THE POPULATION DYNAMICS OF THE ROCK HYRAX *PROCAVIA CAPENSIS* (PALLAS, 1766) IN THE MOUNTAIN ZEBRA NATIONAL PARK

Dissertation

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THE POPULATION DYNAMICS OF THE ROCK HYRAX PROCAVIA CAPENSIS (PALLAS, 1766) IN THE MOUNTAIN ZEBRA NATIONAL PARK

by

L.J. FOURIE

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ABSTRACT

The chief objective of the study was to investigate the population dynamics of the hyrax in the Mountain Zebra National Park (MZNP). To realise this objective information on growth, age determination, reproduction, habitat utilization, behaviour, parasites and mortality had to be gathered.

The growth of hyrax in relation to age is described by means of Stevens asymptotic regression equations. Near asymptotic measurements are attained first in hind foot length (at 30-33 months of age), head/body length (at 37-39 months of age), girth (at 41-48 months of age) and body mass (at 68-70 months of age). Allometric growth of the various body measurements was investigated and useful predictive relationships for mass are presented.

Age determination of hyrax was studied in detail. Cementum annuli counts provided reliable estimates of age. One primary cementum line is formed annually. The dried eye lens mass was an accurate means of age determination up to *c.* 72 months of age. A summary of findings which will facilitate age determination of dead animals or skulls, and live animals, is provided. Reproduction in the hyrax was studied with emphasis on breeding season, age-specific litter sizes, prenatal mortality and lactation. Male hyrax attained puberty at 15-17 months of age or one year later. Females generally attained puberty at 15-17 months of age. One female (1,4% of total shot sample for the specific age group) attained puberty at 4-5 months of age. Middle-aged hyrax had significantly larger litter sizes than younger animals.

Hyrax in the MZNP feed on at least 80 different plant species belonging to 33 plant families. Crude protein of stomach contents and faecal samples showed little seasonal fluctuation implying that hyrax in the MZNP were on a stable quality diet. Female hyrax enjoyed a significantly better quality diet than males for the four month period prior to parturition and during the first two months of lactation. The crude protein values of faecal and stomach samples had a significant correlation. Body fat of male and female hyrax showed seasonal variation related to physiologically stressful periods.

Seasonal differences in activity patterns were demonstrated. The basic structure of hyrax social organization is the multi-female kinship group that is matrilocal. Territorial dominant males maintain harems and exclude all other adult males. Peripheral males occupy areas on the periphery of the activity areas of other members of the hyrax colony. Peripheral males do not form bachelor groups and are normally younger than territorial males.

It is suggested that territorial males are able to monopolize between 3-17 females in a successful and energetic manner. Both natal and breeding dispersal occurred, the former being considerably more extensive than the latter.

The ecto- and endoparasites of hyrax were identified and their burdens quantified over a 13 month period. Juveniles had significantly larger burdens of ectoparasites than did adults.

Information on age-specific mortality was obtained from skulls collected in the field and at black eagles' nests. Losses that occurred in the study population due to caracal and black eagle predation were quantified. Evidence is supplied which indicates that juvenile mortality may fluctuate markedly.

The population dynamics of the hyrax population in the MZNP was studied by the use of time specific life-tables, models on population growth rates, population simulation models and sensitivity analysis. Sensitivity coefficients were used as a predictor of population regulation. Female juvenile mortality was considered to be the main regulating factor. Changes in fecundity schedule are important compensatory mechanisms and also play an important role in the regulation of a hyrax population. Predation, particularly by caracal, is thought to dampen population fluctuations.

CHAPTER I

INTRODUCTION

OBJECTIVES

In the Karoo regions of South Africa the rock hyrax, Procavia capensis, is commonly found in montane and rocky terrain. Marked increases in the hyrax population in the Karoo during the early 1930's (Kolbe 1967) and 1940's (Thomas 1946) and later also in South West Africa (Namibia) (Lensing 1978) caused considerable concern to small stock farmers. This is because hyrax are regarded as competing with lifestock for forage, and can also cause damage to fruit trees, crops and gardens (Hanse 1962).

During 1946 the hyrax was declared vermin (a problem animal) according to ordinance 21 of 1946 (ordinance on the eradication of vermin) issued by the Department of Nature and Environmental Conservation (DNEC) of the Cape Province. In terms of this ordinance rewards were paid for hyrax skins presented at the Divisional Council offices at Cradock in the Cape Province. A total of 298 936 hyrax skins were handed in at these offices during the period 1947 - 1957 (Van Rensburg pers. comm.).

The hyrax was still considered a problem in certain areas of the Karoo after the latter date and the DNEC of the Cape Provincial Administration initiated research on the hyrax in 1961 (Hanse 1962). However, no attempt has subsequently been made to determine the nature and extent of the hyrax problem.

Of 60 questionnaires returned during 1981 by farmers in the Cradock Division 73% did not consider the hyrax as a problem as far as forage utilization was concerned and 68% reported a subjectively assessed decrease in hyrax numbers. More recent reports of the hyrax being a problem animal are sporadic and isolated. During the early 1980's large numbers of hyrax caused damage to gardens in the Plettenberg Bay Municipal area (Louw pers. comm.) and large numbers were also reported in the Tsitsikamma Coastal National Park (Crawford pers. comm.). A re-evaluation of the hyrax as a vermin species in the Cape Province thus seems to be justified, and a scientifically planned survey by the DNEC of the Cape Province is envisaged for the near future (Lensing pers. comm.).

A possible reason for the increase in hyrax numbers in the Karoo during the 1940's has been suggested by Thomas (1946). He felt that the extensive predator control programme involving jackal-proof fencing, trapping and hunting (which became effective at that time) was responsible. Kolbe (1967) reported a change in hyrax's habitats during the same period. He suggested that hyrax had expanded their distribution to colonise additional habitats and became distributed throughout numerous habitats where they used any available shelter (dam walls, dongas, stone walls, burrows, culverts etc.). Considering the long gestation period (7,5 months) and an average litter size of two or three (Millar 1971) the sudden population explosion of hyrax in the arid Karoo seems enigmatic.

Hanse (1962) and Lensing (1978) suggested possible control measures for hyrax in areas where they had become a problem. Before any such measures can be introduced a sound knowledge of the population dynamics of hyrax is essential. However, until now nothing on the population dynamics of hyraces in Southern Africa has been published.

Published research on hyraces of direct relevance to this study is summarized in Table 1. Prior to this study no attempt had been made to conduct a comprehensive investigation of the hyrax in the Karoo region where it had first assumed pest proportions. Detailed information on parasites, habitat utilization, social behaviour and mortality, which are crucial for an understanding of many aspects of population biology of the animal, are lacking. Because of the paucity of information on many facets of hyrax biology the present comprehensive study was initiated. The several aspects studied should serve as a rational basis for further research and in addition this is also the first intensive autecological study of the Cape rock hyrax.

The objectives of this study can be summarized as follows:

1. To determine the growth rate of hyrax to serve as a basis for age determination.
2. To assess criteria of age determination of hyrax as a basis for population analysis.
3. To investigate habitat preference utilization.
4. To define the social organisation of the hyrax.
5. To qualify and quantify seasonal parasite loads and condition in

Table 1: Past research on hyraces, which is of direct relevance to the present study, grouped according to field of study.

Subject	Hyrax species
Reproduction	
Van der Horst (1941)	*Procavia capensis*
Murray (1942)	*Procavia capensis*
O' Donoghue (1963)	*Dendrohyrax arborea ruwenzorii* (Neumann)
Mendelssohn (1965)	*Procavia capensis syriaca* (Schreber)
Glover & Sale (1968)	*Heterohyrax* sp. *Procavia* sp.
Millar & Glover (1970)	*Procavia capensis*
Millar (1971)	*Procavia capensis*
Millar & Glover (1973)	*Procavia capensis*
Millar & Fairall (1976)	*Procavia capensis*
Neaves (1979)	*Heterohyrax brucei*
Steyn (1980)	*Procavia capensis*
Feeding	
Hoeck (1975)	*Procavia johnstoni*, *Heterohyrax brucei*
Lensing (1978)	*Procavia capensis*
Behaviour	
Sale (1965a)	*Heterohyrax syriacus*, *Procavia habessinica*, *Procavia johnstoni mackinderi* (Thomas)
Fourie (1974)	*Procavia capensis*
Hoeck, Klein & Hoeck (1982)	*Heterohyrax brucei*, *Procavia johnstoni*
Age determination	
Roche (1978)	*Procavia capensis syriaca* (Schreber)
Fairall (1980)	*Procavia capensis*
Physiology	
Louw, Louw & Retief (1972)	*Procavia capensis*
Eloff (1981)	*Procavia capensis*
Leon (1981)	*Procavia capensis*
McNairn (1982)	*Procavia capensis*
Rübsamen, Hume & Engelhardt (1982)	*Procavia* & *Heterohyrax* spp.
Population dynamics	
Hoeck (1982)	*Procavia johnstoni*, *Heterohyrax brucei*
General	
Hanse (1962)	*Procavia capensis*

order to interpret mortality schedules.

6. To investigate the population dynamics of the hyrax in the Mountain Zebra National Park, i.e. (i) population structure (age classes and sex ratios), (ii) mortality patterns (age specific, and predation) and (iii) recruitment (breeding season, gestation, litter size, survival rate).
7. To express the resultant data as life tables and population models and to discuss population regulation in the hyrax.

THE ROCK HYRAX *Procavia capensis*

The systematic position of the hyrax

The superficial physical resemblance between the hyrax (Fig. 1) and the guinea pig deceived early taxonomists and consequently it was named *Cavia capensis* or the Cape guinea pig by Pallas (1766). Ever since then the systematic position of this animal has been controversial (see Leon 1981) because it exhibits many bizarre and specialized anatomical features. Early work on the systematic position of the family has briefly been reviewed by Simpson (1945). He classified the Procaviidae together with two extinct families as the order Hyracoidea. Together with the Proboscidea, the Sirenia and several extinct orders the Hyracoids comprise the superorder Paenungulata. This classification is based on similarities in skeletal and soft anatomical structures, particularly the arrangement of the bones of the limbs and the tips of the pedal digits which have poorly developed hooves (Fig. 2) (Hanks 1977). Other common skeletal

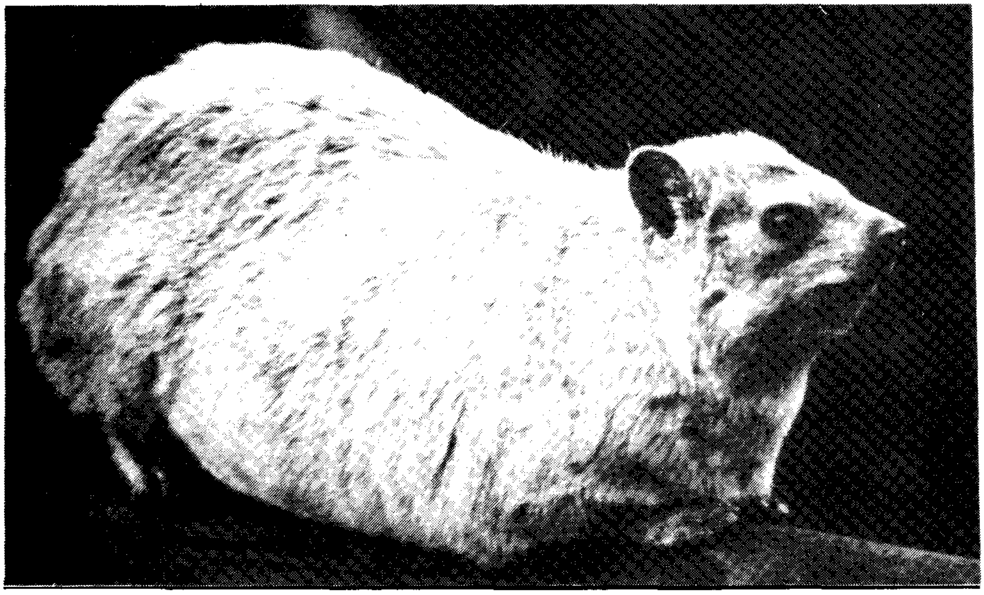

Figure 1: The rock hyrax, Procavia capensis.

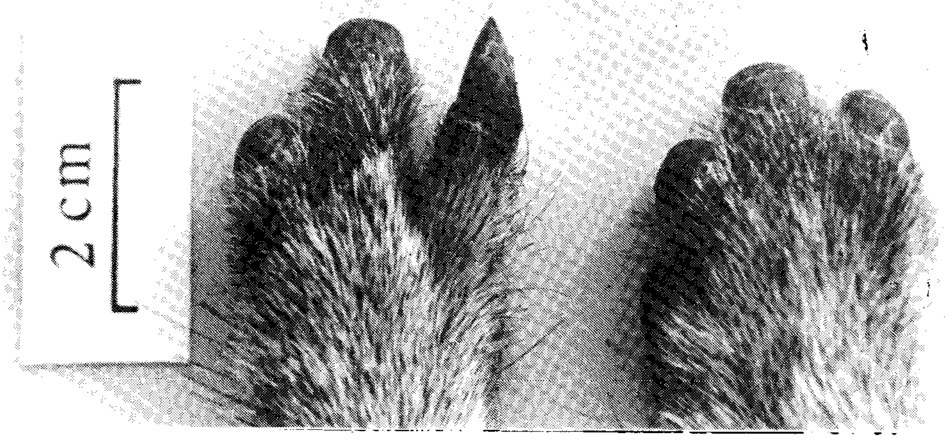

Figure 2: Dorsal view of the left hind foot with three toes and the left front foot with four toes. Note the hoof-like nails, that of the inner toe of the hind foot being modified and used as a grooming claw.

features occur in cranial elements, the enlarged separated incisors and the molar-like appearance of the premolars (Romer 1966).

The skull of the hyrax is stout with deep lower jaws and a post-orbital bar which is partly cartilaginous (Fig. 3). The single pair of upper incisors grow continuously, as in elephants, and are long and curved, whereas the lower pairs are chisel-shaped. There is a wide diastema between the incisors and the premolars in most hyraces but in the genus Procavia this is least evident.

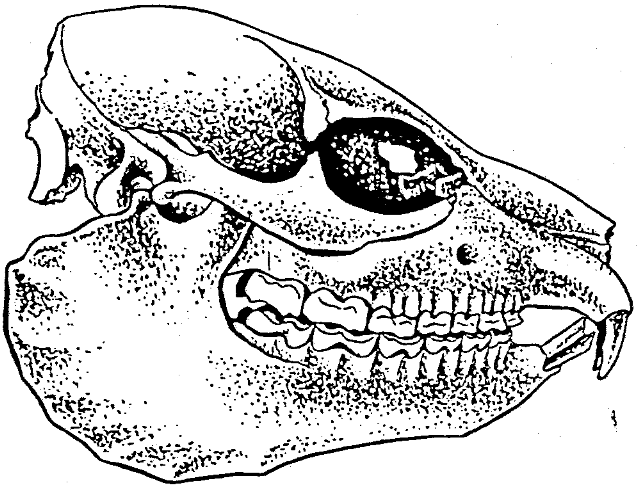

Figure 3: Lateral view of the skull of an adult hyrax, Procavia capensis.

All the species belonging to the three orders are true testicond mammals and the placental and foetal membranes show structural similarities (Wislocki 1928; Wislocki & Van der Westhuizen 1940). A close serological relationship between the hyrax and the elephant has been demonstrated (Weitz 1953) and confirmed by data on plasmaproteins and haemoglobins (Buettner-Janusch, Buettner-Janusch & Sale 1964).

Similarities between the reproduction of the hyrax and the elephant have also been mentioned by Hanks (1977).

Simpson (1945) classifies the rock hyrax* as follows:

Class: Mammalia
Subclass: Theria
Infraclass: Eutheria
Superorder: Paenungulata
Order: Hyracoidea
Family: Procaviidae
Genus: _Procavia_
Species: _capensis_

The genera and distribution of Hyracoidea

Taxonomic affinities within the family Procaviidae are still the subject of controversy. Fox (1933) and Hatt (1933) proposed the use of a single genus, Roche (1972) maintained that there were two genera, while Gray (1868) and Simpson (1945) recognised three genera. Bothma (1971) reviewed the taxonomy of the Procaviidae and retained the three genera _Procavia_, _Heterohyrax_ and _Dendrohyrax_. Since then Hoeck (1978) has found anatomical and behavioural differences between the three genera thus reinforcing the classification of the Procaviidae into

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*"Hyrax" (without indefinite article) is used to denote more than one animal and "hyraces" more than one genus, species etc. (after Sale 1965a).

three genera. A total of 11 species, five belonging to Procavia, three to Heterohyrax and three to Dendrohyrax (with several subspecies) are recognised by Bothma (1971). For the purpose of this study the allocation of species to three genera will be adopted.

All hyrax species are distributed widely and almost solely within Africa. Of the three genera, Procavia has the widest distribution occurring throughout southern Africa and extending through much of Africa north to Arabia, Israel and Syria (Fig. 4a). One subspecies Procavia johnstoni mackinderi (Thomas), the Mount Kenya hyrax, lives in alpine regions (3 200 - 4 650 m above sea level) on Mount Kenya (Kingdon 1971). P. capensis occurs throughout southern Africa including Zimbabwe, Northeastern Botswana and South West Africa (Namibia) excluding the Kaokoveld where it is replaced by Procavia welwitschii (Bothma 1967 & 1971).

Both Heterohyrax and Dendrohyrax are confined to Africa. The former is distributed along the eastern seaboard of Africa but its distribution also extends into central and eastern Angola (Fig. 4b). The most southerly limit of the genus is the northeastern Transvaal, and the most northerly Egypt (Bothma 1971). The arboreal genus Dendrohyrax is confined to the forested areas of Africa and is found largely in the equatorial rain forests of West Africa and the Congo basin (Fig. 4c). It does, however, extend south to the evergreen forest of the eastern Cape Province.

Both Procavia and Heterohyrax occupy a rock-dwelling niche. These two

Figure 4a - c: Geographic distribution of (a) Procavia, (b) Heterohyrax and (c) Dendrohyrax (modified after Bothma 1971 and Kingdon 1971).

genera occur sympatrically in some areas of their distribution, even to the extent of sharing the same rock crevices (Turner & Watson 1965; Hoeck 1975).

CHAPTER II

THE STUDY AREA

INTRODUCTION

The study was conducted in the Mountain Zebra National Park (MZNP) (32°15'S; 25°41'E), comprising an area of 6 536 ha situated 24 km south-west of Cradock in the Cape Province, Republic of South Africa (Fig. 5). Hyrax were also collected on a neighbouring farm, Daniëlshoek.

The MZNP was proclaimed in 1937 when the State purchased the farm Babylons Toren to conserve the Cape Mountain Zebra, *Equus zebra zebra* Linn. During 1964 neighbouring farms were purchased, increasing the size of the Park from 1 712 ha to its present area.

GEOGRAPHY AND GEOLOGY

The southern boundary of the Park follows the summit of the Bankberg mountain range at an elevation of *c.* 1 800 m a.s.l; the highest point in the Park (Spitskop) reaches 1 957 m (Fig. 6). A number of kloofs (ravines) formed by steep-sided northern slopes of the mountain give rise to streams flowing into the Wilgerboom River which drains north north-easterly to join the great Fish River north of Cradock. The most western part of the Park lies in the catchment area of the Kareebosch River, another tributary of the Great Fish River.

The western boundary of the Park runs parallel to a high ridge and

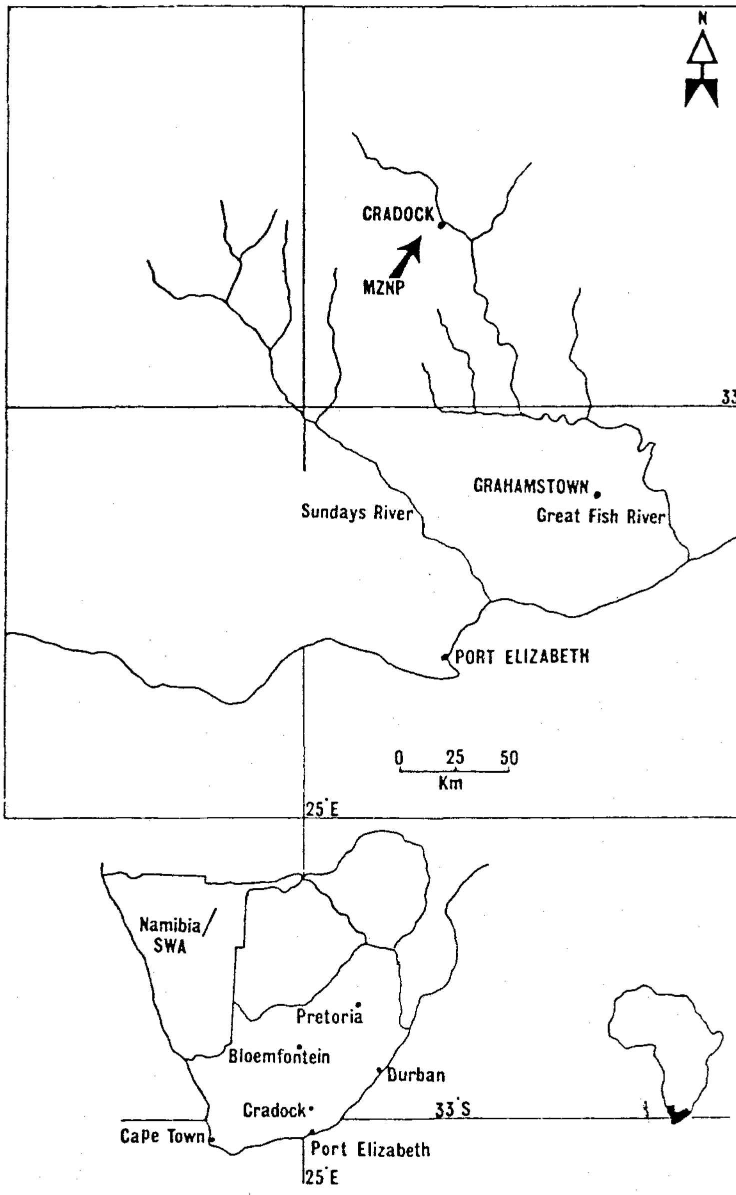


Figure 5: Map indicating the locality of the Mountain Zebra National Park, Cradock, Republic of South Africa.

forms an extensive plateau (1 300 - 1 400 m a.s.l.) to the north, known as Rooiplaat (Fig. 6). There are two small isolated plains in the lower lying regions of the Park, Springbokvlakte and a plain near the old Berghof and Weltevrede homesteads (Fig. 7).

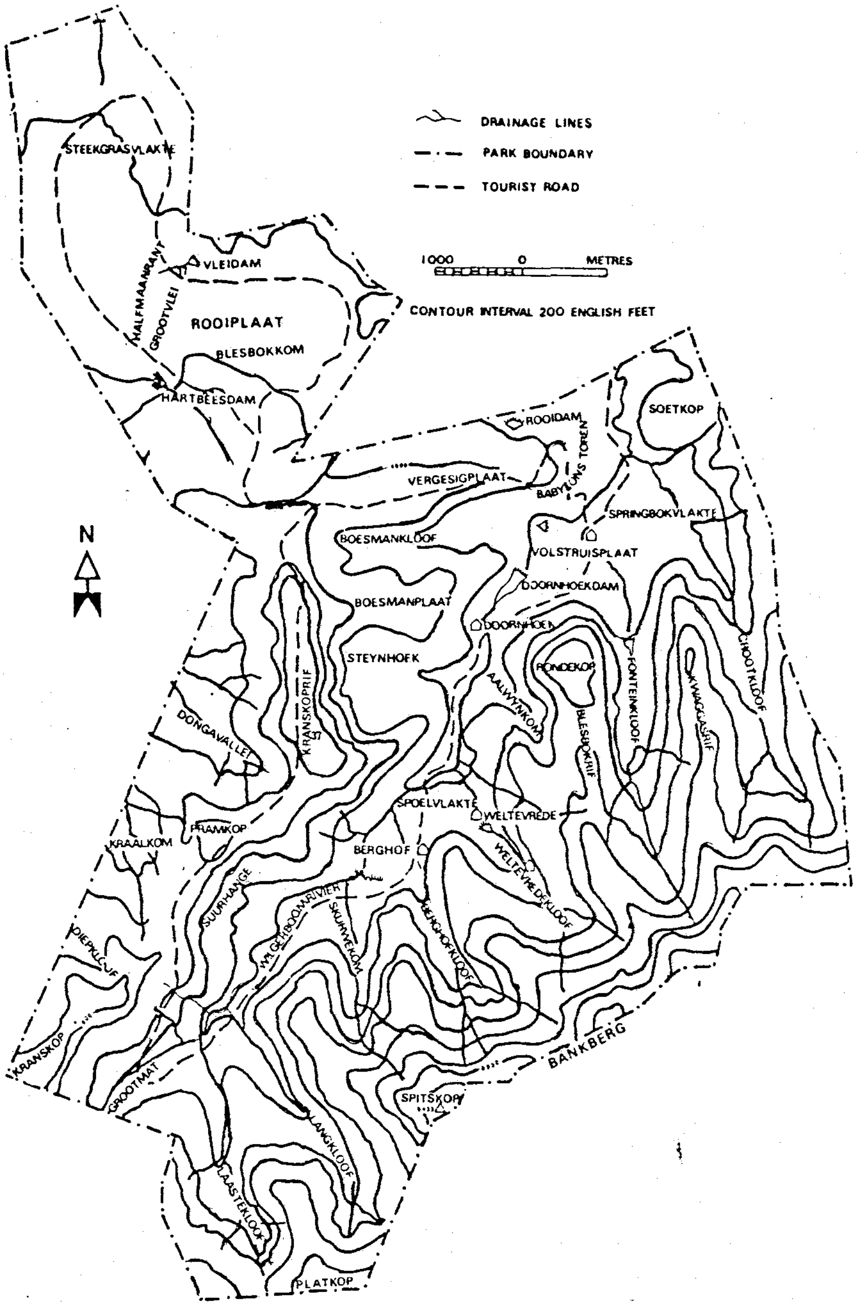


Figure 6: Topographical and locality map of the Mountain Zebra National Park.

A survey of the geological formation in the Park (Toerien 1972) showed that it consists mainly of sandstone, siltstone and mudstone of the Lower Stage, Beaufort Series, Karoo System, with post-Karoo dolerite intrusions. More than half of the Park consists of dolerite. The

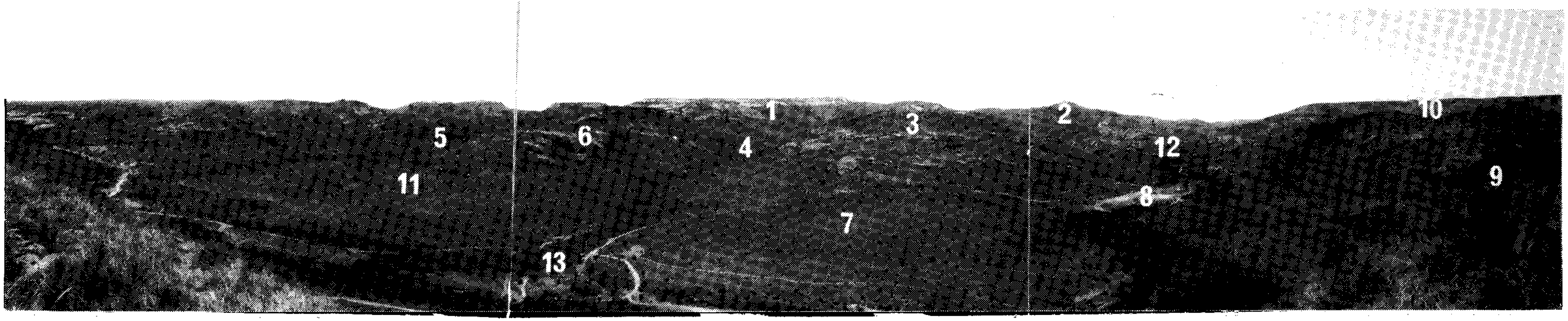


Figure 7: Panoramic view of the Mountain Zebra National Park, Cradock, South Africa.

1 - Bankberg
2 - Spitskop
3 - Rondekop
4 - Fonteinkloof
5 - Grootkloof
6 - Kwaggasrif
7 - Volstruisplaat
8 - Doornhoekdam
9 - Boesmankloof
10 - Kranskoprif
11 - Springbokvlakte
12 - Berghof homestead
13 - Park warden's office

different weathering patterns of dolorite and sandstone, which form large interstices, constitute ideal habitat for hyrax colonies in the Park.

CLIMATE

In view of the mountainous terrain and relatively large altitudinal differences within the Park, local climate variations can be expected. Variations in rainfall, temperature and exposure to wind are clearly manifested in the diversity of vegetation types occurring in the Park.

The climate can generally be described as semi-arid with c. 70% of the rainfall occurring during the summer months, predominantly in February and March. Due to the irregularity of rainfall, mild to severe droughts occur periodically. Air temperatures exhibit major circadian and seasonal fluctuations.

Precipitation

Rainfall recorded (1962 - 1982) at Babylons Toren (Fig. 6) shows an annual mean of 394 mm. The highest monthly mean occurs during March (79 mm) and the lowest during September (10 mm) (Table 2). The month with the highest consistent rainfall is January and the longest periods without rain were two three month periods between June and August in 1966 and 1969.

The rainfall within the Park is markedly influenced by the high

Table 2: Rainfall (mm) recorded in the MZNP during a 20 year period, July 1962 - July 1982.

Month	Mean	Range
January	54,7	20,6 - 117,5
February	59,1	6,0 - 112,5
March	78,6	2,5 - 208,0
April	36,7	8,4 - 66,3
May	21,2	0 - 89,0
June	10,9	0 - 27,0
July	12,3	0 - 45,0
August	19,3	0 - 87,0
September	10,1	0 - 35,0
October	27,0	0 - 68,5
November	31,1	0 - 80,3
December	32,8	0 - 117,0

Bankberg and Kranskoprif areas which also affect its spatial distribution. The areas west of Kranskoprif receive more rain than does the eastern section. The area with the highest rainfall is the Grootmat basin (Fig. 6) while the area with the lowest rainfall is located in the most northerly region of the Park.

Because of the large spatial variation in rainfall within the Park it was decided to use rainfall data recorded at Babylons Toren, Weltevrede homestead, and the farm Daniëlshoek (Table 3) for the purpose of this study. The three recording sites are situated in those parts of the MZNP and on the neighbouring farm where sampling of hyrax took place.

Although most of the precepitation occurs in the form of rain, snow periodically covers the higher reaches of the Park. Hail occurs frequently during the summer months while frost occurs almost nightly during winter.

Table 3: Monthly mean rainfall (mm) recorded at Babylons Toren, Weltevrede homestead and the farm Daniëlshoek during the three year period, January 1980 - January 1983.

Month	Babylons Toren	Weltevrede homestead	Daniëls-hoek	Mean	Range
January	46,3	26,7	28,1	36,5	26,4 - 55,8
February	85,4	65,0	57,3	60,2	29,5 - 80,8
March	52,5	51,7	38,9	47,7	34,0 - 59,1
April	47,6	32,2	41,7	40,5	12,0 - 79,6
May	19,9	11,0	0,4	10,5	0 - 29,0
June	19,8	9,5	10,4	16,3	1,0 - 32,2
July	18,9	17,0	20,8	18,9	0 - 53,5
August	29,2	25,5	31,3	28,6	9,3 - 53,8
September	14,3	10,3	9,7	11,4	1,4 - 18,0
October	40,8	28,4	29,3	32,8	0,5 - 61,9
November	31,7	19,2	27,5	26,1	18,6 - 39,0
December	21,3	17,2	18,7	19,0	1,3 - 29,0

Temperature and Humidity

Ambient temperature and relative humidity were recorded on a thermohygrograph in a Stevenson Screen near the park Warden's office (Fig. 7) for a period of three years 1969 - 1972 (Penzhorn 1975) (Table 4). The mean monthly maximum temperature varied between 29,1°C in January and 15°C in June and the mean minimum temperatures between 13°C in January and -0,1°C in June. In addition to marked variation in daily temperatures major seasonal variations are also evident. Highest maximum temperatures (37°C) were recorded in January and February whereas June and August had the lowest minimum temperature of -7°C.

The monthly mean maximum relative humidity varied between 59% and 87% and the mean minimum between 25% and 40% (Table 4).

Table 4: Monthly mean air temperature and relative humidity recorded in the MZNP during January 1969 - January 1972.

Month	Temperature (°C)				Relative Humidity (%)			
	Maximum		Minimum		Maximum		Minumum	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
January	29,1	18 - 37	13,7	7 - 21	72,5	46 - 96	25,0	14 - 50
February	27,4	15 - 37	12,6	7 - 21	83,4	52 - 95	31,3	14 - 72
March	24,9	13 - 34	11,6	5 - 18	58,9	47 - 94	39,9	13 - 68
April	19,3	6 - 28	6,4	1 - 13	86,5	73 - 95	34,4	16 - 71
May	16,8	8 - 25	3,9	-5 - 13	85,3	58 - 96	35,1	14 - 66
June	15,0	7 - 23	0,4	-7 - 10	83,2	36 - 96	33,7	18 - 57
July	15,8	5 - 22	-0,1	-6 - 8	76,1	42 - 96	29,8	15 - 61
August	17,6	3 - 28	1,0	-7 - 8	69,5	28 - 96	27,8	12 - 80
September	19,4	6 - 32	4,1	6 - 13	65,2	19 - 94	28,4	11 - 87
October	22,8	9 - 35	7,7	1 - 15	73,1	20 - 97	31,4	14 - 92
November	25,4	12 - 36	9,5	1 - 17	74,2	17 - 94	28,0	14 - 69
December	28,2	17 - 36	11,5	4 - 12	75,3	33 - 27	26,6	11 - 46

In order to investigate seasonal variations in the feeding behaviour, activity patterns and parasite loads of hyrax two seasons were defined:

(a) Summer (October - April) with a mean maximum temperature higher than 20°C receiving <u>c</u>. 80% of the annual rainfall;

(b) Winter (May - September) with a mean maximum temperature lower than 20°C and little rainfall.

Daylength

The values utilized for daylength were for latitude 32°30'S (Buys 1978). Recordings (made on 15th of each month) showed that the shortest day occurred in June (10,02 h of light) whereas the longest day occurred during December (14,28 h of light).

Wind

During winter and summer winds come predominantly from a north-easterly direction. Strong winds, which occur during summer, range between south and east.

Recordings of wind distance made at the Agricultural Research Station at Cradock for the six year period (1976 - 1981) indicated that

Table 5: Monthly mean wind distance (km) recorded at the Agricultural Research Station at Cradock for the six year period, January 1976 - December 1981.

Month	Mean	Range
January	211,0	11,6 - 454,8
February	186,7	10,0 - 398,6
March	157,4	10,1 - 395,9
April	140,6	10,9 - 360,4
May	144,4	10,3 - 465,8
June	142,1	10,5 - 432,3
July	154,6	10,1 - 446,7
August	179,4	10,0 - 762,6
September	181,6	10,1 - 454,0
October	211,1	10,0 - 504,5
November	245,9	92,2 - 515,0
December	252,1	84,8 - 461,2

December is the month with the highest mean wind distance (252 km) and April the month with the lowest (141 km) (Table 5).

WILDLIFE

De Graaff & Nel (1970) and Nel & Pretorius (1971) listed 33 small mammal species in the MZNP while Penzhorn (1971) discussed the occurrence and introduction of large mammals into the MZNP. Additions and amendments to the list of mammals, birds and reptiles are given by Grobler & Bronkhorst (1981a,b). The numbers of large animals present in the MZNP during a National Parks Board census (ground counts) conducted during February 1983 are given in Table 6.

Table 6: Estimated numbers of large animals present in the MZNP during a census conducted during February 1983.

Animal species	Number present
Mountain reedbuck (*Redunca fulvorufula*)	500 - 600
Springbok (*Antidorcas marsupialis*)	400 - 450
Blesbok (*Damaliscus dorcas phillipsi*)	80 - 90
Black wildebeest (*Connochaetes gnou*)	155 - 165
Eland (*Taurotragus oryx*)	140 - 150
Red hartebeest (*Alcelaphus buselaphus caama*)	60 - 70
Grey duiker (*Sylvicapra grimmia*)	30 - 40
Steenbok (*Raphicerus campestris*)	30 - 40
Klipsprinker (*Oreotragus oreotragus*)	15 - 20
Kudu (*Tragelaphus stepsiceros*)	25 - 30
Cape mountain zebra (*Equus zebra zebra*)	210
Ostrich (*Struthio camelus*)	49

Several of the known natural enemies of the hyrax (Fitzsimons 1920; Hanse 1962; Sale 1965a; Grobler 1981) occur in the MZNP. Amongst the mammals, the caracal (lynx) (*Felis caracal*) can be considered the main predator. Caracal are sighted frequently in the MZNP and they number *c.* 25 (15 adults and 10 juveniles) (Grobler 1981). Other mammals which may feed on hyrax include the black-backed jackal (*Canis mesomelas*), wild cat (*Felis lybica*), Cape grey mongoose (*Herpestes pulverulentus*) and the Cape fox (*Vulpes chama*) (Hanse 1962).

Several raptor species are known to prey on hyrax and the black eagle (*Aquila verreauxi*) preys extensively on them (Sale 1965a; Gargett 1972, 1977). Two pairs of black eagles are resident in the MZNP and another pair use the Park as their hunting ground (Grobler 1980).

Among the reptiles the Cape cobra (*Naja nivea*) and the puff-adder (*Bitis arietans*), which are both present in the MZNP, are known to take hyrax (Hanse 1962).

The Park contains *c.* 190 bird species; those new to the MZNP not listed by Skead (1965), Penzhorn & Bronkhorst (1976) and Penzhorn (1977) are supplied by Grobler & Bronkhorst (1981a).

VEGETATION

The vegetation of the Cape Midlands is subjected to continuous climatic tension because of the influence of an arid climate from the west and a more moderate climate from the east. A close correlation has been demonstrated in the area between seasonal rainfall and growth of grasses and karoo shrubs (Roux 1966).

The vegetation in the MZNP area is defined as Karroid _Merxmeullera_ Mountain Veld replaced by Karoo for the higher slopes and False Karroid Broken Veld for the northern parts (Acocks 1975).

A detailed phytosociological reconnaissance of the MZNP was conducted by Van der Walt (1980). Based on variations in plant species associations and dominance, 13 stratification classes were recognised and interpreted in the form of a vegetation map (Fig. 8). The vegetation of the MZNP can be divided into three major groups of plant communities (Van der Walt op. cit.): (a) Riparian communities; (b) Valley slopes/summits communities; (c) Plateaux/hot shaly slopes communities.

In the riparian community Van der Walt distinguishes mesic riparian bush (which occurs upstream where soils are moist and strongly leached) from xeric riparian bush (which occurs extensively on the lower alluvial levels of the Wilgerboom River). Prominent plant species present in the riparian community are listed in Table 7.

Approximately 77% of the total Park area is occupied by plant communities of valley slopes and summits. These communities can be classified into two mesic communities and three strongly related xeric communities (Van der Walt 1980). Prominent plant species showing an overall distribution between the mesic and xeric related communities are listed in Table 8.

The third major plant community, namely grass and shrubland, found on

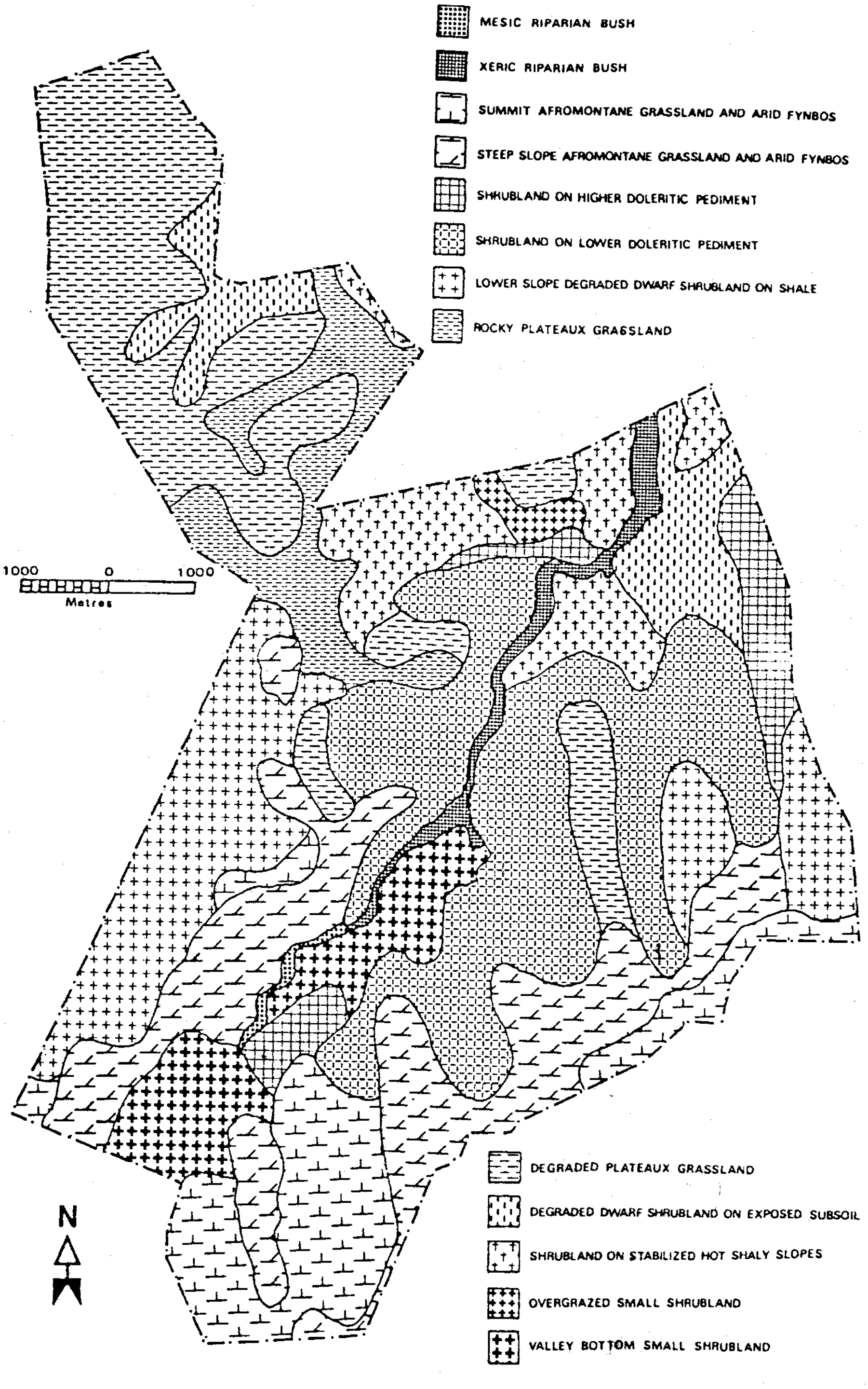


Figure 8: Vegetation map of the Mountain Zebra National Park (after Van der Walt 1980).

Table 7: Prominent plant species of mesic and xeric riparian bush present in the MZNP.

Mesic riparian bush	Xeric riparian bush
Leucosidea sericea TS	*Acacia karroo* T
Rhamnus prinoides TS	*Rhus lancea* T
Rapanea melanophloeos T	*Lycium oxycarpum* TS
Buddleia salviifolia TS	*Diospyros lycioides* TS
Olea africana T	*Artiplex semibaccata* F
Ehrharta erecta AG	*Felicia muricata* DS
Bromus wildenowii PG	*Ballota africana* F
Eragrostis curvula PG	*Garuleum pinnatifidum* F
Carex spicato-paniculata F	*Psilocaulon absimile* F
Berkheya armata F	*Panicum coloratum* PG
Senecio burchellii F	*Stipa dregeana* PG
	Stellaria media F
	Cineraria lobata F
	Teucrium africanum

T - tree; TS - tall shrub; DS - dwarf shrub; PG - perennial grass; AG - annual grass; F - forb.

Table 8: Prominent plant species showing an overall distribution between mesic and xeric related communities of valley slopes and summits.

Plant species	Plant species
Merxmuellera disticha PG	*Felicia filifolia* SS
Eragrostis curvula PG	*Chrysocoma tenuifolia* SS
Themeda triandra PG	*Melobium microphyllum* DS
Aristida diffusa var. burkei PG	*Helichrysum dregeanum* DS
Tragus koeleroides AG	*Lightfootia tenuis* DS
Eustachys paspaloides PG	*Pelargonium quercifolium* MS
Cymbopogon plurinodis PG	*Sutera caerulea* DS
Digitaria eriantha PG	*Senecio burchellii* F
Heteropogon contortus PG	*Lotonis laxa* DS
Aristida adscensionis AG	*Sutera mollis* DS

PG - perennial grass; AG - annual grass; DS - dwarf shrub; SS - small shrub; MS - medium shrub; F - forb.

the northern relatively level sandstone and doleritic plateaux and steep, hot shaly slopes of the Park, shows an overall distribution of grasses and dwarf shrubs. These are listed in Table 9.

Table 9: Grasses and dwarf shrub components showing an overall distribution in plant communities of the plateaux and hot shaly slopes.

Plant species	Plant species
Eragrostis curvula PG	*Melobium microphyllum* DS
Tragus koeleroides AG	*Felicia filifolia* SS
Chrysocoma tenuifolia DS	*Asparagus acocksii* SS
Aristida congesta AG	*Helichrysum dregeanum* DS
Eragrostis obtusa PG	*Walafrida saxatilis* DS
Themeda triandra PG	*Hermannia coccocarpa* DS
Eustachys paspaloides PG	*Lycium cinereum* DS
Indigofera alternans DS	*Phymaspermum parvifolium* DS

PG - perennial grass; AG - annual grass; DS - dwarf shrub; SS - small shrub.

SUMMARY

This study was conducted in the MZNP, an area of 6 536 ha, situated 24 km south-west of Cradock in the Cape province.

The Park is characterized by varying topography. The geological formation in the Park consists mainly of sandstone, siltstone and mudstone of the Lower Stage, Beaufort Series, Karoo System, with post-Karoo dolerite intrusions.

Approximately 70% of the annual rainfall occurs during summer. A large spatial variation in rainfall exists within the Park. Large daily and seasonal variations in air temperatures are evident. The highest maximum temperatures are recorded in January and Febraury whereas June and August have the lowest minimum temperatures. Data on the variation in daylength and wind are presented.

Approximate numbers of the large mammal species occurring in the Park are given and the natural enemies of the hyrax in the Park are mentioned. Amongst these the caracal/lynx and black eagle are the most important.

The vegetation in the MZNP area is defined as Karroid *Merxmeullera* Mountain Veld replaced by Karoo on the higher slopes and False Karroid Broken Veld in the northern parts. Prominent plant species within the three major vegetation types occurring in the park are listed.

CHAPTER III

SAMPLING TECHNIQUES

INTRODUCTION

Destructive sampling is essential for constructing accurate age determination schedules and is a pre-requisite for the understanding of many aspects of animal biology. Valuable quantitive information concerning feeding behaviour, reproductive state and physiological condition can also be obtained in this manner.

Of critical importance to population studies are effective trapping and marking methods which facilitate the study of movement, social behaviour and growth. Skulls collected in the field provide valuable information on natural age-specific mortality.

This chapter describes and critically evaluates the methods used for shooting, capturing and marking hyrax. The collection of skulls is also described.

DESTRUCTIVE SAMPLING

Introduction

Although destructive sampling of hyrax was conducted in the MZNP and on the neighbouring farm, Daniëlshoek, this was done in such a way as to minimize disturbance to the hyrax population within the boundaries of the Park. Where destructive sampling in the MZNP was undertaken it was done in the non-study areas, i.e. those areas where no active trapping was conducted or where observations of marked animals were carried out.

Methods

Two .22 calibre rifles (Standard and Hornet) were used for sampling, both of which were fitted with 3 - 9 x zoom telescopic sights. To minimize wounding, most shots were aimed at the neck. This was also done since the head and all other parts of the body were required for subsequent analyses. The .22 Hornet rifle was effective up to a range of 150 m but because of the large distances over which some hyrax were shot, head and back shots sometimes resulted. These caused considerable damage and reduced the value of carcasses for subsequent analyses. The price of .22 Hornet ammunition is six times that of ordinary high velocity .22 ammunition and subsequently the .22 Hornet was not used after April 1980. Subsequent shooting was conducted with a .22 calibre Standard rifle using high velocity cartridges. The latter were effective up to a range of only 50 m but far less damage was caused to the specimen.

Most shooting was done in the 3 h period after sunrise and the 2 h period prior to sunset. Two methods were employed to shoot hyrax. The first method involved walking along mountain ridges and cliffs. Single animals were shot on sight; but when groups were encountered the nearest animal was shot. The second method which proved to be more time consuming was to hide near a hyrax colony and shoot animals as they emerged.

Results

During the three year field study (January 1980 - December 1982) a total of 589 hyrax were shot in two main sampling areas (Table 10).

Table 10: Number of hyrax shot in the MZNP and Daniëlshoek (January 1980 - December 1982).

Year	1980	1981	1982
MZNP	123	101	75
Daniëlshoek	169	71	50
Total	292	172	125
Mean per month	24,3	14,3	10,4

Discussion

The best times for sampling were found to be early morning when hyrax emerged from refuges and late afternoon just before re-entry. During winter months, hyrax huddled and basked more extensively which facilitated sampling. Strong winds, rain and high ambient temperatures were the main factors limiting shooting success as these environmental factors caused hyrax to shelter in refuges.

CAPTURE

Introduction

Detailed studies of mammal population usually require the collection of data from individually marked animals in the field, and in order to accomplish this, animals have to be captured, marked, released and recaptured at regular intervals. The use of an effective trap causing the minimum amount of injury to animals is indespensable for such studies.

Methods

Trapping hyrax in the MZNP took place at three sites, two near Doornhoek dam and the other next to the laboratory near the Weltevrede homestead (see Fig. 7).

Wire mesh (10 mm apertures) box cages measuring 400 x 400 x 750 mm, with a hinged trapdoor, were used initially. However, because of the severe nasal injuries that occurred, these traps were modified. A wooden box trap (300 x 300 x 750 mm), with a hinged trapdoor above the entrance, was placed at the back of the wire cages (Fig. 9). The door, which only opened inwards, allowed hyrax to enter but prevented those inside from leaving. When caught in a wire cage hyrax took refuge in the dark wooden nest box and were trapped in this way. The trapdoor was held open by a small twig which was knocked down by the hyrax as it entered. Traps were baited with leaves of <u>Olea europaea</u>.

