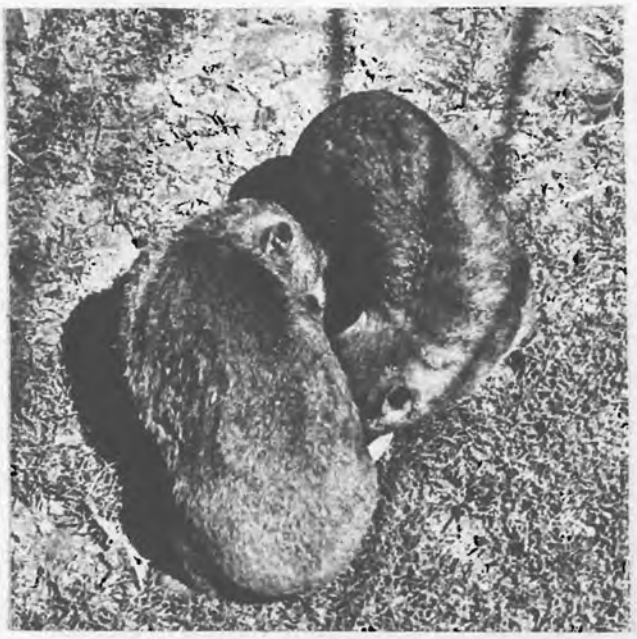
# V SOCIAL BEHAVIOUR OF PROCAVIA CAPENSIS IN CAPTIVITY

## 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.



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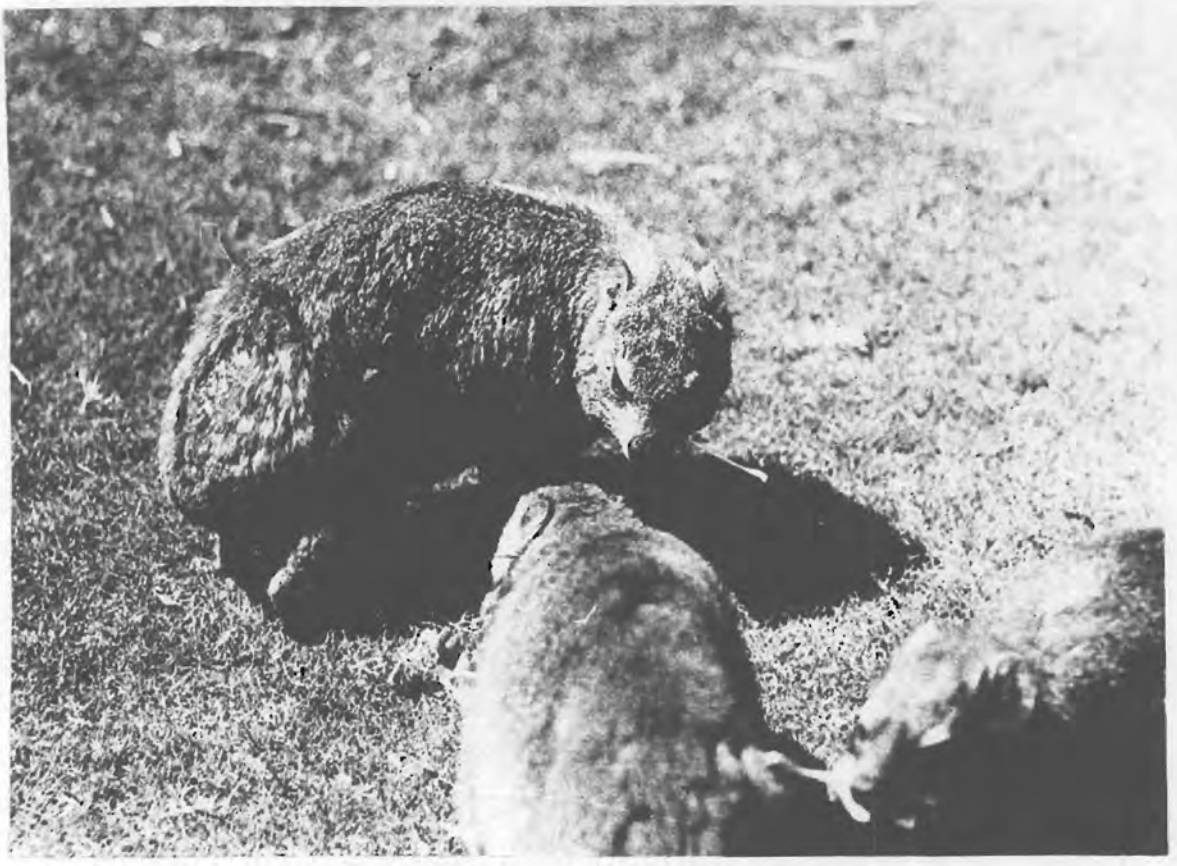

