ACOUSTIC COMMUNICATION AND SOCIAL BEHAVIOUR OF THE ROCK DASSIE, *PROCAVIA CAPENSIS* (PALLAS), IN CAPTIVITY

by

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ABSTRACT

Compared to the paucity of visual, olfactory and tactile signals, acoustic communication is the most important and widely used means of information transfer in *Procavia capensis*. The dassie's sound repertoire consists of 21 vocal, and four nonvocal, sounds. The vocal sounds form a continuum while the nonvocal sounds are discrete. All the sounds appear in more than one situation type although some are more characteristic of one type of situation than another. Elicitation and the type of sound emitted depend on the degree of interest attached to a stimulus and the level of excitement experienced by the animal. The social behaviour of dassies points to a mode of life adapted to cope with the limitations imposed on them by some morphological and physiological features as well as environmental and ecological conditions prevailing in their habitat. It is concluded that poor thermoregulation, diminished size and crevice dwelling probably were the main selective forces in operation during the evolution of the hyracoids, which might have led to the particular behaviour patterns present in *Procavia capensis*.

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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.

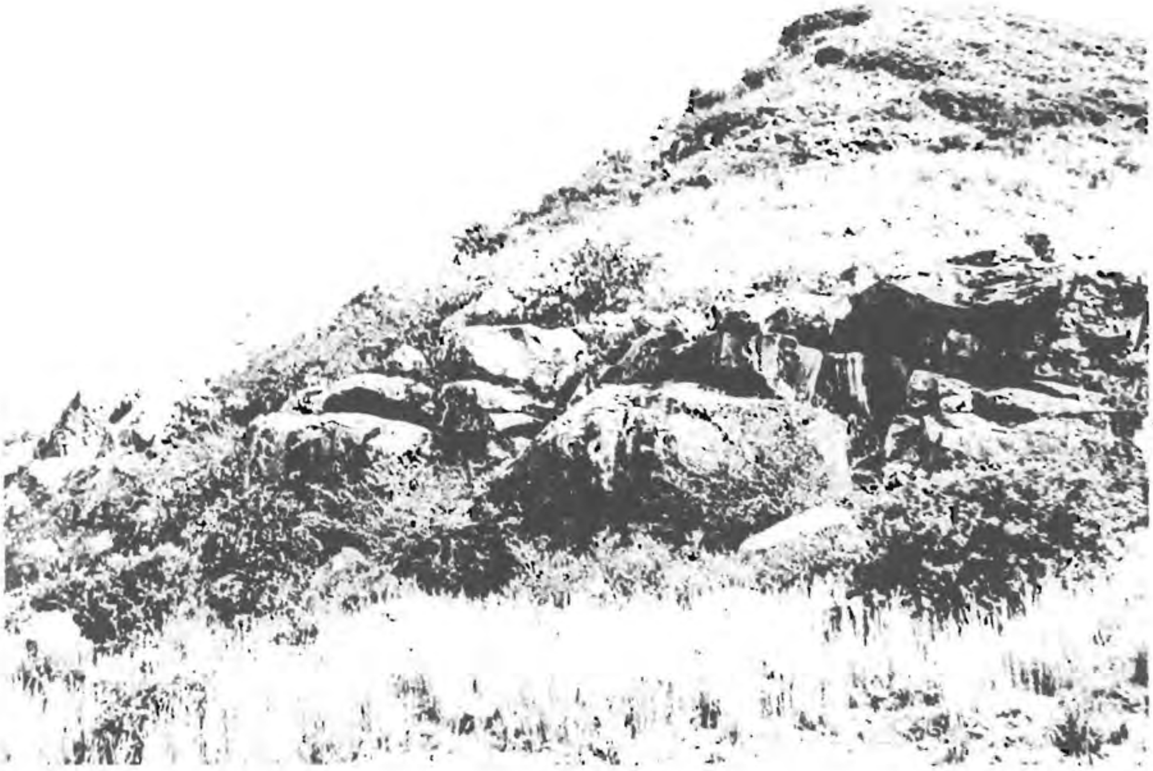
Since a need exists for data on the behaviour of *P. capensis*, a detailed analysis of acoustic communication in this species was undertaken and integrated with observations on other elements of its social behaviour. In this way an attempt was made to interpret the mode of life and general ecological 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 Naudêskop-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 Naudêskop-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 Naudêskop-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 Naudêskop-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 (<u>Procavia capensis</u>) 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.

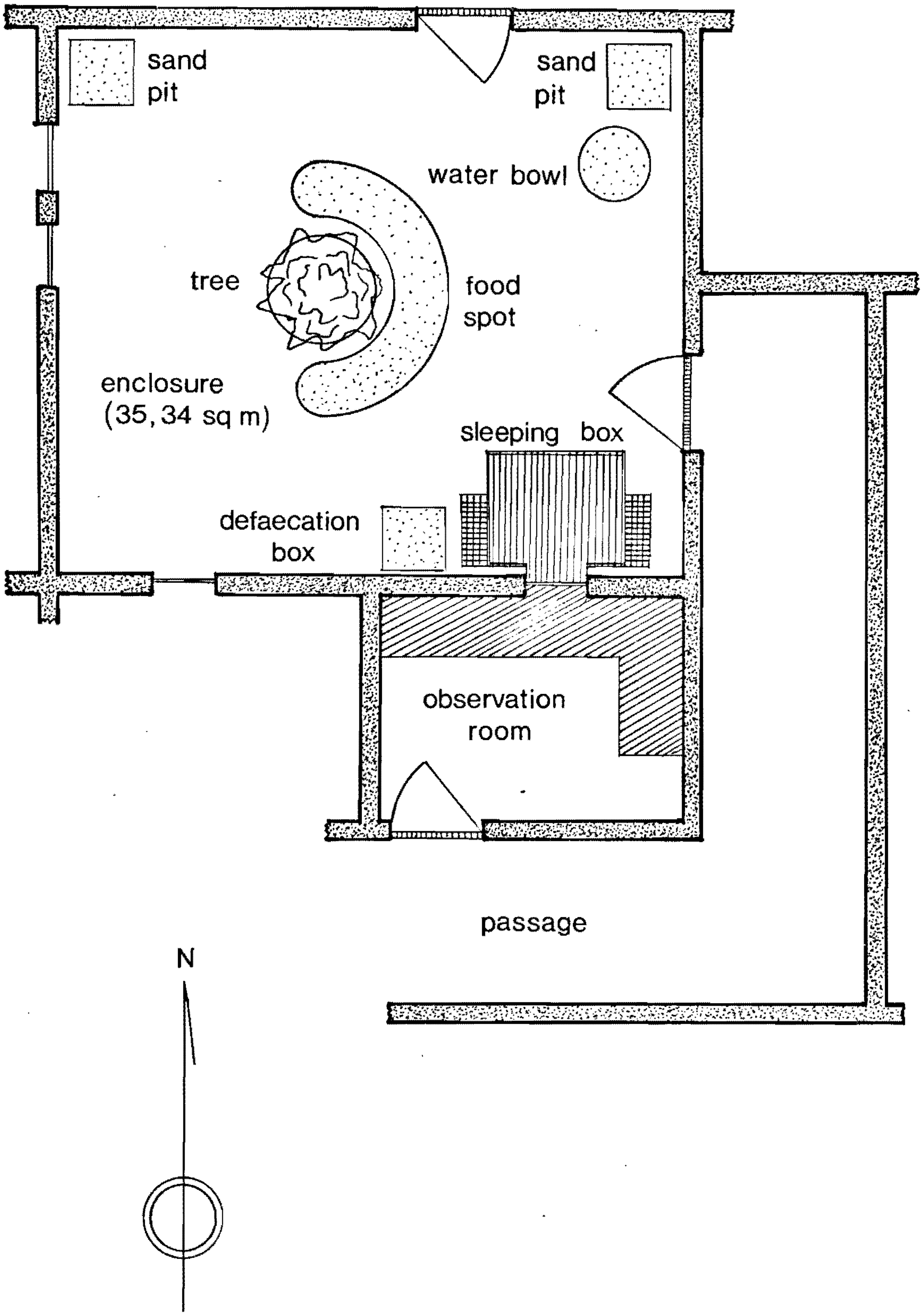
The captive animals transferred to the Zoology Department, University of Pretoria during October 1972 were placed in pairs in wire traps covered with heavy blankets almost 12 hours before the trip. Even though they were in the traps for close to 19 hours they did not show any ill-effects. They were released 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.

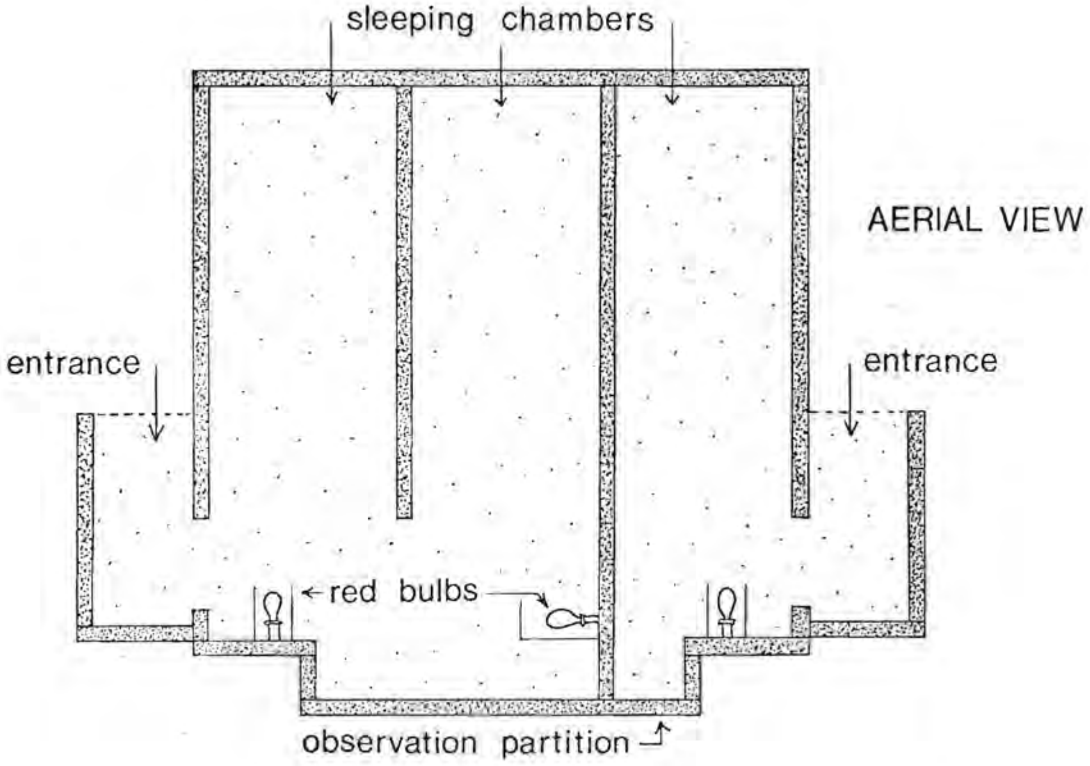
Many authors (e.g. Coe 1962; Kingdon 1971) noted that, in the wild, dassies urinate and defaecate in a specific site. As this is also the case in captive dassies the latrine box was supplied to facilitate cleaning of the enclosure. The bottom of the box was covered with a thin layer of wet sand and some 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.

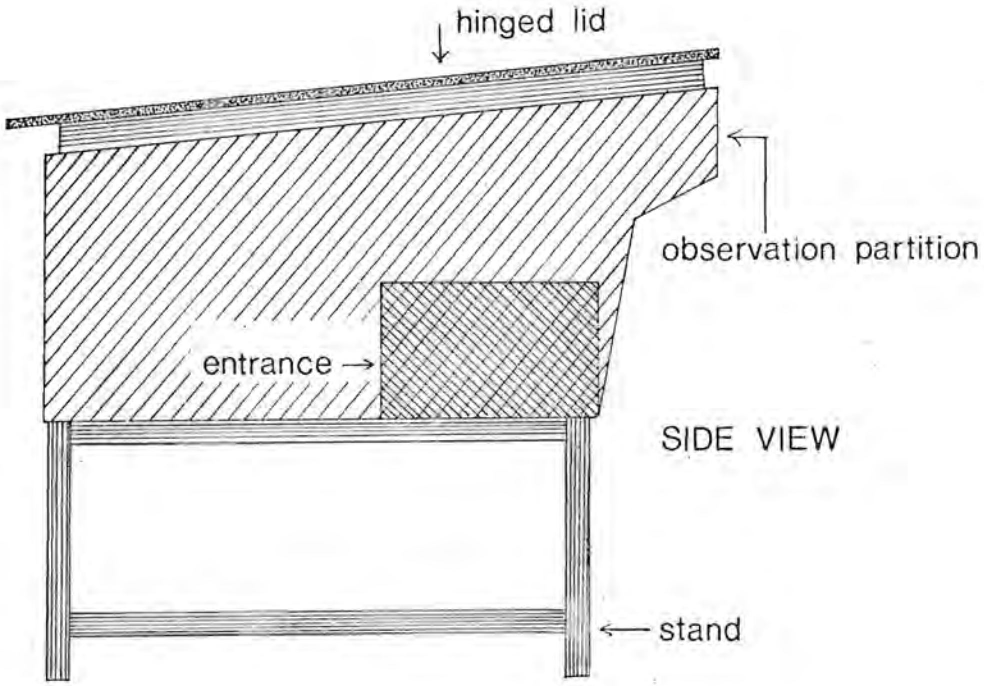
The sleeping box (Fig. 3) consisted of two chambers, measuring 52,5 cm by 47,5 cm by 100 cm and 52,5 cm by 95 cm by 100 cm respectively, each with a separate entrance. The latter chamber was subdivided by means of an incomplete partition. The whole box was raised 81,5 cm above the floor and placed against 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 <u>Procavia capensis</u> 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

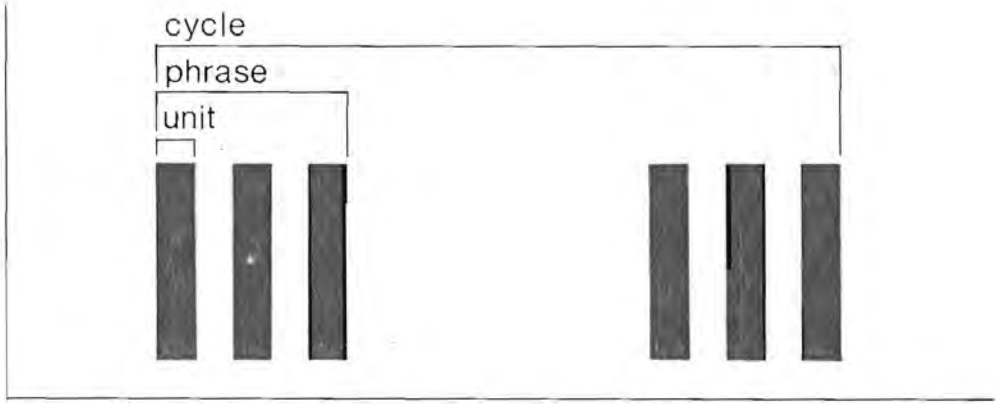
Figure 3: Diagram of the sleeping box used by the captive rock dassies (Procavia capensis) in the Zoology Department, University of Pretoria.

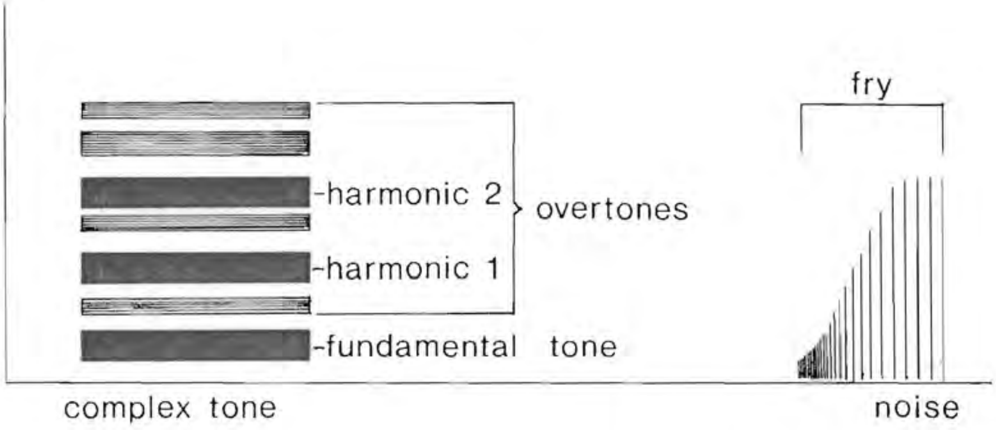
as an essential ingredient or byproduct of motivation and drive. An animal has to be motivated to show an active interest in a certain stimulus and the degree of interest (and consequently the level of excitement experienced) will depend on the general motivational state of the animal at the time. The 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.