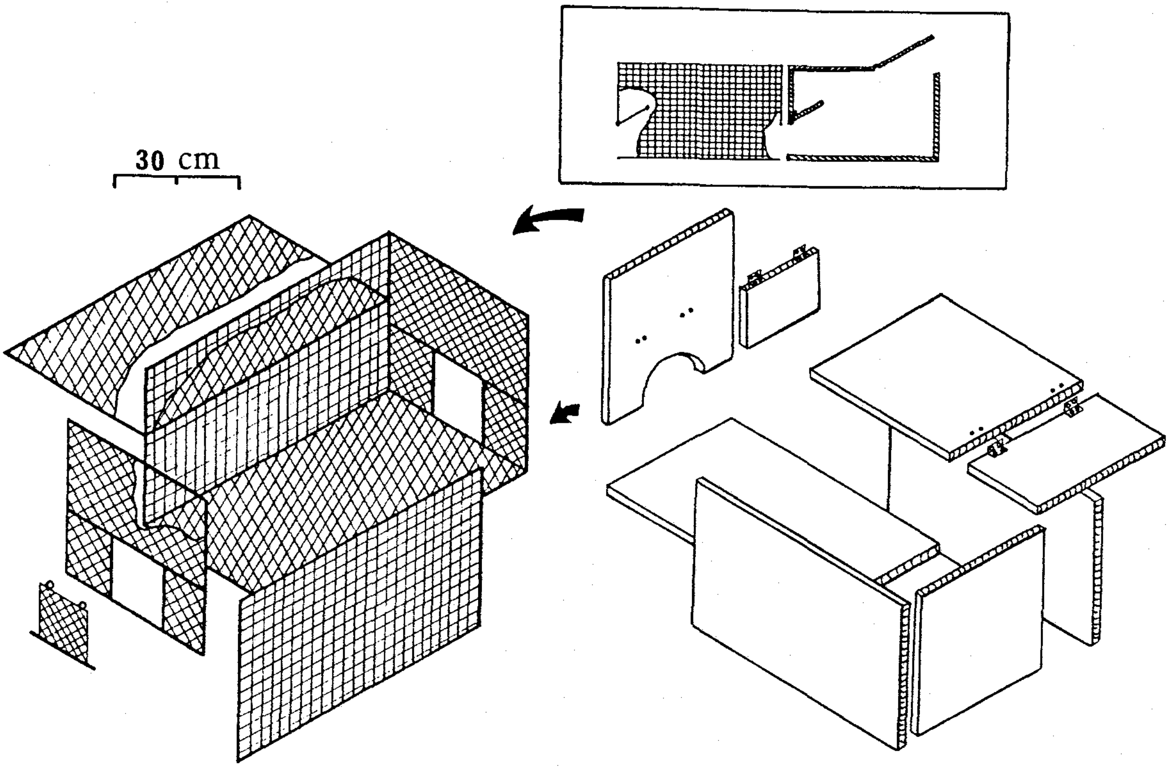


Figure 9: Trap-cage used for capturing hyrax in the MZNP.

In many cases two animals were caught in the same trap. The second animal because it had pushed open the swingdoor and entered the baited wire cage and subsequently the wooden box. Thirteen of these traps were used.

A prebaiting period of 4-6 days, in which baited traps were left open, was allowed. All the traps were placed in close proximity to hyrax colonies. The traps were baited and set at sunset. Throughout the following day they were regularly checked and rebaited at five hourly intervals. Trapping commenced during the dry months (July - October) of 1980 and was terminated in September 1982.

Results

A total of 59 hyrax were trapped and marked during the study period (Table 11). Several recaptures of individual hyrax occurred bringing the total number of captures to 155.

Table 11: Total number of individual hyrax trapped and marked at three trapping sites in the MZNP (July 1980 - September 1982).

MONTH	JUVENILES	ADULTS	TOTAL
July	7	2	9
August	4	-	4
September	31	3	34
October	4	1	5
November	1	2	3
December	-	1	1
February	-	1	1
March	-	2	2
TOTAL	47	12	59

Hyrax entered trap-cages throughout the course of the daylight period and no fixed pattern was discernable. Early morning checks revealed that hyrax very seldom entered traps after sunset.

Prior to attaching the wooden boxes to the trap-cages used in this study, three hyrax of the 38 captured were injured so badly in the traps that they had to be destroyed. None of the hyrax (n = 117) caught or recaptured in the modified traps sustained any serious injuries.

Discussion

Although many authors (Sale 1965a; Millar 1971; Fourie 1972; Fairall 1980; Hoeck 1982) mention trapping hyrax alive, very few describe their traps or mention trapping mortality. Those who do (Sale 1965a; Fourie 1972) have either used wire or steel mesh traps. These traps have obvious disadvantages. Panic stricken animals try to force their way out of the trap-cages and due to their poor near vision (Sale 1970a) sustain serious nasal injuries. Of the 15 hyrax captured by Fourie (1972) seven sustained serious injuries, of which two subsequently died. Care must also be taken not to leave hyrax exposed to direct sunlight for too long a period. Before the traps were modified, one hyrax was found dead in the trap after being exposed for too long to direct sunlight during a hot summer day. Hyrax caught in the late afternoon were left overnight in the boxes, which provided protection against cold winter nights.

Previously captured and marked hyrax seemed to be trap prone resulting in a high incidence of recapture. The most successful month for trapping was September. Although hyrax are known to show some activity on clear moonlit nights (Coe 1962) the reported correlation between trapping success and moonphase (Fourie 1972) is misleading and not proven statistically. Of the 15 hyrax Fourie caught, four were captured at night during first quarter and 11 during fullmoon. However, taking into consideration that his first checking time after baiting the traps the previous evening was 3 h after sunrise the next morning; and that the majority (95%) of trapping times corresponded either with first quarter or full moon; it may very well be that the hyrax had entered the traps after sunrise, prior to the first checking.

In conclusion, the traps designed for this study were very effective, minimizing injuries and providing ample protection during hot summer days and cold winter nights.

MARKING

Introduction

In many animal population studies, the identification of individual animals from a distance is important to gain information on social behaviour, activity patterns and home range. If the animal is large enough and if sexes can easily be distinguished, individuals may be recognised without marking them, merely by conspicuous pelage patterns or markings. In many small to middle-sized animals no obvious sexual-dimorphism or individual characteristics can be distinguished from a distance, thus necesitating the use of a marking system. It is important, however, that the marked animals must be easily identified, marks must be unique and must not inhibit the animal in any way.

Methods

Trapped hyrax were transported to the laboratory in wooden boxes where they were taken out of the boxes by a person wearing thick gloves. Ketamine hydrochloride (Ketalar 100 mg/ml, Parke Davis) at a dosage rate of 20 mg/kg was used as the immobilising agent. The drug causes an anaesthetic state which is characterized mainly by loss of consciousness, profound analgesia, maintained pharyngeal/laryngeal reflexes and with no depression of skeletal muscle tone. Mean immobilization time was 30-40 minutes.

Two methods of marking hyrax were employed, i.e. freeze-branding/ cryo-branding as described by Kambitsch, Wittman & Hemstrom (1969) and Lazarus & Rowe (1975); and ear-tagging. Freeze-branding is a technique used to kill the pigment producing melanocytes in the hair follicles of the animals by use of a supercold branding iron. This results in white instead of coloured hair regrowth. Males were freeze-branded dorso-laterally on the front limbs and females on the back limbs, on both sides. Hair in the area of the branding site was removed by means of a pair of fine scissors and a scalpel and the area was cleaned with 70% alcohol (Fig. 10). Two shapes of solid copper branding irons were used; a bar type (30 x 10 mm) and a round one (30 mm diameter), each of which were 10 mm deep.

The branding irons were supercooled to c. -67°C by placing them in a mixture of dry ice and 95% methanol. They were ready to use when very small bubbles rose from the submerged iron and they were then pressed evenly, but firmly onto the cleaned skin surfaces. Seven seconds were allowed for branding in adults and 4 s in juveniles.

Eartags consisted of stercolite (S.A. Canvas Co. (Pty) Ltd. Port Elizabeth) measuring 60 mm long and 6 mm broad, except for the terminal section which was cut in the form of a square (Fig. 11). Hyrax have small rather soft ears, making tagging difficult. It is important to remove the hair from the outer surface of the ear and to insert the tag as deep as possible in the ear cartilage. A scalpel was used to make an incision in the middle of the ear cartilage, horizontal to the lateral edge of the ear. The narrow part was pushed from the inner surface of the ear through the incision and the loose ends, together with a 10 x 5 mm metal disc with the animals' number engraved on it, were riveted together. The tagged ears were sprayed with gentian violet to prevent infection. The latter procedure was repeated whenever the animal was recaptured. To facilitate the identification of sexes and age classes over long distances in the field, males were tagged on the left ear and females on the right ear. Different tag colours were used for the various age classes.

Results

Due to the long hair of the hyrax, the different shapes of freeze-brands used in order to identify individuals were distorted to such an extent that they were rendered useless. Only after subsequent recapture and clipping of the hair was the original shape discernable (Fig. 12). If the branding iron was applied for too long, scab formation resulted (Fig. 13); if for too short a time, no hair discoloration was noticeable.

The eartags used in this study remained on the ear for two years or longer (Fig. 11) and the tag loss was estimated at less than 10% for the entire study. The main cause of tag loss appeared to be infection.

Discussion

A variety of methods have been used to mark hyrax. Hoeck (1982) used freeze-branding, hair dye and ear tags, but gave no description of branding iron application times or tagging success. Although freeze-branding is a permanent method of marking (Kambitsch et al. 1969) it does, however, have a number of disadvantages as far as the hyrax is concerned. The long hair of the hyrax distorted the different shapes of freeze brands making long distance identification of individuals impossible. Hyrax also sandbath, which makes the pelage dirty, and the white brand difficult to observe from a distance. Animals also had to be transported to the laboratory to be freeze-branded, and this proved to be time consuming, whereas they could be tagged in the field immediately after capture.

Eartagging of hyrax resulted in limited success. Sale (1965a) used circular plastic ear tags which remained on the ear for up to two months, while Fairall & Crawford (1983) used monofilament fish tags with only moderate success. As infection appears to be the main cause

Figure 10: Ear-tagged hyrax with cleaned branding site.

Figure 11: Tag that has been attached for two years to the ear of a hyrax.

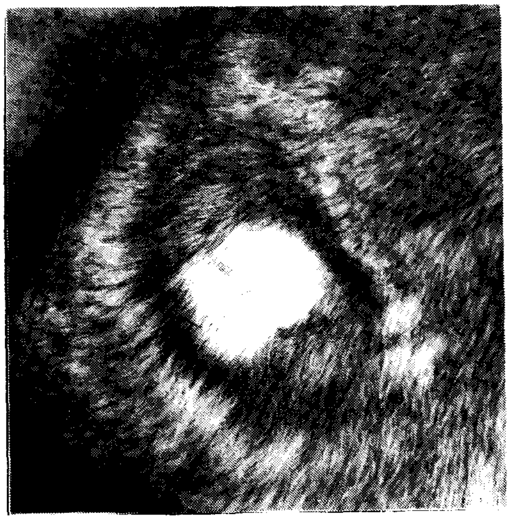


Figure 12: Freeze-branded hyrax showing growth of white hair.

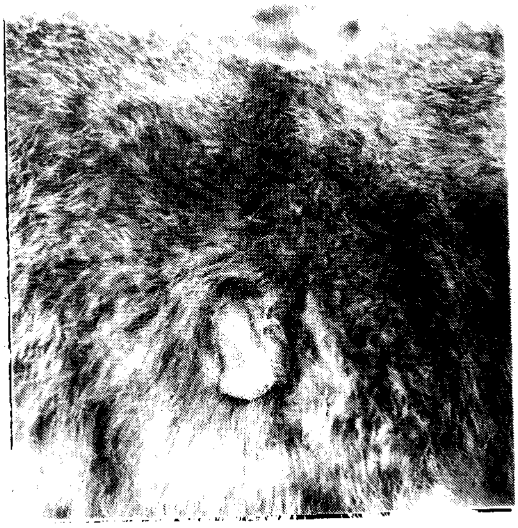


Figure 13: Branding iron applied for too long resulting in scab formation.

of tag loss, it is important to treat all tag sites on recaptured animals with gentian violet. This procedure resulted in tags being retained for a considerable time in the present study.

SKULL COLLECTION

Introduction

Quantification of mortality due to predation, disease and old age is often difficult for natural populations. Wildlife researchers have to resort to indirect methods to obtain this information, for example, collecting skulls in the field.

When sexed and accurately aged, skulls can provide valuable information on population structure and age-specific mortality patterns.

Methods

Throughout the course of this study skulls were collected in the field and at black eagles' nests by myself and staff of the MZNP. As a means of comparing age structure with that of another population within the same district, but with different categories of land use (conservation as opposed to small stock farming) skulls were also collected at black eagles' nests on the farm Rietvlei (c. 40 km south-east of Cradock).

Where the maxilla and mandible were collected together they were placed in a small labelled plastic bag. When either one or the other was collected separately it was also placed in a labelled plastic bag. Upon return to the laboratory, all the maxillae were numbered and sexed, and those which had paired mandibles were stored with these.

Hyrax have sexually dimorphic upper incisors making sexing of the maxillae relatively easy. In both sexes, the upper incisors are approximately triangular in cross-section with the apex of the triangle directed anteriorly (Fig. 14). In males the two anterior surfaces are equal in width, being divided by a definite, centrally-situated ridge. In females, this ridge occurs more medially, with the result that the medial of the two anterior surfaces is markedly narrower than the outer one.

In those cases in which the upper incisors were missing, the sex could still be determined by inspection of the tooth alveolus which has the same shape as the incisors.

Results

A total of 707 maxillae and 294 complete sets of mandibles were collected in the MZNP and the farm Rietvlei during the course of this study (Table 12).

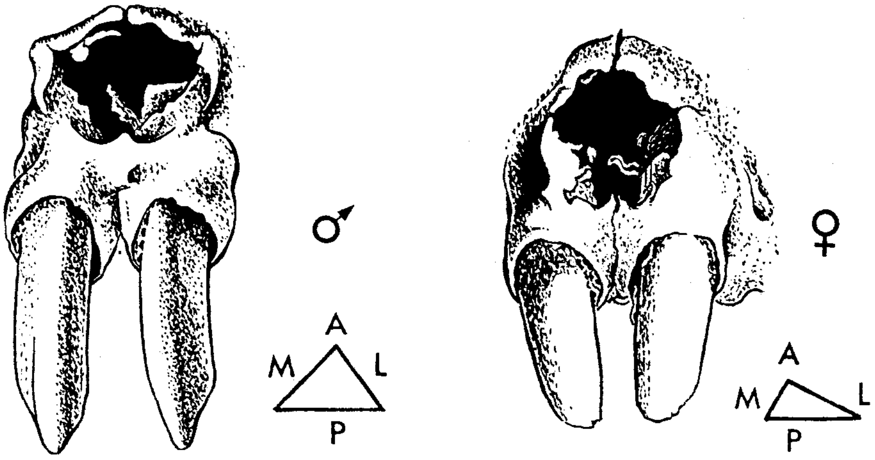


Figure 14: Sexually dimorphic upper incisors of the hyrax, as seen anteriorly and in cross-section (A - anterior; P - posterior; L - lateral; M - medial).

Table 12: Number of maxillae and complete sets of mandibles collected in the MZNP and the farm Rietvlei (January 1980 - December 1982).

Locality	Maxillae	Mandibles (complete sets)	Total
Black eagles' nests (MZNP)	216	138	354
Black eagles' nests (Rietvlei)	61	42	103
Field (MZNP)	430	114	544
Total	707	294	1 001

Skull collection in the field was hampered greatly by the rugged terrain in the MZNP and the dense vegetation on the slopes of the kloofs. The majority of skulls were collected from crevices in and around hyrax refuges.

Skulls of young age classes were under-represented (CHAPTER X).

Discussion

The high number of maxillae in relation to mandibles collected may be attributed to several reasons: firstly, being smaller and thus less conspicuous, the mandibles are more easily overlooked; secondly, the mandibles may have a more rapid rate of deterioration; and thirdly, they may be more readily fractured and consumed by predators and/or scavengers. The above mentioned reasons may also explain the under-representation of skulls belonging to young age classes.

SUMMARY

The methods used for destructive sampling of hyrax are mentioned. A .22 standard rifle was used in an economical and effective way. The best sampling times were early mornings (as the hyrax were leaving their refuges) and late afternoons (just before hyrax entered their refuges).

The live capture of hyrax is discussed and a description of an effective trap-cage is given.

Two methods (ear-tagging and freeze-branding) were used to mark hyrax. These two methods are assessed critically. Prevention of infection in the ears of tagged hyrax, resulted in long retention times of the tags.

The methods used for the collection of skulls are discussed.

CHAPTER IV

GROWTH

INTRODUCTION

Growth can be defined as the measurable increase of an organized system, produced by its assimilation of materials obtained from its environment (Von Bertalanffy 1938). The three quantitative aspects of growth in which zoologists are interested are; growth in time in some dimension of an animal; growth in the relative sizes of two dimensions of a single animal, and changes in shape as a function of time.

According to Hanks (1972) an objective quantitative assessment of growth is essential when comparing growth rates of animals from different environments; in taxonomic studies; when estimating population biomass; and when estimating possible rates of exploitation. Little has, however, been published on growth rates of mammals. This is largely because of the difficulties involved in obtaining body measurements and determining the mass of representative samples, and in addition the limitations of existing age determination techniques (Grobler 1978).

In the present study growth is quantified by measurement of body mass, head/body length, hind foot length and girth and the fitting of such data to Stevens' asymptotic growth equations. The correlations between mass and the measurements of head/body, hind foot length and girth are demonstrated by regression equations.

METHODS

Measurements taken

Measurements of shot hyrax were taken according to standard procedures (Smithers 1973). The following were recorded:

(a) body mass; accurate to 0,01 kg.

(b) stomach mass; accurate to 0,01 kg.

(c) head/body length of the animal lying on its side. This measurement was taken as the direct distance from the tip of the nose to the end of the vertebrae (to the nearest mm).

(d) hind foot length; from the tip of the middle toe to the end of the heel with the foot bent at an angle of 90° to the tibia (to the nearest mm).

(e) body girth; measured directly behind the shoulders (to the nearest mm).

The age of each hyrax was determined according to procedures set out in CHAPTER V.

Data analysis

Theoretical growth curves for the various parameters were calculated using the asymptotic regression equation $y = \alpha + \beta \rho^{x}$ where y tends to an asymptote as x tends to infinity. The equation contains three biologically significant parameters, α representing the asymptotic value of y, β representing the change in y when x passes from 0 - + ∞ (total growth achieved), and ρ representing the growth rate (Stevens 1951). This equation has been computerised by Berjak (pers. comm.) and growth equations were calculated using the Univac computer at the University of Natal, Durban.

Separate equations for pregnant and non-pregnant females were not calculated as adult females were pregnant for the greater part (7,5 months) of the year.

Statistical comparisons between various measurements of the hyrax were made on a Hewlett Packard 91 desk calculator.

RESULTS

Growth in relation to age

The Stevens asymptotic growth equations for the different parameters measured on 450 hyrax are given in Table 13.

Actual growth rates for hyrax were superimposed on the theoretically calculated growth curves (Figs. 15 - 22). The actual growth data on the graphs were expressed as the mean values (±S.E.) for the different age class intervals (CHAPTER V).

Near asymptotic levels were taken as 97% of the value of the theoretically calculated asymptotes. The age at which hyrax attain

Table 13: Stevens asymptotic growth equations for body mass, head/body length, hind foot length and girth measured on 450 hyrax sampled in and around the MZNP.

Sex	Measurement	Equation ($y = \alpha + \beta\rho^x$)	n
♂♂	body mass	$M_t = 3183,78 + [-3010,29(0,9502)^t]$ g	193
♀♀		$M_t = 3307,92 + [-3107,87(0,9523)^t]$ g	227
♂♂	head/body length	$HBL_t = 460,99 + [-250,31(0,9234)^t]$ mm	201
♀♀		$HBL_t = 466,37 + [-246,20(0,9286)^t]$ mm	249
♂♂	hindfoot length	$HL_t = 67,21 + [-29,22(0,9153)^t]$ mm	201
♀♀		$HL_t = 65,99 + [-27,69(0,9213)^t]$ mm	249
♂♂	girth	$G_t = 268,00 + [-156,70(0,9297)^t]$ mm	187
♀♀		$G_t = 270,90 + [-155,10(0,9398)^t]$ mm	215

these levels for the different parameters measured are given in Table 14.

Allometric growth

The relationships between body mass and the measurements of head/body, hind foot length and girth are power functions (Table 15) and are presented in Figures 23 - 28.

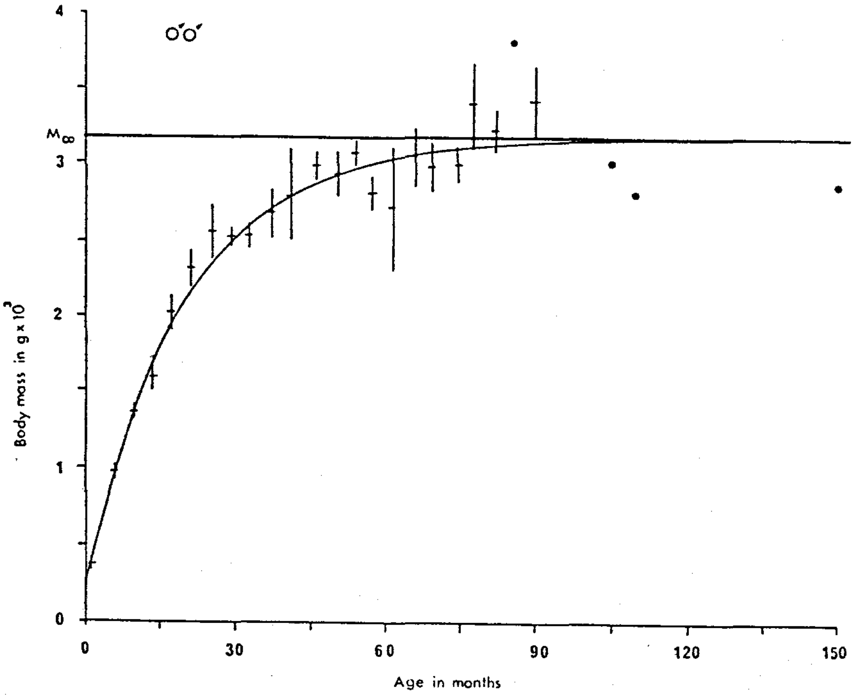


Figure 15: Theoretical Stevens growth curve and actual body masses (means ±S.E.) of male hyrax (n = 193).

(Equation: M_t = 3183,78 + $\left[-3010,29(0,9502)^t\right]$ g; * = single observation)

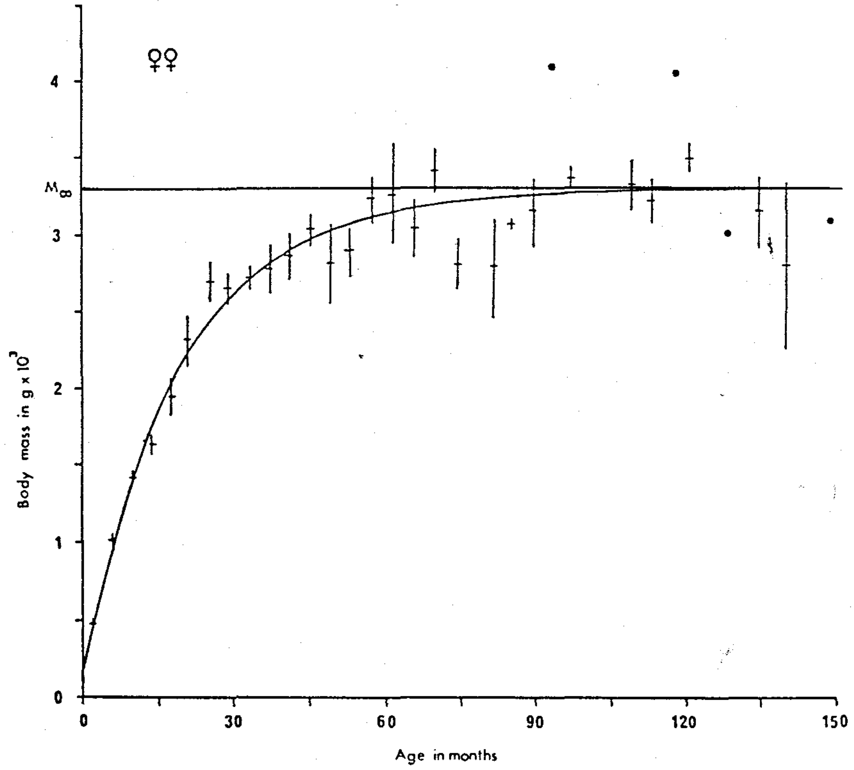


Figure 16: Theoretical Stevens growth curve and actual body masses (means ±S.E.) of female hyrax (n = 227).

(Equation: M_t = 3307,92 + $\left[-3107,87(0,9523)^t\right]$ g; * = single observation)

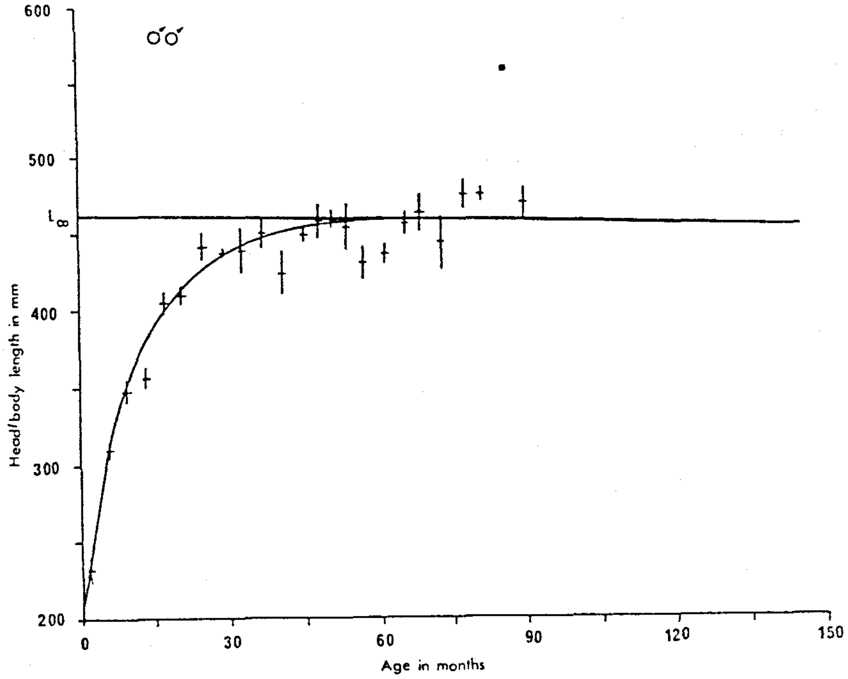


Figure 17: Theoretical Stevens growth curve and actual head/body lengths (means ± S.E.) of male hyrax (n = 201).
(Equation: $HBL_t = 460{,}99 + \left[-250{,}31(0{,}9234)^t\right]$ mm; * = single observation)

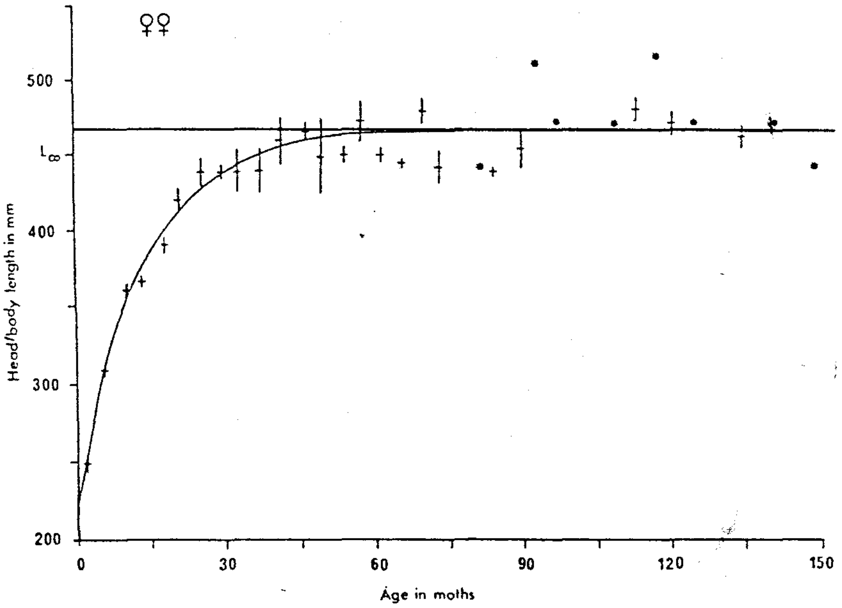


Figure 18: Theoretical Stevens growth curve and actual head/body lenghts (means ± S.E.) of female hyrax (n = 249).
(Equation: $HBL_t = 466{,}37 + \left[-246{,}20(0{,}9286)^t\right]$ mm; * = single observation)

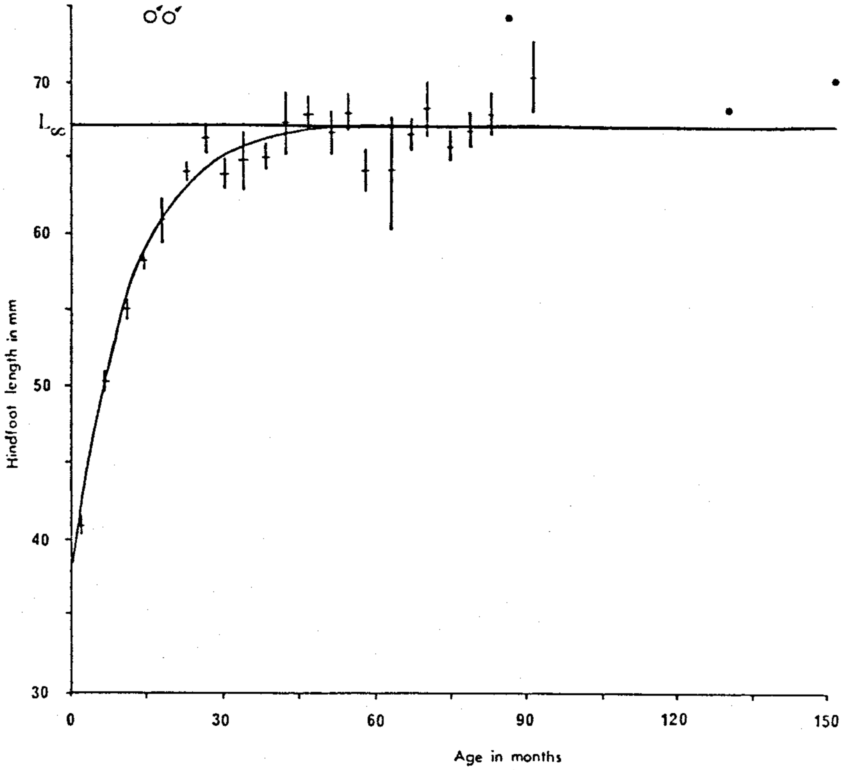


Figure 19: Theoretical Stevens growth curve and actual hind foot lengths (means ±S.E.) of male hyrax (n = 201).

(Equation: $HL_t = 67{,}21 + \left[-29{,}22(0{,}9153)^t\right]$ mm; * = single observation)

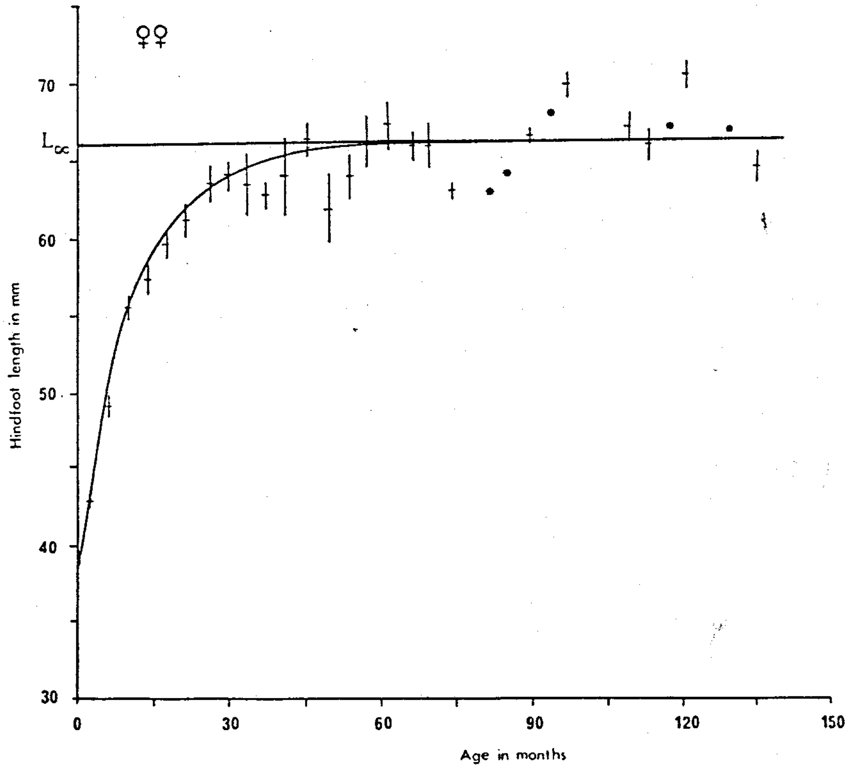


Figure 20: Theoretical Stevens growth curve and actual hind foot lengths (means ±S.E.) of female hyrax (n = 249).

(Equation: $HL_t = 65{,}99 + \left[-27{,}69(0{,}9213)^t\right]$ mm; * = single observation)

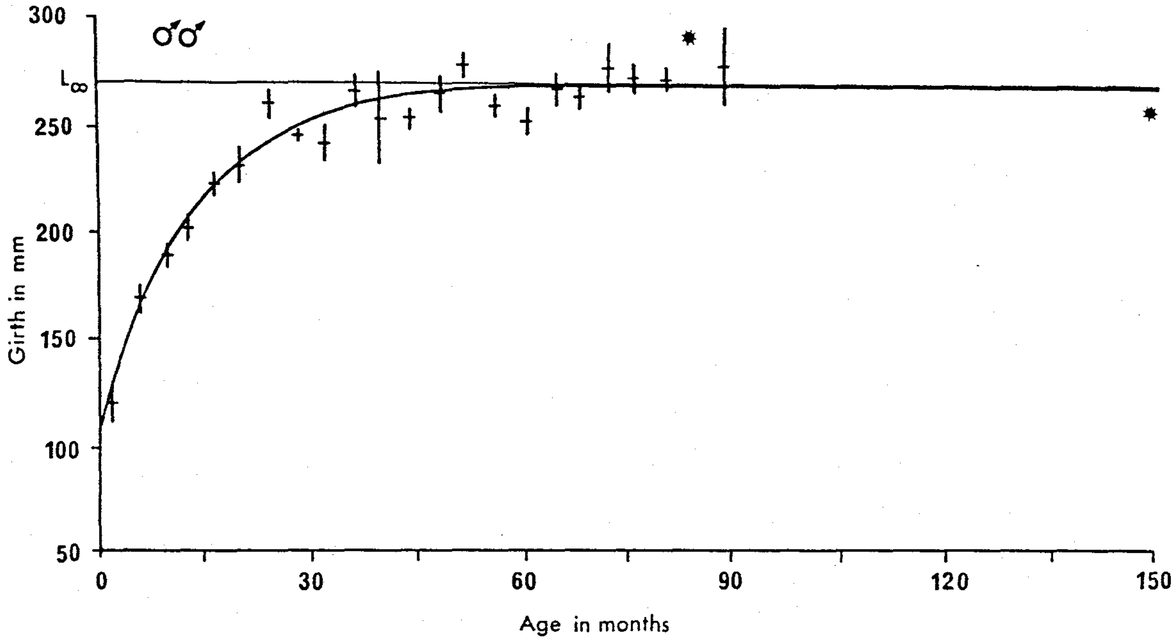


Figure 21: Theoretical Stevens growth curve and actual girths (means ±S.E.) of male hyrax (n = 187).

(Equation: $G_t = 268,00 + \left[-156,70(0,9297)^t\right]$ mm; * = single observation)

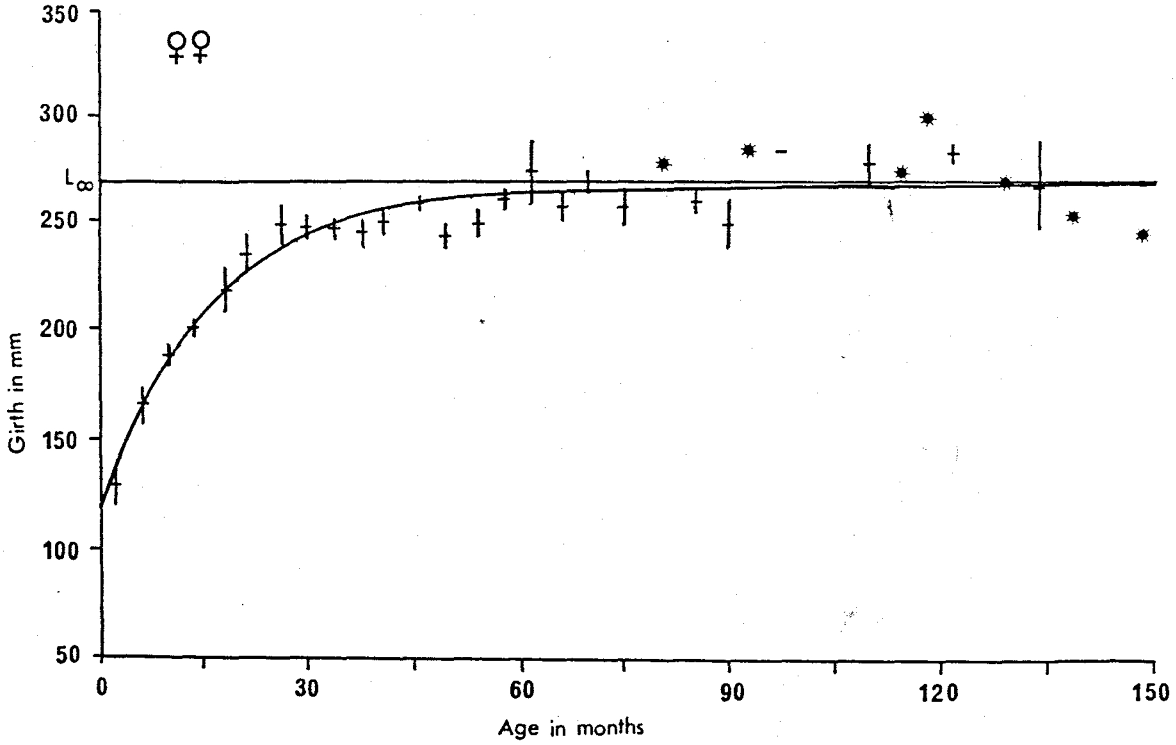


Figure 22: Theoretical Stevens growth curve and actual girths (means ±S.E.) of female hyrax (n = 215)

(Equation: $G_t = 270,90 + \left[-155,10(0,9398)^t\right]$ mm; * = single observation)

Table 14: Near asymptotic levels (97% of asymptote) for the different parameters measured and the age (months) at which these values are attained by hyrax.

Sex	Measurement	Near asymptotic level	Age
♂♂	body mass	3088,27 g	68
♀♀		3208,68 g	70
♂♂	head/body length	447,16 mm	37
♀♀		452,38 mm	39
♂♂	hindfoot length	65,19 mm	30
♀♀		64,01 mm	33
♂♂	girth	259,96 mm	41
♀♀		262,77 mm	48

Table 15: Regression equations demonstrating the relationships between body mass and the measurements of head/body, hind foot length and girth.

Sex	Combination	Equation	r	p	n
♂♂	body mass and girth	$y = 1,27 \times 10^{-2} X^{2,20}$	0,92	0,001	48
♀♀		$y = 7,68 \times 10^{-3} X^{2,30}$	0,93	0,001	52
		(y = mass in g; X = girth in mm)			
♂♂	body mass and head/body length	$y = 1,03 \times 10^{-4} X^{2,80}$	0,99	0,001	45
♀♀		$y = 9,86 \times 10^{-5} X^{2,80}$	0,97	0,001	52
		(y = mass in g; X = head/body length in mm)			
♂♂	body mass and hind foot length	$y = 6,43 \times 10^{-4} X^{3,63}$	0,95	0,001	42
♀♀		$y = 1,12 \times 10^{-4} X^{4,08}$	0,96	0,001	50
		(y = mass in g; X = hind foot length in mm)			

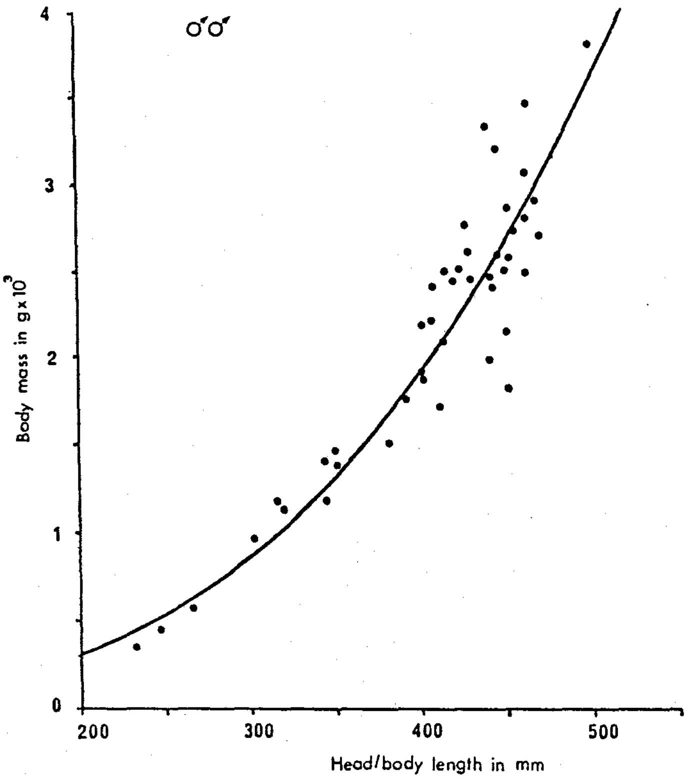


Figure 23: Relationship between body mass and head/body length of male hyrax (n = 45).

(Equation: $y = 1{,}03 \times 10^{-4} X^{2{,}80}$ where y = mass in g; X = head/body length in mm)

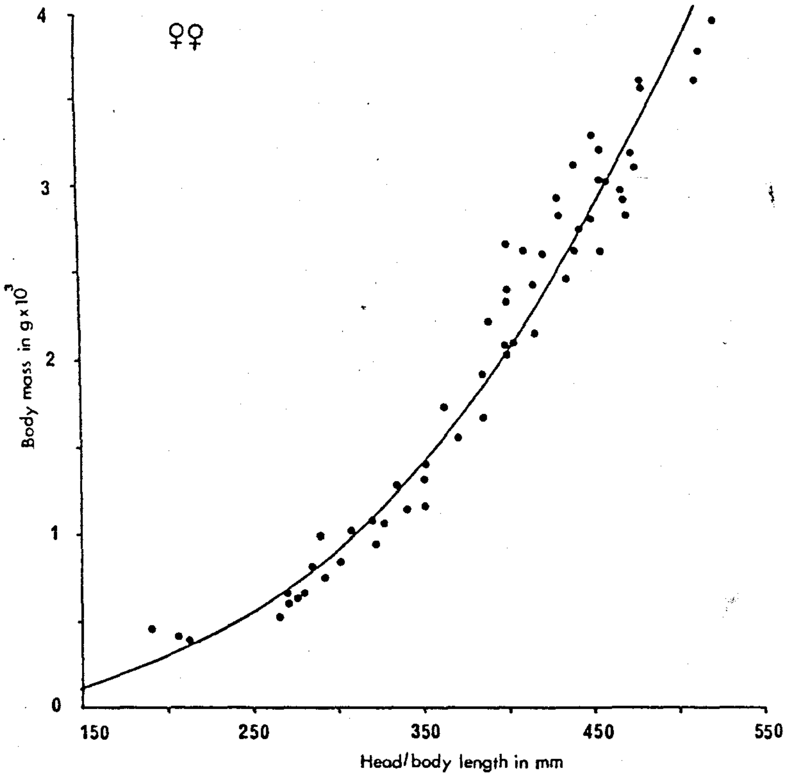


Figure 24: Relationship between body mass and head/body length of female hyrax (n = 52).

(Equation: $y = 9{,}86 \times 10^{-5} X^{2{,}80}$ where y = mass in g; = head/body length in mm)

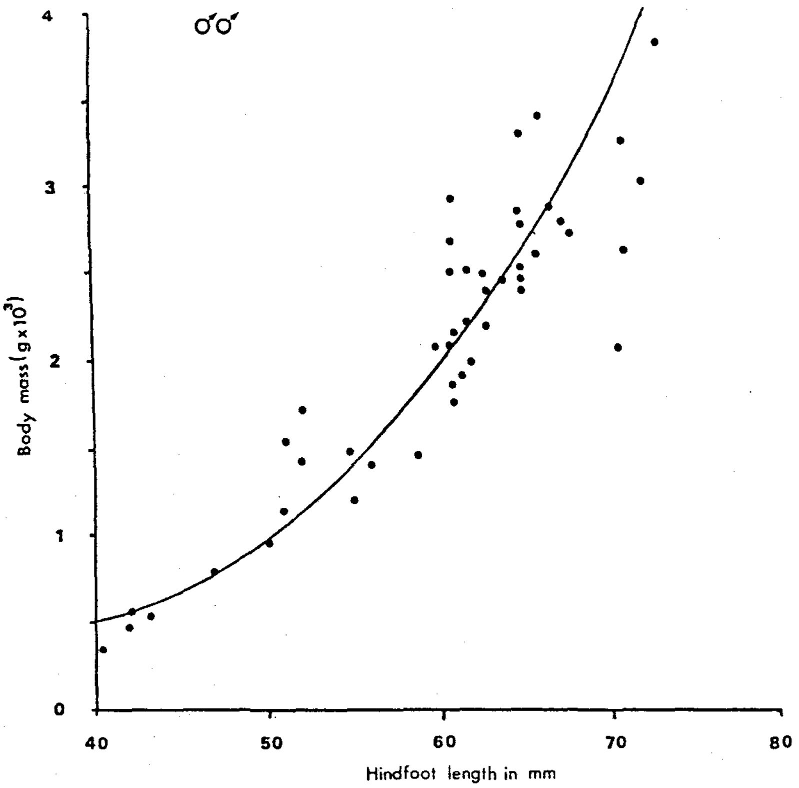


Figure 25: Relationship between body mass and hind foot length of male hyrax (n = 42).

(Equation: $y = 6{,}43 \times 10^{-4} X^{3{,}63}$ where y = mass in g; X = hind foot length in mm)

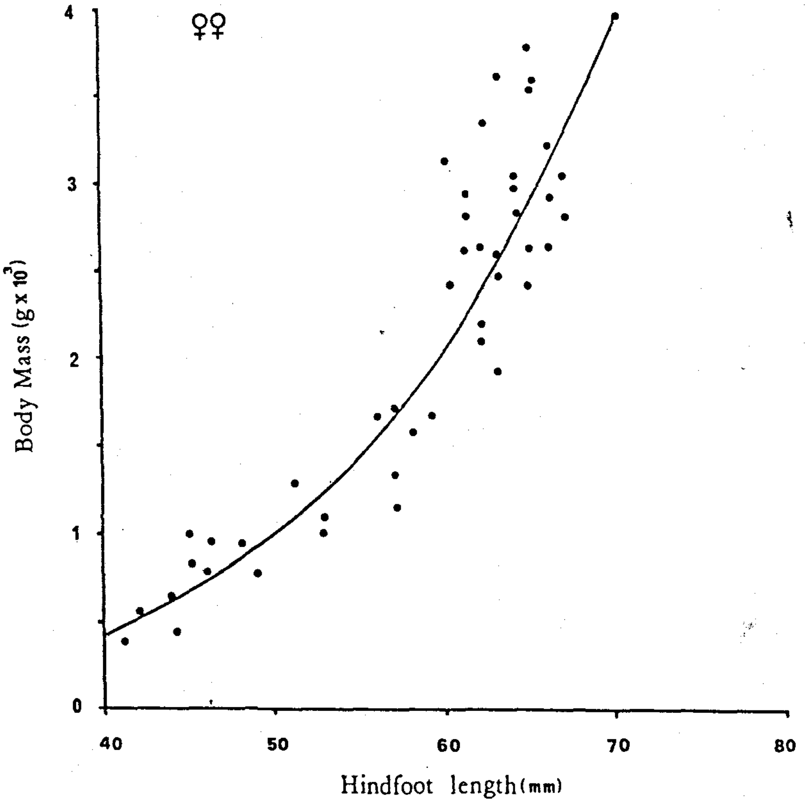


Figure 26: Relationship between body mass and hind foot length of female hyrax (n = 50).

