i>V. macrotis</i> , <i>Alopex lagopus</i> , <i>Fennecus zerda</i> , <i>Urocyon cinereoargenteus</i> , <i>Nyctereutes procyonoides</i> , <i>Lycan pictus</i> , <i>Otocyon megalotis</i>	'Muffen' = whimpering growl	+	♀ ♀ with young, friendly close contact, court- ship, mating, ♂ ♂ providing young with food	friendly close con- tact call, greeting, coaxing, ap- peasement, reassurance	rhythmical se- quence of short, noisy, low-in- tensity sounds	SEITZ (1950), TEMBROCK and OHM- KETTNER (1956), HEYDECKE (1958), TEMBROCK (1960)*, TEMBROCK (1963)*, TEMBROCK (1968)*, TEMBROCK (1970), TEMBROCK (1976a, b)*	data published in TEMBROCK (1976b) in part drawn from the literature (see this publication for further refer- ences)

sonographic analyses are available. These data will be compared with the published information on the respective vocal forms in each family and a general statement on their structure and articulation will be made.

Canidae

One example of a call of the red fox (*Vulpes vulpes*) termed "Muffen" (SEITZ 1950) was available for sonographic analysis (Fig. 1a). It is a short rhythmical sequence of brief, muffled, low-intensity sounds. This vocalization in the Canidae has been dealt with in detail by TEMBROCK (1976a, b); according to his data the structure of this vocal form is fairly uniform in all species of the family that perform it. TEMBROCK makes no statement as to calls functionally equivalent to "Muffen" in those canid species not listed to have it in their repertoire. Surprisingly, "Muffen" receives no mention in either of the surveys of canid vocal communication by COHEN and FOX (1976) and FOX and COHEN (1977). In a detailed study (BRADY 1981) of vocalization in the three neotropical canids *Speothos venaticus*, *Chrysocyon brachyurus* and *Cerdocyon thous*, only in the latter there is a vocalization ("cough") mentioned which may be a structural and functional equivalent to "Muffen". In a comprehensive study of the behaviour of *Speothos* DRÜWA (1976) lists a call termed "greeting scream" which seems to be functionally corresponding to "Muffen" but differs from it in structure. It is a short, rather tonal sound, repeated rapidly.

From these data it seems likely that in the Canidae there are different types of friendly close range sounds, "Muffen" being relatively widely distributed among the species of this family. Despite of structural differences the scheme of a rapid, fairly rhythmical sequence of short single sounds is a common characteristic of these vocal forms. It is not possible to make a general statement on the articulation of these calls.

Felidae

The material collected on friendly close range vocalizations in this family is so am-

Table 2
Friendly close range vocalizations in the Felidae

Species	Vocalization	Observed in ad. ♂ ad. ♀ juv.	Behavioural context(s)	Function(s)	Call structure	References	Comments	
<i>Felis s. silvestris</i> , <i>F. silvestris ornata</i> , <i>F. silvestris</i> f. <i>catus</i> , <i>F. chaus</i> , <i>F. margarita scheffeli</i> , <i>F. nigripes</i> , <i>Prionailurus bengalensis</i> , <i>P. rubiginosus</i> , <i>P. planiceps</i> , <i>Profelis aurata</i> , <i>P. temmincki</i> , <i>Puma concolor</i> , <i>Caracal caracal</i> , <i>Leopardus pardalis</i> , <i>L. tigrinus</i> , <i>L. geoffroyi</i> , <i>Lynchaillus pajeros</i> , <i>Herpailurus yagouaroundi</i> , <i>Leptailurus serval</i> , <i>Pardofelis marmorata</i> , <i>Lynx lynx</i> , <i>L. rufus</i> , <i>Acinonyx jubatus</i> (hybrids of <i>Prionailurus bengalensis</i> and <i>Felis silvestris</i> f. <i>catus</i>)	'Gurren' = gurgle	+	+	+	friendly close contact call, coaxing, appeasement, reassurance	short, noisy, low-intensity sound with rhythmic amplitude modulation	RESCHKE (1960)*, TEMBROCK (1970), PETERS (1978a)*, PETERS (1983a)*, PETERS & TONKIN (unpubl. observations)	a forthcoming publication by PETERS and TONKIN will present structural details of the three relevant felid vocal forms in most species listed here
<i>Neofelis nebulosa</i> , <i>Uncia uncia</i> , <i>Panthera tigris</i> , <i>P. onca</i>	prusten	+	+	+	friendly close contact call, coaxing, appeasement, reassurance	short, noisy, low-intensity sound with rhythmic amplitude modulation	HESSE (1926), POCKOCK (1939), LEYHAUSEN (1950), RESCHKE (1960*, 1966), HEMMER (1966, 1968), SCHALLER (1967), SCHROETER (1971), PETERS (1978a, 1983b)*, MAZAK (1979)	
<i>Panthera pardus</i> , <i>P. leo</i>	puffing	+	+	+	friendly close contact call, coaxing, reassurance, appeasement	rhythmical sequence of short, noisy, low-intensity sounds	RESCHKE (1960)*, HEMMER (1966, 1968), SCHALLER (1972), PETERS (1978a, 1980)*	

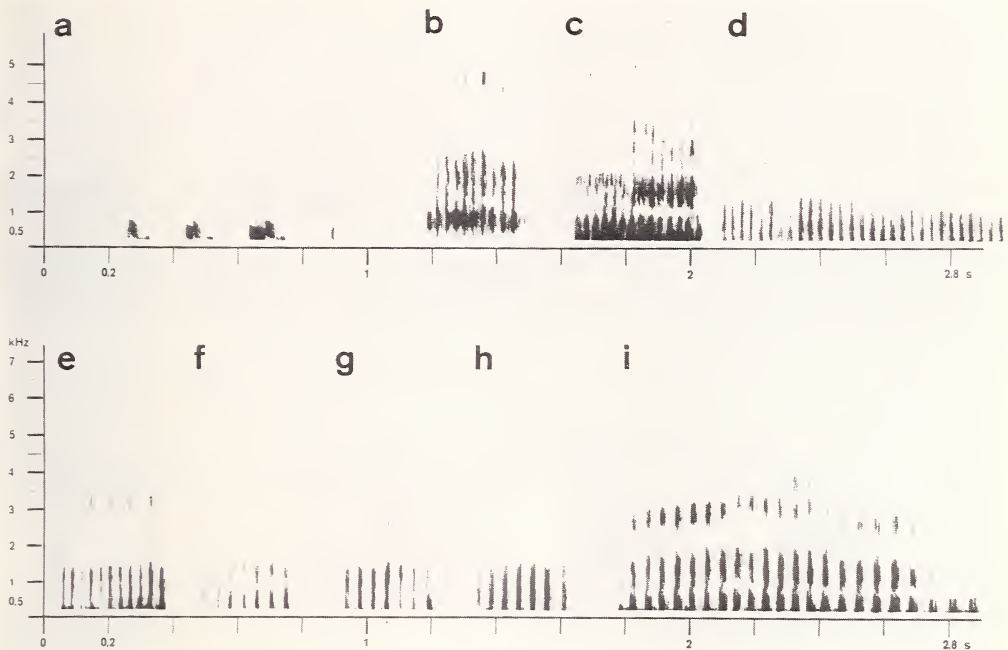


Fig. 1. Canidae: a = Red fox (*Vulpes vulpes*), 'Muffen', ad ♂ (recording G. TEMBROCK). Felidae: b = jaguarundi (*Herpailurus yagouaroundi*), gurgle, ad. ♂. c. serval (*Leptailurus serval*), gurgle, ad. ♂. d-h = African golden cat (*Profelis aurata*), gurgles of 3 adult ♀♀ showing variable duration of single pulses and intervals between them. i = cheetah (*Acinonyx jubatus*), gurgle, ad. (recording G. SCHALLER)

ple (27 of the 37 or so extant species of the Felidae are documented on tape with their respective vocal form) that these data will be presented in detail in a separate publication. Here only a general survey is given.

