

Social behaviour and spatial relationships of the rock hyrax

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Hyraxes associate to form colonies consisting of a dominant territorial male, several adult females and sub-adults and juveniles of both sexes; a peripheral male(s) may be loosely associated with the colony. Five social castes are described. The territorial male monopolizes between three and 17 sub-adult and adult females but the fundamental social unit is the female-bonded group. The sex ratios of hyrax colonies are biased in favour of females, which is attributable to differential mortality and dispersal of sub-adult males. Both juvenile and adult dispersal occur but the former is more extensive. Agonistic interactions occur predominantly between males and are mainly concerned with changes in social rank and territorial defence.

Dassies verenig en vorm kolonies wat bestaan uit 'n dominante territoriale mannetjie, verskeie volwasse wyfies asook onvolwassenes en jongelinge van beide geslagte. 'n Periferale mannetjie(s) mag losweg aan die kolonie verbind wees. Vyf sosiale rolbesettings word verduidelik. Die territoriale mannetjie monopoliseer tussen drie en 17 volwasse en onvolwasse wyfies maar die fundamentele sosiale eenheid is die wyfiegebonde groep. Die geslagsverhouding van die kolonies is ten gunste van wyfies wat toegeskryf kan word aan differensiële mortaliteit en verspreiding van onvolwasse mannetjies. Beide jongeling en volwasse verstrooiing kom voor, maar eersgenoemde vind oorwegend plaas. Strydlustige interaksies vind hoofsaaklik tussen mannetjies plaas as gevolg van verandering in sosiale status en verdediging van territoriums.

Keywords: Behaviour, dispersal, dominance hierarchies, group size, rock hyrax

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Introduction

Local environment can modify the expression of behavioural characteristics of a species so that distinct populations may show different behavioural patterns under different environmental selection pressures (Delany & Hapold 1979). This implies that studies on the behaviour of mammals should be area specific, while results obtained for a particular species will not necessarily apply throughout the species' geographical range. This concept is particularly relevant to the rock hyrax which is widely distributed in Africa.

With the exception of the detailed study of *Heterohyrax brucei* and *Procavia johnstoni* in Tanzania (Hoeck, Klein & Hoeck 1982) little information is available on the social behaviour of hyraxes. Other observations have been made on captive animals (Sale 1965; Fourie 1974) or during field studies of short duration (Meltzer 1967; Turner & Watson 1965; Steyn 1980). In this study the behaviour of the rock hyrax was investigated in order to isolate possible behavioural factors which may regulate hyrax density. Parameters of particular interest and significance are social behaviour, social organization (colony structure and organization) and dispersal, since these may be influenced by density. Dispersal is important in altering the demography of populations as it is a mechanism whereby local densities of mammals can be regulated (Barash 1974; Tamarin 1978). Similarly, information on socially mediated mortality could indicate the degree of density-dependent control of a population (Crook 1970). Behavioural factors that influence population dynamics have been discussed by Fourie (1983) and are reviewed.

Study area and Methods

The Mountain Zebra National Park (MZNP) is 6536 ha in extent and is situated 24 km south-west of Cradock (32°15'S / 25°41'E) in the Cape Province. The climate is semi-arid with 70% (276 mm) of the annual rainfall occurring during the summer months, predominantly in February and March. Mild to severe droughts occur periodically. The area is subject to major diurnal and seasonal temperature fluctuations. Maximum monthly mean temperatures (29,1°C) occur in January whereas July has the lowest monthly mean temperature of -0,1°C. The vegetation in the MZNP is predominantly Karroid *Merxmullera* Mountain Veld, but this is replaced by Karoo Veld on the higher slopes and False Karroid Broken Veld on the northern aspects (Acocks 1975). A significant correlation exists between seasonal rainfall and growth of grasses and Karoo shrubs (Roux 1966).

The social organization (social structure, dominance hierarchy, group size and sex ratios) of hyrax in the MZNP was studied by direct observations over a period of 359 h from January 1982 – May 1983. The hyrax colony site consisted of boulder scree and formed a steep slope. The position of numerous refuge entrances afforded excellent opportunities for behavioural observations. Observations were made with 8 × 30 binoculars from a hide 8 m above ground and 15 m away from the observation colony. Except for four adults, all sub-adults (13 to 24 months; $n = 16$) and adults (>24 months; $n = 18$) were marked using freeze brands and ear tags (Fourie & Perrin 1986). The hyraxes' ages were determined from tooth impressions (Fourie 1983). Juveniles

($n = 34$) were not captured and marked at the observation colony during 1982 but were easily recognizable because of their small size. They could, however, not be individually identified. Observations were made from sunrise to sunset on two occasions each month between February and July 1982. Associations and interactions between mother, infant and juvenile, intraspecific aggression between individuals of the same and different social ranking, and sexual behaviour were studied using the 'all occurrences of some behaviours' technique (Altmann 1974).