(Equation: $y = 1{,}12 \times 10^{-4} X^{4{,}08}$ where y = mass in g; X = hind foot length in mm)

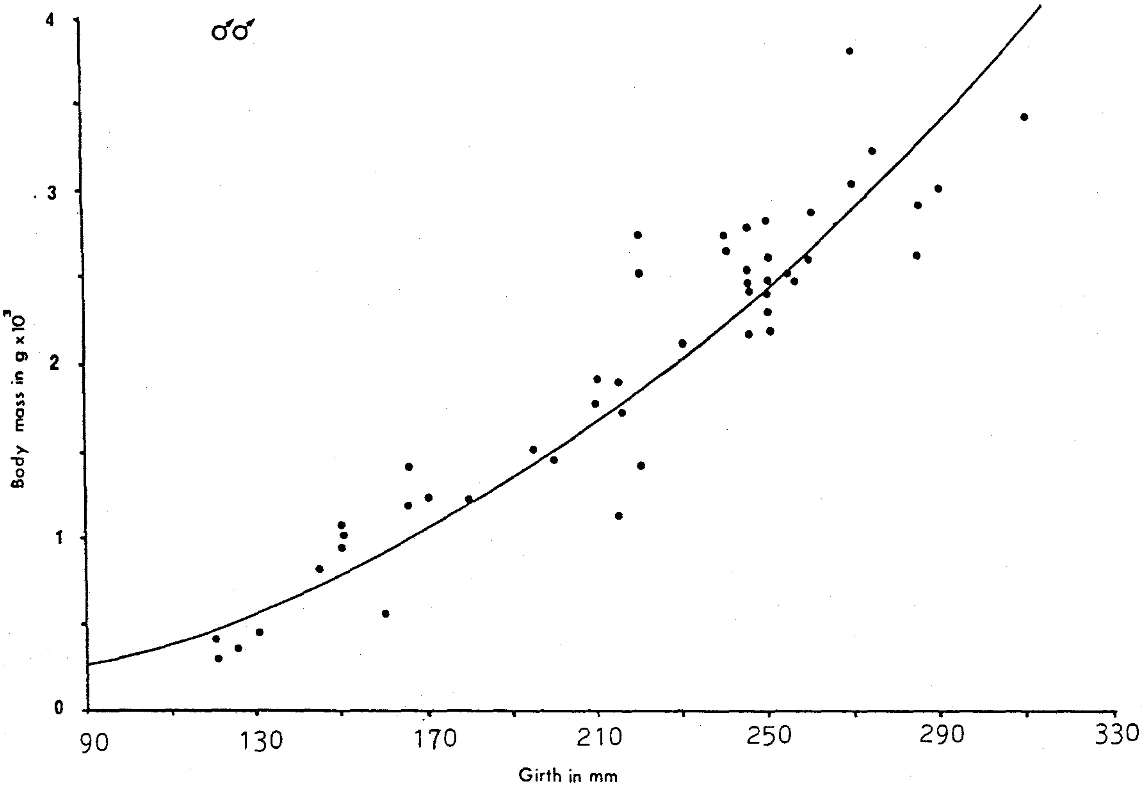


Figure 27: Relationship between body mass and girth of male hyrax (n = 48).

(Equation: $y = 1{,}27 \times 10^{-2} X^{2{,}20}$ where y = mass in g; X = girth in mm)

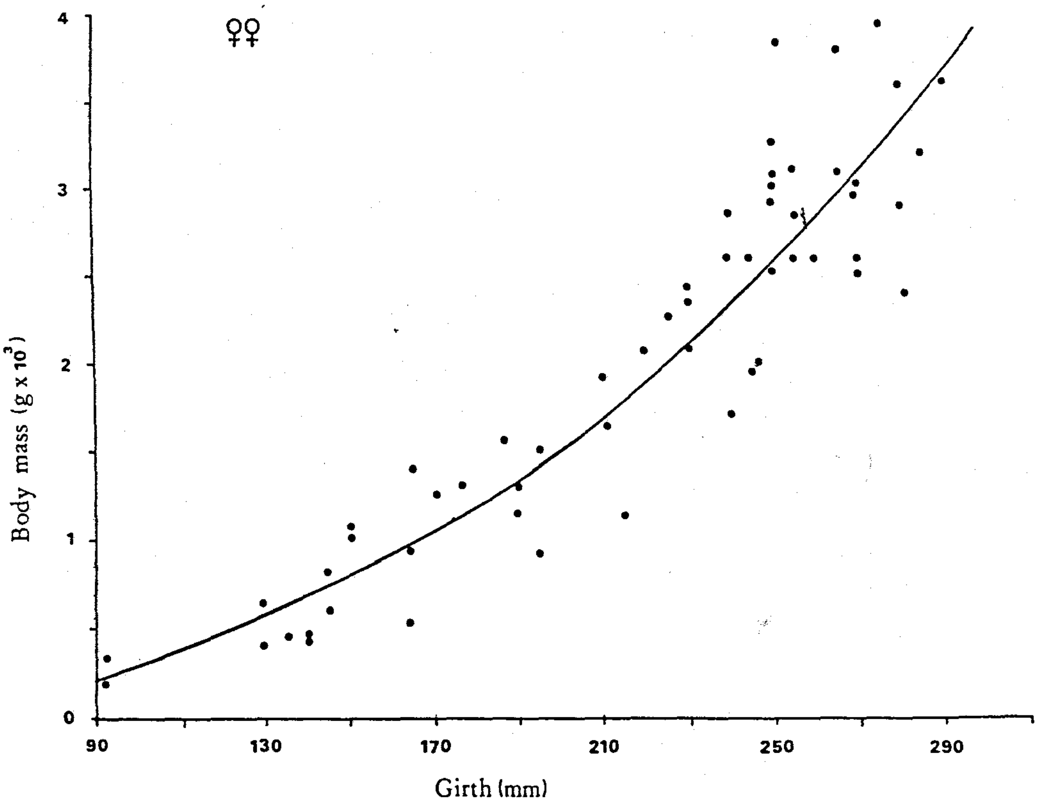


Figure 28: Relationship between body mass and girth of female hyrax (n = 52).

(Equation: $y = 7{,}68 \times 10^{-3} X^{2{,}30}$ where y = mass in g; X = girth in mm)

DISCUSSION

Intensive studies on the growth of captured hyrax up to the age of three years were conducted by Fairall (1980), while Steyn (1980) studied the growth of individuals from a free-living hyrax population at Muden in Natal. Both these authors used the theoretically calculated Von Bertalanffy growth equation to present their data. The Von Bertalanffy theoretical growth equation was shown to have physiologically significant coefficients for fish and crustaceae (Von Bertalanffy 1938). However, this equation has since been criticized by numerous researchers (Hanks 1972; Steyn 1980; Sowler in prep.). Hanks (1972) pointed out that the coefficients of the Von Bertalanffy equation have no significance in terms of the physiology of mammals.

A major disadvantage of this equation is that certain parameters involved in the equation (t_o and k values) have to be calculated beforehand, making the use of this method very time consuming. Fairall (1980) suggested that the observed growth curves for hyrax are sufficiently close to the empirical relationship to make the Von Bertalanffy equation an acceptable discriptive method.

Sowler (in prep.) studied the growth of the fruit bat Epomophorus wahlbergi and used both the Von Bertalanffy and Stevens equations. She found no difference in the growth curves produced, but recommended the use of Stevens' equation because the three biologically significant parameters (asymptote, growth rate and total growth achieved) contained in the Stevens equation make it very useful for comparative studies on growth of species frequenting different habitats and the effect of social pressures (density) on growth.

Although a simple polynomial function could be used which would fit a given set of points better than the Von Bertalanffy or the Stevens equation, Simpson, Roe & Lewontin (1960) pointed out that the great danger of the mathematical method lies in the extraordinary power of a mathematical function to fit observations. Thus the establishment of a satisfactory mathematical expression should not be confused with an elucidation of the underlying biological process. In addition such polynomial expressions cannot be used for comparative purposes.

The results indicate that growth for the different parameters measured took place in three phases. An initial rapid growth phase with almost linear growth lasting c. 15 months, a period of strong curvilinear growth lasting c. 60 months for mass and about 30 months for hind foot length and a third phase during which growth is very slow and is near to the asymptotic level. For age determination purposes, the first and second growth phases represent the time span during which measurements can be used meaningfully. The end of the second growth phase corresponds to 97% of the value of the theoretically calculated asymptotes (Table 14).

A major problem in comparative growth studies is that the measurements taken are often not standardized, making a comparison of results impossible. Three methods of measuring body length of the hyrax have been used (see Fairall 1980; Steyn 1980). The asymptotes of comparable data are given in Table 16.

Table 16: Comparison between the asymptotes obtained for body mass, hind foot length and girth in the present study (n = 450), a captive colony (n = ?) and the Muden hyrax population (n = 101).

Sex	Measurement	Present study	Muden population (Steyn 1980)	Captive colony (Fairall 1980)
♂♂	Body mass (g)	3183	3267	3377
♀♀		3307	3450	2664
♂♂	Hindfoot length (mm)	67,2	68,4	-
♀♀		65,9	68,3	-
♂♂	Girth (mm)	268,0	257,0	327,7
♀♀		270,9	259,9	305,4

From the table it is clear that the asymptotes obtained for this study are fairly similar to those of Steyn (1980). With the exception of female body mass, the captive colony had higher asymptotes.

Although comparisons of the asymptotes are useful they are genetically controlled for the species while the theoretically calculated values depends on the nature of the samples. If the sample consists only of rapidly growing animals which have not reached the asymptote, then there will be no significant drop in measurement for progressively older animals, this being the indication that the asymptote is approaching (Steyn 1980). Thus the asymptote calculation will be an extrapolation on an entirely theoretical basis, and therefore will be overestimated as was the case with the captive colony (Fairall 1980). On the other hand if samples are representative of the total life span of the animals, similar asymptotes and ages at which near asymptotic levels are reached, reflect similar growth patterns.

Observations as to when the asymptotes are reached are made somewhat arbitrarily in the literature. Theoretically the asymptote will never be reached. Thus depending on the scale used the age at which the growth curve nears the asymptotic level may vary greatly. In the present study, a value of 97% of the theoretically calculated asymptotes was taken to represent near asymptotic values (Table 14). Near asymptotic levels were first reached in hind foot length, followed by head/body length, girth and body mass. Although this sequence is consistent with the results obtained by Steyn (1980), her statement that asymptotic measurements are attained at c. 42 months of age differs markedly from the results obtained in this study (Table 14).

The values obtained in this study are significant. The smaller the value of ρ, the higher the growth rate and the sooner the particular measurement will reach the asymptote. The low mean ρ value obtained for hind foot length (0,9183) indicates a more rapid growth rate than was recorded for head/body length (0,9260), girth (0,9348) and mass

(0,9512) respectively. ρ values obtained by Sowler (in prep.) for free-living bats ranged between 0,51 and 0,79 indicating a more rapid growth rate than in the hyrax. Fruit bats raised in captivity showed higher ρ values for similar parameters indicating retarded growth; thus demonstrating the use of ρ values for comparative purposes.

Factors influencing growth were not examined in this study. It is a known fact that nutrition has a marked influence on the growth of animals, and that the quality as well as the quantity and availability of food is of importance (Moen 1973).

Mendelssohn (1965) reported on the influence of domestication on growth of hyrax in a captive colony. During the initial years after the establishment of the colony, males weighed 2 000 g at *c.* 12 months of age. A few years later males of *c.* 14 months attained masses of up to 3 850 g. Similarly, Hanse (1962) measured the mass of 16 young hyrax in captivity on a monthly basis. At 15 months of age the mean mass of hyrax (n = 6) was asymptotic at 3 070 g. This is *c.* 54 months shorter than the true growth period of free-living hyrax recorded in this study.

A variety of measurements have been used to estimate the body mass of mammals (Freeman & King 1969; Howells & Hanks 1975). The importance of body mass is that it reflects body condition and reaches the asymptotic level at a later age than other physical parameters and consequently it is generally an important statistic for management. The mass of a captured animal can only accurately be determined once it has been immobilized with a drug which is usually very expensive. Consequently it is generally the most difficult measurement to obtain and hence researchers attempt to calculate it from other measurements.

Body mass data are reasonably easy to obtain in hyrax. Nevertheless an equation to predict mass may prove useful in those cases where data on mass are not available. Measurements of the hind foot length are fairly easy to obtain from captured animals without immobilization. Hind foot length correlated significantly ($p < 0,001$) with body mass and hence can be used to calculate mass data.

The relationship between body mass and the measurements of single body parameters was in all cases strongly curvilinear and the best correlation was found between body mass and head/body length ($r = 0,99$; $n = 45$ for ♂♂ and $r = 0,97$; $n = 52$ for ♀♀). The correlation between mass and girth gave the lowest $\underline{r}$ values of 0,93 for females ($n = 52$) and 0,92 for males ($n = 48$), but were also highly significant ($p < 0,001$).

SUMMARY

The growth of hyrax in relation to age is described by means of Stevens asymptotic regression equations. Equations for both sexes are provided for growth in body mass, head/body length, hind foot length and body girth. Near asymptotic measurements are attained first in hind foot length (at 30 - 33 months of age), head/body length (at 37 - 39 months of age), girth (at 41 - 48 months of age) and body mass (at

68 - 70 months of age).

The use of the Stevens growth equation is recommended because it contains three biologically significant parameters which are very useful in comparative studies. Allometric growth of the different body measurements is investigated and useful predictive relationships for mass are presented.

CHAPTER V

AGE DETERMINATION

INTRODUCTION

Accurate age determination is an essential pre-requisite for an understanding of many aspects of animal biology; although absolute precision may be more of academic than of practical importance (Spinage 1973). Precise methods of age determination are indispensable to population dynamic studies, and important in comparative anatomy, morphology and taxonomy. Without this information we cannot determine the uniformity of comparable data or variation occasioned by age. Several methods of age determination have been reviewed by Morris (1972) and many of these were evaluated in the present study.

In this study three methods were used for age determination:

(a) Growth; increase in body and skull dimensions, including tooth root length and eye lens mass. Some of the body and skull dimensions were incorporated into predictive age equations. Tooth eruption and replacement and the closure of the proximal epiphysis of the humerus were also investigated.

(b) Toothwear; quantified by tooth measurements.

(c) Cementum annuli.

METHODS

Dentition

Eruption and replacement

In the MZNP the majority of hyrax births occur between mid-November and mid-December (CHAPTER VI). Making use of the date of collection, the skulls of shot hyrax (n = 589) which had been cleaned and labelled, were allocated to chronological age classes ech spanning four months.

The eruption and replacement of mandibular and maxillary deciduous teeth (incisors and premolars) and permanent teeth (molars) in these skulls were recorded against age.

The criteria used to quantify the eruption of teeth (premolars and molars) are illustrated in Figure 29a - f. Eruption patterns/stages were determined on the basis of the following:

(a) tooth not visible;

(b) tooth visible in crypt but with tip of crown not visible above alveolus;

(c) tooth erupting with its tip visible above the alveolus (Fig. 29a);

(d) mid-eruption with the crown height of the erupting tooth approximately half the height of the adjacent tooth (Fig. 29b);

(e) nearly level, with the crown height of the erupting tooth approximately three quarters the height of the adjacent tooth

(Fig. 29c);

(f) crown height of erupting tooth level with that of the adjacent tooth (Fig. 29d);

(g) occlusal surface level with that of a fully erupted adjacent tooth; the enamel/cementum boundary, on the buccal aspect of the tooth, partly raised above the alveolus, but for only part of its length (Fig. 29e);

(h) fully erupted, with the enamel/cementum boundary beneath the crown, on the buccal aspect of the tooth, above the alveolus for the whole length of the tooth (Fig. 29f).

Tooth impressions were made using a super elastic alginate impression (Algiace powder; Sankin Chemical Industry Co. (Ltd), Tokyo, Japan), to investigate tooth replacement and attrition patterns of captured hyrax. The impressions so obtained were made permanent by using a fine-textured dental impression powder.

Replacement schedules were verified by using eight known-aged (9 - 37-month-old) skulls from hyrax originally captured and marked as juveniles.

Attrition patterns

The two oldest skulls (subjectively assessed) from a collection of 1570 were selected in order to assign an upper age limit to the dental classes. The oldest individual maxilla belonged to a male in which only the first and third molars still retained occlusal surfaces. The

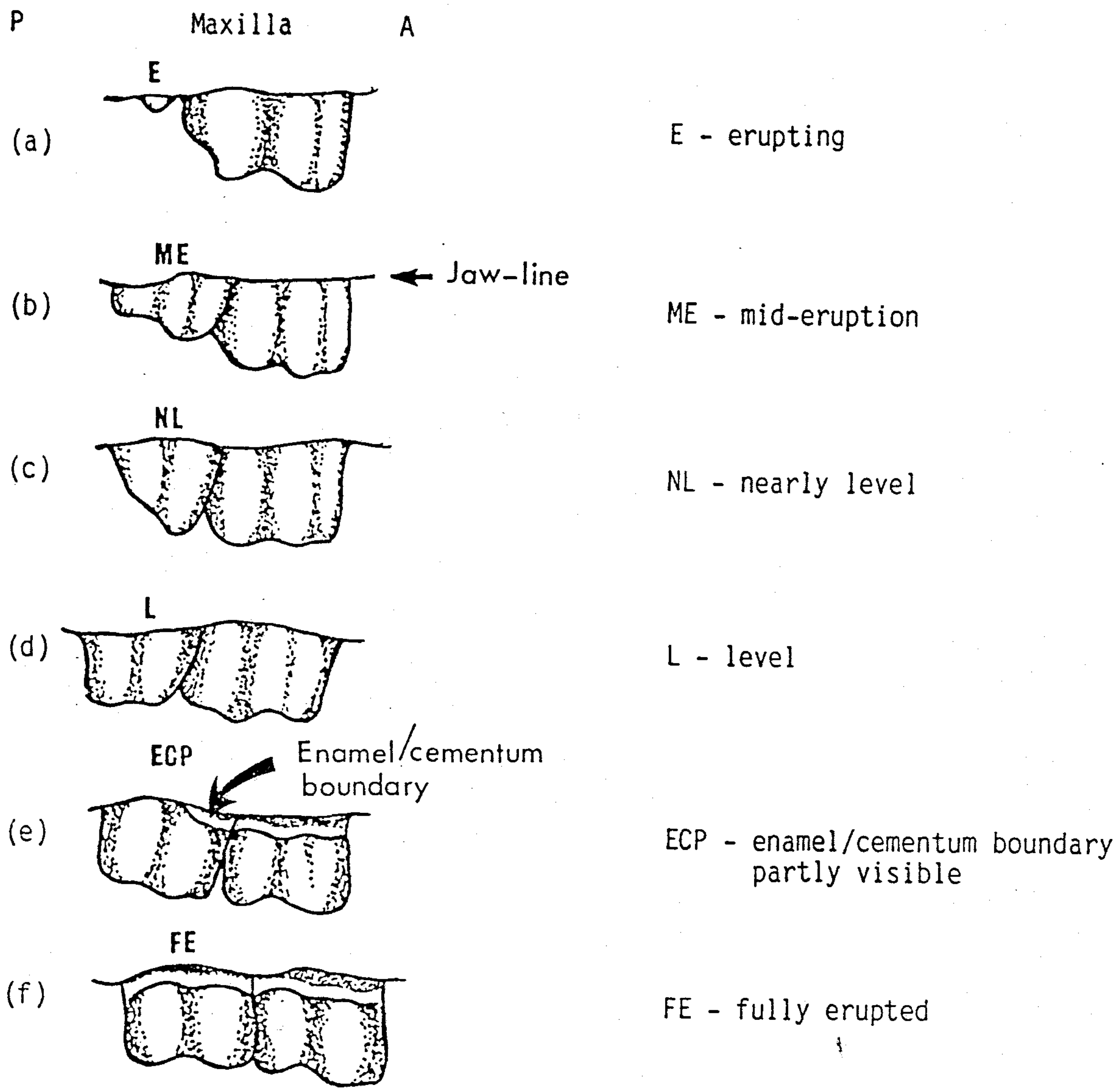


Figure 29a - f: Tooth eruption criteria used for age determination of hyrax (A - anterior; P - posterior).

other teeth were worn down to the roots. Subsequent dental histology revealed that the cementum annuli were so compact as to make any count unreliable. However, the next oldest maxilla belonged to a female and on the basis of cementum annuli counts her age was estimated to be 13 years (see later). For the purpose of this study 14 dental age classes were recognized, comprising 13 annual classes and a fourteenth for the oldest maxilla.

The different wear, eruption and replacement patterns/stages were correlated with the number of cementum annuli (see later). All the skulls of the hyrax that had been shot were allocated to dental age-classes on the basis of tooth eruption and replacement; or for those skulls in which the full complement of permanent teeth were present, on the basis of dental exposure and occlusal wear patterns.

For practical descriptive purposes, six categories of wear were recognised (Fig. 30).

The nomenclature for the description of cones/cusps (and hence patterns) on the maxillary molars follows that of Hall-Martin (1976) (Fig. 31).

Measurement of teeth

The crown heights of the first and third molars in the mandible and maxillae were measured to quantify the wear of teeth. The selection of these teeth for measurement was based on the fact that the first molars erupt just after birth and are worn down to the roots in very old animals, whereas the third molars erupt at c. 24 months of age and the crown heights can still be measured in very old animals.

Appositional growth of mammalian teeth is generally considered to function as a process uplifting the tooth from below to counteract

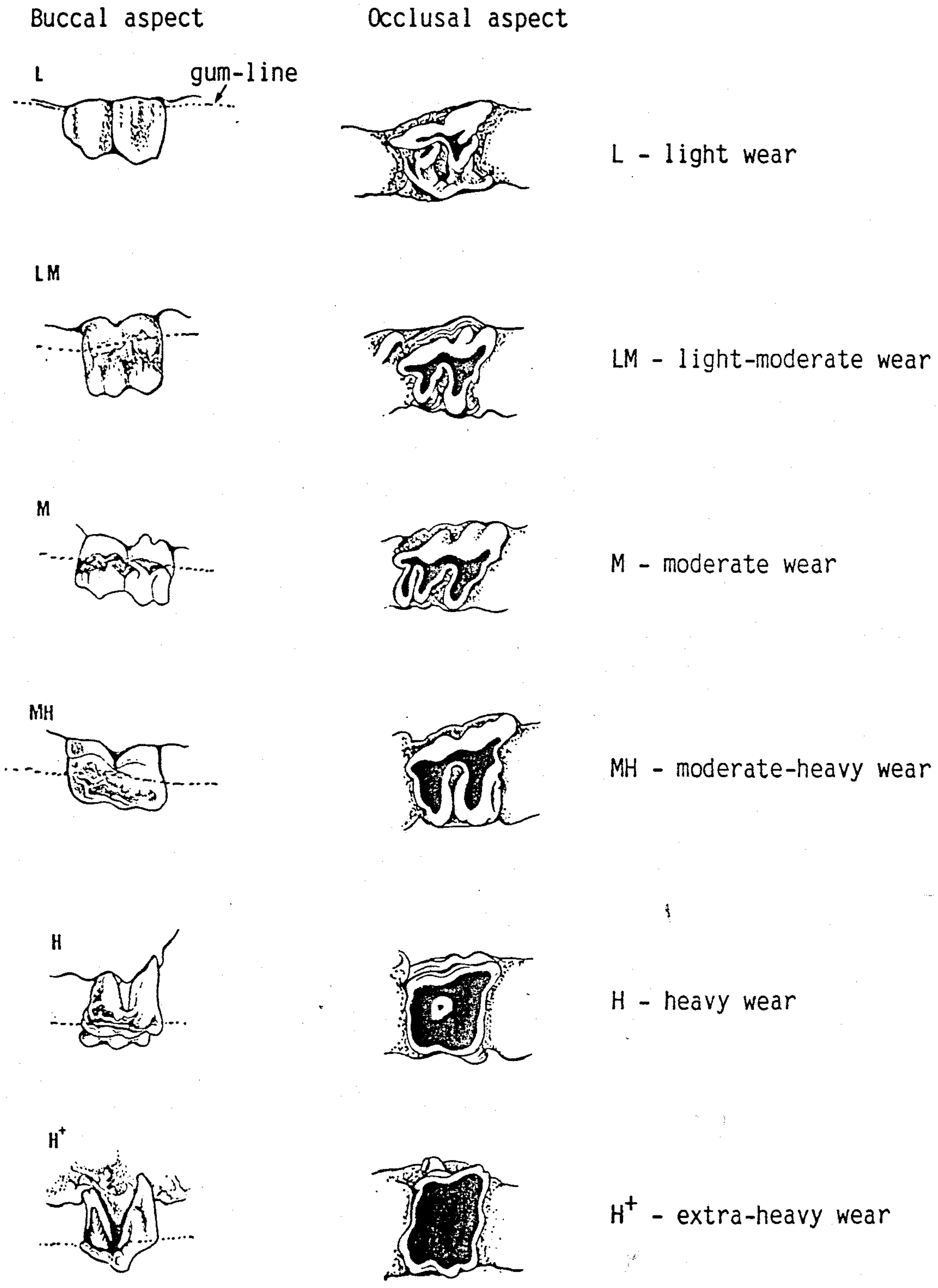


Figure 30: Six categories of wear on hyrax maxillary molars viewed from buccal and occlusal aspects.

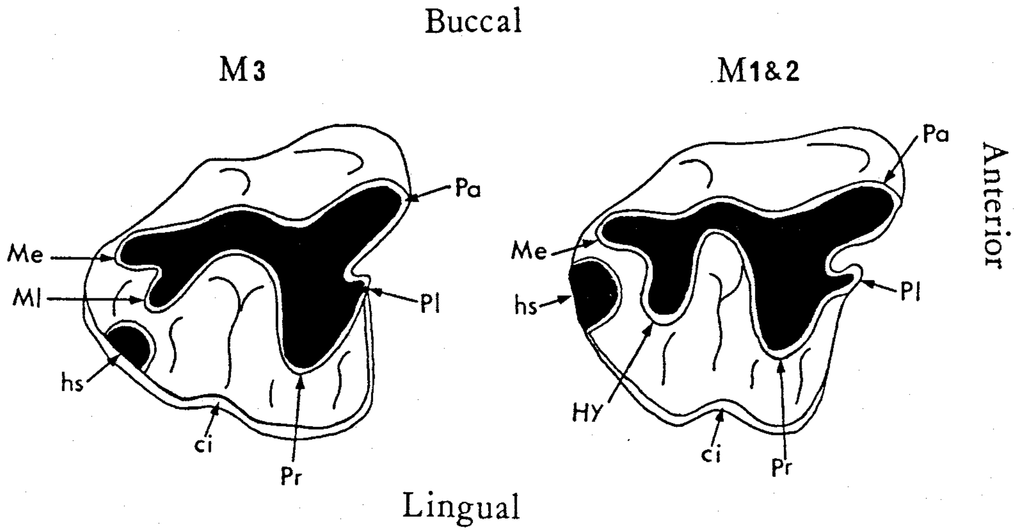
abrasion from above (Grue & Jensen 1979). Bearing this in mind crown height was recorded as the vertical distance from the apical tip of the paracone to the enamel/cementum boundary (adjacent to the anterior root on the buccal side of the tooth for a fully erupted tooth) (Fig. 32). For teeth not fully erupted the measurement was made to the jaw-line.

The root lengths of the first and third mandibular molars were measured on radiographs of the mandibles X-rayed at 100 MA; ±44 KVP for 0,08 s with a FFD of 910 mm. This procedure was necessary because it was difficult to extract teeth without damaging their roots. Root length was taken as the vertical distance from the enamel/cementum boundary to the tips of the anterior root on the buccal side of the tooth (Fig. 32). All measurements were made using dial calipers accurate to 0,05 mm.

Cementum annuli

One male and one female skull from each provisional annual dental class was chosen at random and the maxillary molars extracted. The teeth were decalsified in 5% nitric acid, diluted 1:4 with 10% neutral formalin, and in ethylene diamine tetracetic acid (EDTA) according to Steenkamp's method (1975); processed according to standard histological methods for soft tissue and transverse and longitudinal serial sections made.

Examinations of serial sections were made under a Zeiss microscope at



Main cusps

Pr - Protocone } Lingual
Hy - Hypocone

Pa - Paracone } Buccal
Me - Metacone

Secondary cusps

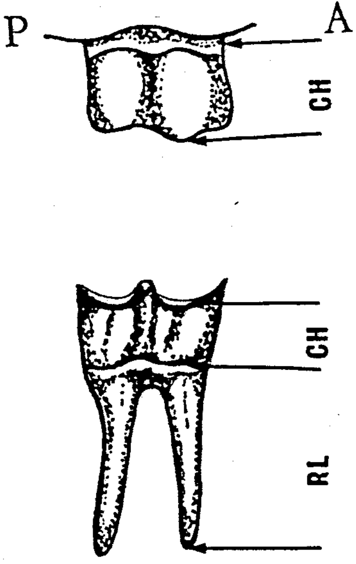
Ml - Metaconule } Median
Pl - Paraconule

hs - hypostyle } Lingual

Other features

Ci - Cingulum

Figure 31: Occlusal views of hyrax maxillary molars showing main features (shaded sections represent exposed dentine).



P - posterior
A - anterior
CH - crown height
RL - root length

Figure 32: Reference points used to obtain the crown height of maxillary molars and the crown height and root length of mandibular molars.

magnifications between 33 and 132. Sections with the most distinct laminations were photographed using a Zeiss photomicroscope. A green filter was used and an overdeveloped 125 ASA plus X-pan film provided good contrast. Photographs were printed on hard paper.

An annual layer consists of two zones, a broad (light band) and a narrow (dark band) which differ in the intensity of their staining reactions and in their optical density (Morris 1972). A description of the different types of dark staining bands/lines is given by Grue & Jensen (1979). Primary lines are well developed and occur at regular intervals, secondary lines are less well defined, and resorption lines are irregular lines resulting from reparative apposition processes.

The number of darkly stained primary lines were counted on the photomicrographs by the author and two independant observers. In those cases in which M^2 and M^3 were used for age determination one and two years were added respectively to the number of lines counted since these teeth erupt c. 12 and 24 months after birth.

Eye lens mass

Both eye balls (or just one in the case where one was damaged) of hyrax shot in and around the MZNP were removed from the orbit and placed in 10% formalin. No more than 8 h elapsed between sampling and subsequent fixation. As the duration of fixation is known to affect accuracy (Friend 1967a) this was standardised to between one and four months in length.

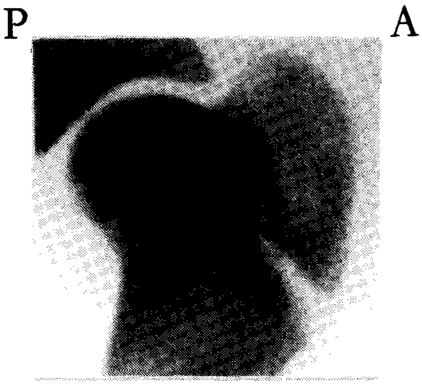
After fixation the eye balls were incised and the lenses removed, cleaned of any extraneous tissue, placed in cleaned vials and dried at 80°C. Drying time depended on size but the largest lenses reached a constant mass at c. 10 days.

After removal from the oven the lenses were allowed to cool in a desiccator where they remained until their mass was determined to within 0,0001 g on a Cahn electrobalance. The balance was recalibrated after every tenth weighing. The mass of single eye lenses was doubled since Steyn (1980) has shown no significant difference (less than 1%) between the masses of the left and right lenses of hyrax.

Epiphyseal closure

Different bones have different rates of epiphyseal closure, and this has been shown for a large number of species (Washburn 1943). The closure of the proximal epiphysis of the humerus occurs after that of the iliac crest, while the vertebrae are the last to close. Fore-limbs are relatively easy to sample and are ideal for X-ray examination, hence it was decided to relate the closure of the proximal epiphysis of the humerus to age.

Fore-limbs of 63 hyrax of varying ages were removed from carcasses at necropsy and then X-rayed at 100 MA; ±44 KVP for 0,08 s at a FFD of 910 mm. In order to quantify epiphyseal closure according to the degree of ossification five closure classes were recognized (Figs. 33a - e).



(a) Open with the epiphyseal area represented by a definite groove of cartilage not replaced by bone.

(b) Open, but with a greater degree of ossification at both the anterior and posterior sections of the epiphyseal plate.

(c) Intermediate, with the epiphyseal plate nearly closed posteriorly.

(d) Intermediate, with the anterior section of the epiphyseal plate nearly closed, and with the posterior section completely closed.

(e) Closed, with no indication of an epiphyseal line.

Figure 33 a - e: Radiographs of the proximal epiphysis of hyrax humeri demonstrating five different epiphyseal closure classes (A - anterior; P - posterior).

Skull measurements

A number of skulls placed in the provisional annual dental age classes were selected at random and the following measurements were made (Figs. 34a - c):

1. Maxilla:

(a) greatest length of the skull,

(b) zygomatic width,

(c) length of maxillary tooth row.

2. Mandible:

(a) greatest length of mandible,

(b) length of the mandibular tooth row.

All the measurements were made to the nearest 0,05 mm with a pair of dial calipers.

Multivariate regression equations

The body (previous chapter) and skull measurement data were subjected to multivariate regression analysis relative to age using a Hewlett Packard 850 mini computer.

RESULTS

Dentition

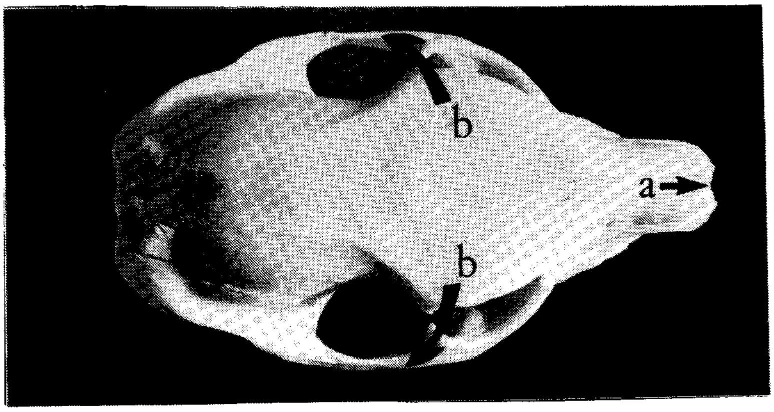


Figure 34a: Measurements made on the maxillae of hyrax: a - a, greatest length of the skull; b - b, zygomatic width.

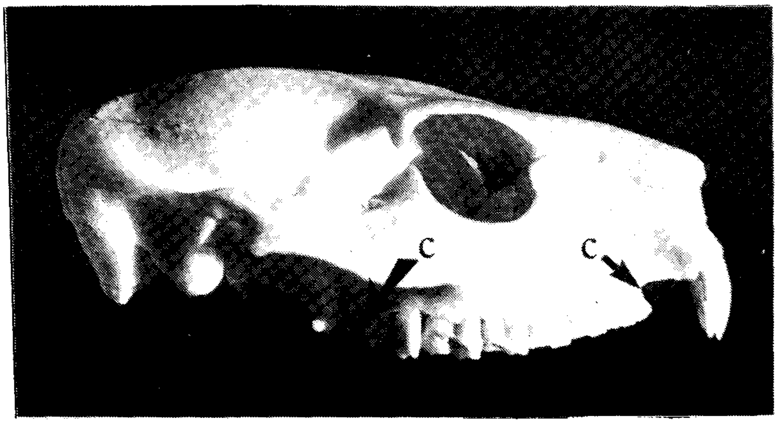


Figure 34b: Measurement made on the maxillae of hyrax: c - c, length of the maxillary tooth row.

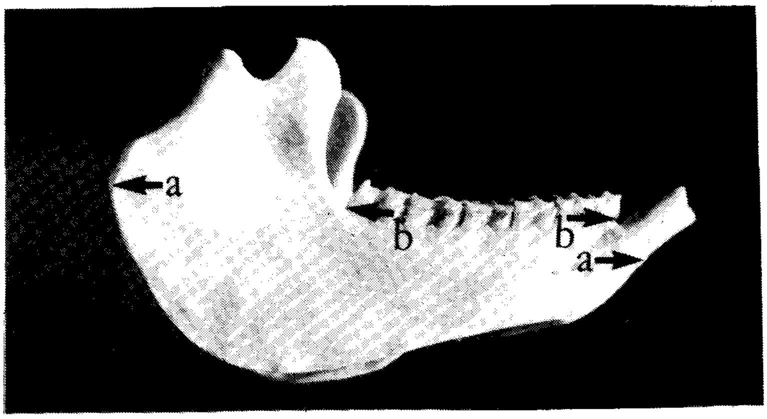


Figure 34c: Measurements made on the mandibles of hyrax: a - a, greatest length of mandible; b - b, length of the mandibular tooth row.

Eruption and replacement

The sequence of tooth eruption and replacement is summarized in Table 17 (see also Fig. 35). It is evident that the maxillary and mandibular teeth have different rates of eruption and replacement. The mandibular molars erupt earlier and are fully erupted before the maxillary molars. M^3 is fully erupted at c. 64 - 72 months.

The tooth eruption and replacement pattern in skulls retrieved from culled known-aged hyrax was consistent with previous results.

Attrition patterns

Sequential changes in tooth wear for hyrax are illustrated in Fig. 35.

Attrition patterns were not uniform and the drawings are representative of average patterns. Wherever possible, key features such as cusp fusion were used to separate classes. In contrast to the maxillary molars no conspicuous cusps are present on the mandibular molars and hence only maxillary molars were used for descriptive purposes. The descriptions of 13 annual age classes are as follows:

Class 1

Light wear on M^1 with dentine slightly exposed on the protocone, protoconule, paracone and metacone. A thin band of dentine is present between the metacone and the paracone.

Table 17: Schedule of tooth replacement in the hyrax.

Maxilla/ Mandible	Age (months)	I1	I2	C	PM1	PM2	PM3	PM4	M1	M2	M3
Maxilla	0 - 4	D	-	D	D	D	D	NL(D)	VC	-	-
Mandible		D	D	D	D	D	D	NL(D)	VC	-	-
Maxilla	5 - 8	D	-	D	D	D	D	FE(D)	ME	-	-
Mandible		D	D	D	D	D	D	FE(D)	ME	-	-
Maxilla	9 - 12	R	-	D	D	D	D	D	L	VC	-
Mandible		R	R	D	D	D	D	D	ECP	E	-
Maxilla	13 - 16	P	-	A	P	P	P	P	ECP	ME	-
Mandible		P	P	A	P	P	P	P	FE	NL	-
Maxilla	17 - 20	P	-	A	P	P	P	P	FE	NL	-
Mandible		P	P	A	P	P	P	P	FE	L	VC
Maxilla	21 - 24	P	-	A	P	P	P	P	FE	ECP	VC
Mandible		P	P	A	P	P	P	P	FE	FE	ME
Maxilla	33 - 36	P	-	A	P	P	P	P	FE	FE	ME
Mandible		P	P	A	P	P	P	P	FE	FE	L
Maxilla	45 - 48	P	-	A	P	P	P	P	FE	FE	NL
Mandible		P	P	A	P	P	P	P	FE	FE	ECP
Maxilla	57 - 60	P	-	A	P	P	P	P	FE	FE	ECP
Mandible		P	P	A	P	P	P	P	FE	FE	FE
Maxilla	69 - 72	P	-	A	P	P	P	P	FE	FE	FE
Mandible		P	P	A	P	P	P	P	FE	FE	FE

I - incisor
C - canine
PM - premolar
M - molar
A - aborted
D - deciduous

R - being replaced
P - permanent
VC - visible in crypt
E - erupting
ME - mid-eruption
L - level

NL - nearly level
ECP - enamel/cementum boundary partly visible
FE - fully erupted

Class 2

Medium wear evident on M^1 with the exposed dentine on the metacone confluent with that on the hypocone. Dentine also exposed on the hypostyle. Light wear on M^2 is apparent with dentine slightly exposed on the protocone, protoconule, paracone and metacone. A thin band of dentine is exposed between the metacone and paracone.

Class 3

M^1 is moderately to heavily worn with the dentine exposed on the hypostyle confluent with that of the hypocone and metacone. Wear on M^2 is light to moderate with the dentine exposed on the hypocone confluent with that on the metacone.

Class 4

Wear on M^1 moderate to heavy, with dentine bands exposed between protocone, paracone, metacone and hypocone more pronounced than in previous class. Wear on M^2 is moderate with dentine exposed on hypostyle. M^3 only lightly worn with dentine exposed on metacone, paracone, protoconule and protocone. A thin dentine band is exposed between the protocone, paracone and metacone of M^3.

Class 5

Heavy wear on M^1 with broad band of dentine exposed between protocone, paracone and hypocone. The wear on M^2 is moderate with the dentine exposed on hypostyle not yet confluent with that on the hypocone. Light to moderate wear on M^3 is apparent with dentine exposed on metacone confluent with that on metaconule.

Class 6

Heavy wear on M^1. In the case of M^2 the wear is moderate to heavy with dentine exposed on hypocone confluent with that on the hypostyle. The wear on M^3 is light to moderate with a relatively broad band of dentine exposed between the protocone, paracone and metacone.

Class 7

Wear on M^1 is heavy with dentine exposed on the protocone almost confluent with that on the hypocone. The wear on M^2 is moderate. Wear on M^3 is moderate with dentine exposure on the metacone, metaconule, paracone and protocone more pronounced than in previous class.

Class 8

Wear on M^1 and M^2 is heavy and with the exception of a thin lingually derived ridge the whole occlusal surface consists of exposed dentine. Wear on M^3 is moderate with dentine now also exposed on the hypostyle.

Class 9

Extra heavy wear on M^1 with the whole occlusal surface consisting of exposed dentine but the lingually derived ridge is still evident. Wear on M^2 is heavy. In the case of M^3 wear is moderate to heavy with a broad exposed band of dentine between paracone and metacone.

Class 10

Wear on M^1 is extra heavy and heavy on M^2. Moderate to heavy wear is apparent on M^3 with exposed band of dentine between the hypostyle and the protocone almost confluent with dentine band between the paracone and the metacone.

Class 11

Wear on M^3 is moderate to heavy with exposed band of dentine between the hypostyle and the protocone almost confluent with dentine band between the paracone and the metacone.

Class 12

Extra heavy wear is apparent on all molariform teeth but none are worn down to the roots.

Class 13

Extra heavy wear on all molariform teeth with M^1 worn down to the roots.

An experienced independent assessor was supplied with 23 hyrax maxillae belonging to the whole range of age classes. He was able, using only the average wear patterns, to place 65% in the correct age class, a further 26% to within one year and the remaining 9% to within two years of the correct age class. When he used wear patterns in conjunction with eruption criteria 70% were placed in the correct age class and the remaining 30% within one year of the correct age class.

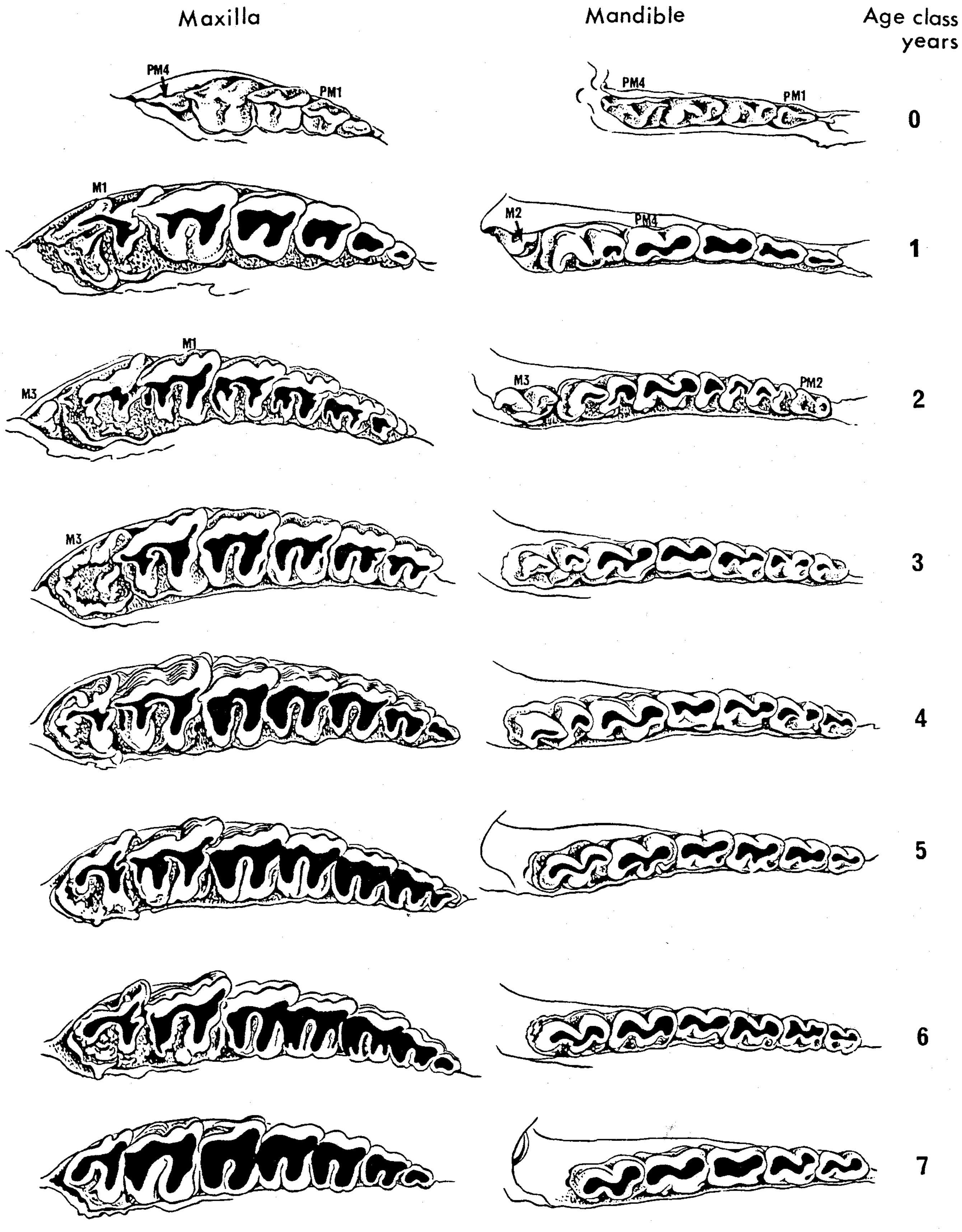


Figure 35: Average age-specific eruption and attrition patterns of the premolar and molar teeth of hyrax.

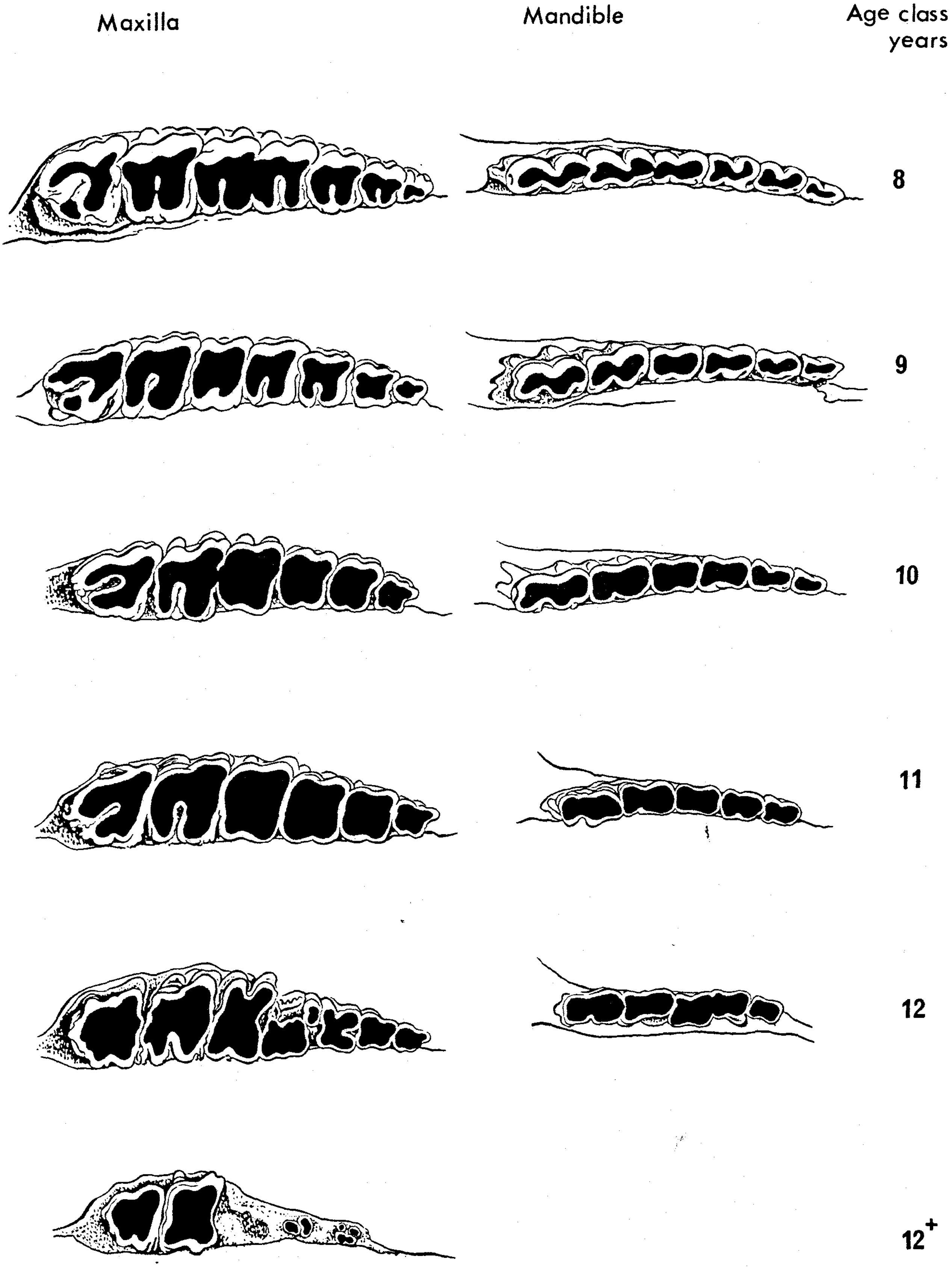


Figure 35 (cont.)

Measurement of teeth

The relationships between crown height of mandibular and maxillary molars (M1 and M3) and dental age are summarized in Table 18 and Figures 36 - 39.

Table 18: Regression equations of crown height (y) of mandibular or maxillary molars (M1 and M3) on dental age (x) for hyrax.

Tooth	Regression equation	r	p	n
M1 (mandible)	$y = 4{,}98e^{-0{,}24X}$	-0.88	0,001	98
M1 (maxilla)	$y = 7{,}94e^{-0{,}27X}$	-0,89	0,001	96
M3 (mandible)	$y = 8{,}40e^{-0{,}17X}$	-0,90	0,001	87
M3 (maxilla)	$y = -0{,}591X + 9{,}215$	-0,90	0,001	92

Change in crown height of the first mandibular/maxillary molar was biphasic with a rapid initial rate of decrease to the age of c. 72 months after which time it decreased more gradually (Figs 36 & 37). Crown height of M_3 had a slower initial rate of decline to c. 96 months of age followed by an even more gradual rate of decrease thereafter (Fig. 38). In the case of M^3 the rate of crown height decrease was constant and the regression line linear (Fig. 39), making this tooth particularly useful for estimating ages of animals older than 60 months.