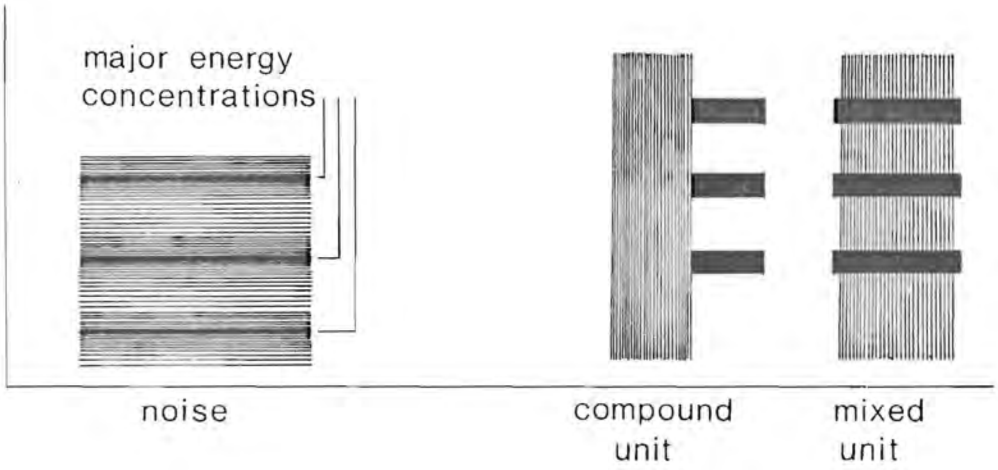
The following terms and definitions used in the description of the sounds of the rock dassie are quoted from several authors as indicated below. Arrangement of the terms attempts to be such that any term needed to explain subsequent ones is placed first. For this reason authors are not quoted chronologically. 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)

"Rhythm	:	A repetition of groups of sounds at regular intervals"
"Succession	:	rep~~i~~etition of units"
"Frequency	:	The number of vibrations or cycles in a unit of time (expressed in cycles per sec: cps or Hz)"
"Noise	:	Sound without definite organisation of frequencies" (This has been termed "non-tonal sound" by Struhsaker (1967)).
"Pitch	:	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
phrase
unit


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.

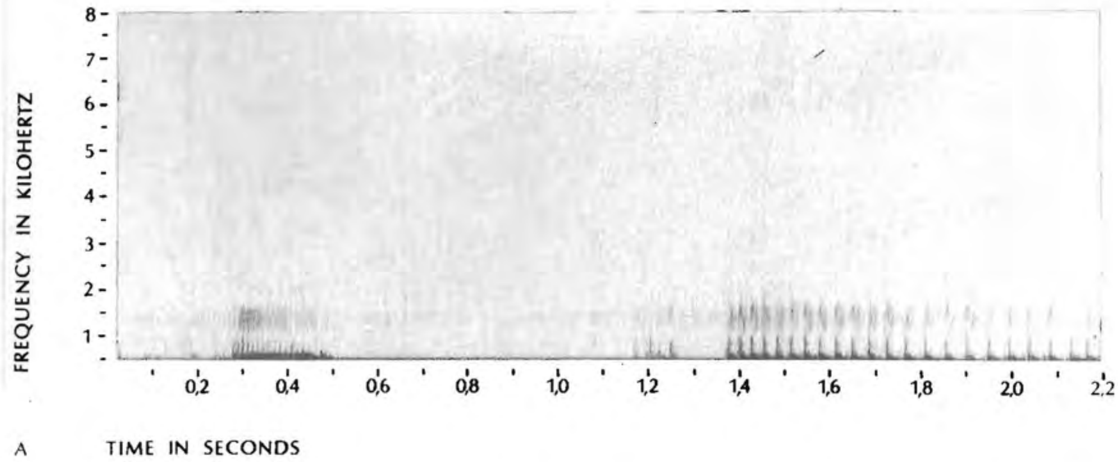
Physical charactersitics of the sounds

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).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FREQUENCY IN KILOHERTZ
8
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6
5
4
3
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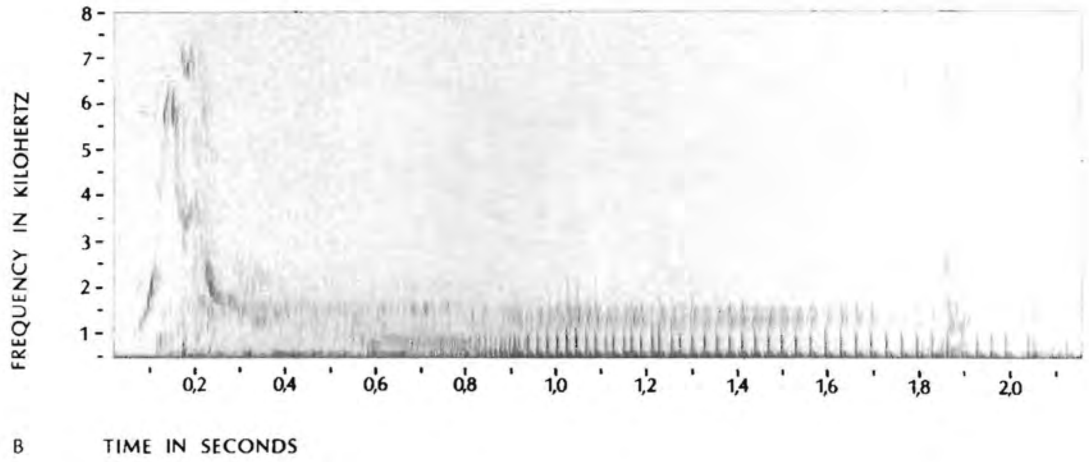
TIME IN SECONDS


B
FREQUENCY IN KILOHERTZ
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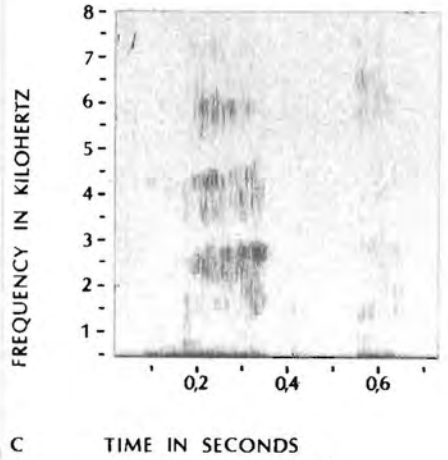
TIME IN SECONDS


C
FREQUENCY IN KILOHERTZ
8
7
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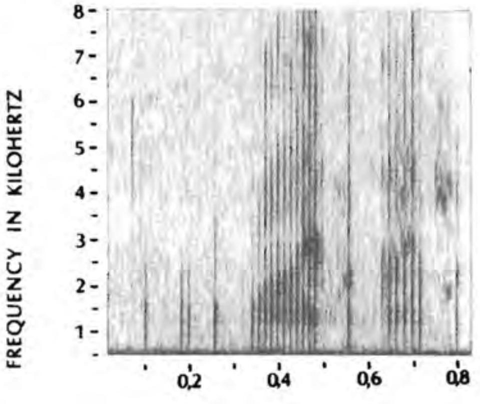
TIME IN SECONDS

Figure 6: Spectrographic representation of _P_. _capensis_ sounds. A. Growl. B. Snarl. C. Spit.


FREQUENCY IN KILOHERTZ
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TIME IN SECONDS

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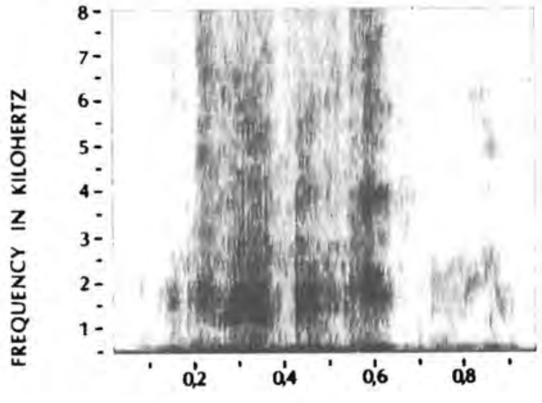
FREQUENCY IN KILOHERTZ
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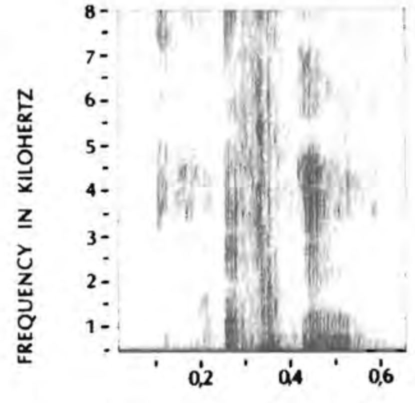
TIME IN SECONDS

B


FREQUENCY IN KILOHERTZ
8
7
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4
3
2
1
0,2
0,4
0,6
TIME IN SECONDS

C

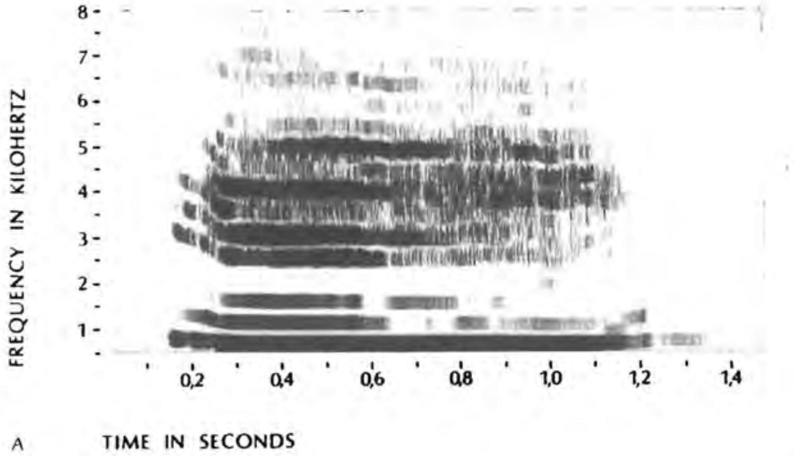
Figure 5: Spectrographic representation of P. capensis sounds. A. Low amplitude grunt. B. Whistle-grunt. C. High amplitude grunt.

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).


FREQUENCY IN KILOHERTZ
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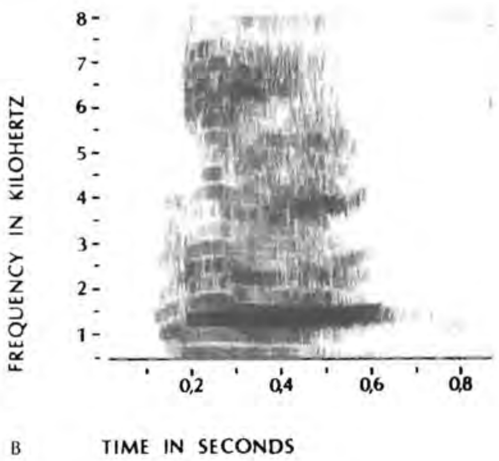
TIME IN SECONDS

A


FREQUENCY IN KILOHERTZ
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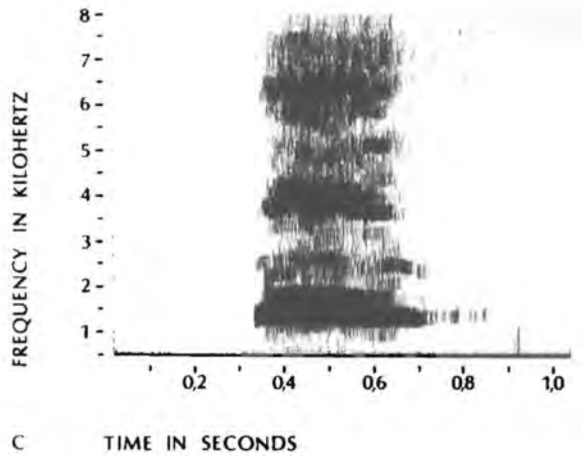
TIME IN SECONDS

B


FREQUENCY IN KILOHERTZ
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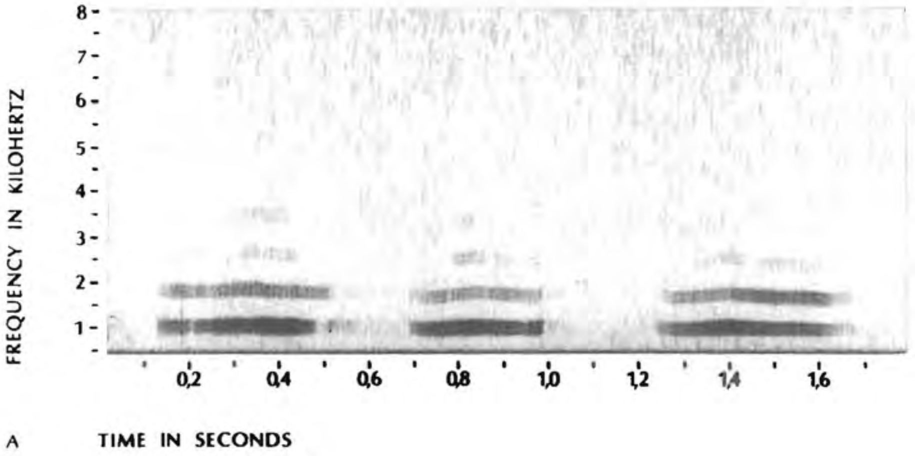
TIME IN SECONDS

C

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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FREQUENCY IN KILOHERTZ
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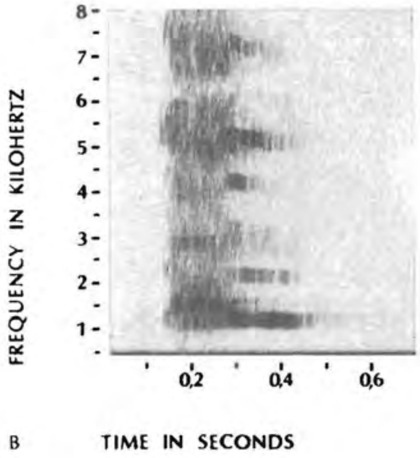
TIME IN SECONDS

A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FREQUENCY IN KILOHERTZ
0,2
0,4
0,6
TIME IN SECONDS

B

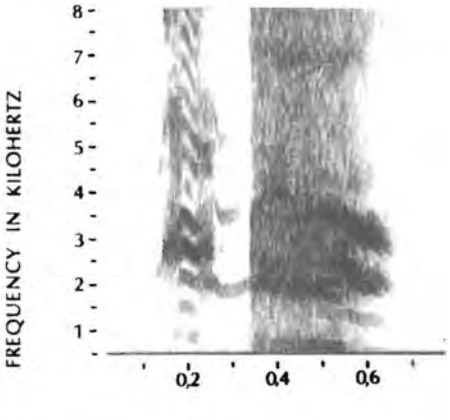
Figure 7: Spectrographic representation of *P. capensis* sounds. A. Low amplitude wail. B. Medium amplitude wail. C. High pitched variation of medium amplitude wail.

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).


