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Acoustic communication in the aardwolf, *Proteles cristatus* (Carnivora: Hyaenidae)

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Abstract

Acoustic signalling behaviour of free-ranging and captive adult and juvenile aardwolves (*Proteles cristatus*) is described, based on sonagraphic analyses of vocalizations and behavioural observations. In addition to relying heavily on olfactory communication, the aardwolf uses diverse acoustic signals when interacting with conspecifics at close and medium range but seems to lack a true long-range vocalization. Vocalizations during agonistic interactions are the most diverse. About half of the species' 9 sound types presently documented belong to graded systems of sounds while the rest probably represents discrete types. It is not yet fully established whether all sound types listed actually function as acoustic communication signals. As far as data are available the acoustic signal repertoire of aardwolves is considerably different from those of the other species of the Hyaenidae.

Introduction

Various studies present data on acoustic communication in the four extant species of the Hyaenidae (taxonomy according to Wozencraft 1993). This is especially true for the spotted hyaena (*Crocuta crocuta*) (Kruuk 1972; Schaller 1972; Henschel 1986; Mills 1990; East and Hofer 1991 a, b). Considerably less is known of vocalization in the brown hyaena (*Parahyaena brunnea*) (Owens and Owens 1978; Mills 1982, 1990), the striped hyaena (*Hyaena hyaena*) (Kruuk 1976; Rieger 1981; Peters 1984), and especially the aardwolf (*Proteles cristatus*) (Koehler and Richardson 1990). While the spotted hyaena is probably one of the most vociferous terrestrial carnivores, the other hyaenid species are considered comparatively silent (Kruuk 1976) and the aardwolf particularly so (Kingdon 1977; Koehler and Richardson 1990; Estes 1991). Nevertheless, a number of different sounds uttered by this species are mentioned in the literature (e.g. Shortridge 1934; Smithers 1971; Estes 1991), all of them described in a non-quantitative manner and in terms inconsistent with terms used in this and other hyaenid species. The purpose of the present study is to give a first quantitative survey of acoustic communication in the aardwolf, including an outline of those aspects of its vocalization behaviour where data are lacking.

Material and methods

In the course of a 28 months field study on the game farm 'Benfontein', situated 10 km south-east of Kimberley, in the Northern Cape Province, South Africa, between May 1991 and August 1993 13 adult aardwolves (6 females, 7 males) were captured by remote immobilisation and fitted with radio-transmitters. After an initial habituation period of two weeks, one of the authors (A. S.) followed them at nighttime in a four-wheel-drive vehicle at a distance of 15–30 m, always in visual contact, aided by the vehicle's headlights and a low-powered hand held spotlight. Notes on the aardwolves' behaviour while vocalizing were recorded on a dictaphone. The volume of the different vocalizations was rated subjectively on an increasing scale from I to V, according to the distance over which they were audible for the human observer under calm conditions (I: 0–10 m; II: 10–20 m; III: 20–30 m; IV: 30–100 m; V: 100–200 m). Recording distances in the field varied between 15 and 40 m of the animal from the switched-off vehicle. Sound recordings were obtained with a Nagra IV-D tape recorder and microphone ECM 1035 AOI Super Cardonic Directional Microphone with windshield at a tape speed of 19.05 cm/second. The relatively great distance and the windy conditions limited the number of recordings which could be analysed and affected the scope and significance of measurements that could be obtained from spectrographic analysis. Vocalizations of three adult females and two adult males were recorded with a quality sufficient for sound spectrographic analysis. Several sounds of one hand-raised female aardwolf cub were recorded at distances between 10 cm and about 2.5 m with an AKG D202 ES microphone without windshield and the same tape recorder and recording speed as described above when it was 5 and $8^1/_2$ months old. Both microphones used have a reasonably flat frequency response in the range of the vocalizations studied. Sound spectrographic analyses were done on a MEDAV SPEKTRO 3 000, version 3.2, 1991. Sonagraph settings for frequency and time ranges and resolutions were chosen according to the structural parameters measured for each vocalization type and can be gathered from the sonagrams figured. Oscillograms of all vocalizations analyzed were checked to avoid overloading. Pulse repetition rate was calculated according to method B given by Scoville and Gottlieb (1978). The calculation was based on number of pulse pairs per train in sounds with pulse pairing and on single pulses in those without pairing. Heavy background noise was removed by filtering if, according to the sonagram, the vocalization appeared to have no frequency components within the range filtered. Filtered sonagrams are identified as such in the figures and details of filtering are given. General structural parameters of the different vocalization types are presented in Table 2. As our sample is relatively small these are unlikely to reflect the whole range of structural variability of the species' vocalizations and/or may not be fully representative for certain vocalization types.

Results

Throughout this publication the term "vocalization" is used for any (communicatory) sound produced by aardwolves, irrespective of whether it is voiced or unvoiced and regardless of mode of sound production. The vocalizations of the aardwolf will be described in a uniform format for juveniles and adults. We first present the types established on the basis of spectrographic analysis. We then describe those for which few or no recordings are available but the observer witnessed them frequently and their occurrence in specific behavioural contexts was typical and fairly common.

We identified nine different vocalizations: "purr", whine, jaw click, lip smack, snarl, growl, bark, squeal, and a whizzing sound (see Tabs. 1, 2). Only for the last vocalization type the description and classification is solely based on the observer's (A. S.) auditory impression.

"Purring"

At about 4 weeks of age a hand-raised female aardwolf cub was heard to produce a fairly sustained, low-pitched, vibrating sound when stroked or when in body contact with her foster parents, in many respects reminiscent of the purring of a domestic cat. Addressees under natural conditions are very probably siblings and/or parents at very close distance. "Purring" probably signals comfort – if it serves a communicatory function at all. A more regular, sustained and more intense production of this sound seemed to reflect the animal's continuing comfort.

The sound was observed repeatedly during the animal's juvenile development and was still present when she was given away at 9 months of age. Then the sound could be heard up to several meters away, being considerably louder than felid purring. Aardwolf "purring" (Fig. 1 a–c) is rather constant in pitch and can go on for minutes, sometimes with very short interruptions of sound production at irregular intervals. Sound intensity varied but there was no regular pattern in this respect, nor was there a regular alternation of sound quality as in felid purring where sound quality differs between exhaling and inhaling. Thus we could not ascertain whether sound production occurred during exhalation and/or inhalation, but exhalation is considerably likelier. During vocalizing the vibration of the body surface was palpable, especially on the chest, neck and abdomen. This vocalization was not observed in the field, neither in juveniles nor in adults, probably because of the large observation distance or because it is only produced while the animals are in the den. "Purring" occurred only at intensity level I. The term "purring" for this aardwolf vocalization is deliberately used in inverted commas to signify that based on the available analysis data it seems to differ from felid purring as will be detailed below.

