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# VOCAL COMMUNICATION IN RACCOONS (PROCYON LOTOR)

by

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(With 8 Figures)  
(Acc. 19-XII-1983)

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## Introduction

By mammalian standards, carnivores are rather vocal animals (EWER, 1973). They use a great diversity of sounds. In canids up to 12 distinct call types are found (FOX & COHEN, 1977). Felid repertoires include about 10 basic types (SCHALLER, 1972; PETERS, 1978, 1980). Although some species have long distance calls at their disposal (*e.g.*, large felids, social canids), most calls are used for close range communication. Structural differences between and within types of close range calls in general are best understood as vocal expression of different moods (DARWIN, 1872; MORTON, 1977, 1982). Many calls follow a code with two physical dimensions: Sound quality and sound frequency. They interact with motivation along a continuum. On one end, aggressive motivation is expressed through harsh, nontonal and low frequency sounds, while on the other end fearful and friendly motivation through tonal and highpitched sounds (MORTON, 1977, 1982).

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Raccoons (*Procyon lotor*) are medium-sized, nocturnal, semi-arboreal and omnivorous carnivores originally restricted to the American continents. Like the other procyonids except the coati (*Nasua narica*), they are solitary. Males and females spend all year in partly overlapping home ranges of an average size of 40 to 100 ha (KAUFMANN, 1982). Except for temporary feeding aggregations (TEVIS, 1947; SHARP & SHARP, 1956), contacts among adults seem to be restricted to a short time during the breeding season in late winter, when one male may breed several females. The cubs are reared by the female alone and persistent bonds between mothers and offspring (SCHNEIDER *et al.*, 1971) and between siblings (FRITZELL, 1977) are found. Communication in raccoons is only poorly known. Casual reports indicate that raccoons possess a variety of visual (TEVIS, 1947; SHARP & SHARP, 1956; BARASH, 1974; MELLEN, 1976; RICARD & DORE, 1977), olfactory (MELLEN, 1976; OUGH, 1982), tactile (MELLEN, 1976) and vocal signals (see references later in the text).

The purpose of this study is to describe the structure, contexts and ontogeny of vocalizations in raccoons and to test whether structure and motivation interplay in the way predicted by MORTON's (1977, 1982) motivation-structural rules. A group of captive raccoons was observed for a full reproductive cycle in conditions permitting all major interactive behaviours among mother and cubs, siblings and unrelated juveniles and adults.

## Methods

The study was conducted at the U.S. National Zoological Park's Conservation and Research Center Front Royal, Virginia, from April 1982 through March 1983. Study animals included one adult male, 5 adult females and a total of 14 young which reached sexual maturity during the study. All animals were individually marked with ear tags and/or collars. The five females were live trapped while pregnant at the Center with Tomahawk traps No. 207 between April 9 and 20, 1982, and introduced to individual cages in an old horse barn.

Every cage, measuring 4.4 × 4.2 × 3.1 m, had a clay floor, 2 or 3 windows and was equipped with many stems and branches and with two dens, fastened 1.3 to 1.5 m above ground. These dens were made from plastic barrels, 60 cm high and 40 cm in diameter and had a round opening in front. On the rear end of each barrel, a plexiglas window, covered with a one-way vision screen, allowed observations of the dens from outside the cage. A 7-watt red light in the den provided illumination. The cages themselves were illuminated by a 100-watt red light bulb. Adjacent cages were separated by a wooden wall and a 85 cm high iron grid, which allowed some contact among the animals. In addition, adjacent cages were linked by round doors of 20 cm diameter.

Between May 7 and June 1, the five females gave birth to a total of 14 cubs (sex ratio, ♂♂: ♀♀, were: 1:3; 2:1; 0:1; 3:0; 2:1). A female from litter 1 and a male from litter 4 were removed for handraising in the 4th week. All others were successfully reared by their mothers. In the autumn, 3 females and one juvenile escaped. In January 1983, a live

trapped adult male was introduced. This male shared the cages with members of 3 families.

The management of the study animals was changed according to the developmental stage of the cubs. Before weaning, all families stayed in their home cage and had no access to other cages. In the post-weaning period, the doors between adjacent cages were opened one by one so that unrelated animals had access to one another. Eventually 3 families (and later the adult male) shared their cages on one side of the observation floor and two families on the other side.

The raccoons were fed daily with 'Nebraska Brand Feline Diet', later with 'Western Plateau Meat Eater Diet' and with 'Ralston Purina Lab. Canine Diet No. 5006' in pellets in a ratio 1:2. Fresh vegetables or fruits were added once or twice weekly. Water was changed daily. The temperature in the unheated barn roughly corresponded to the ambient temperature, though it was buffered from the extremes.

Observations, totalling 520 hours, took place from May 1982 through March 1983. Every family was observed for 2 hours per 4 day period. From birth until 6 months of age, I watched every litter separately, in the winter all 5 at the same time due to the greatly reduced activity. During the breeding season (February through March), the large group of raccoons was observed for 4 hours, the small group for 2 hours per 4 day interval. Additional observations were made during the females' estrus. All observations were conducted in the 6 hours following sunset, when the activity is highest in the wild (SHARP & SHARP, 1956). Every family or group was observed, alternating early or late within this period of time. Besides scan samples of the activity and location of the members of a family and focal animal samples whose results will be reported elsewhere, I noted all vocalization bouts with the location of the caller and the (potential) recipient and their behaviour (when I was able to detect it) during and following a call. Check sheets were used for recording in order to avoid disturbing the animals who remained shy during the study.

Tape recordings of the calls were made with an Uher portable tape recorder (4000 Report IC) at a speed of 9.5 or 19 cm/sec and an Uher microphone (M 514), a Sennheiser directional microphone (MKH 816 T) or a Dan Gibson E.P.M. parabolic microphone (P-200). Calls were recorded from animals either while in their cages or when trapped for weighing and marking in the lab. The tape recordings were analyzed on a Kay sonograph (7029 A) in wide band setting through a frequency range of 2 to 16 kHz, according to the main sound energy of the different calls. The temporal resolution varied therefore from 0.013 (2 kHz setting) to 0.0017 sec (16 kHz setting) and the frequency resolution from 75 Hz (2 kHz setting) to 600 Hz (16 kHz setting). For measuring frequencies, I used plastic overlays, drawn after the sonograph's calibration signals.

The following terms, adapted from EISENBERG *et al.* (1975) and EISENBERG (1976) are used to describe the calls: The smallest distinct parts of sound perceived by a listener are referred to as syllables. They appear as uninterrupted traces in the sonograms or, as in some pulsed calls, as a group of pulses with regular intervals. A phrase is a group of syllables separated by another group by an interval longer than any syllable. A call is a syllable or a phrase distinctive in form. A bout, used mainly in contextual descriptions, is a syllable, one or several phrases of one call, given in close temporal proximity and without behavioural changes in the caller. Two bouts are separated by a change in the caller's behaviour. Tonal calls have distinct, narrow frequency bands and often true harmonics. Mixed calls are composed of a tonal component superimposed by noise. Noisy calls consist of sound not separated in discrete frequency bands. Pulsed calls consist of brief pulses with a wide frequency range which are repeated in fast and regular succession. Three terms describe temporal features of the calls: Brief structures are those lasting less than 0.02 sec, short ones are 0.02-0.6 sec and long ones more than 0.6 sec in duration.

## I. The repertoire and its ontogeny

Based on aural impressions and spectrograms, 13 call types were discerned (Fig. 1, Table 1). Not all calls are used at the same time; some are typical for particular ontogenetic and seasonal phases. Therefore I will briefly describe these phases and the calls characteristic of them before presenting detailed information on the structure and contexts of the calls in section II.

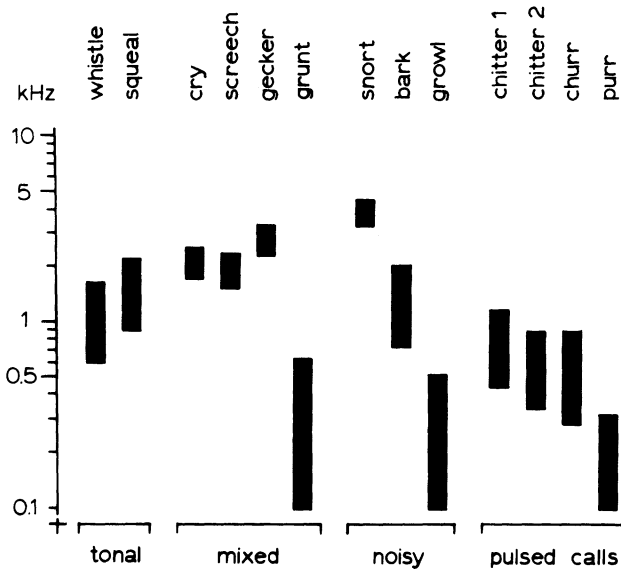


Fig. 1. Frequency features of the 13 raccoon calls. For tonal calls, the bars connect the mean of the lower and upper limit of the fundamental, for all other calls the mean of the lowest and/or darkest band as indicated in Table 1.