As listed in Table 2 there are three different friendly close range vocalizations in the Felidae, each species having only one of these. Only 2 felids have puffing as their friendly close range sound, 4 species prusten and all the rest – very probably also including those species for which no data are available yet – have gurgling. Gurgles (Figs. 1b–i, 2a, b) are soft, short and noisy sounds of about 0.5 s duration with rhythmical amplitude modulation and low in volume. Pulse repetition rate varies between about 10–45 per s in the different species, the call changing its sound character with the varying structure. Prusten (Fig. 2c–g) is also a relatively short (<1 s) and soft call. It is of low intensity, atonal and has a rhythmical amplitude modulation. It is composed of two structurally different pulse sequences, one in the basal and the other one in the upper frequency range (see Fig. 2c). Puffing (Fig. 2h) is a very short (<0.1 s), muffled, noisy sound. Very occasionally it is uttered singly, but usually in a rapid, almost rhythmical sequence of as few as 2–4 sounds, occasionally more. The intervals between the single sounds in a puffing sequence last about 0.2 s.

The three friendly close range vocalizations of the Felidae represent the same structural pattern: a short, rhythmical sequence of short, noisy sound pulses. Basically this characterization applies to gurgling and prusten as coherent vocal forms with rhythmical amplitude modulation as well as to puffing as a sequence of separate single sounds. Gurgling very probably is articulated laryngeally, prusten is likely to contain a laryngeal

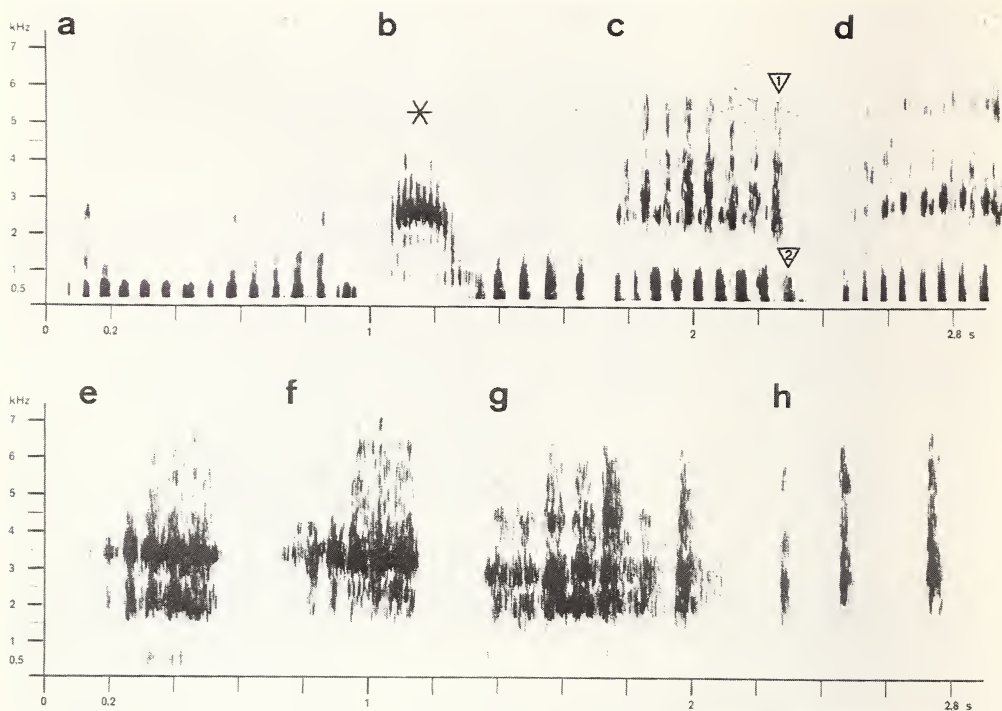


Fig. 2. Felidae: a = cheetah (*Acinonyx jubatus*), gurgle, ad. ♂. b = little spotted cat (*Leopardus tigrinus*), gurgle, juv. ♂. The preceding mew with FM and AM to which the gurgle is coupled is marked with an asterisk (*). c and d = clouded leopard (*Neofelis nebulosa*), prusten, juv. ♀. A pulse of the upper frequency range type is marked '1', a basal range one is marked '2'. e and f = tiger (*Panthera tigris*), prusten, ad. ♀. The basal frequency range pulse sequence is nearly fully reduced, the upper pulses are merged. g = jaguar (*Panthera onca*), prusten, ad. ♀, similar in structure to prusten in the tiger. This sound has a detached last pulse. h = leopard (*Panthera pardus*), puffing, ad. ♀

and a nasal contribution to sound production (PETERS 1983b), and puffing is mainly articulated through the nose, but a minor laryngeal component may also be present.

Hyaenidae

No detailed investigation of the vocal behaviour of any of the 4 species of Hyaenidae (including *Proteles*) using modern analysis techniques has so far been published. Therefore no tabulated survey of friendly close range sounds in this family is given.

I had one recording of vocal communication between a ♀ striped hyaena (*Hyaena hyaena*) and her cub for analysis. In it the ♀ utters a short, grunt-like, low-intensity sound towards the cub calling in distress. The ♀'s vocalization functions as an appeasement/reassurance and coaxing call (Fig. 3a) (RIEGER pers. comm.). A friendly close range sound very similar to this one was heard in a pair of *Crocuta crocuta* at the National Zoo, Washington, D.C. From the description of the vocal repertoire of the spotted hyaena published by KRUUK (1972, pp. 245, 311, 312) it is not clear which vocalization I heard in these animals. Data on the vocal behaviour of the brown hyaena (*Hyaena brunnea*) presented by MILLS (1981) are not detailed enough to make a statement on friendly close range sounds in this species. Because of the scarcity and ambiguity of the data no general

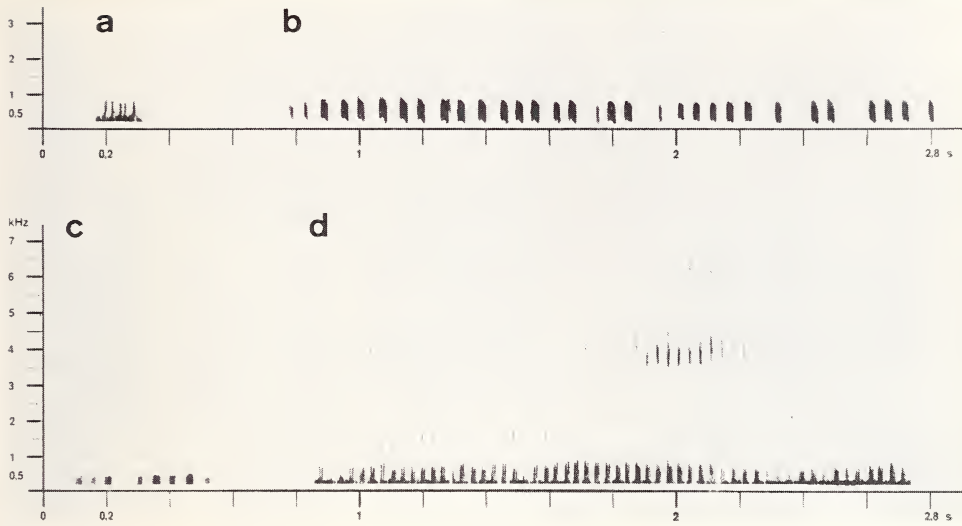


Fig. 3. Hyaenidae: a = striped hyaena (*Hyaena hyaena*), groan, ad. ♀ (recording I. RIEGER). Mustelidae, Mustelinae: b = stoat (*Mustela erminea*), 'Muckern', ad. ♀ (recording A. BENK). Mustelidae, Lutrinae: c = giant otter (*Pteronura brasiliensis*), purr, ad. (recording H. LÜTGENS). Procyonidae: d = raccoon (*Procyon lotor*), chitter 1, ad.

statement on structure and articulation of the relevant vocals forms in the Hyaenidae can be made.

Mustelidae

The subfamilies of the Mustelidae will be dealt with separately because the published information on their friendly close range vocalizations indicates that these differ to a certain extent.