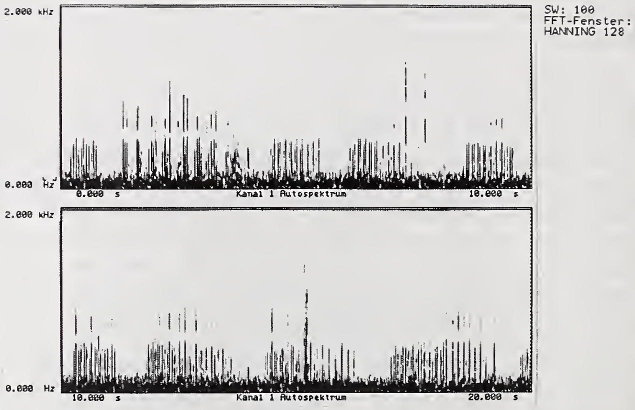
Three continuous recordings of aardwolf "purring" were available for analysis, recorded once when the captive juvenile female was 5 months old. Thus no comments can be made whether its structure undergoes ontogenetic change. These examples of "purring" lasted 30.59 s, 33.07 s and 40.59 s with fairly sustained vocalization, traceable sound production being present for 66.8%, 70.9% and 57.4% of the total recording. Aardwolf "purring" is composed of largely continuous pulse trains of varying duration with a more or less regular sequence of the single pulses (Fig. 1 a). In our recorded sample intervals without sound production between pulse trains lasted between 0.13 and 2.66 ($\bar{x} = 0.6 \pm 0.39$) s ($n = 62$). The recorded pulse trains consisted of 2–36 ($\bar{x} = 15.14 \pm 10.9$) ($n = 65$) single pulses. No regular pattern in the occurrence of these pulse trains was discernible. Of the 65 pulse trains analysed in the whole "purring" sample 28 (43.1%) consisted of ≤ 8 ($x = 4.36 \pm 1.22$) pulses and had an average duration of $\bar{x} = 0.2 \pm 0.11$ s; the remaining 37 (56.9%) pulse trains consisted of ≥ 12 ($\bar{x} = 18.7 \pm 11.1$) pulses and had an average duration of $\bar{x} = 1.65 \pm 0.78$ s.

If each phase without sound production and the subsequent vocalization phase are considered as one "breath", representing one coherent inspiratory (without sound production) and expiratory phase (with sound production), average "breath" duration of this juvenile aardwolf while producing "purring" would be 1.72 s, resulting in an average rate of 34.9 "breaths" per min during the production of this sound. It seems unlikely, though, that each of the very short pulse trains in our recordings of "purring" represents a complete exhalatory phase, and the short phases without sound production directly preceding and following such a pulse train inhalatory phases accordingly.

The sequence of pulses is not regular throughout the duration of a train. Single pulses may be of variable intensity. For varying portions of the duration of the pulse trains, pulses are paired off (Fig. 1 b). During other portions of the pulse trains pulse pairing is less obvious, or they are sequences of single pulses with pulse repetition rates equivalent to the repetition rates of the pulse pairs (Fig. 1 c). Pulses and pulse pairs occurred at a rate of 7.1 – 9.9 ($\bar{x} = 8.47 \pm 0.62$) ($n = 28$) per s. Because of heavy background noise and high input level during the original recording it is not clear whether the energy maximum

▶

Fig. 1. Aardwolf "purring" by a juvenile ♀ 5 months old.
a: A continuous 20 s stretch (upper plus lower sonagram) of "purring" with more or less regularly structured pulse trains of varying duration interrupted by phases without sound production which may represent phases of inhalation.
b: A stretch of 1 s of "purring" with clear occurrence of pulse pairs, nine of which are present here.
c: Another stretch of 2.5 s duration with a less regular sequence of pulses with pulse pairs in the beginning portion and single pulses in the end. These follow each other at about the same repetition rate as the preceding pulse pairs.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SW: 100
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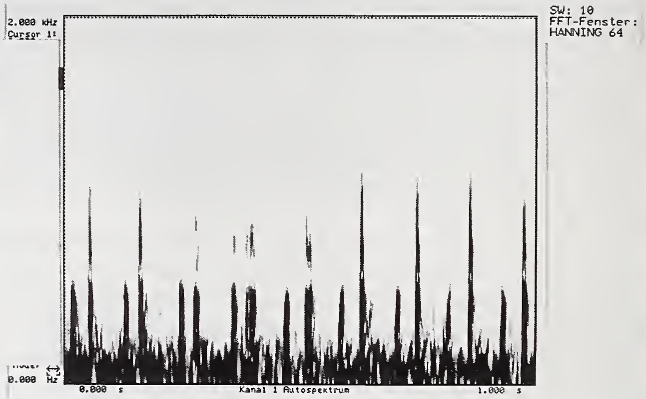
a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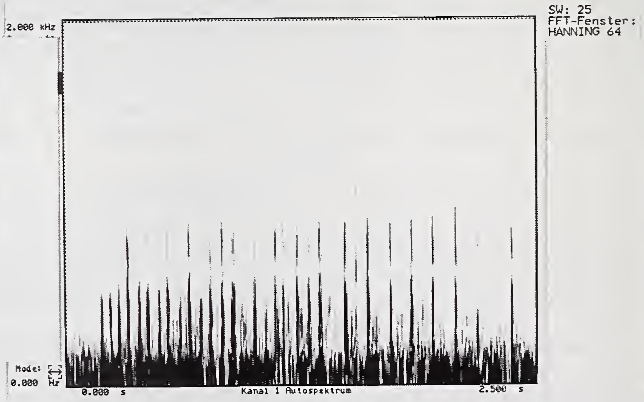
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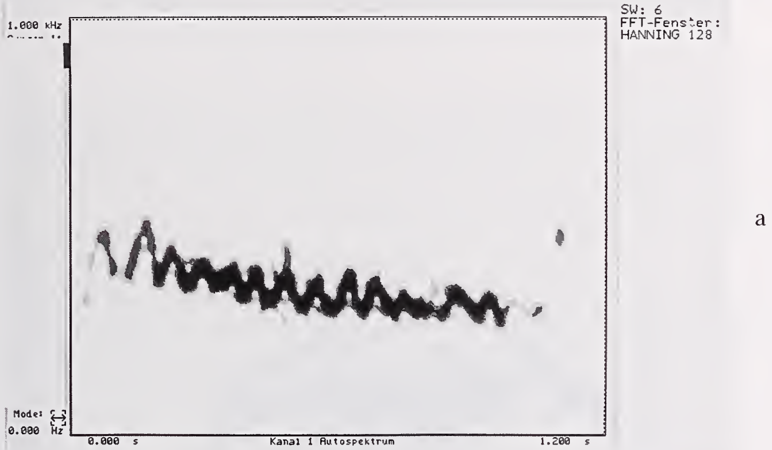
Kanal 1 Autospektrum
2.500 s

c

of "purring" at about 40 Hz actually belongs to this sound. The cause of the differences in pulse structure is unknown. On the basis of the available data it is not possible to make a statement as to the detailed mechanism of sound production in aardwolf "purring" as compared to that of felid purring (Frazer Sissom et al. 1991). Very likely "purring" is a discrete type of vocalization.