### Nestling phase.

Raccoon cubs, 2 to 5 in general and 1 to 4 in the study group, are usually born in May after a gestation period of 63 to 65 days (KAUFMANN, 1982). They are furred at birth, but eyes and ear channels are closed until 3 to 4 weeks of age. In the first month, the deciduous teeth begin to erupt and are gradually replaced by the permanent dentition through the 4th month (MONTGOMERY, 1964). The cubs are usually born in a tree den where they stay for 1½ to 2 months. The first excursions of the study animals away from their litter dens took place between day 48 and 56. Prior to emergence, many behavioural patterns had already developed:

TABLE 1. Structural features of raccoon calls

Parameter	Tonal calls		Mixed calls			
	1. Whistle	2. Squeal	3. Cry	4. Screech	5. Gecker	6. Grunt
	Exhaling mouth	Exhaling mouth	Exhaling mouth	Exhaling mouth	Exhaling mouth	Exhaling mouth
	Call production					
	Temporal characteristics					
<i>Repetition rate</i>						
Syllables/phrase: $\bar{x} \pm s$	1.2 ± 0.4	4.1 ± 3.8	2.0 ± 1.3	3.6 ± 3.7	3.4 ± 3.3	3.4 ± 3.3
Range	1-2	1-20	1-7	1-15	1-14 (25)	1-14 (25)
Number of phrases	40	140	49	32	1-ca. 10	70
<i>Syllable duration</i>						
$\bar{x} \pm s$ sec	0.35 ± 0.10	0.72 ± 0.39	0.32 ± 0.21	0.49 ± 0.12	0.26 ± 0.13	0.01-1.67
Range	0.11-0.57	0.05-1.86	0.13-0.94	0.15-0.68	0.08-0.67	0.01-1.67
Number of syllables	43	90	31	40	28	79
Number of animals	7	young of 3	5	3	5	2 ♀
Age	1.-10. month	litters, 1.-2. month	6. month-adult	2. month	5.-10. month	adult
<i>Intersyll. intervals</i>						
$\bar{x} \pm s$ sec	0.26 ± 0.13					
	Frequency characteristics					
<i>Fundamental frequency</i>						
Lower limit: $\bar{x} \pm s$ kHz	0.6 ± 0.15	0.9 ± 0.25				
Upper limit: $\bar{x} \pm s$ kHz	1.6 ± 0.25	2.2 ± 0.40				
First peak: $\bar{x} \pm s$ kHz	1.05 ± 0.15		2.1 ± 0.35	1.95 ± 0.25	2.8 ± 0.3	0.35 ± 0.05
Second peak: $\bar{x} \pm s$ kHz	1.35 ± 0.30		1.35-2.45	1.5-2.3	2.1-3.35	0.30-0.45
Highest peak: $\bar{x} \pm s$ kHz		2.0 ± 0.4				
	Gradations/simultaneous calls					
			cry-gecker	screech-growl	gecker-cry	—

Parameter	Noisy calls		Pulsed calls				
	7. Snort	8. Bark	9. Growl	10. Chitter 1	11. Chitter 2	12. Churr	13. Purr
	Exhaling nose	Inhaling mouth	Call production Exhaling mouth	Exhaling mouth	Exhaling mouth	Exhaling mouth	Ex- and inhaling mouth
Temporal characteristics							
<i>Repetition rate</i>							
Syllables/phrase: $\bar{x} \pm s$	1.0	1.1 $\pm$ 0.3	1.5 $\pm$ 0.7	2.7 $\pm$ 2.7		11.5 $\pm$ 12.4	up to several hundred
Range	—	1-2	1-4	1-19	1-ca. 20	1-75	
Number of phrases	17	37	76	305		102	
<i>Syllable duration</i>							
$\bar{x} \pm s$ sec	0.50 $\pm$ 0.16	0.10 $\pm$ 0.05	0.50 $\pm$ 0.19	0.35 $\pm$ 0.23	1.25 $\pm$ 0.38		
Range	0.19-0.66	0.02-0.19	0.16-0.80	0.05-1.14	0.69-1.95	0.15-1.32	0.02-2.63
Number of syllables	17	33	43	173	17	$n_{\bar{x}} = 13$	$n_{\bar{x}} = 13$
Number of animals	5	6	6	8	2 adult ♀♀	young of 3 litters, 1. mo.	4 adult ♀♀
Age	5.-8. month	2.-9. month	2.-9. month	3. mo.-adult			
<i>Pulsation</i>							
Pulses/syllable: $\bar{x} \pm s$				8.3 $\pm$ 5.3	16.5 $\pm$ 4.6	13.3 $\pm$ 8.0	(1->100)
<i>Pulse rate</i>							
Pulses/sec: $\bar{x} \pm s$				22 $\pm$ 2.4	14 $\pm$ 0.8	22 $\pm$ 2.4	47 $\pm$ 10.2
<i>Intersyll. intervals: <math>\bar{x} \pm s</math> sec</i>						0.2 $\pm$ 0.05	
Frequency characteristics							
	l	d	ld	ld	ld	d	ld
Mean frequency of lowest/-darkest band: $\bar{x} \pm s$ kHz	4.0 $\pm$ 0.9	1.35 $\pm$ 0.5	0.45 $\pm$ 0.2	0.8 $\pm$ 0.2	0.6 $\pm$ 0.1	0.6 $\pm$ 0.2	0.2 $\pm$ 0.1
Range	2.9-5.4	0.65-2.85	0.25-0.85	0.45-1.3	0.5-0.8	0.5-1.2	0.13-0.5
Gratations/simultaneous calls							
snort-growl	—	—	growl-snort	—	—	churr-squeal	—
			growl-screech				

Autogrooming (2nd week), exploration and interactions like social grooming and social play (4th week). Three calls are typical for the nestling period: Whistle, squeal and churr. All are present at birth (Fig. 2). The latter two are generally restricted to the nestling period and have their highest frequency of occurrence during the first month (Fig. 3). Whistles are still used by juveniles and adults, but they are most frequent during the first two months (Fig. 3). Several other calls were first recorded during the nestling time, but they were infrequent and not as commonly used as the nestling calls.

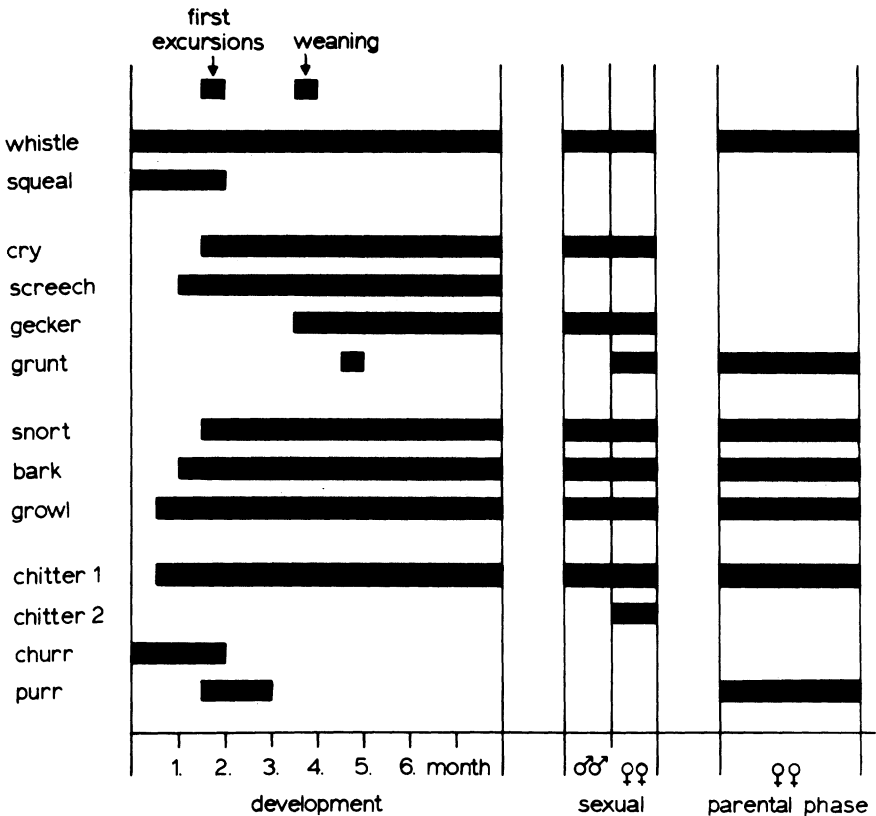


Fig. 2. Development and later use of raccoon calls.

### Juvenile phase.

After first leaving the den, raccoon cubs follow their mothers for increasing amounts of time during their nightly foraging trips (SCHNEIDER *et al.*, 1971). Solid food was first taken by the cubs under observation in the 9th



week. Weaning was accomplished by the 15th or 16th week. By the time of weaning, the juveniles seemed equipped with all basic behavioural patterns. The same holds true for the vocalizations (Fig. 2). With the exception of chitter 2, all calls were first recorded before or around weaning. Juveniles therefore possess nearly the complete vocal repertoire of adults.