FREQUENCY IN KILOHERTZ
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TIME IN SECONDS

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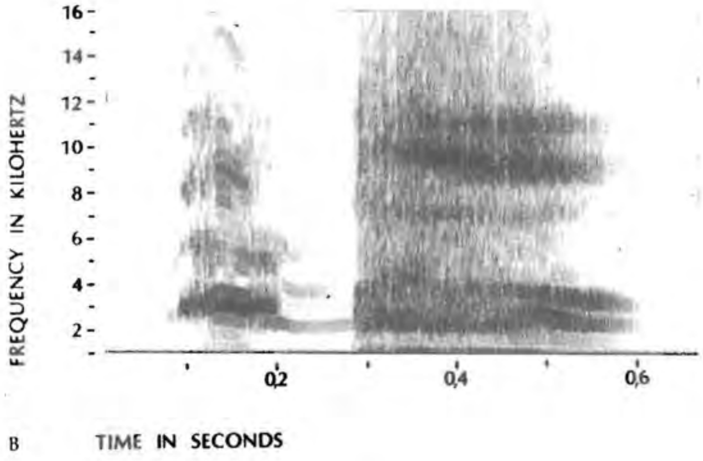
FREQUENCY IN KILOHERTZ
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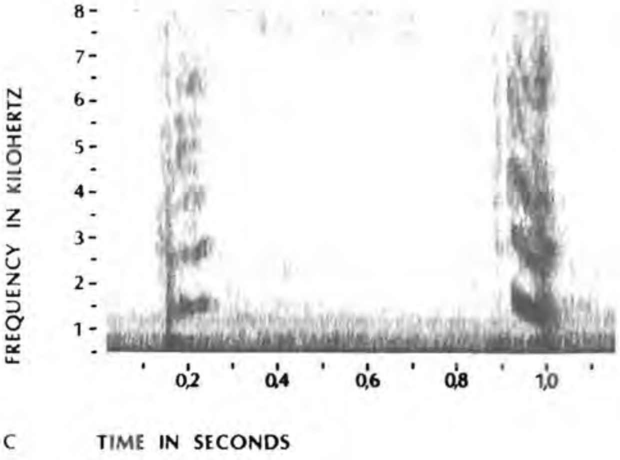
TIME IN SECONDS

B


FREQUENCY IN KILOHERTZ
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TIME IN SECONDS

C

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.

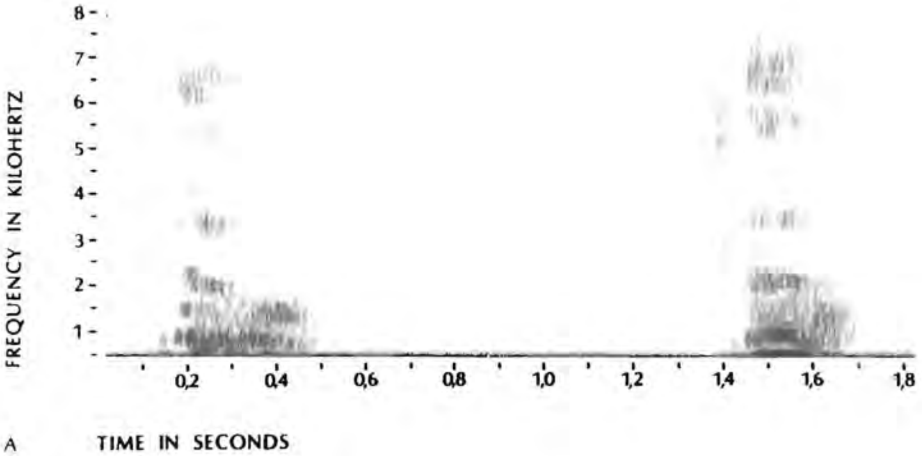
Whine: A more intense form of the coo (i.e. showing a higher amplitude) rising in pitch towards the end of the sound. The fundamental tone frequency rises from 1,0 kHz to 2,0 kHz and is 0,65 sec long. The highest overtone reaches over 8,0 kHz (Fig 10C).

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


FREQUENCY IN KILOHERTZ
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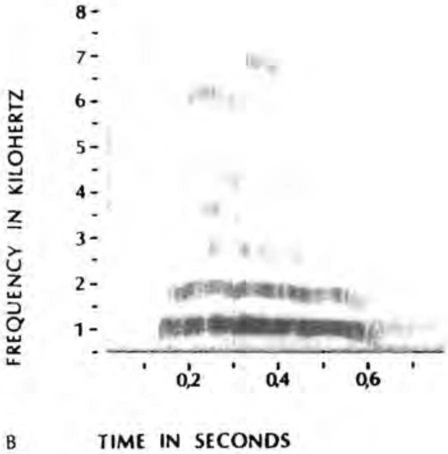
TIME IN SECONDS

A


FREQUENCY IN KILOHERTZ
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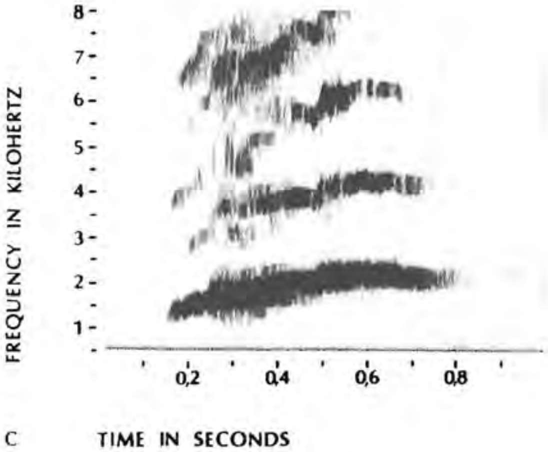
TIME IN SECONDS

B


FREQUENCY IN KILOHERTZ
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0,8
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).

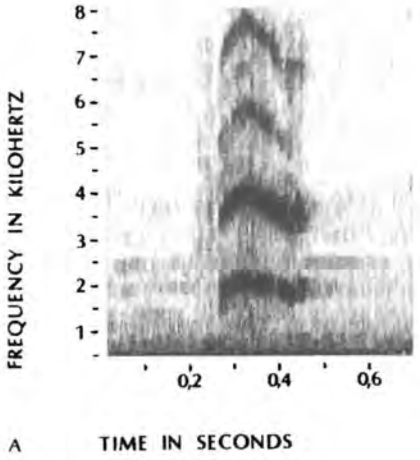
Figure 11: Spectrographic representation of *P. capensis* sounds. A. Squeak. B. Yap. C. Spit (first unit) followed by a short yap (second unit) and a two syllable squeak (third and fourth units, interrupted by intersyllabic inspiration).

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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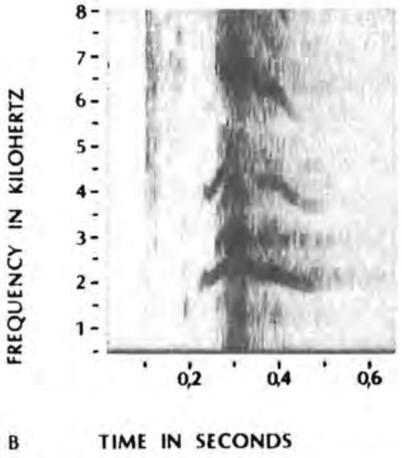
TIME IN SECONDS

A


FREQUENCY IN KILOHERTZ
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TIME IN SECONDS

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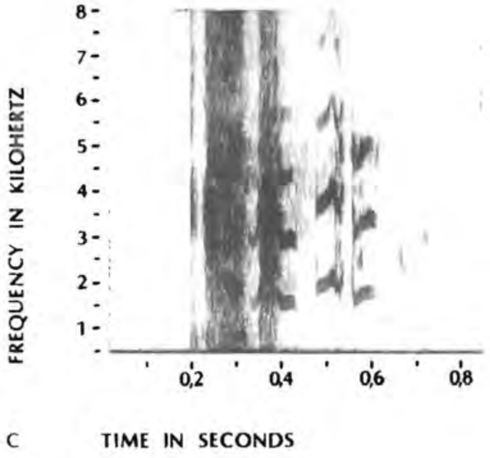
FREQUENCY IN KILOHERTZ
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0,8
TIME IN SECONDS

C

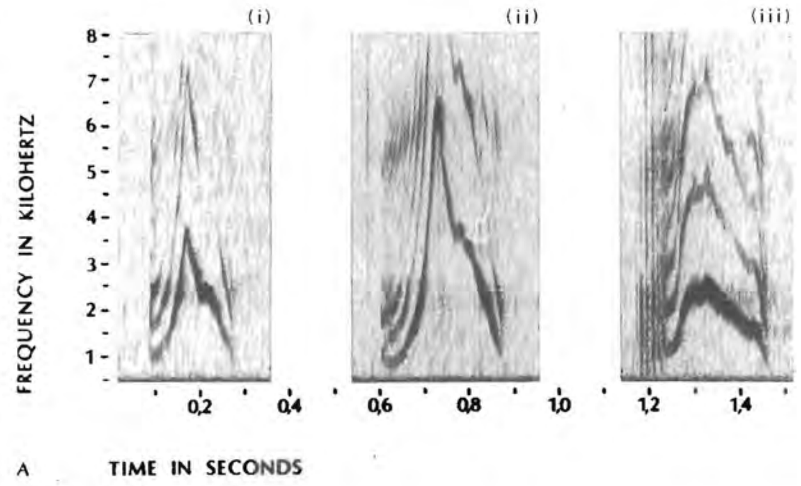
Figure 12: Spectrographic representation of *P. capensis* sounds. A. Sharp bark. B. Repetitious bark.

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.


(i)
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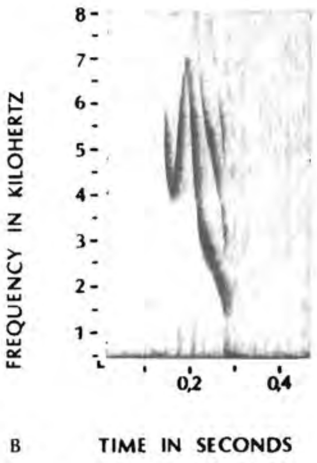
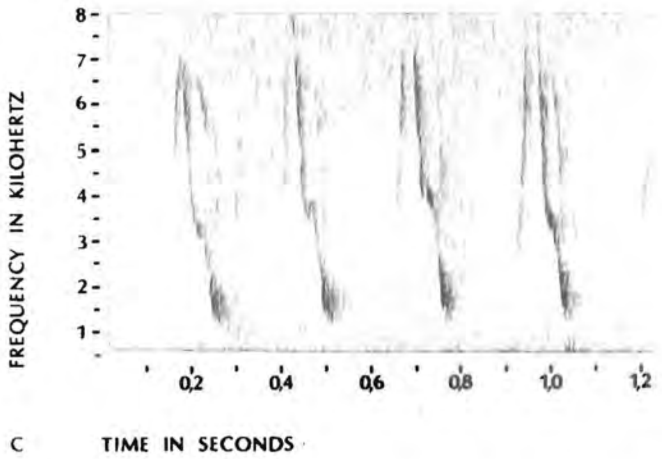
1
0,2
0,4
0,6
0,8
1,0
1,2
1,4
TIME IN SECONDS

A

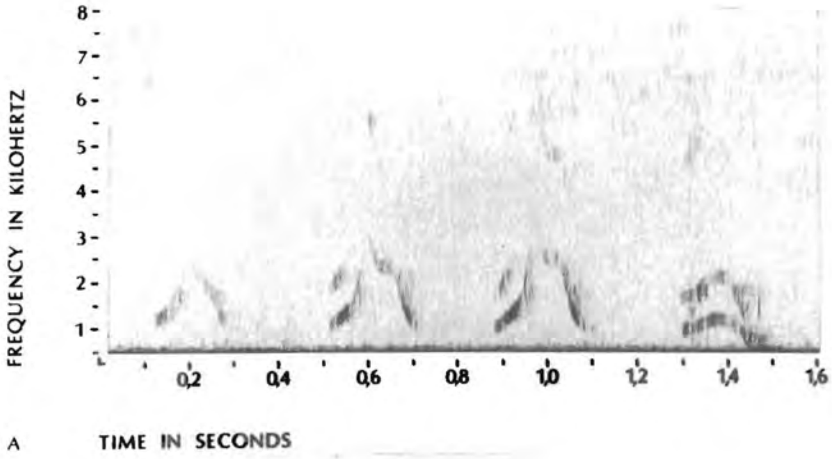

FREQUENCY IN KILOHERTZ
8
7
6
5
4
3
2
1
0,2
0,4
TIME IN SECONDS

B

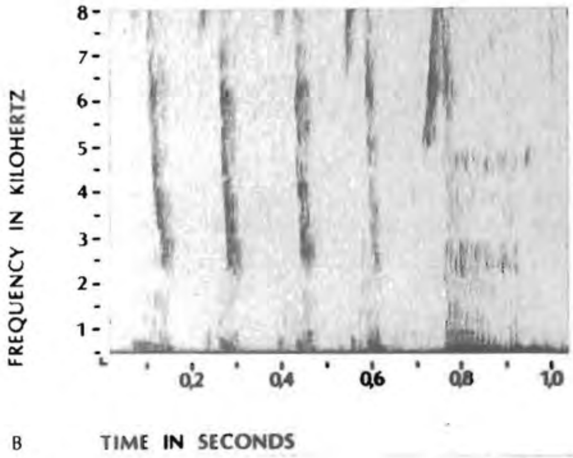

FREQUENCY IN KILOHERTZ
8
7
6
5
4
3
2
1
0,2
0,4
0,6
0,8
1,0
1,2
TIME IN SECONDS

C

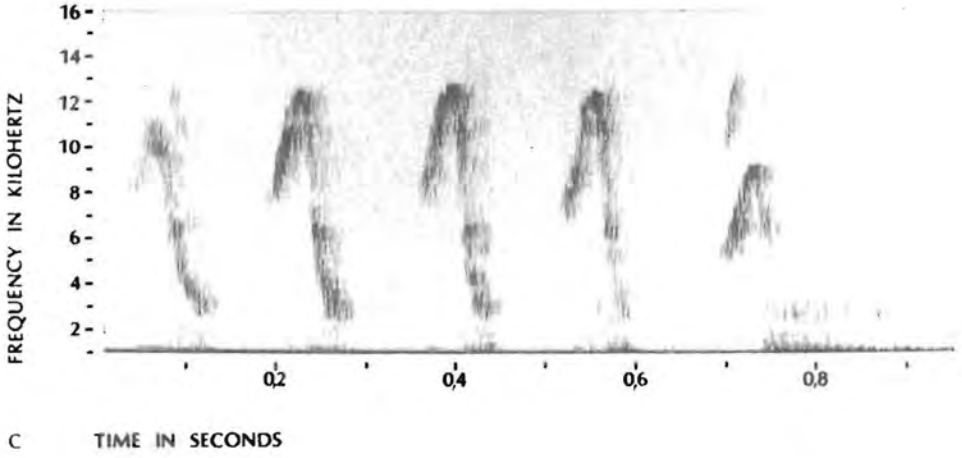
Figure 14: Spectrographic representation of P. capensis sounds. A. Low amplitude whistle chirrup. Note the poorly defined overtones around 5,5 kHz. B. Harsh chirrup. C. The same as B but spectrographically reproduced at half the recorded speed.


FREQUENCY IN KILOHERTZ
8
7
6
5
4
3
2
1
0,2
0,4
0,6
0,8
1,0
1,2
1,4
1,6
TIME IN SECONDS

A


FREQUENCY IN KILOHERTZ
8
7
6
5
4
3
2
1
0,2
0,4
0,6
0,8
1,0
TIME IN SECONDS

B


FREQUENCY IN KILOHERTZ
16
14
12
10
8
6
4
2
0,2
0,4
0,6
0,8
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

	Infants		Juveniles													Adults								
SOUND	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	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.