Whine

Whines (Figs. 2 a–d) are clear tonal calls of variable pitch and degree of frequency modulation (FM). Most whines decrease slightly in pitch towards their end, usually after a short and variable increase in pitch in their beginning. They are comparatively short sounds. Relatively loud whines could be clearly heard for over 100 m but much softer whines also occurred. On one occasion a male followed the scent-marks of a receptive female and when sensing her proximity whined loudly while trotting about 100 m past



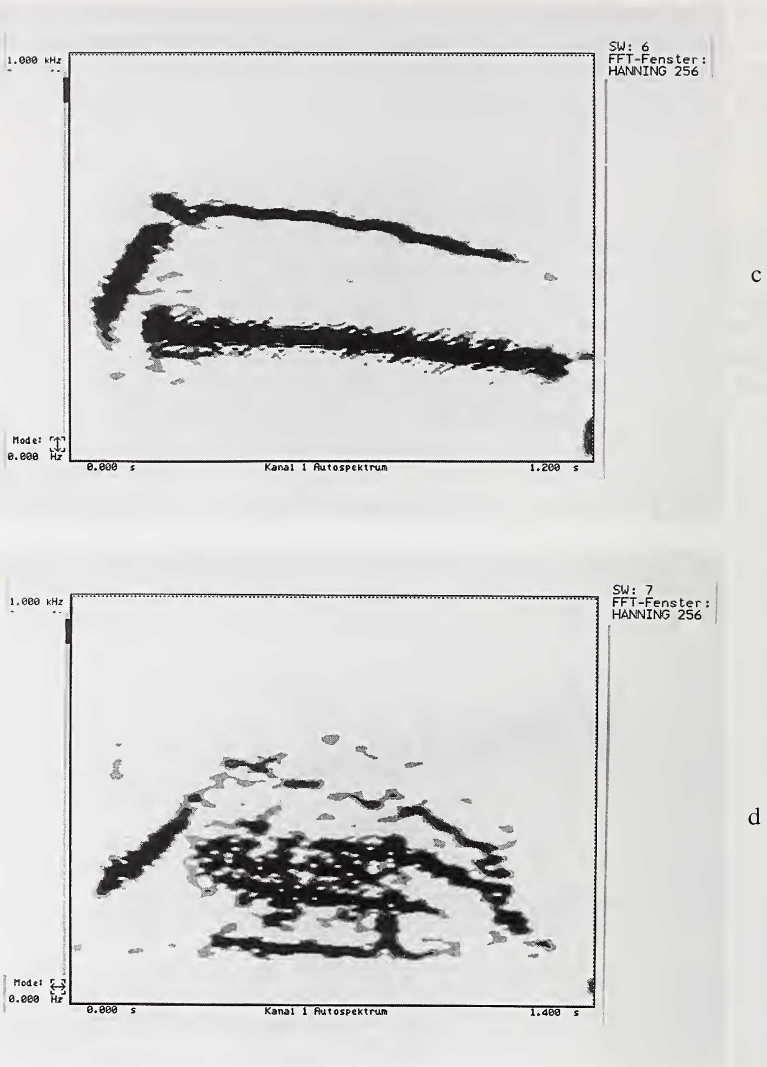


Fig. 2. Whines of adult ♂ aardwolves. Because of adverse recording conditions unequivocal designation of frequency bands (as f0, f1, f2, etc.) showing in the spectrograms is not always possible.
a: Higher-pitched variant of this call with distinct and fairly constant periodical frequency modulation (FM) for the whole of its duration (high-pass filtered >250 Hz).
b: Another variant of higher-pitched whine with little FM which is not periodical (high-pass filtered >280 Hz).
c: Low whine with two harmonically related frequency bands and an incipient sound (band-pass filtered for range 170–700 Hz).
d: Low whine with (at least) 4 harmonically related frequency bands (and likely subharmonics) for a portion of its duration and an incipient sound (band-pass filtered for range 110–690 Hz).

where she was lying behind a hill out of sight from him. Upon hearing him she jumped up and ran after him, caught up and immediately mated with him. Less loud whines were heard from males approaching the den containing the female and cubs when they took up guarding duties. Then they were usually uttered at about 50 m from the den and always when catching sight of the female lying outside of her den. Males also used a soft and high-pitched whine audible for about 30 m repeated up to six times within an interval of about 2 min when trying to solicit eight weeks and older cubs to follow them on short excursions around the den, or when they moved too far from the den when they were older. Males also whined softly when cubs approached to greet them. Females whined when approaching the den after a foraging trip and to solicit cubs to follow them on short foraging trips. When the cubs were still in the den, females used whines to call them out (P. R. K. Richardson, M. D. Anderson pers. comm.). Whines were never heard between two adult males or from cubs towards their parents. Whining outside the mating season was produced mainly by males towards juveniles. Females whined less often and were never heard to produce loud whines towards adult males over longer distances. The intensity of whines rated as level II–IV (for the most intense forms). Whining was used during friendly contact at close and approach at close to medium range. It probably functions as an appeasing and reassuring sound. The reaction of the addressee is in cubs to come out of the den and/or follow when their mother or father whines. A female's reaction to male whining during the mating season was related to her reproductive status. She either rebuffed him vocally and/or actively or followed him. All whines recorded and analyzed were those of ♂♂ during the mating season.

The human observer can roughly classify these calls into two categories according to their pitch: a lower-pitched and a higher-pitched form. The latter can be differentiated further on the basis of FM. This classification does not encompass all whines recorded on tape; some calls were intermediate in pitch or FM. Sonagraphic analysis largely supports this preliminary distinction. We analyzed 11 calls for one variant of higher-pitched and 10 in the other, and 12 calls of the lower-pitched form. Additionally, 4 intermediate calls were provisionally classed with the category they were closest to structurally, 3 with the higher-pitched and 1 with the lower-pitched variant.

Periodical FM was obvious in one variant of the relatively higher-pitched whines (Fig. 2 a) in which only one frequency band is present; it is likely to be the fundamental. FM over the whole duration of the call varied but in the majority of these whines the frequency decreased towards the end of the call. Periodical FM occurred at a rate of 15–20 Hz but was not fully regular in its temporal and frequency characteristics for the whole duration of the call. The frequency change during one FM period of about 60 ms duration can be more than 200 Hz. The other variant of relatively higher-pitched whines usually also showed one frequency band only (probably the fundamental) with variable overall FM but no periodical FM (Fig. 2 b). In the three calls provisonally grouped with this whine variant more than one frequency band showed up in the sonagram.