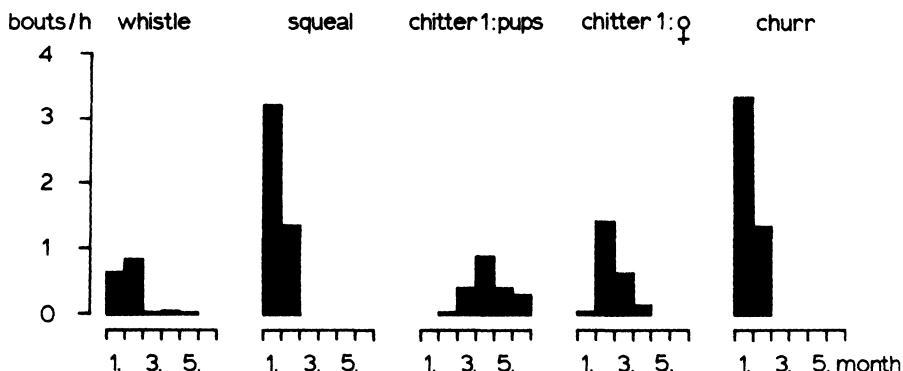


Fig. 3. Frequency of occurrence of the three nestling calls and of chitter 1 during the first 6 months per hour activity time per young or female. The activity time was calculated after 3 min scan samples and divided by the recorded bouts. The total activity time ranged from 10 to 35 hours per month for the females, from 57 to 118 hours for the young.

### Sexual phase.

Up to 60% of wild and captive females are said to reach sexual maturity during their first year (KAUFMANN, 1982). In the population in which the study animals were trapped, the percentage is much lower (SEIDENSTICKER, personal comm.). Males usually do not breed before their second year (KAUFMANN, 1982). Of the study animals, all yearling males copulated during February and March; also at this time, all had bacula of a length (>100 mm) considered to allow successful breeding (SANDERSON, 1961). Four of the five yearling females were successfully bred and gave birth to litters of 3 or 4 cubs in April or May 1983. Although the breeding season is a very vocal time, chitter 2 is the only call restricted to the sexual phase (Fig. 2). All other calls used during this time are also heard during occasional encounters of raccoons at food sources, resting places or from animals meeting while moving about.

### Parental phase.

After mating, female and male raccoons dissociate and with approaching birth, females become aggressive against males and other females. They

rear their litters alone (KAUFMANN, 1982). Two calls, grunting and purring, are by far most frequently utilized by females caring for cubs.

All calls not mentioned as typical for an ontogenetic or seasonal phase are uttered by juveniles or adults in the contexts described in the following section.

## II. Structures and contexts

In this section, structural and contextual features of the calls are presented. The calls are listed in four groups: Tonal, mixed, noisy and pulsed calls. Within the groups, they are organized, based on increasing repetition rate. Summarizing information about the structure of the calls is given in Fig. 1 and Table 1, about the contexts in Table 2. Synonyms of my descriptive terms for the calls are given, provided that there was either structural or clear contextual evidence for the same call in both *Procyon lotor* and *P. cancrivorus*.

### A. Tonal calls

Of the 13 calls found, two are tonal: Whistle and squeal. They are distinct from one another in both their temporal and phonetic characteristics.

#### 1. Whistle (Fig. 4a). (Quieken: LÖHMER, 1976, in *P. cancrivorus*).

*Structure:* Whistles are given as single syllables or in a sequence with intersyllabic intervals exceeding the short syllable duration. The syllables (Fig. 4a) are of bird-like tonal pitch. The fundamental lies between 0.6 and 1.6 kHz and carries the main energy of the moderate or low intensity call; up to two or more harmonics can be found. The fundamental is modulated. Two peaks are usually found, one in the first half of the syllable and one near the end, after which the frequency falls steeply. In more than 80% of the spectrographed calls, the second peak had a higher frequency than the first, resulting in a rising slope between the peaks. Whistles seem not to grade in any other call, but may precede or follow chitter 1's. Whistles are given by animals while stationary or in locomotion with the head lifted and the mouth slightly opened.

*Contexts:* Raccoons up to 6 months in age whistle most often in the den (87%; N = 107 bouts), generally when the female is absent (69%). Whistling occurs after a variety of startling circumstances (Table 3), the most prominent one being an accidental touch by the female or a sibling. Whistles are also given as an answer to a call of the female, for example



when she approaches the cubs in the den and chitters. The handraised young whistled when touched, while moving in a novel environment or when they heard noises after a period of silence.

Juveniles whistle, though rarely, in situations which can be best interpreted as calling to or searching for the mother. For example, a male, 4 months old, played for a long time in a den with another, unrelated juvenile male. All other members of the two families had retired to the elevated branches to rest. As the male left the den, he gave two whistles, then went chattering into the other cage where his mother and brothers rested upon different branches. He approached one of his brothers, stopped after sniffing in his direction, joined his mother who had been watching him, tested and groomed her and finally rested in body contact with her.

During the breeding season, whistles were recorded from males while moving on the ground or when touched by another male without preceding visual contact, from males or females in the pauses of a fight or from males while crouched approaching a dominant male, the only situation in which whistles were addressed to another animal.

Although used in a variety of contexts, whistling may be based on one underlying motivation. It is basically a startling call, given under mild distress and elicited by novel or unusual stimuli and situations.

Only 19% of the whistles given by young raccoons evoked an observable response by the mother of the caller (Table 3). The fact that females approached their young after a whistle suggests that they may be highly attracted by this call although this is contradicted by the small number of responses. This may partly be due to the specific caging situation: The elevated resting places gave the females an excellent overview and allowed them easily to decide whether or not a whistling cub needed their help. Undirected whistles uttered by juveniles or adults were not seen to evoke any specific response other than a turn of the head in the direction of the caller; directed whistles could elicit a chitter 1 from the dominant callee.

2. Squeal (Fig. 4 b-d). (whine: COLE, 1912; cry: WHITNEY & UNDERWOOD, 1952; Quärren: LÖHMER, 1976, in *P. cancrivorus*).

*Structure:* Although squeals are highly variable, several features allow the call to be lumped in a class distinct from all other calls. Squeals are usually fairly repetitive as long syllables alternate with short intervals. The amplitude, too, is highly variable between and even within bouts. In pure

squeals, a fundamental, carrying the main energy, and several harmonics can be found (Fig. 4b). The fundamental increases steeply at the beginning, has an extended phase with a horizontal course in the middle and decreases at the end, covering a range between 0.9 and 2.2 kHz. Superimposed on this general pattern are modulations with a rate of 15 to 25/sec, resulting in a sound reminiscent of a whinneying horse. Squeals often grade from or into churrs or are given simultaneously (Fig. 4c, d). This may indicate a different origin in the vocal apparatus of the two calls. Squeals are likely to be produced by the vocal chords and are uttered through the opened mouth. The caller is lying, sitting or moving. Squealing is not generally linked to a visual display.

*Contexts:* Squeals are uttered almost exclusively by young in the den (99%; N = 268 bouts). Prominent contexts include various aversive situations (Table 3). Squealing by cubs being groomed by the mother was usually restricted to the beginning of a grooming bout when she grabbed the cub and brought it in a position suitable for grooming. When she held the cub quietly, it started gradually or abruptly to churr and squealing ceased. The hand raised pups squealed when having troubles with the milk bottle or when being restricted while trying to walk. These observations jointly suggest that squealing is a distress call, given with varying intensity according to varying degrees of distress.

Even if squealing is uttered undirected, it may be a message particularly for the mother, especially since siblings do not react to one another in the first month when squealing is most frequent. In 96% of all squealing bouts, the young had body contact with her. A considerable percentage of squeals elicited an observable response by the female (Table 3), primarily solicitous behaviours like sniffing or grooming the cub, pulling it with a forepaw to a nipple, carrying it by a grip around the neck or touching it with a forepaw. In some cases, the females looked out of the den as soon as a young started to squeal, most likely a response to detect possible predators attracted by the call which is often of considerable intensity.

## **B. Mixed calls**

Four calls have a mixed structure: Cry, screech, gecker and grunt. All are of low to moderate repetition rate, but are quite different in their amplitude and main frequencies. The loudest call, screech, as well as one of the softest, gecker, belong to this group. Both are relatively high-pitched like the cry. Grunt varies in amplitude, but is constantly low in pitch.