Mustelinae

One recording of trilling ("Muckern") of a free-ranging ♀ stoat (*Mustela erminea*) with young was available for analysis (Fig. 3b). Throughout the entire length of the recording (approx. 15 s) the animal utters short, tonal sounds in a rapid, almost rhythmical sequence. The duration of the single calls averages 0.02 s, that of the intervals between them 0.04 s. In fully rhythmical sections of the sequence 17–19 single sounds are formed within 1 s. These structural details agree well with the data published by Gossow (1970). Structurally similar vocalizations have been described in *Mustela nivalis*, *M. putorius* and *Martes foina* (GOSSOW 1970), *Mustela frenata* (SVENDSEN 1976) and *Poecilogale albinucha* and *Ictonyx striatus* (CHANNING and ROWE-ROWE 1977), all functioning as friendly close range sounds. The functionally equivalent vocal form of juvenile and adult *Eira barbara* has been described as clicking (POGLAYEN-NEUWALL 1975; POGLAYEN-NEUWALL and POGLAYEN-NEUWALL 1976; POGLAYEN-NEUWALL 1978). A sonagram of clicking figured in the 1976 publication shows a rhythmical series of very short noisy clicks, differing from the structure of trilling in the other Mustelinae mentioned.

Thus, within the subfamily Mustelinae friendly close contact calls are rather uniform in structure in the genera *Mustela*, *Martes*, *Poecilogale* and *Ictonyx*, being rapid, largely rhythmical series of brief, tonal sounds, very probably articulated in the larynx. Clicking, the functionally equivalent call of *Eira barbara*, is atonal. However, the basic structural pattern of a rapid rhythmical series of short single sounds is common to all Mustelinae studied so far.

Table 3
Friendly close range vocalizations in the Mustelidae

Species	Vocalization	Observed in ad. ♂ ad. ♀ juv.	Behavioural context(s)	Function(s)	Call structure	References	Comments
Mustelinae							
<i>Mustela erminea</i> , <i>M. nivalis</i> , <i>M.</i> <i>putorius</i> , <i>M. fren-</i> <i>nata</i> , <i>Martes</i> <i>martes</i> , <i>M. foina</i> , <i>Ichonyx striatus</i> , <i>Pocilogale albi-</i> <i>nucha</i>	'Ockern', 'Kollern', 'Muckern', trill, greet- ing call	+	+	friendly close contact call, greeting, coaxing, appeasement, reassurance	rhythmical sequence of short, tonal calls	GOETHE (1940, 1950, 1964), HERTER (1953a, b), HERTER and OHM-KETT- NER (1954), HEIDT et al. (1968), HUFF and PRICE (1968)*, GOSSOW (1970)*, HEIDT and HUFF (1970)*, MÜLLER (1970), SVENDSEN (1976)*, CHANNING and ROWE-ROWE (1977)* POGLAYEN-NEUWALL (1975), POGLAYEN- NEUWALL and POGLAYEN- NEUWALL (1976)*, Pog- LAYEN-NEUWALL (1978) WAYRE (1979), DUPLAIX (1980) DUPLAIX (1980) DUPLAIX (1980)* POULTER (1968) FRANK (1940), GOETHE (1964), NEAL (1977), WAYRE (1979)	see text for a detailed dis- cussion of this vocal form
<i>Eira barbara</i>	clicking	+	+	friendly close contact call, coax- ing, appeasement, reassurance	rhythmical sequ- ence of clicks		
Lutrinae							
<i>Lutra</i> spp. (Old World)	twitter, whickering	+	+	friendly close contact call, coax- ing, appeasement, reassurance	friendly close contact call, coax- ing, appeasement, reassurance		
<i>Lutra</i> spp. (New World)	staccato chuckle	+	+	affiliative close contact call	affiliative close contact call		
<i>Prionura</i> <i>brasiliensis</i>	purr ♦	+	+	friendly close contact ♀ ♀ and ♂ ♂ with young cubs	friendly close contact ♀ ♀ and ♂ ♂ with young cubs		
<i>Enbydra lutris</i>	chuckle	+	+	friendly close contact call, coax- ing, appeasement, reassurance	friendly close contact call, coax- ing, appeasement, reassurance		
Melinae							
<i>Meles meles</i>	'Muckern', whinnying purr, whickering	+	+	friendly close contact call, coax- ing, appeasement, reassurance	friendly close contact call, coax- ing, appeasement, reassurance		

Lutrinae

One recording with several soft, short and noisy calls with rhythmical amplitude modulation of a captive individual of *Pteronura brasiliensis* was available for analysis. The sound has a duration of 0.25–0.6 s and probably functions as a friendly close range vocalization (Fig. 3c). Very probably it is the one described as “purr” by DUPLAIX (1980, p. 559, Fig. 31, top sonagram) which she observed in the field in adult ♂♂ and ♀♀ towards their young cubs. There is scattered information on vocalization in several species of the Lutrinae (cf. HARRIS 1968), much of which is too inexact to be included in this paper. Without giving structural details DUPLAIX (1980) states “*Lutra*, a genus which encompasses New World and Old World species, can be recognized by its unique generic vocalization: the staccato chuckle (New World) or the twitter (Old World), both given in close contact, affiliative context between adults and mother to cubs”. As no structural details for these calls are given it is impossible to classify them as compared to the purr of *Pteronura*.

From the few data available it seems that the species of the Lutrinae have friendly close range sounds that differ in structure; nothing is known about their articulation. However, all these vocalizations seem to follow a general structural pattern, either being short, low-intensity sounds with rhythmical amplitude modulation or short, rhythmical series of brief, low-intensity calls.

Melinae

NEAL (1977, pp. 196, 197) lists a friendly close range sound (“whinnying purr”) in the Eurasian badger (*Meles meles*). This very probably is the same vocal form that was named “Muckern” by FRANK (1940) and “socializing staccato” (literal translation of the German term used) by GOETHE (1964). As there are no exact data on vocalization in any species of the Melinae, no general statement on structure and articulation of friendly close contact sounds in this subfamily of the Mustelidae can be made.

As far as there is enough evidence to draw a general conclusion, friendly close range vocalizations in the various subfamilies of the Mustelidae may have different structures, in some cases even within the same subfamily. Despite all structural diversity the general pattern of rapid, rhythmical repetition of brief sounds is a uniform characteristic of all the vocal forms, series of single calls as well as sounds with rhythmical amplitude modulation.

Procyonidae

Several recordings of friendly close contact calls of juvenile and adult ♂ and ♀ raccoons (*Procyon lotor*) were available for analysis. The sounds of the juveniles have a mixed structure with a rhythmical repetition of a tonal, FM (frequency modulation) component and a noisy click component. The analyzed calls of adults¹ (cf. Fig. 3d) in my sample only show the click component but SIEBER (in litt.) who is going to publish a detailed study of vocalization in the raccoon informed me that both structural elements found in the call of juveniles may also be present in adults¹. The term chosen for this vocal form by SIEBER, “chitter 1”, gives a good idea of its sound quality.

POGLAYEN-NEUWALL (1962, 1976b) described the friendly close contact call in the kinkajou (*Potos flavus*) as chirping (“Zirpen” in the German text). No structural details are given, these have been drawn from the sonagram figured in the later publication (p. 270, Fig. 15). It shows a rhythmical series of 12 very brief sounds produced within about 0.7 s; their structure is not fully clear because of the poor quality of the sonagram. The calls seem to be tonal with very rapid FM. Without presenting any structural data the author lists a grunting sound of ♀ kinkajous probably functioning as a coaxing call towards their young.

¹ Note added in proof: The study is going to be published as SIEBER, J. O.: Vocal communication in raccoons (*Procyon lotor*). Behaviour (in press).

