1. INTRODUCTION

Communication in animals has attracted a considerable amount of interest during recent years and has formed the basis for a large number of research reports and reviews (e.g. Lanyon and Tavolga 1958; Busnel 1963; Sebeok 1968; Sebeok and Ramsay 1969). Detailed analyses of acoustic communication in vertebrates mainly concerned birds (e.g. Thorpe 1961; Armstrong 1963; Greenewalt 1968) and primates (e.g. Andrew 1963; Marler 1965; Altmann 1967; Moynihan 1967), this knowledge of the latter group being regarded as useful in shedding light on the origin of human language (Bastian 1964; Struhsaker 1967; Lancaster 1968).

Interest in mammalian communication systems has expanded considerably during the past two decades and detailed studies on other groups such as rodents (e.g. Waring 1966; Smith 1972; Brooks and Banks 1973) and carnivores (e.g. Reschke 1960; Tembrock 1960; Le Boeuf and Peterson 1969) have been undertaken. This general upsurge in interest, apart from the development of sophisticated apparatus facilitating such studies, probably resulted from more observers realising the important role of communication in the maintenance of group structure. A knowledge of communication in any social species is therefore essential if its social behaviour is to be fully understood.

Past research on the Hyracoidea of southern Africa mainly involved studies on the taxonomy and morphology of especially Procavia capensis. Hahn (1934), Wells (1936), Whitworth (1954), Churcher (1956) and Kitching (1966) described fossil dassies from southern Africa and discussed their relationship with the earlier fossils from eastern, central and northern Africa. The more important taxonomic reviews of recent dassies were presented by Thomas (1892), Gray

(1933), Sale (1960), Bothma (1971) and Roche (1972), while Bothma (1964, 1967) mainly dealt with southern African forms. The distribution of dassies in southern Africa also received attention from Bigalke and Bateman (1962) and Pienaar (1964). George (1874) gave a detailed account of the morphology of dassies in general and Owen (1832), Swart (1970) and Millar (1973), amongst others, described various anatomical features of P. capensis.

The general biology of southern African Hyracoidea received little attention in the past. Until now research has been mainly centred on the physiology (especially reproduction) of P. capensis and the role of dassies in the transmitting of diseases or as host for parasites. Weitz (1953) and Buettner-Janusch, Buettner-Janusch and Sale (1964) commented on the serological relationship between the African elephant and the dassie, while Louw (1971) and Louw, Louw and Retief (1972) reported on aspects of thermoregulation and renal function in P. capensis. Reproduction in the dassie, however, attracted more widespread interest. The mechanisms involved in the control of reproductive processes in P. capensis were investigated by O'Donoghue (1963), Millar (1971, 1972a, 1972b) and Millar and Glover (1970, 1973). Other studies involved research into the dassie's gestation period (Van der Horst 1941; Murray 1942) and placentation and embryology (Turner 1875; Wislocki 1928; Wislocki and Van der Westhuyzen 1940; Sturgess 1948). The parasites and diseases of and transmitted by the dassies of southern Africa have also received some attention, notably so from Bedford (1932a, 1932b), Wagner, Buchanan, Bokkenheuser and Leviseur (1958), Wagner and Bokkenheuser (1961) and Taute (1971).

Although a number of descriptive studies on the behaviour of East African and Syrian hyracoids were done (e.g. Nassonow 1895; Coe 1962; Mendelssohn 1965; Sale 1965b, 1965c, 1965e, 1970a, 1970b), no such reports exist for southern

African dassies apart from short notes by Bothma (1963, 1966) and Siegfried and Geldenhuys (1965) on a few selected aspects of P. capensis behaviour. Communication processes of hyracoids in general have so far attracted little attention from an analytical point of view, although some authors described sounds (see Table 3, page 18 for author references), postures and other components of acoustic, visual, olfactory and tactile communication in terms of function or as causally specific to particular situations. However, apart from Rahm's (1969) oscilloscopic analysis and description of the "cry" of Dendrohyrax dorsalis, no detailed or complete analysis of acoustic communication in the dassie exists in the literature.

When employing a term with such general usage and meaning as "communication", it should be defined within the limits of its use. Such an attempt cannot, however, be made in total disregard of the definitions of animal communication previously proposed by other authors (e.g. Révész 1944; Hockett 1958; Frings and Frings 1964; Carpenter 1969). Most of these definitions were criticised by Tavolga (1968), Lenneberg (1969) and Moles (1969) as being impractical and it would seem as if the term "communication" cannot be universally defined. Hockett and Altmann (1968), however, bypassed the necessity for definition by proposing their approach to animal communication through design-feature analysis. They argued that any discernable property in a process of information transfer affords a criterion more exact than the loose conception of "communication". The term "communication" is therefore either used in combination with another descriptive term or "label" (e.g. "acoustic", "visual", "olfactory", etc.), thereby enabling the observer to select a certain property characteristic of the label and using it as a design-feature, or substituted by a new term (e.g. "vocal behaviour", "visual displays", etc.) to describe particular processes involving information transfer.

Hockett and Altmann (1968) also stated that "If, in a specific social and ecological setting, a particular animal transmits a message to one or more others (or to himself), use is necessarily being made of a channel, or of several channels at once." Keeping the above in mind, acoustic communication is considered a process involving the vocal-auditory channel in the production and detection of sound as a means of information transfer. In the same sense visual, olfactory and tactile communication can be investigated by inquiring about the channel involved.

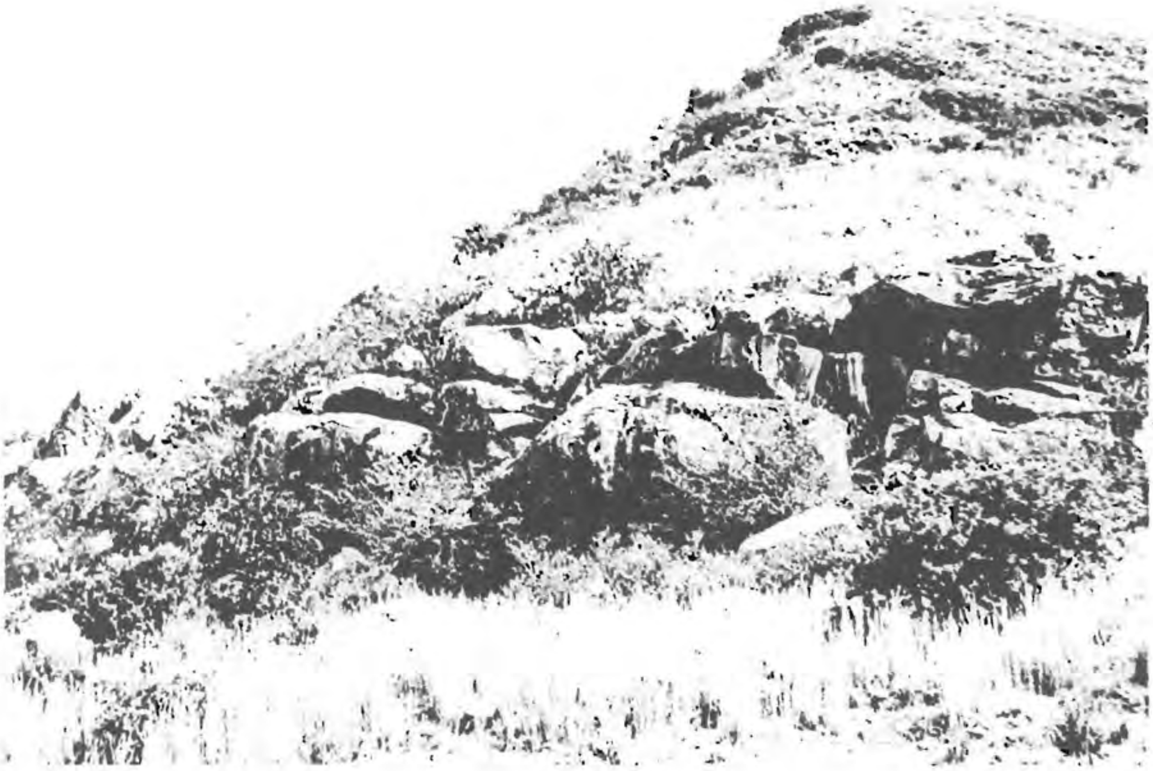
Since a need exists for data on the behaviour of *P. capensis*, a detailed analysis of acoustic communication in this species was undertaken and integrated with observations on other elements of its social behaviour. In this way an attempt was made to interpret the mode of life and general ecological requirements of the rock dassie in terms of the possible evolutionary development of the hyracoid group. Although visual, olfactory and tactile means of communication were also investigated, the main emphasis in this work is placed on acoustic communication since it is probably the most important and widely used mechanism of information transfer in the dassie, as shown by the fact that dassies use 21 vocal and four nonvocal sounds against only four visual signals (dorsal spot flaring and body posture) and one olfactory signal (scent emittance from the dorsal gland).

2. STUDY AREAS

Field studies on dassies were conducted for various lengths of time between January 1971 and December 1973 on the farm Naudéskop-Oost (28°8'S; 28°6'E) 24 km north-west of Bethlehem, Orange Free State. The habitat consists of rocky hillsides covered with shrubs, aloes and grass. Two separate study areas, each supporting an isolated dassie colony were selected. These are separated by approximately 1,6 km of grassland sloping steeply from both areas towards the Vals River running more or less halfway between them. Area 1 (Fig. 1A) is a small cliff on one side of a koppie (Naudéskop) and served as the main trapping area for animals needed for studies in captivity. This area had a dassie population, based on visual counts, of between 50 and 80 individuals. Area 2 comprises a series of low cliffs overlooking a large dam built in a rivulet (Leeuspruit) which runs closeby the cliffs and joins the main river some distance away.

Observations were also made on the farm Liberia, 17 km south-east of Senekal, O.F.S. Here the habitat consists of large crevices in an erosion gully (Fig. 1B), with the surrounding area covered by grass and cultivated prickly pear.

Trapped animals were kept from May 1971 to October 1972 in an enclosure, approximately 3,0 km from area 1 and 1,5 km from area 2, on the farm Naudéskop-Oost. In October 1972 the captive dassies were transferred to an enclosure in the Zoology Department, University of Pretoria. Conditions in the enclosures are discussed in greater detail below.



A

B

3. MATERIAL AND METHODS

Five dassies (three males, two females), approximately five months old and kept in captivity on Liberia, were transferred to the enclosure at Naudéskop-Oost in April 1971. These had been caught in an erosion gully as juveniles of between one and two months old. The other captive animals (10 males, four females) were trapped between May 6 and July 12 1971 at Naudéskop-Oost and placed with the Liberia dassies. These dassies are elsewhere referred to as numbering 11 males and four females (Fourie 1972). This is correct since one of the males escaped and was later recaptured in study area 1. For statistical purposes it was thus treated as two different animals.

Between May 1971 and October 1972 the size of the captive colony was drastically reduced as a result of natural deaths, heavy fighting during the mating season and a few escapes which occurred while trapping was still in progress. By the end of October 1972 only seven dassies (three males and four females - one gravid) remained in the enclosure on Naudéskop-Oost. These were all transferred to Pretoria.

A total of 28 captive animals (18 males and 10 females) were studied over a period of three years, from April 1971 until March 1974. Nineteen of these were born in the wild and their early history is unknown. Nine were born in captivity, three males at Naudéskop-Oost and the rest, three males and three females, in Pretoria.

Not included in the above is one female captured within a week after birth. She came into my possession as a tame juvenile of five months and was kept as a pet until her ninth month, and then placed with the captive colony thus bringing her into contact with other dassies for the first time since birth.

Since many of the young animals matured and grew to adulthood during the period of study, the actual number of animals studied in the three main age groups (adult, juvenile and infant) is given in Table 1. A few individuals were studied for very short periods only before they died or escaped. They are nevertheless included in the Table.

Table 1: Actual number of captive rock dassies (Procavia capensis) in the three main age groups studied between April 1971 and March 1974 at Naudéskop-Oost and the Zoology Department, University of Pretoria.

Age group	Number
Adult (15 months and older)	23 (11 of these were adult at the commencement of the study)
Juvenile (2 to 15 months)	17
Infant (up to 2 months)	9

Field and laboratory procedures

Dassies were trapped with treadle operated, single door wire mesh live traps measuring 25,4 cm by 30,1 cm by 81,2 cm. Cold maize porridge was found to be a successful bait. All the dassies were trapped on clear, windless nights during first quarter or full moon phases in traps placed either in a feeding area or in the food-paths leading to it (Fourie 1972).