Since hyrax spend 95% of their time in an inactive state (Sale 1970), and because of the difficulty in measuring home-range area (Hoeck *et al.* 1982) the concept of a core area was introduced. The core area is defined as the area predominantly used by a colony of hyrax when not on feeding excursions, and includes sleeping holes, huddling and basking sites. In order to describe the area within the core area used predominantly by hyrax with the same social ranking the term area of activity is used. These areas were mapped using natural features at the colony site.

Observations on the spacing of individuals with the same or different social ranking were done concomitant with a study of activity patterns. Every five minutes spot recordings were made using the scan technique (Altmann 1974). An index of dominance (Id) for males belonging to different social rankings was determined using the equation

$$Id = \frac{a-b}{a+b}$$

where a = number of males towards which test male(s) showed aggression and b = number of males which were aggressive towards test male(s) (Hoeck *et al.* 1982). Detailed descriptions of the individual behaviour patterns associated with aggression in captive hyrax have previously been described (Sale 1965; Fourie 1974).

To quantify dispersal to and from the observation colony, hyrax were counted from the hide twice monthly (January to December 1982). Counting commenced at sunrise and continued for a period of 3 h when all individuals had emerged. Intensive field observations to locate marked ($n = 59$) dispersing hyrax were periodically conducted from January 1981 to May 1983; the age and locality of each individual was recorded. From May 1981 to January 1982, 16 rocky outcrops known to be used as core areas were visited on a weekly basis to determine occupancy or shifts *en masse* to adjacent core areas. The observations were of a direct (visual observation) as well as of an indirect (examination of faecal deposits) nature.

Results

Social structure and dominance hierarchy

Hyraxes associate in polygynous groups (colonies) consisting of a dominant territorial male, several adult females, and sub-adults and juveniles of both sexes; a peripheral male may also be loosely associated with the

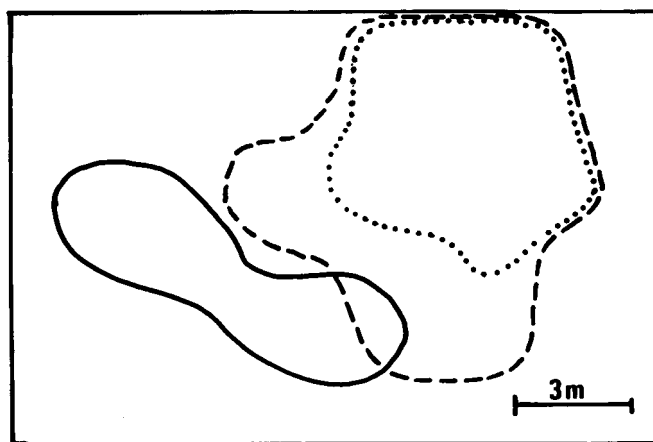


Figure 1 Areas of activity of hyrax belonging to different social rankings at the observation colony at Doornhoekdam in the MZNP (.... area of activity of juveniles and sub-adults; ... area of activity of adult ♀♀ and territorial ♂; — area of activity of peripheral ♂).

colony. The spatial arrangement of these social groups at the study colony is shown in Figure 1. Five social castes, differing in patterns of interaction, spatial dispersion within the core area, and roles in reproduction were identified:

- (i) Juveniles (0 to 12 months) are physically immature and reproductively inactive. They have a large area of activity which overlaps with that of the peripheral male.
- (ii) Sub-adult hyrax (13 to 24 months). Sub-adult females are sexually mature at 16 to 17 months of age. Sub-adult males may attain puberty at 16 to 17 months but more commonly one year later. They are prevented by the agonistic behaviour of the territorial male from mating with females of the same colony. The area of activity of sub-adult hyrax is similar to that of the juveniles.
- (iii) Adult females (> 24 months) are reproductively active and are monopolized by the territorial male. Their area of activity is smaller than that of the sub-adult and juvenile hyrax.
- (iv) Dominant territorial males form part of and influence colony structure. The area of activity of the territorial male is equivalent to that of adult females and all other adult males are excluded from this area. The territorial male actively monopolizes adult females, preventing sub-adult males from mating with females from the same colony and also preventing the peripheral males from mating with sub-adult or adult females attached to the colony.
- (v) Peripheral males occupy areas on the periphery of the area of activity of adult females and the territorial male. They are solitary on rocky outcrops, or are transients moving between colonies. At the observation colony, in the absence of the territorial male, the peripheral male dragged his erect penis, which curved downwards, on the ground and urinated at four different places outside his area of activity (Figure 2). Two of the urinating sites overlapped the area of activity of the adult females and the territorial male, but the peripheral male

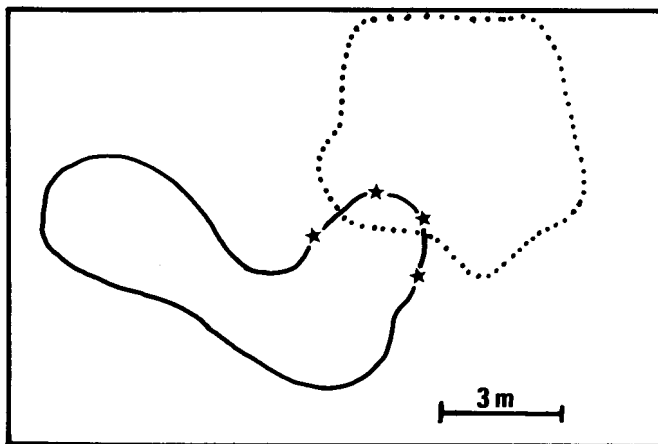


Figure 2 Expanded area of activity of the peripheral male accompanied by urination at four distinct places (marked by asterisks in the diagram) (... area of activity of adult ♀♀; — area of activity of peripheral ♂; * expanded area of activity of peripheral ♂).

did not defend his area of activity. No evidence was found for the formation of bachelor groups. The peripheral male adjacent to a colony may have sensory contact with the group, including the perception of alarm calls and direct visual contact with other members of the group. The peripheral male is characterized by submissive behaviour when confronted by the territorial male. During the temporary absence of the territorial male the peripheral male will mate with the females.

The ages of peripheral males were determined by selectively shooting six isolated individuals. Their mean age was 42,7 months with a range of 17 to 61 months, while the age of the only territorial male captured was 47 months. The dominance ranking for males was linear and age based, i.e. territorial male (1,0) dominant to peripheral male (−0,2) dominant to sub-adult males (−0,5). (Examples illustrating the determination of ranking are discussed under intraspecific aggressive and sexual behaviour.) Dominance ranking was not evident for females and the level of aggressive interaction was low. During 25 different observation periods, ranging from 3 to 12 h, the oldest females were observed performing a guarding function from a vantage point on 19 occasions, whereas the territorial male was seen performing this function on only two occasions.

Group size and sex ratios

Counts conducted (October 1982) at five hyrax colonies categorized as small (<15 animals), and five colonies categorized as large (>15 animals), gave a mean (\pm S.E.) group size of 9,35 (\pm 1,69) and 32,40 (\pm 3,41) respectively.

The group compositions of hyrax comprising colonies at three localities during September 1982 are given in Table 1. Animals were captured, examined, marked and released. The observation colony consisted of 35 hyrax plus the one peripheral male associated with the colony, while the colony situated west of the observation colony

Table 1 Locality, group size, social ranking and age (months) of hyrax at Observation Colony, Western Colony and Laboratory Colony (September 1982)

Observation Colony			Western Colony			Laboratory Colony		
Social ranking	n	Age	Social ranking	n	Age	Social ranking	n	Age
J	24	10–11	J ♂	1	10–11	J ♀♀	3	10–11
SA ♂	1	22–23	J ♀♀	3	10–11	J ♂	1	10–11
SA ♀♀	3	22–23	SA ♀	1	22–23			
AD ♀	1	34–35	AD ♀	1	46–47			
AD ♀	1	58–59	AD ♀	1	118–119			
AD ♀	1	70–71	T ♂	1	46–47			
AD ♀	1	82–83						
AD ♀♀	2	?						
T ♂	1	?						
P ♂	1	?						