Lower-pitched whines (Figs. 2 c, d) usually show 2–4 frequency bands, 2 harmonics (with a ratio of their frequency components of 1:2) usually being significantly more intense than the other (Fig. 2 d). Of the 12 examples analyzed of this form of whine 8 had an initial sound (Figs. 2 c, d) of approximately 0.2 s duration (an average of a little less than 20% of the whole duration of the call). The initial sound consisted of only one steeply ascending frequency band (no additional harmonic as in the rest of the call) with a frequency difference of about 200 Hz between its start and end. In addition to the structural diversity of the calls classified as whines in this study (all recorded in the same general behavioural context), the diverse other functional contexts in which whines occur strongly suggest that further differentiation of this category is appropriate. However, a complete and fully substantiated subdivision of whines or even a division of this category into several vocalization types requires more structural and behavioural data than are available at present. We are still unsure whether they belong to a graded call system or represent discrete vocalizations but the former is more likely.

Jaw click

Muffled sounding clicks were heard at close quarters when an animal was growling. They were audible over about 10 m and thus rated I–(II) on the subjective volume scale. They were most likely generated through forceful closing of the jaws, the clash of the teeth producing the sound. Jaw clicks were used in intra- and interspecific threat behaviour, interspersed with growling or snarling and occurred in conjunction with lip smacks (see below) as opening and closing sounds of the jaws and lips. Usually several of these sounds were produced in a row. Jaw clicks were only witnessed in a wild adult male approached on foot by the observer at about 10 m and in the $8^1/_2$ months old captive female cub when another similar aged male cub approached her. It is not clear whether jaw clicks function as a real acoustic signal or whether they are just a by-product of the closing of the jaws indicating an intention to bite. In a series of 5 jaw clicks (Fig. 3 a) the first 4 clicks follow each other at intervals of about 130 ms, the last click which is weaker than the preceding clicks occurred after an interval of about 50 ms. Jaw clicks represent a discrete sound type.

Lip smack

Lip smacking occurs in the same circumstances and often occurs together with jaw clicks (Fig. 3 a), interspersed between growling or snarling stretches, during intra- and interspecific threat behaviour. We have one recording of a lip smacking sequence without jaw clicks being present in it (Fig. 3 b). Lip smacks, jaw clicks and slight growling where heard once when the observer (A. S.) approached a habituated adult male aardwolf on foot. The animal looked at the observer and opened and closed its lips with a smack, audible for at least 10 m. The other incidence of lip smacking was when a hand-raised female cub was approached by a male cub. The volume of the sound is equivalent to I(–II) on the subjective volume scale. A smacking sound is generated through forceful closing and/or opening of the jaws, lips and cheeks probably contributing to sound production. As with jaw clicks it was not clear whether it functions as an acoustic signal or was an acoustic by-product of the opening and closing of the mouth. At present it is not possible to separate jaw clicks and lip smacks unequivocally on the basis of sound structure. There is a minor clue in the sound quality, that of jaw clicks is relatively harder and more mechanical than lip smacks. The two examples analyzed were recorded in the juvenile ♀ aardwolf when it was $8^1/_2$ months old. In the one sound sequence where both vocalization types seem to occur together we interpret the last sound after a preceding series of 5 jaw clicks as a lip smack (Fig. 3 a). It follows the last jaw click after an interval of about 140 ms. The other series (Fig. 3 b) consists of three sounds without accompanying jaw clicks. The interval between the first two is about 350 ms, that between the second and third sound only about 24 ms. The frequency components with maximum amplitude in lip smacking cannot be established with certainty because the lower frequency range <1 kHz is affected by heavy background noise. Like jaw clicks, lip smacks represent a discrete vocalization type with probably little structural variability. Despite their close temporal association and occurrence in the same behavioural contexts, and the problems in separating them they are listed as distinct sound types because they are produced by different body structures.

Growl

Aardwolf growling is similar to the growl of other terrestrial carnivores. It is a fairly continuous low rumbling, throaty "rrrrrrrrrrr" sound, variably sonorous and usually sustained for some time. It is quite similar to the growling of a large sized dog and is usually louder and sounds more "impressive" than would be expected for a mammal of an aardwolf's size. Its high intensity forms were audible at a distance of up to about 20–30 m, its

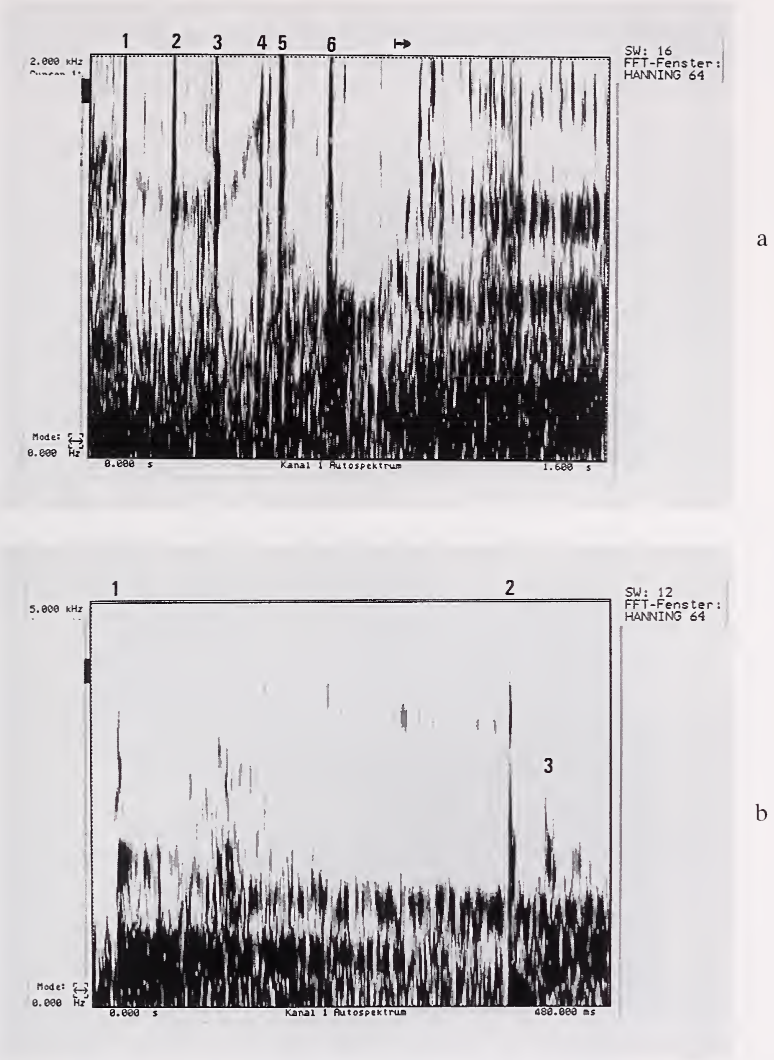


Fig. 3. a: Five jaw clicks (marked '1' to '5') and one lip smack (?) ('6') of a juvenile ♀ aardwolf $8^1/_2$ months old. They are directly followed by growling the start of which is marked by an arrow. b: A sequence of 3 lip smacks (marked '1' to '3') of the same individual. In both sound sequences the positive identification and distinction of the two vocalization types is still equivocal, though. Both recordings with heavy background noise.