Although it was easy to distinguish between individual dassies by means of natural markings and variation in facial structure, an additional marking system was employed to aid identification of individuals when partly obscured by other dassies or objects in the surroundings. Neck bands made from 15 mm wide Saflag nylon coated vinyl strips were used. Each dassie was marked with two colours, one to indicate sex and the other to identify the individual. Black denoted males and white females. Four additional colours (red, green, orange and blue) were cut in 10 mm wide strips and laced through slits in either the black or white bands. Such a combination band was then stapled round the neck of each individual. Although not foolproof, this method served its purpose well enough.

Vocalizations and other sounds made by the dassies were recorded in the field and artificial enclosures on either a Stellavox SP7 battery-operated tape recorder, fitted with a Mono 1:1 NAB head adjusted for Scotch Dynarange 203 magnetic tape run at 38/sec, or on an Uher 4200 Report Stereo tape recorder run at a tapespeed of 19 cm/sec. A Sennheiser MKH 804 super cardoid microphone with a frequency response of 50 to 20 000 Hz was used with both tape recorders; two additional dynamic microphones, an Uher M517 and Uher M537, were also occasionally used with the Uher tape recorder.

Artificial cavities and sleeping boxes in the enclosures were so constructed that these microphones could be placed to within 75 cm of the dassies without disturbing them. For recordings made in the open, a Sennheiser MZW 804 windshield was fitted to the Sennheiser microphone.

As the Scotch 203 magnetic tape series was withdrawn from the market in 1972, Scotch 223 was used as a substitute since then.

A Kay Electric Company model 6061-A Sona-Graph sound spectrograph in conjunction with a Nagra III tape recorder was used to graph the various sounds. Wide band and HS analyses were found to be the most satisfactory. Kay Electric Company Sonogram Paper Type B/65 was used on which the sounds were visually displayed with time (up to 2,4 sec.) as the ordinate and frequency (up to 8 kHz) as the abscissa.

Where it became necessary to examine the physical behaviour of a sound pattern or unit reaching higher than 8 kHz the tape speed on the playback recorder coupled to the sound spectrograph was retarded. In this way all frequencies in the sound were halved or quartered to bring them within the registerable range of the sound spectrograph. In calculating the original frequency at any point on the resulting spectrogram, the corresponding reading on the abscissa was then doubled or quadrupled, depending on the amount of retardation.

The analysis procedure followed was that described by Borror and Reese (1953).

Maintenance of the captive colony

The 120 m^2 enclosure at Naudéskop-Oost was fenced in with chicken wire mesh to a height of 2,5 m on all sides. The fence was given a 50 cm overhang on the inside since a number of dassies managed to clamber up the wire mesh and escaped. Two artificial cavities, each measuring 188 cm by 94 cm by 73 cm (excluding the entrance passages) were covered with soil and rocks to form an outcrop 8 m long, 2 m wide and 1,5 m high inside the enclosure. The roof and sides of each cavity were constructed of corrugated iron sheets and the floor paved with flat stones and smooth bricks.

The enclosure lacked trees and shrubs and the dassies therefore had to be content with shade provided by the outcrop itself. Although shade outside the crevices also seems to be an important aid for the regulation of body temperature in the dassie during the hot hours of the day (Sale 1970a), the protection offered by the artificial cavities appeared to have been sufficient for this purpose.

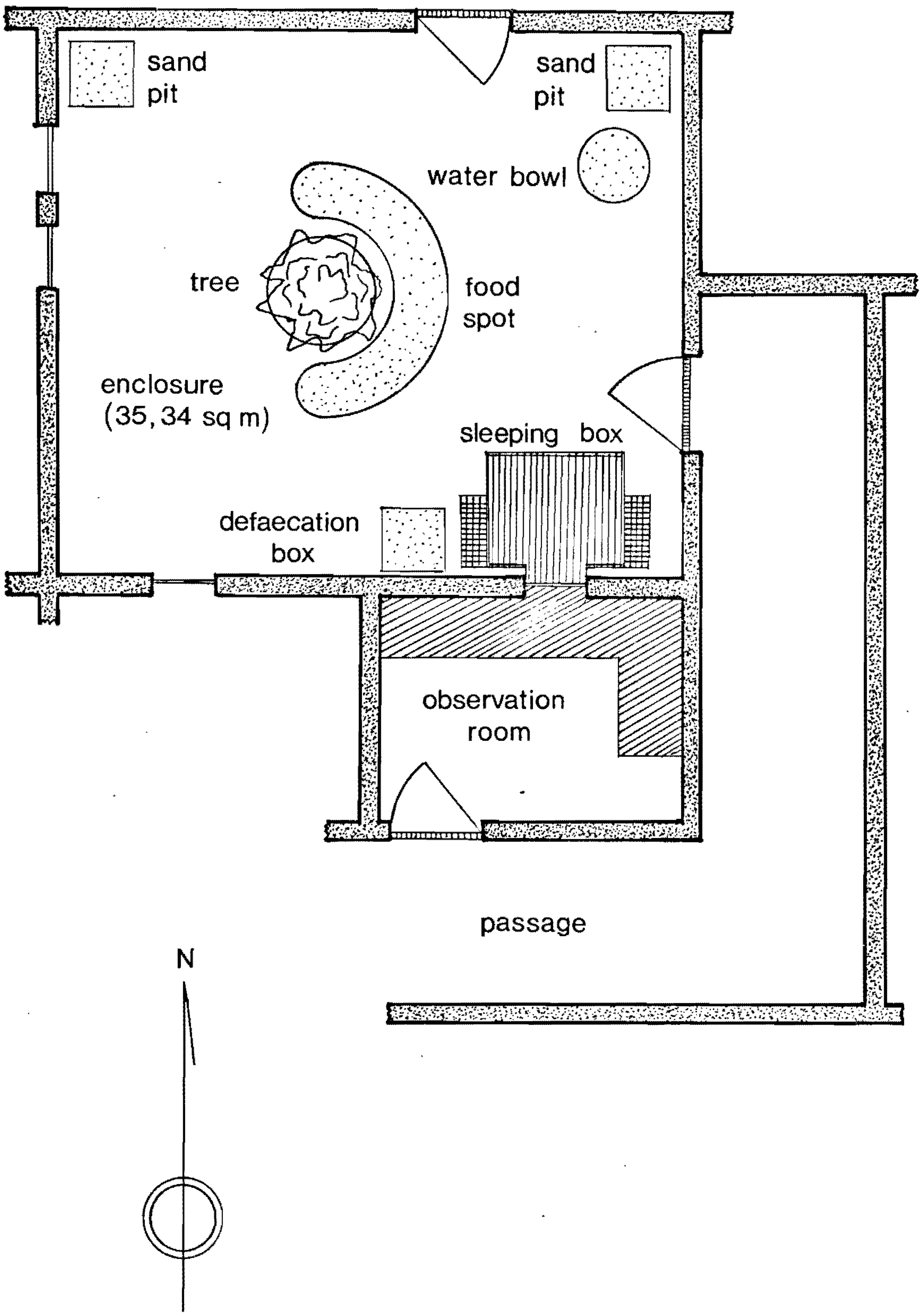
The captive animals transferred to the Zoology Department, University of Pretoria during October 1972 were placed in pairs in wire traps covered with heavy blankets almost 12 hours before the trip. Even though they were in the traps for close to 19 hours they did not show any ill-effects. They were released as a group in a 35,34 m^2 enclosure bordered on three sides by the walls of a U-shaped building situated in a courtyard of the main building, and on the remaining side by a 2,3 m high wall. Fixtures inside the enclosure included a 15 m poplar tree, three 1 m^2 by 12 cm deep open wooden boxes, a water bowl and a subdivided sleeping box (Fig. 2). As the enclosure has a concrete floor, two of the wooden boxes were used as sandpits where the dassies could sandbathe. The third box served as a communal latrine.

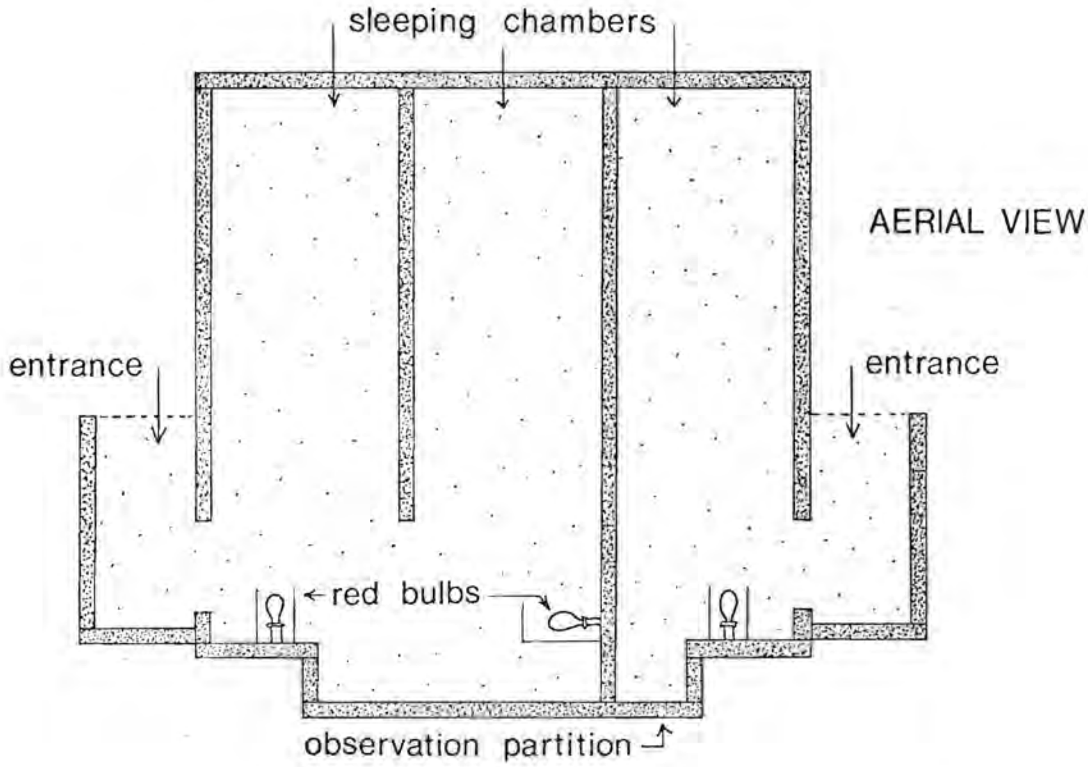
Many authors (e.g. Coe 1962; Kingdon 1971) noted that, in the wild, dassies urinate and defaecate in a specific site. As this is also the case in captive dassies the latrine box was supplied to facilitate cleaning of the enclosure. The bottom of the box was covered with a thin layer of wet sand and some fresh dassie droppings strewn on top. The wetting of the sand stemmed from personal observations which indicated that, if given a choice, dassies would always prefer to perch on an elevation or protrusion of the ground next to a damp spot while defaecating.

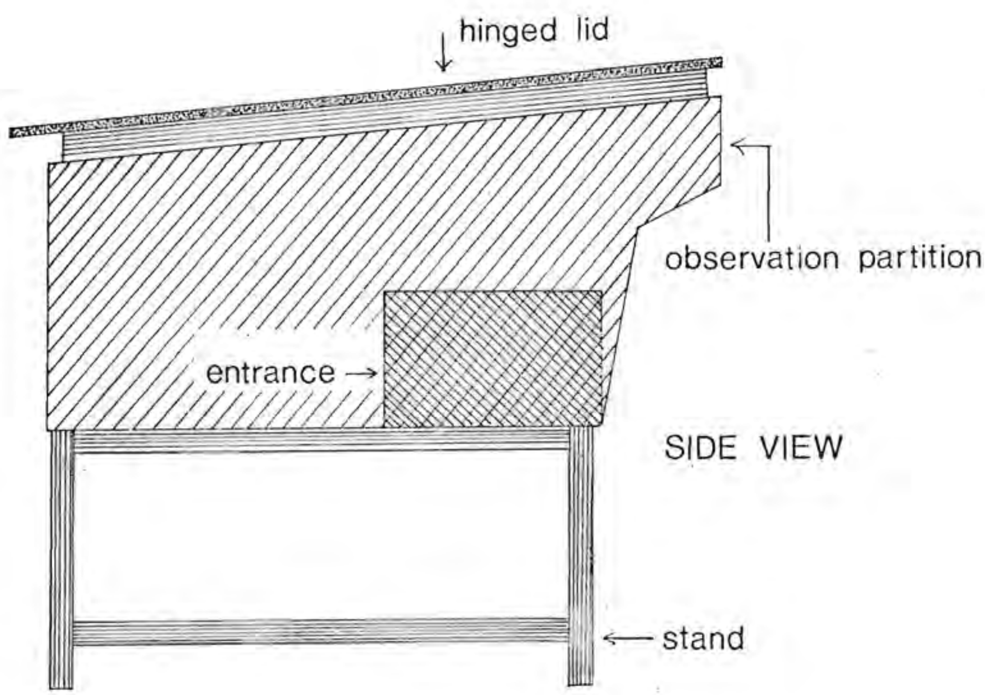
The sleeping box (Fig. 3) consisted of two chambers, measuring 52,5 cm by 47,5 cm by 100 cm and 52,5 cm by 95 cm by 100 cm respectively, each with a separate entrance. The latter chamber was subdivided by means of an incomplete partition. The whole box was raised 81,5 cm above the floor and placed against a window from which the panes had been removed and replaced with hardboard. Observations and recordings inside the box were made from an adjoining room through holes in the hardboard. Three 60W red bulbs provided illumination. The roof of the chambers formed a 20° angle with the base and consisted of two hinged lids so that the chambers could be cleaned and the dassies handled when necessary.