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When dassies feed as a group they disperse over the feeding area, facing away from each other. It sometimes happens that two or more animals, during the course of feeding, approach and try to eat the same portion of food. The result is the same as 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

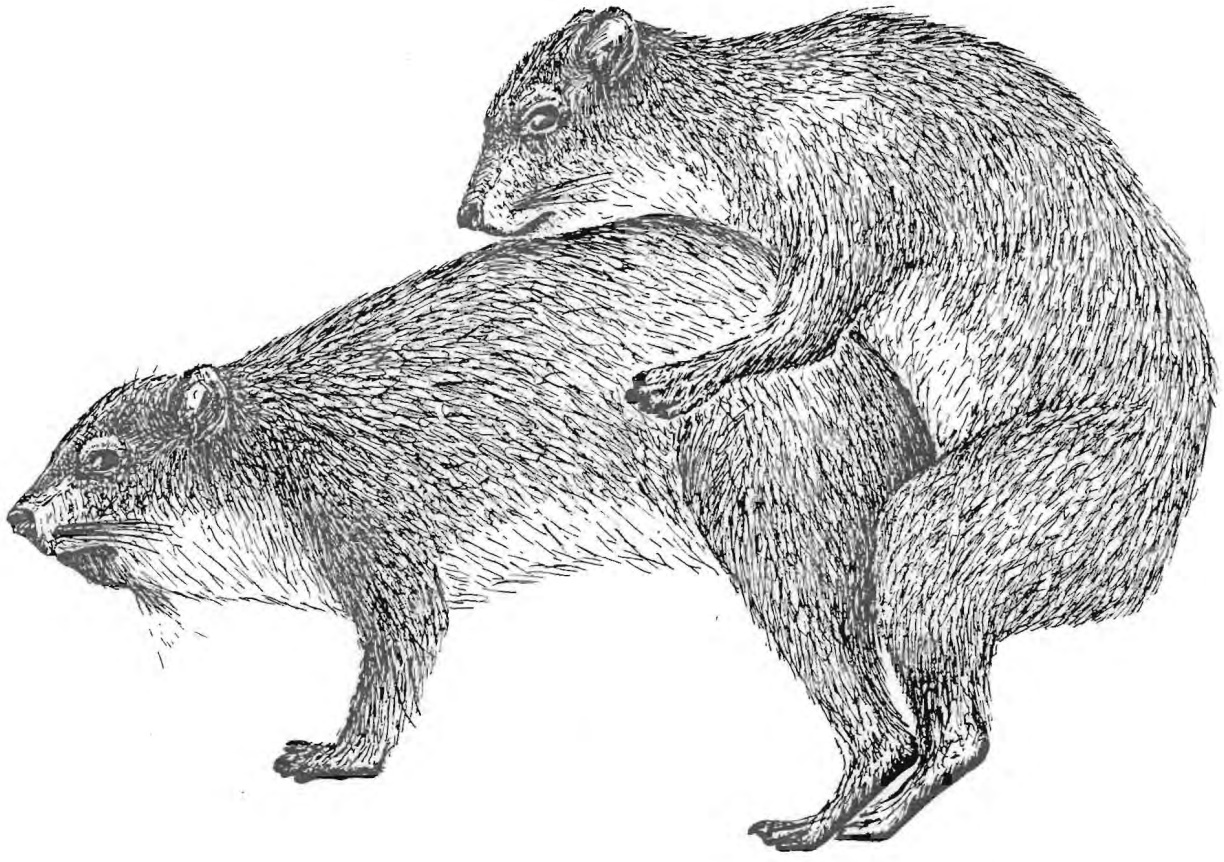
Figure 16: Aggressive and submissive postures assumed by P. capensis. A. Two dassies of equal status feeding from the same food container. Both animals' bodies are curved so that they can keep each other in sight while simultaneously each one is prepared to present its back in submission should the other 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 P. capensis. 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 foetuses. 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 placed 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 dislodged 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