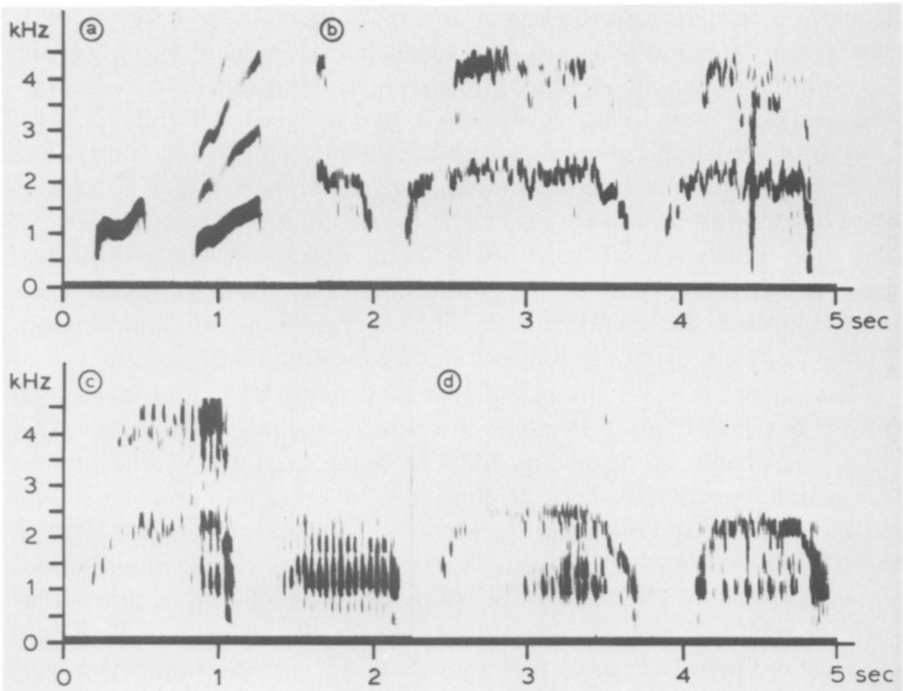


Fig. 4. Tonal calls. a. Two whistles, given with a longer interval as shown here (♀, one month old). b. squal, three syllables out of a longer phrase, the first syllable is cut (young, 5 days). c. squal, grading into a churr; two syllables out of a longer phrase (young, 1 day). d. squal, superimposed to a churr; two syllables out of a longer phrase (young, 2 days).

1. Cry (Fig. 5a, b). (*cri aigu et bref*: RICARD & DORE, 1977).

*Structure*: Cries are moderate to high intensity calls, uttered most often as single syllables, but also in phrases of a few with irregular intervals. The syllable duration varies from brief to long, but most recorded cries were brief or short. The spectrograms (Fig. 5a, b) are characterized by a concentration of energy around 2.1 kHz. These bands may have a modulated structure similar to that of squeals which is superimposed by noise, and they lack the rising and falling slope at the beginning and end. One or several harmonic-like bands may occur. Cries intergrade with geckers as they become more repetitive and more noisy. They share the sharp beginning with geckers; unlike those, they are however rather tonal at the inception. Pure cries are given with no obligatory visual display by animals involved in an interaction.

TABLE 3. Contexts of the nestling calls. The data include observations during the first 6 months. The numbers represent bouts

	Whistle		Squeal		Churr	
	n	%	n	%	n	%
Contexts of the caller						
Searching for, loosing a nipple	2	2	65	43	20	7
Being handled and/or groomed by the female or a sibling	1	1	64	42	257	84
Being accidentally touched by the female or a sibling	28	35	13	8	28	9
Responding to a call of the mother	6	8	—	—	—	—
Apparently sleeping, suddenly awakening	16	20	—	—	—	—
After a noise nearby	14	18	—	—	—	—
Others	13	16	10	7	1	<1
Sum	80	100	152	100	306	100
Behavioral changes in the female after a call						
Female approaches pup	8	9	1	<1	—	—
Female shows solicitous behaviour	4	4	130	52	6	2
Female looks out of the den	5	6	30	12	16	5
No change in the female's behaviour	72	81	91	36	302	93
Sum	89	100	252	100	324	100

*Contexts:* Early cries occurred exclusively in social play. Whenever I was able to detect the immediately preceding behaviour of the players, cries were given by an animal that was being bitten by the other. Later, cries were heard in severe agonistic encounters such as being bitten by a conspecific defending his food. During the breeding season, males or females cried, often intergrading with geckers, while being attacked (39%; N = 62 bouts). Females used cries when they were mounted by a male and tried to escape his grip (32%) or during copulations when the male changed his position abruptly (29%). RICARD & DORE (1977) also heard males crying during copulations. All these contexts, though variable, suggest that the cry is a call expressing immediate pain.

Since cries are always given in complex interactions, it is not surprising that the behavioural sequences continued variably after a cry. Players would stop and separate, or would continue to wrestle. Animals in agonistic encounters often separated immediately or with some delay, but this may be more a consequence of the original attack than of the cry

itself. They could also stay together and get involved in a fight or the caller showed submissive gestures such as licking the mouth of the opponent, lying on the back, or geckering. Coy females freed themselves and ongoing copulations continued despite a cry.

2. Screech (Fig. 5c). (screech: STUEWER, 1943a; scream: WHITNEY & UNDERWOOD, 1952).

*Structure:* Screech, by far the loudest of all calls, is given in single syllables or, more frequently, in phrases of two to 15 syllables. The syllables are short to long and the intersyllabic intervals fairly constant in their short duration. The frequency range covers from 1 to 6 kHz, carrying typically a darker, nearly tonal band in its lower range (Fig. 5c). This band may show a modulated course with a repetition rate similar to that of squeals suggesting a possible derivation of screeching from the squeal. The relationship of the two calls is further suggested since screeching appears in ontogeny at the time the squeals become infrequent (Figs 2, 3). Screeches, given with an open mouth, can be accompanied by urinating or defecating and the call may be superimposed on or grade from or into a growl.

*Context:* Screeching was never heard in the usual caging situation. It was uttered only by animals that were grabbed in the den or netted or caught in the cage. WHITNEY & UNDERWOOD (1952) report similar situations from the wild. They further stated that nearby raccoons will jump out of trees after the screech of a conspecific. The study animals froze in the den or showed alarm behaviour (rush to an elevated place and freeze there) when I opened a den and before a young started to screech. No further responses were therefore seen after screeching. Once, however, a female, whose 50 days old young screeched in the den, came rushing and forced me to leave the cub where it was. There is thus little doubt that screeching is an alarm call, uttered under high distress. In the wild, the call may work to deter a predator by its surprising loudness as well as cause the mother to rush to her pup's defense.

3. Gecker (Fig. 5d).

*Structure:* Gecker is a low to moderate intensity call, given in phrases of a few to about 10 syllables of brief or short duration. The syllables are uttered in a rapid succession during one burst of exhalation. The intersyllabic intervals are short. The syllables show a sharp, click-like onset, carrying energy up to 16 kHz and beyond. One or several discrete energy bands occur between 2.3 and 3.3 kHz (Fig. 5d), superimposed by noise.



Different syllables within the same phrase may differ in the pitch of the bands carrying the highest amplitude, resulting in a modulated pitch throughout the phrase. In some syllables, the click-like units are repeated, giving the syllable a partly pulsed character. Geckers intergrade with cries. A geckering raccoon faces a conspecific with his head lowered and his neck stretched; the ears stand upright or are laid back and outwards and the lips are retracted. In contrast to the former calls, all these characteristics indicate a call directed to a particular recipient rather than a 'two-whom-it-may-concern-call' (ALTMANN, 1967).

*Contexts:* Geckers were given only rarely by young in their first half year, either during social play or when approaching an alien female, the mother or another, dominant young. During the breeding season, the call became frequent and was used by members of either sex. Females not ready to copulate addressed it to approaching or mounting males (33%; N = 99 bouts), often after a series of hostile calls. Some males geckered in front of a coy female (12%), others while approaching or being approached by a dominant male (34%) or during fights (16%). Geckering was frequently linked with or followed by sniffing and/or licking the recipient's mouth. This, the crouched posture and the often clearly subdominant position of the caller in comparison with the recipient suggest that geckering signals active submission and serves subdominant animals to appease dominant ones. Similar, though more tonal calls are used with the same visual displays in the same general contexts by other members of the *Canoidea* (e.g., canids: FOX & COHEN, 1977). Corresponding to this view, geckering has little immediate impact to the recipient's behaviour. Play bouts were more often continued than interrupted after a gecker; dominant animals, approached and/or licked by a geckering conspecific, either shortly licked his mouth or face or did not show any change in the ongoing behaviour. Geckering may, however, be of importance in reducing escalation to violent behaviours.

#### 4. Grunt (Fig. 5e). (growled warning: STUEWER, 1943b).

*Structure:* Grunts are low pitched calls of varying intensity, usually given in phrases of several syllables. The syllable duration is double peaked: Brief and short grunts have a mean duration of 0.20 sec, long ones a duration of 1.3 sec. It is remarkable in terms of signal discreteness that growl, a call of similar frequency (Fig. 1), has an intermediate duration between short and long barks (Fig. 6). Long and short barks can be uttered alone, in one type or mixed phrases. Mixed

phrases usually start with short and end with long syllables. The frequency covers a range from the baseline up to about 2 kHz (Fig. 5e). A dark band is usually found between 0.1 and 0.6 kHz, which may be of rather tonal structure and have regular modulations at a rate of 5 to 15 per sec, although it is noisy in others. Frequency and amplitude of the first inflections in long grunts tend to be higher than in the later ones and only these carry, if any, harmonic-like structures. Grunts are given in a four leg stance with pilo-erection and are accompanied by tail rattling.

*Contexts:* Grunting was recorded exclusively against me and never a conspecific (N = 47 bouts). With two exceptions (a juvenile male and a copulating female), it was restricted to females with young aged less than 5 months. The usual eliciting situation was when a female sniffed or saw me in close proximity to the cubs. One female who grunted regularly at me, often gave some short grunts as she neared and became aware of me. Then she retreated a few steps and uttered some long grunts. Another gave short, noisy grunts after visual contact with me, but used long, mixed grunts after getting aware of my presence, but not of my exact location, by scent.