The dassies were supplied every day with dry lucerne hay in the late afternoon and with fresh vegetables such as carrots, pumpkin and lettuce once or twice a week. Fresh shoots and green leaves of the poplar tree were also extensively utilized.

Figure 2: Diagram of enclosure (not drawn to scale) where captive rock dassies (Procavia capensis) were housed between October 1972 and March 1974 in the Zoology Department, University of Pretoria.


sand
pit
sand
pit
water bowl
tree
food
spot
enclosure
(35,34 sq m)
sleeping box
defaecation
box
observation
room
passage
N


sleeping chambers
AERIAL VIEW
entrance
entrance
red bulbs
observation partition


hinged lid
observation partition
entrance
SIDE VIEW
stand

Two methods of catching dassies in the captive colony were used: in confined spaces a heavy blanket was thrown over the animal which was then quickly grabbed by the head with one hand. The other hand was then placed under the blanket and moved over the back of the dassie up to its neck where it was held tight. The blanket could then be removed. Dassies running loose in the enclosure were caught with a long-handled net and directly gripped by the neck.

4. ACOUSTIC COMMUNICATION IN PROCAVIA CAPENSIS

The vocalizations of the dassie form a continuum of sound, i.e. they appear to be interrelated and with some of their physical parameters intergrading. Within this continuum, however, it was possible to identify 21 fairly distinct sounds on the grounds of a significant change in one or more of the parameters, such as frequency, amplitude and length. The four nonvocal sounds identified are discrete and not interrelated. No quantitative analysis and mean values of parameters (such as the forementioned) were undertaken on a large number of recorded samples of dassie sounds since this study is mainly intended to establish a preliminary basis for future more conclusive investigations. The number of sounds for P. capensis here suggested and the conclusions drawn as to their relationships (see Addendum and Fig. 19) were done only from representative spectrograms (See physical characteristics of the sounds, p. 26, and Figs. 5 to 14).

A list of the vocal and nonvocal sounds of P. capensis is given in Table 2. The consecutive order in which the sounds are presented is quite incidental and does not indicate priority affixed to any sound over another. The name given to each sound does not describe the acoustical properties of the sound in any detail but suggests a certain similarity to the common, everyday sound called by such a name. This follows the suggestion by Jay (1965) that terms used to label signals (visual, acoustic, etc.) should be descriptive of the signal or its physical structure rather than its function.

Table 3 attempts to correlate the names of Procavia sounds (or sounds described for taxa including Procavia)as given by earlier observers of dassies with those here suggested.

Table 2: List of _Procavia capensis_ sounds. Corresponding sounds in different age groups are listed on the same levels. See text for full description.

SOUNDS		
Adults (15 months and older)	Juveniles (2 to 15 months)	Infants (up to 2 months)
Grunt	Grunt	-
Growl	Growl	-
Snarl	Snarl/Spit	Spit
Wail	Yelp	-
Wail-bark	Rasp	-
Hiccup and cough	-	-
Hoarse moan	-	-
Coo	-	-
Whine	-	-
Squeak	Squeak	-
Yap	Yap	-
Sharp bark	Sharp bark	-
Repetitious bark	-	-
Squeal	Squeal	-
Whistle and whistle chirrup	Whistle and whistle chirrup	(? Soft twitter)
Harsh chirrup	Harsh chirrup	-
Harsh twitter	Harsh twitter	Harsh twitter
-	-	Soft twitter
Sneeze	Sneeze	Sneeze
Snort	Snort	-
Pant	-	-
Teeth gnashing	Teeth gnashing	Teeth gnashing

Table 3: Comparison of names used in the literature for the sounds of dassies belonging to the genus Procavia.

Name of Procavia capensis sound used in present study	Synonymous name with original author	Taxon for which used
Hiccup	? Hoarse squeaking noise (Sale 1965b)	Procavia johnstoni mackinderi
Coo	Whinnying type of noise (Sale 1965b)	P. johnstoni mackinderi
Whistle chirrup	Deep guttural twitter (Sale 1965b)	P. johnstoni mackinderi
	Whistles (Hoffmeister 1967)	Procaviidae
	? Scolding squeaks (Hoffmeister 1967)	Procaviidae
	Twittering contact call (Kingdon 1971)	Procavia
Harsh chirrup	? Chatters (Hoffmeister 1967)	Procaviidae
	? Clucking sounds (Hoffmeister 1967)	Procaviidae
Harsh twitter	Loud chirping noise (Flower 1932)	?
	Staccato squeal (Bothma 1963)	P. capensis
	Twittering noise (Sale 1965b)	P. johnstoni mackinderi
	Begging call (Sale 1965b)	P. johnstoni mackinderi
	? Scolding squeaks (Hoffmeister 1967)	Procaviidae
	Bird-like chirrup (Kingdon 1971)	Procavia
	Twitter (Kingdon 1971)	Procavia
Growl	Growling (Sale 1965c, 1970a)	Procavia
	Growling (Kingdon 1971)	Procavia
	Growling (Matthews 1971)	Hyracoidea
	Shrill squeak (Burton 1951)	Procaviidae
	Warning cry (Sale 1960)	Hyracoidae
Sharp bark	Sharp coarse note of alarm (Coe 1962)	P. johnstoni mackinderi
	Alarm cry (Bothma 1963)	P. capensis
	Loud roar of alarm (Kingdon 1971)	Procavia
	Bark (Kingdon 1971)	Procavia
	Warning note (Matthews 1971)	Hyracoidea
	Alarm note (Matthews 1971)	Hyracoidea

Table 3 (Continued)

Name of *Procavia capensis* sound used in present study	Synonymous name with original author	Taxon for which used
Repetitious bark	Mewing note (Coe 1962)	*P. johnstoni mackinderi*
	Territorial call (Mendelssohn 1965)	*P. capensis syriaca*
	Male sexual calling (Sale 1970a)	*Procavia*
	Cry (Kingdon 1971)	Procaviidae
	Croak (Kingdon 1971)	*Procavia*
	Mewing note (Matthews 1971)	Hyracoidea
Squeak	Whistle-like call (Bothma 1963)	*P. capensis*
	Short, low-pitched squeak (Sale 1965c)	*Procavia*
	? Warning whistle (Tembrock 1968)	Hyracoidea
	Low intensity whistle (Kingdon 1971)	*Procavia*
Teeth gnashing	Teeth grinding (Kingdon 1971)	*Procavia*

Since there is a general lack of sound spectrograms in the literature for the Hyracoidea in general, apart from a series of oscillograms presented by Rahm (1969) for the "cry" of Dendrohyrax dorsalis, and in some cases also of detailed descriptions of dassie sounds, this comparison can only be regarded as tentative.

As is evident from Table 4 (see also situations eliciting the sounds, p. 42), the various P. capensis sounds are not situation specific, i.e. every sound is produced in more than one, sometimes apparently quite different situations. It thus became necessary to determine what controls the type of sound given. Kiley (1972) stated that the type of sound emitted appears to depend on the level of "excitement" of the animal and that in contexts where vocalization occurs, excitement is commonly elicited by a "frustration situation". Furthermore, there must be a stimulus within a situation that evokes vocalization. The interest an animal shows in a given stimulus determines the level to which the animal becomes excited. It thus follows that the interaction between stimulus interest and level of excitement controls the type (or structure) of the sound emitted (see Addendum) and when it will be given. Consequently the same stimulus may evoke different sounds. This view was also applied in this study.

Definition of terms

Use of the terms "excitement" and "frustration situation" in the text follows Kiley's (1972) definitions, namely that "... an increase in excitement is defined as an increase in locomotion with the performance of more different activities more often", and that "A frustration situation is ... defined as one in which the animal wants something, is waiting for something, or is thwarted from obtaining something." It should be emphasised, however, that the term "excitement" is not intended as a substitute for the concepts "motivation" or "drive", since that would mean an over-simplification of an already mechanistic approach. Excitement is here regarded

TABLE 4 : The percentage involvement of each Procavia capensis sound in the various situations in which it occurs. Calculation of the percentages were made from an analysis of tape recordings of dassie sounds and from field notes. Sounds were recorded (and analysed) only as regards particular situations, and not as to their percentage contribution to the total repertoire in a given observation period. Observation times for particular situations (and sounds) were therefore not necessarily equal.

	SITUATION AND PERCENTAGE SOUND INVOLVEMENT										
SOUND	Aggressive threat	Defensive threat	Fear	Startled	Alertness	Appeasement	Anticipation: pleasant	Frustration	Contact retained	Contact prevented	Pain
Grunt	73%	27%									
Growl	68%	32%									
Snarl	46%	54%									
Spit		82%		18%							
Wail			51%					49%			
Wail-bark			53%					47%			
Yelp			62%					38%			
Rasp			60%					40%			
Hiccup			36%					17%			47%
Cough			36%					17%			47%
Hoarse moan			56%					44%			
Coo					29%	71%					
Whine			28%		10%			32%		30%	
Squeak			10%	54%	18%			18%			
Yap			41%	43%	16%						
Sharp bark			36%	37%	27%						
Repetitious bark*											
Squeal	28%					58%		14%			
Whistle				14%	14%	31%	18%		23%		
Whistle chirrup						21%	27%		25%	27%	
Harsh chirrup						68%				32%	
Harsh twitter			15%					33%		32%	20%
Soft twitter						34%	28%		38%		
Snort	39%				61%						
Pant*											
Sneeze**				32%	68%						
Teeth gnashing	27%	26%			21%			26%			

* Situations uncertain

** Percentages exclude sneezes associated with nasal irritation

Figure 3: Diagram of the sleeping box used by the captive rock dassies (Procavia capensis) in the Zoology Department, University of Pretoria.

as an essential ingredient or byproduct of motivation and drive. An animal has to be motivated to show an active interest in a certain stimulus and the degree of interest (and consequently the level of excitement experienced) will depend on the general motivational state of the animal at the time. The definition of excitement, as given above, however provides the observer with a workable parameter against which a behaviour pattern can be judged in order to establish the degree of motivation or drive involved.

The following terms and definitions used in the description of the sounds of the rock dassie are quoted from several authors as indicated below. Arrangement of the terms attempts to be such that any term needed to explain subsequent ones is placed first. For this reason authors are not quoted chronologically. Self-explanatory terms used in the text are not described here. Figure 4 presents an idealized illustration of some of the terms described below in the form of stylized sonograms.

Bondesen and Davis (1966)

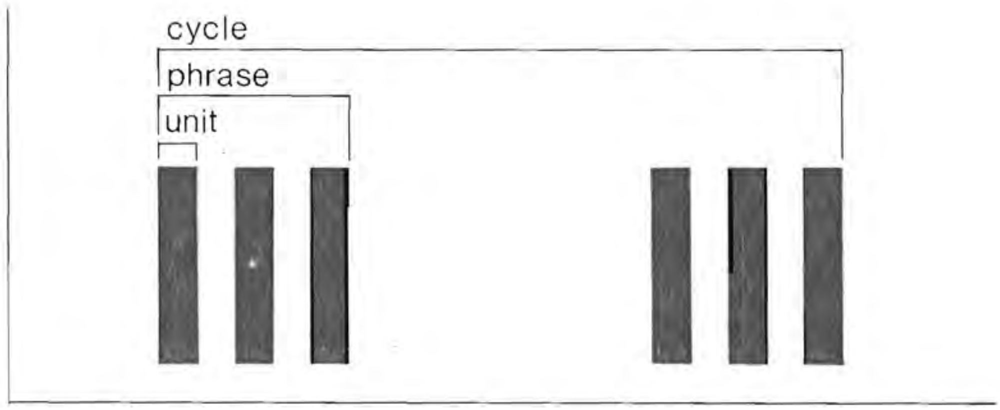
"<u>Rhythm</u> : A repetition of groups of sounds at regular intervals"

"<u>Succession</u> : repetition of units"

"<u>Frequency</u> : The number of vibrations or cycles in a unit of time (expressed in cycles per sec: cps or Hz)"

"<u>Noise</u> : Sound without definite organisation of frequencies" (This has been termed "non-tonal sound" by Struhsaker (1967)).