Table 4
Friendly close range vocalizations in the Procyonidae

Species	Vocalization	Observed in ad. ♂ ad. ♀ juv.	Behavioural context(s)	Function(s)	Call structure	References	Comments
<i>Procyon lotor</i>	twitter	+	♀ ♀ with young	friendly close contact call, coaxing		KAUFMANN (1982)	
<i>Procyon cancrivorus</i>	'Zirpen', 'Girren'	+	friendly close contact	friendly close contact call		LÖHMER (1976)	
<i>Bassariscus astutus</i>	whistle- grunt (?), chuck (?)	+	friendly close contact	social tolerance	rhythmical se- quence of short, tonal sounds with rapid FM	TOWELL and TOWELL (1978), WILLEY and RICHARDS (1981)*	contradiction in function of vocalization between re- ferences
<i>Bassariscus sumichrasti</i>	clicking and/or chirping (?)	+	friendly close contact	clicking: friend- ly close contact call chirping: ap- peasement, reassurance		POGLAYEN-NEUWALL (1973)	
<i>Bassaricyon</i> sp.	'Fiepen' = cheep	+	friendly close contact, court- ship	friendly close contact call, coaxing	rhythmical se- quence of short sounds	POGLAYEN-NEUWALL and POGLAYEN-NEUWALL (1965), POGLAYEN- NEUWALL (1976a)*	structure of vocalization not definite in published sonagrams
<i>Nasua nasua</i>	quiet chitter and/or con- tact call (?)	+	♀ ♀ with young, friendly close contact	friendly close contact call		KAUFMANN (1962), SMITH (1980)	
<i>Potos flavus</i>	'Zirpen' = chirp	+	♀ ♀ with young, courtship, mating	friendly close contact call, coaxing, ap- peasement, reassurance	rhythmical series of short, low-intensity sounds	POGLAYEN-NEUWALL (1962, 1976b*)	structure of vocalization not fully clear in published sonagrams

Thus it seems possible that this species has two different friendly close contact vocalizations. The interpretation of the structure of the relevant vocal form of *Bassaricyon* described by POGLAYEN-NEUWALL and POGLAYEN-NEUWALL (1965) and POGLAYEN-NEUWALL (1976a) poses problems. The later publication includes three spectrograms (sonagrams d, d1, e; pp. 216–218) of the tweet, termed “Fiepen” in the German text. The apparent structural differences between the calls in these three sonagrams are in part probably due to echo and overloading. The following structural details of the olingo’s tweet were taken mainly from sonagram d1. It is a short, tonal call with rapid FM and approximately 0.15 s duration, repeated relatively rhythmically at a rate of about 1–3 calls per s. Two friendly close range sounds were listed for the Central American cacomistle (*Bassariscus sumichrasti*) by POGLAYEN-NEUWALL (1973): clicking and chirping, the latter being analogous to the chirping of *Potos*. Although no structural details are presented it may be inferred from the author’s descriptions that the chirp is a tonal call, probably produced in the larynx. Clicking is likely to be noisy and rhythmical mouth and tongue movements accompany its articulation.

The vocal repertoire of the ringtail (*Bassariscus astutus*) is well documented in a paper by WILLEY and RICHARDS (1981). Some data on ontogenesis of vocalization in this species are found in TOWEILL and TOWEILL (1978); this publication includes material already analyzed by BAILEY (1974). POGLAYEN-NEUWALL and POGLAYEN-NEUWALL (1980) also give some information on vocalization of the ringtail. The friendly close contact call of this species is the whistle-grunt, a bi-component sound (WILLEY and RICHARDS 1981), repeated rhythmically. The grunt component (only its structure is clearly discernible in the sonagram figured) lasts about 0.02 s and shows rapid FM. Probably it is a laryngeal sound.

The data available on friendly close range calls in the Procyonidae suggest that in this family both tonal and noisy calls are represented. There is some evidence that both types may be present in the same species (*Bassariscus sumichrasti*, *Potos flavus*) and there are relevant vocal forms that have both a tonal and a noisy structural component (*Procyon lotor*). All tonal calls resp. tonal components show rapid FM and are uttered in rhythmical succession. Noisy calls resp. noisy components either are a series of clicks or a coherent sound with rhythmical amplitude modulation. Thus the general structural pattern of a rhythmical series of short sounds is realized in all these forms. Because of lack of unequivocal evidence no general statement on the mode of articulation of these vocal forms in the Procyonidae can be made.

Regardless of their disputed systematic grouping (cf. THENIUS 1979), a comment on the relevant vocalizations of the red panda (*Ailurus fulgens*) and the giant panda (*Ailuropoda melanoleuca*) is given here. Both species’ friendly close contact calls are relatively high-pitched, clear and tonal with AM (amplitude modulation) and rapid FM (Fig. 8a, b). The twitter of *Ailurus* (SIMPSON 1869; ROBERTS and KESSLER 1979; ROBERTS 1981) and the bleat of *Ailuropoda* (KLEIMAN et al. 1979; PETERS 1982; KLEIMAN 1983) are similar in structure. Usually one full phase of the rhythmical FM and AM in these two vocal forms is about 0.1 s long.

Ursidae

Behavioural and structural details on friendly close contact sounds of those ursid species for which recordings were available were presented in PETERS (1978b). Prior to this paper this sound of the Polar bear (*Ursus maritimus*) had been described as chuffing by WEMMER et al. (1976). Chuffing is likely to belong to the repertoire of all ursids with the exception of the spectacled bear (*Tremarctos ornatus*). This species’ functionally equivalent call is described in PETERS (1978b). In addition to the bear species listed to perform chuffing in that paper, personal observations confirmed its presence in *Helarctos malayanus* and *Melursus ursinus*, in the latter species also proven by a sonagram published by TEMBROCK (1975, p. 60, Fig. 6b). Contrary to the original description of chuffing by WEMMER et al.

Table 5
Friendly close range vocalizations in the Ursidae

Species	Vocalization	Observed in ad. ♂ ad. ♀ juv.	Behavioural context(s)	Function(s)	Call structure	References	Comments
<i>Ursus arctos</i> ssp., <i>U. maritimus</i> , <i>U. americanus</i> , <i>Selenarctos thibetanus</i> , <i>Helarctos malayanus</i> , <i>Melursus ursinus</i>	'Lippenklappen', chuffing	+	+	+	friendly close contact call, greeting, coaxing, appeasement, reassurance	rhythmical sequence of short, noisy, low-intensity sounds (two separate structural components may be present, both are noisy)	see text for a detailed discussion of structure and articulation of these ursid vocal forms
<i>Tremarctos ornatus</i>	'Trillern' = trilling	+	+	+	friendly close contact call, greeting, appeasement, reassurance	SCHEIDER (1933), MEYER-HOLZAPPEL (1957), TEMBROCK (1968)*, TEMBROCK (1975)*, WEMMER et al. (1976)*, LAURIE and SEIDENSTICKER (1977), PETERS (1978b)* ROTH (1964), ECK (1969), PETERS (1978b)*	

(1976) this vocalization has two structural components, each of which varies in its relative development and may be even fully reduced (cf. Figs. 4e-g, 5a-d, 6a-c; the different structural components are marked in 4g). Generally chuffing is a short, rhythmic series of brief, noisy sounds.

The term trilling conveys the quality of the call of *Tremarctos* that is functionally equivalent to chuffing. It also has two structural components (cf. Fig. 4a-d; structural components marked in 4b), one of them click-like and noisy, the other a tonal element with rapid FM. Likewise, both structural components in trilling vary in their relative development. The examples of trilling analyzed were of an individual less than 1 year old, so its structure in adults has still to be established.

The data on vocalization in *Ursus americanus* presented in JORDAN (1979) include two forms that have some structural similarity with the two components of chuffing but their temporal arrangement differs strikingly from chuffing and these sounds of the American black bear function as a threat. As I have no personal observations of vocal behaviour in this species these conflicting data cannot be interpreted.