J — juveniles; SA — sub-adult; Ad — adult; T — territorial; P — peripheral.

comprised eight hyrax. Owing to the rugged terrain at the western site it was impossible to capture and determine the numbers of peripheral males associated with the colony. The four juvenile hyrax captured next to the field research laboratory stayed on their own and were not associated with any adult hyrax.

The sex ratio (1,0 ♂ : 1,2 ♀) of 35 juvenile hyrax captured during 1980–1981 did not differ significantly from parity ($p < 0,1$). The sex ratio of all hyrax present at the observation colony during January 1982 was 1,0 ♂ : 1,4 ♀, while in November 1982 it was 1,0 ♂ : 2,4 ♀. This represents a significant shift in the sex ratio.

Social behaviour

Spacing within the group

Early morning observation ($n = 23$) indicated that hyraxes with different social rankings emerged from specific refuge holes at the colony site (Figure 3). The adult females and territorial male occupied the central area while juveniles and sub-adults were more peripheral. Once emerged, the hyrax moved about within their respective areas of activity. However, there was a tendency for juvenile and sub-adult hyrax to occupy the peripheral areas of their area of activity throughout the day. The areas of activity for individual hyrax were not determined. However, the areas of activity for juveniles and sub-adults were 85 m², that of adult hyrax 41 m² and the area of activity for the peripheral male 46 m². The area of activity for the juveniles and sub-adults differed significantly from those of the adult hyrax and peripheral male ($\chi^2 = 14,68$ and 11,10; $p < 0,005$).

Circumstantial evidence suggests that young, older than one month of age, do not share sleeping holes with their mothers. Young emerged from different holes and at different times from the mothers. When adult females

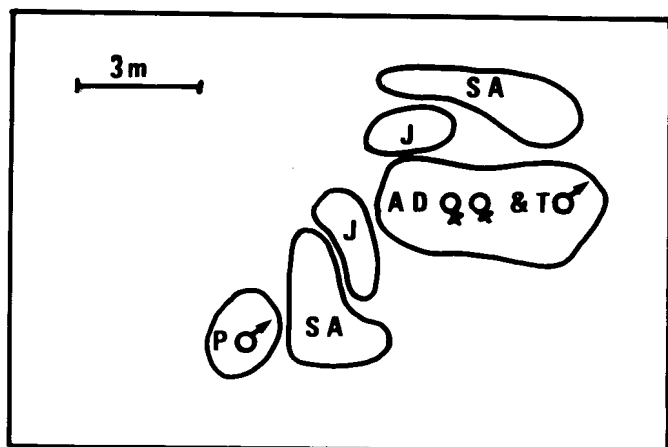


Figure 3 The spacing of hyrax of different social rankings within areas of activity (SA — sub-adults; P — peripheral; J — juvenile; T — territorial).

emerged the young hyrax moved towards them and were suckled. It appeared as if young were sometimes suckled by non-maternal females. On one occasion four juveniles were seen to suckle on a 23-month-old female. Female hyrax of this age group normally only have litters of between one and three ($n = 13$; Fourie 1983). In this particular case an older female acted aggressively towards one of the juveniles, but the 23-month-old female did nothing to protect the juvenile. Young often climbed on their mothers' backs or basked with them, and sometimes followed adult females on short foraging excursions.

Juveniles (about five months old) tended to congregate forming nursery groups (Figure 4), and during basking were often in close bodily contact. Social play amongst juveniles was observed on 86 occasions during 113 h of observation. It consisted mainly of mock mating and chasing one another in and out of holes and crevices.

Intraspecific aggressive behaviour

In general the level of agonistic behaviour was low.



Figure 4 A nursery group of juvenile hyrax.

Table 2 Quantified aggressive interactions recorded (113 h of observation) between hyrax belonging to the same and different sub-groups

Individuals involved	Occurrence
J → J	20
T ♂ → SA ♂	8
P ♂ → J	4
SA ♂ → J	4
T ♂ → P ♂	3
SA ♂ → SA ♂	3
AD ♀ → J	2
AD ♀ → SA ♂	1
SA ♀ → SA ♂	1
SA ♀ → J	1

T — territorial; P — peripheral; AD — adult; SA — sub-adult; J — juvenile.



Figure 5 Male hyrax (36 months old) with bite wounds on neck and shoulder.