Root length measurements did not provide a good correlation with age. M_1 obtained a maximum root lengthin hyrax at c. 36 months of age after which root length decreased. M_3 reached a maximum root length at c. 96

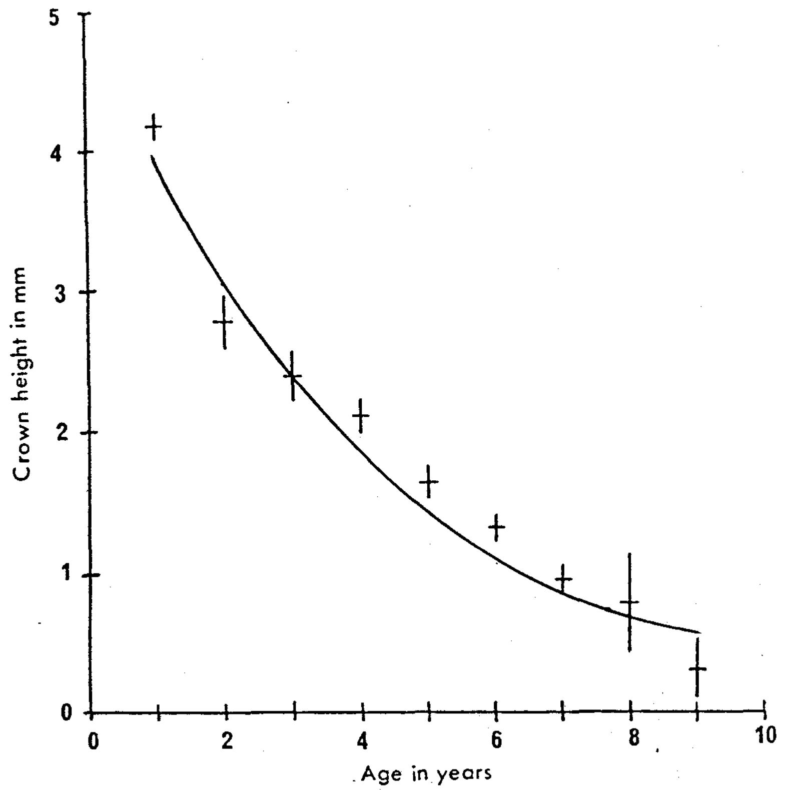


Figure 36: The relationship between crown height of mandibular M1 and age (means ± S.E.).

(Regression equation: $y = 4,98e^{-0,24X}$; $r = -0,88$; $p < 0,001$ and $n = 98$)

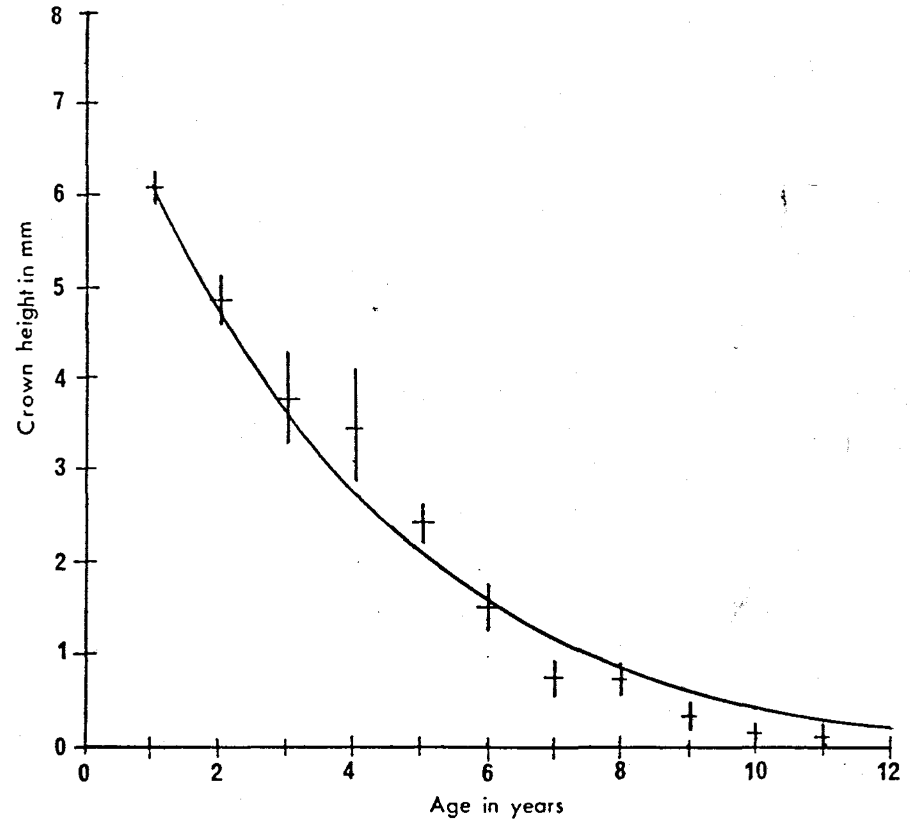


Figure 37: The relationship between crown height of maxillary M1 and age (means ± S.E.).

(Regression equation: $y \doteq 7,94e^{-0,27X}$; $r = -0,89$; $p < 0,001$ and $n = 96$)

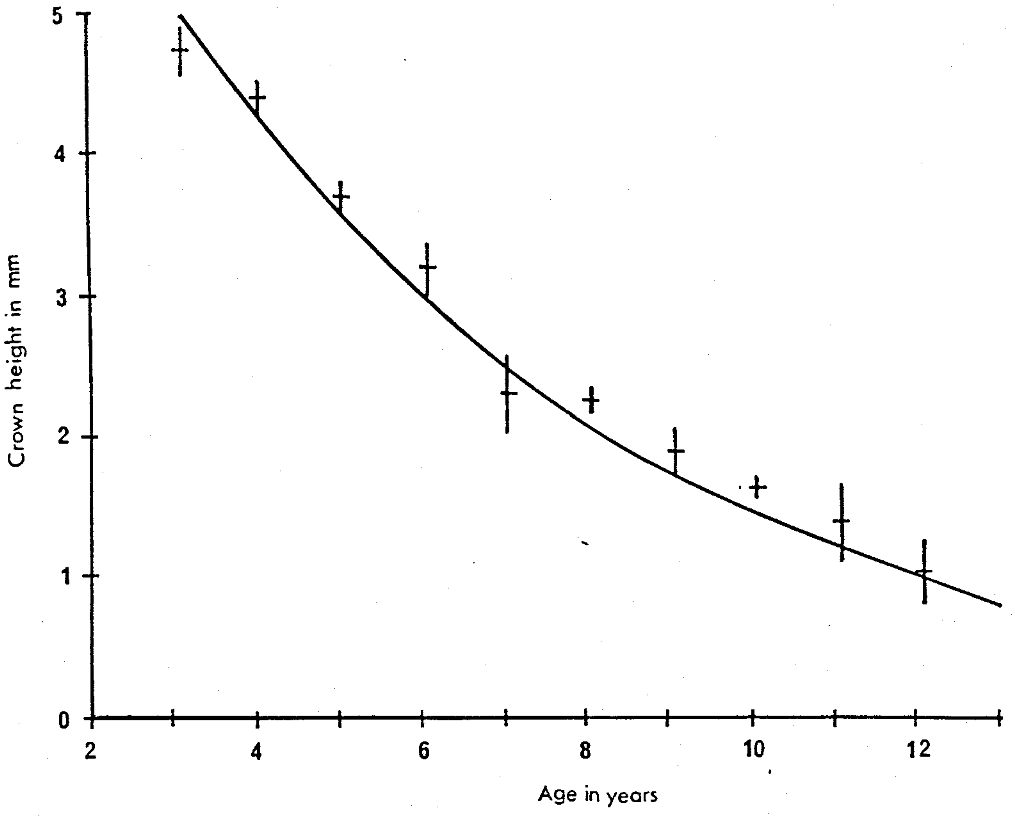


Figure 38: The relationship between crown height of mandibular M3 and age (means ± S.E.).

(Regression equation: $y = 8{,}40e^{-0{,}17X}$; r =-0,90; P < 0,001 and n = 87)

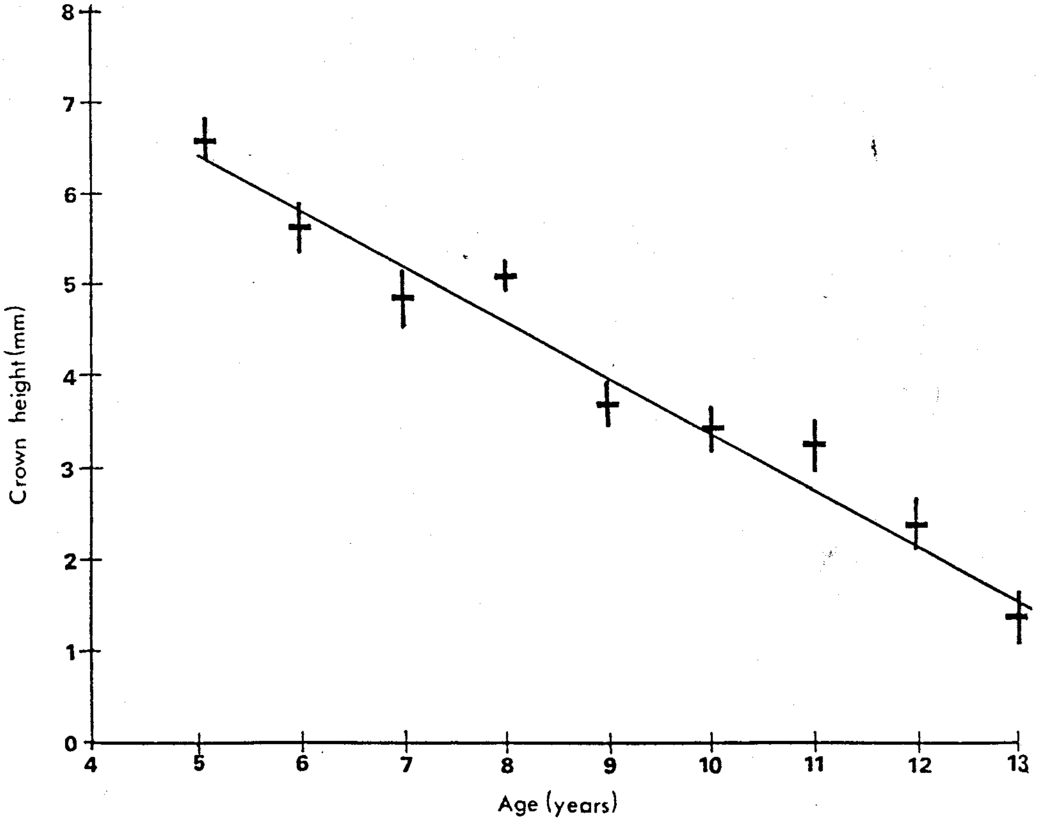


Figure 39: The relationship between crown height of maxillary M3 and age (means ± S.E.).

(Regression equation: y = -0,591X +9,215; r=-0,90; P < 0,001 and n = 92) months after which root length decreased rapidly. Mean values ($\pm$S.E.) for the different measurements are summarized in Table 19.

Table 19: Mean values (mm) and standard errors for root length measurements of mandibular M1 and M3 of hyrax.

Age (months)	M1	±S.E.	n	M3	±S.E.	n
12	5,93	0,22	9			
24	6,85	0,18	10	4,00	0,33	10
36	7,05	0,20	10	5,49	0,10	10
48	6,62	0,21	9	5,32	0,14	9
60	6,29	0,19	10	5,69	0,21	10
72	6,51	0,16	8	6,05	0,20	8
84	6,13	0,20	8	6,03	0,22	8
96	5,53	0,24	3	6,73	0,37	3
108	5,55	0,13	9	5,65	0,15	9
120	5,05	0,05	2	5,00	0,00	2
132	5,65	0,16	3	5,13	0,22	3
144	4,93	0,23	3	4,62	0,37	3

Cementum annuli

From known-aged material it was established that one primary cementum line is formed annually. Photographs of primary cementum lines of hyrax aged one, two and nine years respectively are illustrated in Figures 40 - 42.

There is a very high correlation coefficient (0,98; $p < 0,001$) between the number of cementum lines and age (in years), which can be represented by the regression equation $y = 0,301 + 0,932x$ (where y = number of primary cementum lines and x = age in years (Fig. 43).

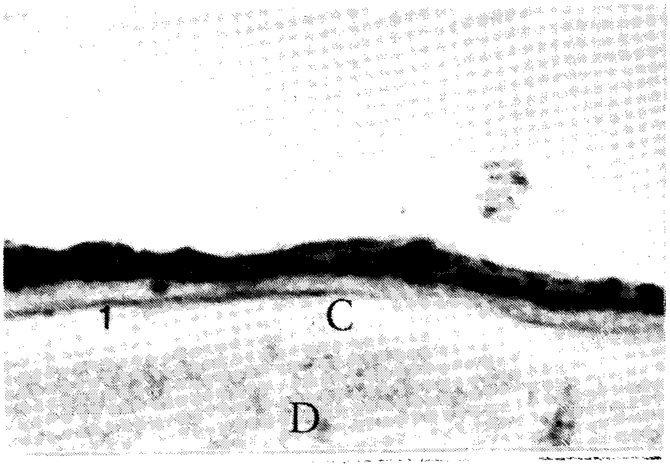


Figure 40: Photomicrograph of a cross-section of the M^1 root of a one-year-old hyrax showing a single primary cementum line (C - cementum; D - dentine)(X 528).

Figure 41: Photomicrograph of a longitudinal section of the root of the M^1 of a two-year-old hyrax showing two primary cementum lines (C - cementum; D - dentine)(X198).

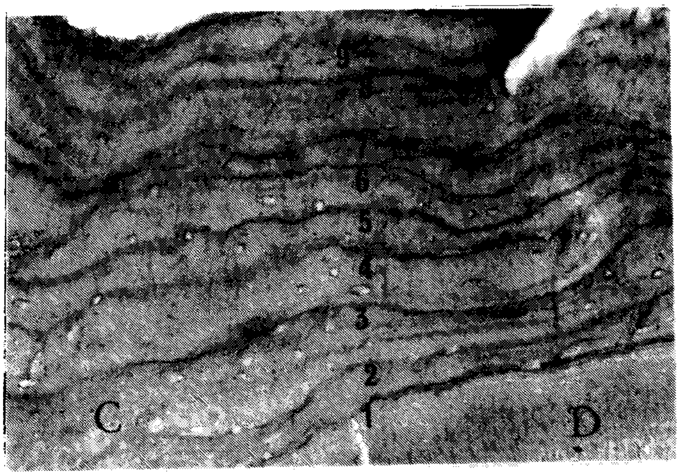


Figure 42: Photomicrograph of a cross-section of the root of the M^1 of a hyrax estimated to be c̲. 9 years old. Note nine clear primary cementum lines (C - cementum; D - dentine)(X 198).

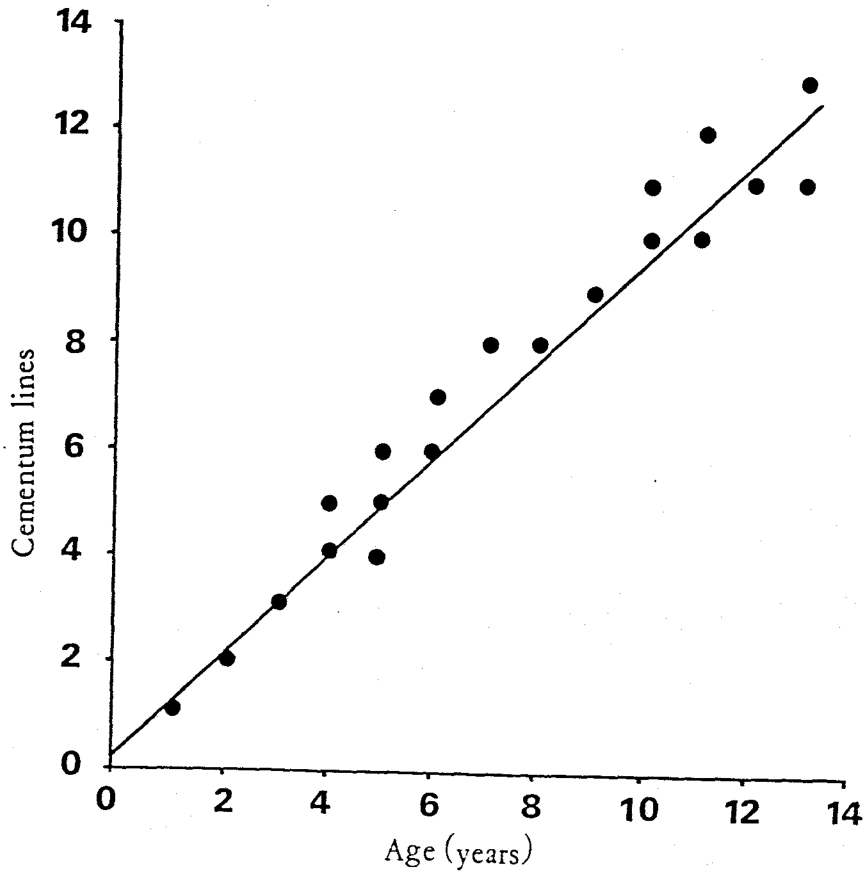


Figure 43: Relationship between dental age and number of primary cementum lines in molariform teeth of hyrax. (Regression equation: $y = 0{,}301 + 0{,}932X$; $r = 0{,}98$; $p < 0{,}001$ and $n = 22$).

To validate the accuracy of the method the author and two independent observers counted the cementum lines on 13 photographs of tooth sections. A comparison of their counts is given in Table 20.

None of the counts differed by more than one from the expected number of lines (dental age class). In all three cases the counts did not differ significantly ($p > 0{,}10$; Chi-Square test) from the expected value.

Secondary lines were encountered in all tooth sections from adult hyrax. Their appearance was, however, very inconsistent.

Table 20: A comparison of the number of cementum lines counted by the author and two observers on the same set of 13 photographs. The expected number of lines was taken to correspond to the dental age class (in years).

Expected number of lines	Observer (A)	Observer (B)	Author
1	1	1	1
1	1	1	1
2	2	2	2
3	3	3	3
5	6	4	5
6	6	5	5
7	7	6	6
8	8	7	7
9	10	9	9
10	10	10	10
11	11	11	10
12	12	12	11
13	12	13	12

Eye lens mass

The correlation between eye lens mass and age for hyrax ($n = 450$) is represented by the power curve $y = 20{,}71\ x^{0{,}409}$ (Fig. 44) with a correlation coefficient of 0,98 ($p < 0{,}001$: where y = dry eye lens mass in mg and x = age in months). The mass of the eye lens increases throughout life and the growth of the lens is typically biphasic with an initial rapid phase lasting c. 50 months followed by a more reduced rate of increase through middle and old age. The accuracy of age estimation utilizing the lens mass decreases with age, particularly after 75 months of age (Fig. 44).

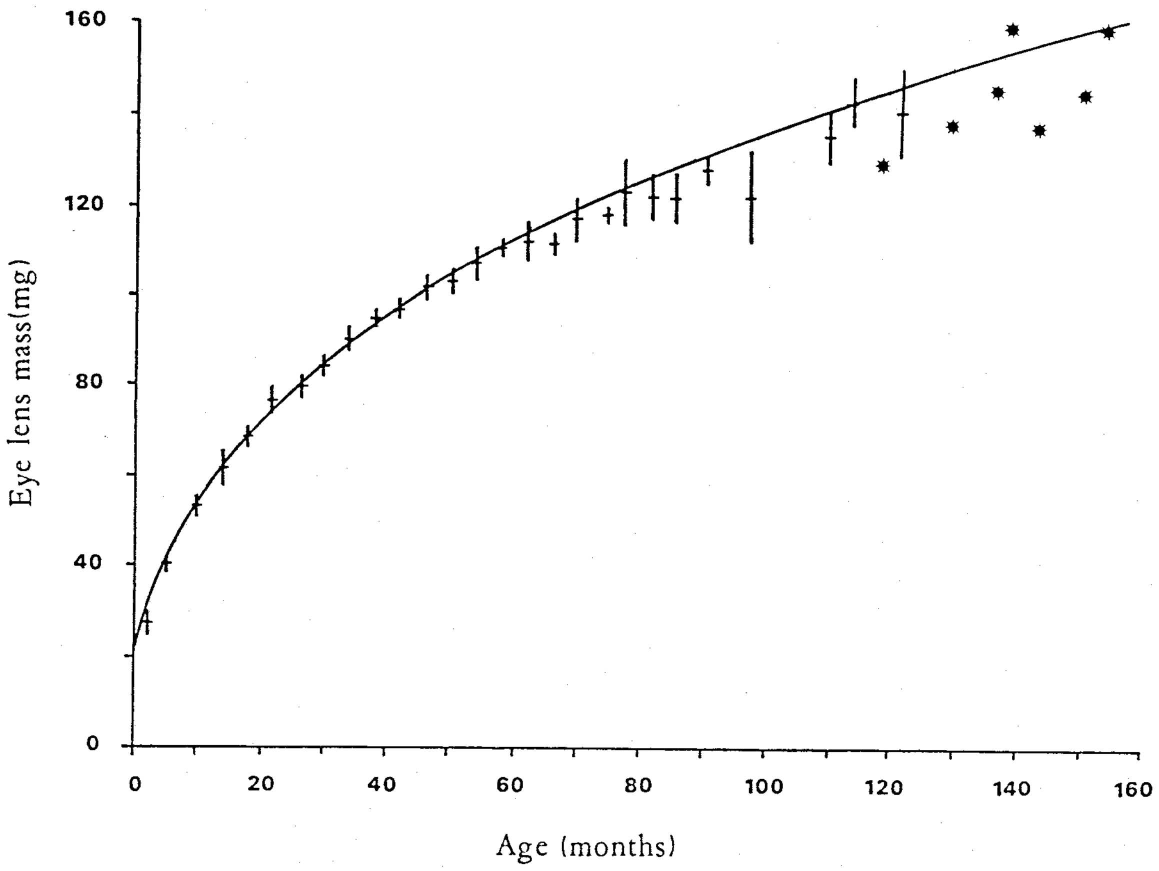


Figure 44: The relationship between eye lens mass and age of hyrax (means ±S.E.). Regression equation : $y = 20,71\ x^{0,409}$; r = 0,98; $p < 0,001$ and n = 450 (* = single observation).

Epiphyseal closure

The relationship between class of epiphyseal closure and age (as determined by dental characteristics) is illustrated in Fig. 45 and represented by the regression equation $y = 9,38\ x^{1,26}$ ($r = 0,91$; $p < 0,001$ and n = 63: where y = age in months and x = class of epiphyseal closure). The proximal epiphysis of the humerus is completely closed at an average of 74 months of age. Due to the large overlap in the age range for the different classes of closure (Table 21) absolute ages cannot be determined reliably by this method. However, age-related categories can be recognized with fair accuracy, (but not precision), as evidenced by the significant correlation coefficient obtained.

Table 21: Mean ages (months) and range for the classes of closure of the proximal epiphysis of the humerus of unsexed hyrax.

Closure class	n	Mean age (months)	Range
1	9	14,58	6 - 18
2	16	23,25	18 - 28
3	12	30,00	24 - 40
4	20	61,89	36 - 88
5	6	74,00	52 - 108

No significant difference ($p > 0,5$; t-test) between sexes as regards epiphyseal closure was observed.

Skull measurements

The mean values (±S.E.) for the different mandibular and maxillary measurements are summarized in Table 22. With the exception of mandibular and maxillary tooth row lengths, which did not differ significantly ($p > 0,05$; t-test) for males and females, statistically significant differences ($p < 0,05$) were found between males and females for all parameters investigated.

The increase in skull dimensions is triphasic with an initial rapid growth rate up to the age of <u>c</u>. 24 months, followed by a period of more rectilinear growth up to the age of 84 months, after which little

Table 22: Age-specific cranial measurements (mm) of the hyrax (means ± S.E.).

Age (months)	Sex	Greatest length of the skull	S.E.	n	Zygomatic width	S.E.	n	Maxillary tooth row length	S.E.	n	Greatest length of mandible	S.E.	n	Mandibular tooth row length	S.E.	n
12	♂♂	73,6	1,5	5	41,4	1,0	6	29,2	2,8	8	59,3	1,9	7	29,8	0,5	8
	♀♀	74,5	1,2	6	41,4	0,5	6	29,1	0,9	6	58,2	1,9	7	28,1	1,7	7
24	♂♂	83,8	1,1	7	49,2	1,0	7	35,7	0,5	8	70,4	1,3	6	34,6	0,4	6
	♀♀	82,8	1,2	8	47,7	0,7	8	35,9	0,5	8	71,1	1,5	8	35,7	0,4	8
36	♂♂	86,2	1,5	6	51,1	1,4	6	37,8	0,5	6	72,5	1,4	6	36,7	0,5	6
	♀♀	83,3	0,7	6	48,3	0,8	6	37,6	0,6	6	71,0	1,4	6	35,7	0,7	6
48	♂♂	88,4	1,1	6	52,5	1,2	7	37,3	0,7	8	75,6	1,2	5	35,5	1,1	5
	♀♀	86,6	1,4	6	50,4	0,6	5	38,1	0,8	7	73,7	1,5	5	36,1	1,1	5
60	♂♂	87,1	1,3	6	52,1	1,1	5	36,5	0,3	6	74,9	0,8	4	36,3	0,8	4
	♀♀	86,9	3,9	2	50,5	1,0	5	37,2	0,8	6	75,2	1,5	6	35,4	0,5	6
72	♂♂	89,8	1,5	5	52,2	0,7	4	37,4	0,5	5	75,4	0,6	5	36,1	1,0	5
	♀♀	86,8	0,4	5	51,4	0,6	5	36,4	1,1	5	73,8	0,5	5	34,6	0,8	5
84	♂♂	91,8	2,2	5	55,5	0,9	5	36,4	0,6	5	76,9	1,2	5	36,3	0,5	5
	♀♀	87,2	2,3	3	52,6	0,6	3	35,3	0,4	5	74,1	2,0	3	33,9	0,5	4
96	♂♂	89,7	2,2	5	55,9	0,6	5	36,8	0,7	5	-			-		
	♀♀	86,8	2,4	6	50,3	0,9	5	35,9	0,7	6	78,4	0,7	4	33,8	0,8	4
108	♂♂	87,8	2,8	2	52,2	1,4	2	35,4	0,7	3	78,6	-	1	33,7	-	1
	♀♀	91,5	1,1	6	55,1	1,1	5	37,2	0,6	7	78,4	0,6	5	37,4	0,9	5

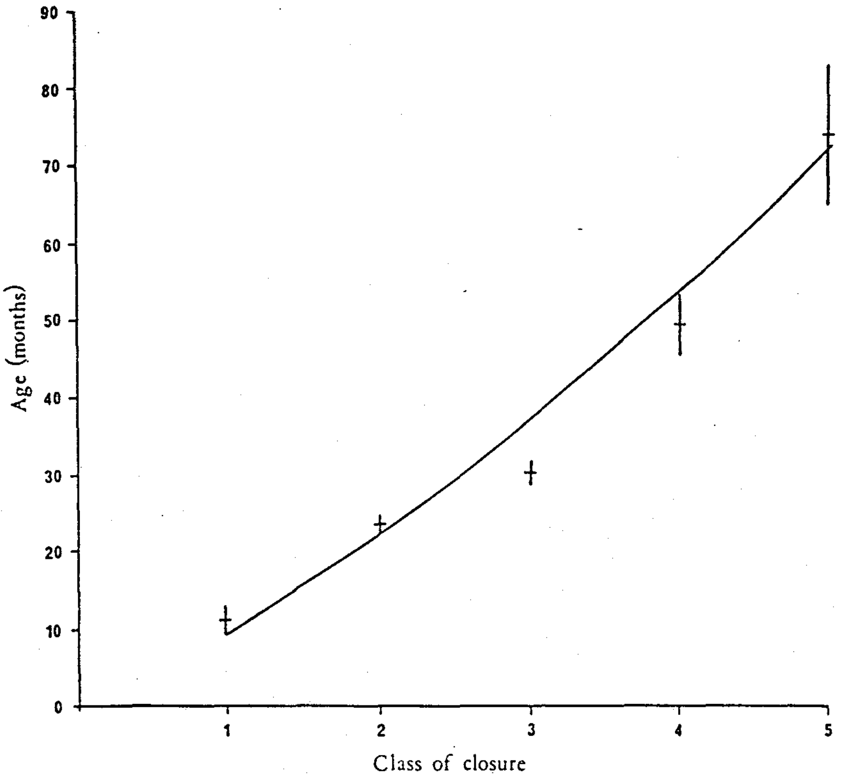


Figure 45: The relationship between the classes of closure of the proximal epiphysis of the humerus and age of hyrax (means ± S.E.). Regression equation: $y = 9{,}38x^{1{,}26}$; $r = 0{,}91$; $p < 0{,}001$ and $n = 63$.

or no growth occurs. Mandibular and maxillary tooth rows increased in length up to the age of 34 - 48 months (Table 22) after which time they decreased due to the loss of premolars.

Regression equations for the various skull measurements relative to age (up to 84 months) are summarized in Table 23.

Statistically, but not biologically, significant correlations exist between skull dimensions and age. After 24 months of age skull measurements cannot be used to obtain accurate age estimations (Table

22).

Table 23: Regression equations for skull measurements (y) against age (x) of hyrax up to 84 months of age.

Measurement	Sex	Regression equation	r	p	n
Greatest length of	♂♂	$y = 58{,}95X^{0,101}$	0,84	0,001	40
the skull	♀♀	$y = 62{,}58X^{0,080}$	0,78	0,001	36
Zygomatic width	♂♂	$y = 31{,}13X^{0,131}$	0,82	0,001	40
	♀♀	$y = 32{,}10X^{0,113}$	0,87	0,001	38
Greatest length of the mandible	♂♂	$y = 44{,}27X^{0,133}$	0,83	0,001	38
	♀♀	$y = 44{,}90X^{0,124}$	0,77	0,001	40

Multivariate regression equations

The body measurements fitted to a multivariate regression equation were head/body length (HBL), girth (G) and hind foot length (HL). Body mass was considered too prone to environmental influence to be a good criterion for age determination and it was omitted from these analyses. In females age (months) = 0,1206 HBL + 0,1903 G + 0,1408 HL - 70,05 and in males age (months) = 0,1196 HBL + 0,1670 G + 0,1194 HL - 62,04.

These regression equations did not give reasonable estimates of age and the use of the equations is not recommended.

Skull measurements incorporated into multivariate regression equations were greatest length of the maxilla (ML), zygomatic width (ZW) and crown height of the first maxillary molar (M). For males (skulls) age is represented by age (years) = 0,1295 + 0,0440 ML + 0,0431 ZW - 0,7035 M and for females age (years) = -4,1984 + 0,0701 ML + 0,0858 ZW - 0,6320 M.

When tested with the raw data for skulls up to the age of 84 months, 97% of the skulls were aged to within one year of the dental age-class using the multivariate regression equations.

DISCUSSION

Dentition

Tooth eruption and replacement

The chronology of tooth eruption and replacement is an accepted means of age determination in wildlife research (Spinage 1973; Hall-Martin 1976). However, in critical studies of age determination, Steenkamp (1975) found that tooth eruption alone could not be regarded as a reliable measure of age due to the tremendous variation that occurs in tooth eruption times within a species. Weiner & Purser (1957) found considerable variation in the exact time of eruption of the incisors of sheep due to genetic and environmental factors. Spinage (1973) has, however, claimed that differences in eruption chronology due to different nutritional levels are unlikely to be significant causes of variation.

Comparison of the present data with results obtained from a captive hyrax colony fed a high protein diet (Fairall 1980) confirms Weiner & Purser's findings (1957). Eruption occurred sooner in the captive colony with the major differences being the eruption of M^2 at 8 months of age compared with 9 - 12 months in the present field study. In addition M^3 erupted at 15 months compared with 17 - 20 months in the present study.

Although the classes used by Steyn (1980) for age determination in a wild hyrax population at Muden in Natal differ slightly from those used in the present study, the results obtained are comparable. However, M_1^1 was visible in the crypt at 0 - 4 months of age in this study whereas no mention was made of the appearance of this molar in hyrax 0 - 5 months of age in the Muden study.

Of considerable significance to age determination is the slow development of M^3 which is fully erupted only at c. 72 months. A similar pattern of eruption has also been recorded for Procavia capensis syriaca by Roche (1978). He described tooth eruption and replacement in 22 known-aged skulls (collected in Israel) and by Steyn (1980) for P. capensis in Muden. Fairall (1980) found M^3 to be fully erupted at 36 months but stated that the discrepancy between his and other observations might be due to the different criteria used to determine when teeth are fully erupted.

It is evident from the literature that a major source of variation is the replacement time for incisors, this can take place between 8 - 17 months (Roche 1978; Fairall 1980; Steyn 1980).

Provided the date of collection within the study area is known, hyrax skulls up to the age of 36 months can be aged with a high degree of accuracy (to within ±1 month) by using eruption and replacement criteria. This method can also be used with a fair degree of accuracy (±12 months) for hyrax up to the age of 72 months. The major variation affecting accuracy after 36 months of age is the slow development rate of M^3 making age class distinctions difficult when used in isolation. However, errors of more than 12 months are unlikely. For all practical purposes hyrax aged less than 36 months sampled during the course of this study, can be considered as 'known-aged' material.

Attrition patterns

In contrast to carnivorous animals, herbivores tend to have broader, flatter teeth, which show marked changes on the occlusal surfaces because of the abrasive action of opal-phytoliths and accidentally ingested gritty bodies (Baker, Jones & Wardrop 1959; Spinage 1973). This causes enamel to erode and exposes dentine at ever increasing rates.

Tooth wear patterns are the most readily available means of determining age and have been used extensively by wildlife biologists throughout the world (Spinage 1973). However, since tooth wear is affected by diet (quality, fibre content, opal-phytoliths and sand)

(Baker et al. 1959; Steenkamp 1975) comparisons within species should be made on individuals frequenting the same habitat. Since attrition tends to follow a negative exponential curve (Spinage 1973), because as opposing surfaces become smoother so the friction between them decreases, there is a tendency to overestimate the age of younger animals and underestimate that of older age classes (Gilbert & Stolt 1970).

When eruption/wear, age estimates of elk were compared with actual age, only 50% agreement was recorded when the animals were placed in specific age groups (Keiss 1969). Individual biologists placed an average of four white tailed deer out of every 10 examined into a different age class (using eruption/wear patterns) than that determined by cementum annuli counts (Gilbert & Stolt 1970).

Hyrax sampled in this study frequented the same habitat and the variability in tooth wear patterns observed probably resulted from genetic differences in dentine and enamel hardness. Nevertheless wear patterns used alone provided a fairly accurate indication of age (65% agreement for specific age classes). The accuracy was further enhanced (70% agreement) when wear patterns were used in conjunction with tooth eruption patterns.

Age determination of animals using tooth wear characteristics may be improved by correlating wear to other dental variables (Hall-Martin 1976; Perrin 1979). A further improvement may be to use various features on single teeth, for example attrition, periodontosis, secondary dentine and cementum apposition, root resorption and transparency of the root. By summing numerical scores for these criteria the method has been used in humans with a high degree of accuracy (Gustafson 1950). The more recently devised scoring method by Demirjian, Goldstein & Tanner (1973) also illustrates the above principle when applied to human teeth.

In conclusion, tooth wear can be effective in assessing the general age structure of a large sample, for, although it lacks exact precision this method has the advantage of rapidity. In addition the method can be applied to dead as well as to living animals by using tooth impressions. Since visual examinations of jaws are often the only means of age determination and since fairly accurate results have been obtained, the use of this technique is justified in the hyrax, especially when used in parallel with other methods.

Measurement of teeth

Results on crown height measurements are consistent with the negative exponential rate of decay reported in the literature for a variety of mammals (Spinage 1973; Aitken 1975; Perrin 1979). The rate of decrease for M^3 was linear, most probably because of the slow growth rate and the protected position of the tooth at the back of the maxillary tooth row. Since there is a large overlap in values accompanied by small differences in mean values, which are masked by progressive age, tooth measurements when used alone are of little value for age determination. However, they supply useful information in doubtful cases of wear patterns such as in old animals (>72 months).

The same criticism levelled against crown height measurements also applies to root length measurements. In addition the X-ray technique is too expensive to use on a parameter yielding doubtful results.

Cementum annuli

The time of cementum line formation and the causative factors have been the source of much discussion and speculation. The two popular hypotheses being that a shortage of food or a more severe climate reduces growth at particular times of the year and that compact, dark staining lines in the cementum are formed as a consequence (Spinage 1973 & 1976; Aitken 1975). The other hypothesis favours the endogenous effect where seasonal fluctuations in physiology due to the annual reproductive cycle cause cementum growth to vary (Kolb 1978).

The presence of one clear primary cementum line in 12-month-old juvenile hyrax (which are not sexually mature) suggests that primary line formation is related to seasonal changes in environmental parameters (temperature, photoperiod and rain). The occurrence of inconsistent, faint secondary lines in adults, however, suggests that their formation may be related to aspects of the annual reproductive cycle (rutting, parturition and lactation) and that it may depend on the overall physiological condition of the animal.

The uncertainty that exists as to the causal factors in incremental line formation can probably only be eliminated after in depth physiological and metabolic studies. However, the method of determining absolute age of animals by cementum counts has a sound theoretical bases and when critically used can yield very accurate results (Grue & Jensen 1979).

Counting cementum annuli has been used to determine the absolute ages of many mammals in various geographical regions. Most success has been obtained with animals from northern temperate regions (Novakowski 1965; Inukai & Kadosaki 1974; Grue & Jensen 1979).

A comparison of ages assigned to hyrax by dental characteristics and by the number of cementum annuli revealed total agreement between the two methods in 55% of cases (n = 22), and agreement to within one year in 95% of the cases. Since the number of cementum annuli appears to be an accurate criterion for age determination (Adams & Watkins 1967; Keiss 1969), the disparity between the two age determination methods indicates that dental characteristics may only give an approximate estimate of animals' true age, particularly in aged animals.

A possible source of error in cementum annuli counts in aged animals is the resorption of cementum commencing at the root apex. Hansard, Comar & Davis (1954) have found that the typical excretion rate of unabsorbed calcium showed a three-fold increase in aged cattle. The cementum counts of an aged animal can thus only provide a minimum age, as an unknown number of lines are likely to have been resorbed

(Spinage 1973).

Fairall (1980) devised age determination methods for the hyrax in captivity up to the age of 36 months. He concluded that counting cementum annuli can be used accurately and absolute age in years is equal to the number of dark staining lines plus one. He made no mention, however, as to which tooth was used, and since there is c. 24 months difference in eruption times between M^1 and M^3, comparison of the results obtained in the present study with those of Fairall is difficult. It is worth mentioning that results obtained for similarly aged coyotes, from widely spaced geographical regions, differed by 12 months in the formation of the first incremental line for the same tooth. This implies that as far as cementum annuli counts as an age determination method are concerned, the applicability of this method for animals occurring in widely separated geographical regions should be verified first.

Eye lens mass

The lens of the eye is an ectodermal structure and grows continuously. Owing to its unique location little, if any, of the lens is worn away in life and consequently it is one of the more accurate methods of age determination in mammals (Morris 1972). Lord (1959) first showed how the dry mass of the eye lens can be used for age estimation in cotton- tail rabbits. Since that time numerous studies related to lens mass have been conducted on small (Gourly & Jannett 1975; Perrin 1979) and large (Novakowski 1965; Hall-Martin 1976) mammals. It is evident from the literature that the greatest success has been obtained with small to medium sized mammals, notably rabbits (Morris 1972).

Potential sources of error when using the eye lens mass technique have been mentioned by Friend (1968). When standardized procedures and sophisticated micro-electrical balances are used some of these sources of error can be eliminated and precise results obtained (Perrin 1979). It is possible to discard those lenses of which the masses are suspect and to grade the remainder according to their reliability, but this introduces subjectivity.

Fairall (1980) discarded dried eye lens mass as a reliable age determinant for hyrax above the age of 24 months. Steyn (1980), however, obtained a correlation coefficient of 0,95 between dried lens mass and dental age criteria for hyrax and concluded that it is a reliable index of age. A high correlation coefficient of 0,98 between dental age criteria and dried eye lens mass in the present study supports Steyn's (op. cit.) conclusion. A comparison of the results obtained for the Muden hyrax population in Natal (Steyn 1980) and in the present study is difficult since means and standard errors were not given for the Muden population. However, manipulation of the regression equation $y = 0{,}01X^{0{,}40}$ (where y = single lens mass in g and x = age in months) provided for the Muden colony and that obtained for the present study showed MZNP hyrax to have consistently heavier eye lenses (Table 24). The difference is significant ($p < 0{,}001$; t-test), and since both studies showed similar results for tooth eruption and replacement age, the estimation of the ages, based on eye lens mass, of hyrax up to the age of 72 months should also have been fairly similar.

Table 24: Comparison of eye lens masses (mg) obtained for the Muden hyrax population and that for hyrax sampled in and around the MZNP based on manipulation of the regression equations obtained.

Age (months)	Muden population dried lens mass (mg)	Present study dried lens mass (mg)	Difference (mg)
6	41,0	43,1	2,1
12	54,0	57,2	3,2
18	63,6	67,6	4,0
24	71,3	76,0	4,7
30	78,0	83,3	5,3
36	83,9	89,7	5,8
42	89,2	95,5	6,3
50	95,6	102,6	7,0
60	102,9	110,5	7,6
70	109,4	117,7	8,3
80	115,4	124,3	8,9
90	121,0	130,5	9,5
100	126,2	136,2	10,0

The apparent differences may be genetically based in which case they will be consistent with the results obtained by Bothma, Teer & Gates (1972), who found that known-age cottontail rabbits occurring in different geographical areas had different dried eye lens masses. Alternatively the differences may be due to different periods of time allowed for fixation of the lenses (< 0,5 months for the Muden population and 1 - 4 months for the present study). Friend (1967a) found that if the eye lenses of rats were fixed for less than 0,5 months their masses were unlikely to be comparable with those of lenses fixed for 1 - 10 months. Another possible cause for the differences could be disparities in nutritional status for the two populations. It has, however, been shown that nutritional status does not influence the growth of lenses of young rats (Friend 1967b) and deer (Friend & Severinghaus 1967). This may also be true for hyrax but must be verified.

A possible refinement of the eye lens mass technique is to assay the insoluble lens protein (Otero & Dapson 1972), and according to the authors this is an extremely accurate method. This technique has been used in white-tailed deer (Ludwig & Dapson 1977), but is, however, time consuming and impractical to use on large samples.

In conclusion it can be stated that the dried eye lens masses of hyrax provide an accurate method of age assessment up to _c_. 72 months of age. The inaccuracies after 72 months of age may not be due to shortcomings of the technique, but rather are a direct consequence of the difficulties involved in determining the exact age of aged animals from dental criteria (in the absence of known-aged material). The major disadvantage of the eye lens technique is that it can only be used in animals that have recently died.

Epiphyseal closure

Growth takes place in the long bones of young mammals in a cartilaginous zone between the diaphysis (shaft) and epiphysis (head). When adult size is attained this zone ossifies and the epiphysis and diaphysis become solidly fused (Hale 1949). Unfused epiphyses are therefore an indication of continuing growth and may serve as a guide to age (Bothma et al. 1972). Observation of epiphyseal closure has been used effectively for many years by medical science to age primates and laboratory animals and has subsequently been used to age wild animals (Thomsen & Mortensen 1946; Carson 1961; Dubock 1979).

The method used in this study is fairly subjective. A more objective way would have been to use the changing ratio of bone length and epiphyseal closure. Morris (1970), however, has shown that in the hedgehog, as bones become larger and the gap gets smaller, the gaps eventually become so small that measurements are inaccurate. This results in large discrepancies in the ratio value based upon comparisons with the relatively enormous length of bone.

Since the results for hyrax indicate that only age-related categories (juveniles, sub-adults and adults) can be recognised the use of this technique is very limited (Bothma et al. 1972; Dubock 1979). It does, however, have the advantage that by using X-rays, it can be applied to live animals. If only dead animals are used, epiphyseal closure can be studied visually without using expensive X-ray apparatus.

Skull measurements

Skull dimensions have been examined as a method of age determination on many animals (Van Bree, Jensen & Kleijn 1966; Bothma et al.

1972). They can only be used with a fair degree of accuracy for a short period of time relative to the life span of the animal (Aitken 1975; Grobler 1978). Hoffmeister & Zimmerman (1967) demonstrated that skull dimensions gave accurate results for cottontail rabbits that had not yet reached adulthood.

The hyrax is a slow growing animal and maximum size is only reached at _c_. 72 months of age. Yet, its skull dimensions increase rapidly for 24 months, thereafter changes take place more slowly thus limiting the use of these criteria for the accurate age determination of adults. Since tooth eruption and replacement schedules can provide more accurate results, the use of skull dimensions is not recommended.

Multivariate regression equations

The multivariate regression equations compiled in this study yielded disappointing results. I believe that individual variation in the parameters incorporated into the equations was a possible source of error. Some of the raw data tested gave precise results whereas the majority yielded results with errors of such a magnitude as to reject the use of the equations entirely. Fairall (1980), however, compiled multivariate regression equations effective for ageing captive hyrax up to 36 months of age. The growth of the captive colony was possibly more uniform than that of free-living colonies because of a more stable diet. In addition the SPSS package used by Fairall (op. cit.) incorporates a more refined method of determining these equations.

Multivariate regression equations employing skull measurements and molar height measurements yielded more positive and useful results than those making use of other measurements. This was possibly due to the fact that these dimensions are not normally subject to large seasonal variations, nor are they seriously affected by nutritional status and habitat differences, as are certain of the body measurements (Morris 1972).

General discussion

To determine the true life span of mammals, Petrick (1977) developed the formula $y = c\sqrt{x}$ where y = life-span, c = 41,2 (constant), and x = first life cycle (twice the gestation period plus the period of puberty). In applying this formula to the hyrax, a life-span of between 182 and 231 months was calculated (Fourie 1978). The highest recorded age for a hyrax (female Procavia capensis syriaca Schreber, in captivity) is 148 months.

The oldest skull (maxilla) collected at a black eagle's nest during the course of this study had belonged to an animal estimated to be c. 168 months of age. It thus seems as if the maximum age indicated by the age classes used in this study approximates actual longevity.

The following summary of results should facilitate age determination in hyrax:

(a) Dead animals/skulls

1. The dried eye lens mass can be used for accurate estimates up to c. 72 months of age (chronological age can be read off from Fig. 44).
2. The stage of tooth eruption can be examined in either jaw. The corresponding stage of eruption with its chronological age can be found in Table 17.
3. In those animals in which the teeth are fully erupted wear patterns should be used in conjunction with tooth measurements (Figs. 36 - 39) and eye lens masses (Fig. 44).
4. In addition to the above mentioned procedures the predictive multivariate regression equations (for skulls) provide age estimates (within ±12 months) up to c. 84 months of age.
5. Single body measurements (head/body length, hind foot length and girth) provide estimates (within ±3 months) up to 24 months of age. In this respect the theoretical growth curves (Figs. 17 - 22; CHAPTER IV) are useful.
6. The single most reliable parameter for age determination is the number of primary cementum lines. One primary line is formed annually. If M^2 or M^3 are used one and two years must be added to the number of lines counted respectively since these teeth erupt approximately one and two years after birth.

(b) Live animals

1. Certain single body measurements provide age estimates (within ±3 months) up to the age of c. 24 months (Figs. 17 - 22; CHAPTER IV).
2. Tooth impressions provide accurate information on tooth eruption/ replacement and wear patterns. The same procedure as that for dead material can be followed.
3. Relative age classes can be obtained by X-raying fore limbs.

Using these procedures it is possible to determine the age of most animals up to the age of 72 months to within 12 months. Thereafter the possible error increases because of the greater variability found in older animals and because tooth wear patterns are also more variable; however, the error in prediction is still unlikely to exceed 24 months.

SUMMARY

The methods used for age determination of hyrax were growth (skull and tooth dimensions, eye lens mass, tooth eruption and replacement and the closure of the proximal epiphysis of the humerus), tooth wear and the counting of cementum annuli.

A schedule of tooth replacement in the hyrax is provided. The third maxillary molar erupts fully at c. 64 - 72 months of age. Drawings of the sequential changes in tooth wear for 13 annual classes, as well as

a description of each class, are provided. Crown height and root length when used alone are of little value for age determination. Cementum annuli counts provided reliable estimates of age. One primary cementum line is formed annually.

A growth curve for dried eye lens masses is supplied. The dried eye lens mass of hyrax provide an accurate means of age determination up to _c_. 72 months of age.

The closure of the proximal epiphysis of the humerus was not an accurate means of age determination. Since only age related categories (juveniles, sub-adults and adults) can be recognised the use of this technique is limited.

Skull dimensions in the hyrax increased rapidly during the first 24 months of age, thereafter changes took place more slowly, limiting the use of this method for the accurate age determination of adults.

Multivariate regression equations incorporating body measurements and skull measurements are provided. The use of the multivariate regression equation incorporating body measurements did not furnish accurate estimates of age and its use is not recommended. Multivariate regression equations employing skull measurements gave reasonable estimates of age, to within _c_. 1 year for hyrax skulls up to the age of seven years.

A summary of results to facilitate age determination of dead animals is provided.

CHAPTER VI

REPRODUCTION

INTRODUCTION

In any study of population dynamics, age-specific fecundity, onset of puberty, breeding season, prenatal mortality and the effect of environmental factors on these parameters are fundamental questions. This chapter investigates these parameters and supplements the data on hyrax reproductive biology. Conflicting reports in the literature on hyrax biology are discussed.

Since the reports by Thomas (1946), Hanse (1962) and Kolbe (1967) on the population explosion of hyrax in the Cape Midlands and Karoo during the 1930's and 1940's the only pertinent study conducted in these areas was that by Millar (1971). Since he did not use accurate age determination methods, however, the value of his results are limited. The only other investigation on a natural population of hyrax, relating reproduction to environmental factors, was that by Steyn (1980) at Muden in Natal.

Since environmental factors are known to affect litter size and prenatal mortality (Millar 1971), and because hyrax show a regional variation in litter size (Sale 1969), any investigation of reproduction is area specific and may not necessarily apply throughout the species range.