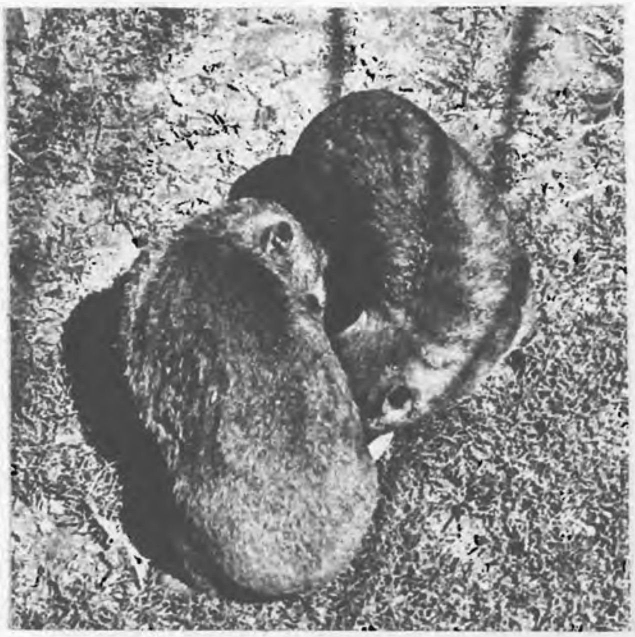
V SOCIAL BEHAVIOUR OF PROCAVIA CAPENSIS IN CAPTIVITY

Aggressive and submissive behaviour

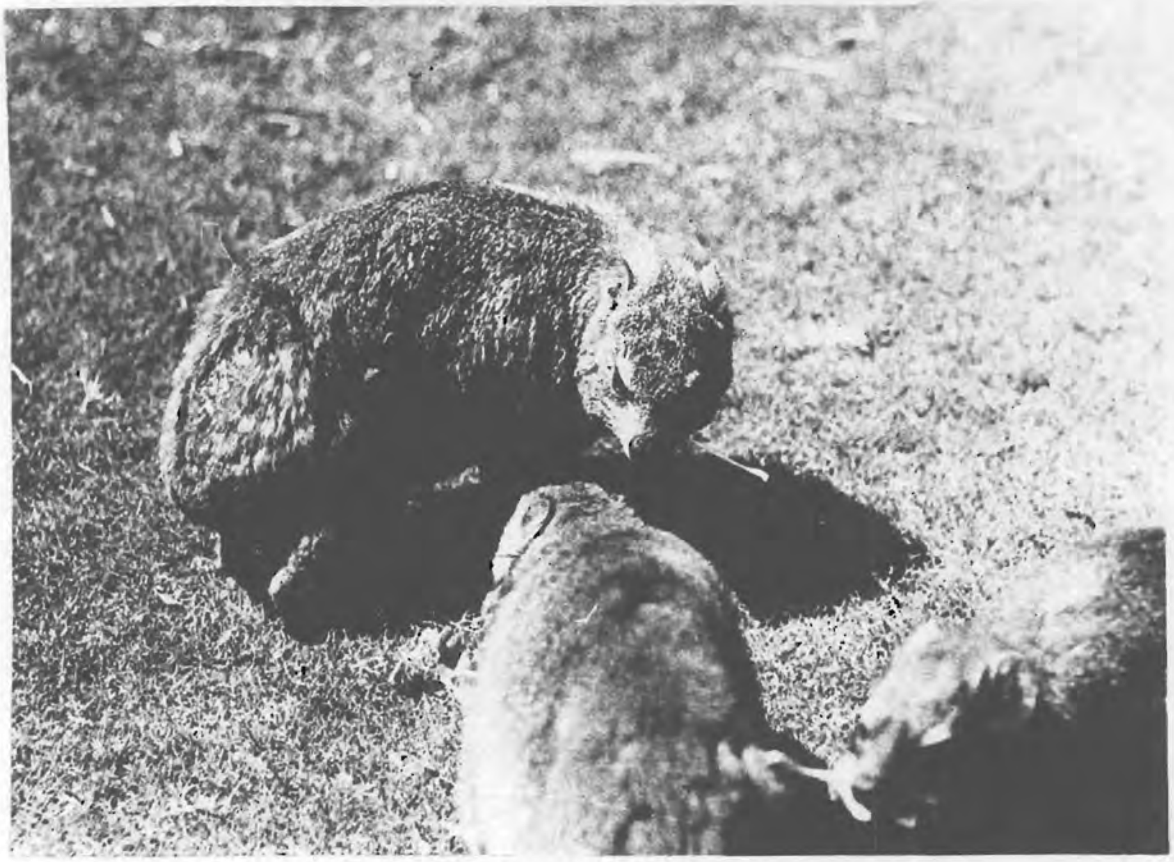
Aggression in the dassie is marked by distinct behaviour patterns, some of which (especially those in which the erection of dorsal spot hair plays a dominant role) are described in detail by Sale (1970a, 1970b) for the East African species of Procavia and Heterohyrax. Sale's descriptions are to a great extent also applicable to P. capensis.

Threat and appeasement behaviour are usually accompanied by characteristic sounds and postures which may differ in intensity of expression depending on the type of situation eliciting this behaviour. The most often observed and perhaps most basic type of threat and appeasement behaviour is shown during head-on encounters between two dassies, at least one of which must be adult or nearing adulthood, during feeding or huddling. The older or dominant animal may then show mild threat behaviour which is indicated by a slight raising of the neck hair and dorsal spot hair, grunts and growls. This complex signal probably acts audio-visually to convey the aggressive intentions of the dassie. Appeasement gestures, following threat behaviour, are generally characterised by backing away by the subordinate animal (Sale 1970a, 1970b). This involves a slight curving of the body so that the back is turned towards the aggressor, while at the same time the subordinate's head is turned backwards in order to keep the other dassie in sight (Fig. 16). The back presentation, a non-flaring of the dorsal spot and a series of squeals and chirrups serve to indicate submissiveness.

Although dassies as a rule tend to avoid face-to-face encounters, it is not always possible to do so where they huddle or heap inside the sleeping box. Young dassies, trying to climb onto the backs of adults, often cause incidents of threat behaviour. They, however, quickly respond with the well-defined pattern of appeasement behaviour described above.



A



B

When dassies feed as a group they disperse over the feeding area, facing away from each other. It sometimes happens that two or more animals, during the course of feeding, approach and try to eat the same portion of food. The result is the same as that described for the head-on encounter except that, since both animals are usually highly motivated in obtaining the food, serious threat indicated by maximum dorsal spot flaring, growling, snarling and even a chase or rapid bite by one of the dassies is not uncommon.

As a rule the dassie shows a marked degree of aggressiveness during feeding. Infants, however, are usually tolerated in this respect and are sometimes allowed to take food directly from an adult's mouth. In this way the infant learns its food preferences (Mendelssohn 1965). A definite advantage can be seen in correct food selection within a short feeding period and is perhaps the reason for adults showing this type of behaviour towards infants.

Dassies are also extremely aggressive towards any intruder while they feed, even if they are used to other species sharing the same confined space with them. Siegfried and Geldenhuys (1965) reported dassies killing crowned cranes (Balearica regulorum) but could not establish under what circumstances. The birds used the same food trough as the dassies and were found dead in its vicinity although Stanley cranes, ducks and geese, which also fed from the trough, were never attacked. It is possible that only crowned cranes ventured near the dassies while they were feeding, probably ignoring their threatening growls and therefore eliciting an attack. F.F. Kolbe (pers. comm.) mentions the same response towards guinea-pigs. Although dassies quickly grow accustomed to regular visitors and may in such cases fail to show signs of threat in most situations normally marked by such behaviour (Sale 1966b), they will always act aggressively during close contact situations while feeding.

In potentially dangerous interspecific encounters (e.g. when a dassie is chased by a predator such as a dog) the dassie flees towards shelter without first showing any threat displays. If cornered, however, the dassie turns around, facing the danger and emits growls and snarls interspersed with a gnashing of the teeth. The dorsal gland hair and the hair over the neck and rump regions are fully raised and the dassie will actually attack and bite the predator if it ventures too close. This method of defense is ususally very effective in discouraging the predator.

During the mating season males become noticeably more aggressive, especially towards each other. Fighting is not uncommon (Coe 1962; Sale 1970a) and serves the purpose of establishing which male will be dominant and thus copulate with the females. When two males are highly motivated and both persist in serious threat displays towards each other, fighting is inevitable. This results in one being forced into submissiveness or else killed, usually after a number of fights.

In the captive colony, which contained three adult males at the beginning of 1973, two of the males on a number of occasions simultaneously attacked the third (until then the dominant male) during the onset of the mating season. Most of the attacks followed on an approach of a receptive female by the third male, or his mere presence near her during group feeding periods. He was also only allowed movement within a small portion of the camp bordering the food area and was quickly chased back by one or both of the other males should he venture outside this area. This male was repeatedly attacked and seriously injured over a period of two weeks and eventually died within a week of the last attack, a time during which he rarely fed or moved about. After his death aggression, displayed in the same pattern as described above, increased between the remaining two males and resulted in the death of one of them.

Although many authors described territoriality in the dassie (e.g. Mendelssohn 1965; Griner 1968), results from my captive colony are equivocal. Kingdon (1971), however, recognized a specific threat behaviour pattern in the dassie as such and stated that they "are very territorial and will threaten intruders of the same species or will attack enemies as a group." He illustrated this by refering to Hanse (1962) who, in South Africa, "watched fourteen adult hyraxes converge on a young jackal and succeed in intimidating it with sudden movements and barking threats."

Anxious and watchful behaviour

Behaviour which is intermediate between threat and escape is often difficult to classify (Hall 1965). In the dassie anxiousness (here regarded as a medium level of excitement) is usually displayed when an intruder approaches within the tolerance-distance of the group but not close enough to elicit threat behaviour from the dassies, e.g. when a human enters the camp or takes up position between the animals and the food source close to feeding time. The dassies which showed this type of behaviour usually were in a safe position, for instance on a branch in the tree.

Amongst the adults the dominant male, under the circumstances described above, was the only one to display alertness, watchfulness and slight frustration by flaring his nostrils, snorting and sometimes squeaking, especially when some of the younger dassies or the tame female cautiously approached the food and thus the observer. This manner of mildly threatening the observer and simultaneously alerting the approaching juveniles was more easily elicited during the mating season.

In juveniles and young adults curiosity, in the sense at least that the animals try to keep the source of disturbance in sight, may often lead to "excited" or "anxious" behaviour being shown. They tend to approach the food even with the observer partly obstructing the way or else peep from the safety of the sleeping box, occasionally emitting squeaks and yaps, should the observer remain motionless close to the food. With the slightest movement on the side of the observer, the young dassies would jump back inside the sleeping box only to appear seconds later and continue in the same fashion. The tame female, however, displayed this behaviour pattern only towards strange persons.

Although a debatable point where animals are concerned, "fear" could be seen as highly excited or intensely anxious behaviour, often elicited when a dassie is startled by the sudden appearance of a predator at close range. A quick jump and high amplitude squeak by the dassie, followed directly by head-long flight, mark this behaviour pattern. Van der Poll (1972) also described intense fear in the dassie at the sight of flaming fire, responding to it by emitting "een harde balkende kreet" (a loud braying cry).

Sexual behaviour

Glover and Sale (1968) described seasonality regarding reproduction in Procavia and Heterohyrax in East Africa while Millar and Glover (1970) were the first to draw attention to this fact concerning P. capensis in South Africa. Dassies mate between February and July in South Africa but timing varies according to the locality, i.e. as the latitude decreases the copulatory period occurs later in the year and is longer in duration. This is suggestive of photoperiod providing the environmental cue for the mating season (Sale 1969; Millar 1971, 1972a, 1972b; Millar and Glover 1973). Although mating usually does not occur later than July, copulation with conception may in captivity, however, occur as late as October, as suggested by the birth records of dassies bred in the National Zoological Gardens in Pretoria (Brand 1963).

The gestation period is around 230 days (Van der Horst 1941; Murray 1942; Mendelssohn 1965; Sale 1965a; Millar 1971, 1972a) with most births being recorded during November and December. Litter size is reported by Millar (1971, 1972a) to increase with the age of females, the mean litter size ranging between 1,5 (lowering Thursby-Pelham's (1924) mean figure of 2,0) and 3,5 (extending Van der Horst's (1941) mean figure of 3,3).

Maturity is reached at an age of between 16 and 17 months (i.e. during the second mating season after birth) and the animals are sexually able to partake in mating. Millar (1971, 1972a), however, reported one-third of females and a few males reaching puberty four to five months after birth.

The behaviour of dassies during the mating season differs markedly from their behaviour during the rest of the year. Mendelssohn (1965) makes the point that P. c. syriaca males become very intolerant of other adult males during the mating season. He further states that "Some adult males may, even during the mating season, tolerate the presence of sexually mature, sixteen-month-old males, but will never tolerate the presence of twenty-eight-month-old or older males." Regarding this statement, Glover and Sale (1968) pose the following question "Does this mean that the young (16 month) males are, in fact, not sexually active but that all the older males are both sexually mature and active?" The fact that fighting only occurs between a dominant polygamous male and fully grown rivals, each occupying a restricted piece of ground (bachelor males tend to group together outside the mating season) while younger adults, moving about freely in the camp, were largely tolerated by all other males, is certainly suggestive of a positive answer to this question. Glover and Sale (1968) consequently suggested that, during the mating season, male dassies may be grouped into three reproductive categories, the sexually immature or juvenile animals, adult animals in a sexually quiescent state, and sexually active adults. These categories seem to apply to male P. capensis in South Africa as well, if judged by the difference in behaviour patterns associated with the mating season. The subdivision of adult dassie males in those that show an active interest in females and those that do not probably corresponds with categories two and three mentioned above. Captive males entering their first mating season as sexually mature animals (i.e. 16 months old) usually do not partake in mating if older males are present in the colony. As a rule, these young adults were never involved in fighting and their presence was usually tolerated by older males. Should any of them, however, happen to show interest in an adult female when feeding close together or walking close by, they would be chased away abruptly by the dominant male or even more than one older male simultaneously if dominance has not been finally established.

Juvenile males were allowed freedom of movement within the camp by all members of the colony, also within close proximity of receptive females, with little or no aggression shown towards them by adult males. The same applied to young adult females. Sexually active males, however, were individually restricted to specific portions of the camp. The interesting point in this arrangement was that these males did not defend their "home bases" but that fighting did occur in neutral areas. A neutral area is indicated by the presence of a female in any portion of the camp, even if it happens to be a male "home base", in this case then regarded neutral for as long as the female remains within its boundaries. Should the male occupant show an interest in the female and not leave the spot instead, the dominant male will immediately run towards him and try to chase him off. If the occupant persists in holding his ground a fight develops.

Copulatory behaviour has as yet not been described in the literature. According to Mendelssohn (1965) copulation by captive dassies probably takes place at night. This is not the case in South African dassies since copulation was observed during all times of the day.

When a receptive female is approached by a male she turns around and presents her hind quarters. The male then sniffs her genital region, sometimes while she urinates, and attempts to mount. The female then usually walks slowly from under the

Figure 16: Aggressive and submissive postures assumed by *P. capensis*. A. Two dassies of equal status feeding from the same food container. Both animals' bodies are curved so that they can keep each other in sight while simultaneously each one is prepared to present its back in submission should the other attack. B. A subordinate dassie approached by a dominant one. The subordinate's body is curved for the same reason as that in A above while the dominant animal does not demonstrate this posture. Note the bare patch on the subordinate dassie's back where it was bitten repeatedly on previous occasions and also the ears pressed flat against the head which is a sign of alertness.

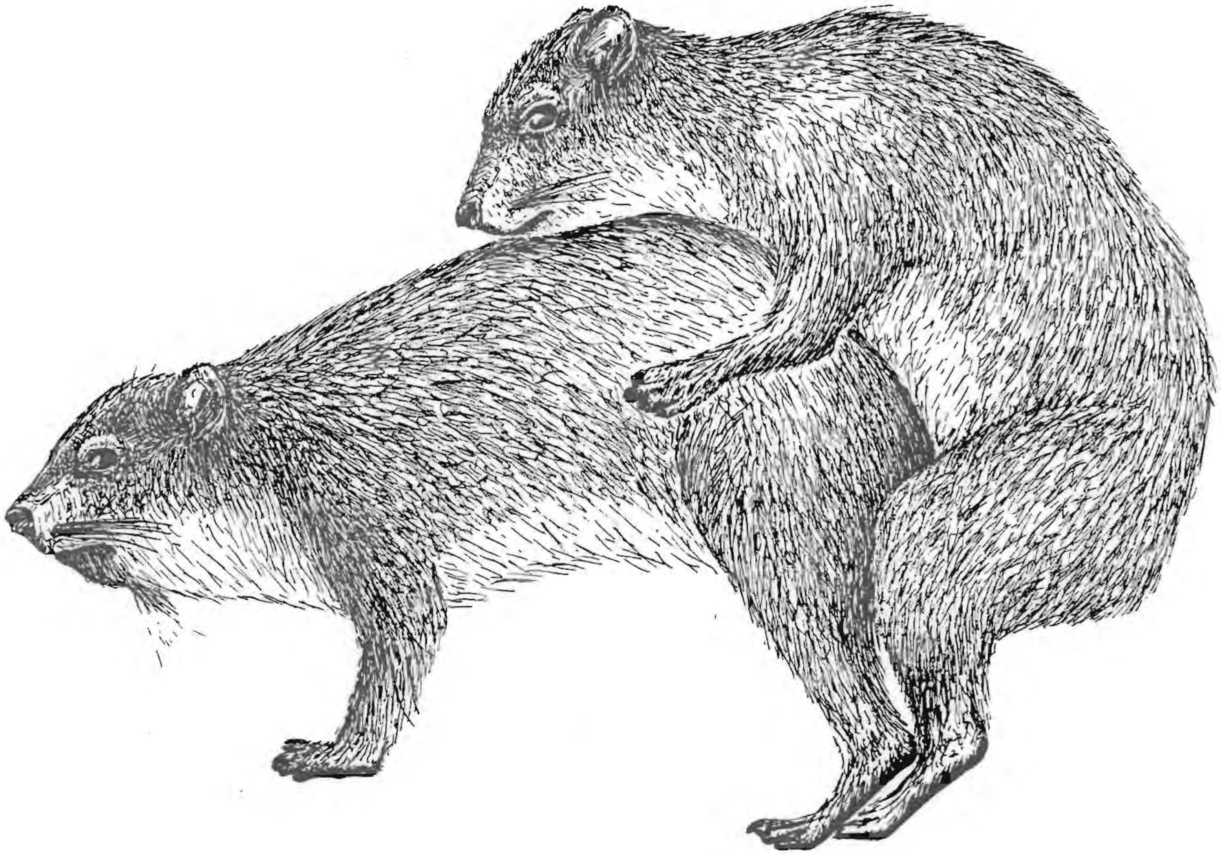
(Photographs by F.F. Kolbe)

male while he follows closely. This procedure is repeated a number of times before the female finally allows the male to mount and copulate. The female places her hind legs wide apart while standing with an arched back. The male places his hind feet next to the female's and presses his front legs to her side just behind the ribcase (Fig. 17). Ejaculation probably occurs within 10 seconds of penetration. E.J. Waanders (pers. comm.) watched several copulations amongst captive dassies in the National Zoological Gardens and according to him the males placed their front legs far to the front over the ribcase, head against the left shoulder blade of the female and grasped the neck hair of the female firmly between the teeth. This pattern has not been observed in the captive colony used in this study and the question remains whether the postures assumed by the study animals while I watched them did in fact accompany copulation with penetration or only represented attempted copulation, and whether successful and attempted copulation require different postures.