The response of young to the grunting of their mother depends on their age. In pups aged less than 55 days I could not detect any response; they even continued to sleep in the den. Older young, however, always showed a response, which varied depending on their physical location. Cubs in the den froze (1 × observed); on branches they either approached their mother (2 ×) or looked in the direction she was grunting (1 ×). Staying on the ground or, a few times, on branches, they showed alarm behaviour (16 ×). Thus, grunting is a warning call of the mother to her young whose adaptive response matures when it is needed, namely when the pups start to leave the den. For a potential predator, the same call could also have a deterrent function.

### C. Noisy calls

The three calls belonging to this group, snort, bark and growl, are easily separated from one another by their different origin in the vocal apparatus and by consistent differences in their temporal and frequency features (Fig. 1, Table 1).

#### *Structures.*

1. Snort (Fig. 7a, b). (hiss: WHITNEY & UNDERWOOD, 1952; BARASH, 1974; MELLEN, 1976).

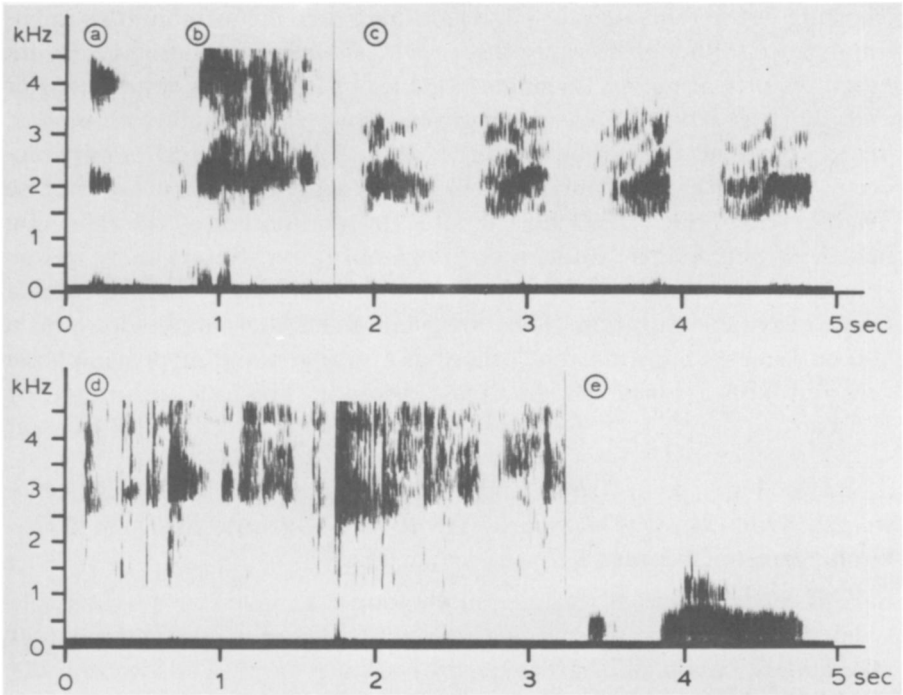


Fig. 5. Mixed calls. a. short cry ( $\sigma$ , 8 months). b. long cry (adult  $\varnothing$ ). c. screech; four syllables out of a longer phrase ( $\varnothing$ , 2 months). d. gecker; part of a phrase ( $\varnothing$ , 5 months). e. grunt; phrase containing one short and one long syllable (adult  $\varnothing$ ).

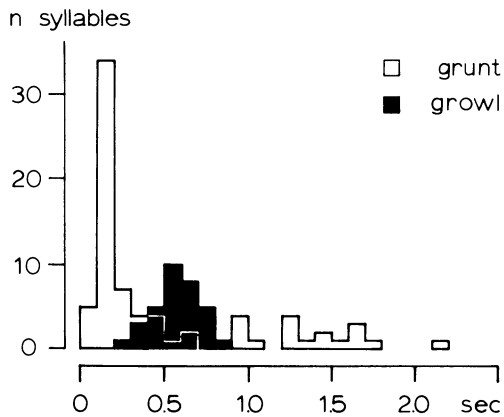


Fig. 6. Syllable duration of grunts (white) and growls (black). Growls of animals less than two months old are not considered.

Snorting is the sole nasal sound considered to be of communicative importance, although several others such as sniffing or sneezing may be heard. Snorts are given as single syllables of low to moderate intensity and short duration. The spectrograms (Fig. 7a, b) show a burst of dispersed sound energy between 1.5 and 13 kHz. Several bands may occur, though none of them has a higher amplitude than the others. There is, however, often a horizontal shift in amplitude as the calls fade in, then get louder until they stop abruptly. Snorts may occur simultaneously with growls (Fig. 7b), with which they share the same range in syllable duration. They are often given alternating with growls and barks or with grunts. The caller has a sitting, standing or lying position and faces a conspecific at a close distance. The ears are upright or laid back.

2. Bark (Fig. 7d, e). (short and sharp barks: COLE, 1912; cough-like snarls: STUEWER, 1943a; snarl: TEVIS, 1947; grunt: MELLEN, 1976; Drohgrunzen: LÖHMER, 1976 in *P. cancrivorus*).

Bark is an explosive, brief and usually loud call, given mostly in single syllables with a variable energy distribution. There is one or sometimes several dark bands, all characterized by a sharp onset. The lowest or the second band carries the main energy. The mean frequency of the darkest band is higher than in the other explosive call, growl. Barks seem not to grade into any other call, but are often given in sequences with others, either preceding or following snorts and/or growls. The caller faces a conspecific at a close distance; the ears are laid back and often the teeth bared.

3. Growl (Fig. 7b, c, d). (growl: COLE, 1912; HAMILTON, 1936; MELLEN, 1976; snort-growl: TEVIS, 1947).

Growls are loud calls of moderate repetition rate. The syllables are short. The main energy is arranged in a band between the baseline and 0.5 to 1.0 kHz. The frequency seems to decrease as the animals grow older. The main frequency of growls given by 3 raccoons less than 2 months old was  $0.75 \pm 0.10$  kHz, the one in 3 other individuals, 3 to 8 months old, was  $0.35 \pm 0.05$  kHz. The syllable duration, however, seems to increase with increasing age: The mean syllable duration in the younger cubs was  $0.25 \pm 0.10$  sec, in the older ones  $0.57 \pm 0.14$  sec. Growls intergrade and occur simultaneously with snorts (Fig. 7b) and screeches. Growls are usually given in standing position with pilo-erection. The caller's head, facing a conspecific, is held downwards and his ears look upright. This

position is either held while growling or, as in more intensive growls, is followed by a fast upward movement of the head while calling or even by an attack jump or a short pursuit.

### *Contexts.*

The three noisy calls are all used chiefly in intraspecific, hostile contexts (Table 4). Young in their first half year addressed most calls to young of other litters, although they had had access to each other only after the end

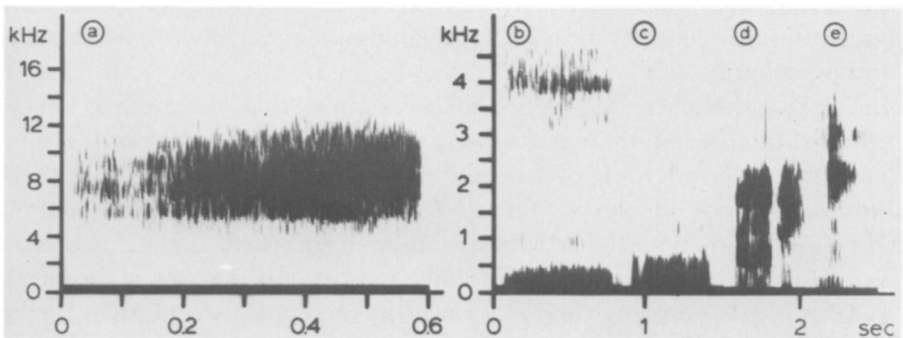


Fig. 7. Noisy calls. a. snort ( $\sigma$ , 7 months). b. snort, superimposed to a growl ( $\sigma$ , 7 months). c. growl ( $\sigma$ , 4 months). d. growl, followed by a bark ( $\varnothing$ , 2 months). e. bark ( $\sigma$ , 6 months).

of the 4th month. The females, too, called mostly to members of other families and never to their own cubs. For all three calls, defensive contexts were most prominent, although ontogenetically all were first used during social play. Snorting and barking were heard most frequently from animals which had been approached while resting. Growls were prominently used for defending food. Offensive contexts, that is an animal who snorts, barks or growls while approaching another, were rare and for most instances accounted a single, low ranking female.

During the breeding season, females were far more often callers than males. They prominently snorted and barked to defend themselves against approaching or mounting males. During copulations the males called while preventing other males from displacing them. Rarely, the females used these calls to get rid of an interruption. Members of either sex could snort, bark or growl when being attacked or during fights.