Agonistic behaviour consisted mainly of threat behaviour (growling and flaring of dorsal gland hairs), chasing, and in a few instances biting. Aggressive interactions between the different sub-groups are summarized in Table 2. From a shot sample (November–May; $n = 224$) it was evident that bites piercing the skin (Figure 5) were generally inflicted on the ears, neck, shoulders and rump. Of the 16 shot hyrax with severe fresh bite wounds, 14 were adult males, and 12 of these 14 were less than four years old. The remaining two males were seven and 11 years old respectively.

Sexual behaviour

Three categories of males attempted copulation with

females in oestrus, i.e. territorial males, peripheral males and sub-adult males.

During the peak of the mating season (April) the territorial male moved through the colony in search of receptive females and sniffed fresh urine deposits almost continuously. Of the 19 copulations observed, 17 were with adult females and only two with sub-adult females. Receptive females were observed to approach the territorial male cautiously with the hair around the dorsal gland erected, they would then sniff the anogenital region of the territorial male before presenting their hind-quarters to the male. The territorial male responded by sniffing the anogenital region of the female before mounting. Seven sub-adult females and 10 adult females were present at the observation colony during the peak mating period (April), giving a total of 17 females being monopolized by the territorial male.

During the peak of the mating season an unknown peripheral male was observed on a rocky outcrop 20 m from the observation colony. He periodically uttered calls and took part in mating. Of the 12 observed peripheral male copulations, 11 were with sub-adult females and only one with an adult female. Generally the adult females showed little interest in the peripheral males. The peripheral males often followed the sub-adult females on foraging excursions and it is possible that some copulations took place at feeding sites.

An attempt by a peripheral male to follow a sub-adult female into her area of activity caused the territorial male to charge and chase away the peripheral male. In the absence of the territorial male, the peripheral male uttered rutting calls and made wailing sounds (whereas the territorial male infrequently uttered rutting calls but never made wailing sounds). On one occasion two sub-adult females responded to the calls, moved towards the peripheral male and one of them was mated. In the presence of the territorial male copulation by the peripheral male with sub-adult females was prevented by overt aggression. One sub-adult female, however, followed the peripheral male from the refuge site, and copulation occurred.

Only two attempted copulations were recorded between sub-adult males and sub-adult females, and in both instances the territorial male intervened and chased the sub-adult males into their refuge holes.

Defaecation

Although it has been reported that hyraxes have communal dung middens (Sale 1965; Louw, Louw & Retief 1972; Steyn 1980), observations made during the present study failed to confirm this. Numerous white urine stains found on rock faces and the accumulation of faecal pellets at the base of many boulders at refuges would seem to indicate otherwise. Piles of faeces found at the entrances to hyrax refuges are probably a consequence of their inactive (basking) life style. Certain hyrax may show a constancy in urinating and defaecating sites, but this can be explained by segregated area utilization and socio-spatial factors.

Dispersal

Emigration and immigration

Dispersal of young from their birth site is termed 'juvenile dispersal' whereas 'adult dispersal' is the movement between breeding sites of adult individuals that have reproduced (Greenwood 1980). Changes in the percentage composition of various age categories in the observation colony from January to December 1982 are illustrated in Figure 6 a-c. Only 29% of the original juvenile hyrax were present at the end of the year; although juveniles declined from April onwards, a more marked decline took place from September when juveniles were 10 months of age. Dispersal of sub-adult hyrax differed according to sex. Sub-adult males emigrated from the colonies at the onset of the mating season (March to May) at the age of 15 months, whereas sub-adult female numbers stayed fairly constant during the mating season, but declined from June and only 25% were present at the end of the year.

The territorial male of the observation colony was displaced by a peripheral male during April, and the peripheral male was replaced in the same month by a transient male so the total numbers of adult males remained constant. Adult female numbers declined from June to September and after one year adult females constituted 75% of the original number. During October the only incidence of immigration was recorded; two adult females joined the colony.

Of the 35 hyrax marked as juveniles at the observation colony, 10 were later seen during field observations. Male dispersers were seen in isolation in the proximity of other colonies, whereas females were seen within other colonies. Information on dispersal distances, relocation sites and the age of dispersers is summarized in Figure 7. Dispersal distances were small, ranging from 250 to 500 m.