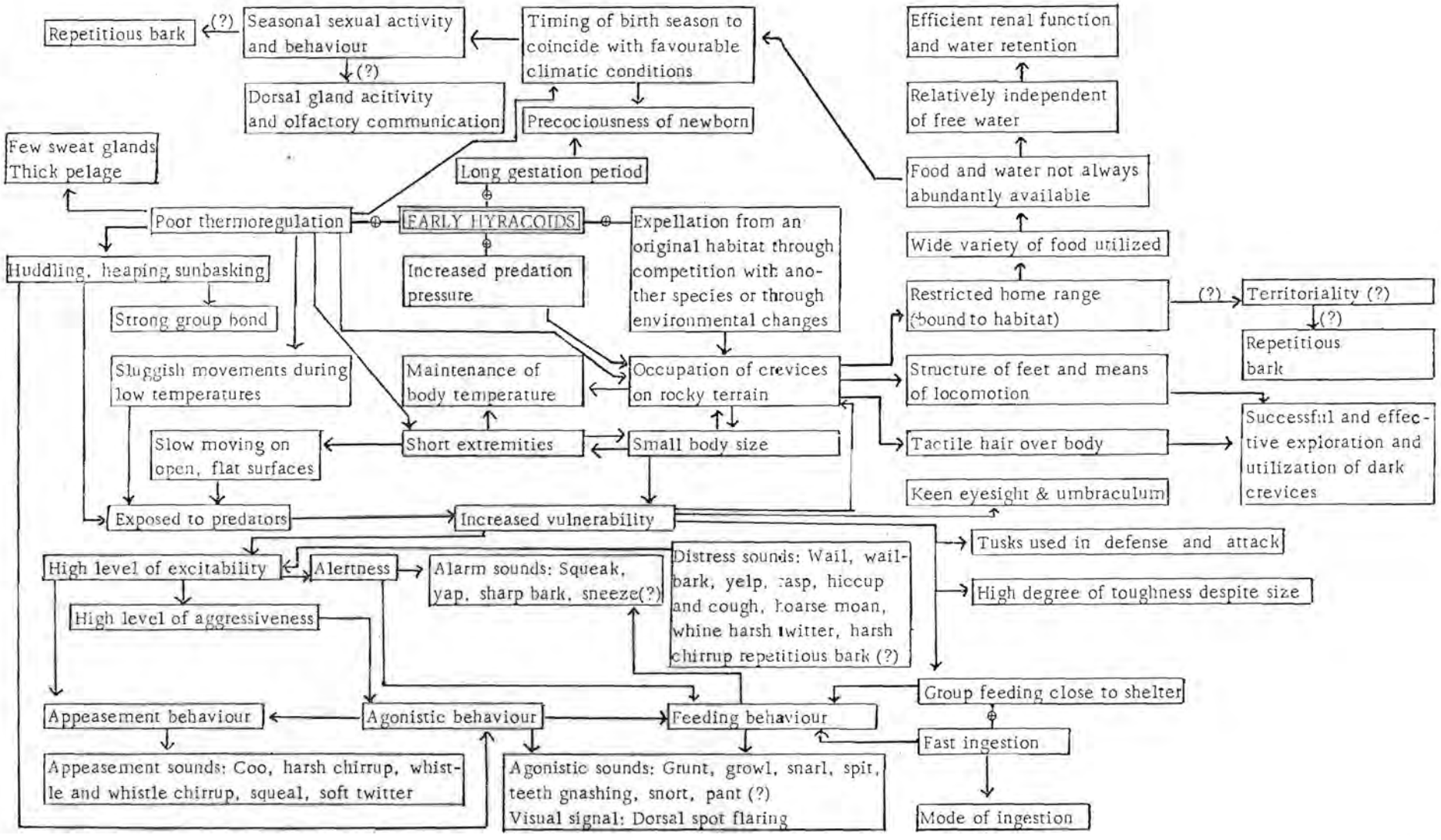
The results presented and discussed in the preceding pages necessitate some concluding remarks about the possible origin and evolutionary development of the communication system and general social behaviour patterns in the rock dassie in relation to its ecological requirements.

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



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 regarding of the repetitious bark is still unclear and speculations ~~in~~ 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 over-specialization, 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 Naudéskop-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 hitte-regulering, 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.