"<u>Pitch</u> : the subjective interpretation of frequency, but it is sometimes partly dependent upon the intensity of the sound as well as the frequency. (That is two sounds of the same frequency but of different intensity may be said to have a different pitch)"


cycle
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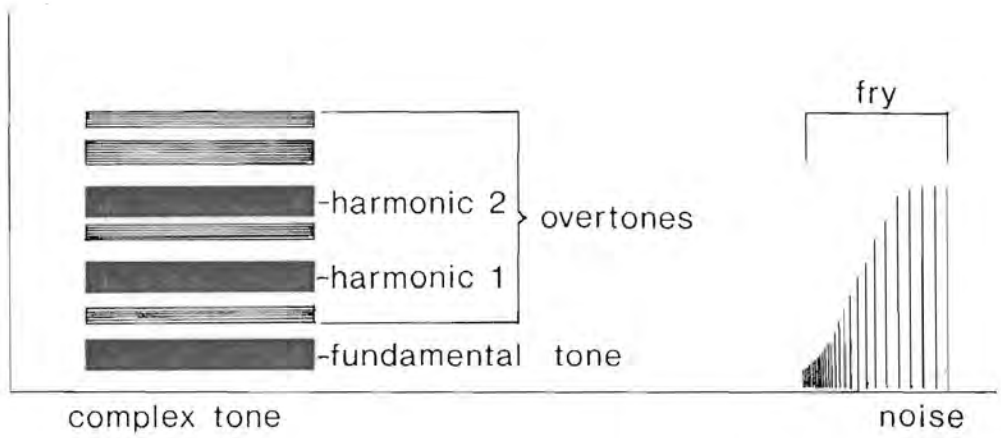
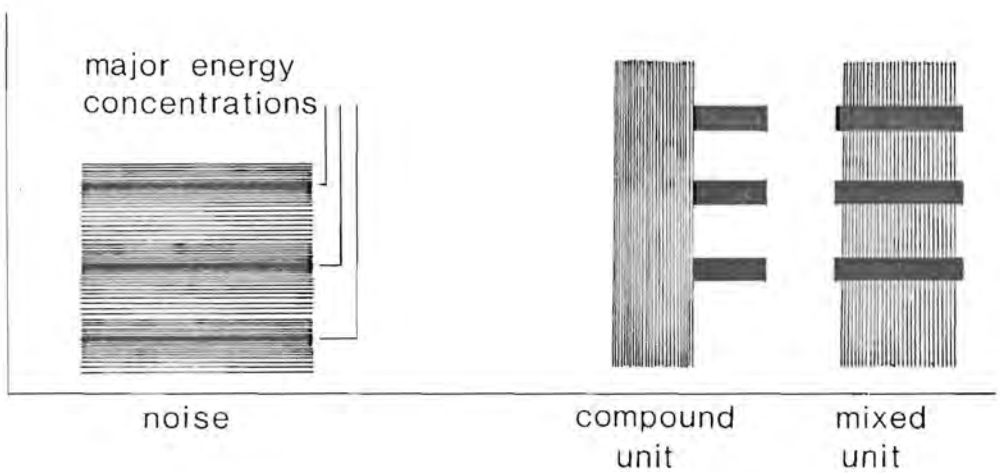

fry
-harmonic 2
overtones
-harmonic 1
-fundamental tone
complex tone
noise


major energy concentrations
noise
compound unit
mixed unit

"Tone	:	a sound sensation having pitch"
"Simple tone	:	(pure tone) a sound sensation characterized by its singleness of frequency"
"Complex tone	:	a sound sensation characterized by more than one frequency"
"Fundamental tone	:	the component of lowest frequency in a complex tone"
"Overtone	:	a component of a complex tone having a frequency higher than the fundamental"
"Harmonic	:	a component of a complex tone having a frequency which is an integral multiple of the fundamental"
"Glissando (slur)	:	continuous change in frequency (ascending or descending)"
"Tempo	:	the speed at which a sound production is performed"
"Amplitude	:	The extent of a vibratory movement. (Represented on the sound-spectogram as a function of coloring density, or by means of the Amplitude display method as a function of height)" This was classified arbitrarily by ear as low, medium or high judged by the relative loudness of the sounds.

Andrew (1962)

"Click	:	A very narrow column of noise" (This has also been termed a "transient but discrete signal covering a wide range of frequencies" by Brooks and Banks (1973)).

Kiley (1972)

"Fry is the term used for a structure which occurs when the call is of low tonality. It consists of a series of short clicks occurring in quick succession ... Fry probably represents periodic dampening of the sound by the lips of the glottis coming together."

Struhsaker (1967)

"Unit : The unit is the basic element of a ... sound or call, and is represented as a continuous tracing along the temporal (horizontal) axis of the sonogram."

"Phrase : The phrase is a group of units that is separated from other similar groups by a time interval greater than any time interval separating the units within a phrase." (A group of phrases forms a cycle - Bondesen and Davis (1966)).

"Compound unit : A compound unit is composed of both nontonal and tonal sounds that appear as a continuous tracing on the sonogram."

"Mixed unit : Units composed of both tonal and nontonal sounds that are rather superimposed on one another are called mixed units. The tonal and nontonal aspects are more or less separated by differences in frequency."

"Distribution of major energy of nontonal sounds: The distribution of the major energy of a nontonal sound is represented and thus determined by the darkest portion of the tracing on the sonogram. This distribution is generally over a smaller range than the frequency range of nontonal sounds. The distribution of major energy of nontonal sounds is described by an upper frequency (highest pitch of major energy) and a lower frequency (lowest pitch of major energy)."

("Nontonal sounds" correspond to "noises" of Bondesen and Davis (1966)).

Figure 4: Stylized sonograms to illustrate some of the terms used in the text for description of the physical characteristics of P. capensis sounds.

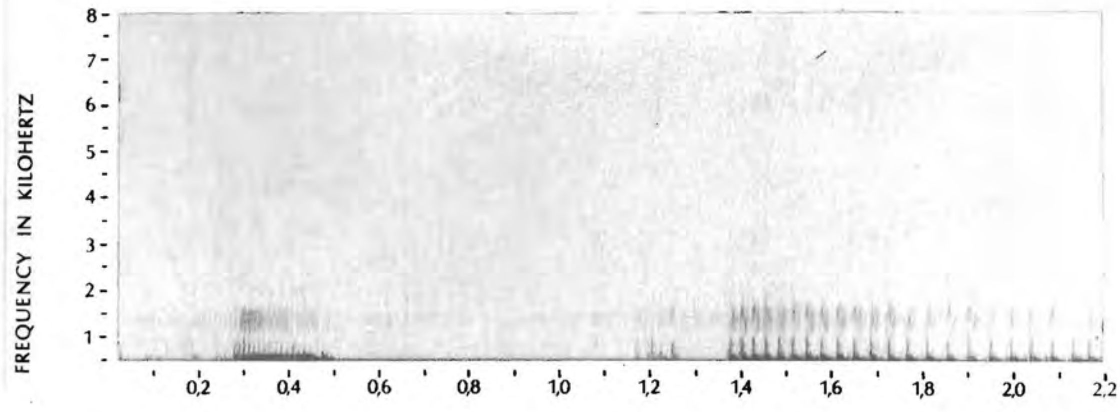
Physical charactersitics of the sounds

Grunt: At low amplitude it is a long drawn-out noise characterised by fry (i.e. composed of varying number of clicks showing rhythm) and with peak frequencies not exceeding 2,0 kHz (Fig. 5A). There is a tendency for retardation in the tempo of click succession towards the end of the sound. It may also be given in association with whistles (Fig. 5B). At high amplitude it is a short, forced noise of 0,25 sec duration. Fry is absent and major energy is distributed around 2,5 kHz, 4,25 kHz and 6,0 kHz (Fig. 5C). There is a tendency towards expression as a mixed unit but the tonal component is largely obscured by the noise. Since the mouth remains closed during production of the grunt, the sound is filtered which causes the main structural differences between the grunt and the growl.

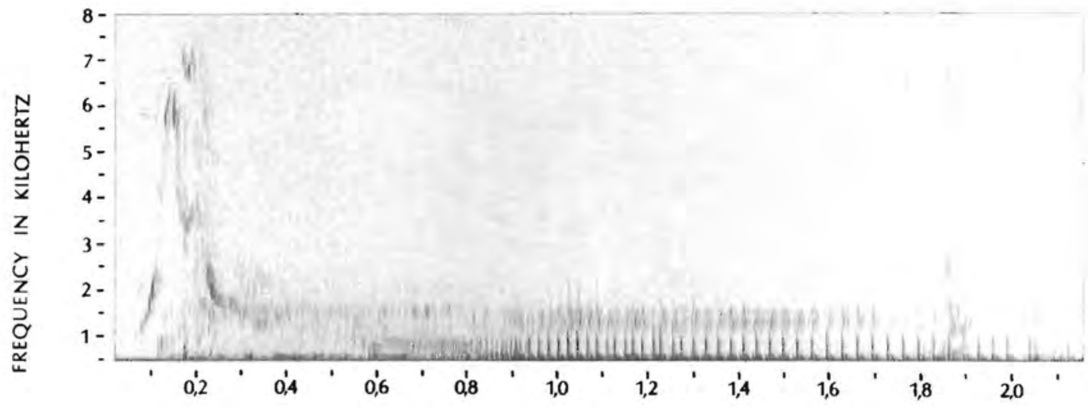
Growl: Basically the same as the grunt, but since the mouth is open during production of this sound and therefore acting as an open-ended resonating chamber, some differences can be noted. Fry is present with a faster succession of the clicks which do not show retardation of tempo towards the end of the unit. Peak frequencies may reach above 8,0 kHz. The growl is a noise with no tendency towards a mixed unit (Fig. 6A) although it often forms part of a compound unit.

Snarl: A high amplitude extension of the growl. It comprises a broad frequency band noise of short duration (0,1 - 0,2 sec), usually rapidly repeated to form a phrase (Fig. 6B).

Spit: The spit or infant snarl is also a broad frequency band noise where fry may sometimes be recognised, but more often than not it forms a single blended unit of 0,12 sec duration which is rapidly repeated once or twice to form a phrase (Fig. 6C).



A TIME IN SECONDS



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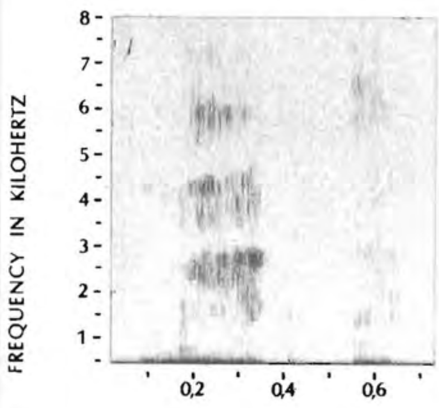
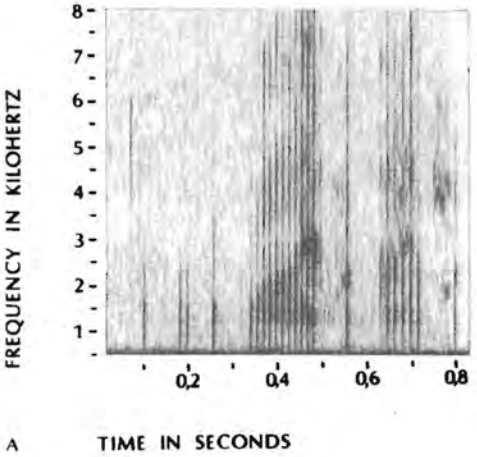


C TIME IN SECONDS

Figure 6: Spectrographic representation of P. capensis sounds. A. Growl. B. Snarl. C. Spit.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TIME IN SECONDS

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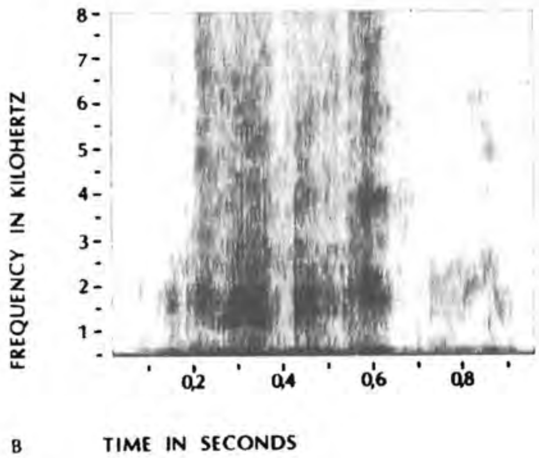
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TIME IN SECONDS