Observations of the behaviour accompanying these calls and in trapped animals, in which these calls are likely evoked indicate that

snorting, barking and growling may be based on different degrees of arousal. A slow approach of a person to a trapped animal usually elicits a snort, which may grade into or be followed by growls if the person stays close for some time. A fast or sudden approach leads to growls, sometimes alternating with barks. While snorting the ears of the caller may take on every position from upright to laid back. In growling, they usually stand upright and the attack or pursuit (intention) sometimes following indicates an animal strongly ready to defend his resource if the callee does not retreat. Barking, often given with an open mouth threat and sometimes followed by a bite, but with a facial expression also indicating fear, is used most likely by animals in a conflict between fear and aggression.

The response of the callees are no less complex than the contexts of the callers. Often, when there is a subsequent reaction, one of the opponents leaves the place after any of the three calls, therefore suggesting that they have a distance increasing effect. But all of these calls are parts of complex interactions. Furthermore they were used among animals individually known to each other (which may also be the case in the wild: BARASH, 1974), holding different places in the apparent hierarchy. It is therefore not surprising that after a snort, bark or growl it is not always the callee that leaves, if anyone does. Depending on who calls to whom, caller or callee may retreat, both may stay while facing each other, one may attack if its opponent shows no sign of submission or, in contrast, a subdominant may instantly retreat after the first growl of a dominant. The specific functions of the different calls (if they are irrespective of the accompanying displays) can therefore not be derived without examining the relations among the individuals who are concerned, a problem to be dealt with elsewhere.

#### D. Pulsed calls

Four calls, all repetitive to a variable extent, have pulsed syllables: Chitter 1, chitter 2, churr and purr. The purr is clearly distinct from the others by its high pulse rate and its low frequency. Churr and chitter 1 differ in their repetition rate and their phonetic structure, but have the same mean pulse rate. Chitter 2, though structurally resembling chitter 1, is characterized by its low pulse rate.

1. Chitter 1 (Fig. 8a, b, c). (whimpering cry: COLE, 1912; low grumbling purr, soft snore: TEVIS, 1947; Girren (Zirpen): LÖHMER, 1976, in *P. carnivorus*).

TABLE 4. Callers, recipients and contexts of snorting, barking and growling during development, parental and sexual phase. The numbers represent bouts. Were different calls given by one animal during one encounter, every call type is counted only once. Graded calls (snort-growls) are listed in either of the two calls

	Young, 1.-6. month						Females with young						Breeding season					
	snort		bark		growl		snort		bark		growl		snort		bark		growl	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
	Callers and recipients																	
Against siblings/own young	14	17	18	27	29	37	—	—	—	—	—	—	—	—	—	—	—	—
Against alien young	64	78	49	73	41	52	4	—	—	—	—	—	—	—	—	—	—	—
Against mother	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Against alien adult female	3	4	—	—	6	8	2	—	—	—	—	—	—	—	—	—	—	—
Against observer	1	1	—	—	3	4	3	—	—	—	—	—	—	—	—	—	—	—
Male against male	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Male against female	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Female against male	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Female against female	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sum	82	100	67	100	79	101	9	—	—	—	—	1	—	—	—	—	—	—
	Contexts of the callers																	
Being approached, touched while	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
- resting, grooming, exploring	46	60	24	50	17	27	4	—	—	—	—	—	—	—	—	—	—	—
- feeding, drinking, dousing	15	20	4	8	23	36	—	—	—	—	—	—	—	—	—	—	—	—
Female, approached and/or mounted by male	1	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Female, approached by female while standing or in locomotion	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Male, defending female during copulation	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
During social play or fights	9	12	15	32	13	21	—	—	—	—	—	—	—	—	—	—	—	—
Getting aware of observer	1	1	—	—	3	5	3	—	—	—	—	—	—	—	—	—	—	—
Approaching a resting/grooming animal	1	1	3	6	5	8	—	—	—	—	—	—	—	—	—	—	—	—
Approaching a feeding animal	4	5	1	2	2	3	—	—	—	—	—	—	—	—	—	—	—	—
Approaching a copulating pair	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sum	77	100	48	100	63	100	9	—	—	—	—	1	—	—	—	—	—	—

*Structure:* Chitter 1 is a call of moderate repetition rate and varying intensity, given rarely as single syllable, usually in phrases of a few and quite often in bouts of several phrases. The syllables are brief to long, depending on the number of pulses per syllable. The pulses include two different parts, both pulsing at the same rate, but often with slight delay in respect to one another. One is a click-like structure of very brief duration (below 20 msec), carrying energy up to 8 kHz in some calls (Fig. 8b), being only outlined below 4 kHz in others (Fig. 8c). The other structure is usually of longer duration (up to 40 msec) and its energy is often divided into harmonic-like bands (Fig. 8a, b). The fundamental contour follows a M- or W-like course, depending on which lines are accentuated. Both parts of a pulse are often linked in the fundamental band by noisy darkening which result in a distinct horizontal band over the whole syllable (Fig. 8a-c). The few spectrograms from chitter 1's of a pup 24 days of age (the earliest record of this call, not included in Table 1) show a lower pulse rate of 13 to 19 pulses per sec. Chitter 1 does not grade into any other call. It is sometimes given preceding or following whistles. Chattering raccoons call in any position or in locomotion. Although several behaviours, such as testing a conspecific with the forepaws or sniffing, can accompany the call, there is generally no visual display and the caller does not regularly face another at a close range.

*Contexts:* Unlike any other call, chitter 1 is regularly given by raccoons of every age and sex class except neonates. It therefore includes different contexts. Nevertheless, its use is restricted to a few situations in any of the phases (early development, sexual and parental phase; Table 5).

Raccoon pups and juveniles utter chitter 1's mainly as they approach the stationary or follow the moving mother. They often continue to chitter or even start only as they reach her while sniffing and/or testing her with the forepaws. The handraised ones chattered while expecting food or while seeing or hearing me outside the cage without being able to reach me. These observations, and the fact that the highest frequency of chitter 1 occurs around weaning (Fig. 3), suggest that young use chitter 1 as a begging call. This is further supported by the observation that chattering 1 increases in juveniles as they get more and more hungry. The female's response to the chitter 1's of her young varied with their age. As the young grew older, the females responded less often with establishing, but more with breaking the contact. However, this was also the case if she was approached by a silent young and may therefore indicate a general feature of the pre- and postweaning time rather than a specific response to this particular call.



More than half of all chitter 1 bouts did not lead to any observable response by the female. This is of special interest if one looks at the chitter 1's given by the female and the regular responses of the young.

Females with young chattered not only less than did their young, but also with a temporal peak at a different time, namely in the second month (Fig. 3), around the time their cubs began to leave the den. Two contexts were prominent. A female chattered to lead the way to the food after she had descended from her resting place or she chattered after feeding while going back to rest or to inspect the young in the den. The other context occurred after visual contact with me at some distance or after sniffing out of the cage and is therefore likely to express a soft warning to the young. The pups responded in 90% of the bouts, either by approaching her, by making visual contact with her or by giving a call themselves (whistle, chitter 1).

Chitter 1's uttered by males and, rarely, by females during the breeding season, were given most often by animals moving or running on the ground or upon branches. Some males also called during copulation attempts, whereas they stayed silent during successful mounts. Quite often, yearling males and females approached their mothers while chattering even after her next estrus. The animals surrounding a chattering raccoon at this time seemed to pay little attention to the caller and no response other than an occasional head turn in his direction was observed.

Despite the variety of contexts, chitter 1 may be based on a few underlying motivations. On one hand, several contexts can be described as situations in which animals try to achieve a goal unachievable without a conspecific (such as milk in the young or a female for the males in the reproductive time). On the other hand, chitter 1 serves as a leading call for females with young and is in this case a strong cue for summoning the cubs.

2. Chitter 2 (Fig. 8e). (grumble: WHITNEY & UNDERWOOD, 1952; roucoulement: RICARD & DORE, 1977).

*Structure:* Chitter 2 is a very low intensity call, uttered in bouts of one to some dozens of long syllables. The intersyllabic intervals are also long and often exceed the syllable duration. The syllables contain up to more than two dozen pulses lasting for 65 to 80 msec. The pulse rate is therefore the lowest of all pulsed calls. As in chitter 1, the pulses consist of two different elements (Fig. 8e): A lambdoid element, carrying energy up

TABLE 5. Prominent contexts of and behavioural responses to chitter 1 during development, parental and sexual phase. The numbers represent bouts

	Young up to 6 months		Females leading young		Breeding season	
	n	%	n	%	n	%
Contexts of the caller						
Young/yearling following mother	130	68			28	31
Young sniffing and/or testing mother, trying to suckle	27	14				
♂♂ (exceptionally ♀♀), moving on ground or upon branches	18	10			46	51
Mothers before, after feeding			23	56		
Mothers after sniffing out of the cage or getting aware of the observer			12	29	3	3
Mothers before, during and after moving their cubs			6	15		
♂♂ approaching a like-aged ♀ or trying to copulate					5	6
Others	16	8			8	9
Sum	191	100	41	100	90	100
Behavioural responses of the recipient <sup>1)</sup>						
	Female after a chitter 1 of a cub		Cub after a chitter 1 of the mother			
	n	%	n	%		
Approaching, following	10	5	17	44		
Establishing sight contact	26	14	8	20		
Giving a call (chitter 1, whistle)	2	1	9	23		
Breaking contact by going away	44	23	—	—		
Others	5	3	1	3		
No behavioural response	103	54	4	10		
Sum	190	100	39	100		

<sup>1)</sup> Chitter 1's during the breeding season are not considered as usually not even a recipient could be made out.

to 6 kHz, alternates with a longer element whose main energy is concentrated between 0.35 and 0.9 kHz. It may also carry energy above and shows a lambdoid structure then as well. Chitter 2 has no graded transitions into other calls and is uttered with no visual display.