Very little can be added to the comprehensive description by Sale (1965b) of parturition in East African dassies. Basically the same pattern was observed in <u>P. capensis</u>. From a few days to a month before parturition gravid females became noticeably more aggressive towards other members of the colony, especially adult males which were driven out of the sleeping quarters. The slightest disturbance by an observer elicited wails characteristic of excitement (as a result of frustration) interspersed with fear. Immediately prior to and during parturition a female in labour was left alone while the younger members of the colony, especially non-gravid females, continuously emitted whistle chirrups while inquisitively watching the parturient female from a distance.

In one case the firstborn of a litter of five succeeded in climbing onto the mother's back while the third birth was

Figure 17: Copulation posture assumed by *P. capensis*. Note the arched back of the female and the position of the feet of the male.



still in progress. Climbing of the young onto the mother's back soon after birth was observed in all cases, a behaviour pattern serving a number of important functions which are discussed in the next section.

Births followed each other rapidly in all cases except one where the female gave birth to two males within 10 minutes of each other and then took five, 17 and 19 hours respectively for the remaining three which were stillborn, the delay probably brought about by the lack of movement in the foet~~e~~us~~u~~es. During all of this time the parturient female hardly rested, periodically showing abdominal contractions accompanied by coughs and harsh moans, and never fed. After the last birth she tore at the membranes, not ingesting any, and licked at the birth fluids.

Mother-infant behaviour

The moment a newly born dassie struggles free from the birth membranes, not actively assisted by its mother in any way, it is capable of looking after itself in most ways, even perhaps able to survive without being nourished by its mother (Griner 1968). Precociousness might be expected in an animal of such small size and comparatively long gestation period allowing enough time for development. At birth the eyes are open, a milk dentition in an advanced state of eruption is present, the pelage is thick and fully developed, and infants immediately start moving about. Within a day they begin to nibble on solid food. These features seem to apply to the Hyracoidea in general (Mollaret 1962; Roche 1962; Mendelssohn 1965; Sale 1965b; Millar 1971) although Nassonow (1895) mentions a newborn Syrian dassie lying almost motionless and with closed eyes for quite a while. He, however, reasons that it probably was the result of the cold air temperature at the time.

While the newborn struggles from the birth membranes the mother occasionally licks or sniffs it. This is probably the first social-contact action by the mother towards the infant which may serve to draw the attention of the young for possible imprinting and also to introduce the object towards which the young dassie can direct its climbing behaviour. As soon as the infant straightens its legs it climbs onto the mother's back, succeeding only after several attempts. This strong tendency for the newborn to climb onto the mother's back probably serves a number of important functions. Sale (1965b) suggested that the young in this way come into contact with the dorsal gland of the mother, so being marked with her scent, and that the mere fact of being perched on an object further serves as a preparation for adult watchfulness. Sale furthermore viewed the infant climbing behaviour to be of great stimulus value in the imprinting process since it constitutes the first clearly defined social-contact action on the part of the newborn in relation to the mother.

It was observed in two cases that newborn infants directed their initial climbing behaviour towards a non-lactating female and used the mother only to suckle on. On the other hand, even if both these activities were initially directed towards the mother, most infants were seen to suckle on any lactating female, nuzzle for teats in any other adult dassie or climb onto any adult's back within hours after birth. Apart from the fact that these observations indicate a rather loose mother-infant bond, it is also suggestive of the imprinting process not necessarily involving the mother but that any dassie which happens to be close by when the infant is born and which is capable of providing in either or both the above mentioned needs (i.e. to suckle or climb on) will suffice. The direction of these activities towards the mother is, however, much more frequent since she is in a position to elicit and receive the first attentions from the infants.

On the whole it would thus seem that climbing behaviour in the infant, apart from preparation for adult watchfulness, probably plays an important role in the association of the newborn not only with the mother, but also with the group. Since it is known that dassies will chase off or even attack any strange dassie introduced to adult males in a colony (Kingdon 1971) and that adult males sometimes kill newborn infants (Roche 1962; Mendelssohn 1965), a distinct signal safeguarding the young dassie against attacks may be expected. Physically associating with any adult by climbing onto its back, at the same time being marked with the scent of the dorsal gland, could thus have the advantage of immediate recognition and acceptance of the infant as part of the colony, whether it is visually or olfactoraly perceived.

Female dassies in general show little interest in their young, apart from feeding them. In cases of mild frustration, such as when the infants are palced outside the safety of the sleeping box or want to suckle and cannot find the mother, they emit harsh twitters to which the mother responds with coos and whines. She approaches the young, thereby placing herself in contact with them, and lead them back to shelter or allow them to suckle. As soon as the infants are able to find the way back to the sleeping quarters on their own, there is a marked decrease in the incidence of harsh twitters. After they are weaned the voicing of harsh twitters disappear almost completely but are in fact retained in the original form throughout life to be heard only when extreme fear or pain is experienced at the hand of a predator.

Harsh twitters in infants usually elicited a response from a large number of adults in the colony, especially if the young were injured and in pain. Such responses include rapid sharp barks by the dominant male and even positive attacks on me by adult females while I held the twittering infant.

Soft twitters, emitted during suckling, indicate satisfaction on the part of the infant and serve as an appeasement sound to calm the mother (Sale 1965b). These sounds later probably give rise to the chirrup series, retaining the original function; the whistle chirrup given during renewed contact (greeting) with other members of the colony and the harsh chirrups for appeasement of an aggressive superior.

Until they are weaned after three to five months, the young dassies do not venture far from shelter (Mendelssohn 1965; Sale 1969). In the captive colony they usually sunbasked in the entrances to or huddled close together inside the sleeping box.

Behaviour of juveniles

Although juvenile participation in a number of social situations have been described two distinct patterns associated with juvenile behaviour, namely play and curiosity, need special mention.

Play in the dassie has been mentioned by Nassonow (1895), Eismann (1897), Bothma (1966), Sale (1970a), and Smithers (1971) but detailed descriptions are lacking. In the captive colony no indication of social play was ever observed but individual juveniles sometimes showed undirected movements such as darting off over a short distance and jumping in a sideways manner or bouncing on all four legs which suggests playfulness. I often elicited play in a five-month-old tame female. When tapped on the muzzle with a finger she would roll over on one side, dragging herself forward with the two legs closest to the floor while gently biting at the finger. When I swiftly moved a hand from one side of her body to the other, pinching her firmly during each movement, the same reaction was elicited. In this case she would lie flat on her belly, trying to follow the hand with her head and attempting to bite it. When confusion about the position of the fast moving hand arose she would dart off, run in a circle, return and immediately roll over on reaching me. She would then gently bite at my hand and repeat the entire performance when the slightest indication of participation is given. On some occasions she initiated the performance described above by nibbling on the hands or feet of a person; the slightest reaction on the human's part immediately triggered play. Vocalizations accompanying the bites or emitted in response to the pinching included whistle chirrups and squeals.

Another striking feature of the juvenile dassie is its curiosity, a quality appearing within a few weeks after birth and remaining easily recognizable until about eight months of age.

Once I was followed in the field for about 20 metres by two approximately four-month-old dassies. They moved cautiously from rock to rock and showed themselves fully only for as long as I stood quite still. At times they appeared from behind a rock so close to me that they could almost be touched. In the captive colony young dassies invariably approached me (seated motionless next to the food spot) and sniffed at me after watching me for various lengths of time (sometimes up to one hour) from the safety of the sleeping box entrances. They seldom approached directly but usually jumped down from the sleeping box, remaining still for some time and then slowly came forward with the belly close to the ground and the neck and body stretched out, a posture enabling them to retreat instantly if necessary.

This type of behaviour was rarely observed in adults and is possibly, together with the ready acceptance of captivity by the dassie, the main reason why they are easily tamed when younger than seven months.

Spacing within the group

One week after release into the enclosure in Pretoria each adult animal occupied its own specific spot where it would rest and sunbask during the day. Some of the dassies selected spots in the tree while others occupied spots on the floor of the enclosure or roof of the sleeping box.

A fork in the main trunk of the tree, approximately six metres from the ground, provided a neutral spot where the tree occupants heaped onto one another during the early morning, late afternoon and during the night. Otherwise only one adult female, and after her death two younger females, occupied this fork permanently. It was not necessarily the dominant animals which occupied the highest branches or centrally situated spots in the tree but rather a question of "first come, first served" in regard of the most comfortable and easily reached positions closest to the main trunk. Younger dassies which ventured into the tree for the first time at about seven months of age had to be content with the slender branches higher up in the tree. Inside the three-chambered sleeping box, however, no selection of a specific corner or chamber was evident although, during the mating season, young mature males always used a chamber not occupied by the dominant male.

Juveniles only showed a tendency for spot selection at the age of seven to twelve months. When they were one year old an urge to leave the colony became evident and all dassies in this age group tried to escape. They were then allowed to leave and enter the enclosure freely for a period of two weeks which resulted in them inhabiting ventilation holes in the main building and only visiting the enclosure during group feeding times. None of the other animals showed this tendency. When the one-year-olds were forced to stay inside the enclosure after the two week period, they appeared restless until the start of the mating season about two months later. Only after the mating season attempts at escape by the same animals were again recognized.

It was also noted that the upper and lower incisivi were shed and replaced with permanent teeth at one year of age. A correlation, if any between the shedding of the front teeth, nearing of sexual maturity and the tendency to leave the colony is, however, dubious. Under natural conditions this may well be the age at which dassies nearing sexual maturity tend to establish a new colony.

The dassie requires its own individual minimum space in which to carry out activities such as sunbasking, shade resting and feeding (Sale 1970b) although these activities do not take place in the same spot. Since the dassie is not an intensely social animal, avoidance of bodily contact during these activities limits the expression of the animal's aggressive nature towards a conspecific. Maintenance of a minimum distance between two dassies is facilitated through the use of vocalizations and dorsal spot flaring. During cold temperatures the dassie needs to huddle close to other members of the group in order to conserve body heat. Although this situation necessitates bodily contact, a minimum distance between the faces of the animals is still necessary and results in the dassies performing huddling and heaping in a radiating fashion, i.e. facing away from each other (Sale 1970a). It would thus seem as if the dassie is forced to act socially through, in the words of Mendelssohn (1965), "the heightened thigmotaxis and gregariousness of hyrax during low temperatures."

The behaviour of dassies under environmental conditions other than low temperatures strongly suggests that they are at most unsocial gregarious animals. Evidence of this includes the absence of a strong mother-young bond (Sale 1965b), a complete lack of social grooming, the solitary existence of Dendrohyrax, and the low threshold of intraspecific aggression in both sexes of especially adult Procavia (Sale 1970a).

Daily routine

Sale (1970a) mentioned that the rock dassie is a very inactive animal and spends approximately 95% of the day resting. He also stated that a resting dassie may be involved in one of three basic social groupings, namely heaping, huddling and solitary resting, and defined these groupings as follows:

"Heaping normally involves three or more animals that have packed themselves very tightly together, some of the group being raised up on the backs of the others which are crouching on the ground."

"Huddling is similar to heaping but does not involve animals being raised up on the backs of others i.e. there is a single tier, all crouching on the ground but in close lateral contact with one another."

"Whereas in heaping and huddling the hyrax clump together in a tight formation, in ... 'solitary resting', the animals tend to be scattered and although sometimes lying in twos or threes, they are never in physical contact with other members of the group."

The daily routine of my captive animals usually started at sunrise when they appeared in the entrances of the sleeping box. Here they sat awhile before proceeding directly to the roof of the sleeping box or their individual resting places in the tree, often defaecating on their way at the communal latrine. Generally, near inactivity and sluggish movements marked the dassies' behaviour for the first four to five hours after sunrise. This is probably closely associated with their known poor thermoregulation (Turner and Watson 1965; Taylor and Sale 1969; Sale 1970a; Bartholomew and Rainy 1971; Louw 1971; Louw, Louw and Retief 1972; Millar 1973).

When the sun rose high enough to shine directly inside the enclosure the dassies on the floor, or the roof of the sleeping box fully exposed themselves to the rays by stretching out on their bellies, sometimes turning over on their sides. They never showed heaping outside the sleeping box but often huddled during the initial stages of sunbasking. As sunbasking progressed, however, they gradually dispersed to their individual sunbasking spots for solitary resting. Dassies which spent most of their time in the tree showed a strong tendency for heaping. Sometimes as many as four animals sat on top of each other in a fork in the tree for long periods during the mornings and occasionally for a whole day during the winter. When the sun reached their individual resting spots on the branches, however, they moved off to sunbask. In the tree heaping replaced huddling which could not be carried out successfully.

After the early morning chill, about one to two hours after sunrise, most of the dassies moved towards the food spot where they soon assembled for the first group feeding period of the day which usually lasted 20 to 30 minutes. At the end of this feeding period the dassies returned to their respective resting spots to bask in the sun, or to groom themselves.

The dassies frequenting the floor of the enclosure and roof of the sleeping box utilized shade from time to time, and avoided prolonged exposure to direct sunshine on hot days. As the tree occupants seldom left their resting places, except to defaecate at the latrine box on the ground or for casual feeding in the branches of the tree, the air temperature in the tree probably never rose too high.

The second group feeding period started about two hours before sunset and lasted twice as long as the morning one. Between the two main feeding periods individuals often fed casually at the food spot but the dassies inhabiting the tree, however, seldom descended. They utilized leaves and fresh shoots in the tree or, during winter, stripped large portions of the branches of bark.

At nightfall most dassies retreated to the sleeping box where they huddled and heaped until sunrise. During the night they would at intervals, sometimes for prolonged periods, scratch themselves or shift position, the latter usually accompanied by aggressive and appeasing vocalizations. The inhabitants of the tree, however, stayed there, even during winter months and only moved inside the sleeping box on extremely cold nights. Fox (1933), Mendelssohn (1965) and F.F. Kolbe (pers. comm.) mentioned dassies contracting pneumonia and dying as a result if exposed to intense cold for prolonged periods.

Food and feeding

At the start of both of the dassies' two main group feeding periods the juveniles approached the food first, followed by the dominant male and females. Young males arrived last and usually fed on the fringes with the juveniles and dominant male occupying the centre. During this time the animals were spaced evenly and fed at great speed.

Dassies consume a large variety of plants (Turner and Watson 1965; Sale 1965c; 1966a; Kolbe 1967; Millar 1972a). Highly poisonous plants are reported to have little effect even when taken in large quantities by some species of dassie (Sale 1965d; Dobroruka 1973). My colony ate every kind of vegetable and fruit supplied, including lettuce, carrots, cauliflower, pumpkin, peaches, apples and oranges. They preferred carrots and lettuce, however, and could be easily enticed by these into feeding as a group at any time of the day or night. Two juveniles also ate large quantities of minced meat whenever presented with it, even if fresh greens were simultaneously supplied.