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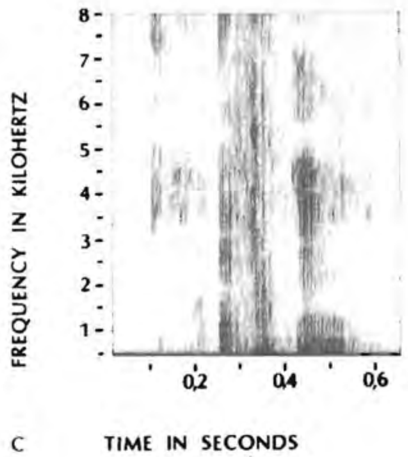
FREQUENCY IN KILOHERTZ
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TIME IN SECONDS

C

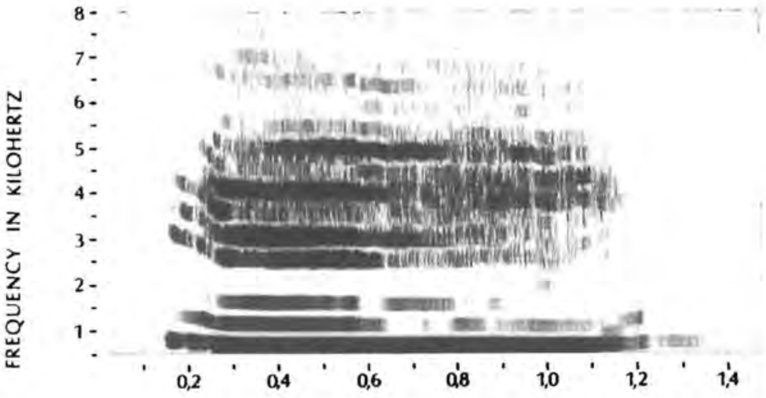
Figure 5: Spectrographic representation of P. capensis sounds. A. Low amplitude grunt. B. Whistle-grunt. C. High amplitude grunt.

Wail: At low amplitude this relatively long (1,0 - 1,5 sec) complex tonal sound has a fundamental at 0,1 - 0,5 kHz with overtones reaching 7,0 kHz and harmonics reaching 5,0 kHz. Apart from the slight drop in pitch at the beginning it demonstrates a characteristic stability in pitch (Fig. 7A). It is usually repeated at 1 - 2 sec intervals. (The medium amplitude wail is shorter (0,5 - 0,6 sec) and the evenness of the respective frequency bands tend to become distorted by fry and unorganised noise. The sound is slightly higher pitched with the fundamental tone at 1,0 kHz (Fig. 7B). (High pitched variations show the fundamental also at 1,0 kHz but with two harmonics at 3,7 kHz and 6,5 kHz respectively, and a number of overtones distorted through noise (Fig. 7C).

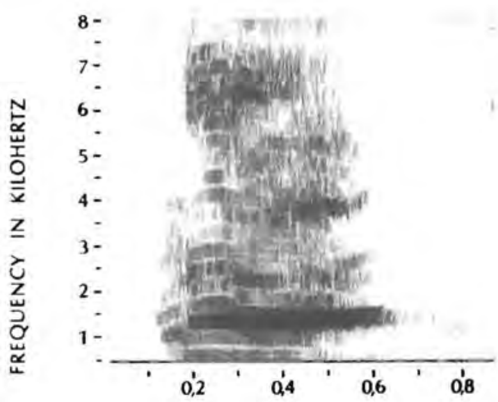
A wail-like "weeping" sound was recently brought to my attention by F.F. Kolbe (in litt.). It is a soft nasal wail expressed as a complex tonal sound of low pitch. Each unit has a duration of 0,2 - 0,45 sec and consists of a fundamental at 1,0 kHz and two to four harmonics which show a decrease in amplitude with increase in frequency from the fundamental to the highest harmonic (Fig. 8A). It may be repeated up to three times at 0,2 - 0,25 sec intervals.

Wail-bark: Constitutes a 0,4 sec mixed unit where the tonal component is largely obscured by noise during the first half of the sound, probably as a result of the sudden expiratory movement. The tonal part lies between 1,0 and 7,0 kHz but the noise part reaches above 8,0 kHz (Fig. 8B).

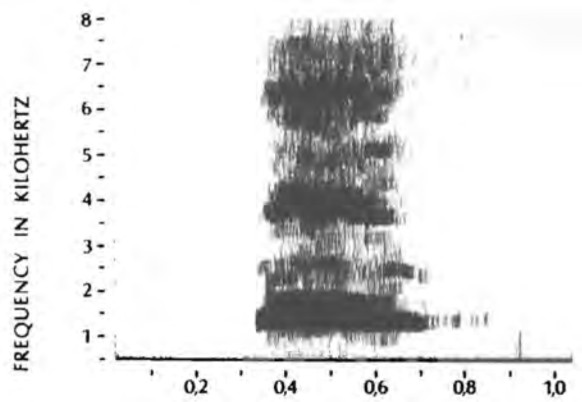
Yelp: The yelp or juvenile wail is a complex tonal sound with a tendency towards a mixed unit. The fundamental tone lies around 3,0 kHz and the overtones, which appear as arched bands showing a gradual rise and fall in pitch, reach up to 15,0 kHz. A soft harmonic squeak usually terminates the sound (Figs. 9A and 9B).



A TIME IN SECONDS

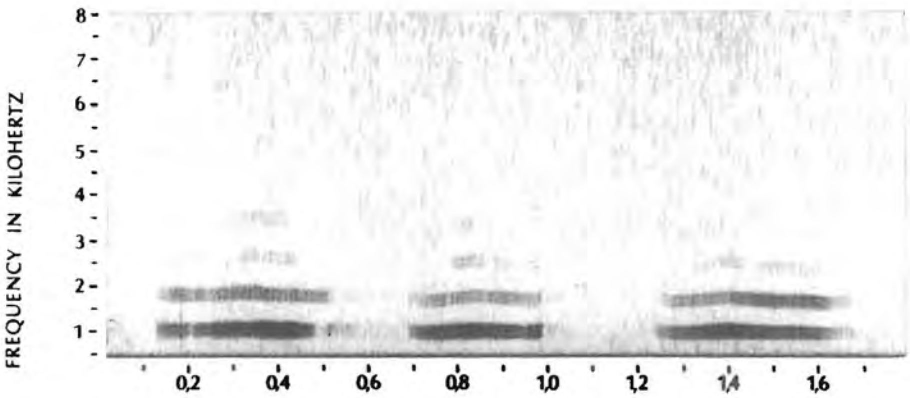


B TIME IN SECONDS



C TIME IN SECONDS

Figure 8: Spectrographic representation of P. capensis sounds. A. Wail-like "weeping" sound (from a tape recording by F.F. Kolbe). B. Wail-bark.



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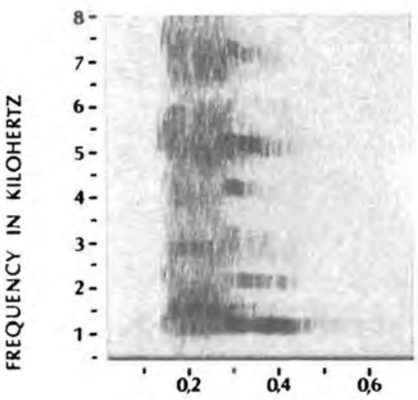


B TIME IN SECONDS

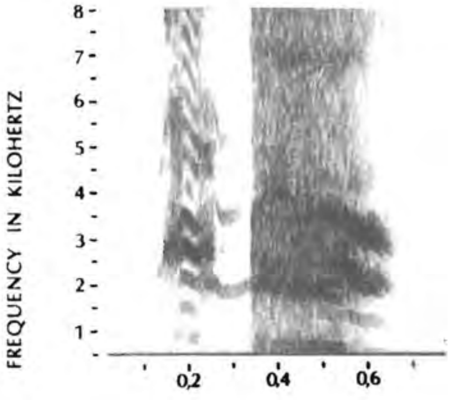
Figure 7: Spectrographic representation of P. capensis sounds. A. Low amplitude wail. B. Medium amplitude wail. C. High pitched variation of medium amplitude wail.

Rasp: The rasp or juvenile wail-bark has a duration of 0,3 - 0,35 sec. It is a broad spectrum mixed unit with the noise part dominating. The tonal component has a fundamental at 0,5 kHz and high amplitude overtones at 2,0 kHz, 4,0 kHz, 9,5 kHz and 11,5 kHz respectively. Fry, occurring towards the end of the unit, is noticeable only when the taperecorded sound is reproduced at half the natural speed (Figs. 9A and 9B)..

Hiccup and cough: The hiccup is a phrase composed of two units, each 0,1 - 0,12 sec long and with an inter-unit interval of 0,6 - 0,65 sec. The whole phrase may be regarded as a compound unit with a narrow noise band introducing the first unit and terminating the second unit. To some extent the tonal component resembles a squeak (see below and Fig. 11A) separated into two halves. Overtones in the first unit show a rise in frequency and the opposite in the second unit. Peak tonal frequencies lie below 8,0 kHz (Fig. 9C). The first unit may sometimes be given without being followed by the second unit. In this case it is termed a cough.

Hoarse moan: A 0,3 - 0,4 sec mixed unit with the tonal component dominating in the lower frequencies. Noise is present in the form of ill-represented fry. The fundamental frequency of the tonal component lies at 0,5 - 0,75 kHz followed by at least two overtones between 1,0 and 2,0 kHz respectively. In the noise part two or three major energy concentration bands are present between 5,0 and 7,0 kHz. If repeated, it is usually at 0,9 - 1,0 sec intervals (Fig. 10A).

Coo: A 0,5 sec complex tonal sound with at least one clear harmonic and three to five overtones. The fundamental lies at 0,75 kHz and shows very little change in pitch (Fig. 10B).



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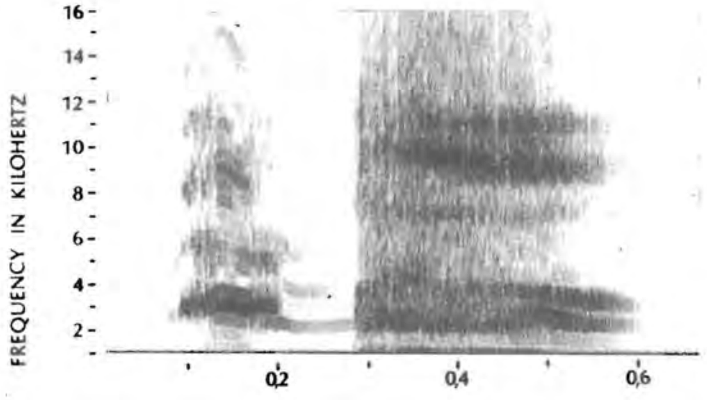

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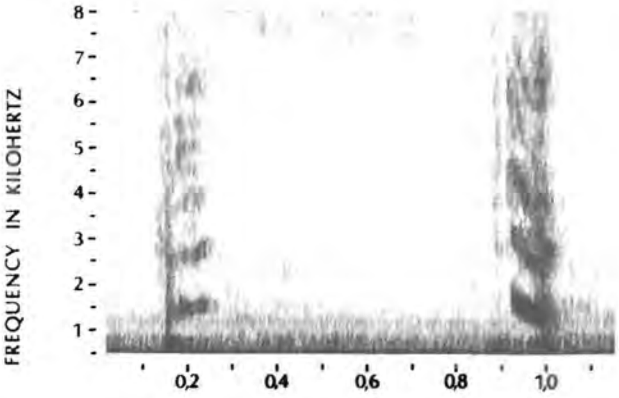


C TIME IN SECONDS

Figure 9: Spectrographic representation of P. capensis sounds. A. Yelp (first unit) and rasp (second unit), respectively given by two different juvenile dassies. B. The same as A but spectrographically reproduced at half the recorded speed. C. Hiccup. First unit termed a cough since it may be given without being followed by the second unit.