intensity is rated at II–III on the subjective scale; low intensity forms of growling rate at level I. Growling at low to medium intensity and relatively short duration was produced during expiration only, the longer phases of expiratory sound production interrupted by only relatively short phases of inspiration without vocalization. Sometimes a sound was also produced during inspiratory phases. With increasing duration and intensity sound production was more likely to continue over the short inspiratory phase between two adjacent expiratory phases. These voiced inspiratory phases in growling sounded like inspiratory snarling and are very similar to it in structure, indicating a close relationship

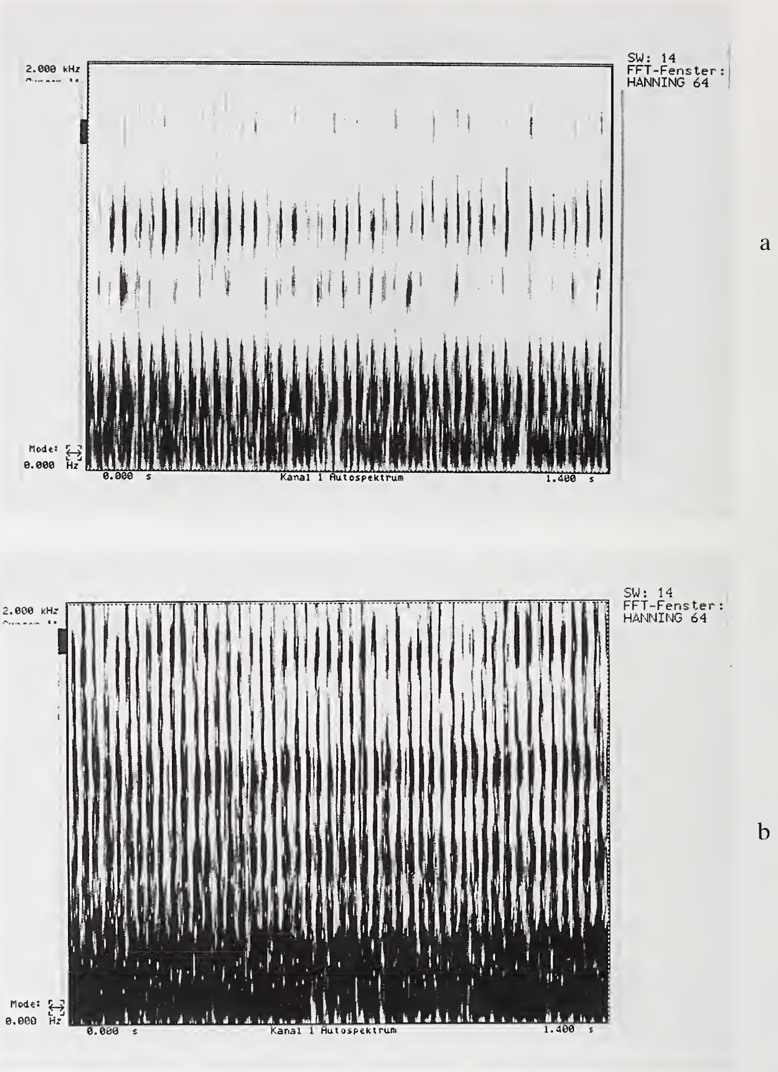


Fig. 4. Growling of a juvenile ♀ aardwolf $8^1/_2$ months old.
a: Growling of little sonority with clear representation of single pulses.
b: Growling of higher sonority in which the single pulses are not as distinct as in a. and less well separated from each other.

between growling and snarling. Nevertheless, we prefer to separate growling proper here from snarling proper. The criteria to separate the 'pure' forms of the two vocalization types are listed in the section on snarling.

Growls were used as a defensive threat towards conspecifics and heterospecifics, usually together with snarls, and often preceding barks. Aardwolves seem to lack an acoustic signal of offensive threat; attacking individuals were always silent with the exception of the whizzing sound in one individual (see below). In the wild growling was most often heard during the mating season when females growled at courting males who tested their receptivity through slight and short attacks (Richardson 1985, 1987). It was used throughout the year and heard first in wild cubs at 6 weeks of age. As in the three other vocalizations that occur during agonistic behaviour (snarling, jaw click, lip smack) growling could only be analysed in a juvenile ♀ $8^{1}/_{2}$ months old. Our subjective acoustic impression is that the structure of these vocalization types in animals of this age is very similar to that in adults.

Growling (Figs. 4 a, b) of variable intensity and sound character can go on for 10 s and more without interruption of sound production. Short (inspiratory) intervals of at least 1 s duration interrupted sound production but several inspiratory and expiratory phases of sound production could also follow each other without interruption of vocalization. The

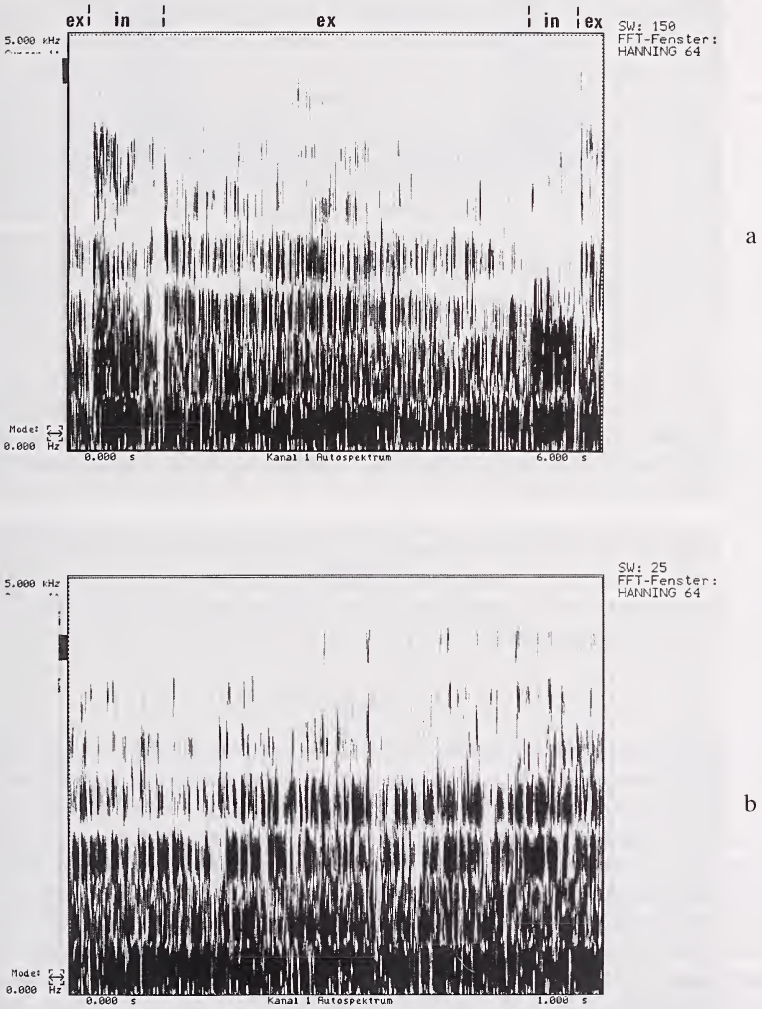


Fig. 5. Snarling of a juvenile ♀ aardwolf $8^{1}/_{1}$ months old.
a: A stretch of 6 s with continuous sound production during in- and expirative phases of respiration (marked 'in' resp. 'ex').
b: One second of expirative snarling. Pulsation is less pronounced, single pulses are much less clearly separated and the structure of the sound is noisier than in growling.

sonority of the sound changed over its duration. Pulsation was very obvious and regular in the exhalatory phases of growling with a pulse repetition rate of 30–35 pulses per s. The inhalatory phases were much less clearly pulsed; a pulse repetition rate could not be determined.