Various authors have contained that chuffing is produced by the lips (SCHNEIDER 1933; MEYER-

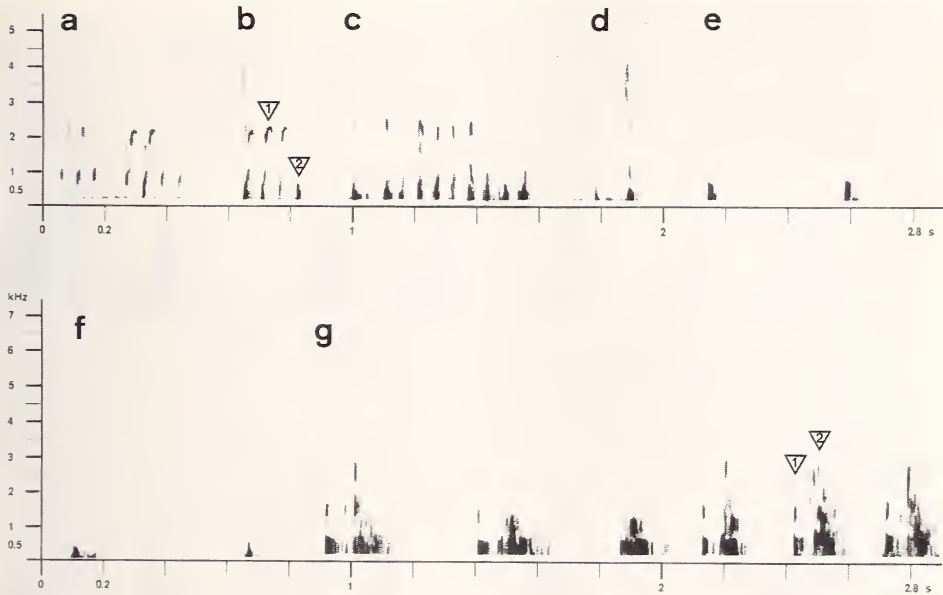


Fig. 4. Ursidae: a–d = spectacled bear (*Tremarctos ornatus*), trilling, juv. ♀. In b a tonal FM component is marked '1', a basal frequency range noisy one is marked '2'. The examples show the variable relative development of the two structural components in this call of *Tremarctos*. e–g = Himalayan black bear (*Selenarctos thibetanus*), chuffing, ad. ♀. In g the popping sound is marked '1', the subsequent forceful exhalatory sound is marked '2'.

HOLZAPFEL 1957; TEMBROCK 1968; WEMMER et al. 1976), also indicated by its German name "Lippenklappen". SCHNEIDER (1933) and WEMMER et al. (1976) present detailed descriptions of the articulatory process, in both cases stating that rhythmical forceful exhalation is imparting a movement on the lips which generates the sound. Personal observations of various bear species performing chuffing with varying relative development of its two structural components indicate that the click-like popping sound very probably is produced by lip and/or cheek movements and the chuffing sound proper (as described by WEMMER et al. [1976]) is a forceful exhalatory jet from the opening mouth. It is not clear in which way trilling of the spectacled bear is produced.

Despite all structural variability of chuffing and the difference in structure between chuffing and trilling these friendly close contact sounds of the Ursidae represent the same basic structural pattern: a rhythmical series of short, broad-band sounds. Whereas chuffing is a sequence of single sounds, trilling cannot be classified yet in this respect.

Viverridae

Friendly close range calls of two viverrid species were available for analysis, the large Indian civet (*Viverra zibetha*) and the fossa (*Cryptoprocta ferox*). The recordings in the former species are of two adult ♀♀, in the latter of an adult ♂. The relevant vocalization of *Viverra zibetha* (Fig. 6e, f) is a rapid, largely rhythmical series of a few low-intensity, brief and noisy bursts of sound, very occasionally only one such sound is produced. The recorded sequences consist of 2–9 single sounds and last between 0.15–0.96 s. The single sounds are about 0.02 s long with intervals of approximately 0.1 s between them. The vocalization of *Cryptoprocta* also is a rapid, rhythmical series of short, low-intensity and

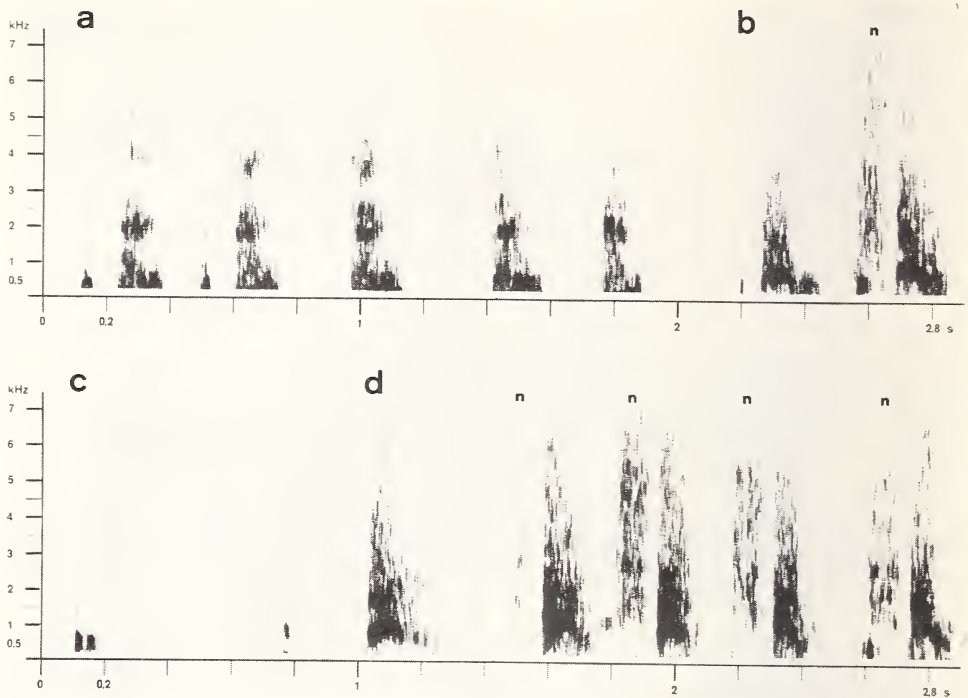


Fig. 5. Ursidae: a = Polar bear (*Ursus maritimus*), chuffing, ad. ♂. In the beginning of the sequence both structural components of this vocal form are fully developed, the end only consists of the exhalatory jets. b = Kodiak bear (*Ursus arctos middendorffi*), chuffing, ad. ♂. This individual is peculiar in performing a nasal inhalatory sound (marked n) in front of most of the exhalatory jets. c = Kodiak bear, chuffing, ad. ♀. This example of chuffing only consists of the popping sound. d = Kodiak bear, chuffing, ad. ♂; same individual as in b with same peculiar structure of call

noisy sounds. The sonograms of this call reveal a rather complex structure (Fig. 6d) which cannot yet be fully understood because of the relatively poor quality of the recordings. Because of different structural components in this vocalization and their temporal arrangement it seems likely that two sources contribute to its articulation. This sound of *Cryptoprocta* was briefly mentioned by VOSSELER (1929) but is not listed by ALBIGNAC (1973). In various species of the Viverridae coughing was described as a friendly close contact sound by EWER and WEMMER (1976) and especially WEMMER (1977), the latter publication presenting sonograms of this call in *Genetta tigrina* and *Viverricula indica*. Coughing is a rapid, rhythmical series of brief, noisy sounds. In the former species each sound in the sequence is bi-partite with a tonal laryngeal and a subsequent noisy nasal component, in the latter only one type of noisy sound pulse is present. The "hoquet" (GANGLOFF and ROPARTZ 1972) of *Genetta genetta* as its functional equivalent has the same bi-partite structure as coughing in *Genetta tigrina*, suggesting two sources of sound production, too (unpublished data, recordings kindly provided by DR. J.-J. ROEDER). The full range of structural variability and the phylogenetic relationship of the various friendly close range calls listed as coughing in the Viverrinae and Hemigalinae by WEMMER (1977) and the relevant vocalizations of *Viverra zibetha* and *Cryptoprocta* described here are not yet understood.