METHODS

Collection of material and measurements

Shot hyrax were dissected on return to the laboratory and the following data were recorded:

1. Combined testes mass, with the epididymes removed, to the nearest 0,1 g (measured on a Metler analytical balance).
2. Number of corpora lutea in each ovary.
3. Number of embryos/foetuses in each uterine horn.
4. Signs of embryonic or foetal resorption.
5. Mass of the foetuses to the nearest 0,1 g (measured on a Metler analytical balance).
6. Crown to rump (stump of tail) length of foetuses lying in a natural position (to the nearest 0,1 mm with a pair of dial calipers).

All the reproductive tracts, foetuses and testes were stored in labelled bottles containing 10% formalin.

Calculation of foetal age

Huggett & Widdas (1951) developed an equation correlating foetal mass with age. This equation ($M^{\frac{1}{3}} = a\ (t - t_o)$ where $M^{\frac{1}{3}}$ = cube root of foetal mass, t = foetal age, t_o = intersect on the t-axis and a = specific foetal growth velocity) was used in the present study to calculate foetal age. As individual foetal mass at any stage of pregnancy varies according to the number of foetuses present (Millar 1971; Van der Merwe & Skinner 1982), with foetuses belonging to small litters being heavier, the more reliable measure of total litter mass was used.

The mean litter mass (±S.E.) for the five heaviest litters sampled was 658 (±42) g. The gestation period of the hyrax is c. 230 days (Murray 1942; Millar 1971). The intersection on the t-axis is given by Huggett & Widdas (1951) as c. 0,2t for mammals with a gestation period between 100 - 400 days and 0,2t will therefore be 46 days (0,2 x 230) for the hyrax. The specific growth velocity, a, was calculated to be 0,0472 ($a = \frac{M^{\frac{1}{3}}}{t - t_o}$) and the equation employed to calculate foetal age utilising Huggett & Widdas' formula was $t = \frac{M^{\frac{1}{3}}}{0,0472} + 46$.

Histology

The two methods used to determine the sexual status of male hyrax were histological sections of the testes, and testes smears. Testes used for histological examination were fixed in 10% formal-saline and Bouin's fluid respectively, embedded in paraffin wax, sectioned at 6 - 8 µm using a rotary microtome, and stained with haemotoxylin and eosin according to standard histological procedures (Peacock & Bradbury 1973).

Stained preparations were photographed using Kodak 125 plus X-pan film on a Zeiss photomicroscope.

Smears of the dissected testes and epididymes were made on glass slides and examined at x 400 magnification for the presence of spermatozoa.

Field observations

Information on copulation, lactation and first sightings of juveniles was gathered during 359 h of direct observation from a hide at a large hyrax colony (40 - 56 animals). The adult animals in this colony had been individually marked and their ages determined from tooth impressions.

Additional information was gained during a further c. 900 h spent while shooting hyrax and on field work.

RESULTS

Male reproductive biology

Gross anatomy

The male urinogenital system is illustrated in Fig. 46. The intra-abdominal testes are attached to the ipsilateral kidneys by a firm peritoneal attachment, the left kidney being situated slightly more caudally than the right.

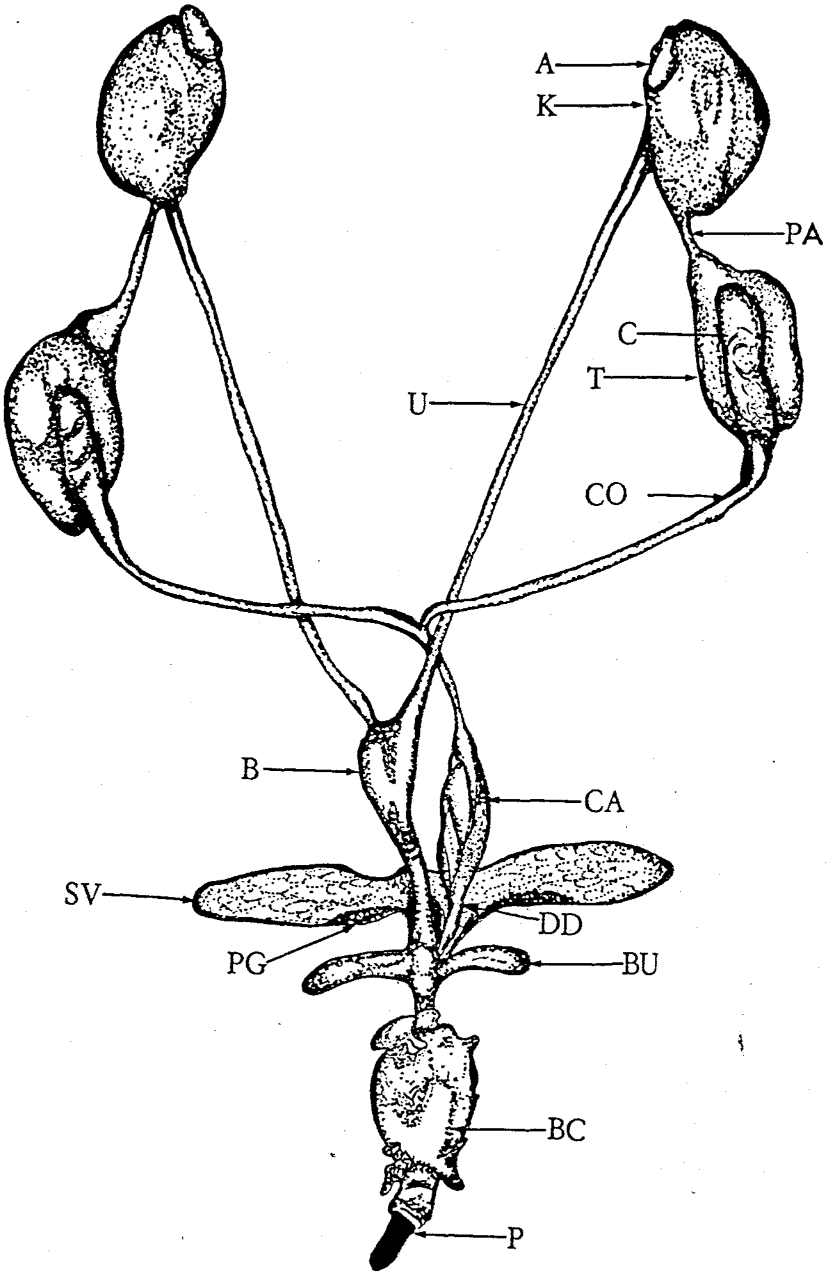


Figure 46: Ventral view of the male urinogenital system of the hyrax.

A - adrenal gland
K - kidney
PA - peritoneal attachment
C - caput epididymis
T - testis
U - ureter
CO - corpus epididymis
B - bladder

CA - cauda epididymis
SV - seminal vesicle
DD - ductus deferens
PG - prostate gland
BU - bulbo urethral gland
BC - bulbo cavernosus muscle
P - penis

Fat tissue is formed abundantly around the testes. The testicular artery arises from the inferior renal arteries and no pampiniform plexus is evident.

The testicular excurrent duct is extensively coiled along the length of the testis and forms the caput epididymis. It straightens to form the corpus epididymis and crosses over the ureter to reach the pelvic cavity. At the entrance to the pelvis the duct joins its contralateral partner to form the cauda epididymis. Both the cauda epididymis and the seminal vesicles empty into the pelvic urethra. The prostate tissue adheres to the caudal surface of the seminal vesicle. The bulbo urethral glands are situated on the dorso-lateral surfaces of the urethra.

The penis is of the vascular type in which erection is produced primarily by vascular engorgement of the cavernous tissue. The opening of the penis is situated immediately below the anus.

Attainment of puberty

Histological examination and testis smears showed that no hyrax (n = 16) less than 15 months old, sampled in March and April during 1980 - 1982, had reached puberty. Only two of the seven hyrax, between the ages of 15 and 17 months, sampled during the same period had attained puberty (Table 25).

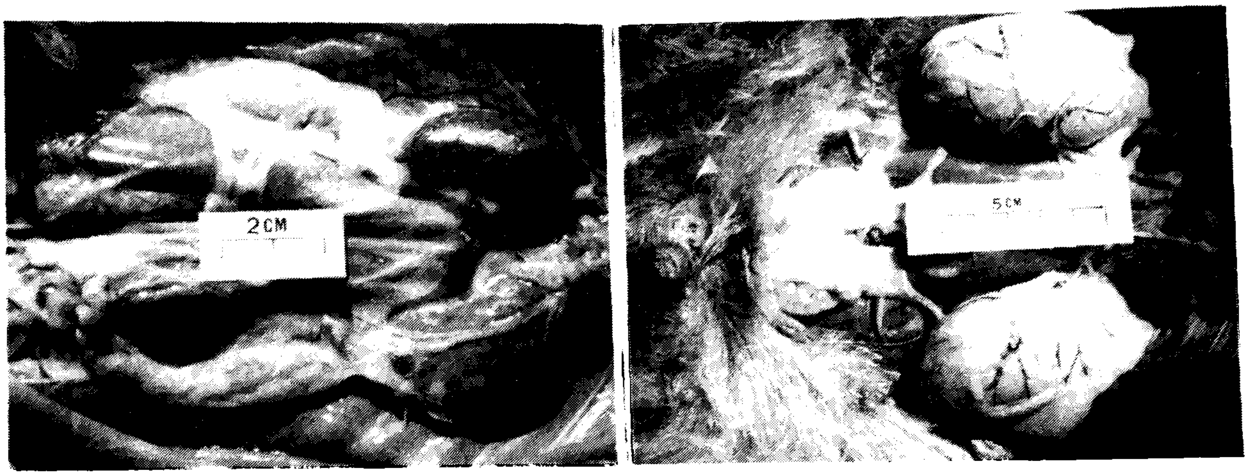
Table 25: Dates of collection, combined testes mass (g) and results of testes smears of seven hyrax between the ages of 15 and 17 months.

Date of collection	Combined testes mass (g)	Testis smear
19.04.80	4,6	negative
01.03.81	4,1	negative
18.04.81	3,2	negative
20.03.81	3,7	negative
19.03.82	57,6	spermatozoa
23.03.82	75,1	spermatozoa
20.04.82	6,3	negative

Not one of the four hyrax between the ages of 15 and 17 months collected during 1980 - 1981 were sexually active. However, two of the three hyrax of this age group collected in 1982 had sexually active testes and their testes masses were 15 times greater than those of their prepubertal counterparts (Table 25, Figs. 47a & b).

All males examined (n = 11) between the ages of 27 and 29 months had spermatozoa in their testes.

A histological section of the testis of a 4-month-old prepubertal. male hyrax is illustrated in Fig. 48. This section shows seminiferous tubules with a small diameter and reduced seminiferous epithelium and no spermatogenic activity. A section of the testis of a pre-pubertal 17-month-old hyrax is shown in Fig. 49. Although the seminiferous tubules are slightly larger in diameter and the tubule lumen is wider, no spermatogenic activity is evident and the seminiferous epithelium is still much reduced. However, a testis section of a 17-month-old sexually active hyrax shows extensive spermatogenic



(a) (b)

Figure 47: Regressed testes of a prepubertal 17-month-old hyrax (a), and enlarged testes of a sexually active 17-month-old hyrax(b).

activity and spermatids in the seminiferous tubules which have a wide lumen and thickened epithelium (Fig. 50). This is similar in appearance to that of a testis of a sexually active 29-month-old hyrax (Fig. 51).

Reproductive senescence

Male reproductive senescence was not encountered in this study. The testes of a 12-year-old male (collected in April) was producing spermatozoa.

Seasonality of sexual activity

Male hyrax are sexually active between February and May as indicated by testes mass (Fig. 52), the presence of spermatozoa, and observations of copulations in the field. April was the month of peak sexual activity and this was manifested by the larger number of

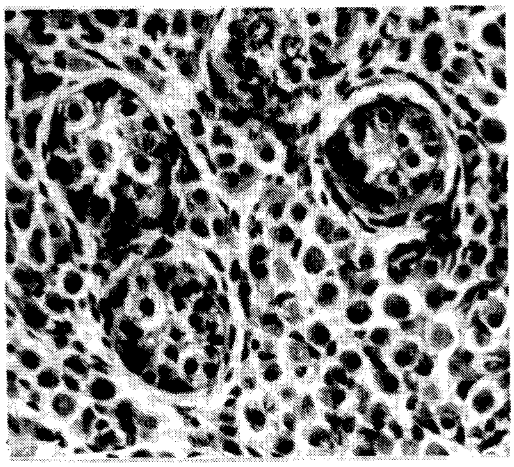


Figure 48: Photomicrograph of the testis of a prepubertal four-month-old hyrax (X 100).

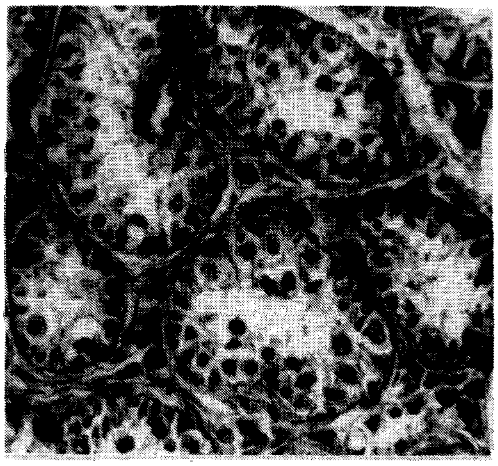


Figure 49: Photomicrograph of the testis of a prepubertal 17-month-old hyrax (X 100).

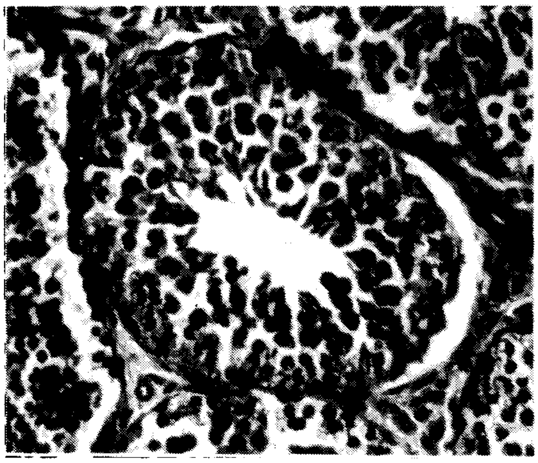


Figure 50: Photomicrograph of the testis of a sexually active 17-month-old hyrax (X 100).

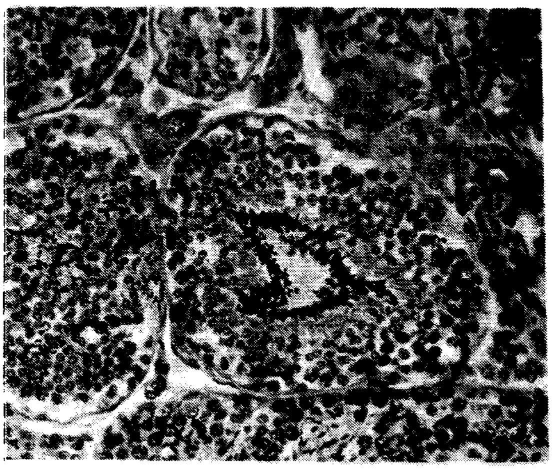


Figure 51: Photomicrograph of the testis of a sexually active 29-month-old hyrax (X 70).

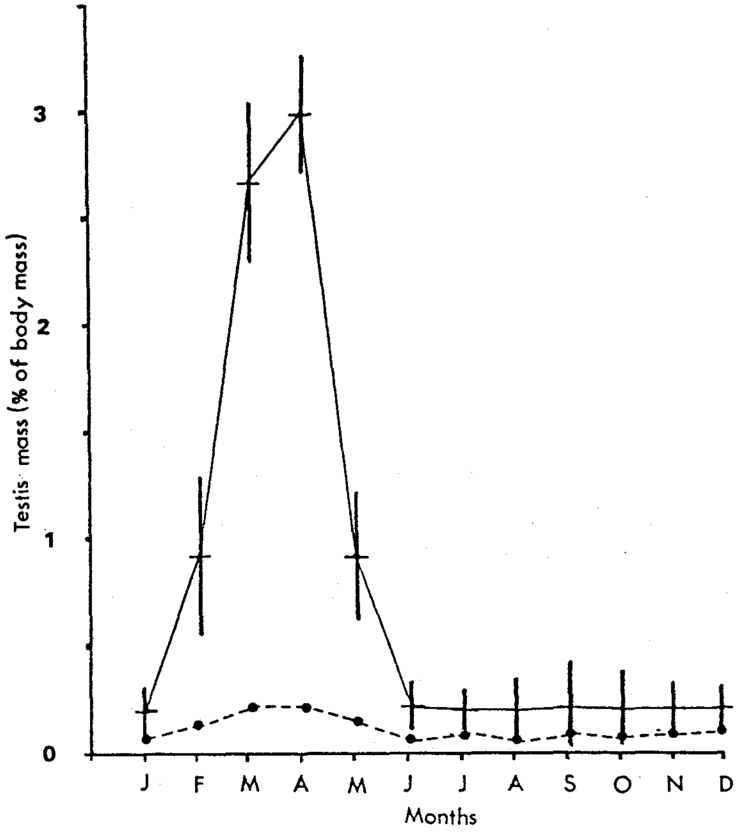


Figure 52: Mean (±S.E.) combined testes mass for sexually active and quiescent hyrax (n = 75) older than 15 months and combined testes mass of prepubertal hyrax (n = 30) (broken line) younger than 17 months. The values are expressed as a percentage of total body mass for a 12 month period (January - December).

copulations observed (15) in comparison with March (8) (observation periods were approximately equal).

The mean value (±S.E.) for combined testes mass of sexually active hyrax during the peak mating period (March and April) was 80,7 (±7) g and that for prepubertal hyrax older than 12 months 4,4 (±0,5) g. For sexually quiescent adult males the mean value (±S.E.) was 6,2 (±0,4) g. Because testes mass is related to body mass ($r = 0,53$; $p < 0,05$) (for sexually active males collected during March and April) it was decided to express combined testes mass as a percentage of total body mass to limit statistical variation (Fig. 52). From Fig. 52 it can be seen that hyrax testes were markedly smaller during June - January than during February - May thereby defining a sexually quiescent phase.

The temporal relationship between rainfall, temperature, photoperiod and testes mass is illustrated in Fig. 53. The onset of spermatogenic activity coincided with a decrease in photoperiod and in mean monthly maximum temperature. Although not constant the three months (January - March) immediately prior to the period of peak sexual activity had

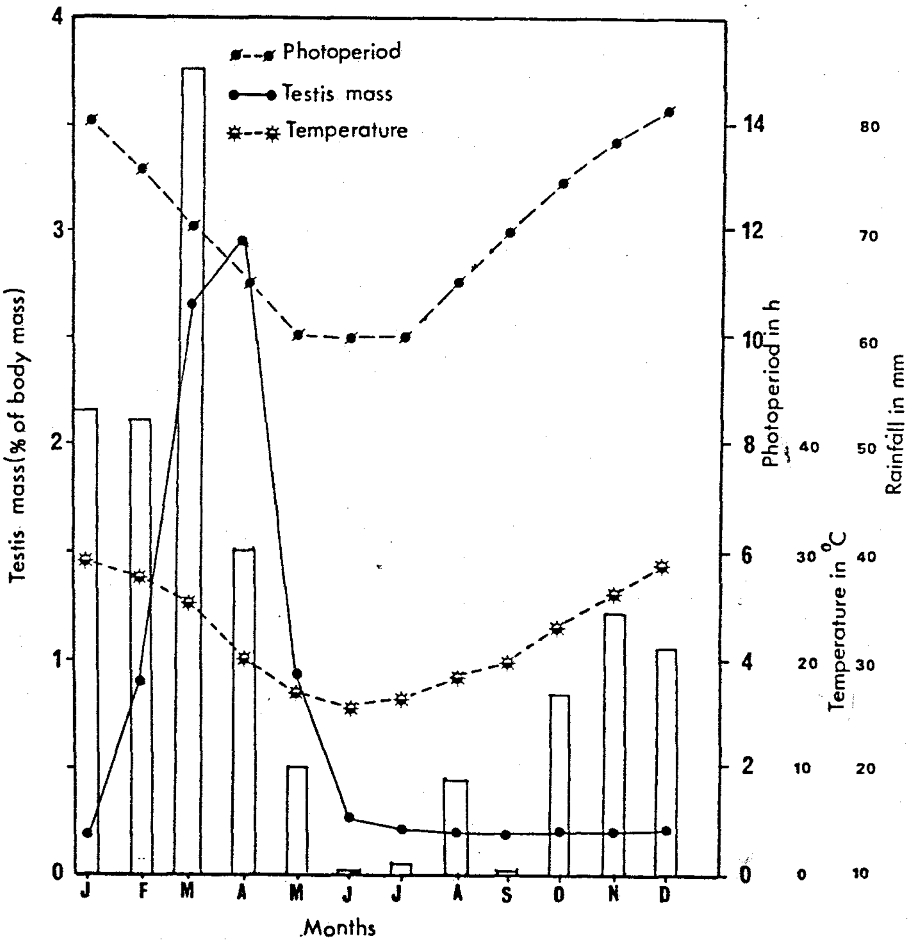


Figure 53: Relationship between testes mass (expressed as percentage of total body mass) and photoperiod (h), rainfall (mm) (histogram) and mean monthly maximum temperature (°C) for a 12 month period (January - December).

the highest mean monthly precipitation, with March having the highest mean monthly rainfall. Mean monthly rainfall decreased after March.

Female reproductive biology

Gross anatomy

The female urinogenital tract is illustrated in Fig. 54. Corpora lutea of parous hyrax can clearly be seen on the irregularly shaped ovaries which are suspended from the dorsal body wall. The oviduct enters the bicornuate uterus ipsilaterally and the two uterine horns become confluent in the pelvic cavity to form the body of the uterus. The vagina extends into the urogenital sinus in which the urethral opening is also situated. The clitoris is situated caudal to the urogenital sinus and the ureters and bladder lie dorsal to the vagina.

Attainment of puberty

Of the female hyrax examined (n = 72) in their first year of life only one (1,4% of total sample) had attained puberty by the age of 4 - 5 months. The mass of this female at 9 months of age was 1600 g compared with a mean (±S.E.) of 1 250 (±51) g for prepubertal females of the same age. One female shot at the age of 22 months had not conceived, and since ovulation is a seasonal phenomenon, this hyrax could only become pregnant at 27 - 29 months of age. However, this female may have been sexually mature but remained unfertilised.

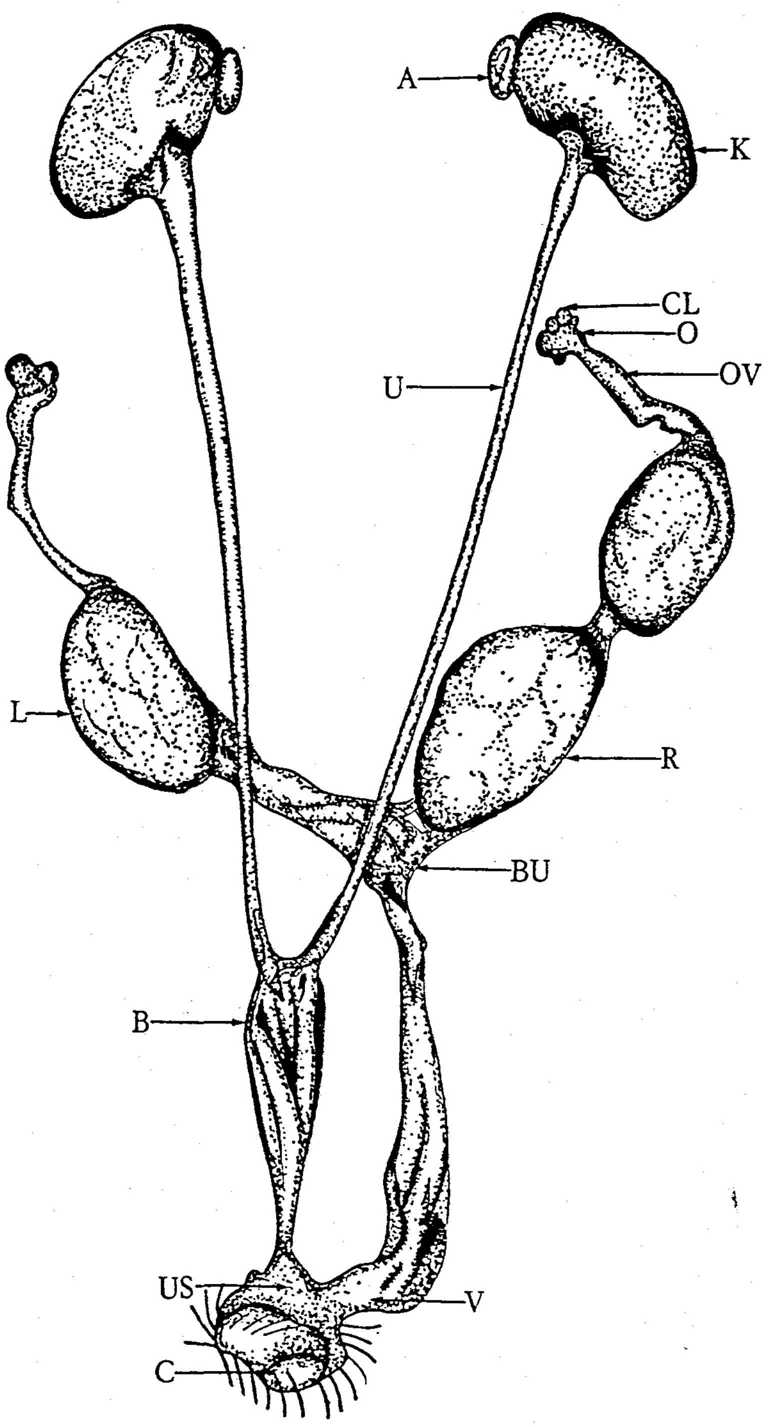


Figure 54: Dorsal view of the urinogenital system of a female hyrax.

A - adrenal gland
K - kidney
U - ureter
CL - corpora lutea
O - ovary
OV - oviduct
C - clitoris

US - urogenital sinus
BU - body of uterus
B - bladder
V - vagina
R - right uterine horn with two foetuses
L - left uterine horn with one foetus

Reproductive senescence

Of the adult females examined (n = 204) only two (five and seven years old respectively) did not conceive in the particular year of examination. No abnormalities of their reproductive tracts were evident. The oldest female collected (13 years old - based on cementum annuli counts) in this study had two normal foetuses in her uterus.

Ovulation and implantation

Examination of the reproductive tracts of 95 females indicated 144 corpora lutea in the left ovaries compared with 114 in the right ovaries. In individual females it was also usual for one ovary to have more corpora lutea than the other (Fig. 55).

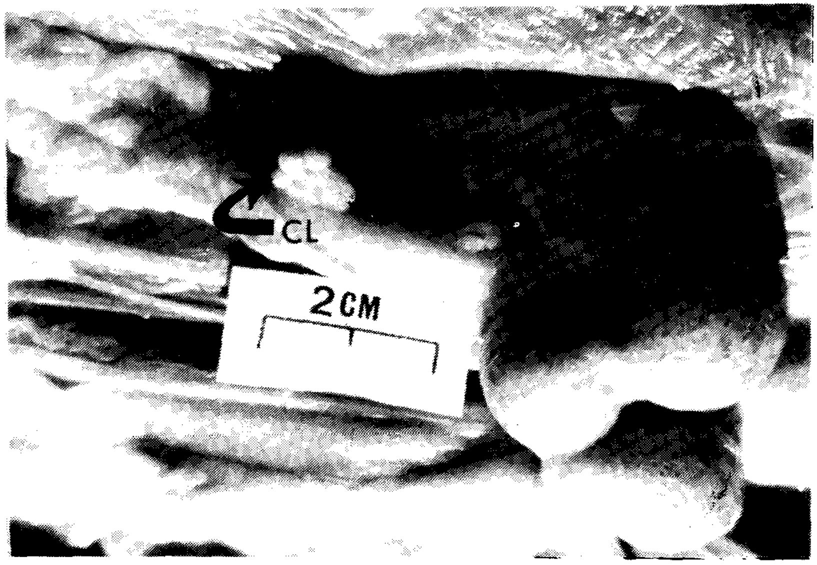


Figure 55: Female reproductive tract of the hyrax showing three corpora lutea (CL) in the left ovary, two foetuses in the left uterine horn and one in the right uterine horn.

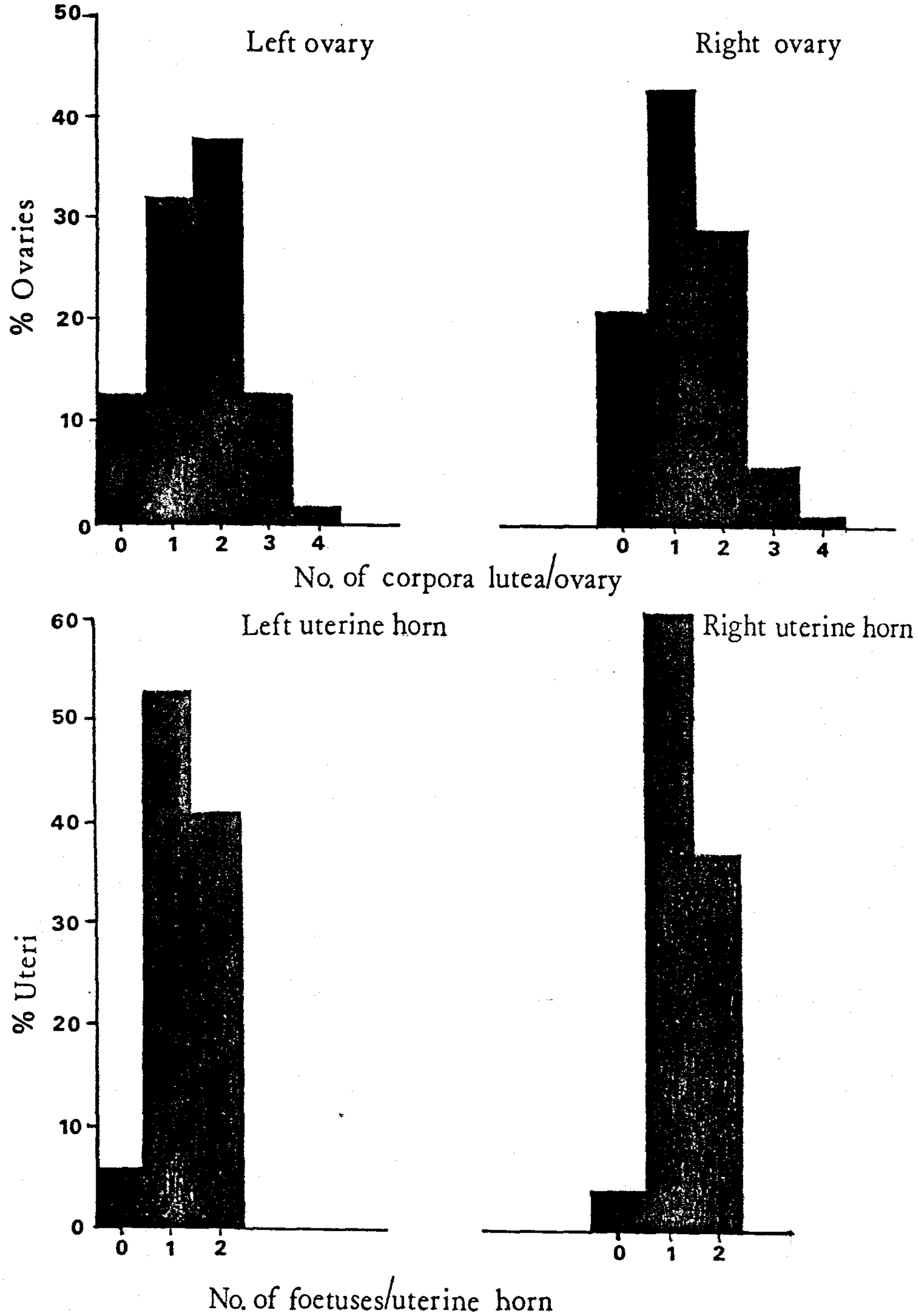


Figure 56: The numerical frequency of corpora lutea and foetuses in the left and right halves of the reproductive tracts of 95 female hyrax.

Despite this difference foetuses were equally distributed between left and right uterine horns (Fig. 56). The more even distribution of foetuses was caused by transuterine migration of the ova and occurred in 38% of the females examined.

Conception, gestation and parturition

The Huggett & Widdas (1951) theoretical foetal growth curve used to calculate foetal ages of hyrax is illustrated in Figure 57. This

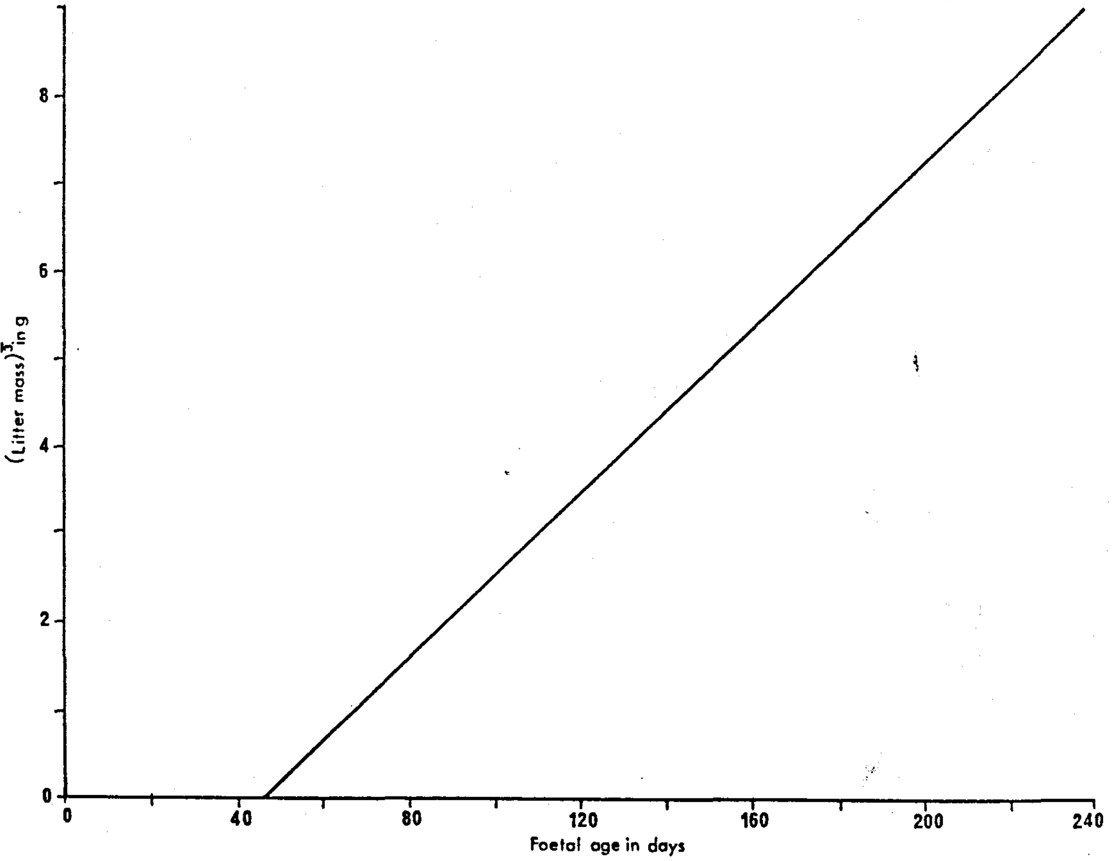


Figure 57: The Huggett & Widdas theoretical foetal growth curve. (Equation: $M^{\frac{1}{3}} = 0,0472\ (t-46)$)

method was only applied to litters consisting of two or more foetuses, for when it was used when only one foetus was present (Fig. 58) the predicted birth dates were incorrect when compared with results obtained from field observations and actual birth dates.

The regression equation when the cube root of litter mass was plotted against date of collection (number of days) (Fig. 58) was $M^{\frac{1}{3}} = -3{,}65 + 0{,}0443X$ ($r = 0{,}95$; $p < 0{,}001$ and X = date of collection). The line intersects the t-axis at 87 days (26 May). The modal class for birth was 278 days (3 December) and by subtracting 230 days (length of gestation period) a value of 48 days (17 April) was obtained (modal

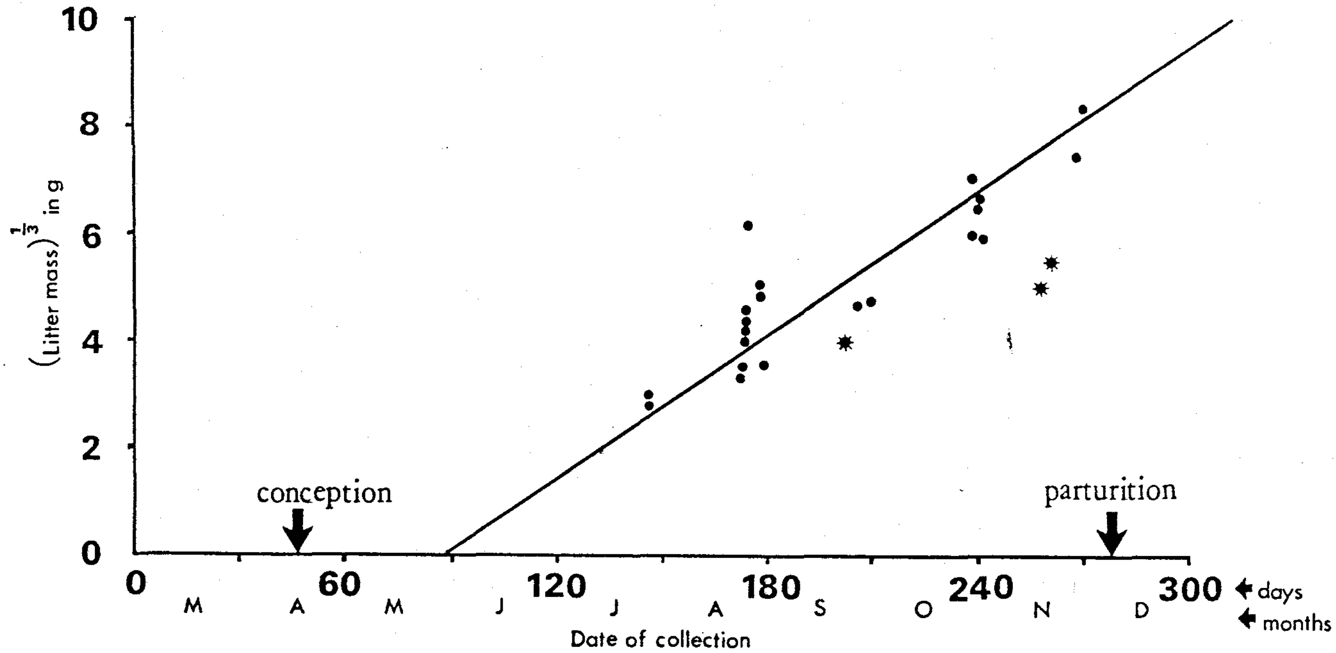


Figure 58: Total foetal growth of hyrax in the MZNP; the regression equation is presented by $M^{\frac{1}{3}} = -3{,}65 + 0{,}0443X$ ($r = 0{,}95$; M = litter mass and X = date of collection); foetal growth is presented by $M^{\frac{1}{3}} = 0{,}0443\ (t-39)$ (*litters consisting of one foetus).

class of conception). In order to obtain the t_o-value 48 days (17 April) was subtracted from 87 days (26 May). Actual total foetal growth is represented by $M^{\frac{1}{3}} = 0,0443\ (t-39)$ (Fig. 58). The specific growth velocity is 0,0443 and is close to the 0,0472 obtained from the theoretical curve.

The temporal distribution of conception and birth dates is illustrated in Figure 59.

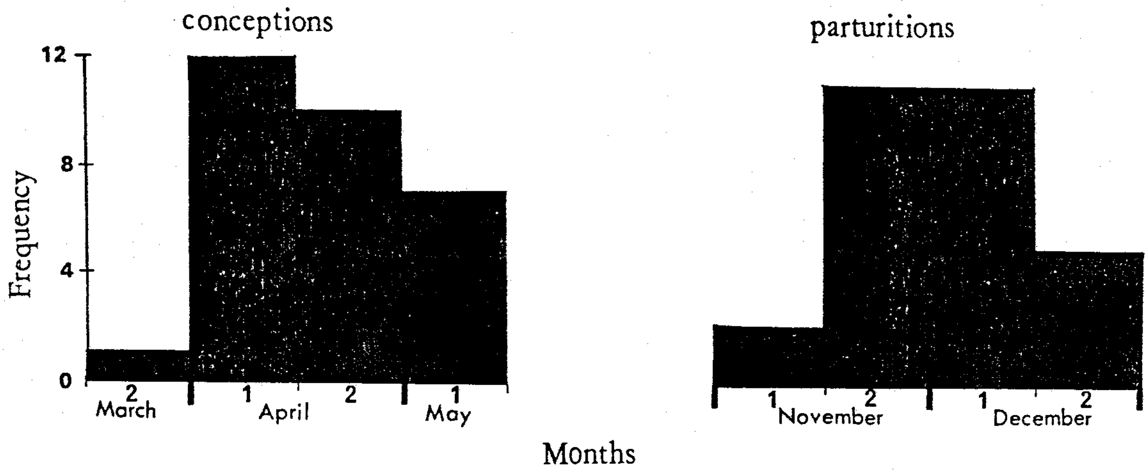


Figure 59: Seasonal frequency distribution of conception and parturition.

Young hyrax first emerged in the MZNP in the second half of November. Estimations of the accumulated percentage of females that had given birth at each occasion on consecutive examinations are summarized in Table 26.

The fact that calculated birth dates and actual birth dates agree clearly illustrates the accuracy of calculating birth dates from the theoretical foetal growth curve.

Table 26: The accumulated percentage of hyrax in the MZNP that had given birth, as recorded during consecutive collections in November and December (1980 - 1982).

Date	No. of ♀♀ examined	Acc. % of ♀♀ that had given birth
15 November	4	0
30 November	13	31
22 December	13	92

The relationship between crown to rump measurements (CR) and foetal age (F_t) is given by the equation $CR = -38{,}26 + 0{,}82F_t$ ($r = 0{,}99$; $p < 0{,}001$ and $n = 26$) (Fig. 60).

Age-specific fecundity

The mean (±S.E.) age-specific litter size and range for hyrax litters ($n = 95$) sampled during the study period are given in Table 27.

Young and very old hyrax had smaller litter sizes than middle-aged animals. The largest mean litter size of 3,36 foetuses was recorded for females belonging to age class five.

In order to compare age-specific fecundity statistically three broad age classes were used, i.e age classes 0 - 1, age classes 2 - 8 and age classes 9 - 12. Age classes 0 - 1 differed significantly ($p < 0{,}001$; t-test) from age classes 2 - 8.

The frequency distribution of the various litter sizes is illustrated

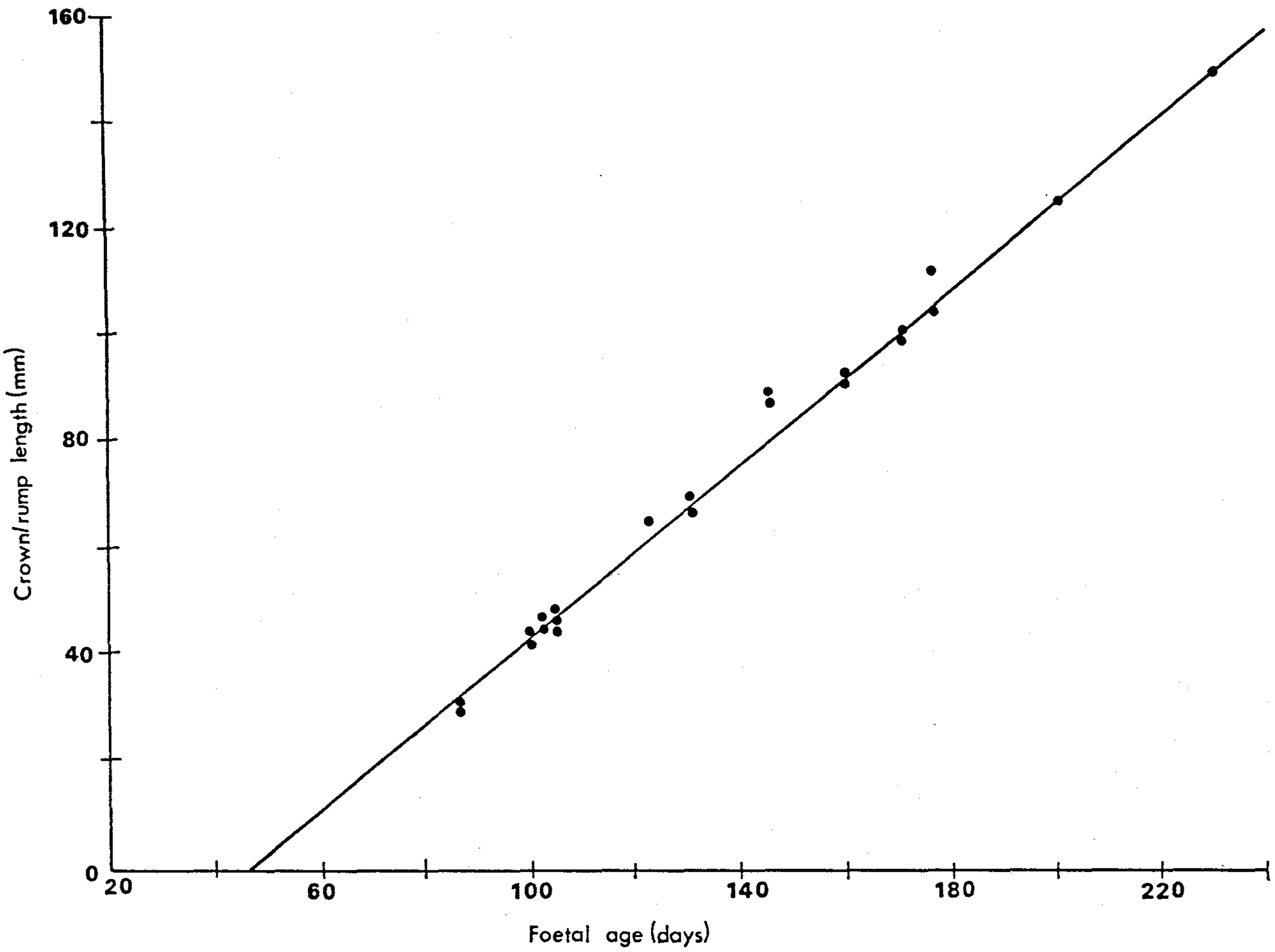


Figure 60: Crown to rump measurements (CR) of hyrax foetuses plotted as a function of foetal age (F_t). (Regression equation: $CR = -38,26 + 0,82F_t$; $r = 0,99$; $p < 0,001$ and $n = 26$)

in Figure 61.

In order to determine the possible effect of rainfall on follicular growth, which is initiated about three months before ovulation (Steyn 1980), and hence ovulation rates, age-specific litter sizes for 1980 - 1982 were compared statistically. However, due to small sample sizes for the various years, statistically valid comparisons could only be made for age classes (years) two and five (Table 28).

Table 27: Mean (±S.E.) age-specific litter sizes and ranges for hyrax litters (n = 95) sampled during the period January 1980 - December 1982 in and around the MZNP.

Age class (years)	Mean litter size	S.E.	Range	n
0	2,00	-	-	1
1	2,08	0,24	1 - 3	13
2	2,46	0,16	1 - 4	24
3	3,00	0,23	1 - 5	17
4	2,55	0,15	2 - 3	12
5	3,36	0,17	2 - 4	14
6	2,75	0,25	2 - 3	4
7	3,00	0,41	2 - 4	4
8	-	-	-	-
9	2,00	0,00	-	2
10	2,00	-	-	1
11	2,50	0,50	2 - 3	2
12	2,00	-	-	1

Table 28: Comparison between age-specific litter size and mean monthly rainfall (mm) (January - April).

Year	Mean monthly rainfall (January - April)	Mean litter size Age class (years)			
		2	n	5	n
1980	42,28	2,42	12	3,60	5
1981	53,73	2,38	8	3,33	4
1982	42,70	2,75	4	3,40	5

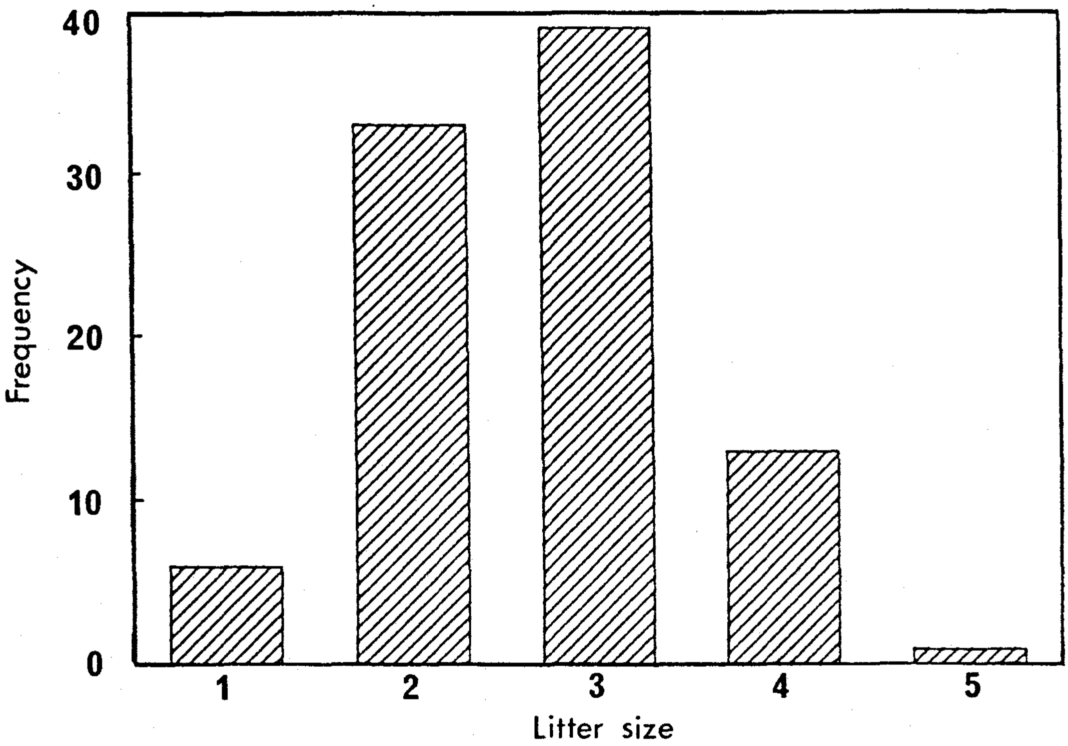


Figure 61: The frequency distribution of litter sizes (n = 95) of hyrax in and around the MZNP.