Snarl

Snarls are louder, distinctly more voiced and rather more tonal, higher in pitch, and much less clearly and regularly pulsed than growls (Fig. 5 b); short, intense outbursts may sound like a roar. Aardwolf snarls are very similar to snarls of a large dog, rating at III on the subjective volume scale in its most intense forms. Like growling snarling is a sustained vocalization usually continued for some time. However, contrary to growling, sound production generally occurred during both in- and expiratory phase of respiration, although it was not necessarily continuous during both phases (Fig. 5 a). Inspiratory phases of snarling were higher in pitch and much shorter than the expiratory phases. Together with growling and barks, snarls of aardwolves were heard during intra- and interspecific agonistic encounters and were part of the species' defensive display. The sender seemed to be more strongly agitated than during growling, resulting in more hectic vocalizing. Snarling was usually uttered in agonistic situations at close range as a high-intensity defensive threat, rising out of a growl and, with withdrawal of the addressee, tapering off into a growl again. If the opponent further approached snarling broke and rose into a bark or a short series of barks. Snarling was only heard during serious agonistic encounters when the opponent of the sender attempted to bite or make physical contact. It was first heard when juveniles were about eight months old but it is very likely that it is already present much earlier during ontogeny. In adults it was heard from both sexes during fights and in the mating season when the sender was pressed hard, as females having to defend themselves against frustrated courting males (Sliwa 1996) or males fighting over mating rights of females (Richardson 1987).

Stretches of fairly continuous snarling lasted for up to 20 s. A concentration of sound energy in broad, somewhat noisy frequency bands was visible in the sonagrams, an indication of the more voiced and tonal character of snarling compared to growling and the differences between the two respiratory phases. We currently assume that snarling and growling form a graded sound system.

Bark

Barks in aardwolves were the loudest form of defensive vocalization. The barks were often heard over 200 m distance, and could even be heard when the animal was deep down in a den. We rated them at IV–V on our subjective intensity scale. Barks varied in sound from a hoarse cough to a fully explosive bark. They were relatively deep like that of a large-sized dog. Barks were most often heard in the wild during the mating season. Females barked at males testing their receptivity through little attacks. Barks of the female coincided with lunges of the testing male. They usually grew out of a preceding growl or snarl and generally tapered off into growling and/or snarling. The addressee was more likely to retreat when the sender barked, and if the addressee did not retreat, actual fighting proceeded. Increasing stress, like the approach of the addressee, led to a higher repetition rate of barks. Barks were first heard in six weeks old cubs. During territorial encounters only the chased animal barked defensively. During a serious fight of two adult males at the height of the mating season, only some low intensity growling was heard. Females whose receptivity was tested by males through circling around them and slight attacks growled continuously and often barked on seeing the male approach from 10 m away. Most of the recorded barks were produced by females in their dens. Very few barks

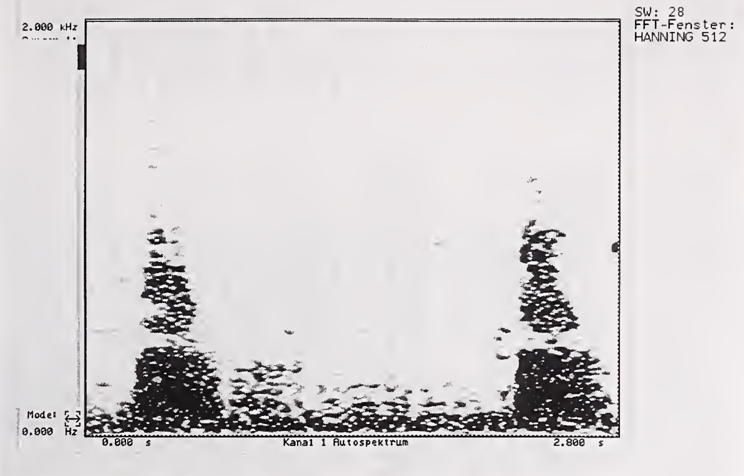


Fig. 6. Two barks of an adult ♀ aardwolf. Structural characteristics of this vocalization type as showing in the sonagram are affected by the fact that the animal was recorded while vocalizing in its den. The original duration of the interval of about 15 s between these barks was shortened in the analysis. Recording with high level of background noise.

could be recorded in animals which were above ground but all of these were so far away from the observer that the recording quality was poor. Therefore the material on which the structural analyses are based is limited. Barks (Fig. 6) were short sounds. Their frequency distribution was atonal.

Squeal

Handling the feeding bowl at feeding time caused the hungry hand-raised aardwolf cub to give a loud, sometimes staccato-like squealing sound, in anticipation. These squeals increased to a more continuous loud squeal of a bleating quality with opened mouth which further graded into even louder continuous squeals with increasing frustration. Similar sounds could be heard when a mother returned to her den and the cubs were struggling to suckle. The volume varied between II and III on the subjective volume scale, the sender's mouth opening slightly with increasing intensity of squeals. They were heard in wild cubs of about three months at close quarters and in the hand-raised female cub at about two months and were still uttered when she was 9 months of age but they were never observed in adults. Squeals seem to have a begging role.

All recordings of squeals are of the ♀ juvenile at an age of 5 months. Their quality is poor due to background noise and therefore no sonagram is figured. Squealing can be interrupted into short staccato-like sounds but usually goes on for several seconds. Long stretches of squealing sounds can follow each other, only interrupted by short phases of inspiration. It is largely tonal and variable in pitch with up to 4 harmonics with some variable FM. In all calls the fundamental f0 is the most intense harmonic. Due to our limited sample and the poor quality of the recordings no statement can be made about the variability of these calls. It is also not clear whether squealing of juvenile aardwolves is a discrete or a graded sound type, although the latter is more likely. Possible structural relationships between squealing and whining cannot be clarified on the basis of our material.

Table 1. Vocal repertoire of aardwolves (*Proteles cristatus*). General characterization of vocalization types.