Bark-eating under drought conditions has been reported by Sale (1965c) for *P. habessinica jacksoni*. My dassies demonstrated the same habit during winter months but this behaviour in my study cannot be attributed to a scarcity of food and free drinking water since both were always abundantly available.

Food is taken in large amounts by gripping it between the molars and chewing it in a sideways fashion. Large solid pieces of food such as carrots are grabbed with the front teeth and a small piece broken off through a whiplash action of the head. It is then passed to the molars where it is chewed. Sometimes the front feet are used to steady or hold down large pieces of vegetables so that a piece can be broken off. When drinking, the dassie sips through slightly opened lips and does not use the tongue to lick.

Although Hendrichs (1963) reported rumination in captive *P. capensis*, Sale (1966a) disagrees and is supported by the fact that chewing movements in the absence of ingestion often accompany two distinct behaviour patterns, one totally unrelated to feeding. As noted above, an aggressive dassie gnashes its teeth when growling, a movement resembling chewing. I often elicited this pattern in a dassie by slowly walking towards one while making chewing movements and loudly gnashing my teeth. The other situation eliciting chewing movements in a dassie is the sight of specially favoured food placed at the food spot during group feeding time and then being guarded by a person. The dassie in question is then probably eager to ingest the food but is afraid to approach it. A frustration situation therefore arises and the chewing movement may thus be an illustration of appetitive behaviour.

Individual behaviour

Dassies affected self-grooming by scratching themselves with the long claw-like nails on the hind feet, or combing the fur with their lower incisors, occasionally biting in the pelage to dislodge~~d~~ dirt which became stuck. Dustrolling by the captive dassies in the sand boxes provided often took place during the late afternoon. Dassies have a number of ectoparasites (Bedford 1932a, 1932b; Taute 1971) and dustrolling could, in addition to grooming, be a method of restraining infections.

A dassie seldom slept lying outstretched with closed eyes. The animals usually huddled in an upright position with the legs drawn close to the body, belly flat against the ground, and staring fixedly ahead. The tame female and some of the juveniles, however, showed a "relaxed" way of sleeping on one side with closed eyes when tucked under a blanket.

In all, three stages of awareness in the dassie were recognized. These were: 1. An active alertness indicated by movement of the ears, twitching of the nose and a raised head; 2. Semi-awareness indicated by a passive motionless upright lying posture during which the fur is ruffled and the gaze fixed (especially noticeable in infants immediately after suckling). This stage is usually present during sunbasking although ruffling of the fur is only seen while the animal is still cold. If potential danger is noticed during this stage, it immediately passes into stage 1 which then, depending on the severity of the danger, may or may not be followed by the sounding of alarm and flight; 3. Total unawareness during which the body is relaxed, stretched out in an upright position or on one side, and the eyes are closed. While in this stage, a dassie may be touched or even picked up without being awakened. This may be regarded as the only time when a dassie really is asleep, and probably only evident when in the dark of the crevices under natural conditions, or when it is completely safe and does not fear intrusion by a predator.

Social communication: The utilization of tactile, olfactory and visual signals by the dassie

Although this study was mainly concerned with acoustic communication in P. capensis (discussed in more detail above), other means of communication (i.e. tactile, olfactory and visual) are also utilized by the dassie.

Sale (1970b) considered the adaptive significance of three skin derivatives in the dassie, namely the dorsal gland, dorsal spot and widely distributed tactile hair, and noted how these structures are used by the dassie in social communication and underground habits.

Tactile hair are distributed more or less evenly over the body of the dassie except for concentrated clumps around the muzzle, on the underside of the chin and above the eyes. These hair are probably particularly useful when the dassie moves in crevices which are totally dark inside. Another possible function may be sought in the feeding behaviour of the animals. When one of the long vibrissae on the rump of a feeding adult dassie was lightly touched, the animal immediately responded with a soft grunt which indicated mild aggression. Light touching of an ordinary body hair did not elicit this reaction.

The necessity for the dassie to maintain a certain minimum distance from a conspecific while feeding, in order to avoid elicitation of aggression, has been noted above and has also been remarked on by Sale (1970b) who described the role of dorsal spot flaring in P. johnstoni as a visual signal in this respect. In P. capensis dorsal spot flaring is not often seen and they sometimes feed relatively close together without any apparent signs of aggression. Should the tactile hair of a feeding dassie, however, register the presence of another dassie without the latter being visually perceived by the former, signs of aggression became evident. The intruder then swiftly moved away or turned his rump towards the other while uttering appeasing vocalizations. Close bodily contact between two or more dassies was never observed apart from activities which required heaping or huddling.

The role of the dorsal gland in social communication is still not clear, but increased secretions resulting in a stronger odour around the dassie during the mating season suggests a function in this regard. Hvass (1961) and Sale (1970b) provided evidence that the dorsal gland functions maximally in both males and females during the mating season and that males probably locate females entirely by smell. R.F. Ewer (pers. comm.) also mentioned dorsal spot flaring and scent emittance through the dorsal gland in Dendrohyrax during threat behaviour. The possible function in recognition of colony members and importance of the marking of newborn with the scent of an adult member of the colony has already been mentioned above. These observations indicate a pertinent use of olfactory signals in the social bahaviour of the dassie.

Sale (1970b) presented evidence of the combined use of visual and olfactory signals in the male during courtship behaviour in P. johnstoni, the strong scent serving as a reinforcement of dorsal spot flaring which conveys the male's intentions to the female. In P. capensis dorsal spot flaring during courtship has not been observed but other visual signals such as the male approaching the female in a crouched posture, belly pressed close to the ground while dragging himself forward, probably serves a similar function. It is possible that in species with a lightly coloured dorsal spot (such as P. johnstoni) flaring as a visual signal is much more frequent and constitutes an important and successful method of information transfer, easily perceived because of its contrast to a dark background by conspecifics even at close range. In P. capensis with a dark dorsal spot, however, flaring is not so common. It still serves to indicate aggressiveness in some situations, as mentioned above in connection with aggressive behaviour, but has probably lost most of its original functions. Since perception of a slightly darker spot on a dark background of fur at close range by an animal with alleged poor near vision (Sale 1970a, 1970b) might present identification problems, it is likely that tactile, olfactory and acoustic means of communication gained priority over subtle visual signals in such situations (or at least function to reinforce and identify them). All except two sounds made by the dassie, as well as tactile and olfactory signals, function at close range only which suggests a strengthening of this view.

Apart from dorsal spot flaring, the function and significance of which in the absence of other communicative signals is not quite clear, only three distinct, visually perceptable signals were identified in P. capensis. These were: 1. Back presentation with or without head turning by a subordinate animal in response to threat from a dominant animal or from a male towards a female during courtship, which indicates submissiveness and non-aggressive intentions; 2. A crouching posture assumed by a male when slowly approaching a receptive female, also indicating an appeasement gesture; 3. Any sudden, running movement by a member of the colony during feeding or sunbasking periods which immediately elicited flight towards shelter from all other members, even without an accompanying sharp bark.

6. GENERAL DISCUSSION AND CONCLUSIONS

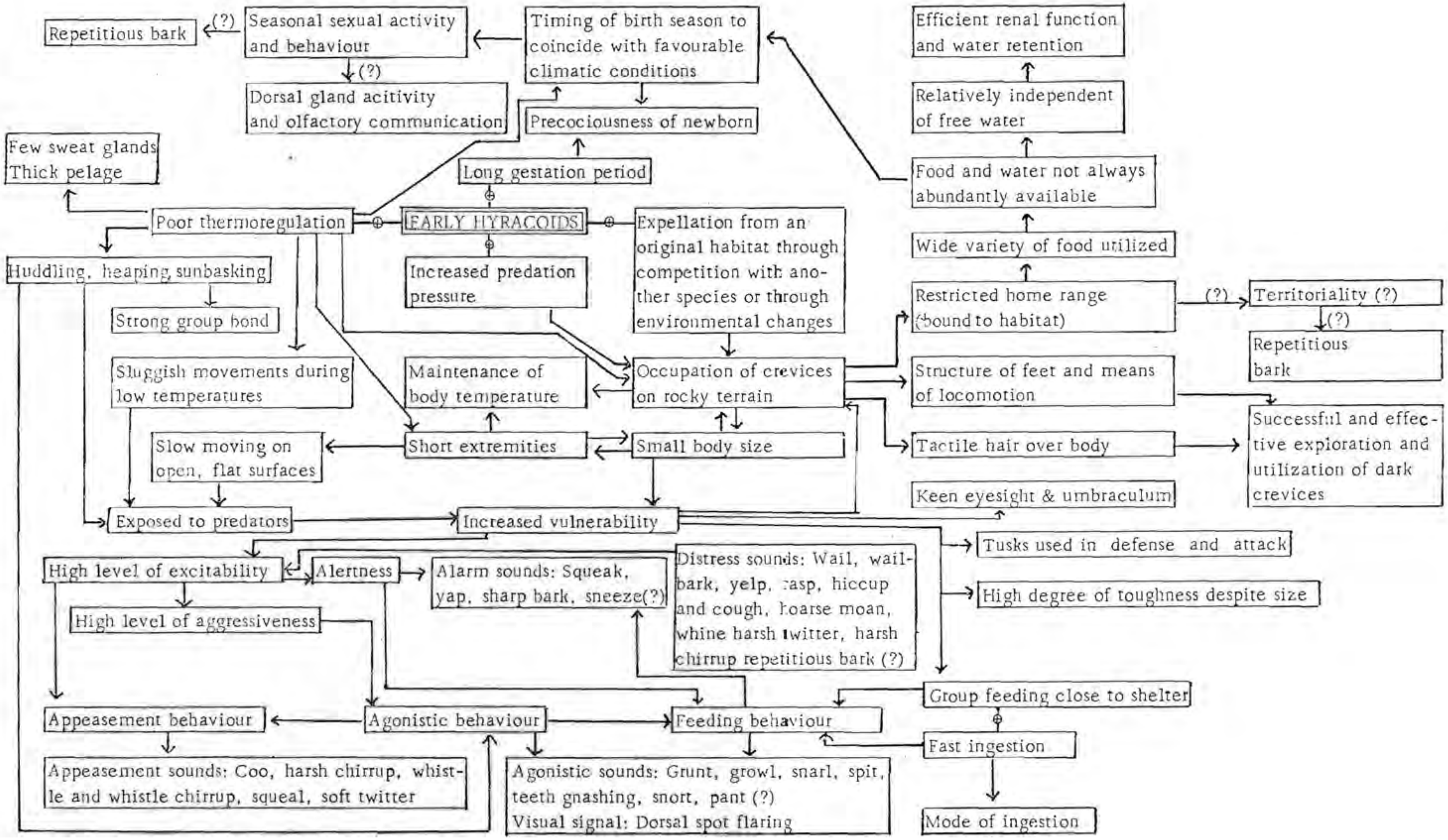
The results presented and discussed in the preceding pages necessitate some concluding remarks about the possible origin and evolutionary development of the communication system and general social behaviour patterns in the rock dassie in relation to its ecological requirements.

In view of the arguments of Crook (1970), it is important to distinguish between two types of evolutionary processes, that of natural selection and social selection, which both act as major sources of biological modification. Petrucci (1906, In: Crook 1970) concluded that spatial dispersion, group composition and relations between individuals were directly responsive to the environment and that the factors programming the system included such features as food supply, predation and the requirements for sexual reproduction in differing habitats. In reaction to Petrucci's reasoning Crook stresses the importance of socio-ecology and remarks that "Social structure as a group characteristic ... is a dynamic system expressing the interactions of a number of factors within both the ecological and the social milieux that influence the spatial dispersion and grouping tendencies of populations within a range of lability allowed by the behavioural tolerance of the species ... Because a major requirement for biological success is for the individual to adapt to the social norms of the group in which it will survive and reproduce it follows that a major source of genetic selection will be social..." With this in mind the general social behaviour patterns of the dassie, of which communication in general forms an integral part, are taken as resulting from the demands imposed on them by certain morphological and physiological features (such as small size and poor thermoregulation) as well as environmental and ecological conditions (such as fluctuations in availability of food, predation pressure, etc.) with which the animals have to cope in order to survive.

Figure 18 represents a summary of the events which might, in the course of hyracoid evolution, have given rise to the social structure, behaviour patterns and certain associated morphological and physiological features present in Procavia capensis. For obvious reasons this view can only be regarded as highly speculative and is therefore not intended to indicate the events which eventually led to the make-up of the modern dassie but rather to pose some questions.

As regards Fig. 18, two points need mentioning. Firstly, it was necessary to make some assumptions as to the probable characteristics of the early giant hyracoids (there probably was a progressive decline in size towards modern forms), some of which were presumably retained in present-day forms. Poor thermoregulation and a long gestation period on the physiological side and, on the ecological side, the occupation and utilization of crevices in rocky outcrops probably resulted from increased predation pressure, interspecific competition for a specific niche or environmental changes such as suggested by Turner and Watson (1965). Secondly, any diagramatic presentation of probable evolutionary events is bound to falsify their true temporal distribution, and even more important, the interrelationships of these events when they are viewed independently of each other as singular forces functioning at any specific point in time. It is therefore important to view Fig. 18 in totality rather than along isolated lines.

As already suggested, poor thermoregulation was probably a feature of the early hyracoid stock and was retained in recent forms. Adaptations to cope with this problem may thus be expected to have arisen quite early in the evolutionary history of the dassie. The possible routes which might have been taken include physiological selection for better thermoregulation, and/or morphological and behavioural adaptations to cope with the problem of maintaining a constant body temperature. Taylor and Sale (1969) and other workers found that the dassie in fact does possess the usual physiological


Repetitious bark
(?)
Seasonal sexual activity and behaviour
(?)
Dorsal gland acitivity and olfactory communication
Timing of birth season to coincide with favourable climatic conditions
Precociousness of newborn
Efficient renal function and water retention
Relatively independent of free water
Food and water not always abundantly available
Few sweat glands Thick pelage
Long gestation period
Poor thermoregulation
EARLY HYRACOIDS
Expellation from an original habitat through competition with another species or through environmental changes
Wide variety of food utilized
Huddling, heaping sunbasking
Increased predation pressure
Restricted home range (bound to habitat)
(?)
Territoriality (?)
(?)
Repetitious bark
Strong group bond
Sluggish movements during low temperatures
Maintenance of body temperature
Occupation of crevices on rocky terrain
Structure of feet and means of locomotion
Successful and effective exploration and utilization of dark crevices
Slow moving on open, flat surfaces
Short extremities
Small body size
Tactile hair over body
Keen eyesight & umbraculum
Exposed to predators
Increased vulnerability
Tusks used in defense and attack
High degree of toughness despite size
High level of excitability
Alertness
Alarm sounds: Squeak, yap, sharp bark, sneeze(?)
Distress sounds: Wail, wail-bark, yelp, rasp, hiccup and cough, hoarse moan, whine harsh twitter, harsh chirrup repetitious bark (?)
High level of aggressiveness
Group feeding close to shelter
Appeasement behaviour
Agonistic behaviour
Feeding behaviour
Fast ingestion
Appeasement sounds: Coo, harsh chirrup, whistle and whistle chirrup, squeal, soft twitter
Agonistic sounds: Grunt, growl, snarl, spit, teeth gnashing, snort, pant (?)
Visual signal: Dorsal spot flaring
Mode of ingestion

mechanisms for regulating their temperature but to aid these mechanisms bask in the sun to warm up or increase evaporation in the heat by panting, salivating and grooming. Louw et al. (1972) suggested that dassies, by means of their well-defined behaviour pattern, particularly cyclic feeding behaviour, avoid the stress of high ambient temperature and low humidity by retreating to the protective micro-climate of rock crevices. As a result, selection pressure for superior thermoregulation at high atmospheric temperatures has been largely absent and the animals are poor thermoregulators from the physiological viewpoint. Louw et al. (1972) conclude that the sunbasking, resting and feeding behaviour pattern of the dassie, supported by efficient renal function, possibly were the main contributing factors to its success.

Sunbasking and shade resting during the hot hours of the day to help overcome the problem of maintaining a fairly constant body temperature, and conservation of body heat during low ambient temperatures (e.g. during the night or early morning) through huddling and heaping behaviour certainly would have been advantageous. This largely might have contributed to the development of a strong group instinct. In addition to the development of a thick pelage, few sweat glands and short extremities restrained unnecessary loss of body heat through radiation and sweat evaporation. At the same time, however, these attained features would have hampered the loss of excessive body heat during high ambient temperatures and compensating characteristics were necessary.