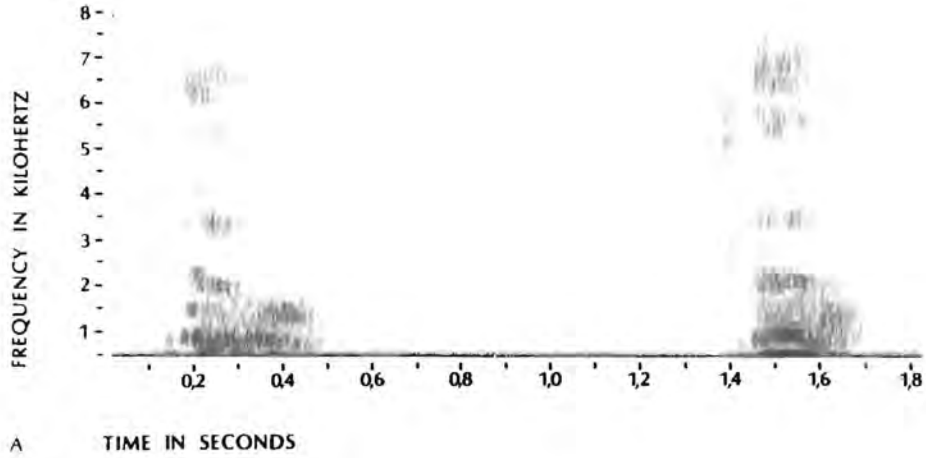
Whine: A more intense form of the coo (i.e. showing a higher amplitude) rising in pitch towards the end of the sound. The fundamental tone frequency rises from 1,0 kHz to 2,0 kHz and is 0,65 sec long. The highest overtone reaches over 8,0 kHz (Fig 10C).

Squeak: The squeak is a complex tone of approximately 0,2 sec duration. The fundamental tone lies at 0,23 kHz with several harmonics (the number depending on the amplitude of the sound) above it. It furthermore shows an abrupt rise and fall in pitch, giving the impression of a complete glissando (Fig. 11A).

Yap: The yap is a mixed unit with the tonal part superimposed on a "spit-like" noise. This sound lasts 0,3 sec with the harmonic structure slightly blurred and sometimes totally obscured by noise. It is given at medium amplitude (Fig. 11B). The yap is sometimes given in combination with other sounds, e.g. preceded by a spit and followed by a two syllable squeak showing an intersyllabic inspiratory interruption (Fig. 11C).

Sharp bark: This sound is a noise of 0,6 sec duration and with major energy concentrations around 1,5 kHz, 3,0 kHz, 4,5 kHz and 7,5 kHz. The distribution of these concentrations suggests a harmonic structure which indicate the possibility of the sharp bark being a mixed unit with noise dominating the sound (Fig. 12A). The sharp bark is seldom repeated by the same animal, but if so, it never forms a phrase.

Repetitious bark: This comprises a phrase composed of two or three noise units, the first of which is always longer than the succeeding units. The first unit may rarely be given as a single discrete bark. Even if this happens, it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TIME IN SECONDS

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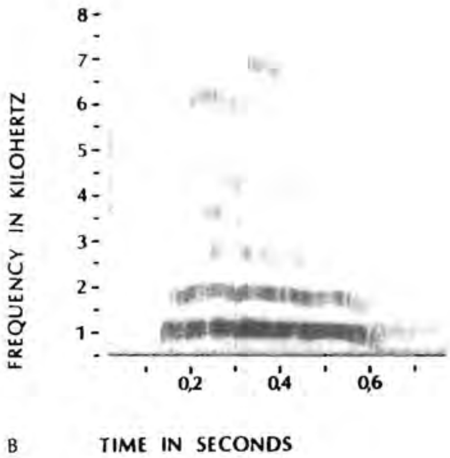
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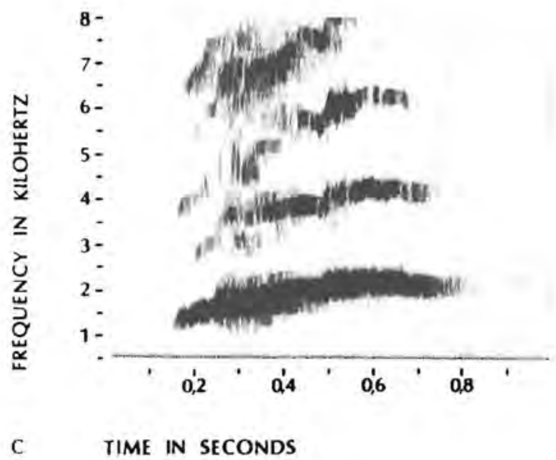
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TIME IN SECONDS

C

Figure 11: Spectrographic representation of P. capensis sounds. A. Squeak. B. Yap. C. Spit (first unit) followed by a short yap (second unit) and a two syllable squeak (third and fourth units, interrupted by intersyllabic inspiration).

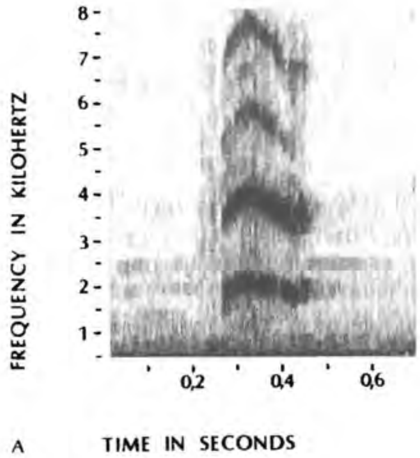
Figure 11: Spectrographic representation of P. capensis sounds. A. Squeak. B. Yap. C. Spit (first unit) followed by a short yap (second unit) and a two syllable squeak (third and fourth units, interrupted by intersyllabic inspiration).

Figure 10: Spectrographic representation of P. capensis sounds. A. Hoarse moan. B. Coo. C. Whine.

is repeated together with phrases to form a cycle which may stretch over several hours. In a phrase of three units, the first unit is approximately 0,45 sec long, and the second and third units each 0,2 - 0,3 sec. The interval between the first and second units is usually shorter (0,15 sec) than the interval between the second and third units (0,2 sec). In total the phrase lasts for approximately 1,4 sec and an interval of 1 - 2 sec between phrases in a cycle is usual. In all the units major energy is concentrated around 1,25 kHz, 2,5 kHz and 4,0 kHz, which is suggestive of a mixed unit as indicated by a possibly obscured harmonic structure. The 2,5 kHz energy concentration band (the most prominent) is often seen as a narrow noise band introducing the first unit, linking all three units and terminating the last unit (Fig. 12B).

Squeal: This sound is closely related to the whistle (see below) and shows wide variation in structure. The typical squeal is a 0,2 sec complex tonal sound with the fundamental tone rising and falling sharply between 0,75 kHz and 4,0 kHz. Two or more clearly defined overtones may be recognised with the peak frequency around 7,0 kHz (Fig. 13A (i)). At high amplitude the fundamental peak rises to 6,5 kHz and the peak frequency of the highest overtone stretches well above 8,0 kHz (Fig. 13A (ii)). The squeal is often given in association with grunts and growls to form compound units (Fig. 13A (iii)).

Whistle and whistle chirrup: The whistle may either be expressed as a simple tone or as a complex tone. It is 0,1 - 0,15 sec long and is characterised by its swift fluctuation in pitch, the fundamental tone ranging between 1,2 kHz and 7,0 kHz (Fig. 13B). The whistle may be given as a single sound or be repeated (usually the latter) at 0,1 sec intervals to form a phrase of varying length, i.e.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TIME IN SECONDS

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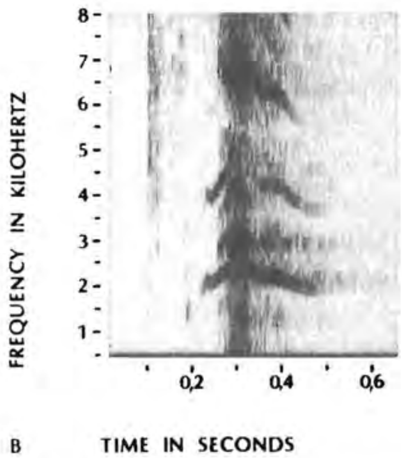
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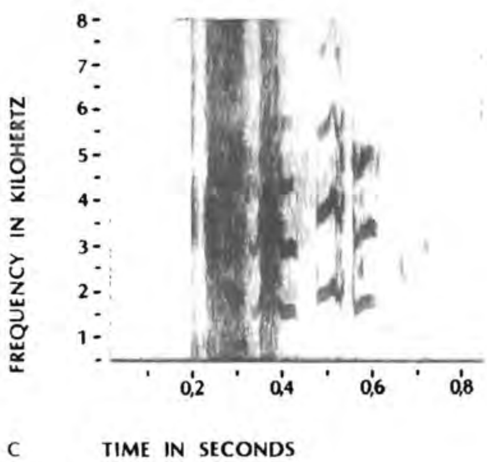
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TIME IN SECONDS

C

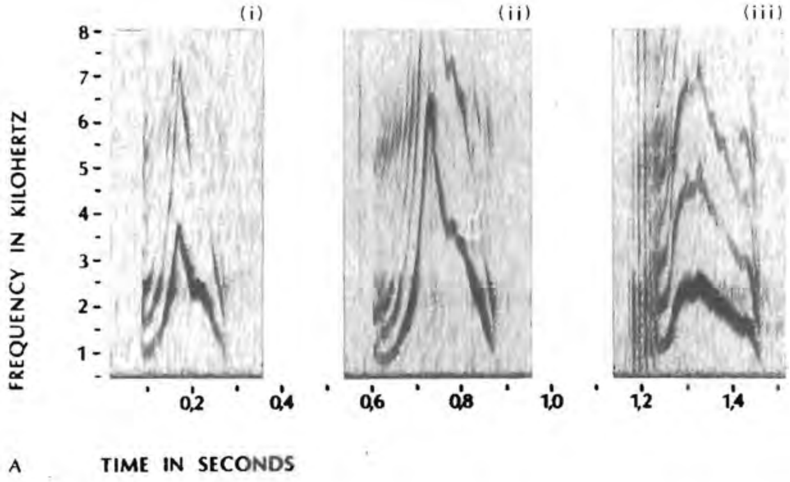
Figure 12: Spectrographic representation of P. capensis sounds. A. Sharp bark. B. Repetitious bark.

the whistle chirrup (Fig. 13C). At low amplitude there is a considerable drop in pitch with the fundamental tone forming an asymmetrical arch between 1,0 kHz and 3,0 kHz. One or two poorly defined overtones, around 2,0 kHz and 5,5 kHz respectively, may be recognised. Each unit in the whistle chirrup is approximately 0,2 sec long and spaced from the next unit by a 0,15 - 0,2 sec interval (Fig. 14A).

Harsh chirrup: The harsh chirrup constitutes a phrase composed of a varying number of simple tonal units separated by 0,07 sec intervals. Each unit is 0,09 sec long, starting at 7,0 kHz, rising sharply to reach a peak at 13,0 kHz, and falling abruptly to terminate at 2,0 kHz (Figs. 14B and 14C). It is sometimes combined with a gruntlike noise to form a compound unit in which case the pitch of the tonal part is slightly lower.

Harsh twitter: Because of overmodulated sound recordings, the spectrographic analysis of harsh twitters was unsuccessful and therefore no spectrogram is included here. However, it would seem that each harsh twitter usually comprises two units, the first a broad spectrum noise with major energy concentration around 4,0 kHz and the second a simple tone of varying pitch, starting at 7,5 kHz, falling to 5,5 kHz, rising again to 7,75 kHz and falling finally to terminate at 3,5 kHz. Apparently there is a very small interval between these two units. If repeated, as is the case, it forms a phrase of varying length with 0,1 sec intervals between successive phrases. The duration of a single unit is approximately 0,3 sec. Sometimes a triple-unit twitter terminates a phrase.