*Context:* Chitter 2 (N = 127 bouts) has been heard only from females during copulations. Females start uttering it soon after being mounted,

probably when intromission takes place. The rhythm of the call follows closely the pelvic thrusts of the male (see also RICARD & DORE, 1977). The call becomes somewhat louder as the copulation goes on and lasts to its end or until the pair is approached by another raccoon or until one of the partners changes its position abruptly. No behavioural changes in the male were detected after the onset of the female's chitter 2.

3. Churr (Fig. 8d). (purr: WHITNEY & UNDERWOOD, 1952; schnurren: LÖHMER, 1976, in *P. carcivorus*).

*Structure:* Churr is a low to moderate intensity call of high repetition rate. The phrases contain up to 75 syllables, either short ones or long ones, rarely mixed. The intersyllabic intervals are of fairly uniform, short duration. The main energy is usually concentrated in the lowest of the up to 6 bands which has a slightly lower mean frequency than chitter 1. The mean pulse rate is the same as in chitter 1. The syllables, however, are of longer duration and contain more pulses. The pulses seem of simpler construction than those of chitter 1's since only one element is repeated (Fig. 8d). It consists of a W- or M-like form, sometimes with the bars apart, sometimes compressed to a click. The simpler structure of churr pulses may be caused by a different position of the jaws while calling. Churrs unlike chitter 1's are given with the mouth open. Churrs, uttered in various positions, but not in locomotion, may be given simultaneously or intergrade with squeals (Fig. 4c, d).

*Contexts:* Churrs were recorded almost exclusively from pups in the den (98.5%; N = 327 bouts). The most common situation was when a female took one of the cubs and held it with her forepaw<sup>r</sup> to lick its anogenital region to stimulate urination or defecation. Other parts of the body are also licked and nibbled by the female and the pups churr then as well. They start usually right after the female has begun with her rhythmic movements of licking or nibbling and continue until this tactile stimulation stops. There was usually no change in the female's behaviour after the onset of a pup's churr (Table 3). In the second month, as the young started to groom each other more frequently, churrs were also uttered in this situation suggesting a rather mechanical response to tactile stimulation. In the handraised pups, two situations led to churring almost exclusively during the first 1½ months: Either being stimulated with a paper towel in the anogenital region or being petted in any part of the body, but for the longest period during development, around the neck. In hungry pups, churring was likely accompanied by a rapid opening and

closing of the jaws which produced an audible noise and the appearance of saliva in the corners of the mouth. Only once was churring given by a pup actually suckling from the bottle. In all other cases the handraised pups either churred, or they suckled. The same holds true for the mother raised cubs. Churring becomes very infrequent or ceases after the young start leaving the den. This is surprising insofar as the main eliciting situations last for weeks (stimulation for elimination) or months (social grooming) after this time.

4. Purr (Fig. 8f). (purr: WHITNEY & UNDERWOOD, 1952).

*Structure:* Purring phrases, calls of low intensity, are the most extended calls heard from raccoons, lasting up to several min and containing up to several hundred syllables. The syllables vary considerable in duration. Often, several short syllables are followed by one long one, probably reflecting one in- and exhaling cycle. The pulse rate is far higher than in any other pulsed call. The structure of the pulses seems to be simple, churr-like. The mean frequency of the lowest band, usually carrying the main energy, is lower than in the other pulsed calls (Fig. 8). Some spectrograms miss any bands above that near the baseline, some have up to three further bands. Purring occurs in sitting or various lying positions and the caller shows no simultaneous visual display. No gradations have been detected nor is purring preceded or followed by any other call.

*Contexts:* Purring in adult females occurred almost exclusively during nursing (99%; N = 84 bouts) and was therefore temporally confined to the first four months of their cub's life and spatially almost entirely to the litter den. Only a few nursing bouts were observed without purring. A fairly usual sequence was the following: After a resting bout, the female approaches the den where the cubs are resting, too. She enters and starts to lick a young, while the others search for a nipple and begin to suckle. After grooming one or several young, one after the other, she takes a sickle-shaped position and starts to purr when all cubs suckle quietly. After several min, the regular rhythm of purring gets faster until it stops and the female leaves the den. The young usually do not change their behaviour when the female starts to purr. A few times, a cub who was out of the den entered when the female began to purr.

Purring in young was heard only 19 times between the end of the 2nd and the end of the 3rd month from young being groomed by the mother or a sibling or during nursing bouts. These contexts are the same as those in which churring occurred earlier. This, in addition to the similar

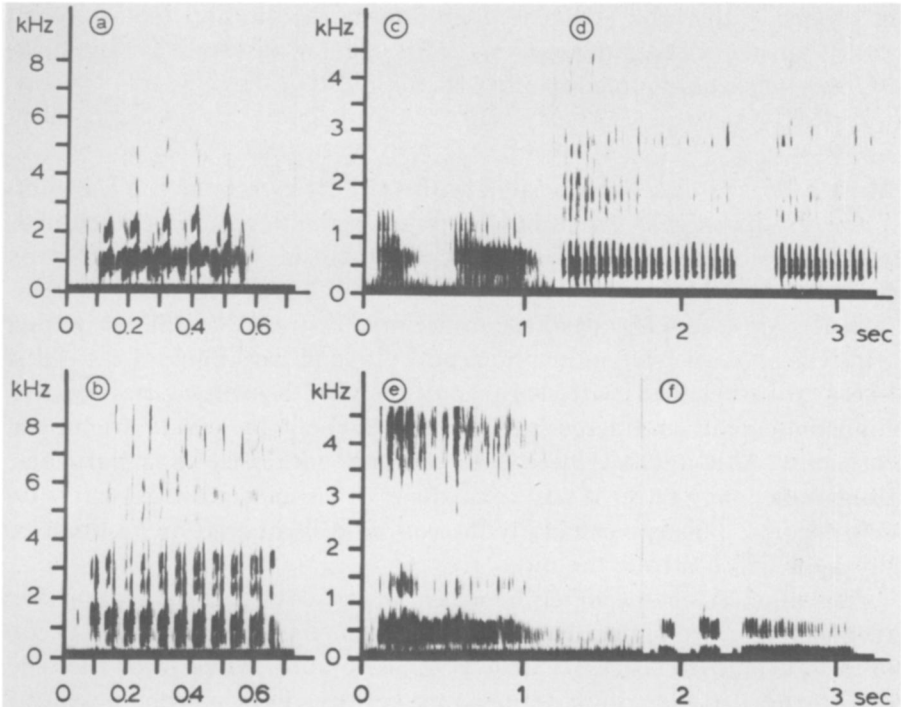


Fig. 8. Pulsed calls. a. chitter 1 ( $\sigma$ , 1 month). b. chitter 1 of the same  $\sigma$ , 7 months old. c. chitter 1 ( $\sigma$ , 4 months old, another individual as in a and b). d. churr; two syllables of a much longer phrase, the second is cut (young, 10 days). e. chitter 2; one syllable (adult  $\sigma$ ). f. purr; two short and one long syllable out of a much longer phrase (adult  $\sigma$ ).

structure of churrs and purrs suggests that the churr is the ontogenetic forerunner of the purr.

## Discussion

### *Structure.*

Most raccoon calls are clearly separated from one another by either phonetic and/or temporal features. The repertoire is therefore largely discrete. Nevertheless, graded transitions between calls or simultaneous utterance of two calls are found. With 13 basic call types, 78 call-to-call gradations could theoretically occur, but only 4 were found (Table 1). Various degrees of stereotypy occur with discrete signals. While some are highly variable in respect to frequency, quality and temporal features (squeal, cry, gecker, grunt), two patterns may generate higher stereotypy

in others: Either the syllables are uniform in duration (snort, bark, growl) or the calls are repetitive with regular intersyllabic intervals (screech) or even double repetitive as the pulsed calls.

#### *Contexts.*

Most calls are closely associated with one or few contexts (Table 2). Three groups of calls given under similar motivations can be discerned. Distress calls are utilized in situations where the caller is likely to be fearful or frightened. Different calls express different degrees of distress. Whistles are uttered by nestlings under mild distress. Squealing covers a wide range of aversive motivations and the high variability of the call is likely to correspond with various degrees of distress. Cries express immediate pain and screeches are uttered only by highly frightened raccoons. Although all these calls are not addressed to a particular conspecific, they have, if any immediate, a distance reducing effect on conspecifics. This is particularly the case in calls uttered by nestlings or juveniles which attract the mother.