The precipitation for the periods January - April 1980 - 1982 was fairly similar. No statistically significant differences ($p > 0{,}10$; t-test) were found between the mean litter sizes during the three year period.

Foetal sex ratio

The foetal sex ratio (0,96 ♀♀: 1,00 ♂♂) (n = 106) did not differ significantly ($p > 0{,}50$; Chi-Square test) from parity.

Prenatal mortality

Prenatal mortality was determined by comparing the number of corpora lutea in the ovaries and the number of foetuses in the uterus (Table 29).

Table 29: Age-specific prenatal mortality of foetuses in 95 gravid female hyrax collected in and around the MZNP.

Age class (years)	1	2	3	4	5	7	9	11
% litters with foetal loss	31	25	41	25	7	25	50	50
% foetuses lost	13	9	12	9	2	8	20	33
n	13	24	17	12	14	4	2	2

Prenatal loss of foetuses was highest in young and very old animals. When prenatal mortality was compared with the original ovulation rate it was evident that those females who shed one or five ova respectively had the highest prenatal loss rates. In the groups shedding 2 - 4 ova, prenatal loss increased with the number of ova shed (Table 30).

Table 30: Number of ova shed (no. of corpora lutea), frequency of occurrence, sample size and percentage prenatal loss in 95 female hyrax.

No. of corpora lutea	Frequency of occurrence	% prenatal loss	n
1	1	50	2
2	6	20	31
3	9	21	43
4	6	37	16
5	2	67	3

There is a significant negative correlation ($-r = 0{,}95$; $p < 0{,}05$) between rainfall during the gestation period and prenatal mortality (Table 31).

Table 31: Total rainfall (mm) during the gestation period (April - November) of the hyrax and percentage prenatal mortality as recorded for the period 1980 - 1982.

Year	Rainfall (April - November)	% prenatal mortality
1980	78,5	9,37
1981	204,5	8,75
1982	294,1	7,30

The only observed occurrence of foetal resorption was seen in a four-year-old female. In all other cases prenatal mortality was thought to be due to embryonic or foetal resorption at an early stage or due to foetal abortions.

Lactation

Both the pelvic (one pair) and the pectoral (two pairs) mammae were used for suckling (Fig. 62).

From field observations and the expression of milk from the mammary glands of captured and shot hyrax it was found that young are suckled soon after birth. They are weaned at 1 - 4 months of age (mean ($\pm$S.E.) = 2,3 ($\pm$0,2) months). A few lactating females were found during March,

Figure 62: Juvenile hyrax suckling from pectoral and pelvic mammae.

but none in April, implying that young were weaned before conception took place.

Seasonality of sexual activity

The temporal relationship between conception and parturition dates, and environmental factors is illustrated in Figure 63.

Conception dates coincided with a period of decreasing rainfall, photoperiod and mean monthly maximum temperatures. Parturition coincided with the period of maximum photoperiod, a mean (±S.E.) maximum monthly temperature of 27 (±1) °C and a mean (±S.E.) monthly rainfall of 23 (±5) mm. The latter factors are associated with nutritious and abundant forage production (CHAPTER VII).

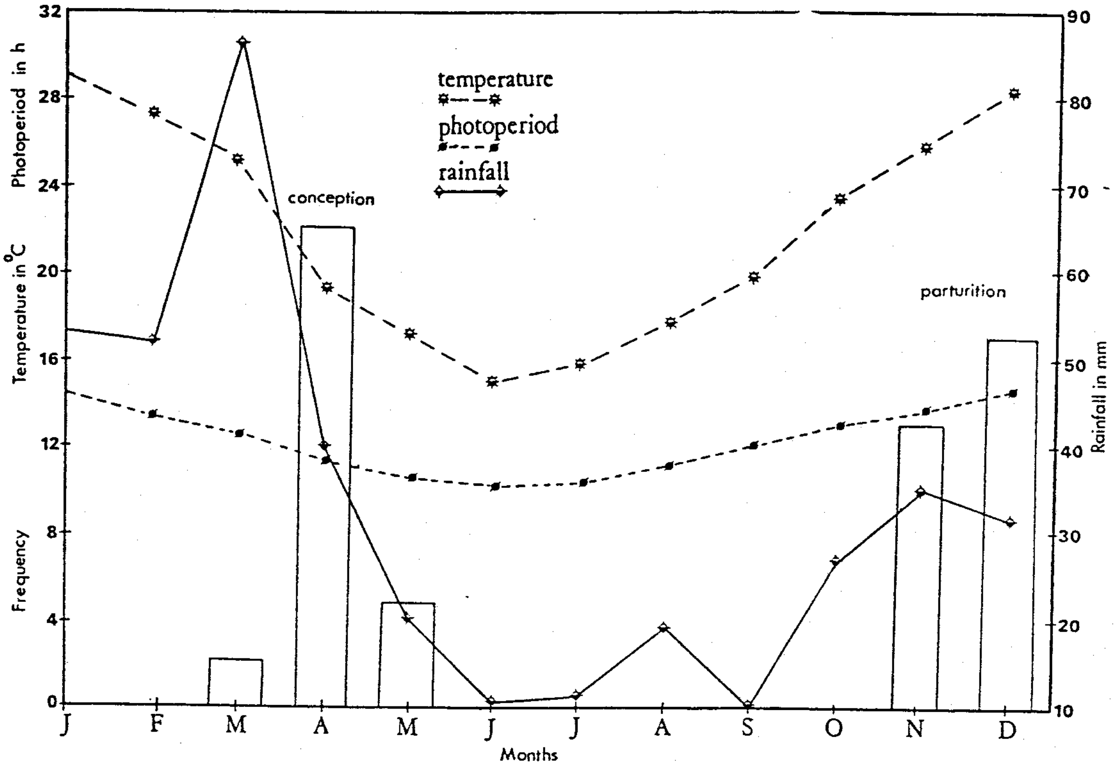


Figure 63: Frequency distribution of conception and parturition dates and the mean monthly rainfall (mm), photoperiod (h) and maximum temperature (°C) over a 12 month period (January - December). Climatological data represents long term means.

DISCUSSION

Gross anatomy

The general morphology of male and female reproductive tracts of hyrax in the present study is consistent with that reported in the literature (Millar & Glover 1970; Hanks 1977; Steyn 1980).

Attainment of puberty

Males

Published data on the attainment of puberty in the hyrax is somewhat conflicting. Millar (1971) and Steyn (1980) state that the majority of males attain puberty at 15 - 17 months of age. However, Millar (1971) also found that two 4 - 5-month-old male hyrax (comprising 30% of the total sample for an age group) at the kloof area of Lake Mentz (Cape Province, R.S.A) had reproductively active testes. Sale (1965a) studied a captive colony of Mount Kenya hyrax (Procavia johnstoni mackinderi) and found that sexual maturity was reached before two years of age. Glover & Sale (1968) interpret Mendelssohn's (1965) report to mean that old males will only tolerate other males younger than 16 - 17 months during the mating season, thereby implying that these younger males were perhaps reproductively inactive. This observation is consistent with the results obtained in the MZNP. Attainment of puberty in males occurs at 15 - 17 months of age or one year later. Male hyrax of 15 - 17 months of age are, however, not allowed by the territorial male to mate with members of the multi-female kinship group (CHAPTER VIII).

Van der Merwe & Skinner (1982) studied the reproductive pattern of P. capensis in the Willem Pretorius Game Reserve (Orange Free State, R.S.A). Although they gave no ages they stated that males with a mass of less than 2 200 g were sexually immature. The 16 - 17-month-old male hyrax in the present study, as well as those studied by Fairall

(1980) and Steyn (1980), had a mass of less than 1 900 g. It is thus evident that any 16 - 17 month old males observed by Van der Merwe & Skinner (1982) would indeed still have been immature. Their results also revealed that some of the males with a mass of 2 300 - 2 900 g had a combined testes mass of only 2 - 5 g during the peak period of male sexual activity. This suggests that these adult males were in a sexually quiescent state.

Females

Millar (1971) and Steyn (1980) state that most females attain puberty at 15 - 17 months of age. Two of the females studied by Steyn (1980) had failed to reach puberty at this age and a hyrax (Procavia johnstoni mackinderi Thomas) kept in captivity only became sexually mature at an age of about 30 months (Sale 1969). Millar (1971), however, reported that 33% of the Lake Mentz (kloof) and 14% of the drier Lake Mentz (noors) females had attained puberty at an age of 4 - 5 months. A prepubertal period of some 8 - 10 months is suggested for Dendrohyrax arborea ruwenzorii Neumann (O'Donoghue 1963).

Millar (1971) suggested that the age at which puberty is reached is dependent on the body growth rate and nutrition. Although this has been shown to be the case for a variety of mammals (Zejda 1966; Sadleir 1969; Fritts & Sealander 1978) the results obtained in the present study and that of Steyn (1980) require further explanation. The mean mass of about 700 g for 4 - 5-month-old females reported by Millar (1971) is less than the equivalent figure (812 g) for the present study, and the figure of 800 g obtained from the growth curves compiled by Steyn (1980). These results clearly indicate a more rapid growth rate for hyrax studied by Steyn (1980) and in the present study, than for those in Millar's (1971) study. Yet only 1,4% of the females in the present study, and none of those studied by Steyn (1980), attained precocious puberty. There was also no precocious puberty in the captive colony of Mount Kenya Procavia studied by Sale (1969) or the captive colony of Procavia studied by Mendelssohn (1965). One would expect that the presumably higher level of nutrition of the captive colonies would lead to precocious puberty, but this was evidently not the case. The higher incidence of precocious puberty in the better vegetated regions of Lake Mentz as compared with the drier regions (Millar 1971) supports the view that the level of nutrition may affect live mass and hence puberty.

The overall pattern of attainment of puberty in hyraces is difficult to understand and in the absence of precise data explanations are only speculative. Although precocious puberty in females may primarily be due to a high growth rate and plane of nutrition, other factors may also be of importance. It is possible that attainment of puberty might be secondarily inhibited by social factors; although no study relating this or density to the attainment of puberty (in the hyrax) has been undertaken. The attainment of puberty in males at an age greater than 15 - 17 months may be related to social pressures mediated through the territorial male. Since mass may be important in determining dominance status, males having a high growth rate may also attain precocious puberty. The high incidence of female precocious puberty reported by Millar (1971) and the very low incidence found in this study may possibly reflect a lower population density for the populations studied by Millar.

Ovulation and implantation

The high incidence of transuterine migration of ova found in this study is consistent with that reported in the literature (O'Donoghue 1963; Millar 1971; Steyn 1980). It seems that the main purpose of transuterine migration of the ova is to bring about a more even distribution of foetuses in the uterine horns since the ovaries have an uneven rate of ovulation with the left ovary being more active.

Conception, gestation and parturition

From the dates on which copulation was observed and the first appearance of juveniles in the MZNP, a gestation period of 7,5 months was calculated. This period is consistent with that reported in the literature (Murray 1942; Millar 1971).

The rate of foetal growth obtained in this study is equivalent to that derived for hyrax at Lake Mentz, i.e $M^{\frac{1}{3}} = 0{,}047\ (t-41)$ (Millar 1971) and very similar to that for a population at Muden; $M^{\frac{1}{3}} = 0{,}0508\ (t-46)$ (Steyn 1980), and in the Willem Pretorius Game Reserve ($M^{\frac{1}{3}} = 0{,}0457\ (t-46)$ (Van der Merwe & Skinner 1982).

Leitch, Hytten & Billewicz (1959) compared the non-reproductive premating mass of females with the foetal mass of their new born litters in 114 species of mammals. To predict litter mass they evolved the equation $N = 0{,}5408\ M^{0{,}8523}$, where N is equal to litter mass and M the premating mass of the adult female. When an average premating mass of 2 830 g for female hyrax is used in this equation the calculated litter mass at birth is 472,2 g. This is 28% less than the actual mean birth litter mass of 658 g. Leitch et al. (1959) noted that values of N significantly above the one predicted occur either in domesticated species, where nutrition or selective breeding may have interfered, or wild rodents with unusually long gestation periods for their size. The high neonatal mass of the hyrax and the long gestation period may indicate that present day hyraces may have descended from a much larger animal (Sale 1965b; Millar 1971). This hypothesis is supported by fossil evidence which shows that the anatomically similar hyracoids were up to three times as large as the living species (Kitching 1966; Whitworth 1954).

The highly significant correlation obtained in this study between foetal crown to rump measurements and foetal age is useful for predicting birth and conception dates in the absence of data on mass.

Age-specific fecundity

A discussion of hyrax breeding strategies is given in CHAPTER XI. Sale (1969) has commented on the litter size patterns of hyraces. He reported that the genus Procavia shows a higher litter size at more temperate latitudes than near the tropics (Table 32), and speculated

Table 32: Litter size data for _Procavia_, _Heterohyrax_ and _Dendrohyrax_ (adapted from Steyn 1980).

Species	Place	Mean litter size	Range	n	Source*
Procavia species	Israel	3,2	1 - 6	36	Mendelssohn (1965)
	Egypt	2,57	1 - 5	14	Flower (1932)
	East Africa	1,9	1 - 3	45	Sale (1965c)
	Tanzania	2,4	1 - 4	14	Hoeck (1982)
	South Africa (Zoo)	2,23	1 - 5	66	Brand (1963)
	South Africa (Orange Free State)	2,4	1 - 5	49	Van der Merwe & Skinner (1982)
	South Africa	3,2	2 - 4	9	Sale (1969)
	South Africa (Karoo)	2,39	1 - 4	±114	Van der Horst (1941)
	South Africa (Karoo)	2,65	1 - 5	95	Fourie (1983) (present study)
	South Africa	5,2	1 - 6	11	Wislocki & Van der Westhuizen (1940)
	South Africa (Natal)	2,71	1 - 4	24	Steyn (1980)
	South Africa (Uitenhage)	2,26	1 - 4	38	Sapsford (1969 unpubl.)
	Zimbabwe (Matopos)	2,00	1 - 3	12	Wilson (1974 unpubl.)
	United States of America (San Diego) (Zoo)	±3,00	1 - 6	-	Griner (1968)
Heterohyrax species	-	1,8	-	±6	Roche (1962)
	East Africa	1,6	-	±6	Allen and Lawrence (1936)
	East Africa	1,7	1 - 2	16	Sale (1969)
	Tanzania	1,6	1 - 3	55	Hoeck (1982)
	United States of America (Zoo)	2,2	-	±6	Hollister (1924)
Dendrohyrax species	Uganda	-	1 - 2	57	O'Donoghue (1963)
	East Africa	1,0	1	14	Sale (1969)
	Zimbabwe (Matopos)	1,83	1 - 2	12	Wilson (1974 unpubl.)

* For references used in the table, but not included in the list of references, see Steyn (1980).

that a possible reason for this may be lower mortality (due to disease) for hyrax living in the tropics. Perhaps overlooking the fact that due to the relatively high temperatures and rainfall in the tropics more stable and productive environments with a high level of nutrient availability prevail. Contrary to the situation in temperate regions where marked seasonal variations in nutrient availability occur resulting in severe juvenile mortalities (CHAPTER X). High litter sizes for temperate regions may thus be a reflection of higher mortalities not only due to predation or diseases but due to periodically limited nutrient availability. For Heterohyrax and Dendrohyrax small litter sizes, which are typical for their respective genera, have been reported (Sale 1969).

The use of mean litter sizes to compare hyrax populations from different geographical regions, or even from the same area, can lead to misinterpretation of population growth trends or ovulation rates, unless these comparisons are made on a time and age-specific basis. Significant differences were found between the litter sizes of young and middle-aged animals in this study. No significant difference for mean age-specific litter sizes, between years was evident in the present study. It is interesting that mean precipitation (January - April) was fairly similar for each year during the study. Millar (1971) states that adverse nutritional conditions influence litter size, primarily by decreasing ovulation rates, and that these nutritional effects are probably mediated by the anterior pituitary and decreased release of gonadotrophins. A similar observation has also been made for the bank vole (Zejda 1966). The results obtained on age-specific ovulation in the present study strengthen Millar's (1971) claim.

Prenatal mortality

Commenting on the decline in fecundity in aged mice Jones & Krohn (1961) suggested that this phenomenon is likely to be due to defects in the hormonal control of the ovary or of the uterine environment rather than loss of oocytes *per se*. Changes associated with age in the connective tissue and stroma of the uterus, cervix and vagina may interfere with the normal passage of sperm or with the zygote and may cause delays in fertilisation or implantation.

The inability of the ageing uterus to sustain developing foetuses may also be of importance. Of the six litters collected from hyrax older than eight years, two (33%) had suffered prenatal mortality which may be a reflection of this inability.

Four (29%) of the primiparous hyrax (n = 14) lost a foetus. This may be due to the fact that the additional burden of pregnancy in young animals, still in a rapid growth phase, is too energy expensive thereby causing resorption/abortion of embryos/foetuses. Prenatal mortality may further be enhanced by adverse nutritional conditions. Millar (1971) reported that 43% of female hyraces in the dry areas lost a foetus compared with the 7,2 - 24,3% of females examined in the better vegetated areas of Lake Mentz. The significant correlation between prenatal mortality and precipitation during gestation, recorded in this study is consistent with the results of Millar (1971). Controlled experiments by De Wet Louw (1978) on angora goats showed a considerable increase in prenatal mortality in undernourished ewes compared to those on a higher plane of nutrition.

Van der Merwe & Skinner (1982) have questioned the validity of determining prenatal mortality based on a comparison of the number of corpora lutea with the number of embryos/foetuses. They argue that because one cannot determine whether the ova are fertilized or not, it may be that many, if not all, are not fertilized. Thus the loss of ova may be a common phenomenon in the hyrax. However, one of the principle factors of natural selection favouring internal fertilization is to minimize the energy expenditure of producing large numbers of ova. The author suggests that, except in the case of physical disability of the uterus, a high probability of fertilization of each ovum is likely. Further, the close correlation between adverse environmental conditions and prenatal mortality observed in this study and that of Millar (1971) suggests a causal effect.

Lactation

The cessation of lactation before conception in mid-March, implies a causal relationship between the end of lactation and the onset of follicle growth (Steyn 1980). The results obtained on lactation are similar to the observations of Sale (1965a), Griner (1968) and Steyn (1980). In contrast, the report by Millar (1971) of a five-month and of Hoeck (1977) of a six-month lactation implies that lactation proceeds well into pregnancy.

Seasonality of breeding

Proximate causes

The three month period (January - March) immediately prior to the peak period of sexual activity is characterized by a decrease in photoperiod, and mean maximum monthly temperature. The long term mean monthly rainfall data show a steady increase during this period with a maximum in March (CHAPTER II). The effect of these environmental factors on the vegetation is reflected in a marked increase in the deposition of fat in females, after the cessation of lactation. Male hyrax show a gradual increase in deposited fat reserves during January - March and a marked depletion of fat reserves immediately after the mating season (CHAPTER VII).

When these abiotic (temperature, photoperiod, rainfall) and biotic (vegetation) factors are viewed in the context of hyrax reproductive biology, the cause of the time of the mating season becomes apparent. Both males and females are at a peak of physiological condition prior to mating.

High quality nutrition prior to mating is also essential for follicular growth, optimal ovulation rates (Pinter & Negus 1965; Millar 1971; Van der Merwe & Skinner 1982) and for optimum rate of spermatogenesis (Millar & Fairall 1976). The last mentioned authors have demonstrated that spermatogenesis and testosterone production decrease on a low plane of nutrition.

Since hyrax have abdominal testes their body temperature is probably indicative of testicular temperature; suggesting that the temperature at which spermatogenesis is adversely affected in the hyrax is higher than that for a mammal with a scrotum (Millar & Glover 1973). Hyrax have a labile body temperature (Taylor & Sale 1969). Thus the period of decreasing maximum ambient temperatures prior to mating may be a selective advantage because spermatogenesis may be less energy consuming and more effective at these lower temperatures.

Neaves (1979) comments on the reasons for the short duration of seasonal mating in male hyrax and suggests that because of the high degree of intraspecific aggression during mating, a prolongation of the period of sexual activity, beyond the minimal requirement for successful breeding, could jeopardize survival. The marked depletion of male fat reserves immediately after the mating season, and the onset of the winter season with low rainfall and ambient temperatures, implies that these environmental factors ultimately control the duration of the mating season. Male hyrax adapt to this through their behaviour.

Millar & Glover (1973), who experimentally altered photoperiod, reported that a critical rate of decrease in photoperiod is the proximal cause of breeding activity in the hyrax and that temperature and precipitation may have a modifying effect. Millar (1971) demonstrated that the breeding season changes with a decrease in latitude. The mating season occurs later and lasts longer in the lower latitudes until, at the equator, there is a tendency for successful reproduction to take place throughout the year (Sale 1969) (Fig. 64). Neaves (1979) however, reported that an equatorial colony of lesser rock hyrax (Heterohyrax brucei) studied by him, resembled Procavia capensis from temperate latitudes in respect of seasonal occurrence of testicular activity and parturition. Yet Sale (1969) was unable to demonstrate any discreet seasonal occurrence of mating/births for P. habessinica or Dendrohyrax arboreus ruwenzorii Neumann at the equator. Since photoperiod and temperature are fairly constant in tropical regions, Sale (1969) suggested that the tropical species synchronise reproduction with rainfall. The main link between breeding and precipitation being the availability of the right quality of food at the time of lactation and weaning.

It seems evident from the literature that in temperate high latitudes the proximate cause of the timing of the mating season in the hyrax is photoperiod, but rainfall and vegetation may have a modifying influence. For those hyrax occurring in lower latitudes and in the tropics breeding activity is further modified in response to temperature, rainfall and the consequent changes in vegetation.

Ultimate causes

The birth dates of hyrax in the MZNP coincide with high ambient temperatures, a long photoperiod and the onset of the summer rains.

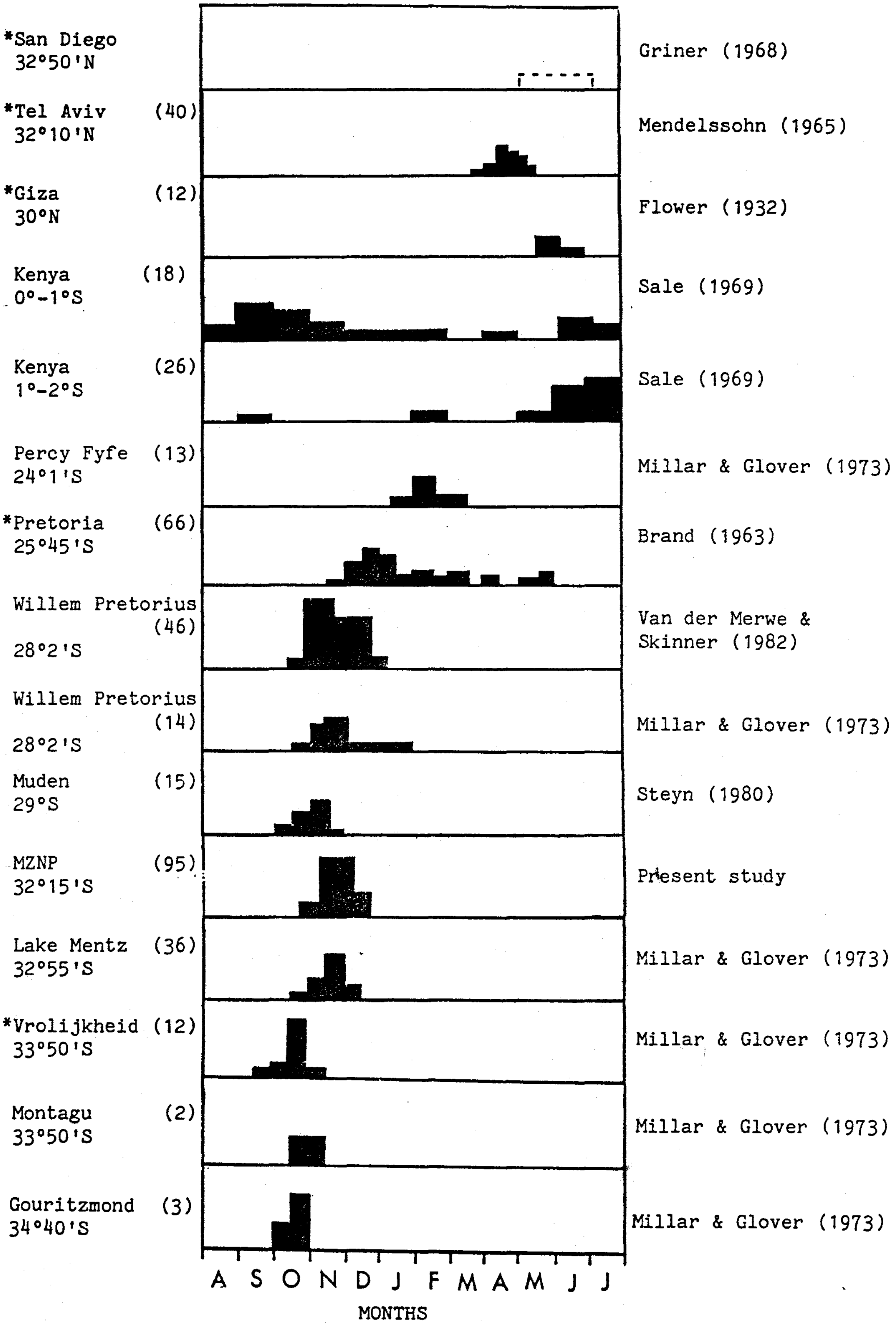


Figure 64: Frequency distribution of births of hyraces (Procavia) at different latitudes. Number of litters shown in brackets; broken line for San Diego encloses the extremes of recorded births (adapted from Millar Glover (1973)).

* Captive colonies

The quality and quantity of vegetation are high (CHAPTER VII) and this is important since juveniles eat green material soon after birth. Suckling young place an additional energy burden on females, which in the absence of favourable nutritional levels can lead to a marked lowering of physiological condition. The high ambient temperatures during the parturition period are important for plant growth. They may also be advantageous for the juveniles, which because of their poor thermoregulatory ability (McNairn 1982), are succeptible to both bacterial and viral pneumonias (Mendelssohn 1965).

The ultimate cause for the timing of the breeding season in hyrax seems to be a combination of temperature, rainfall and consequent growth of vegetation (i.e food resources) and the effects of this on both the needs of lactating females and juveniles.

SUMMARY

The gross anatomy of the urinogenital tracts of male and female hyrax are described.

Male hyrax attain puberty at 15 - 17 months of age or one year later. Females generally attain puberty at 15 - 17 months of age. One female (1,4% of the total sample), however, attained puberty at 4 - 5 months of age.

The left ovaries were more active than the right ovaries, but foetuses were evenly distributed between the uterine horns.

Conception and parturition dates of female hyrax were calculated from the Huggett & Widdas (1951) theoretical foetal growth curve. The modal date of conception was 17 April and the modal parturition date was 3 December.

Data on age-specific litter sizes are supplied. Middle-aged hyrax had significantly larger litter sizes than young hyrax.

The foetal sex ratio did not differ significantly from parity.

Prenatal mortality was determined by comparing the number of corpora lutea in the ovaries and the number of foetuses in the uterus. Young and very old animals had the highest prenatal loss of foetuses. Low rainfall during the gestation period increases prenatal mortality.

Hyrax are weaned at 1 - 4 months of age with a mean value of 2,3 months.

The environmental factors that influence breeding in the tropics differ from those that operate in the northern and southern temperate regions of the Hyracoid's distribution. In temperate regions photoperiod is the main proximate factor with temperature and rainfall being subsidiary. In the tropical regions where photoperiods are fairly constant the breeding season is modified in response to rainfall and the consequent changes in vegetation. The ultimate cause of the timing of the breeding season is the availability of abundant and nutritious food resources.

CHAPTER VII

HABITAT UTILIZATION

INTRODUCTION

For an organism to survive, it must be adapted to a particular niche which includes not only to the physical space it occupies, but also its functional role in the community (Odum 1971). Although the environment in any locality has its own characteristics of vegetation, resources, climate and seasonality, the individual (through its behaviour) selects its own ecological niche by using those components of the environment which are essential for its survival (Delany & Happold 1979). Thus any attempt to evaluate the relationship between an animal and its habitat should in each case be area-specific with a multidisciplinary approach that includes behavioural characteristics and an assessment of habitat condition and trends.

The three basic requirements of animals are food (including water), shelter and space. A multitude of studies have been conducted to investigate animal populations in relation to their environment, in particular their food resources. Each animal ingests food, digests it and uses it metabolically to meet its current needs which may change depending on its activity and productivity (Moen 1973). Any attempt to evaluate the feeding habits of a population should take into account the dynamic nature of the energy requirements for specific groups of animals (comprising different sexes and age groups) through time.

The determination of population condition is an important aspect of the population dynamics of mammals. The body condition of an animal serves as an important link between growth, reproductive rate and nutritional level of individuals and populations at different seasons, and under a variety of environmental conditions. The two ways of defining population condition are; physiological condition (Hanks 1981) and demographic vigour (Caughley 1971, 1977). The physiological condition of an animal, according to Hanks (1981), is closely linked to its chances of living or dying and as such is an important factor influencing mortality (Coblentz 1975; Hanks, Cumming, Orpen, Parry & Warren 1976). Caughley (1971, 1977) favours the demographic approach to the assessment of condition. He suggests that it should be expressed by a single statistic that combines the vigor of each age and sex class in a population. He also proposes the use of the survival-fecundity rate of increase, symbolised by r_s, which he terms demographic vigour, noting that any change in the environment will usually result in a rapid change in r_s. According to Hanks (1981), demographic vigour, which provides an assessment of the dynamics of a population, is a valuable adjunct to physiological condition. An index that measures physiological condition need not necessarily be equated to nor predict demographic vigour. In addition to the above-mentioned methods of measuring population condition, Hanks (1981) suggests that population resilience should be measured. This would provide a wild-life manager with an indication of the anticipated response of a population to continued environmental stress or ameliorative management practices.

In order to study the hyrax in relation to its environment in the MZNP,and to emphasise those factors which may influence the population dynamics, the following aspects were investigated:

(a) Composition and diversity of the diet in relation to season and rainfall.

(b) Phenological changes of vegetation and their seasonality in relation to environmental factors for those plants important in hyrax diet.

(c) Qualitative aspects of the diet by determination of crude protein and neutral detergent fibre in relation to season and rainfall.

(d) Physiological condition using body fat and serum cholesterol levels in relation to age, sex, physiological stresses and season.

(e) The feeding habits of hyrax, including mode of ingestion, feeding level and foraging patterns.

In addition, a description of hyrax refuges is given and the temperatures within the refuges are quantified.

METHODS

Collection of carcasses

Ten hyrax were shot in the MZNP each month for 12 consecutive months (April 1981 - March 1982) in order to examine stomach contents at different seasons to determine food selection. Sampling took place during the late afternoon to ensure the collection of animals with full stomachs, and during the last week of each calendar month to allow for discreet time units between consecutive samples. The time and place of collection was recorded for each hyrax, body measurements were taken (CHAPTER IV & V), and body condition monitored.

Because of the heterogeneity of the vegetation within the MZNP sampling was confined to three areas (Fig. 65) representing different plant communities. These sampling areas consisted mainly of shrubland on higher doleritic pediment and xeric riparian bush in riverine and

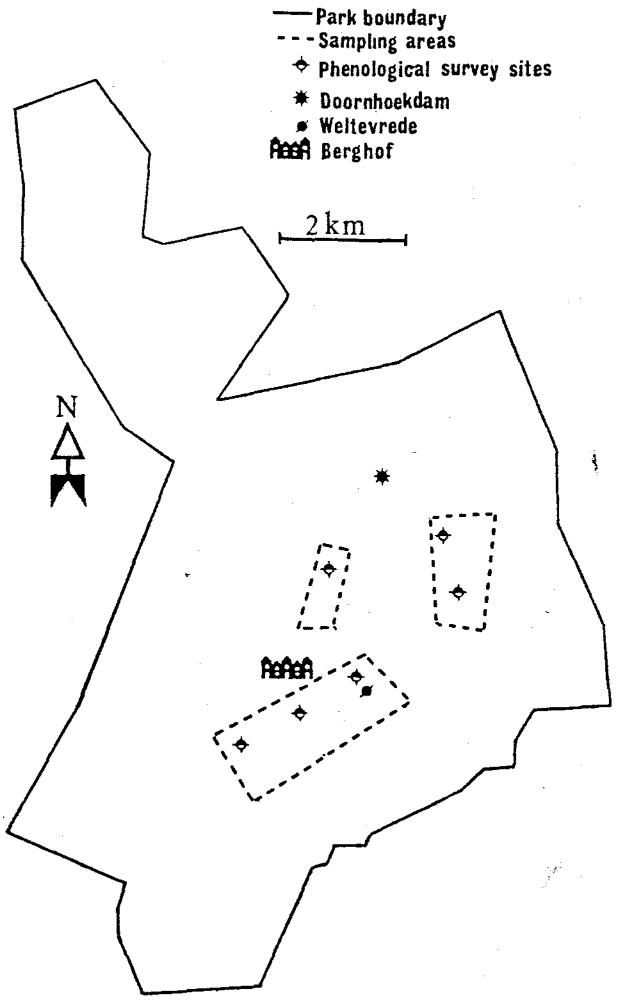


Figure 65: Sampling areas and phenological survey sites used during the study on feeding habits of the hyrax in the MZNP.

kloof areas.

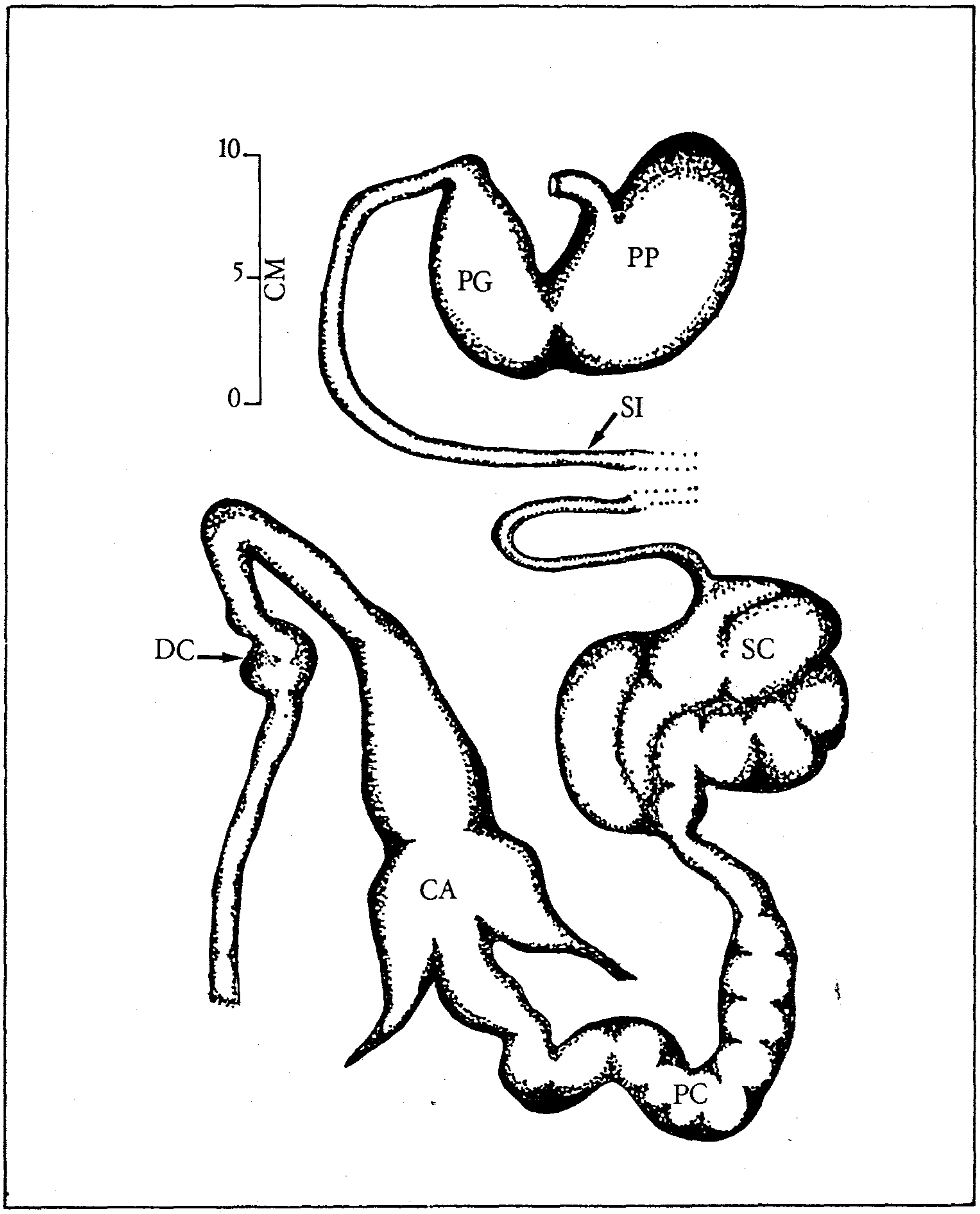
Stomach content analysis

A variety of names have been used to describe the different parts of the digestive system of the hyrax (Clemens 1977; Leon 1981; Rübsamen, Hume & Engelhardt 1982). The terminology used in this study follows that of Rübsamen et al. (1982) which was based on a macroscopic and microscopic examination of the gastrointestinal tract conducted by Rahm (1980, as cited by Rübsamen et al. 1982).

The method used to quantify diet was based on the observation that plants ingested by hyrax are laid down in distinct layers in the pars proventicularis (proximal half of stomach) (Fig. 66), (Rübsamen, et al. 1982) where they are retained for 4 h after ingestion (Clemens 1977). Almost no mixing of the ingested plant species occurs during this time (Rübsamen, et al. 1982).

Because hyrax ingest their food rapidly (Sale 1965c) the plant material ingested is coarse (Fig. 67) and in many cases whole leaf segments can be isolated. This greatly facilitates identification of plant species.

The different layers of ingested plants (Fig. 68) in the pars proventicularis were carefully separated. Plants were identified to species or genus level on gross morphological characteristics from a key compiled for common plant species utilized by hyrax.



PP - pars proventicularis
PG - pars glandularis
SI - small intestine

SC - sacculated caecum
PC - proximal colon
CA - colonic appendages
DC - distal colon

Figure 66: Gastrointestinal tract of the hyrax.

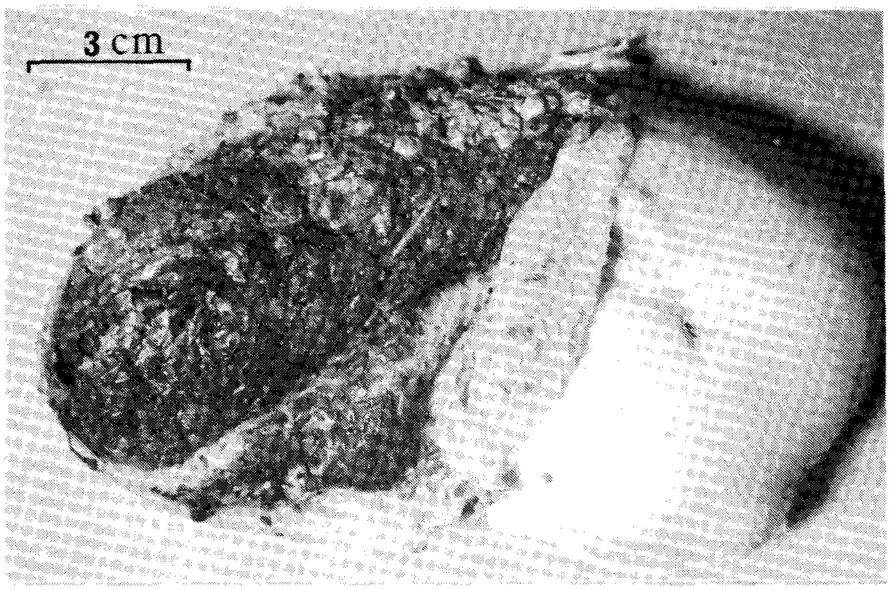


Figure 67: Stomach of the hyrax showing coarseness of ingested food.

Figure 68: Stomach of the hyrax illustrating formed layers of ingested food.

Identification was aided by the characteristic odours (from the liberation of volatile oils) of many Karoo plants. No attempt was made to identify individual grass species and they were simply categorised as monocotyledons (grasses). The wet mass (accurate to 0,01 g) of the different plant species in each stomach was determined on a Metler analytical balance and these plants were then dried in a draught oven at 80°C to constant mass after which they were reweighed. Plant species with a mass of less than 1 g were not dried and simply labelled as "trace". In cases where identification of a plant layer(s) was not possible the mass was determined, the sample dried, reweighed, and labelled as "unidentified". The different plant components (leaf, stem, flower and fruit) ingested were recorded.

Plants difficult to identify were placed in labelled bottles containing FAA (formol-acetic-alcohol) and taken to the sample area when next visited for direct field comparison with plants at the site. The herbarium at the MZNP research station was also extensively used for the identification of plant components from stomach samples.

The composition of stomach contents was related to rainfall and the phenology and seasonality of the vegetation. The moisture content of stomach samples was recorded as was the total amount of food ingested per day.

Plant phenology and seasonality of the vegetation

In order to examine the phenological changes of the vegetation in the areas in which hyrax were sampled, six predetermined and fixed sites (see Fig. 65) within these areas were selected and visited at the end of each month for a period of one year. Those plants known to be eaten by hyrax were monitored on a monthly basis. Relative leaf densities, which were equated with growth in the present study, were subjectively assessed and reproductive phases recorded. Grasses were recorded as green or dry and the formation of new grass blades and flowering cycles were observed. Plant growth changes were related to the annual rainfall pattern in the MZNP.

Principal and preferred food-plant species

Petrides (1975) regards principal foods as those which an animal population eats in the greatest quantities while preferred food species are regarded as species which are proportionately more "frequent" in the diet of an animal than in the available environment. Thus in order to define food preferences and principal foods a measure of food availability must be obtained (Barnes 1976). Because of the arboreal feeding habits of the hyrax (Sale 1965a; Hoeck 1975) it is impossible to ascertain the number of trees and tall shrubs which they can climb and which are available. In addition feeding in the MZNP may take place a considerable distance (> 500m) from refuges. Because of the above-mentioned factors and the heterogenous nature of the vegetation, any attempt at defining and quantifying food availability is likely to result in serious bias. Food preferences and principal foods are thus used in a more arbitrary way in the context of plant phenology and seasonality and feeding habits.

Chemical analysis of stomach contents and faeces

Samples of the various plant species were dried and collected in proportion to their prevalence in the stomachs of hyrax in order to determine food quality. Faecal pellets were also collected from the recta of all hyrax sampled and placed in labelled bottles. Analyses for crude protein (CP) and neutral detergent fibre (NDF) in stomach contents and faecal samples were done using the method of Goering & Van Soest (1970).

Correlations between stomach and faecal CP were examined in order to assess the value of the chemical composition of faeces as an index of food quality and availability at any season.

Physiological condition

Body fat

Fat deposits are a commonly used criterion for the description of physiological condition (Hanks 1981). However, the removal of all fat and the expression of this fat as a percentage of the carcass mass is an expensive, tedious and time consuming task. An alternative method whereby an estimate of visible deposited fat can be obtained is to remove the fat immediately around the kidneys and to calculate the kidney fat index (KFI) (Caughley 1970; Monro & Skinner 1979).

Since fat is not formed extensively around the kidneys of the hyrax (Steyn 1980), but rather caudal to the kidneys, especially around the gonads, the use of a KFI is not justified. The method used in this study was to subjectively apply a body fat ranking (BFR) on a scale from 1 - 5 as follows:

(a) 1BFR - no visible fat around the kidneys, gonads or in the lower abdomen (Fig. 69a).

(b) 2BFR - a small amount of visible fat around the caudal portion of the kidneys as well as around gonads.

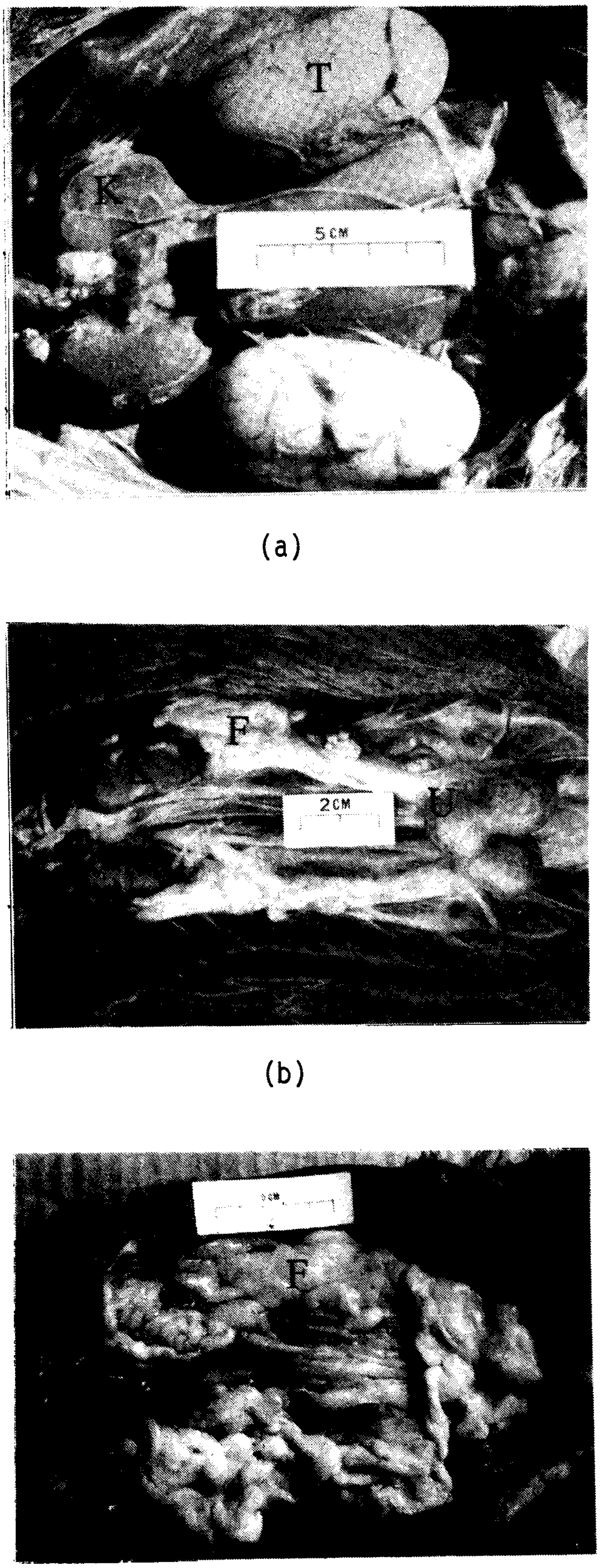
(c) 3BFR - fat covering caudal portion of the kidneys and extending down into the body cavity but not entirely covering gonads (Fig. 69b).

(d) 4BFR - visible fat extending towards the proximal portion of the kidneys and completely covering the gonads.

(e) 5BFR - large amount of fat around proximal and caudal portions of the kidneys and completely covering the gonads (Fig. 69c).

Juveniles (0 - 12 months old) had little or no visible fat deposits and were not used for comparative purposes.

In order to quantify the subjectively assigned BFRs, 27 hyrax were analysed in detail. Five belonging to each BFR, except for the first; in which seven hyrax were used (in order to obtain a wider



(a)

(b)

(c)

Figure 69 a - c: Ventral view of the lower abdomen of the hyrax illustrating three different body fat rankings; (a) no visible fat=rating one; (b) intermediate amount of fat=rating three; (c) large amount of fat=rating five (K - kidney; T - testis; F - fat; U - uterus).

range for this ranking). They were cleaned of gastrointestinal contents and their entire bodies dried at 70°C in a draught oven to a constant mass. The carcasses were sectioned into blocks of c. 3 x 3 cm by means of a circular saw, and these were finely ground with a Spencer Larson mill. The body fat was then extracted using ether-distillation in the Soxhlet apparatus (Allen, Grimshaw, Parkinson & Quarmby 1974). BFR and total body fat content were correlated, and the BFR patterns were related to rainfall and physiological stressful periods (rutting, gestation and lactation).

The sequence of fat mobilization was determined by observing deposited fat in males prior to the rut (good condition), and during and after the rutting period (poor condition).

Serum cholesterol

Fifty hyrax of both sexes were shot during February - November 1982 at a rate of c. 5 per month. The jugular veins of these animals were severed immediately and 5 ml of blood collected in clean labelled glass tubes which were placed in a cooled polystyrene holder. The blood samples were allowed to clot and the liquid portion was centrifuged for 5 min at 8 000 r.p.m. The serum thus obtained was collected and stored in a deep freeze at c. -20°C. Serum cholesterol levels were determined on a Bio-Dynamics Unimeter (Kodon House, 26 McArthur Street, Durban). Mean monthly serum cholesterol levels were correlated with BFRs and rainfall patterns within the MZNP.

Field observations

Feeding behaviour at a colony next to Doornhoek dam (CHAPTER II) was observed from sunrise to sunset twice a month for a period of six months (February - July 1982). The observation period thus included three summer and three winter months. (The observations formed part of the study on activity patterns and the methods employed are fully discussed in CHAPTER VIII).

Because of the rugged terrain in the MZNP and the habit of hyrax of frequenting riparian thickets, movement of individual animals could not be followed. Thus it was not possible to determine the exact time any particular individual spent daily on active feeding. All hyrax that left refuges (they were known to feed in adjacent areas) were recorded as foraging. This included actual feeding, time spent looking for feed or time spent at transit zones during foraging excursions. Foraging patterns for winter and for summer were related to ambient temperature changes and wind velocity.