Soft twitter: Recordings of soft twitters could also not be used for analytical purposes. These sounds seem to resemble whistle chirrups as phrases of varying length composed of single unit tonal sounds.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TIME IN SECONDS

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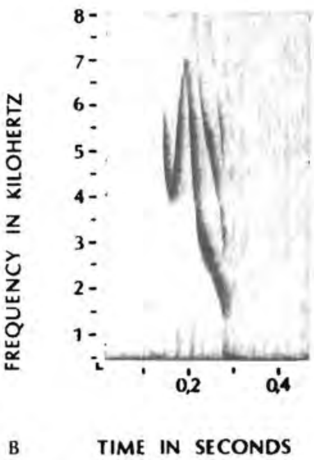
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TIME IN SECONDS

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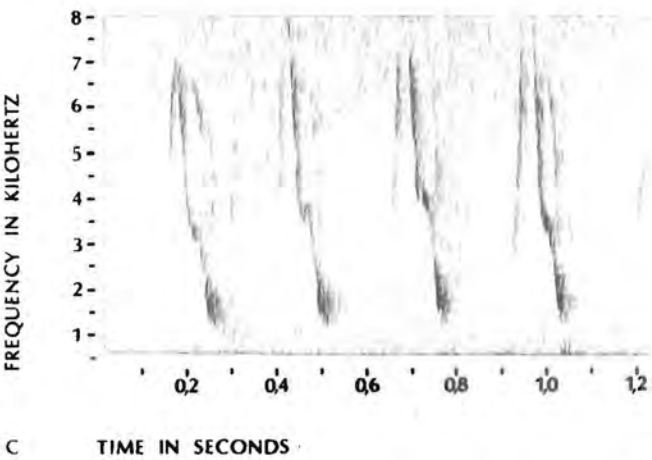
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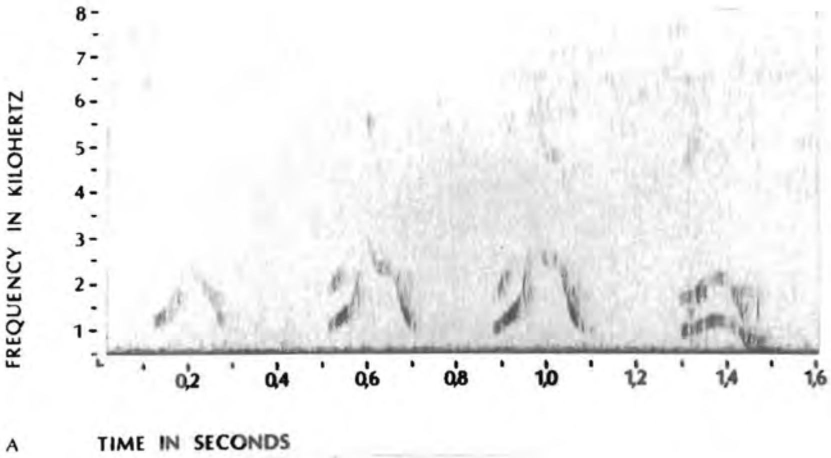
TIME IN SECONDS

C

Figure 14: Spectrographic representation of P. capensis sounds. A. Low amplitude whistle chirrup. Note the poorly defined overtones around 5,5 kHz. B. Harsh chirrup. C. The same as B but spectrographically reproduced at half the recorded speed.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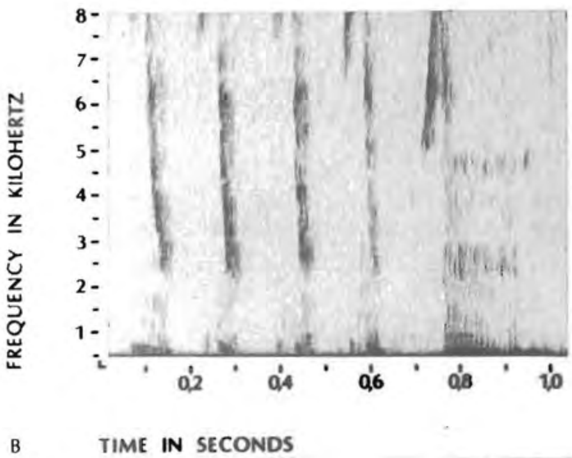
TIME IN SECONDS

A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TIME IN SECONDS

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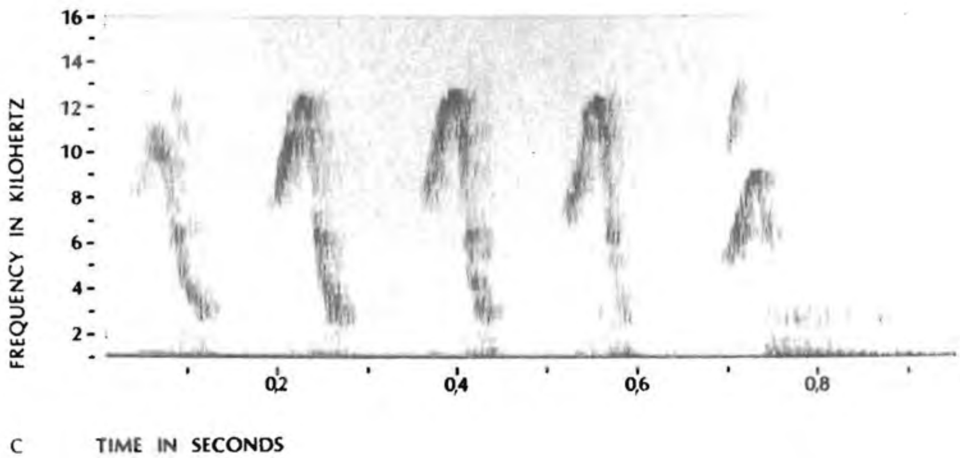
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TIME IN SECONDS

C

Sneeze, snort, pant and teeth gnashing: These sounds were not spectrographically analysed. They are nonvocal and can all be described as noises.

Situations eliciting the sounds

Grunts, growls, snarls, and to a lesser extend also spits, are some of the most often used sounds in the dassie's repertoire, either independently or as part of compound units. Situations which elecit these sounds may vary greatly, but they are all characterized by aggressive or defensive threat behaviour patterns.

There is a notable tendency for the grunt, growl and snarl to occur in a specific order when two or more of them are elicited by a certain situation. A predictable grading from a low amplitude grunt rising gradually through a medium amplitude growl and terminating in a high amplitude snarl is frequently shown. This is evidence of the interrelationship of these three sounds since the amplitude variations depend entirely on the level of excitement of the vocalizer.

When an adult dassie is cornered and threatened with a stick or gloved hand slowly pushed towards it, it remains freezed until the object is approximately 25 cm away. If the object is moved still closer, the mouth gradually opens while the upper lip is drawn back to show the upper incisors to their full extent. The dassie also emits growls sometimes accompanied by, or alternated with, teeth gnashing. When the object reaches a separating distance of only a few centimetres, the animal suddenly emits a snarl, at the same time thrusting the head forward and inflicting a rapid bite. The dassie continues growling and hangs onto the object for a while after which it resumes its original position.

Basically the same pattern is shown when two or more dassies (usually males) act aggressively towards each other. When two animals are feeding too close together, i.e. with heads less than 5 cm apart, the dominant one will utter a grunt or growl and the other will respond similarly, thus also assuming a threatening attitude, or may act appeasingly by emitting a rapid series of whistles, squeals, growl-squeals and harsh chirrups. If neither gives way in such a face-to-face encounter it results in the dominant animal emitting a snarl, followed by fighting interspersed with snarls and bites from both animals. The same sequence of events often occurs inside the sleeping cavities where a number of dassies huddle together and the level of excitement in a dominant animal is markedly higher because of the proximity of subordinates.

Infants and young juveniles subjected to the same treatment as mentioned above (i.e. threatened with a stick after being cornered) utter spits which correspond with the adult snarl. In those stages where an adult would have growled, the infant merely opens the mouth, draws back the upper lip and prepares to strike.

The wail, wail-bark, yelp and rasp are usually given in response to a persistent threat stimulus with which the animal cannot cope by defensive threat or running away. Such a persistent threat stimulus was applied by chasing a dassie for some time, eventually allowing it to hide in a small box and then prodding the animal repeatedly with a stick. The dassie thus experiences a frustration situation because of the persistence of the stimulus and consequently demonstrates a high enough level of excitement to start vocalizing.

The situations eliciting the wail and wail-bark (or yelp and rasp in juveniles) show similarities to those situations eliciting grunts, growls and snarls (or spits). It is therefore not surprising that all these sounds may be heard in the same situation. Not all the animals subjected to the treatment mentioned above responded with wails and wail-barks, but all of them gave the grunt-growl-snarl sequence. It thus appears that the threshold for elicitation of wails and wail-barks is extremely high and that only a small number of dassies can be excited to a level where the threshold may be overcome.

When the wail (or yelp) starts it is represented in the form described above (see physical characteristics and Figs. 7A and 9A). If I stopped prodding the animal and stood back, even moving out of sight, the wailing (or yelping) did not stop abruptly but petered off into a high pitched, low amplitude variation. When I again approached the animal, the wail (or yelp) gradually grew in amplitude and reached its original form when the stick was brought within 10 cm of the dassie's head. In between the wails, grunts and growls, and sometimes also teeth gnashings, were produced. When the stick was brought closer than 5 cm to the animal's head, a high amplitude wail-bark (or rasp) was emitted, directly followed by a snarl (or spit) and a bite on physical contact. Yelping may stop within five minutes after total removal of the threat stimulus but wailing usually persists for long periods, sometimes for up to an hour. This suggests that the animals remain excited for lengthy periods.

F.F. Kolbe (in litt.) describes a wail-like sound emitted by a female and mentions an accompanying "shedding of tears" through the nose during production of the sound. According to him the female was apparently extremely excited by the twitter of her young and probably also frustrated by the presence of an observer. Due to lack of comparable information this sound is regarded here as a variation of the wail purely on the grounds of the frustration situation which apparently elicited the sound and also because of its somewhat vague spectrographic affinities with the wail (compare Figs. 7A and 8A).

During production of the wail and yelp the mouth is barely opened and the mouth corners are drawn back, resulting in the lips being stretched tight and most of the teeth and gums becoming visible. With production of the wail-bark and rasp the mouth is wide open.

The hiccup, cough and hoarse moan are emitted only by females in labour. The hiccup and gasp coincide with the contractions accompanying labour while the hoarse moan is given in response to climbing behaviour of a new-born trying to get onto the back of the mother while she is still in labour. The hoarse moan was also emitted when I on one occasion ventured too near a parturient female. These sounds were never observed outside the context of parturition.

Both the coo and the whine are emitted only by females and are commonly heard during the period after parturition and until the infants are weaned.

When the young want to suckle they emit soft twitters and the mother responds by cooing which serves to direct the young towards her. She may occasionally coo while suckling is in progress, probably calming the infant in this way. Should the young, however, be frustrated and highly excited, as might be the case when they are separated from the mother while outside the sleeping box or when they are hurt, they emit harsh twitters. The mother then reacts with a strong whine or harsh chirrup while running towards them. Whines were also produced when I disturbed a female while she suckled her young.

Coos and whines were also emitted by a female, peeping from the sleeping box entrance, when juveniles of eight months (not necessarily her offspring) approached food in my presence. The young dassies responded to this cooing with immediate flight towards shelter.

The squeak and yap is only produced when a dassie is startled, such as when suddenly and unexpectedly confronted at close quarters. This behaviour is especially marked in juveniles and young adults. The proximity of the startling stimulus, which might be a person or predator, determines which of the two sounds will be given. If the stimulus is far enough to allow the dassie time for reaching shelter safely if necessary, the animal is only mildly excited and the squeak is emitted. Accompanying locomotor activities include a stretching of the neck and limbs, but no flight. Should the stimulus be close enough to be potentially dangerous, the dassie gets more excited and the yap is produced. Flight towards shelter (i.e. the sleeping box) follows immediately. The animal, however, does not remain out of sight for a long period, but reappears in the entrance of the sleeping box within 10 seconds to two minutes and repeatedly squeaks while keeping the stimulus in sight. A dassie would do this for up to 10 minutes providing the stimulus remained stationary. With the slightest movement by the stimulus, the dassie emits a yap and jumps out of sight.

When a juvenile is unexpectedly grabbed this usually results in a combination of sounds being produced, one of them the yap which is often followed by a spit and bite.

The sharp bark has been mentioned by most authors writing about the dassie. This is not surprising since it is a very carrying sound and is easily elicited by approaching a colony of dassies in the wild. Many authors (see Table 3) described the sharp bark as an alarm cry or warning cry, an apt description since it functions in most situations where emitted to alert members of the colony to possible danger in the form of a predator. In the wild the sharp bark of a dassie noticing danger may be echoed by other members of the colony while fleeing towards shelter. This is especially the case when the dassies are surprised while feeding on open terrain some distance away from their crevices.

In captivity the sharp bark is not so commonly heard, for a number of reasons. Dassies adapt very quickly to a new environment and get habituated to objects and people which they then readily accept as part of their environment. However, putting in a sudden appearance while they feed usually elicits the sharp bark. Only one dominant animal (male or female) at a time in the colony was responsible for introducing sharp barks, this dassie's place being taken by another within a few days should the first animal be removed from the colony.

The sharp bark is a high amplitude sound with considerable carrying power and elicits immediate flight towards shelter by all members of the colony, including the vocalizer. If the feeding dassies merely need to be alerted, use is being made of squeaks which is of low amplitude and audible only over a short distance. When hearing squeaks while feeding, all members stop chewing and raise their heads. If a sharp bark does not follow, they resume their feeding activities. Sometimes squeaks, if given at slightly higher amplitude and pitch than those serving to alert the dassies without eliciting flight, cause the animals to run for a few metres, stop, look around and return to the food.