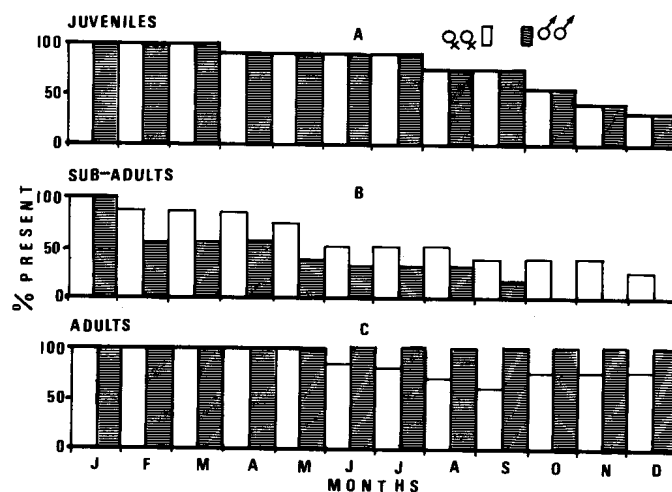


Figure 6 (a) — (c) Changes in the percentage of juveniles, sub-adults and adult hyrax present during the period January–December 1982 at the observation colony at Doornhoekdam.

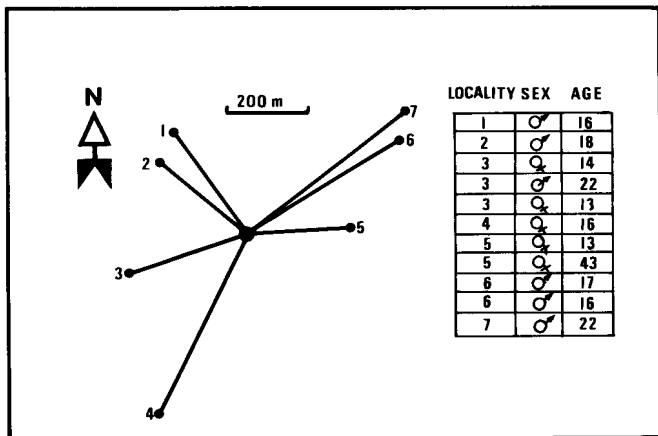


Figure 7 Direction and distance moved from the observation colony at Doornhoekdam by dispersing hyrax of different ages (in months) and sexes.

Shifts of colonies

Of the 16 hyrax colonies monitored over a nine-month period, 12 remained stationary while four were absent from their refuges for periods ranging from two to six weeks. Certain identified hyrax refuges were vacated for extended periods of three to six months. The observation colony and the western colony were spatially stable throughout the course of the study.

Discussion

Social organization

The basic structure of hyrax social organization is defined here as the female-bonded group. There may be one or more peripheral males associated with the polygynous groups, and these peripheral males also have a linear social ranking (Hoeck *et al.* 1982). The peripheral male with the highest social ranking may displace the territorial male.

Results obtained in this study confirm that polygynous colonies are not actively defended (Hoeck *et al.* 1982); i.e. do not vary owing to local environment. The small area within the colony which is actively defended by the territorial male is a result of the female hyrax's gregarious nature and male competition for females. Dominance hierarchies proposed for males in this study are consistent with the results obtained by Hoeck *et al.* (1982). Although not observed, the territorial male may mark his area of activity in a way similar to that of the peripheral male. Scent marking with urine and/or faeces is common amongst ungulates (Grau 1976; Ebling & Stoddard 1978) and is frequently associated with dominance and area utilization. Urine markings by peripheral and territorial male hyrax are believed to perform these functions.

Hyrax group sizes are variable (Sale 1965; Hoeck *et al.* (1982). The availability of suitable shelter and floorspace within a refuge can most probably be considered as the main group-limiting factors. Provided, however, that sufficient shelter is available the results of this study and

that of Hoeck *et al.* (1982) have shown that a territorial male can monopolize three to 17 females.

Body mass has been shown to be a major factor in winning intraspecific combats (Hoeck *et al.* 1982). Since males only reach their asymptotic mass at five to six years of age (Fourie 1983) it is suggested that territorial males are usually older animals, while it has been established that peripheral males are generally younger than four years.