It was shown by Taylor and Sale (1969) and Louw et al. (1972) that the dassie possesses a fairly low heat tolerance and makes use of additional features to guard against body temperature rising too high. These are shade resting and occasional retreat to the crevices where ambient temperature is considerably lower than outside on hot days (Sale 1966b;

Bartholomew and Rainy (1971) sweat evaporation from the surface of the foot-soles to which sweat glands are restricted (Sale 1970a; Barholomew and Rainy 1971) and panting, salivation and grooming under extremely high ambient temperatures (Taylor and Sale 1969; Louw *et al*. 1972). The restriction of sweat glands to the footsoles had the advantage that it can be exposed to the air when necessary or otherwise held flat against the ground or rock when loss of heat through sweat evaporation was not desireable. Sale (1966b) and Bartholomew and Rainy (1971) showed that the ambient temperature inside crevices varies fairly little if compared with that outside the crevices and favours the maintenance of a constant body temperature by the dassie. This favourable condition in combination with interspecific competition and increased predation pressure might have contributed to selection pressure eventually leading to dassies occupying rocky outcrops and utilizing existing crevices.

Turner and Watson (1965), however, explain the evolution of the kopje-dwelling habit in rock and tree dassies as follows: "... we consider Hyracoidea to have been originally forest-dwelling, as is the present-day *Dendrohyrax validus*. At some stage, possibly as the forest started to give way to woodland, a form took to grazing and lost some forest dwelling features. As the forests continued to recede, this woodland hyrax, already separated from the forest forms in diet and habits, became confined to the small islands of forest and woodland associated with kopjes. The change involved from living in hollow tree trunks to living in rock crevices would not seem to be great.

"At the same time arboreal forms, initially quite different in habits from the ground-living hyrax, became confined to kopjes and developed the same adaptations for kopje life. So the arboreal and groundliving hyrax reconverged. But no convergence of diet or feeding habits took place because space considerations inside the kopje never allowed populations to put pressure on the food resources.

"The authors consider the separation of diets and feeding habits to be so pronounced as to be unlikely to have arisen from food competition in the past".

The dassie's sluggish movement during low temperature (especially noticeable in the early morning) together with a decline in body size which might have accompanied shortening of the extremities as the result of a need to use the more abundantly available smaller crevices for shelter (Sale 1966a) certainly made the dassie more vulnerable and thus easy prey for a larger number of aerial and other predators when they huddled, heaped, sunbasked or fed away from the crevices. A number of features present in the dassie might at least partly have evolved as a consequence of increased vulnerability. These include a high degree of toughness despite their small size, keen eyesight and sharp constantly growing upper incisors which are their sole means of active defense against predators and for attack in intraspecific agonistic situations. In addition, sunbasking left the dassie wide open to aerial attacks from various birds of prey, such as the black eagle (Aquila verreauxi) which preys mainly on dassies (Brown 1963; Visser 1963). The light-shielding umbraculum in the eye of the dassie (probably contributing to spotting birds of prey approaching from the direction of the sun) is suggested by Millar (1973) to have evolved in response to a selection pressure resulting from predation by raptorial birds. In this regard the advantage of being able to keep the eyelids open without the possibility of damaging the eyes when looking directly into the sun, is evident. Probably as a result of this adaptation the dassie never blinks its eyelids, the quick wetting of the eyes by a nictitating membrane being sufficient.

Behaviour patterns which probably acquired their characteristic structure as a result of increased vulnerability of the dassie outside the crevices are feeding behaviour, watchfulness and agonistic behaviour. Feeding is performed as close to shelter as possible and although individuals may feed intermittently during any time of the day, two main group feeding times occur which in turn are characterized by the fast ingestion of large amounts of food over a short period, thereby limiting exposure to predators.

Watchful behaviour in the dassie is especially noticeable during group feeding sessions and when they recline on the rocks. Increased vulnerability probably led to a general rise in alertness which, together with the development of an efficient alarm system through warning signals such as the sharp bark, became useful during times of exposure to possible attacks by predators.

Another result of an increase in vulnerability could have been a rise in the general level of excitability in the dassie which might have led to a higher level of aggressiveness. Fixation of a high level of aggressiveness, together with the imposed close contact during heaping and huddling, might then have resulted in an outspoken intraspecific agonistic behaviour in the dassie. Of this the well-defined appeasement behaviour patterns bear evidence which probably was a direct consequence of the development of intraspecific aggression (Sale 1970a). The general lack of social grooming, restricted play behaviour, loose mother-infant bond and the mechanisms operating to keep animals spaced apart during feeding to avoid fighting, stress the important effect of a high level of intraspecific agonism on the social behaviour of the dassie.

The occupation of crevices on rocky terrain by early hyracoids necessitated a number of adaptations in order to utilize their new environment effectively. As already mentioned, the extra safety ensured by small crevices which barred large predators entering it, might have contributed to the dassie acquiring its small body size. Two other morphological features which probably arose as a result of their utilization of crevices are the long tactile hair over the whole of the body which facilitated effective exploration of their underground habitat (Sale 1970b), while the general structure of the feet made swift and agile movements over rough rock surfaces possible.

Since the dassie does not dig tunnels but makes use of natural crevices for shelter from which it never ventures far, it is largely bound to its habitat. This restriction in home range probably led to the dassie acquiring a taste for a wide variety of plant food (Sale 1965c; Turner and Watson 1965). In spite of this, however, food and water within the limits of their home range usually are not always abundantly available during all seasons of the year and the dassie consequently grew relatively independent of free water. This fact is amplified by their extremely efficient renal function which allows for maximum water retention under such conditions (Louw 1971). Another important adaptation which probably arose in connection with scarcity of food during certain times of the year is the timing of the birth season to coincide with early summer after the first rains when food again becomes available in sufficient quantities. This, together with the general advantages of favourable climatic conditions on thermoregulation and thus on the survival of newborn dassies, are most likely the main reasons for the development of the dassie's seasonal sexual activity and associated behaviour as was also concluded by Sale (1969). Millar (1971) and Millar and Glover (1973), however, showed that birth takes place in the summer throughout South Africa, although there is a complete reversal of rainfall season from winter in the Cape to summer in the Transvaal. This fact does not entirely support the above mentioned ideas and shows that the timing of the birth season is perhaps not primarily concerned with the provision of food to newborn dassies.

The precociousness of the newborn dassie probably is the result of an interaction between increased vulnerability and the timing of the birth season which led to the assumedly long gestation period of the early hyracoids being retained.

Sounds and other signals used by the dassie in communication as part of its social behaviour patterns probably largely arose as a result of an increase in the level of excitability through increased vulnerability. It is, however, interesting to note that the most extensive means of information transfer by the dassie is made through the auditory channel if compared with other possible channels. This fact strongly suggests that communication channels other than the auditory channel (i.e. tactile, olfactory and visual channels) were only brought into operation during the evolution of the dassie where they could serve a certain purpose better and more effectively than by acoustic means.

Visual communication is restricted to dorsal spot flaring and a few characteristic postures, all connected with agonistic behaviour during feeding or defense as described in the previous chapter. Olfactory communication functions in reproductive behaviour and mother-infant relationship through the scent of a secrete produced by the dorsal gland (especially noticeable during the mating season) and also in the "greeting ceremonies" when two dassies briefly sniff each other in the nasal regions in the course of an encounter when leaving or entering the entrance to a cavity. The evolutionary development and consequent use of the dorsal spot in dassie communication pose somewhat of a problem, largely because their functions in social behaviour remain obscure. These two morphological features probably evolved to serve a wider function in the early hyracoids and were only retained in the modern dassie to provide reinforcement, perhaps in a minor way, to certain visual signals (postures) and acoustic signals. Tactile communication is concerned with the maintenance of distance between individuals during feeding through use of the tactile vibrissae distributed over the whole body and, although not in the true sense of communication, also with exploration of crevices. This form of communication otherwise involves extremely subtle signals commonly in operation whenever physical contact is made with another animal. It is for this reason that tactile communication is difficult to detect and thus probably immensely underrated as far as its complexity and importance are concerned. Since the mode of life of the dassie necessitated the main emphasis to be placed on acoustic communication it is perhaps not surprising that this means of information transfer became fairly comprehensive and diversified (see Table 2 and discussion of sounds in Chapter 4).

Furthermore, the nature and function of behaviour patterns and signals in all communication channels employed by the dassie feature the common characteristic of drawing as little attention to any participant as possible, unless advertising over a large distance is the actual goal. Of all the identified signals in the dassie only the sharp bark, repetitious bark and in some species with a white or yellow dorsal spot (e.g. *P. johnstoni mackinderi* or *Dendrohyrax arboreus*) the flaring of the dorsal spot are observable over a considerable distance. The sharp bark advertises in a to-whom-it-may-concern manner the presence and severity of potential danger, eliciting head-long flight to shelter from all members of the colony. This acoustic signal is probably reinforced by the flaring of the dorsal spot in such situations. It may therefore benefit the safety of the animals while simultaneously performing its secondary function of restraining intragroup agonism. The causation and function of the repetitious bark is still unclear and speculations ~~in~~ regarding its evolutionary development will thus not be ventured into.

In an overall view of the dassie, its ecological requirements and mode of life, it is indeed interesting to note that this group so successfully inhabited, survived and diversified over almost the whole of the African continent and Syria, despite the morphological, physiological and ecological limitations imposed on these animals. Their success evidently stems from adaptations which, without resulting in overspecialization, allowed them to utilize their environment effectively and also to readily adapt to changing or generally unfavourable environmental conditions, even if a fair amount of their normal requirements are not met during such a change as was shown by their easy acceptance of captivity or occupation of untraditional soil fissures in an erosion gully (Fig. 1) in order to utilize new food sources close by.

The dassie's unspecialized ways, although complex in structure are moreover reflected in its behaviour and communication patterns which are fairly generalized and contextual rather than specific and discrete in meaning and execution. This is perhaps one of the reasons which contributed to the dassie for many years being regarded as uninteresting and therefore largely ignored since its description and introduction to the scientific world by Pallas (1766). Fortunately the past four decades showed an upsurge of interest in this peculiar animal and many investigators were rewarded with excellent research results which formed the basis for this and other studies.

SUMMARY

The acoustic communication and social behaviour of a colony of captive rock dassies were investigated for various lengths of time between April 1971 and October 1972 in an enclosure at Naudéskop-Oost, 24 km northwest of Bethlehem, O.F.S. The animals were then transferred to an enclosure in the Zoology Department, University of Pretoria and kept under observation until March 1974.

Acoustic communication, if compared with visual, olfactory and tactile systems also utilized by the dassie, constitutes the most important, complex and widely used means of information transfer. An analysis of the physical characteristics of the sounds showed that the vocalizations are interrelated and form a continuum of sound. Within this continuum, however, there exists 21 fairly distinct vocal sounds which are linked through intermediate variations and combinations. The four nonvocal sounds identified are unrelated and discrete.

None of the sounds of the dassie is characteristic of any particular situation but occurs also in other, sometimes seemingly quite unrelated situation types. Most sounds are nevertheless more characteristic of a certain situation than another but not restricted to it. This gave rise to the suggestion that the elicitation and type of sound given depend on the level of excitement (usually the result of a frustration situation) experienced by an animal and the amount of interest affixed to a particular stimulus. If the stimulus interest is high, the level of excitement rises in consequence and the sounds given in response tend to be of high amplitude, high pitch and long duration. The opposite also holds true.

Observations on the ontogeny of dassie sounds showed that infants possess only five sounds, three vocal and two

nonvocal. Between two and 15 months of age, i.e. during juvenilehood, all other sounds appear except the five vocal sounds characteristic of adult females and one vocal sound given only by sexually mature males. The infant dassie also makes no use of combination sounds whereas juveniles and adults, in addition to acquiring a large number of new sounds, enlarge their repertoire through combinations and intermediate sounds. It is concluded that there probably is an important shift in stimulus interest from the infant to the juvenile age group, likely to be the result of the number of novel stimuli presented to the juvenile upon leaving the shelter of the cavities.

The dassie is generally very aggressive and shows threat behaviour in the form of dorsal spot flaring, grunting, growling, snarling and biting under most circumstances involving close contact between conspecifics. A well-defined pattern of appeasement behaviour through body postures, squeals, whistle chirrups and harsh chirrups makes it possible for the animals to feed close together or huddle and heap.

When exposing themselves to potential attacks by predators during feeding periods or when sunbasking on the rocks, dassies display a general alertness and watchfulness. Alarm signals in the form of squeaks, sharp barks and sudden running movements elicit immediate flight towards shelter by all members in the colony.

Seasonality as regards reproduction is evidenced by their mating behaviour which occurs between January and July, reaching a peak during late March to early April. During this time the incidence or rival fighting between sexually active males is markedly higher than at any other time of the year and often results in the death of a number of them. The dorsal gland also functions optimally during this time and probably plays an important role in the identification and location of a female by a male.

The gestation period is around seven and a half months and parturition occurs in early summer. Infants are precocious and relatively independent of the mother at birth. The climbing of the infant onto the mother's back soon after birth probably plays an important role in the association of the newcomer with the mother and also with the group, apart from preparing the infant for adult watchfulness. The mother-infant bond is, however, weak. Infants are weaned within three to five months. Although juveniles are inquisitive in nature, they exhibit an almost complete lack of play behaviour.

Adults show a tendency to space out evenly over the available area and select their individual sunbasking or resting spots. These spots are each occupied permanently by the same animal during these activities. Inside the sleeping box, however, they all huddle in a corner and no spot selection is evident. During low temperatures dassies huddle or heap and only move off to their individual spots when the ambient temperature becomes tolerable.

Two group feeding periods are recognized, one in the early morning and the other in the late afternoon. Casual feeding by individuals, however, often takes place during any time of the day but the amount of food ingested is considerably less than during group feeding periods.

It is concluded that the social behaviour patterns, of which acoustic and other communication processes form an integral part, probably arose as a result of the demands imposed on the dassie by certain morphological and physiological features as well as environmental and ecological conditions with which the animals have to cope in order to survive. Of these poor thermoregulation, diminished size and crevice dwelling probably were the most important selective forces in action during the evolutionary development of the hyracoid group which eventually resulted in the mode of life exhibited by the present-day rock dassie.

OPSOMMING

'n Ondersoek na die akoestiese kommunikasie en sosiale gedrag van klipdassies in gevangenisskap is uitgevoer met tussenperiodes van wisselende duur vanaf April 1971 tot Oktober 1972 in 'n kamp op Naudêskop-Oost, 24 km noordwes van Bethlehem, O.V.S. Die diere is daarna oorgeplaas na die Departement Dierkunde, Universiteit van Pretoria en verder bestudeer tot Maart 1974.

Akoestiese kommunikasie, indien vergelyk met visuele, olfaktoriese en tassisteme ook deur die dassie benut, omvat die mees belangrike, komplekse en dikwels gebruikte wyse van inligtingsoordrag. 'n Ontleding van die fisiese eienskappe van die geluide toon dat die vokalisasies onderling verwant is en 'n klankdeurlopendheid vorm. Binne hierdie deurlopendheid bestaan daar egter 21 taamlik duidelik onderskeibare vokale geluide wat aan mekaar geskakel word deur intermediêre variasies en kombinasies. Die vier nie-vokale geluide geïdentifiseer, is onverwant en vorm elk 'n onafhanklike eenheid.

Geen een van die geluide van die dassie is kenmerkend van enige besondere situasie nie maar kom ook in ander, soms klaarblyklik heel onverwante situasies voor. Meeste geluide is nietemin meer kenmerkend van 'n sekere situasie as van 'n ander maar is nie beperk tot daardie situasie nie. Dit het aanleiding gegee tot die gedagte dat die ontlokking van en die tipe geluid gegee op die graad van opgewondenheid (gewoonlik die gevolg van 'n frustrasie situasie) wat deur die dier ondervind word, berus asook op die mate van waarde wat die dier aan 'n besondere prikkel heg. Indien belangstelling in die prikkel hoog is, styg die graad van opgewondenheid in ooreenstemming en die geluide wat daarmee gepaard gaan, neig om 'n hoë amplitude, hoë frekwensie en lang duurte te toon. Die teenoorgestelde is eweneens waar.