During the mating season there is a higher incidence of sharp barks amongst captive dassies, especially so by the dominant male. When I, during this period, talked to or handled the tame female in full view of the dominant male, it almost without exception elicited sharp barks and squeaks from him.

It is also interesting to note that no response could be detected in animals actually out of reach of any danger, even if the sharp bark is sounded. Dassies inside the sleeping box or up in the tree never responded while those on the floor of the enclosure always fled.

The repetitious bark has only rarely been heard in my captive colony. F.F. Kolbe (in litt.), however, mentions frequent calling by males in his captive colony at any time of the day, all year round.

The stimulus for the elicitation, and the function, of the repetitious bark is not quite clear. Mendelssohn (1965) ascribes a territorial function to this sound while Kingdon (1971) mentions the probability of both a territorial and sexual function. Matthews (1971) holds a different view and states that "... it can scarcely be of territorial meaning in a creature so tied to a restricted range, nor is it likely to be sexual in view of the structure of the social groups." Since results from my captive colony are equivocal, no conclusions can be drawn in this regard.

Squeals are associated with mild frustration in aggression situations. When given in combination with grunts and growls they demonstrate mild aggression, as is the case when two males approach the same piece of food and their heads come close together. On the other hand, squeals may accompany harsh chirrups and whistles where they illustrate mild fear of an aggressive conspecific and serve as appeasement sounds.

Whistles, whistle chirrups and soft twitters are associated with contact situations. Soft twitters are often heard in between suckles, probably as an expression of satisfaction, or when the young dassie renews contact with the mother as when it, separated from the mother for a while, is again introduced to her. To this the mother responds with coos. The tame female readily emitted whistle chirrups when spoken to or when gently stroked on the back, demonstrating that this sound is also given in a situation of security and satisfaction.

Harsh chirrups indicate frustration arising from situations where aggression from a conspecific is experienced. Where harsh chirrups by a subordinate dassie follow the grunt-growl-snarl sequence of a dominant dassie, they function as appeasement sounds.

Harsh twitters were emitted by dassies of both sexes and all age groups. It is also the first sound a new-born dassie makes. Depending on the amplitude at which these sounds are given, the harsh twitters of infants indicate a certain degree of frustration. When having difficulties in finding teats, infants emit low amplitude twitters. Medium amplitude variations result from separation from the mother with which they try to establish contact while high amplitude twitters are given when actual pain is experienced. In the last two cases the mother responds by running towards her offspring, establishing contact with them as quickly as possible. Harsh twitters resulting from pain, e.g. when an infant is hurt by a predator, leads the mother to actually attack. In fact, any adult member of the colony, usually those closest to the hurt infant (or adult) will come to its aid. This would probably also happen in the wild as well, should a predator seize a dassie.

The nonvocal sounds of the dassie, i.e. the sneeze, pant, snort and teeth gnashing, were not frequently heard and their function in acoustic communication is still uncertian. Normal nasal irritation, e.g. when smoke is blown in the face of a dassie, produces a sneeze. However, it was also observed that dassies sneeze when they, for instance, appear on a rock ledge and suddenly become aware of an unmoving person at close quarters and on the same level. If the person moves they utter yaps and dart off for shelter. The sneeze is probably associated with a sudden but mild change in the level of excitement of the animal which results in it becoming notably alert.

The pant has been heard inside the cavities constructed in the enclosure at Naudéskop-Oost and consists of one or two quick, complete respiratory movements, starting with expellation of air, probably through an open mouth. Nothing more is known about panting except that it sometimes precedes a grunt-growl-snarl sequence.

Snorting often precedes a sharp bark or squeak and is a very soft sound barely audible over more than six metres. It is, however, easily identified over a distance since it is accompanied by a flaring of the nostrils and the contraction of abdominal muscles. The mouth is closed and air is expelled through the nose.

Teeth gnashing usually accompanies growls but may also be associated with wails and wail-barks. Infants were seen to imitate the chewing movements associated with teeth gnashing under similar situations, i.e. when confronted by danger at close quarters. Teeth gnashing probably functions as a threat signal or perhaps as a displacement activity such as when dassies are barred from reaching food during periods usually associated with group feeding. They may then stare at the food while making chewing movements.

Ontogeny of the sounds

From birth until adulthood there is a general increase in the variety of sounds produced by the dassie (Table 2). Some of the sounds (e.g. soft twitters) function only for a short period or else are replaced with completely new sounds (e.g. yelp or rasp replaced by wail and wail-bark). A few other sounds also function only during specific periods of the dassie's life (e.g. the females' hiccup which is used only during parturition), while some sounds are emitted throughout life with little change in structure (e.g. harsh twitters).

Figure 15 summarizes the age at which each sound is emitted for the first time and, if a temporary sound, for how long it is included in the dassie's repertoire before it ceases to function or is replaced by another sound.

The following points emerged from general observations:

1. During the first two months of its life the infant dassie at most possesses only five sounds, three vocal and two nonvocal. At birth the soft twitter and harsh twitter are already present while the spit, sneeze and teeth gnashing, although they sometimes appear within a week or two, are heard from three to four months of age. Of these sounds only the harsh twitter, sneeze and teeth gnashing are retained throughout life, with slight modifications in structure as the result of changes of the vocal apparatus, nasal cavity and teeth in the growing animal. There is, however, a marked change in the incidence of emittance of these sounds with increase in age. In the infant harsh twitters are often heard in frustrating situations such as loss of contact with the mother, isolation, when in pain or when thwarted from renewing contact with the mother when she emits coos or whines. In weaned juveniles and adults harsh twitters are rare and only heard when pain, accompanied by fear (e.g. when grabbed by a predator) is experienced.

2. Between the age of two and 15 months the dassie's sound repertoire broadens considerably. With the exception of the hiccup, cough, hoarse moan, coo and whine, all produced by adult females, and the repetitious bark of sexually mature males, all other dassie sounds appear during this period of juvenilehood.

The spit, the equivalent of the adult snarl, is replaced under aggression situations by the grunt-growl-snarl sequence

Figure 15: Summary of the age at which each P. capensis sound emerges, how long it remains in the repertoire if a temporary sound and when it is replaced by a new sound.

----- : Age at which the sound starts or ceases to function.

+++++ : Age at which the sound was recorded to be optimally functional.

AGE IN MONTHS

SOUND	Infants (1 2)	Juveniles (3 4 5 6 7 8 9 10 11 12 13 14 15)	Adults (16 17 18 19 20 21 22 23 24)
Spit	++++++	++++------	
Grunt		--------++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Growl		--------++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Snarl		--------++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Yelp		+++++++++++++++++++++++++++++---------	---------
Rasp		+++++++++++++++++++++++++++++---------	---------
Wail		---------	---------++++++++++++++++++
Wail-bark		---------	---------++++++++++++++++++
Hiccup and cough			+++++
Hoarse moan			+++++
Coo			+++++
Whine			+++++
Squeak		++++++++++++++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Yap		++++++++++++++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Sharp bark		++++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Repetitious bark			----------------------+++++
Squeal		-------+++++++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Whistle		++++++++++++++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Whistle chirrup		-------+++++++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Harsh chirrup		-------++++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Harsh twitter	++++++	++++++++++++++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Soft twitter	+++++-	-----	
Sneeze	++++++	++++++++++++++++++++++++++++++++++++++	++++++++++++++++++++++++++++
Snort		-------+++++++++++++++++++++	++++++++++++++++++++++++++++
Pant			+++++++++++++++++++++++++++
Teeth gnashing	++++++	++++++++++++++++++++++++++++++++++++++	++++++++++++++++++++++++++++

during the fifth or sixth months of life. Up to that stage the spit only functions as a defensive threat signal where some degree of fear is experienced. When the dassie shows a tendency for and is capable of active defense and attack, the grunt-growl-snarl sequence is introduced. The soft twitter is likewise replaced with a more elaborate and functionally more effective series of appeasement sounds. These include the squeal, whistle, whistle chirrup and harsh chirrup. The only other juvenile sounds which are later replaced by adult sounds are the yelp and rasp which change to the wail and wail-bark respectively. This replacement occurs between 12 and 19 months of age, i.e. around the time when sexual maturity is reached.

There is, as with the infant sounds, also a marked difference in the incidence of production of some sounds between juveniles and adults. The sharp bark is seldom given by juveniles while sqeaks, yaps, squeals and chirrups are fairly common. In adults the opposite tends to be true. Grunts, growls, snarls and the nonvocal sounds including sneezes, snorts, pants and teeth gnashings are all rare in infants and juveniles but are more often used the older the animals become.

3. All of the few sounds associated with the infant dassie are unspecific as to situation and tend to occur in sometimes seemingly unrelated situation types. No combination sounds are present during any time of infanthood. On the other hand, the juvenile dassie acquires a relatively great number of sounds and in addition also makes use of intermediate sounds and combinations, thereby enlarging the basic repertoire considerably. The reason for these changes probably lies in the big difference in mode of life between the infant and the juvenile and consequently the greater number of novel stimuli encountered by the juvenile upon leaving the shelter of the cavities. There thus seems to be an important shift in stimulus interest (see below) from one age group to the next.

Discussion

As already stated, the interest an animal shows in a given stimulus determines the level to which the animal becomes excited and the interaction between stimulus interest and level of excitement controls the type (or structure) of the sound emitted. The same stimulus may thus evoke different sounds. This was indeed found to be the case in the dassie. If the stimulus interest is low the animal is not very excited and vocalizes less often. In such instances the vocalizations exhibit a low frequency and amplitude. The opposite also holds true (see Addendum and fig. 20). The tame female, for example, would vocalize differently depending on how hungry she was. When starved for two days and then shown bread which was placed approximately 1,5 metres above her, she tried to get to the food by jumping on all objects (such as the roof of the sleeping box) closest to it or running to and fro on the floor watching the bread. All the while she emitted squeals and whistle chirrups at moderate pitch and amplitude. If the bread was held within one centimetre out of her reach, she became very excited and repeatedly emitted squeals, whistle chirrups, grunts and growls at high pitch and amplitude. She would also act aggressively by snarling and biting if touched under these circumstances. On the other hand, she would show diminished interest in the bread and emit only whistle chirrups of low amplitude and pitch, accompanied by very little locomotion, if fed a few hours before. When presented with bread immediately after a feeding period she showed little interest, did not vocalize and would at most sniff the food and perhaps nibble on it for a short while. If barred from reaching the bread she simply ignored it.

The types of stimuli which might evoke vocalizations are, of course, numerous. One interesting stimulus is, however, a sound from an animal which elicits the same or a different sound from conspecifics. A sound serving to change the general level of excitement in other members of the group so that an increase in their vocalization activity results, is said to have emulative characteristics (e.g. the harsh twitter of an infant dassie). Harsh twitters, if emitted when an infant dassie is grabbed by a predator, might elicit sharp barks and squeaks from adults which are sometimes accompanied by an attack on the intruder. Examples of emulative sounds are the sharp bark, repetitious bark, coo, whine, harsh twitter and soft twitter. Sometimes no external stimulus can be identified as responsible for evoking a certain vocalization. The repetitious bark appears to be controlled by physiological factors since it is more frequently heard during the mating season.

It was mentioned above that some sounds are more characteristic of a certain situation, although they also occur in others (e.g. the sharp bark which is more characteristic of situations in which an intruder is noticed during group feeding periods). Consequently it may be assumed that these sounds have specific meanings. Smith (1968) suggested that it is the context rather than the sound that is important for message transfer. Kiley (1972) furthermore concludes that "... vocalizations do not convey information concerning the specific motivational state of the animal, that is, whether it is for example aggressive or sexual, but rather they convey information concerning the degree of interest attached to the stimulus." She, however, adds that this is a generalization and that in some animals there are indeed sounds which are more situation-specific (such as the squeal of the horse).

It was also pointed out by Kiley (1972) that there exists a tendency for vocalizations, at least in mammalian species, to show similarity in structure depending on the function of the sound. The dassie's sounds conform to this idea, i.e. sounds which need to be easily located, such as contact sounds (e.g. coo, soft twitter, whistle chirrups) are usually long with an asymmetrical shaped fundamental, low amplitude and thus do not carry far, while those sounds showing an advantage in not advertising the location of the vocalizer, such as warning sounds (e.g. sharp bark, squeak, yap) which function to alert other members of the group, are short, non-repeated (or rapidly repeated once or twice only) and usually of high amplitude and frequency.

Figure 13: Spectrographic representation of P. *capensis* sounds. A(i). Medium amplitude squeal. A(ii) High amplitude squeal. A(iii). Growl-squeal. These three variations do not necessarily follow in the order or at the time intervals indicated on the spectrogram. They are represented in this way solely because they tend to form part of the same sound sequence. B. Whistle. C. Whistle chirrup given at medium amplitude.