WEMMER (1977) specifically stated that of the viverrid species he investigated, the

Table 6
Friendly close range vocalizations in the Viverridae

Species	Vocalization	Observed in ad. ♂ ad. ♀ juv.	Behavioural context(s)	Function(s)	Call structure	References	Comments	
<i>Herpestes edwardsi</i> , <i>H. ichneumon</i> , <i>Mungos</i> <i>mungo</i> , <i>Helogale par-</i> <i>vula</i> , <i>Suricata suricatta</i>	'Muckern', 'Kontakt- laut', con- tact keeping call	+	+	+	friendly close contact call, coaxing, greet- ing, appease- ment, reassur- ance	rhythmical se- quence of short, low-intensity, tonal sounds (?)	DÜCKER (1957, 1960, 1962, 1965), EWER (1963), ZANNIER (1965), MARQUARDT (1976)	call structure according to last unpub- lished refer- ence
<i>Genetta genetta</i> , <i>G. ti-</i> <i>grina</i> , <i>Civettictis civet-</i> <i>ta</i> , <i>Viverricula indica</i> , <i>Fossa fossa</i>	'Muckern', 'l'appel', contact call, coughing	+	+	+	friendly close contact call, coaxing, greet- ing, appease- ment, reassur- ance	rhythmical se- quence of short, low-intensity noisy calls (two separate struc- tural compo- nents may be present)	DÜCKER (1957, 1965), SCHAUBENBERG (1964), ZANNIER (1965), EWER and WEMMER (1974)*, WEMMER (1977)*	see text for a detailed dis- cussion of these vocal forms in the Viverridae

Paradoxurinae *Nandinia binotata*, *Paguma larvata* and *Paradoxurus hermaphroditus* do not perform coughing, and in connection with these species he mentioned no vocal form functionally equivalent to coughing. Recordings exist, however, of friendly close range sounds of a ♀ and ♂ *Nandinia binotata* during courtship and attempts at mating (TONKIN unpubl. observations) which represent short, muffled, noisy sounds of low volume with a short-phased rhythmical amplitude modulation. As the recordings of this call are not of adequate quality for sonographic analysis no detailed statement about its structure can be made. In a recent publication on another species of the Paradoxurinae, *Arctitis binturong*, WEMMER and MURTAUGH (1981) list a nasal blowing sound of ♀♀ and ♂♂ during courtship that functions as a contact-promoting vocalization. The authors do not comment whether several of these sounds may be sequential.

Information on the structure of the contact keeping call of *Helogale parvula* is based on MAIER et al. (1983) and an unpublished thesis by MARQUARDT (1976). This species' relevant vocalization is a short, rhythmical series of low-intensity, brief, tonal sounds with FM. The same structure is found in the functionally equivalent vocalizations ("cris de contact") of *Galidia elegans* (cf. Fig. 7) and *Mungotictis decemlineata* (ALBIGNAC 1973). No call with a comparable structure is listed for *Herpestes auropunctatus* by MULLIGAN and NELLIS (1975), the only detailed analysis of the vocal repertoire of a herpestine viverrid published so far.

From the relatively few established data available in the Viverridae it is already evident that there are different types of friendly close contact calls in this family. Regardless of

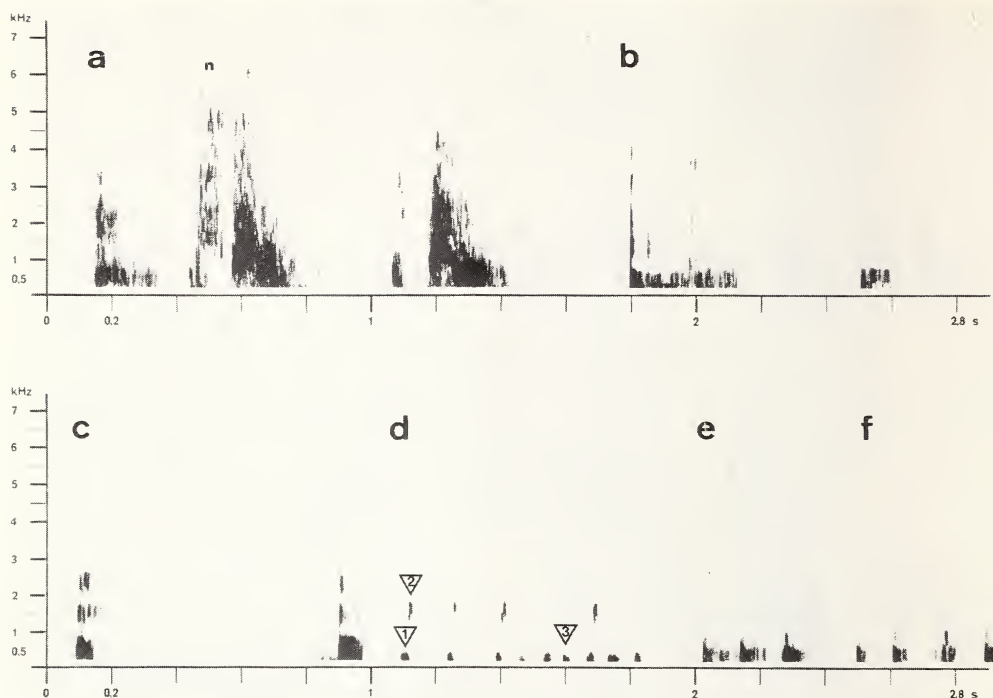


Fig. 6. Ursidae: a = Kodiak bear (*Ursus arctos middendorffi*), chuffing, ad. ♂; same individual as in Fig. 4 b and d. In this example the third exhalatory jet is preceded by a popping sound. The nasal inhalatory sound is marked n. b and c = European brown bear (*Ursus arctos arctos*), chuffing, ad. ♀. In the chuffing of this ♀ the popping sound is prevailing. Viverridae: d = fossa (*Cryptoprocta ferox*), ad. ♂. The different structural components in this vocal form are marked 1, 2, 3. e and f. = large Indian civet (*Viverra zibetha*), coughing, ad. ♀ (recording B. A. TONKIN)

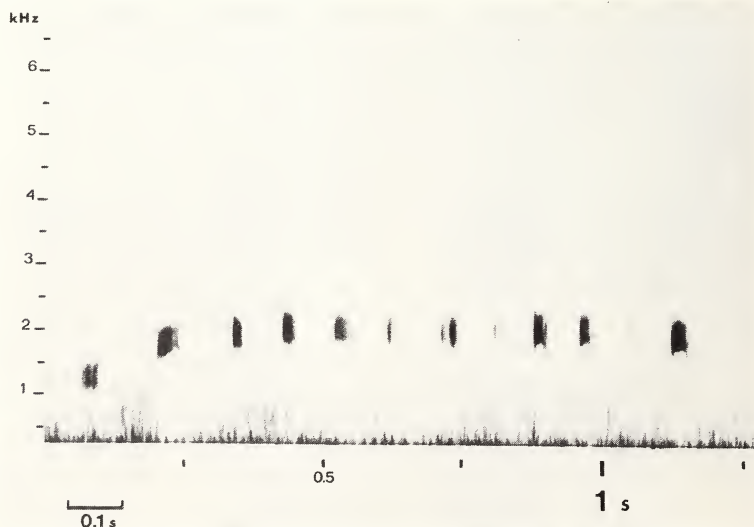


Fig. 7. Viverridae: ring-tailed mongoose (*Galidia elegans*), friendly close contact call, ad. ♂

all differences in structural detail and very probably also in mode of articulation, the vocalizations listed here represent a uniform structural pattern: all are rhythmical series of short, low-intensity sounds. If the structural characterization of the relevant vocal form of *Nandinia* given above is confirmed by sonographic analysis, short, noisy sounds of low volume with rhythmical amplitude modulation would be another type of friendly close contact call in the Viverridae, also conforming to the general structural pattern outlined in this publication.