Vocalization type	Description	Frequency of occurrence	Sender	Behavioural contexts	Body posture and facial expression of sender	Reaction of addressee
“purring”	similar to domestic cat purr but not continuous	?	juvenile ♂♂ and ♀♀, adults ?	relaxed close contact	lying down, relaxed, eyes (halfway) closed	?
whine	short clear tonal sound of variable pitch	seasonally common	adult ♂♂ and ♀♀	sender approaching addressee	head low, body crouched or upright, varies with sound intensity, ears flattened	variable: no reaction → approach
jaw click	soft clicking sound	uncommon	♂♂ and ♀♀, subadults and adults (?)	addressee approaching sender	head low, ears flattened, hair erected	?
lip smack	soft smacking sound	uncommon	♂♂ and ♀♀, subadults and adults (?)	addressee approaching sender	standing errect, ears pointing forward	?
growl	fairly sustained low rumbling sound	seasonally common	♂♂ and ♀♀, all age classes	addressee approaching sender	head low, ears flattened, hair erected	variable: retreat → attack
snarl	similar to snarl of a dog or cat	seasonally common	♂♂ and ♀♀, all age classes	addressee approaching sender	head low, ears flattened, hair erected	variable: retreat → attack
bark	similar to bark of a large-sized dog	seasonally common	♂♂ and ♀♀, all age classes	addressee approaching sender	crouched, hair erected, mouth open	variable: **retreat** → attack
squeal	sustained high-pitched cry of variable intensity and tonality	?	juvenile ♂♂ and ♀♀	nursing	variable, moving, head stretched forward	caregiving, nursing
whizzing sound	hollow whistle sound	seasonal, uncommon (?)	adult ♀♀ (?)	sender approaching addressee	running, ears flattened	variable: no reaction → flight

Table 2. Vocal repertoire of aardwolves (*Proteles cristatus*). Structural characterization of vocalization types.

Vocalization type	Duration [s]	Frequency range [kHz]	Frequency distribution	Relatively intensive range [kHz]	Maximum intensity [kHz]	Generated during expiration inspiration	Main variable structural parameters	Comments
"purring" n = 65	0.07–3.67 $\bar{x} = 1.12 \pm 0.93$ (continuous pulse trains)	< 1.8	atonal, pulsed	< 0.14	0.04 ?	ex (+ in ?)	duration, pulsation	analyses adversely affected by low intensity
whine n = 37	0.44–1.86 $\bar{x} = 0.943 \pm 0.304$	< 0.7	tonal	0.26–0.43	0.35	ex	pitch, frequency modulation	sample heterogeneous
jaw click	series: 0.5 (5 clicks) single click: 0.012	0 – > 5	atonal	< 0.6 and 1–2.3	1.7	–	number of and intervals between single sounds in series	sample very small
lip smack	series: 0.4 (3 smacks) single smack: 0.013	0 – > 5	atonal	< 0.85 and 1.5–2	?	–	number of and intervals between single sounds in series	sample very small
growl	– > 10	< 3	atonal, pulsed	< 0.5	approx. 0.35	ex + (in)	duration, pulsation, sonority	
snarl	ex: 1.7–5.2 in: < 1	– > 4.5	atonal/(tonal), (pulsed)	< 2	ex: 0.3 in: 0.38	ex + in	duration, tonality	
bark	< 0.5	? – > 4.5	atonal	0.1–1	approx. 0.5	ex	?	analyses insufficient
squeal	variable	0.2–1 ?	tonal/(atonal)	< 0.5	0.24–0.42	ex	pitch, frequency modulation	sample very small
whizzing sound	approx. 2–3	?	tonal?	?	?	ex?	?	not tape recorded

Whizzing sound

A whizzing sound was heard during agonistic encounters of a female aardwolf running up to a 'courting' male, standing close, while facing away from the female. The sound is high-pitched, continuous for several seconds, ascending in pitch and fairly constant in its intensity. The female uttered this sound when starting to run fast and straight for the male, sound production stopping when reaching the male. It is somewhat reminiscent of a hollow whistle but we cannot liken it to a sound known to us in any other animal species. The whizzing sound is audible for at least 30 m thus ranking at III on the volume scale. When the male did not move away the female tried to bite him and sometimes a short low-intensity fight could ensue. In the context observed whizzing might function as an aggressive threat to warn the addressee of the immediate danger of physical attack. It is unclear how it is produced and whether it represents an acoustic signal. We were not able to record this sound in the wild and therefore are not able to describe it in a technical manner but it was heard more than 20 times in predictable circumstances. Nevertheless, as this whizzing sound was heard in only one female, although repeatedly during the mating season over three years, it cannot be ruled out that it represents an idiosyncrasy of this individual. Our observations do not allow a definite statement about its variability but the whizzing sound seems to be a discrete sound type.

Discussion

Being considered a solitary and relatively silent species (Kingdon 1977; Koehler and Richardson 1990; Estes 1991), only staying together with conspecifics for a brief period during the mating season and for considerable time while raising its cubs, the aardwolf's acoustic signal repertoire as described here appears to be fairly diverse, especially during agonistic behaviour. Although our data are limited they represent a considerable improvement of the previous state of knowledge and understanding of acoustic communication in this species.

Smithers (1971, 1983), Richardson (1985), Skinner and Smithers (1990), and Estes (1991) reported that when defending themselves and fighting aardwolves emit growls, hoarse barks, and roars of surprising depth and volume for such a small animal. It is likely that these vocalizations are equivalent to the agonistic sound repertoire described here as growling, snarling and barking. Koehler and Richardson (1990) mentioned a soft clicking sound produced by opening and closing of the mouth as the lowest form of threat. This fits well with the jaw clicks and/or lip smacks described in this study but these authors did not differentiate between two sound types. Cubs are said to make a clicking noise very much like the warning clicks of termites (Bartlett and Bartlett 1967), in addition to barking and growling softly (Smithers 1971). The latter two vocalizations were also observed by us but it is not clear what these clicks of cubs actually represent and whether they are connected with the jaw clicks mentioned by Koehler and Richardson (1990) and in the present study. For some aardwolf vocalizations mentioned in the literature it is difficult to correlate them with the species' acoustic signals as described in the present publication. Langden (in Shortridge 1934) reported on whistling calls between mates which may refer to the whines described here. According to Wilhelm (in Shortridge 1934) aardwolves have a howl similar to that of a striped hyaena. As no technical study of striped hyaena vocalization exists this statement cannot be assessed. Estes (1991) expressly stated that the three vocalization types warning clicks, whistle, and howl need confirmation but he did not specify on the basis of which evidence they are less likely to be actually present than the other ones mentioned in the literature. The vocalization types snarl and lip smack have not been expressly named and described in the literature on the aardwolf before. It is likely that they were subsumed under growling and jaw clicking respectively. The following vocalizations cannot be identified from descriptions in the literature and hence constitute newly described types: "purr", squeal, whizzing sound. As no technical data are given for the vocalization type 'soft squeal' listed in juveniles and adults of the spotted hyaena by Kruuk (1972) and Mills (1990) it is not possible at the moment to establish its exact nature as compared to the juvenile aardwolf squeal described here. The same is true for various vocalizations termed 'snarl', 'growl' and 'whine' or variants of these in the striped (Kruuk 1976), spotted (Kruuk 1972; Mills 1990) or brown hyaena (Mills 1990). As vocalization types of different species in the same genus, family, and order ought to be given the same name only if they are homologous, the use of these terms in different species of the family Hyaenidae is preliminary.