To supplement the data on stomach content analysis direct observations on hyrax feeding were made from the hide (CHAPTER VIII) using 8 x 30 field glasses, and also during the many hours spent on sampling hyrax. In each case the plants and component utilized were identified. Occasionally indirect methods (examination of vegetation in the immediate vicinity of refuges) were used.

Refuge requirements

Field observations throughout the MZNP and neighbouring farming areas were conducted to determine the types of refuge used by hyrax as well as their topographical and spatial distribution.

The physical nature of refuge sites was also investigated. Temperature changes within refuges were recorded by means of a thermister probe placed 2 m within the refuge and attached to a Grant temperature recorder (Grant instruments, Ltd., Cambridge). Recordings were made at hourly intervals for a period of a week during summer (January) and winter (August). At the same time the ambient temperature was recorded on a thermohygrograph placed in a Stevenson screen.

RESULTS

Carcasses collected

Of the 111 hyrax collected during the 12 month period four had empty stomachs and consequently 107 stomachs were used for content analysis. The sample consisted of 43 adult females, 38 adult males, five sub-adult females, 11 sub-adult males, 12 juvenile males and two juvenile females.

Composition and diversity of the diet

Thirty-five plant species, excluding grasses (which were treated as a group) were identified from the stomach contents. The various plant components are ranked in order of quantitative prevalence in Table 33. During field observations a further 45 plant species, utilized by hyrax (including the seven grass species commonly utilized by these animals) were recorded, giving a total of 80 plant species belonging to 33 plant families. This is *c.* 16% of the 496 plant species identified in the MZNP. These plants and grasses and their various components ingested by the hyrax are summarized in Appendix A.

Variation in the composition of the diet (% dry mass) on a monthly basis is summarized in Table 34. The plant species are arranged in order of their quantitative prevalence for each month.

The pattern of utilization of the 10 quantitatively most important plants and grasses and their relative growth (based on leaf densities during the 12 month collection period) are graphically presented in Figs. 70*a* - *k*.

Table 33: The plant species identified and ranked by quantitative (dry mass) prevalence in the stomach contents of 107 hyrax examined during a 12 month period (April 1981 - March 1982).

KEY (adapted from Van der Walt 1980)

T - TREE
TS - TALL SHRUB
MS - MEDIUM SHRUB
SS - SMALL SHRUB
DS - DWARF SHRUB
E - EPIPHYTE
C - CLIMBER
S - SUCCULENT
F - FORB

Growth form	Plant species	Frequency	% of total diet
	Grasses	79	22,2
T	Acacia karroo	46	19,0
T	Olea europaea	23	10,5
SS	Felicia filifolia	25	8,0
TS	Grewia occidentalis	36	5,3
T	Cussonia paniculata	20	4,3
TS	Maytenus heterophylla	14	3,7
SS	Pentzia spp.	10	3,1
C	Clematis brachiata	17	2,4
TS	Lycium oxycarpum	12	2,2
TS	Diospyros lycioides	8	2,1
MS	Clutia pulchella	3	1,3
SS	Lotonis divaricata	3	1,1
SS	Blepharis capensis	3	0,9
TS	Rhus lucida	12	0,8
MS	Lycium cinerium	5	0,8
S	Aloe striata	2	0,7
E	Viscum capense	2	0,6
C	Asparagus spp.	9	0,5
S	Opuntia sp.	4	0,5
SS	Cadaba aphylla	1	0,4
S	Aloe striatula	4	0,3
F	Ballota africana	2	0,3
S	Platythyra haeckeliana	2	0,3
T	Celtis africana	2	0,2
DS	Nemesia flaneganii	1	0,2
S	Delosperma sp.	2	0,2
SS	Psilocaulon sp.	1	0,2
B	Moraea polystachya	2	0,2
DS	Nenax microphylla	1	0,1
S	Aloe broomii	1	0,1
SS	Turbina oenotheroides	1	0,1
	Unidentified dicotyledons		7,4
	Trace:		
DS	Indigofera sp.		<0,1
SS	Sutera astropurpurea		<0,1
SS	Solanum sp.		<0,1
T	Rhus lancea		<0,1

Table 34: Composition of stomach contents of 107 hyrax sampled in the MZNP over a 12 month period (April 1981 - March 1982). Values given for each month represent the mean and are expressed as a % of the total diet during that month on a dry matter basis.

KEY (adapted from Van der Walt 1980)

(a) Growth form
T - tree
TS - tall shrub
MS - medium shrub
SS - small shrub
DS - dwarf shrub
C - climber
S - succulent
F - forb
E - epiphyte

(b) Plant component
L - leaves
Fl - flowers
Fr - fruit
St - stems

Growth form	Plant species	Plant component	Frequency	% of total diet
APRIL (n = 8)				
	Grasses	L	6	29,2
T	*Olea europaea*	L	2	17,1
TS	*Diospyros lycioides*	L	2	12,6
SS	*Felicia filifolia*	L Fl	5	12,2
T	*Acacia karroo*	L	2	10,0
TS	*Grewia occidentalis*	L	3	8,1
T	*Cussonia paniculata*	L Fl	3	2,8
TS	*Rhus lucida*	L	3	1,1
C	*Clematis brachiata*	L	1	0,9
SS	*Turbina oenotheroides*	L	1	0,7
S	*Aloe striatula*	L	1	0,4
MS	*Lycium cinerium*	L	1	0,3
S	*Opuntia sp.*	S	1	0,2
	Unidentified dicots.			5,12
	Trace:			
F	*Indigofera patens*	L	1	<0,1
MAY (n = 10)				
T	*Acacia karroo*	L	5	28,6
	Grasses	L	9	20,7
SS	*Blepharis capensis*	L	1	7,4
TS	*Maytenus heterophylla*	L	3	5,2
TS	*Grewia occidentalis*	L	6	4,6
C	*Clematis brachiata*	L	1	4,3
TS	*Lycium oxycarpum*	L Fr	3	4,1
T	*Cussonia paniculata*	L Fr	4	3,5
T	*Olea europaea*	L	2	2,8

TS	*Diospyros lycioides*	L Fr	1	2,8
C	*Asparagus* sp.	L Fr	3	1,2
	Unidentified dicots.			14,1
	Trace:			
SS	*Felicia filifolia*	L	1	<0,1
JUNE (n = 10)				
T	*Olea europaea*	L	4	25,3
T	*Acacia karroo*	L	5	21,0
TS	*Maytenus heterophylla*	L	2	14,0
	Grasses		8	7,1
S	*Opuntia* sp.	S	1	5,4
TS	*Grewia occidentalis*	L Fr	5	4,0
TS	*Lycium oxycarpum*	L	3	3,3
SS	*Felicia filifolia*	L	1	2,1
TS	*Diospyros lycioides*	L	1	1,4
S	*Aloe striatula*	L	1	1,2
S	*Aloe striata*	L	1	1,1
DS	*Pentzia* sp.	L St	1	1,0
T	*Cussonia paniculata*	L	1	0,2
	Unidentified dicots.			13,0
JULY (n = 8)				
T	*Acacia karroo*	L	3	14,1
T	*Olea europaea*	L	4	14,0
T	*Maytenus heterophylla*	L	3	12,2
TS	*Lycium oxycarpum*	L Fr	4	10,7
MS	*Clutia pulchella*	L St	2	8,8
	Grasses		7	7,3
TS	*Grewia occidentalis*	L	3	4,0
MS	*Lycium cinerium*	L	2	3,6
SS	*Pentzia* sp.	L St	1	3,5
TS	*Rhus lucida*	L Fr	3	2,6
C	*Clematis brachiata*	L St	3	1,8
SS	*Felicia filifolia*	L Fl	2	1,6
C	*Asparagus* sp.	L Fr	3	1,3
S	*Delosperma* sp.	L St	1	0,8
	Unidentified dicots.			14,3
	Trace:			
T	*Rhus lancea*	L Fr	1	<0,1
SS	*Sutera astropurpurea*	L St	1	<0,1
AUGUST (n = 8)				
TS	*Grewia occidentalis*	L	2	22,0
C	*Clematis brachiata*	L St	4	15,6
SS	*Lotonis divaricata*	L Fr	1	10,3
T	*Cussionia paniculata*	L	2	7,2
SS	*Felicia filifolia*	L	3	6,8
SS	*Cadaba aphylla*	L	1	6,6
TS	*Lycuim oxycladum*	L Fr	1	6,4
MS	*Clutia pulchella*	L St	1	4,4

MS	Lycium cinerium	L	1	3,8
*S	Platythyra haeckeliana	L St	1	3,5
S	Opuntia sp.	S	2	2,2
S	Delosperma sp.	L St	1	2,1
C	Asparagus sp.	L	2	2,1
	Grasses		2	2,0
	Unidentified dicots.			2,6
	Trace:			
SS	Sutera astropurpurea	L St	1	<0,1
SEPTEMBER (n = 9)				
SS	Felicia filifolia	L Fl	5	47,3
	Grasses		8	21,8
S	Aloe striata	Fl	2	5,9
T	Cussonia paniculata	L	2	5,7
C	Clematis brachiata	L	4	4,9
TS	Grewia occidentalis	L	3	4,4
SS	Pentzia sp.	L	1	0,9
TS	Lycium oxycarpum	L	1	0,8
TS	Maytenis heterophylla	L	1	0,8
TS	Rhus lucida	L Fr	1	0,6
B	Moraea polystachya	Fr	2	0,4
MS	Lycium cinerium	L	1	0,1
SS	Blepharis capensis	L	1	0,1
C	Asparagus sp.	L	1	0,1
	Unidentified dicots.			6,2
OCTOBER (n = 9)				
T	Olea europaea	L	3	22,3
	Grasses		6	21,3
T	Acacia karroo	L	4	19,6
E	Viscum capense	L St	1	4,6
SS	Felicia filifolia	L	2	4,8
TS	Diospyros lycioides	L	1	4,1
T	Cussonia paniculata	L	1	2,8
SS	Pentzia sp.	L Fl	1	2,7
S	Aloe striata	Fr	1	2,2
T	Celtis africana	L	1	1,9
SS	Lotonis divaricata	L Fr	1	1,7
S	Platythyra haeckeliana	L St	1	1,0
F	Ballota africana	L St	1	0,9
	Unidentified dicots.			10,6
	Trace:			
C	Asparagus sp.	L	1	<0,1
NOVEMBER (n = 10)				
T	Acacia karroo	L Fl	8	36,8
	Grasses		8	35,4
TS	Grewia occidentalis	L Fl	3	8,8
TS	Maytenus heterophylla	L Fl	2	5,2
SS	Blepharis capensis	L	1	3,9
*TS	Rhus lucida	L Fr	2	2,4

T	*Olea europaea*	L	2	3,7
TS	*Rhus lucida*	L	1	2,8
S	*Aloe striatula*	Fl	2	2,8
C	*Clematis brachiata*	L	1	0,7
SS	*Felicia filifolia*	L	1	0,3
	Trace:			
C	*Asparagus* sp.	L	1	<0,1
SS	*Pentzia* sp.	L	2	<0,1
TS	*Diospyros lycioides*	L	1	<0,1
DECEMBER (n = 10)				
	Grasses	L Fl	6	40,2
T	*Acacia karroo*	L Fl	4	20,7
T	*Olea europaea*	L	2	10,8
T	*Cussonia paniculata*	L	2	6,0
SS	*Lotonis divaricata*	L Fr	1	2,9
TS	*Grewia occidentalis*	L	1	2,1
DS	*Nenax microphylla*	L Fr	1	1,6
T	*Celtis africana*	L	1	1,2
SS	*Felicia filifolia*	L	1	0,7
C	*Clematis brachiata*	L	1	0,5
	Unidentified dicots.			12,6
	Trace:			
TS	*Maytenus heterophylla*	L	1	<0,1
S	*Aloe striatula*	Fl	1	<0,1
SS	*Solanum* sp.	Fr	1	<0,1
MS	*Clutia pulchella*	L	1	<0,1
C	*Asparagus* sp.	L	1	<0,1
TS	*Lycium oxycladum*	L	1	<0,1
JANUARY (n = 9)				
T	*Acacia karroo*	L Fl	6	31,9
T	*Olea europaea*	L	2	20,2
SS	*Pentzia* sp.	L St	4	12,6
	Grasses		4	12,0
T	*Cussonia paniculata*	L	2	5,8
TS	*Maytenus heterophylla*	L	2	4,2
SS	*Felicia filifolia*	L	1	1,6
SS	*Psilocaulon* sp.	L St	1	1,3
TS	*Grewia occidentalis*	L	1	0,8
S	*Aloe broomii*	Fr	1	0,5
F	*Ballota africana*	L St	1	0,2
	Unidentified dicots.			8,9
	Trace:			
MS	*Clutia pulchella*	L	1	<0,1
C	*Asparagus* sp.	L	1	<0,1
TS	*Diospyros lycioides*	L	1	<0,1
FEBRUARY (n = 8)				
	Grasses	L Fl	8	56,9
TS	*Grewia occidentalis*	L	4	9,6

SS	*Pentzia* sp.	L	1	9,1
T	*Acacia karroo*	L	3	8,2
T	*Olea europaea*	L	1	8,2
C	*Clematis brachiata*	L Fl	1	3,6
TS	*Diospyros lycioides*	L Fr	1	3,0
TS	*Maytenus heterophylla*	L Fr	1	1,8
	Trace:			
TS	*Rhus lucida*	L	1	<0,1
MS	*Clutia pulchella*	L	1	<0,1
C	*Asparagus* sp.	L	1	<0,1
MARCH (n - 8)				
T	*Acacia karroo*	L	6	28,6
	Grasses	L Fl	7	27,3
T	*Cussonia paniculata*	L	3	12,4
TS	*Diospyros lycioides*	L Fr	2	6,5
SS	*Felicia filifolia*	L	1	4,8
T	*Olea europaea*	L	1	4,0
TS	*Grewia occidentalis*	L	3	3,7
E	*Viscum capense*	L St Fr	1	2,3
DS	*Nemesia flaneganii*	L St	1	2,2
SS	*Pentzia* sp.	L	1	1,5
C	*Clematis brachiata*	L	1	1,3
	Unidentified dicots.			5,0
	Trace:			
C	*Asparagus* sp.	L Fl	1	<0,1

Acacia karroo showed peaks of utilization during May, November, January and March. *Grewia occidentalis* showed a distinct peak of utilization during August. The greatest quantity of *Felicia filifolia* was utilized during September whereas *Olea europaea* showed three distinct peaks of utilization during June, October and January. *Lycium oxycarpum* was most utilized during July, *Maytenus heterophylla* during June and utilization of *Clematis brachiata* showed a distinct peak during August. It is interesting to note that most of the *C. brachiata* material ingested consisted of dry leaves and stems. *Diospyros lycioides* was utilized in the greatest quantities during April and *Pentzia* spp. during January. The utilization of *Cussonia paniculata* was the highest during March whereas the utilization of

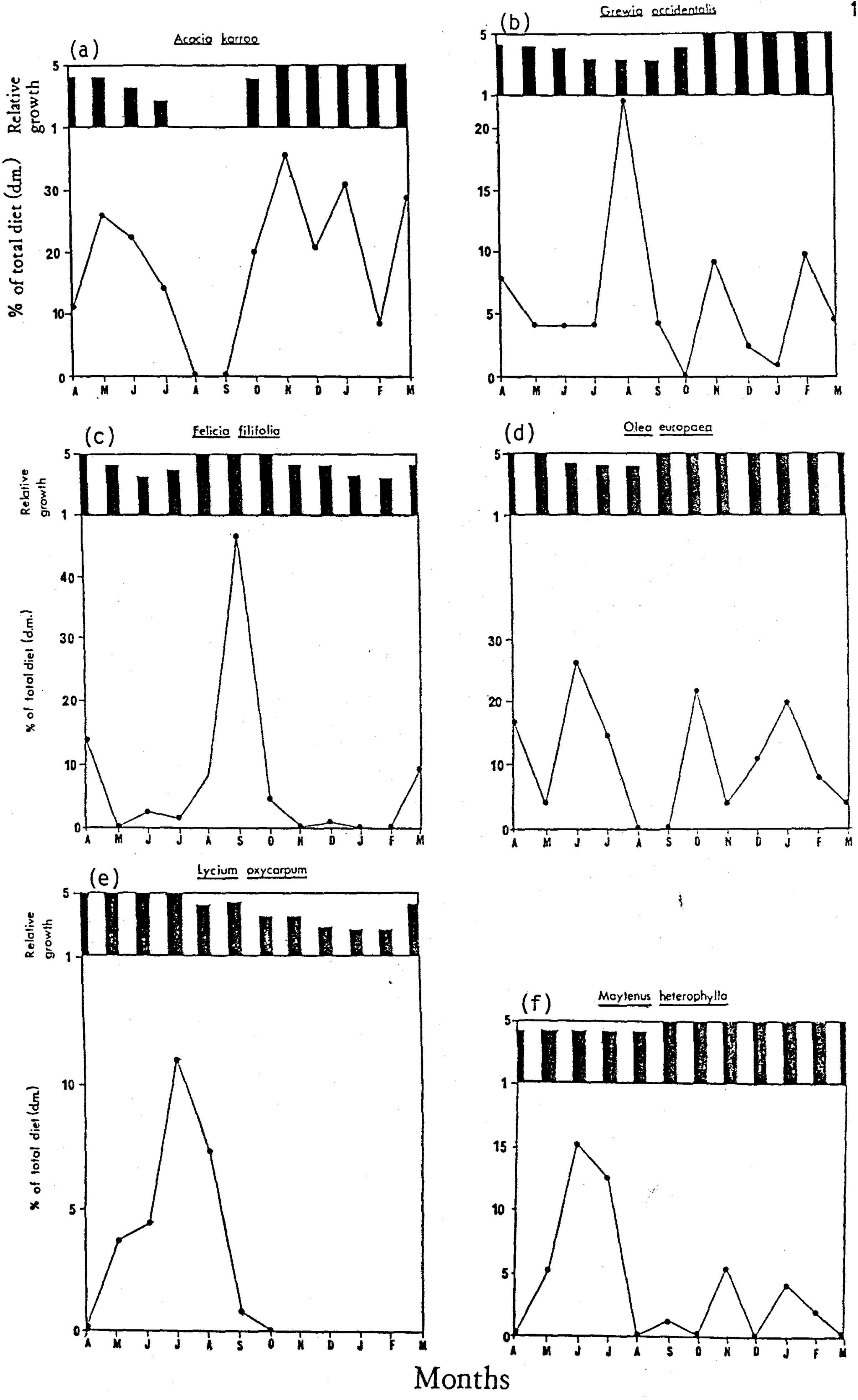


Figure 70 a - k: Graphical presentation of monthly ingestion (expressed as % of total on a dry matter basis) of 11 plant species for April 1981 - March 1982. Shaded bars represent relative growth.

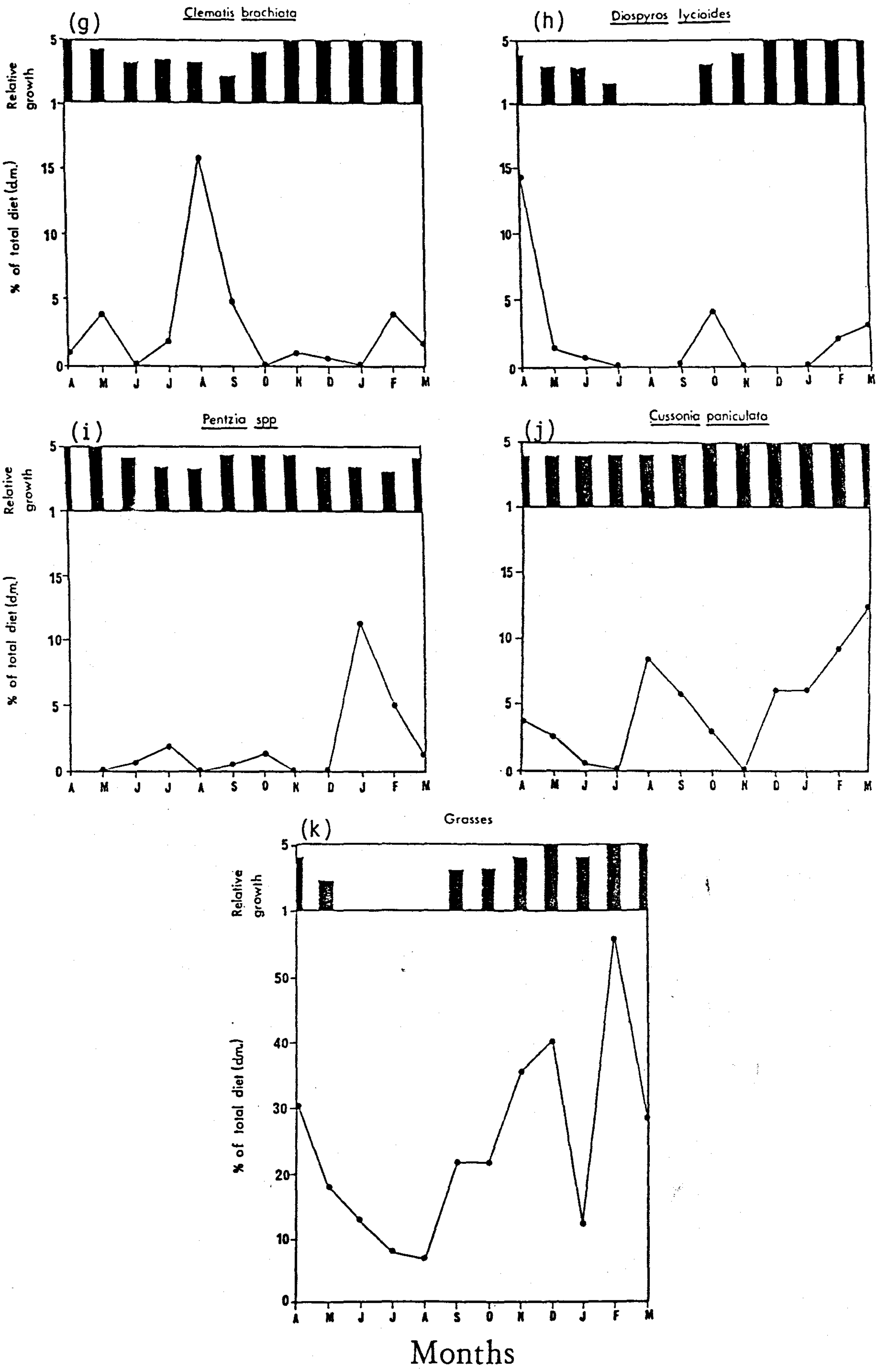


Figure 70 (cont.)

grasses reached a peak during February.

The different utilization of Acacia karroo, Felicia filifolia, Grewia occidentalis and grasses is compared in Fig. 71.

For general descriptive purposes the diet components of the hyrax can be divided into four major classes, namely, trees, shrubs, grasses and others (succulents, climbers and unidentified plant species). Variations in these four classes expressed as a percentage of the diet (dry matter) during the study period are graphically presented in Fig. 72. Trees were browsed throughout the year with September having the lowest value of 6% and January the highest of 58%. In general the

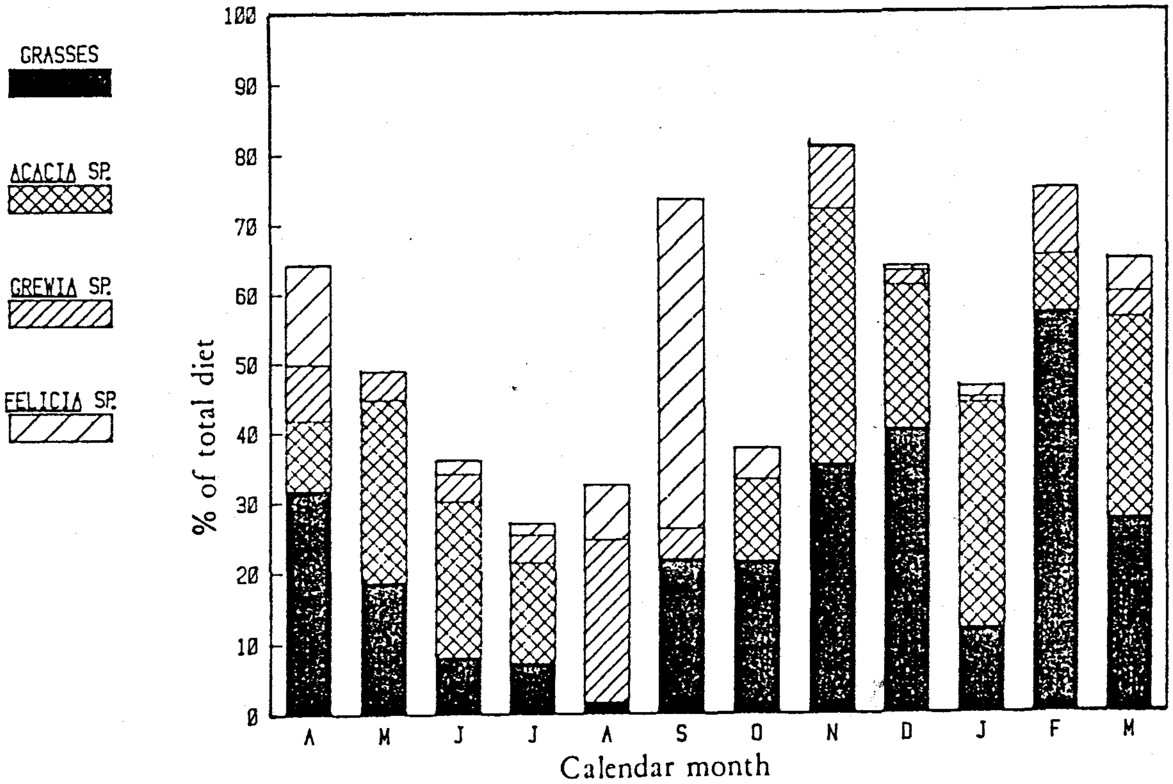


Figure 71: The differential utilization by hyrax during a 12 month period of four plant species (expressed as % of total diet).

intensity of tree browsing corresponded with the most active part of the overall growth cycle (October - March), however, a marked decrease in tree browsing was evident during February (Fig. 72).

Shrubs were browsed throughout the year with the highest ingestion (64%) occurring during August and the lowest (8%) during December (Fig. 72).

Grazing took place throughout the year and the contribution of grasses to the total diet closely followed the growth activity of the grasses. The lowest value recorded for the utilization of grasses was 2% during August and the highest value (57%) during February. In comparison

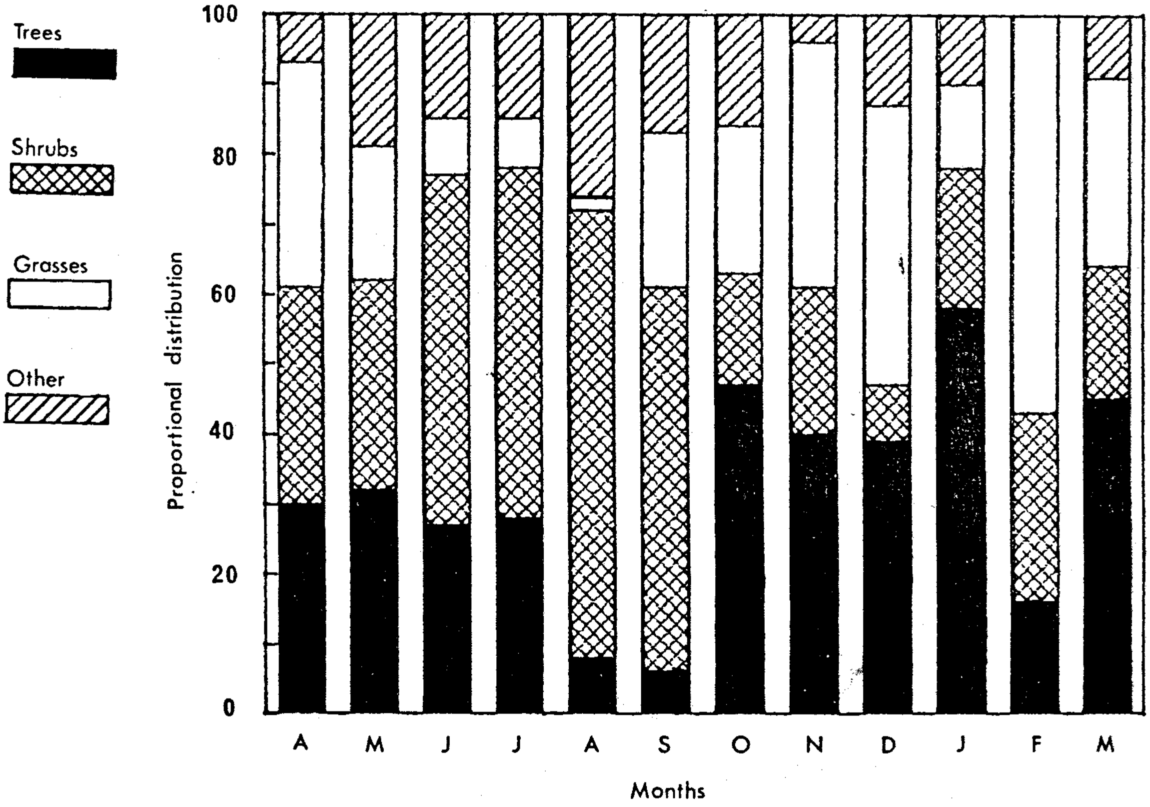


Figure 72: The proportional distribution of the four major plant classes in the diet of the hyrax over a 12 month period (April 1981 - March 1982).

Table 35: The mean % moisture content of plants collected from the pars proventicularis of 107 hyrax stomachs during April 1981 - March 1982.

Month	% moisture content	n
April	76	38
May	75	45
June	74	35
July	74	44
August	80	24
September	74	39
October	76	28
November	79	26
December	78	27
January	69	25
February	77	22
March	72	29

with the preceeding and following months there was a marked decline in the utilization of grasses during January (Fig. 72).

Climbers were eaten throughout the year whereas succulents were eaten in the greatest quantities during the winter. The highest utilization percentages (14,0% - 14,3%) for unidentified dicotyledons were recorded during May - July. The diversity of plants utilized during winter was greater than that utilized during summer; this was also manifested in the greater proportion of unidentified plants ingested during the winter months (Table 34).

The variation in moisture content of plants collected from the pars proventicularis of the stomach is summarized in Table 35.

The lowest mean value recorded was 69% during January which is the hottest month of the year (CHAPTER II). The highest value (80%) was recorded during August the month during which the greatest quantity of succulents was utilized. Winter values did not differ significantly ($P > 0,5$; t-test) from those for summer.

To obtain an indication of total dry mass intake per day, assuming that the stomach is filled once per day (see later), the 10 heaviest stomachs from a total of 589 (total shot sample) were selected (Table 36).

Table 36: Mean (±S.E.) body mass (g) and stomach mass (g), and stomach mass expressed as a % of total body mass for 10 filled hyrax stomachs.

Mean body mass (g)	S.E.	Mean stomach mass (g)	S.E.	% of body mass	S.E.
3550	104,1	576,6	27,7	16	0,8

The filled stomach of the hyrax can account for c. 16% of its total body mass. In order to determine the daily dry matter intake 80 g (mean mass of stomach tissue) was subtracted from the stomach mass and the mean moisture content of the ingesta was taken as 75% (see Table 35). Mean total dry matter intake was thus calculated as 34,97 g dry matter $kg^{-1}day^{-1}$.

To determine whether there was any quantitative difference between adult males and reproductive females as regards the amount of food ingested during the last four months of pregnancy (August - November) and during the first two months of lactation (December - January) the masses of stomach contents of adult males (n = 59) and pregnant females (n = 71) were measured, and expressed as g dry matter kg^{-1} day^{-1} (Table 37). Moisture content of the ingesta was arbitrarily taken as 75% for all months (Table 35).

Table 37: The mean stomach fills (g dry matter kg^{-1} day^{-1}) of 59 adult male and 71 pregnant female hyrax sampled during the period August - January throughout the course of this study.

Month	♂♂ (g dry matter kg^{-1} day^{-1})	n	♀♀ (g dry matter kg^{-1} day^{-1})	n
August	21,94	7	21,89	12
September	25,75	11	28,05	19
October	25,14	9	22,29	7
November	25,85	9	21,96	6
December	22,68	12	25,19	13
January	19,95	11	30,30	14

No statistically significant differences ($p > 0,5$) between males and females were found for the four month period August - November. However, values for females during lactation (December - January) were consistently higher and significantly different ($p < 0,05$; t-test) from those of males.

Plant phenology and seasonality of the vegetation

Relative leaf densities (growth) for the quantitatively most important plant species utilized by the hyrax have been presented in Figs. 70a - k. The plants constituting the major portion of the hyrax diet have growth cycles which achieve maximum growth and development synchronously (for example *Acacia karroo* and *Grewia occidentalis*) or asynchronously (for example *Felicia filifolia* and *Diospyros lycioides*). Growth of the grasses is stimulated during late winter by rainfall and increasing temperatures (CHAPTER II). Maximum growth of this component is achieved during late summer (February - March) with a depression in growth during midsummer (January) coinciding with high ambient temperatures. The peak flowering period for perennial grasses utilized by the hyrax is between February and April.

Small shrubs extensively utilized by the hyrax (see Table 33) fall into two categories of growth activity, those showing maximum growth during late winter (notably *Felicia filifolia*) and those showing maximum growth during late summer - early winter (March - May), for example *Pentzia* spp. Flowering cycles of the former group coincided with maximum growth, whereas the flowering cycle of the latter group preceeded the maximum growth phase by about one month.

Important tall shrubs in the diet of the hyrax show the following growth and reproductive cycles: *Lycium oxycarpum*, maximum growth and reproductive cycle during April - July; *Maytenus heterophylla* during September - March; *Grewia occidentalis* during November - March; and *Diospyros lycioides* during December - March.

Maximum growth of *Acacia karroo*, a tree important in the hyrax diet, occurs during October - March with the initiation of the reproductive cycle occurring during November. Most trees of this species shed their leaves during the severe winter months of August and September. Those in protected areas (riverine thickets), however, retain their leaves. Olea europaea trees are frost-resistant and retain their leaves throughout the year. Active leaf formation, however, takes place from September - March. The growth activity of Cussonia paniculata is similar to that of Olea europaea. Inflorescences are formed on these trees during March and August.

The climber Clematis brachiata, which forms an important component of hyrax diet, occurs in the dense vegetation found around lower lying hyrax refuges. This plant is not frost-resistant and green plants are only found in protected frost-free areas such as riverine thickets, whereas those in unprotected areas are dry. Active growth takes place during October - April and the reproductive cycle is initiated during January.

Principal and preferred food-plant species

Based on their contribution to the total diet, phenological changes in the vegetation and subjective assessment of availability of plant species utilized by hyrax in the MZNP, and making allowance for feeding habits and behaviour (see later) the following assumptions have been made:

(a) Principal foods of the hyrax were grasses and the tree Acacia karroo.

(b) Preferred foods were the trees Olea europaea and Cussonia paniculata; tall shrubs Maytenus heterophylla, Grewia occidentalis, Lycium oxycarpum and Diospyros lycioides; the small shrubs Felicia filifolia and Pentzia spp; and the climber Clematis brachiata.

Chemical analysis of stomach contents and faeces

The mean monthly stomach and faecal CP and stomach NDF values are summarized in Table 38.

Table 38: Mean monthly (±S.E.) CP values (% of dry mass) of stomach and faecal samples and NDF (% of dry mass) of stomach contents of hyrax sampled during April 1981 - March 1982.

Month	CP (stomach)	S.E.	n	CP (faeces)	S.E.	n	NDF (stomach)	S.E.	n
April	17,27	0,76	7	16,58	0,81	6	55,62	2,45	7
May	16,63	1,54	9	15,63	1,32	10	56,66	2,06	7
June	15,19	0,57	8	15,42	0,51	8	54,82	1,43	6
July	15,82	0,72	5	14,80	0,73	7	50,14	0,59	4
August	14,87	1,12	8	14,58	1,00	9	52,21	1,60	8
September	13,86	0,68	7	13,86	0,66	6	51,03	2,05	5
October	14,75	1,44	4	14,95	0,23	4	52,84	-	1
November	14,83	0,72	10	14,97	0,89	7	54,82	1,26	10
December	17,04	0,50	9	16,85	0,73	8	53,04	1,68	8
January	14,93	0,82	7	12,79	0,56	5	53,06	1,74	6
February	18,49	0,21	2	16,27	2,12	2	52,54	0,33	2
March	14,36	0,78	7	14,63	0,61	8	-	-	-

No significant seasonal differences ($p > 0,5$; t-test) between stomach content and faecal CP values were evident. The lowest CP value (13,86%) for stomach content was recorded during September and the highest value (18,49%) during February. Faecal CP showed a lowest mean monthly value (12,79%) during January and a highest value (16,85%) during December. A highly significant correlation ($r = 0,83$;

$p < 0,001$) was found between stomach content and faecal CP values. The regression line is expressed by $y = 2,59 + 0,84X$, where X = % CP in faeces and y = % CP in stomach contents (Fig. 73).

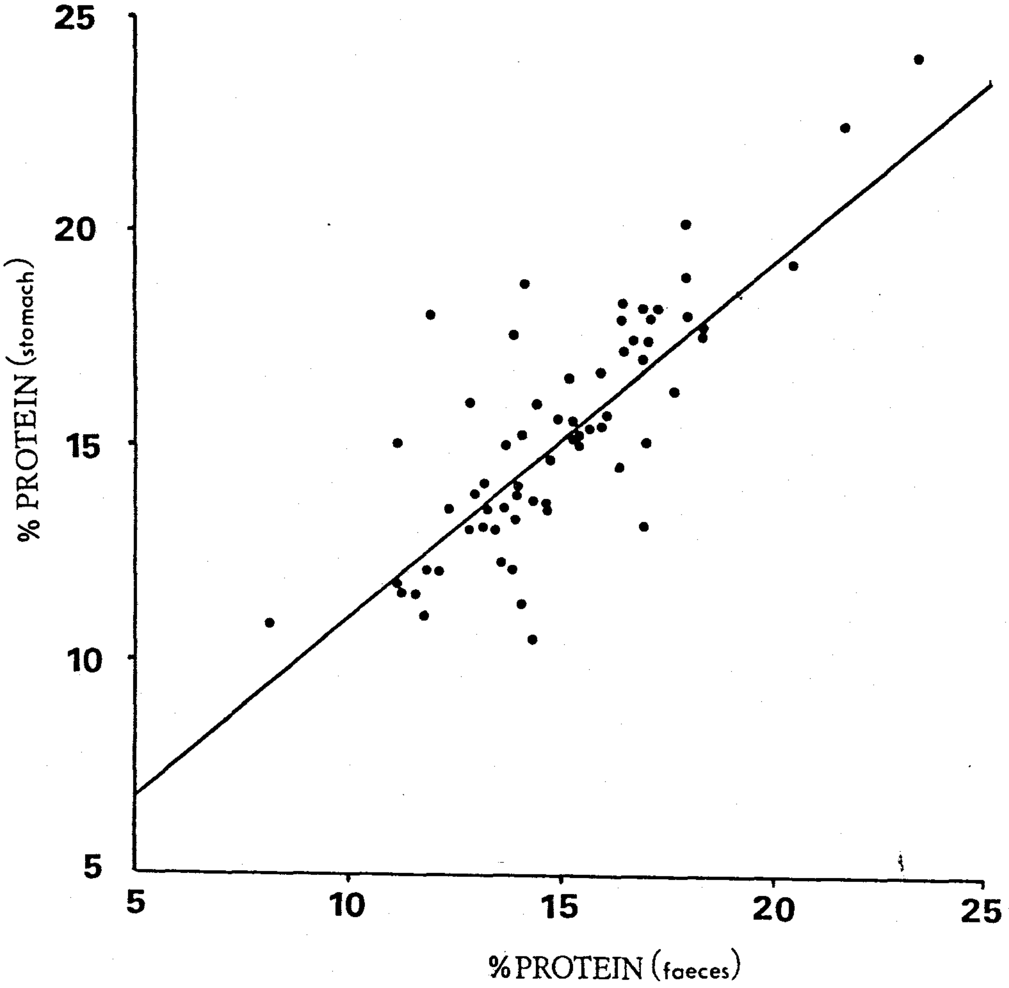


Figure 73: Correlation between stomach and faecal CP (% dry mass). (Regression equation: $y = 2,59 + 0,84X$; $r = 0,83$, $p < 0,001$ and $n = 69$)

A comparison between the CP values of the stomach contents of male and female hyrax during a six month period (August - January), which includes the last four months of pregnancy and the first two months of lactation, is summarized in Table 39.

Table 39: A comparison between mean monthly stomach CP values (±S.E.) of male and female hyrax during a six month period (August - January).

Month	♂♂ CP (% dry mass)	S.E.	n	♀♀ CP (% dry mass)	S.E.	n
August	14,65	1,92	5	14,82	1,16	4
September	13,28	0,82	3	14,81	0,70	3
October	14,04	0,76	2	15,22	0,29	2
November	13,68	0,59	5	15,99	1,15	5
December	16,68	0,87	3	17,17	0,75	6
January	13,50	0,27	3	15,10	1,18	4

A comparison on a monthly basis showed female hyrax to have significantly higher mean monthly CP values ($p < 0,02$; t-test) than male hyrax. CP values of stomach contents, rainfall and diet composition (ratio of graze to browse) are graphically presented in Fig. 74. There is no significant correlation ($r = 0,06$; $p > 0,10$) between mean monthly rainfall and the CP values of the stomach contents. The low CP value of the stomach contents during January, the hottest month of the year, was accompanied by a reduction in grazing (Fig. 74). The highest stomach content CP values (February) correspond with the month during which the highest graze to browse ratio was recorded.

An indication of the degree of digestibility of the feed was obtained by NDF analyses of the stomach contents. This showed the lowest value (50,14%) to occur during July and the highest value (56,66%) during May. In general NDF value showed little seasonal variation (see Table 38).

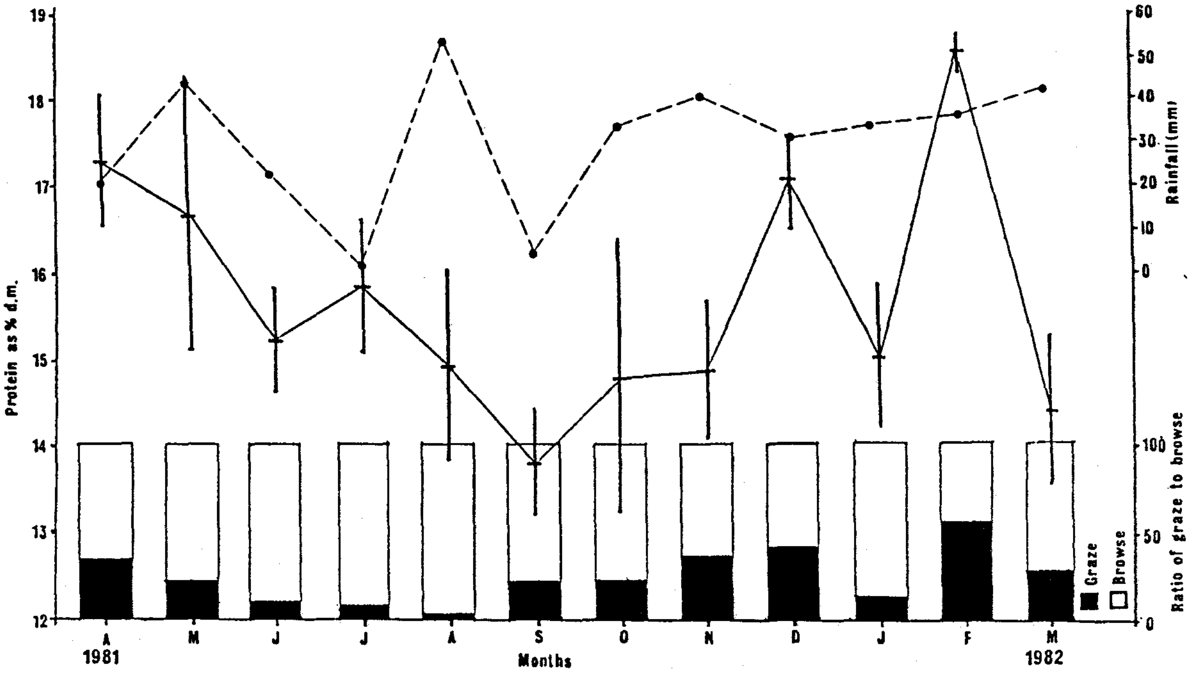


Figure 74: The stomach content CP values (mean ±S.E.) of hyrax, mean monthly rainfall (mm) and the ratio of graze to browse during a 12 month period (April 1981 - March 1982).

Physiological condition

Body fat

The total body fat analyses of 27 hyrax belonging to five different body fat rankings are summarized in Table 40. The correlation between total crude body fat and the subjective BFR is given by $y = 18,34x^{0,3081}$ ($r = 0,86$; $p < 0,001$) where y = total crude body fat and x = BRF (Fig. 75).

Body fat rankings for male (n = 196) and female hyrax (n = 218) during the period April 1980 - May 1982 are graphically presented in Figures 76a & b. Physiologically stressful periods and rainfall are indicated

Table 40: The mean (±S.E.) total crude body fat values (% of dry mass) for 27 hyrax belonging to five different BFRs.

BFR	1	2	3	4	5
$\bar{x}$	18,33	23,54	26,04	27,87	29,72
±S.E.	1,41	0,81	0,33	0,59	0,86

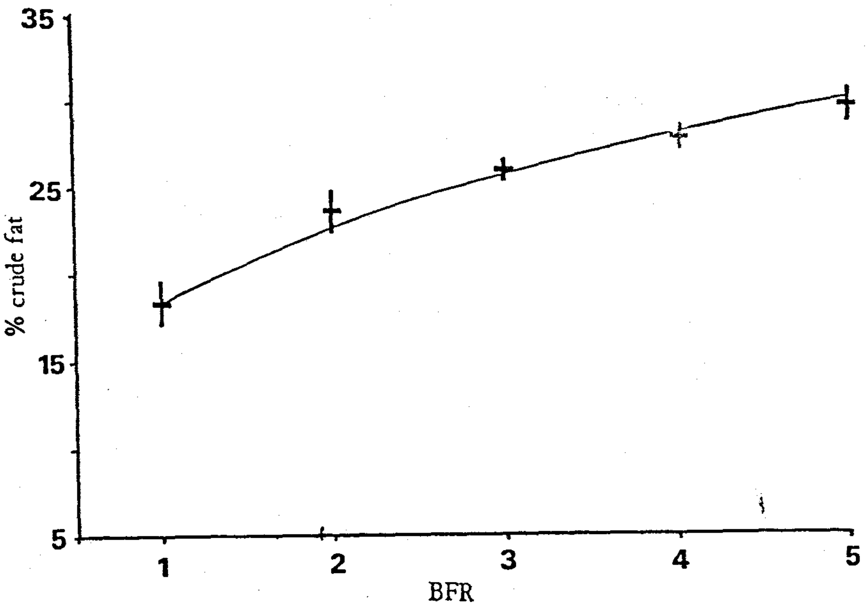


Figure 75: The relationship between % crude body fat and the subjective BFR (mean values ±S.E.) for 27 hyrax.

(Regression equation: $y = 18{,}34x^{0{,}3081}$; $r = 0{,}86$; $p < 0{,}001$ and $n = 27$).

by superimpositions on these graphs. A comparison between the mean monthly BFR for male and female hyrax showed a significant difference ($p < 0{,}05$; t-test) over the entire period. The mean monthly BFR of males for the May - July period (following peak rutting) was significantly ($p < 0{,}05$ and $p < 0{,}01$; t-test) lower than that of females

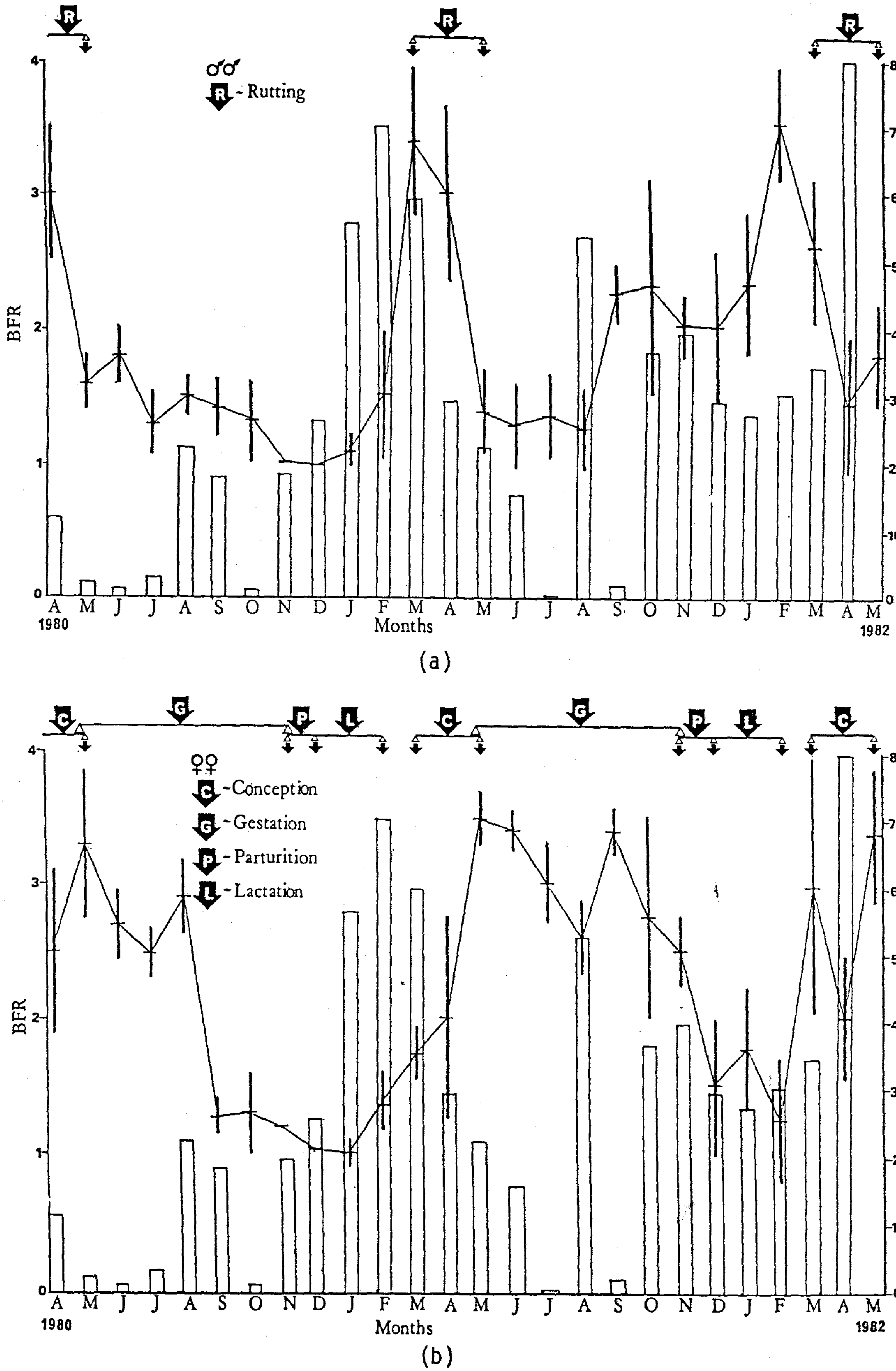


Figure 76 a & b: Mean (±S.E.) monthly BFR values for male (a) and female (b) hyrax during a 26 calendar month period. Mean monthly rainfall (mm) and the different reproductive phases are superimposed on the graphs.

during the same period. The BFR for females during gestation declined from May - November or December and these values differed significantly from male values ($p < 0,05$ and $p < 0,01$; t-test) during the same period. The mean monthly BFR values of females during lactation were consistently but not significantly ($p > 0,1$) lower than those of males collected during the same months (Figs. 76a & b). No statistically significant ($p > 0,5$) relationships between rainfall and BFR of either male or female hyrax were found.