Social behaviour

The observation colony provided data on the partitioning of space within the core area. It is hypothesized that hyrax with a low social ranking (juveniles, sub-adults and peripheral males) act as a buffer zone between ground predators and reproductively active hyrax but experimental verification is required. The separation of sub-adults and juveniles from adult females and the territorial male is important in limiting agonistic behaviour (including infanticide) between hyrax of different social rankings. Hanse (1962) reported an incident in which five adult female hyrax killed 16 juveniles of about four weeks of age, while adult male hyrax are also known to kill newborn infants (Mendelssohn 1985). It is suggested that spatial separation of groups of young hyrax within the colony may be advantageous for their own survival.

The majority (88%) of serious injuries sustained in agonistic interactions are inflicted by males and most (86%) of these are apparent in males younger than four years, corresponding to peripheral males in age. Bite wounds sustained by old males possibly reflect their inability to defend intracolony territories because of deteriorating physical condition. Bite wounds on females are evidence of aggression from males; a phenomenon reported previously by Sale (1965), Steyn (1980) and Hoeck *et al.* (1982).

The displacement of territorial males in late April by peripheral males, can be correlated with deterioration in the physiological condition of the territorial male. In late April, following the peak mating period, the energy cost incurred in mating and defending a territory must be great, the territorial male is vulnerable to social displacement since his physical condition, unlike that of the peripheral male, has most likely declined. A challenge between the peripheral male and the territorial male often results in death of either individual (Hoeck 1982).

The sniffing of urine stains and the anogenital region of the female probably aids the territorial male in olfactory recognition of the physiological state of the females. Increased secretion from the dorsal gland may also be implicated. However, since females sometimes solicit males through posturing and also respond to the calling of a male, auditory and visual stimuli must also play an ancillary role.

Because of limited female dispersal, sub-adult females will usually be kin. If the territorial male is displaced annually (or biannually) as seems likely, incestuous matings are prevented. Similar constraints on inbreeding operate in the yellow-bellied marmot (Armitage 1974); in both

species, territorial/colonial males are born at colonies different from those at which they become dominant.

Extensive juvenile dispersal was recorded, which may reduce inbreeding and increase individual fitness (Greenwood, Harvey & Perrins 1978). Juvenile dispersal reported by Hoeck (1982) involved age classes (12 to 30 months) different from those identified in this study. Dispersal also occurred over longer distances (> 2 km). Hyrax studied by Hoeck (1982) had to disperse over plains with little cover, predation pressures were high and dispersing hyrax had to complete their journey as soon as possible. Since running speed of hyrax is likely to be positively correlated with size, dispersal at an older age could be of selective importance. In the MZNP, however, the rugged montane terrain can provide sufficient cover for dispersing hyrax. This would favour dispersal at an early age and also dispersal over shorter distances. Population density, however, should also be considered.

Juvenile dispersal is here divided into two categories. Hyrax leaving their natal colony prior to the onset of sexual maturity are termed 'early' dispersers, while those which leave after achieving sexual maturity (and the mating season) are termed 'late' dispersers. Since early dispersal is independent of agonistic interactions of colony members it possibly occurs because of endogenous factors. Early juvenile dispersion is temporally associated with the onset of summer rains, increasing temperatures and the availability of high quality forage. This early dispersion may be of considerable significance to the species ecology (colonization, demography and genetic constitution).

Late dispersal is biased toward males and is a result of the agonistic behaviour of the territorial male. It occurs at the termination of mating and the growing season, and may be caused by intraspecific competition for limited forage (and cover). It is probably of less biological significance than early juvenile dispersion in colonization but may contribute to regulating local population density and gene composition.

The incidence of adult dispersal amongst females is low while adult dispersal of males is common. These phenomena are a consequence of social organization and natural selection.

Shifts of hyrax colonies have previously been reported (Sale 1965; Meltzer 1967; Hoeck 1975). Observations reported here and the results of a previous study (Fourie 1983) suggest that these shifts are related to the availability of forage. Supporting evidence for this contention is the fact that hyrax colonies close to riparian thickets, which can supply abundant forage all year round, remained stable throughout the course of this study.

Conclusion

Local environment does not alter hyrax social structure and dominance hierarchies. Hyrax group size, age at dispersal, dispersal distances, and feeding behaviour (Fourie 1983), however, are modified in response to different environmental selection pressures. Additional information on the origin of peripheral males, change-

overs with territorial males, temporal shifts in female hierarchies, group size and structure is needed to obtain a better understanding of hyrax social organization. Further elucidation of hyrax social organization may assist in the understanding of the evolution of social organization in related species.

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