Discussion

The data presented here on friendly close range vocalizations in all families of the terrestrial Carnivora clearly reveal a general structural pattern (irrespective of all differences in structural detail): a relatively rapid, rhythmical series of brief, low-intensity sounds. This pattern is either realized as a rhythmical sequence of separate single sounds or as a coherent sound with rhythmical amplitude modulation. Purely from the structure of a call it is sometimes hardly possible to distinguish between the two types; cf. Fig. 3b and c, the first

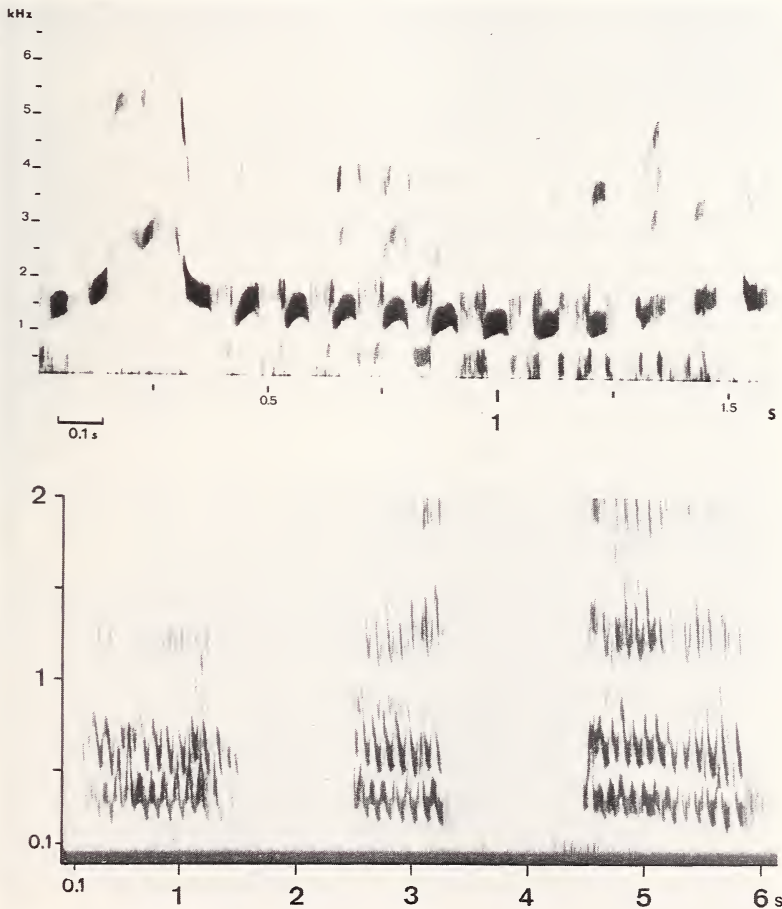


Fig. 8. (above): red panda (*Ailurus fulgens*), twitter, ad. (recording I. RIEGER); (below): giant panda (*Ailuropoda melanoleuca*), bleat, ad. ♂

representing the former type of sound, the second the latter, both in the Mustelidae. From the point of view of articulation, such distinction is an unequivocal reality only in these expiratory vocal forms if a call with amplitude modulation is produced during an uninterrupted phase of exhalation and a series of separate sounds is formed with a separate burst of exhalation each for each single sound and a phase of inhalation between any two adjacent sounds. There is no evidence, however, that the latter form of articulation is prevailing in any of the relevant sounds sequences listed. As the single sounds in all of them are relatively low in volume and little respiratory exertion is required to perform a few of them in rapid succession, like in puffing of the Felidae, such series are produced in one single phase of exhalation, each sound in its own exhalatory burst, without inhalation in between. This mode of articulation, however, is also true for prusten in the Felidae, an example of a friendly close contact call with rhythmical amplitude modulation. This emphasizes that the two structural variants in these vocal forms represent one uniform structural principle. One pointer to the distinction between the two types – independent of the details of coordination of articulation with respiratory cycles – may be the occurrence of solitary sound pulses not forming a part of a rhythmical pattern, which leads to the conclusion that series formed of several of these sounds are a succession of separate single sounds. They are no unequivocal criterion for the classification of a vocal form, though, if truncated forms of a coherent sound with rhythmical amplitude modulation may be performed with just one AM phase.

Most of the friendly close contact calls of both structural variants listed are noisy but tonal sounds with FM are also represented and both may occur in the same family, in some cases even as structural components of a call of a species (cf. raccoon, spectacled bear). It seems likely that most terrestrial carnivores (the relevant vocal forms of about 36 % of the approximately 240 extant species are listed here) have friendly close range calls that conform to the general structural pattern outlined in the publication. On the other hand, some species probably have no friendly close contact sound according to this scheme, although to the best of my knowledge there is very few data to support this hypothesis in any species studied in this respect in detail so far. Many terrestrial carnivores perform one or several types of vocalization in the functional contexts of appeasement, reassurance, greeting, coaxing or friendly close contact that are structurally different from the one(s) listed here, i.e. they may have several vocal forms with these functions not all of which exhibit the same structural pattern. No statement as to the structure of these calls is made. The data presented here only demonstrate that the structural pattern of a rapid, rhythmical series of brief, low-intensity sounds is widespread in calls with these functions in all families of the terrestrial Carnivora. Definitely not all carnivore vocal forms with these basic structural characteristics are friendly close range calls.

Friendly close contact sounds with a structure similar to the scheme outlined in the terrestrial carnivores have been described in a fair number of mammalian species from various taxa. Table 7 lists some of these from taxa phylogenetically as widely separated as the Marsupialia and the Primates. This table is no complete review of the literature, though (cf. e.g. KILEY [1972] for the relevant vocal form of the Artiodactyla, the grunt). The structural classification of the calls in the table according to the two variants present in terrestrial carnivores is based on the details given by the authors cited which are not unequivocal in all cases. No pinniped species is listed in Table 7 but there is some information on their relevant vocalizations (STIRLING and WARNEKE 1971; WINN and SCHNEIDER 1977; TRILLMICH and MAJLUF 1981). None of these publications lists a vocal form that occurs in all friendly functional contexts named in the terrestrial carnivores but the tonal pup attraction calls of adult ♀♀ in some *Arctocephalus* species in parts have distinct rhythmical AM.

Despite the wide distribution of a rhythmical AM pattern in the friendly close contact calls of the Mammalia it is unlikely that many recent groups share it due to its presence in

Table 7

Friendly close range vocalizations in various mammalian taxa, structurally similar to functionally equivalent calls in the terrestrial Carnivora

Order Family	Species	Vocalization	Structural pattern	References
Marsupialia				
Didelphidae	<i>Didelphis marsupialis</i> , <i>D. virginiana</i> , <i>Marmosa robinsoni</i> <i>Marmosa murina</i>	click	A ¹	REYNOLDS 1952; McMANUS 1970; EISENBERG et al. 1975
Dasyuridae	<i>Dasyurus albopunctatus</i>	buzz	B	CHARLES-DOMINIQUE 1983
Phalangeridae	<i>Trichosurus vulpecula</i>	click	A	EISENBERG et al. 1975
Macropodidae	<i>Macropus rufus</i>	click	A	WEMMER and COLLINS 1978 EISENBERG et al. 1975
Edentata				
Dasypodidae	<i>Dasyopus novemcinctus</i>	chuck	A	CHRISTENSEN and WARING 1980
Proboscidea				
Elephantidae	<i>Elephas maximus</i>	growl	B	McKAY 1973
Perissodactyla				
Equidae	<i>Equus caballus</i>	nicker	B	KILEY 1972
Tapiridae	<i>Tapirus terrestris</i> , <i>T. indicus</i>	click	A	HUNSAKER and HAHN 1965; RICHTER 1966
Artiodactyla				
Suidae	<i>Sus scrofa</i>	grunt	B	KILEY 1972; KLINGHOLZ and MEYN- HARDT 1979; KLINGHOLZ et al. 1979
Bovidae	<i>Budorcas taxicolor</i> <i>Tragelaphus angasi</i> , <i>T. scriptus</i>	grunt click	B A	ALTMANN 1980 JACOBSEN 1974; ANDERSON 1980
Primates				
Cebidae	<i>Ateles fuscipes</i> , <i>A. geoffroyi</i>	whinny	A	EISENBERG 1976
Cercopithecidae	<i>Cercopithecus aethiops</i> <i>Cercocebus albigena</i> , <i>C. galeritus</i>	grunt grunt	B A	CHENEY and SEYFARTH 1982 GAUTIER and GAUTIER 1977
Hylobatidae	<i>Hylobates concolor</i>	close contact call	A	TEMBROCK 1974
Rodentia				
Capromyidae	<i>Plagiodontia aedium</i>	cluck	A	EISENBERG 1974
Dasyproctidae	<i>Dasyprocta punctata</i> , <i>Myoprocta pratti</i>	purr	A	KLEIMAN 1972; EISENBERG 1974
Caviidae	<i>Cavia aperea</i> , <i>C. porcellus</i> , <i>Galea musteloides</i> , <i>Microcavia australis</i> <i>Dolichotis patagonum</i>	purr cluck	A A	ROOD 1972; EISENBERG 1974; BERRYMAN 1976 EISENBERG 1974