Klein dassies uiter tot op die ouderdom van twee maande slegs vyf geluide, drie vokaal en twee nie-vokaal. Tussen twee en 15 maande ouderdom tree al die ander geluide tevoorskyn behalwe die vyf vokale geluide kenmerkend van volwasse wyfies en een vokale geluid eie aan geslagsrype mannetjies. Heel klein dassies maak ook nie gebruik van kombinasie geluide nie terwyl jong en volwasse dassies, bykomend tot die verkryging van 'n groot aantal nuwe geluide, hulle repertoire vergroot deur die gebruik van kombinasies en intermediêre geluide. Die gevolgtrekking word gemaak dat daar waarskynlik 'n belangrike verskuiwing in prikkelbelangstelling vanaf die klein- tot die jong-dassieouderdomsgroep plaasvind en dat dit die gevolg is van die aantal nuwe prikkels waarmee die jong dassie vir die eerste keer in aanraking kom sodra hy die veiligheid van die skeure verlaat.

Dassies is oor die algemeen baie aggressief en toon dreigende gedrag deur oopswaaiing van die dorsale kol, grom-, knor- en snougeluide te uiter of selfs te byt onder omstandighede waar noue kontak tussen dassies plaasvind. 'n Goedgedefinieerde patroon van kalmeringsgedrag deur liggaamshoudings, klageluide, fluit-runnike en harde runnike maak dit moontlik dat die diere naby mekaar kan vreet of teen- en oormekaar kan lê.

Wanneer dassies tydens voedings- of sonbakperiodes hulself aan moontlike aanvalle deur roofdiere blootstel, toon hulle 'n algemene wakkerheid en waaksaamheid. Waarskuwingstekens in die vorm van piep- en blafgeluide asook vinnige hardloopbewegings ontlok onmiddelike vlug na veiligheid in al die lede van die kolonie.

Seisoenaliteit betreffende voortplanting word aangetoon deur hulle paringsgedrag wat tussen Januarie en Julie plaasvind en 'n piek bereik gedurende laat Maart tot begin April. Gedurende hierdie tyd is die insidensie van mededingingsgevegte tussen geslagtelik aktiewe mannetjies merkbaar hoër as gedurende enige ander tyd van die jaar en lei dikwels tot die dood van 'n hele paar. Die dorsale klier funksioneer ook optimaal gedurende hierdie tyd en speel waarskynlik 'n belangrike rol in die identifikasie en lokalisering van 'n wyfie deur 'n mannetjie.

Die draagtydperk is ongeveer sewe en 'n half maande en parturisie vind in die vroeë somer plaas. Pasgebore dassies is prekosiaal en relatief onafhanklik van die moeder. Die kleintjie klim kort na geboorte op die moeder se rug, 'n gedragspatroon wat waarskynlik 'n belangrike rol speel in die vereenselwiging van die nuweling met sy moeder asook met die res van die groep. Dit dra moontlik ook by tot voorbereiding van die jongeling vir volwasse waaksaamheid. Die moeder-kleintjie verhouding is egter baie los. Klein dassies word binne drie tot vyf maande na geboorte gespeen. Alhoewel jong dassies baie nuuskierig van natuur is, toon hulle feitlik volkome afwesigheid van speelgedrag.

Volwasse dassies toon 'n neiging om eweredig oor 'n beskikbare ruimte te versprei en elkeen 'n eie sonbak- of ruslêplek uit te soek wat permanent slegs deur homself besoek word. Binne die slaapkas lê hulle egter almal teenmekaar in 'n hoek en tree nie selektief op ten opsigte van lêplek nie. Gedurende lae temperature kruip dassies styf teenmekaar en beweeg slegs na hulle onderskeidelike lêplekke wanneer die omgewingstemperatuur draaglik word.

Twee gesamentlike voedingsperiodes kan herken word, een in die vroeë oggend en die ander in die laat middag. Individue mag egter gedurende enige tyd van die dag voed maar die hoeveelheid voedsel so ingeneem is heelwat minder as gedurende die gesamentlike voedingsperiodes.

Die gevolgtrekking word gemaak dat die sosiale gedragspatrone waarvan akoestiese en ander kommunikasieprosesse 'n integrale deel vorm, waarskynlik ontstaan het as gevolg van sekere morfologiese en fisiologiese eienskappe asook omgewings- en ekologiese toestande waarmee die diere moet kan saamleef om sodoende te kan voortbestaan. Onder hierdie is swak hitteregulering, verminderde liggaamsgrootte en 'n lewenswyse in rotsskeure waarskynlik die mees belangrike selektiewe kragte wat in werking was gedurende die ewolusionêre ontwikkeling van die Hyracoidea en wat uiteindelik oorsprong gegee het aan die lewenswyse van die hedendaagse klipdassies.

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ADDENDUM

Following discussion of this study with Prof. A. Alexander and Dr R.P. Millar, it was considered necessary to further clarify and support some of the statements made in the foregoing text. My thanks are due to them for advice on this matter.

The following questions are dealt with here:

1. How representative are the spectrograms selected to illustrate the different Procavia capensis sounds?

2. How are the sounds interrelated to form a continuum?

3. Can the statement that there is a tendency for the frequency and amplitude of the sounds to increase with increase in excitement (and vice versa) be quantitatively supported?

From the tape recordings and general observations on dassie sounds, it became apparent that some degree of variation in sound production and utilization exists among individual dassies. For that reason each sound recorded on tape was listed against the individual which emitted the sound and was temporarily assigned a name, e.g. grunt, growl-squeal, whistle, etc. A particular sound name (e.g. grunt) was then selected and two examples of the sound as performed by each individual dassie on different occasions, were spectrographically analysed. These spectrograms were visually inspected and the structural appearance most regularly displayed was consequently regarded as representative of the sound. The spectrogram closest resembling this general appearance was thus used for analytical and demonstrative purposes (see also p. 16). Following this procedure with all the sounds, every sound was again judged against the representative sound and permanently named or renamed if necessary. In this way intermediate sounds, i.e. sounds falling outside the range of individual variation but still displaying features of the distinct sounds, could also be determined. The intermediate sounds pointed to a gradual change from one structural sound type to the next, i.e. a continuum of sound. Along this continuous line stages could be recognized where enough significant changes in structure (mainly in amplitude, frequency, length and tonality) were present to regard any stage as distinctly different from previous stages. These stages were regarded as distinct sounds, the interrelationships of which are illustrated in Fig. 19.

In Fig. 20 the frequency, amplitude and level of excitement associated with each dassie sound are compared. Although not strictly applicable to all dassie sounds, the general tendency for a higher level of excitement to be characterized by sounds showing a higher frequency and/or amplitude, is clearly illustrated. The similarity between the level of excitement and amplitude is especially noticeable. The amplitude categories (low, medium low, medium, medium high and high) were judged by ear according to relative loudness while the same categories for the levels of excitement were, according to the amount of locomotor and vocalizing activities involved, determined as follows:

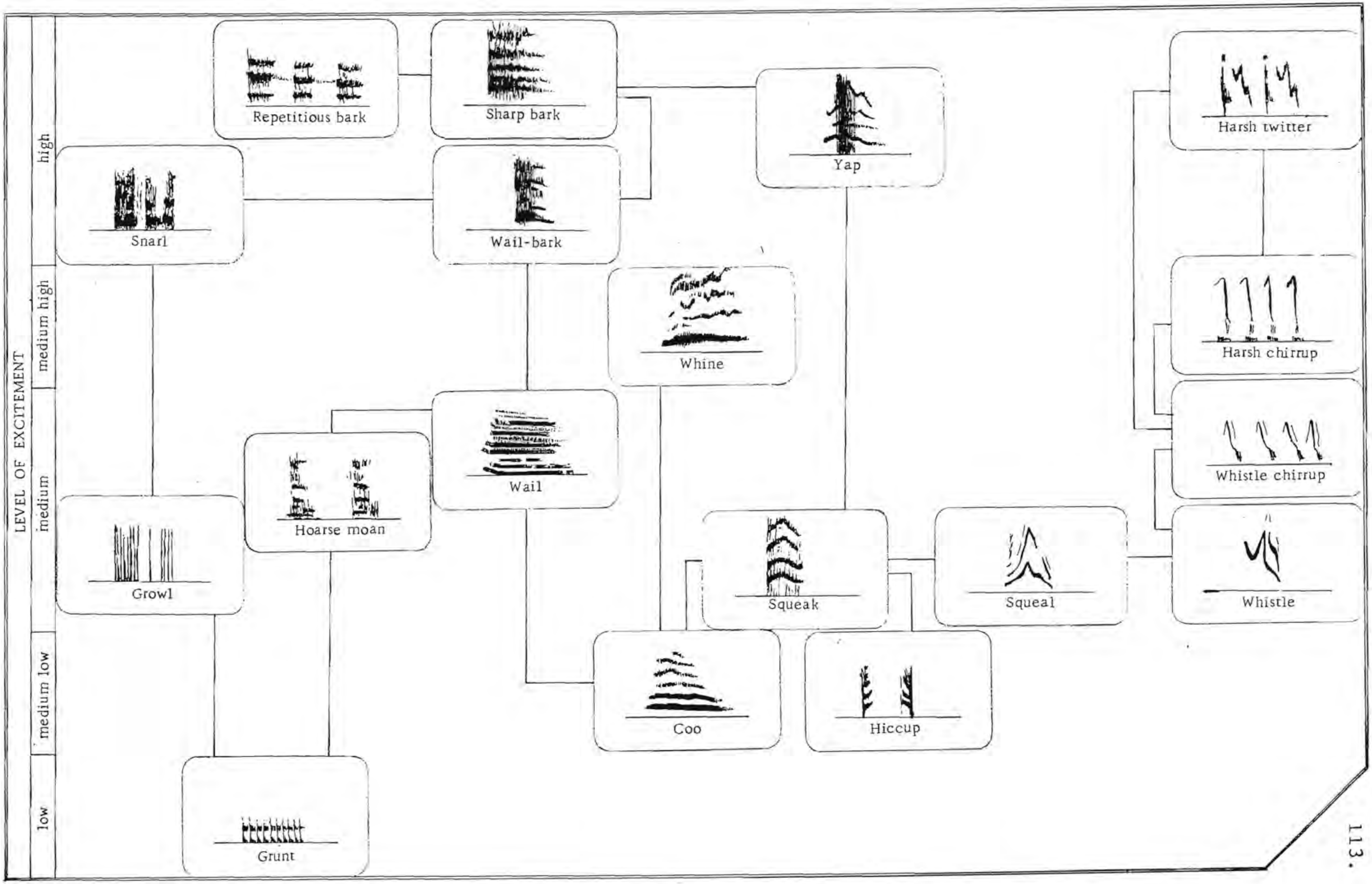
Low: Animal fairly relaxed, lying down or standing still. Casual raising or turning of the head in the direction of the stimulus, ears relaxed. Very little vocalizing activity.

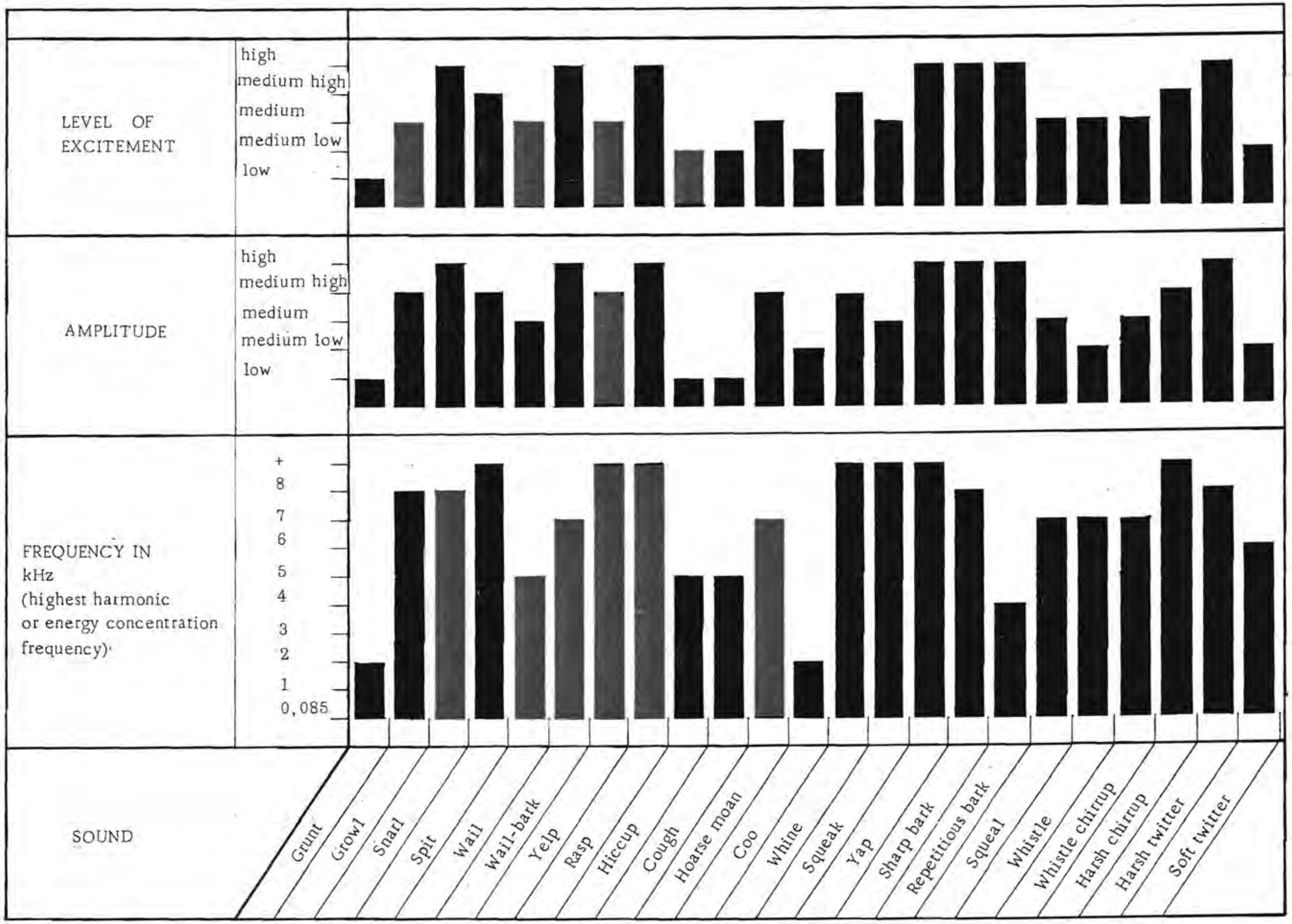
Medium low: Walking or casual feeding. Slight alertness indicated by frequent ear pricking or looking directly at the stimulus. Little vocalizing activity.

Medium: Increase in postural tonus, arching of back, raised head, body raised high on legs, dorsal spot flaring, retraction of upper lip, ears drawn flat against head. Jumping and moderately fast running over a short distance (usually not more than one or two metres). Increase in vocalization activity.

Medium high: Rapid locomotion over short distances and for short periods. Increase in vocalization activities with sounds repeated more often and at higher amplitudes.

Figure 19: Schematic illustration of the interrelationships of the adult *Procavia capensis* vocal sounds based solely on physical characteristics. It is suggested that these sounds form part of a continuum and that the level of excitement experienced by an animal in response to a particular stimulus determines the type and structure of the sound given. A rise in excitement does not necessarily imply that every sound along a particular line in the continuum will be given. Intermediate sounds, not included in the diagram, are represented by the interconnecting lines, which again does not imply pathways that have to be followed in situations, e.g. where the level of excitement rises or decreases.


LEVEL OF EXCITEMENT
high
medium high
medium
medium low
low
Repetitious bark
Sharp bark
Yap
Harsh twitter
Snarl
Wail-bark
Whine
Harsh chirrup
Wail
Hoarse moan
Whistle chirrup
Growl
Squeak
Squeal
Whistle
Coo
Hiccup
Grunt


LEVEL OF EXCITEMENT
high
medium high
medium
medium low
low
AMPLITUDE
high
medium high
medium
medium low
low
FREQUENCY IN kHz (highest harmonic or energy concentration frequency)
+
8
7
6
5
4
3
2
1
0,085
SOUND
Grunt
Growl
Snarl
Spit
Wail
Wail-bark
Yelp
Rasp
Hiccup
Cough
Hoarse moan
Coo
Whine
Squeak
Yap
Sharp bark
Repetitious bark
Squeal
Whistle
Whistle chirrup
Harsh chirrup
Harsh twitter
Soft twitter

High: Rapid locomotion for longer periods over greater distances. Maximum dorsal spot flaring, fighting and biting movements. Great vocalizing activity with more frequent repetition of sounds at high amplitudes and for longer periods.