It is well documented that intraspecific communication in aardwolves primarily relies on olfaction and scent-marking (Kruuk and Sands 1972; Richardson and Bearder 1984; Richardson 1990, 1991; Sliwa 1996). However, for immediate, short to medium range communication they possess a fair-sized repertoire of expressive visual and vocal signals. The size of the acoustic repertoire with its discrete sound types and graded vocalizations seems to be similar to those of *Hyaena* (Kruuk 1976) and *Parahyaena* (Mills 1990) but smaller than that of *Crocuta* (Kruuk 1972; Mills 1990). As all published information on vocalization in the three other species of the Hyaenidae is non-technical a comparison of their acoustic signal repertoires with that of the aardwolf can only be provisional. It cannot be ruled out that *Proteles* has more vocalization types than described here. This is especially true as close-range observations of females with cubs are lacking, and vocal communication generally plays an important role in this behavioural context in Carnivora, especially from the time when the young start to leave the den until they become independent (Peters and Wozencraft 1989). Moreover, a numerical comparison of acoustic repertoire size (as established by the human investigator on the basis of sonagraphic analysis) is unlikely to be a direct measure of the communicative potential the repertoire offers to the sender, especially if applied in combination with other signalling modes. In most behavioural situations in which vocalization occurs in *Proteles* visual signals are used at the same time. The aardwolf's agonistic sound repertoire is relatively diverse, including the wide-spread terrestrial carnivore sounds growling, snarling, and barking. According to the agitation of the sender, their intensity, and the likelyhood of ensuing aggressive action of the sender they can be arranged in the following ascending order: jaw click and lip smack → growl → snarl → bark. Thus, barks represent the most intense threat vocalization signalling that the sender is prepared to attack the addressee upon its further approach. Considering the very close functional proximity and the structural similarity of growls and snarls, the fact that one can easily change into the other and the fact that barks can arise from growling or snarling with hardly interrupting sound production it would be interesting to know the precise mechanisms of sound production in these vocalization types. However, we do not interpret barking as belonging to the graded system formed by growling and snarling because it clearly differs from these in structural characteristics, and vocalizations with intermediate structure did not occur.

We did not list hissing as an agonistic sound. It is present in the other extant families of the superfamily Feloidea, the felids (Wemmer and Scow 1977), viverrids (Wemmer 1977), and very probably also herpestids (Earlé 1981) as the phylogenetically closest relatives of the Hyaenidae (Hunt and Tedford 1993). However, this type of sound is also found in species of different families of the superfamily Arctoidea (sensu Wyss and Flynn 1993) as in the red panda (*Ailurus fulgens*) (Roberts and Gittleman 1984) or several *Mustela* species (Gossow 1970). Within longer recording stretches of snarling and growling in our aardwolf material there are a few short periods with low-intensity exhalatory noise which may represent hissing. Our observations and the quality of these recordings are not good enough to make a definitive statement in this respect, though. Hissing was not listed as a vocalization type in any of the other species of the Hyaenidae (*Crocuta*: Kruuk 1972; Mills 1990; *Hyaena*: Kruuk 1976; *Parahyaena* Mills 1990) for which vocalization data were published and by any of the earlier publications dealing with acoustic communication in the aardwolf.

Further data are also necessary to establish the exact nature of "purring" in the aardwolf described here as compared to purring proper in the Viverridae (Wemmer 1977) and Felidae (Peters 1981; Frazer Sissom et al. 1991). Deane (1962) mentions a sound termed purring in the spotted hyaena. Based on the behavioural context given for this sound it is highly unlikely that it is equivalent to aardwolf "purring" or felid purring but its exact nature remains questionable.

So far neither jaw clicking nor lip smacking have been reported as acoustic threat signals in any species of the Hyaenidae, Felidae, Viverridae, or Herpestidae. If they function as genuine acoustic signals in *Proteles* they probably represent an autapomorphy of this species. The only other species of the Carnivora which are known to produce sounds by opening and closing of the jaws and lips during agonistic behaviour are in the family Ursidae (Jordan 1976), including the giant panda (*Ailuropoda melanoleuca*) (Peters 1985; Schaller et al. 1985) and the red panda (*Ailurus fulgens*) (Roberts and Gittleman 1984). The similarity of these sound signals between the aardwolf and the Ursidae is very likely to be explained by convergent evolution; the respective adaptive significance of these sounds in the two taxa and whether they evolved under equivalent functional constraints is open to question. Aardwolves lack any type of intense long range vocalization and the same seems to be true for the striped hyaena (Kruuk 1976) and the brown hyaena (Mills 1990). So, no other hyaenid species seems to have a vocalization type comparable to the whoop of the spotted hyaena (Kruuk 1972; Henschel 1986; Mills 1990). Mills (1990) mentions more vocalization types in the last species which may not be shared by any other species of the Hyaenidae.

All vocalizations of the aardwolf described in this study require better characterization in their typical structure, their range of variability and some of them possibly further differentiation on the basis of more recordings of appropriate quality and detailed behavioural observations. It is essential that the exact nature of the whizzing sound is established on the basis of sonagraphic analyses. Studies are desirable to check whether aardwolves have further vocalization types in addition to the ones described here. Because of the difficulties in observing and tape recording aardwolf acoustic communication in the field it seems appropriate to plan future studies into this topic with a mixed approach of observing wild and captive individuals.

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Zusammenfassung

Lautliche Kommunikation beim Erdwolf, Proteles cristatus (Carnivora: Hyaenidae).

Auf der Grundlage von Beobachtungen an freilebenden und in Menschenobhut gehaltenen Tieren und sonagraphischer Auswertung von Tonbandaufnahmen wird die lautliche Kommunikation juveniler und adulter Erdwölfe (*Proteles cristatus*) beschrieben. Zusätzlich zu den vorwiegend genutzten geruchlichen Signalen besitzen Erdwölfe eine Reihe von Lautäußerungen, die sie zur Verständigung mit Artgenossen über geringe bis mittlere Entfernung einsetzen. Eine spezifische Lautform zur Verständigung über größere Entfernungen (>500 m) ist nicht ausgebildet. Die Lautformen im Zusammenhang agonistischen Verhaltens sind am vielfältigsten. Von den bisher für die Art belegten 9 Lauttypen gehört ungefähr die Hälfte zu Lautkontinua, bei denen Übergänge zwischen einzelnen Typen auftreten. Bei den anderen handelt es sich wahrscheinlich um diskrete Typen. Es ist allerdings nicht gesichert, ob alle hier beschriebenen Lautformen des Erdwolfs wirklich zur akustischen Verständigung eingesetzt werden. Soweit dies anhand der bisher vorliegenden Beobachtungen zu beurteilen ist, unterscheidet sich das Lautrepertoire der Art deutlich von dem der anderen Arten der Hyaenidae.

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