Hostile calls on the other hand are always directed to a particular recipient and are generally accompanied by visual displays. They are used to defend resources, a mate or oneself (snort, bark, growl) or the cubs (grunt). Calls and accompanying gestures have a repelling effect, the most impressive in the case of a grunting mother warning her cubs.

Contact calls are given by raccoons approaching another in a non-aggressive intention (gecker, chitter 1) or by animals which are already in body contact with one another and involved in a non-aggressive interaction (chitter 2, churr, purr), thus by friendly motivated animals. Contact calls used among distant animals have an attracting function, the most obvious one in chitter 1's exchanged between mother and young. The calls uttered while having body contact evoke no overt response at all. They are likely to serve as excitation indicators by changes in repetition rate (GOULD, 1971, 1983) and to have tonic effects (SCHLEIDT, 1973) in maintaining the ongoing behaviour of the recipient.

#### *Structure-motivational relations.*

The structural similarity of the calls applied in similar motivations is striking. All distress calls are relatively high in frequency and either tonal or have tonal components. Hostile calls are noisy and only grunting may have a tonal element. Contact calls are pulsed (at least partly in geckering) and mainly non-tonal. The first two groups fit excellently with motivation-structural rules (MORTON, 1977, 1982) and represent con-

trasting stimuli as TEMBROCK (1967) states for attracting (affin) versus repelling (diffug) signals. Between the different distress and hostile calls, structure and motivation interplay largely as predicted by MORTON. The increasing frequency from growl to bark to snort parallels a change from aggression to a conflict between aggression and fear as indicated by the facial expression. The basic frequency of cries and screeches, calls given under high distress, are higher than those of whistles, a call uttered while mildly distressed. Intra-call variation shows similar trends in some calls: *e.g.*, grunts, given by a female facing an intruder are noisy, while those uttered before the intruder is spotted (and by a female likely to be more fearful) contain tonal elements.

The contact calls, however, deviate from motivation-structural rules. Though used in clearly non-aggressive contexts, they are rather low in basic frequency and noisy in quality. The reasons for these deviations may differ in contact calls generally used by distant and those by animals in body contact. Chitter 1's utilized between mother and cubs have an attracting effect. Finding each other in dense habitat is facilitated by properties making the call easily locatable such as the pulsed structure and the wide frequency range (MARLER, 1967). The calls used in body contact (chitter 2, churr, purr) and accompanying long lasting interactions (copulating, social grooming, nursing) are linked with vibrations of the whole body in the rhythm of the pulses of the call. These vibrations are transmitted to the recipient. It is possible that this tactile stimulation is more important than the acoustic event in stimulating the partner. This is indicated by the fact that handraised cubs which have stopped suckling for almost being satiated, can be caused to start anew by tactile stimulation. Similarly, a purring female may stimulate the cubs mechanically to continue suckling when the milk flow gets low. Or a female uttering chitter 2's may promote ejaculation in the male by her tactile stimulation rather than by the call.

#### *Comparisons with other species.*

Compared to other procyonids, the vocal repertoire of raccoons seems surprisingly rich. For other species, between 7 and 9 calls are reported (ringtail, *Bassariscus astutus* 9: TOWEILL & TOWEILL, 1978, 7: WILLEY & RICHARDS, 1981; cacomistle, *Bassariscus sumichrasti* 7: POGLAYEN-NEUWALL, 1973; coati, *Nasua narica* 8: KAUFMANN, 1962; kinkajou, *Potos flavus* 9: POGLAYEN-NEUWALL, 1976a; olingo, *Bassaricyon sp.* 8: POGLAYEN-NEUWALL, 1976b). It would, however, be premature to conclude that

raccoons possess more calls than do their relatives. Barely two studies have been performed in the same way. The apparent differences may reflect a lack in our knowledge rather than true differences among species, especially since the repertoire of raccoons contains no call group which is not found in other procyonids and other carnivores as well. Tonal, squealing distress calls are common in all procyonids and the giant panda (*Ailuropoda melanoleuca*: PETERS, 1982; KLEIMAN, 1983), in canids (FOX & COHEN, 1977), mustelids (GOSSOW, 1970), viverrids (WEMMER, 1977) and mongooses (MULLIGAN & NELLIS, 1975). Whistling sounds emitted in startling contexts are shared between procyonids (ringtail, olingo, *loc. cit.*) and felids (SCHALLER, 1972). Harsh calls utilized by aggressive animals are typical for all carnivores (EWER, 1973). Chitter-like contact or appeasing calls, too, are found in all carnivore families (PETERS, in press). Pulsed mating calls occur in ringtails (WILLEY & RICHARDS, 1981), kinkajous (POGLAYEN-NEUWALL, 1976a), olingos (POGLAYEN-NEUWALL, 1976b) and in the distantly related binturong (*Arctictis binturong*: WEMMER & MURTAUGH, 1981). Churr- and purr-like calls in body-contact situations are produced by other procyonids (coati: KAUFMANN, 1962), by bears (PRUITT & BURGHARDT, 1977), felids (PETERS, 1981), viverrids (WEMMER, 1977) and hyenids (DEANE, 1962, in EWER, 1973). Thus, in many species of different carnivore families calls of similar general structure are applied in similar contexts. This suggests that the pattern found in raccoon vocal communication with rather highpitched and tonal distress, harsh hostile and pulsed and repetitive contact calls is a widespread phenomenon within the carnivores.

### Summary

The study describes structure, ontogeny and contexts of raccoon (*Procyon lotor*) vocalizations and investigates whether structure and motivation interplay in the way predicted by general motivation-structural rules (MORTON, 1977, 1982).

Observations during a full reproductive cycle in a mixed group of captive raccoons indicate that they use an elaborate vocal repertoire including 13 calls (Table 1). Two calls are tonal (whistle, squeal), three noisy (snort, bark, growl); four have a mixed structure (cry, screech, gecker, grunt) and four have pulsed syllables (chitter 1, chitter 2, churr, purr). Though some calls grade into one another, the repertoire is largely discrete.

Three calls are present at birth and form the nestling repertoire. The adult repertoire gradually develops through the time of weaning (Fig. 2). Several calls are characteristic for the sexual and parental phase.

Most calls are associated with one or a few contexts (Table 2). Four calls are utilized by animals while distressed and have an attracting effect on others. Four calls express hostile motivation and repel other animals. Five calls are used by animals approaching another or having body contact; they serve in promoting or maintaining contact.



Calls used in similar contexts show remarkable structural similarities. Distress calls are tonal or mixed, hostile calls noisy in accordance with motivation-structural rules. Contact calls deviate in being noisy and low in basic frequency. Possible reasons are discussed. A comparison of the vocalizations in other carnivores reveals that the structure-motivational pattern found in raccoons is a wide-spread phenomenon in carnivores.

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### Zusammenfassung

Die Arbeit beschreibt Struktur, Ontogenese und Kontexte der Lautäusserungen von Waschbären (*Procyon lotor*) und untersucht, ob Struktur und Motivation in der Weise zusammenspielen, wie dies durch die 'motivation-structural rules' von MORTON (1977, 1982) vorausgesagt wird.

Beobachtungen in einer gemischten Gruppe gekäfigter Waschbären während eines Fortpflanzungszyklus von der Geburt bis zur folgenden Paarungszeit ergeben, dass die Art über ein reiches akustisches Repertoire von 13 Rufen verfügt (Tab. 1). Zwei Rufe sind tonal (whistle: Fiepen, squeal: Quären), drei geräuschhaft (snort: Schnaufen, bark: Bellen, growl: Knurren); vier haben eine gemischte Struktur (cry: Schreien, screech: Kreischen, gecker: Keckern, grunt: Grunzen) und vier haben gepulste Silben (chitter 1 und 2: Zirpen 1 und 2, churr: Surren, purr: Schnurren). Obwohl einige Rufe ineinander übergehen, ist das Repertoire weitgehend diskret.

Drei Rufe sind bei der Geburt vorhanden und bilden das Nestlings-Repertoire. Die meisten Rufe der Adulten treten bis zur Zeit der Entwöhnung erstmals auf (Abb. 2). Verschiedene sind typisch für die Paarungs- und Aufzuchtphase.

Die meisten Rufe werden in einem oder wenigen Kontexten gebraucht (Tab. 2). Vier sind Distress-Rufe und haben eine anziehende Wirkung auf Artgenossen. Vier Rufe drücken feindliche Stimmung aus und wirken distanzvergrößernd. Fünf Rufe werden von Tieren geäussert, die sich einem anderen annähern oder Körperkontakt haben; sie dienen zur Herstellung oder Aufrechterhaltung von Kontakt.

Die Rufe, die in ähnlichen Situationen verwendet werden, zeigen auffällige strukturelle Ähnlichkeiten. Distress-Rufe sind tonal oder gemischt, feindliche Rufe geräuschhaft, entsprechend den motivation-structural rules. Kontaktrufe hingegen haben eine abweichende Struktur, da sie geräuschhaft und von eher niedriger Frequenz sind. Mögliche Gründe dafür werden besprochen. Ein Vergleich der Lautäusserungen anderer Arten ergibt, dass Entsprechungen zwischen Struktur und Motivation, wie sie bei Waschbären vorliegen, ein unter Raubtieren weitverbreitetes Phänomen sind.

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