¹ A – rhythmic series of short, low-intensity sounds; B – short, low-intensity sound with rhythmic amplitude modulation.

the relevant vocal form of a common ancestor. It is much more likely that the relative structural uniformity of these vocalizations is a result of convergent evolution in the various groups at different taxonomic levels, sometimes even within the same family. The respective friendly close range sounds probably developed independently, derived from phylogenetically unrelated vocal forms specific to each group. The main argument to support this view is the fact that already within the terrestrial Carnivora these calls are articulated in strikingly different ways and therefore cannot be homologous (EISENBERG 1974; EISENBERG et al. 1975; PETERS 1978a). There are differences in this respect even within one family like e.g. in the Felidae or the Ursidae. Friendly close contact calls in the Marsupialia are also produced in different ways (cf. EISENBERG et al. 1975; WEMMER and COLLINS 1978). There may be friendly close range sounds in different higher mammalian taxa that share a common phylogenetic origin but this will be difficult to establish. Vocal forms like chuffing in the Ursidae, gurgling in the Felidae, trilling in the Mustelinae or "Muffen" in the Canidae that are widespread in their respective taxa and articulated in the same way in each case and in which all structural variants are linked by intermediate forms, very probably are homologous in all species that have it in their repertoire.

The hypothesis of convergent evolution of the majority of friendly close range calls with the structural pattern outlined in the various mammalian orders and in the families of the terrestrial Carnivora (in some instances even within families of this order) calls for an explanation which functional influences could have led to the independent evolution of their uniform structural characteristics. Discussing these calls in the Marsupialia EISENBERG et al. (1975) stated: "Cluck- or click-like calls indicative of the sender's location appear to suggest strong selection for structural similarity in call form to render them audible and localizable." The same reasoning very probably applies also to the relevant calls of the terrestrial Carnivora and the other taxa. This hypothesis seems valid even though all calls listed are used at close distance where sender and addressee(s) of the sound signal often can localize each other visually or are already in visual contact. All friendly close range sounds of the terrestrial carnivores dealt with here exhibit at least two structural characteristics that facilitate the localization of the sound source emitting it (cf. MARLER and HAMILTON 1966; MARLER 1967; ERULKAR 1972; BROWN et al. 1979; GOUREVITCH 1980; BROWN 1982). The last author argues that in primates low-intensity locatable calls at close range facilitate the establishment of visual contact and can help focus the attention on the vocalizer. These aspects very probably are also important in other mammals. It seems noteworthy that these calls are especially frequent in ♀♀ with young and in ♀♀ and/or ♂♂ during courtship, both behavioural contexts in which it is highly adaptive for the vocalizing animal to provide the addressee(s) with information about the sender's location and for the addressee(s) to receive this information.

It is obvious that rhythmicity is a key feature in these friendly close contact sounds but it is likely that other structural characteristics like e.g. their sound quality, emission rate, muffled character, etc. are adaptations to their functions listed, but no experimental evidence can be presented to support these hypotheses. Vocalizations like purring in felids and viverrids (PETERS 1981) or the nursing sound ("Summen") of ursids (SCHNEIDER 1933) may have functions in mother-young communication that are similar to those of the friendly close range sounds listed. Moreover, they exhibit rhythmical AM but their articulation is more or less continuous for minutes on end and normally they are produced while animals are in direct bodily contact. Thus, if their rhythmical AM is functionally significant, it cannot be so because of selection for locatability of the sound source. Furthermore, rhythmical AM is also found in a similar form in growling of carnivores, an aggressive threat sound. These are indirect hints that rhythmical AM cannot be the only key feature in the friendly close contact calls described in the various taxa.

TEMBROCK (1967, 1971, 1977) and MORTON (1977, 1982) formulated general motivational-structural rules in animal vocalization. According to both authors' models a close

range appeasement sound would be predicted to be a high-pitched, tonal call. Many of the friendly close contact calls from various mammalian taxa listed here, most of them also functioning as appeasement sounds, differ totally from this structure: they are noisy, broad-band sounds, relatively low in register.

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Zusammenfassung

Zur Struktur freundlicher Nahkontaktlaute landlebender Carnivora (Mammalia: Carnivora: Fissipedia)

Freundliche Nahkontaktlaute von Arten aus allen Familien der landlebenden Carnivora (Canidae, Felidae, Hyaenidae, Mustelidae, Procyonidae, Ursidae, Viverridae) werden beschrieben. Alle diese Lautformen zeigen einen einheitlichen Grundaufbau: eine ziemlich schnelle, rhythmische Abfolge einiger kurzer Lautpulse. Dieses allgemeine Strukturschema ist entweder in Form einer rhythmischen Sequenz von kurzen Einzellaute oder als zusammenhängender Kurzlaut mit rhythmischer AM ausgebildet. Die Mehrzahl der in dieser Untersuchung aufgeführten Laute ist von geräuschhaftem Aufbau, es kommen aber auch tonale Formen mit FM vor. Freundliche Nahkontaktlaute mit einem von dem hier skizzierten Strukturschema abweichenden Aufbau sind bei den landlebenden Carnivora auch ausgebildet, und sicher sind nicht alle ihre Laute mit einer entsprechenden Struktur freundliche Nahkontaktlaute. Diesem Lauttyp der landlebenden Carnivoren im Aufbau sehr ähnliche Laute entsprechender Funktion sind bei einer Anzahl von Säugetieren aus unterschiedlichen Taxa bekannt. Trotz der weiten Verbreitung dieses Strukturschemas bei freundlichen Nahkontaktlauten der Mammalia ist es wenig wahrscheinlich, daß es sich darin um eine vielen Gruppen gemeinsame ursprüngliche Ausbildung, also ein symplesiomorphes Merkmal, handelt. Vielmehr deuten die Zusammenhänge bei den landbewohnenden Carnivora, für die das umfangreichste Belegmaterial vorhanden ist, darauf hin, daß es sich hier um ein Lautmuster handelt, das mehrfach konvergent innerhalb verschiedener Gruppen entstanden ist, jeweils auf der Grundlage von für die jeweiligen Taxa spezifischen Lautformen. Diese Annahme wird wesentlich dadurch gestützt, daß diese Nahkontaktlaute auf sehr unterschiedliche Weise erzeugt werden – teilweise sogar innerhalb derselben Familie –, also nicht homolog sind. Als wahrscheinlichste Ursache für diese Konvergenz sind Selektionseinflüsse anzunehmen, die trotz der relativ geringen Intensität dieser Laute und ihres Einsatzes im Nahbereich auf ihre möglichst gute Ortbarkeit hinwirkten; weitere einheitliche Struktureigenschaften dieser Lautformen stellen sicherlich auch stammesgeschichtliche Anpassungen dar, lassen sich aber in diesem Zusammenhang nicht eindeutig umreißen.

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Age determination and morphological characteristics of Wild mink from Maryland, USA

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Abstract

A total of 169 wild mink were collected during the 1976-1979 trapping seasons in Maryland. Three aging techniques were applied: 1. aging by cementum annuli, 2. the presence or absence of the zygomatic suture, and 3. size of the suprascapular tubercle. The age distribution was 111 juveniles to 58 adults and the sex ratio was 108 males to 61 females (177 males/100 females). Significant correlations were found for testes weight, epididymides weight, spleen weight, nasal length and nasal width with age for male mink. Significant correlations were found for spleen weight, kidney weight, liver weight, nasal length and nasal width with age for female mink. Spermatogenic activity began in mid-December and continued through February.

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