The sequence of fat mobilisation was observed to be first subcutaneous then abdominal and this was followed by bone marrow fat (deduced from the fact that hyrax with a BFR of one showed a wide range of total body fat).

Serum cholesterol

The serum cholesterol concentrations (mg %) of hyrax ($n = 50$) determined during a 10 month period (February - November 1982), ranged from 50 - 100 mg %. The mean monthly serum cholesterol concentrations for nine of the 10 months were almost constant and varied between 73,0 - 80,0 mg % (Table 41). Only two samples, however, were analysed during October and the mean concentration of these was 55 mg %. The correlation between mean monthly rainfall and mean monthly serum cholesterol concentrations is not significant ($r = -0,52$; $p > 0,05$). No significant ($p > 0,1$) correlation between BFR and serum cholesterol concentration could be shown.

Table 41: Mean (±S.E.) monthly serum cholesterol concentrations (mg %) for the 10 month period February - November 1982.

Month	Serum cholesterol (mg %)	±S.E.	n
February	74,0	5,86	3
March	73,0	4,51	7
April	73,3	1,76	3
May	79,8	5,57	6
June	74,3	4,68	7
July	80,0	4,11	7
August	80,0	-	2
September	78,0	4,14	6
October	55,0	5,00	2
November	73,4	5,70	7

Feeding behaviour

The upper incisors, because of their structure and wide spacing, are not used extensively when feeding. The two pairs of lower incisors are flattened and incised to form comb-like structures used in grooming. Field observations have shown that if food material is a little out of reach hyrax may use their incisors to pull leaves nearer or to break them off simply by retracting their necks. The incisors may also be used during casual feeding spells when feeding intensity is low. The normal mode of browsing, however, is to turn the head sideways and use the cutting edges of the premolars and molars. The plant material obtained in this way is ingested through the side of the mouth. Figures 77 and 78 show hyrax indulging in casual feeding. During the severe drought of 1983 plant material in the close proximity of refuges was devoid of leaves and Figure 78 shows a hyrax feeding on dry twigs using the cutting edges of the premolars and molars.

Frequently tender shoots held between the premolars and molars are defoliated by the hyrax pulling its head sideways and stripping the leaves.

Hyrax observed in the MZNP did not use their fore-paws extensively for manipulating food. In order to reach further they sometimes sit on their hindlegs and use their fore-paws to force down a slender branch. They have never been observed to carry food into their refuges.

Ingestion of food is rapid and little time is spent on mastication. No evidence of rumination was found although hyrax sometimes grind their teeth when confronted giving the impression of rumination.

Feeding level

Hyrax can feed as close as *c.* 1 cm to the ground. The ability of hyrax to climb trees that have sloping trunks or accessible branches (Fig. 79) enables them to utilize the whole strata of vegetation available in the MZNP. Heavy and continual browsing of principal and preferred tree and shrub species have often altered their natural growth forms. Figure 80*a* - *c* illustrates two growth forms brought about by hyrax feeding on the preferred food tree *Olea europaea*.

Figure 77: A hyrax browsing with leaves projecting out of the side of its mouth.

Figure 78: A hyrax browsing on dry twigs using the cutting edges of its premolars and molars.

Figure 79: A hyrax browsing in a tall shrub (Lycium oxycarpum) and balancing on a slender branch.

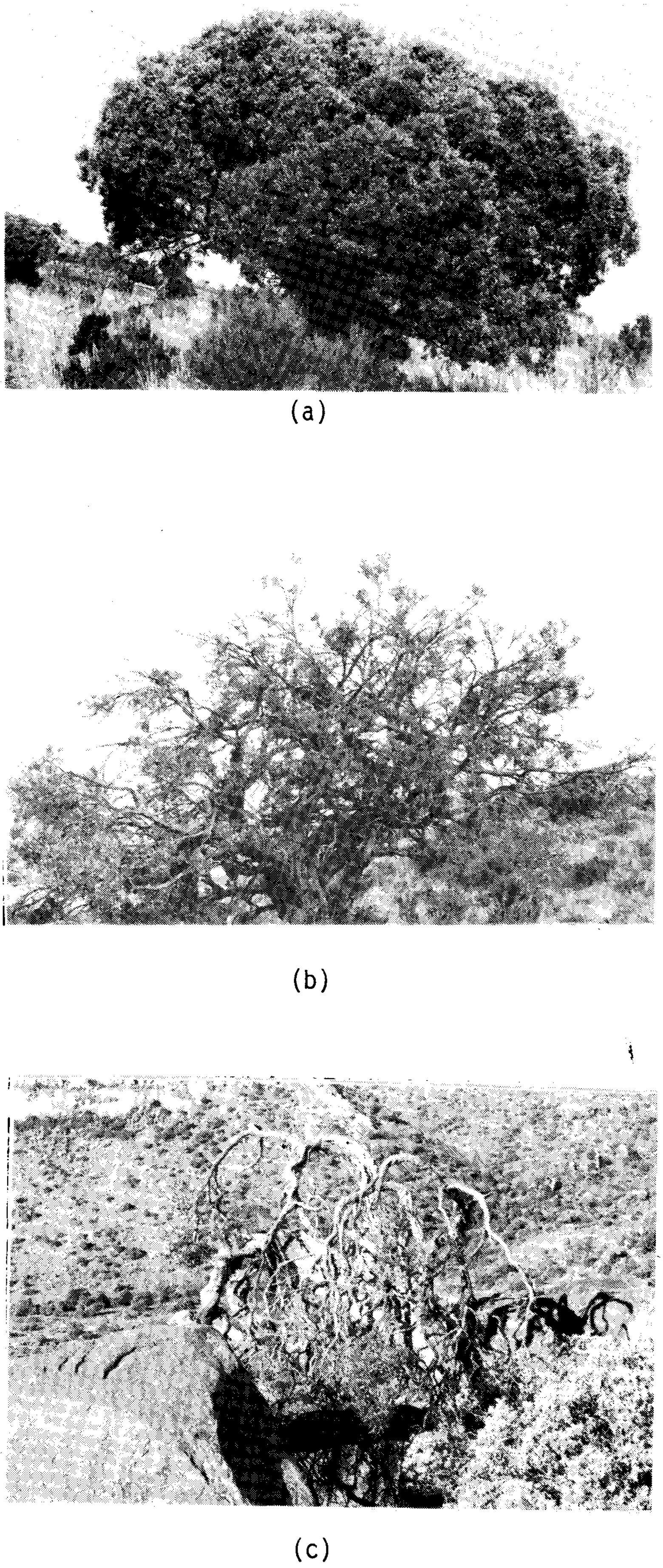


Figure 80a - c: Olea europaea not browsed by hyrax (a), intermediately browsed (b) and heavily browsed (c).

Group foraging patterns

Juveniles up to five months of age and adults show distinct differences in foraging patterns and will be discussed separately.

(a) Juveniles

Juveniles up to three months of age feed only in the close proximity of refuges and under the surveilance of adults. Distinct group feeding (Fig. 81) involving all or some of the juveniles may occur as many as four times a day and may last for 10 - 30 min. The initiation of group feeding is abrupt whereas its termination may be gradual. Hyrax between three and five months of age will feed only up to a distance of 40 m away from refuges, even during extremely adverse conditions such as the severe drought of 1983. Distinct early morning and late afternoon group feeding periods, however, were discernible. Hyrax older than five months of age displayed foraging patterns similar to those of adults.

(b) Adults

The foraging patterns of adult hyrax (expressed as % of total activities) were recorded for a total of 11 days during a six month period (February - July) at the observation colony. These foraging patterns in relation to environmental conditions are graphically represented in Figures 82_a_ - _k_.

Figure 81: A group of juvenile hyrax involved in group feeding in close proximity to refuges.

No definite pattern was discernible for the summer months and hyrax tended to commence foraging during any time of the daylight period. During winter, the foraging normally coincided with the 2 h preceeding sunset (Figs. 82_f_ - _k_). Early morning foraging excursions during winter were rare.

A composite diagram in which all summer and winter foraging observations are combined is presented in Figure 83.

When engaging in a group foraging excursion, hyrax never leave their refuges as a group, but individuals leave the refuge sites at intervals of 10 - 15 min. Figure 84 presents the foraging patterns of four marked hyrax on a specific day. They left the refuges over a period of 2 h and returned to the refuges during a period lasting 3 h.

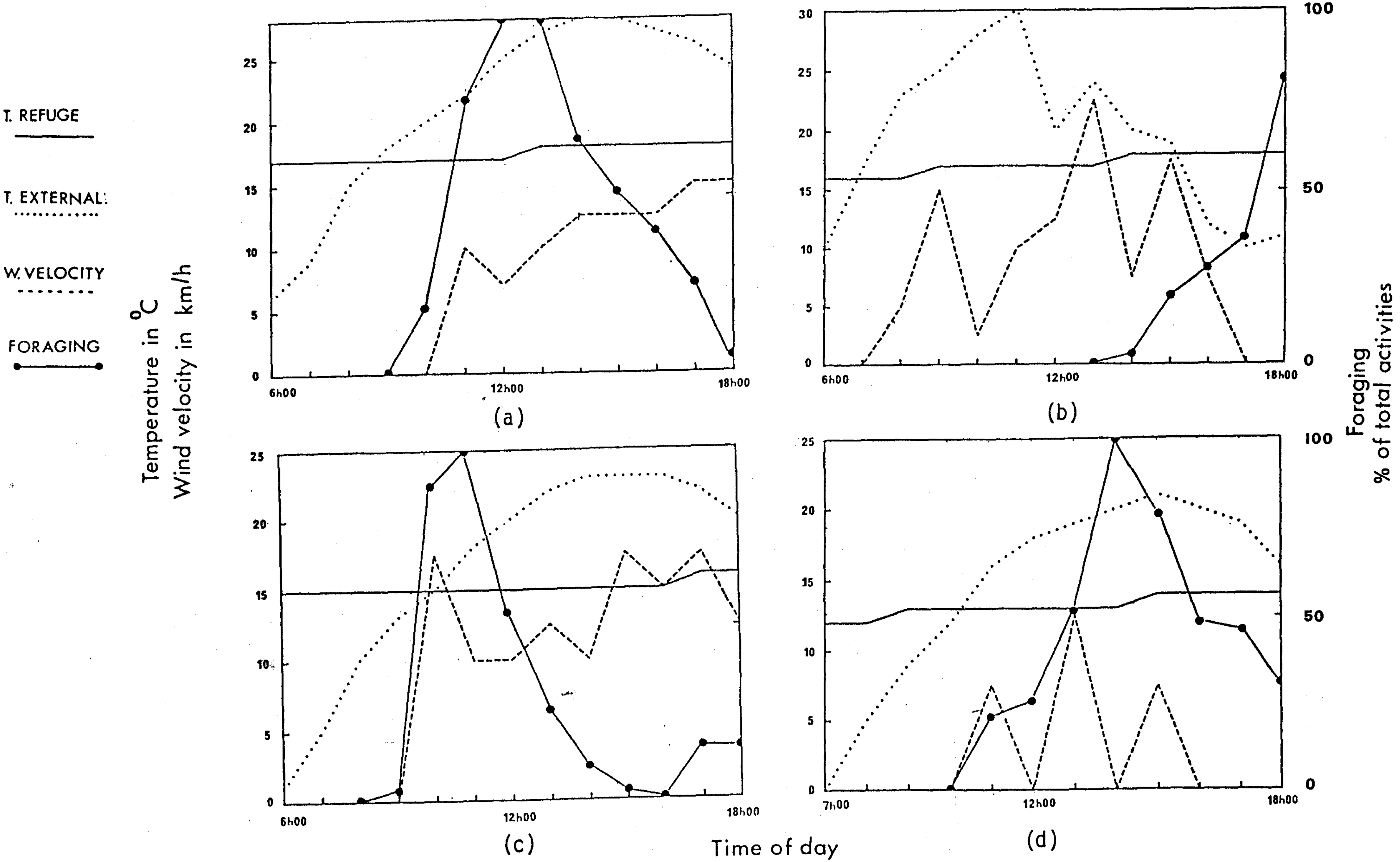


Figure 82 a - k: Foraging of hyrax (expressed as % of total activities) in relation to ambient temperature (°C), temperature within refuges (°C) and wind velocity (km/h) for five days in summer (a - e) and six days in winter (f - k).

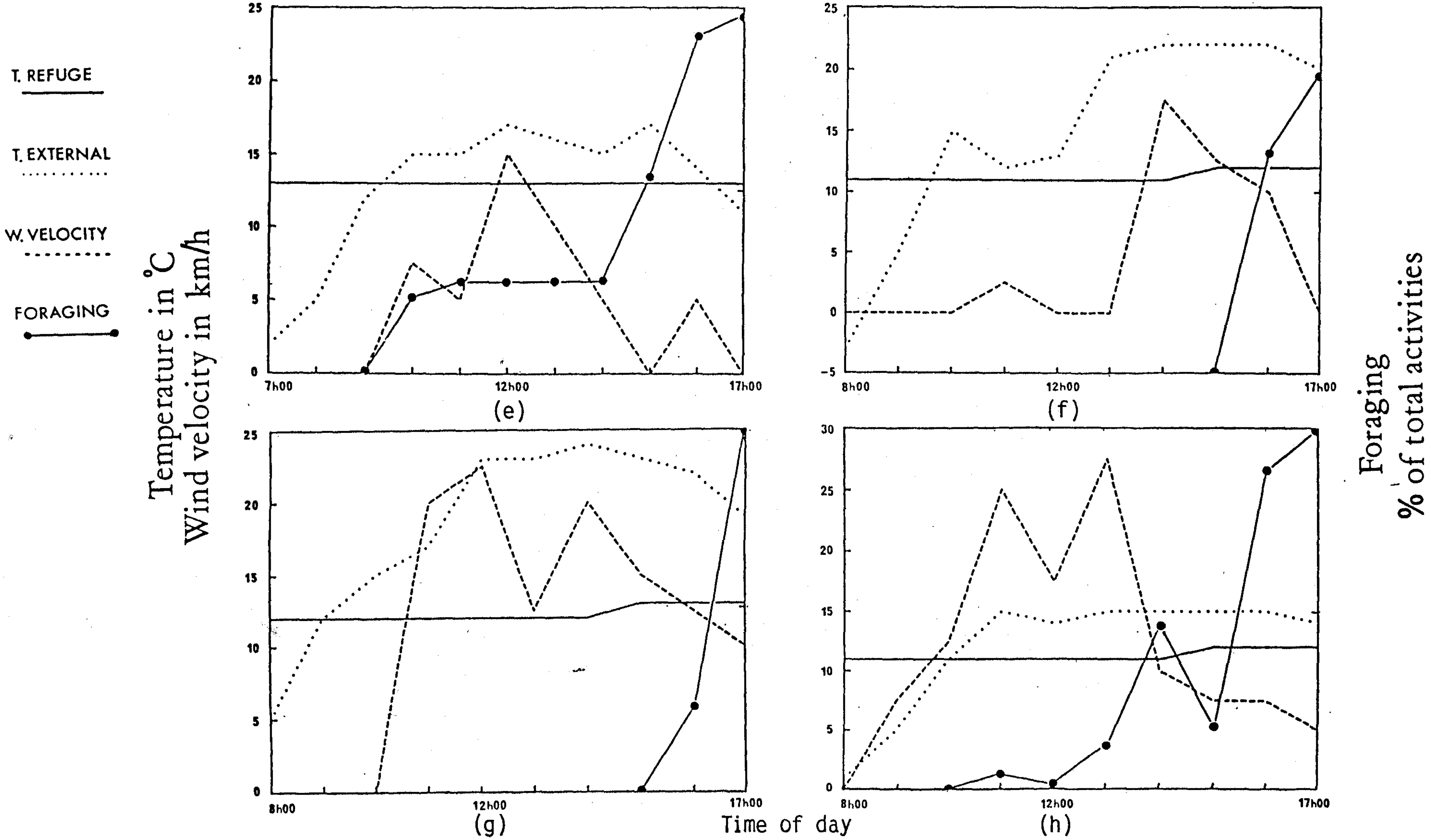


Figure 82 (cont.)

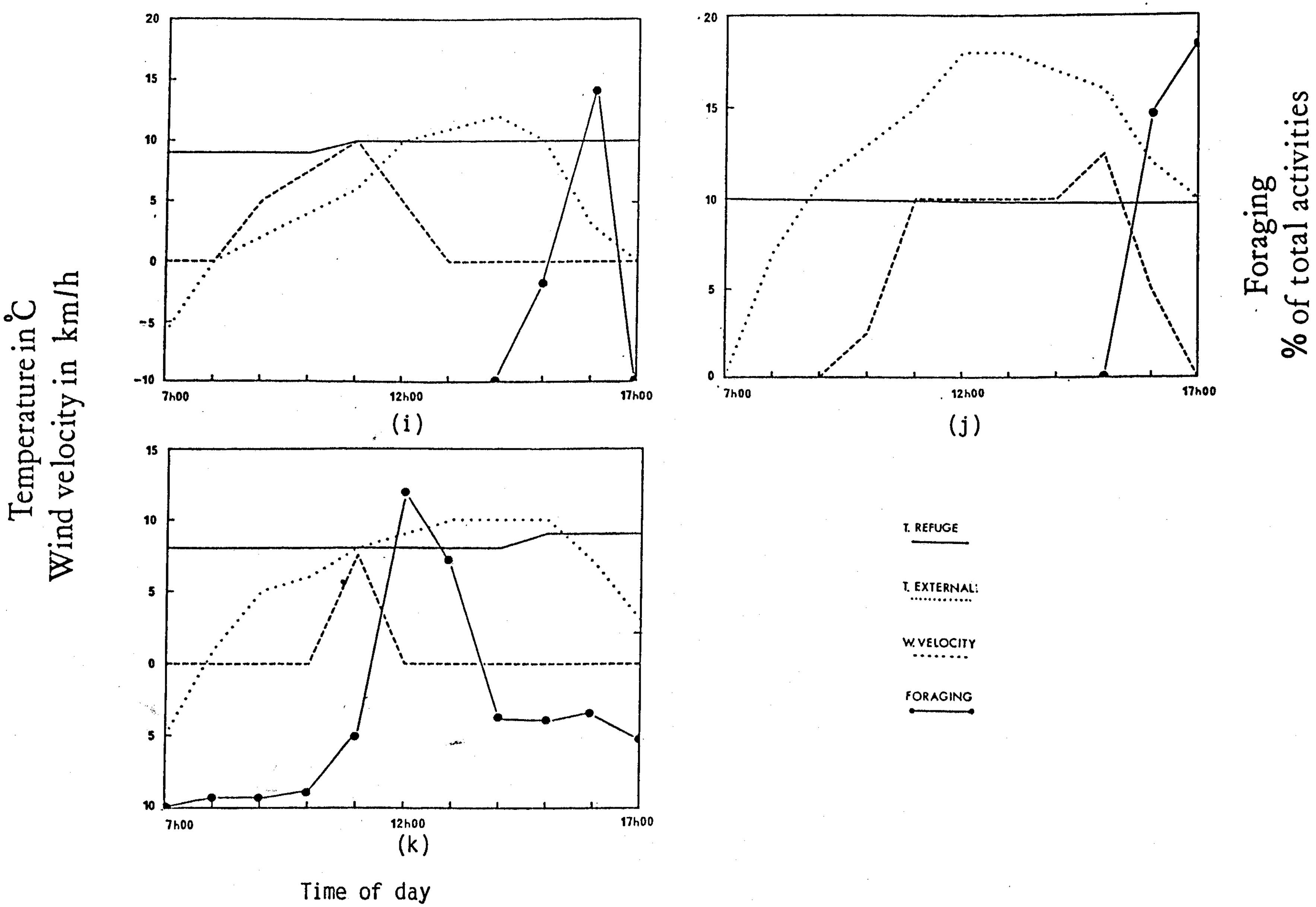


Figure 82 (cont.)

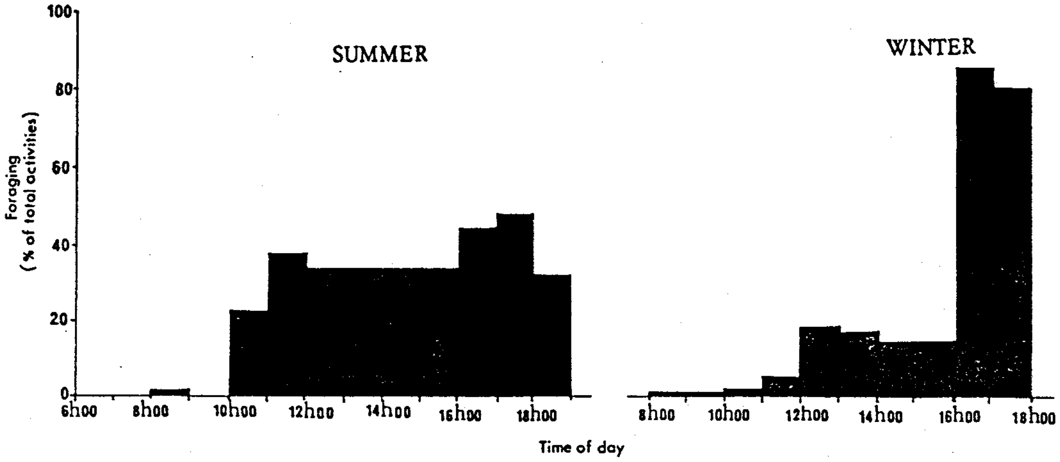


Figure 83: Foraging times of hyrax during summer and winter in relation to time of day (based on 11 days of observation).

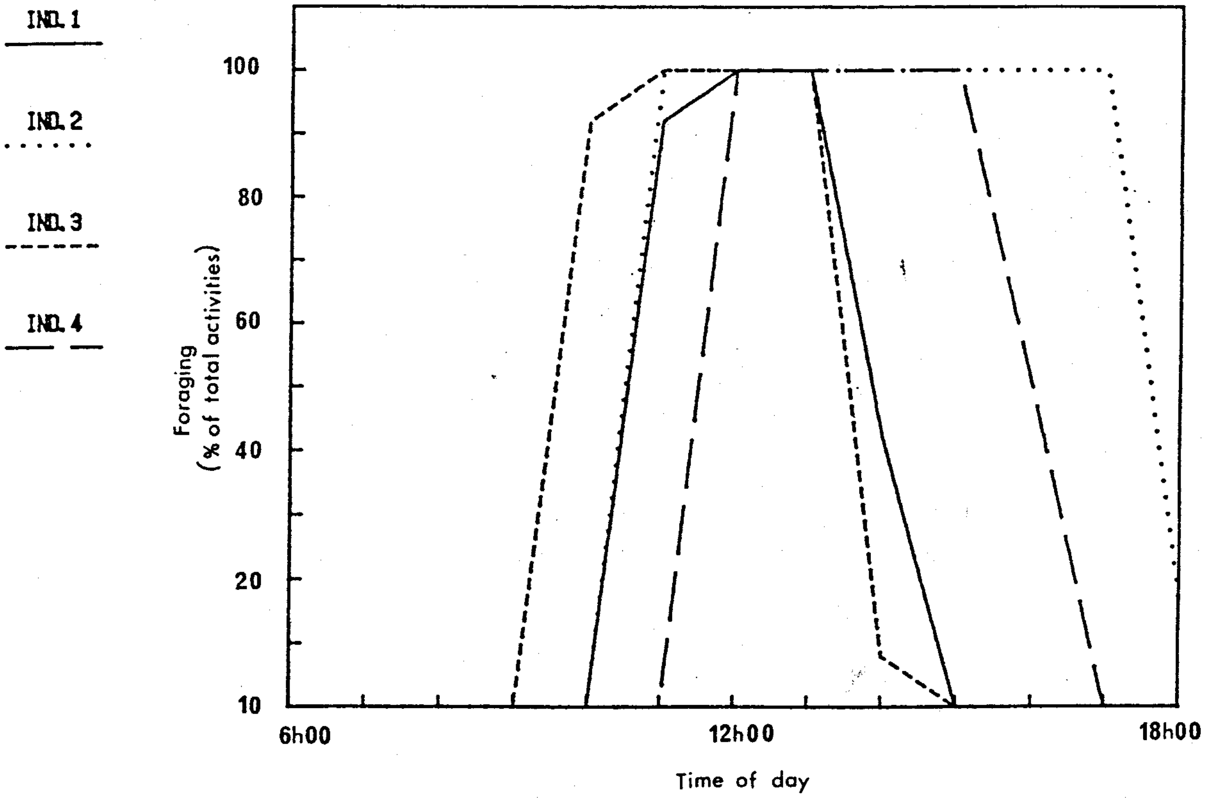


Figure 84: Foraging patterns of four marked hyrax observed for one day from sunrise to sunset (values expressed as % of total activities).

Foraging times for individual animals ranged from 0,5 - 8 h with a mean (±S.E.) time of 2,37 (± 0,27) h.

No obvious relationship between the commencement of foraging and environmental factors such as wind and temperature was evident. Early morning foraging during cold winter months was, however, rare. During rain hyrax entered their refuges and no feeding was observed during these periods.

Foraging times for different hyrax colonies within a specific area were not synchronised. This was established by field observations as well as comparisons of stomach fills of hyrax shot throughout the day on a specific day (Table 42).

Table 42: Hyrax stomach fills expressed as a % of body mass of 12 hyrax shot on the same day in a specific area.

Time of day	Stomach fill expressed as % of body mass
06h30	5
06h40	4
08h45	12
09h50	9
10h20	13
11h45	9
12h35	12
14h30	8
15h20	14
18h10	10
18h20	17
18h50	14

Hyrax were observed to feed as far as 500 m and even further away from their refuge sites. The tendency to forage extended distances away from their refuge sites was particularly noticeable for hyrax inhabiting hill slopes. These hyrax frequently frequented riparian thickets.

Figure 85 illustrates typical pathways used by hyrax at Grootkloof in the MZNP. In many cases clear hyrax footpaths can be seen. On descending from hillsides hyrax make use of transit zones. These are areas which may provide them with temporary protection and which may be used for periods of basking, but are not used for residence. On hillsides these zones normally consist of crevices, boulder scree (Fig. 86) or stacked boulders. On the plains the disused holes of other animals such as antbear (Fig. 87) and mongoose may be used.

Foraging excursions over extended distances (> 500 m) from refuge sites were observed throughout the year and were not confined to the dry winter months.

Hyrax feeding was not observed during night time, even on moonlit nights (based on casual observations by myself and staff in the MZNP).

Casual feeding

Casual feeding of both juvenile and adult hyrax took place intermittently throughout the day. This type of feeding was, however, confined to the close proximity of the refuge site.

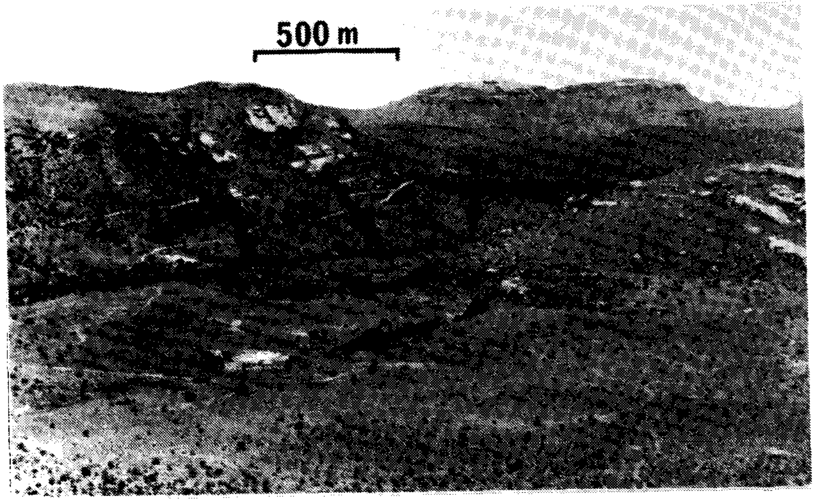


Figure 85: Typical pathways (indicated by arrows) used by hyrax in Grootkloof(MZNP) when on foraging excursions.

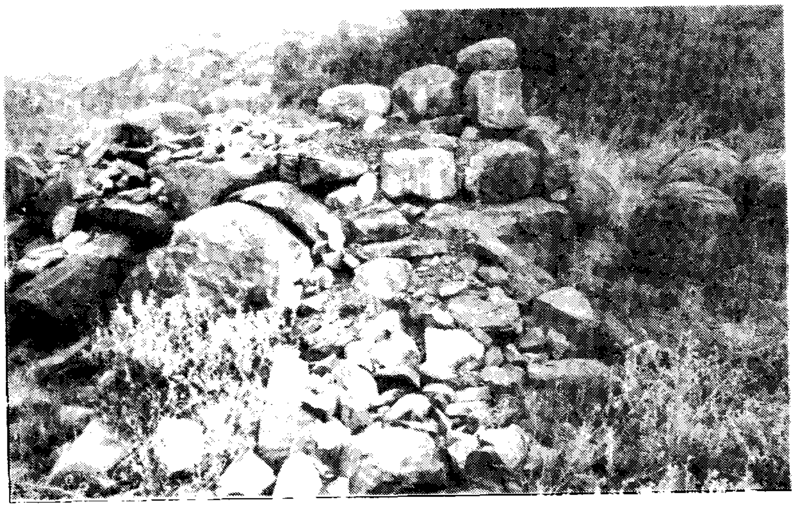


Figure 86: Transit zone used by hyrax in the MZNP.

Figure 87: Disused hole of an antbear used as a transit zone by hyrax in the MZNP.

Refuge requirements

Refuges used by hyrax are found throughout the MZNP at different altitudes, from the bottom of ravines to the crests of the mountain ranges without apparent selection for specific slopes (gradient, north or south facing). The only extensive area in which hyrax refuges do not occur is the Rooiplaat plateau. Refuges are, however, found along the perimeter of the plateau.

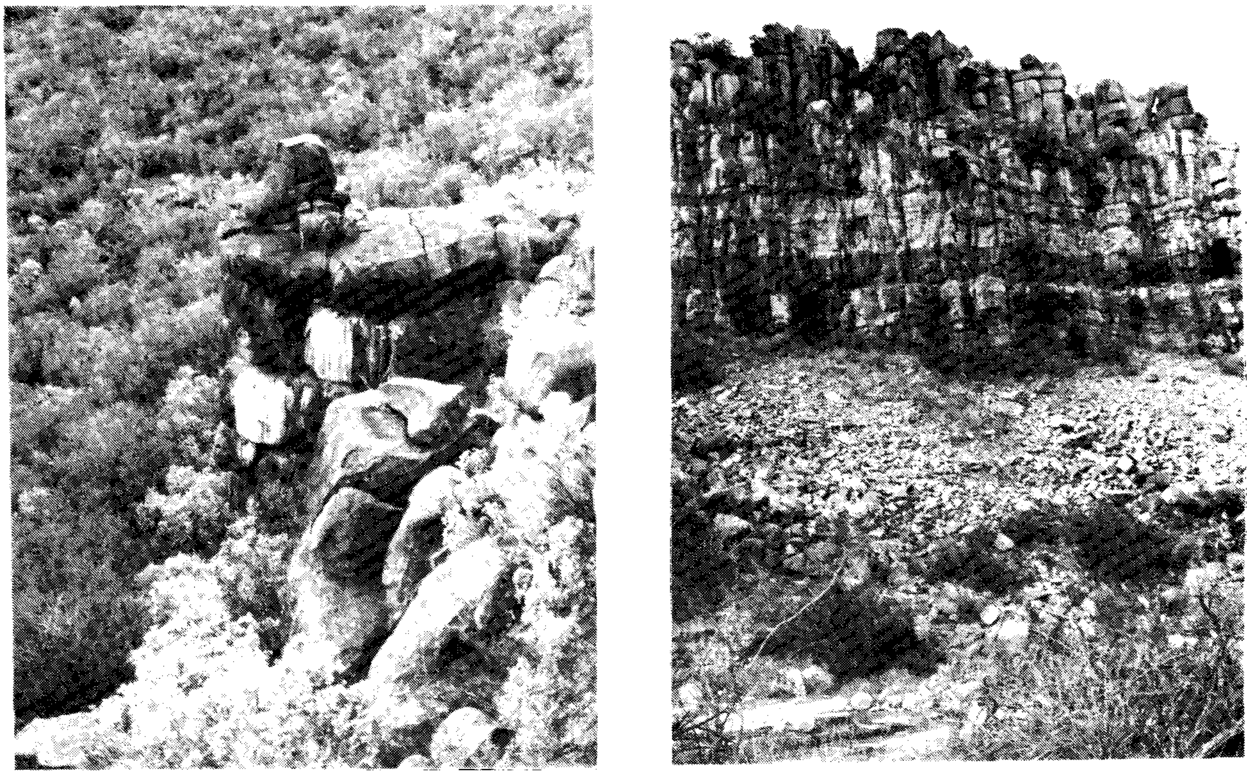
Refuges commonly used by hyrax in the MZNP and surrounding farming areas are:

(a) Dolerite boulders formed by intrusive volcanism and exposed erosion (Fig. 88a). Joints formed by shrinkage when the dolerite cooled and solidified. On being exposed these joints offered lines of entry into the rock for the agents of weathering and erosion. The resulting loose rock, crevices and ledges provide the hyrax with excellent refuge sites.

(b) Boulder scree (Fig. 88b). Exfoliation of dolerite because of weathering causes rock-falls of flat flagstone-shaped boulders. Wet weather and mechanical weathering cause rock-falls of sandstone which fragments on impact with the ground. The piles of rock formed in this manner at the base of a cliff afford many holes and crevices ideal for hyrax refuge sites.

(c) Road sides (Fig. 89). Boulders used or boulder scree excavated during the construction of roads form many holes and crevices used by hyrax.

(d) Rocky outcrops or sheets of dolerite. These function as natural



(a) (b)

Figure 88 a & b: Dolerite boulders formed by intrusive volcanism and exposed erosion (a) and boulder scree (b) commonly used by hyrax as refuges.

Figure 89: Boulder scree used in construction of roads serve as an ideal hyrax refuge.

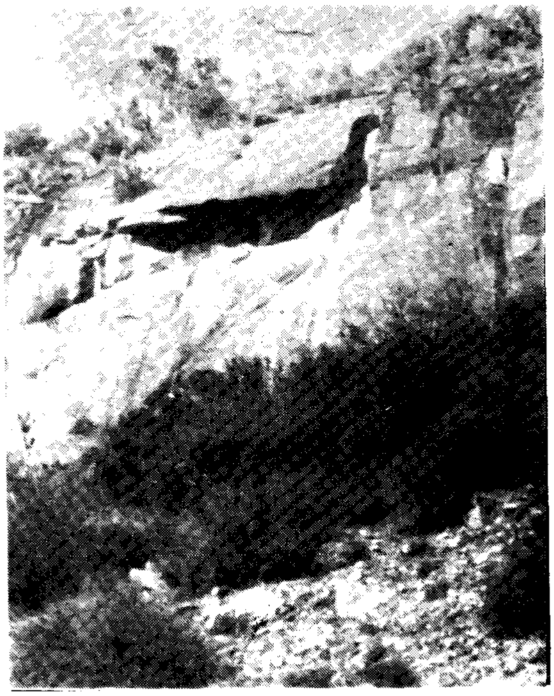


Figure 90: Dense vegetation at the base of a sheet of dolerite.

water catchment systems stimulating growth of dense vegetation (Fig. 90), consisting of both palatable and unpalatable shrubs and trees at their bases. Hyrax frequently use these clumps of vegetation as foraging sites.

It is impossible to establish the number, usage or size of holes used by hyrax as refuges. The size of the entrance to crevices and holes used as refuges is, however, such that it prevents the entrance of the caracal, the chief predator of hyrax in the MZNP.

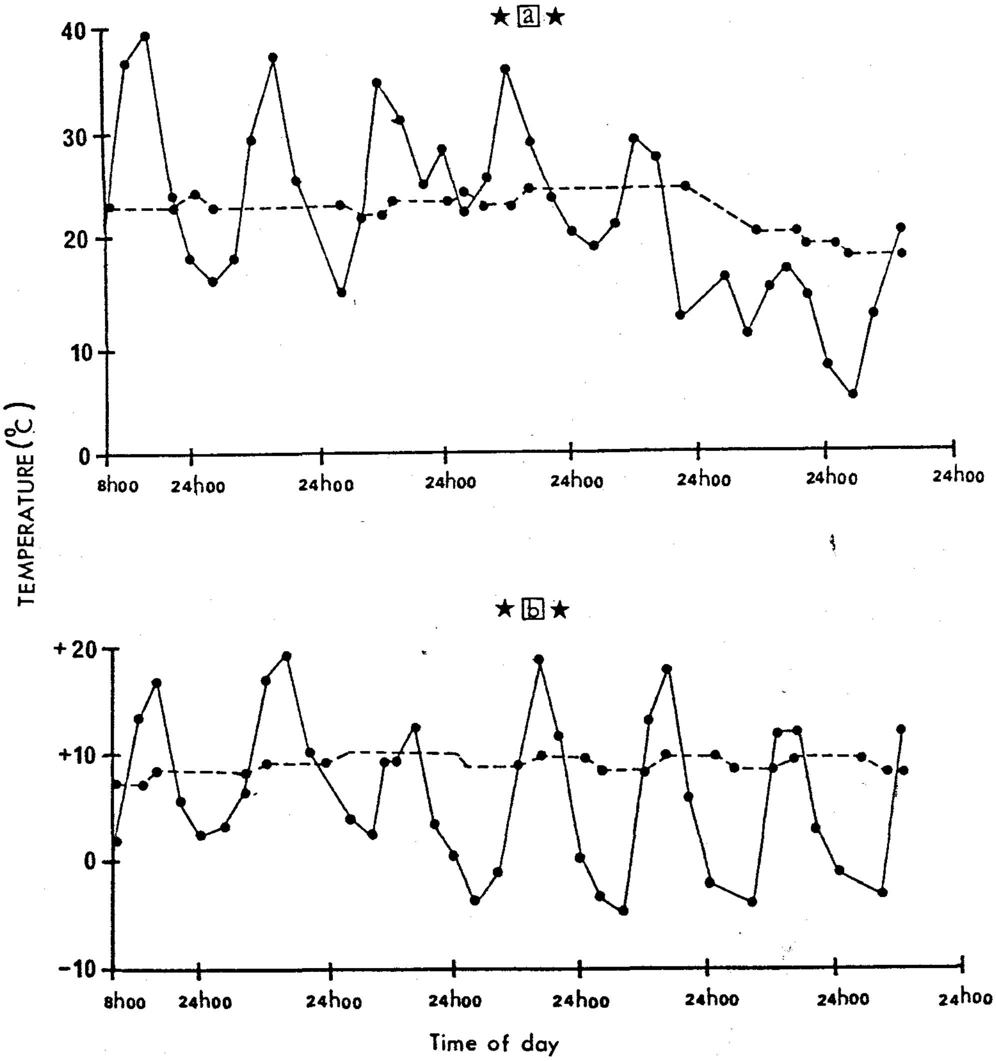


Figure 91a & b: The variation in ambient temperature (solid line) and temperature within a hyrax refuge (broken line) during seven day periods in January (a) and August (b).

No evidence was found of hyrax digging or altering the natural refuge sites.

A comparison of the temperature changes within a refuge and ambient temperature for a period of seven days during summer and during winter is summarized in Figures 91a & b.

Ambient temperature during summer ranged between 4 and 39°C, whereas the temperature within the refuge varied between 18 and 24°C (Fig. 91a). During winter the ambient temperature varied between -5 and 19°C whereas the temperature within the refuge varied between 7 and 10°C (Fig. 91b).

DISCUSSION

Composition and diversity of the diet

A variety of methods can be used to determine the feeding habits of herbivorous animals. Those commonly used involve macro- and microscopic examination of stomach contents (Sparks & Malechek 1968; Hall-Martin 1974; Drodz 1975) or microscopic examination of faeces (Stewart & Stewart 1970; Voth & Black 1973). The only known attempt to date to determine feeding habits of hyrax from stomach contents was by Lensing (1978). Differences in the feeding habits of two sympatric hyrax (*P. johnstoni* and *Heterohyrax brucei*) have also been recorded by noting differential tooth wear (Walker, Hoeck & Perez 1978).

The methods used in this study provided excellent quantitative data and the methods are recommended for future hyrax feeding studies. A prerequisite, however, is a sound knowledge of the vegetation in the study area.

Although hyrax in the MZNP utilize a wide variety of plant species, only 10 plant species (and the grasses) each constitute more than 2% of the total diet on a dry mass basis, i.e. these plant species form c. 83% of dietry biomass (Table 33). Supporting evidence for the marked diversity in the diet of the hyrax is provided by Sale (1965c), Turner & Watson (1965), Hoeck (1975) and Lensing (1978).

Hoeck (1975) reported that only 2 - 11 plant species form 90% of the staple diet of H. brucei in the Serengeti National Park (Tanzania). Sale (1965c) reported that faecal analyses showed that Procavia mackinderi johnstoni (Thomas) also took insects in addition to vegetation. Since no insects were recovered from the stomachs of hyrax in the MZNP it can be assumed that they do not form part of the diet of these animals. Since only traces of insects occurred in the scats examined by Sale (1965c), it is possible that the insects present had been ingested accidentally and that the hyrax had not eaten them intentionally. A case of cannibalism in Heterohyrax syriacus hindei (Wroughton) has also been reported by Sale (1965a). An adult male and a juvenile female ate the entire hindfoot (including bone) and part of the ear of another adult male.

While there is some dispute as to whether Procavia spp. are predominantly grazers or browsers (Sale 1965a; Turner & Watson 1965; Hoeck 1975), the results of this study (confirmed by Lensing 1978) show that P. capensis in Southern Africa is mainly a browser and that grazing depends upon the seasonal availability of grasses. Total intake of grasses on a dry matter basis constituted less than 25% of the total year-round diet. The leaves of trees and shrubs formed the major portion of the diet, and were browsed throughout the year. Browsing also bore a strong relationship to phenological and growth phases. Flowers and fruits were frequently utilized when available.

The report by Sale (1965d) who observed P. habessinica in Kenya to feed on the poisonous plant Phytolacca dodecandra without any ill effects, is of interest. Mendelssohn (1965) also recorded that hyrax feed on poisonous plants in Israel. The only plant which is known to be poisonous at certain times of the year (Hobson, Jessop & Van der Riet Ginn 1970) and is eaten by hyrax in the MZNP, is Diospyros lycioides. According to Sale (1965a) the insusceptibility of hyrax to poisonous plants most probably is due to the functioning of the peculiar hindgut. In this respect caecal microbial detoxification and hydroxilase enzymes of the liver may be important. Co-evolution between the hyrax and poisonous food plants is also likely.

Since faecal pellets were not observed in any hyrax stomachs examined and since faecal ingestion was not observed, coprophagy does not seem to take place. Woodall (1977) found that coprophagy in the water vole (Arvicola terrestris) increased significantly with an increase in the fibre content in the diet. However, since the NDF values obtained for the stomach contents of hyrax in the MZNP showed no marked seasonal changes the fibre content of their diet is probably such that there is no need for coprophagy. Coprophagy is, however, often associated with vitamin release in the hindgut. Absence of coprophagy in Procavia spp. has also been noted by Sale (1965a, 1966a) and for P. capensis by Leon (1981).

Daily dry matter intake by hyrax in the MZNP is similar to the 33,6 g dry matter kg^{-1} day^{-1} recorded for P. johnstoni mackinderi (Thomas) by Sale (1966a), and 32,86 g recorded by Leon (1981) for P. capensis. Leon (op. cit.) also calculated a dry matter intake of 31,67 g dry matter kg^{-1} day^{-1} after extrapolation of Lensing's (1978) results. Comparison of the daily food (dry matter) intake of various animals is summarized in Table 43. Values obtained are similar to those for sheep (35,5 g dry matter kg^{-1} day^{-1}). Since the ratio normally increases as body mass decreases (Sale 1965a), hyrax have a modest food intake for their size and this may be a significant factor contributing to the ability of rock hyrax to inhabit areas where vegetation is sparse or of a poor nutritional quality.

Although this study did not allow for the examination of differences between total feed intakes of male and female hyrax, some interesting trends are discernible. There is a slight but insignificant difference in feed (dry matter) intake between males and females for the two month period prior to parturition (Table 37). However, during the two month lactation period, female values were

Table 43: A comparison of the daily food (dry matter) intake of various mammals (adapted from Sale 1966a).

Species	Body mass (kg)	g dry matter kg^{-1} day^{-1}
Rat	0,3	50
Howler monkey	3	238
Procavia (MZNP)	3,2	34,97
Procavia (Kenya)	3,3	33,6
Wallaby	5	280
Wombat	9	63
Sheep	60	34,5
Zebra (Grevy)	409	20
Beef cattle	800	15
Giraffe	1134	28
Elephant (African)	3409	29

significantly higher than those of males. It is a well documented fact that dry matter intake in domestic stock drops significantly prior to parturition because of the space occupied by the foetus(es) (Forbes 1968) and increases markedly during lactation (Hadjipieris & Holmes 1966) in response to the greater energy requirements (Kaczmarski 1966; Migula 1969; Robinson 1980). Higher food intake by female hyrax during lactation would seem to be consistent with this observation. Controlled experiments under laboratory conditions with both male and female hyrax are, however, necessary to confirm these trends, since the quantity of feed ingested may vary in response to the composition of the food; with the crude fibre content affecting the quantity consumed (Hume, Rübsamen & Engelhardt 1980; Leon 1981). If however, female feed intake is shown to decrease prior to parturition, this may, during times of drought (or restricted feed availability) result in a markedly decreased intake of energy. This will cause the rapid depletion of stored energy reserves and thus seriously affect the viability of young (Thorne, Dean & Hepworth 1976; De Wet Louw 1978).

It can be concluded from the moisture content analysis of vegetation ingested that plant species are not primarily selected for their moisture content, except during August when there is evidence suggesting selection for plant species with a high moisture content, such as succulents (Table 34 & 35). Lensing (1978) reported similar observations for P. capensis in S.W.A. (Namibia).

The fact that hyrax were not seen drinking water, although they are known to drink free water (Steyn 1980) is consistent with the findings of Leon (1981) and Meltzer (1976). The latter mentioned authors reported that the food ingested by hyrax is sufficient to satisfy the water needs of the animals. Hyrax can, however, not exist indefinitely on dry food without water (Louw 1971).

The mean rate of water turnover measured in hyrax under conditions of ad libitum food and water is up to 60% lower than that of other eutherian mammals (Rübsamen, Heller, Lawrenz & Engelhardt 1979). The low water requirements of the rock hyrax is mainly due to an efficient renal concentrating mechanism (Louw et al. 1972), a low evaporative water loss (Rübsamen & Kettembeil 1980) and a low faecal water loss (Rübsamen et al. 1979). When the water content of the vegetation is very low, additional water can be saved by increasing the urine concentration to maximal values (3 200 m

Osm. kg^{-1}) equivalent to that of the camel (Louw et al. 1972), and by reducing faecal water content to 56% (Rübsamen, et al. 1979). Under conditions of severe drought additional water can be saved by a shift in body temperature (Rübsamen et al. 1982). This causes the oxygen consumption to decrease by up to 20% thereby also reducing the evaporative water loss (EWL). Of even greater significance is the fact that at ambient temperatures above 35°C the hyrax becomes hyperthermic during periods of water restriction (Rübsamen & Kettembeil 1980). This can result in a reduction of EWL of more than 50%. The hyrax also has the ability to reduce water turnover rate and to tolerate a substantial decrease in body mass in response to dehydration (Rübsamen & Kettembeil 1980). Under these conditions of dehydration, food intake is lowered resulting in reduced daily excretion of solutes (particularly K^+ and urea) and thus a minimal loss of water in the urine (Maloiy & Sale 1976).

The low water requirements of the hyrax, its effective adaptive mechanisms reducing water loss, and the ability of the animal to feed on a wide diversity of plant species may be major factors contributing to its wide range and broad niche.

Plant phenology and seasonality of the vegetation

The findings on plant phenology and seasonality are consistent with those obtained for relative growth and reproductive phases of plants in the Eastern Mixed Karooveld (Vorster & Roux 1983). The shrub and grass components of the diet are differentially influenced by seasonal rainfall. The grasses are stimulated by rain falling during the period September - February, whereas shrubs are invigorated by rains falling mainly during August - March. Fluctuations in seasonal rainfall are regarded to be one of the main causes of the instability and the dynamic nature of the vegetation of the Eastern Mixed Karooveld (Roux 1966).

A major factor affecting the nutrient contents of a plant is its phenological stage of development (Westoby 1978). Different nutrients tend to co-vary in their concentration within plant tissues, and are thus commonly diluted by the increase in cell wall components that occurs with time and age. The variety of plants in the MZNP (Van der Walt 1980) and the fact that each displays a different growth peak during the year can provide the hyrax with high quality nutrients throughout the year. This emphasises the food-potential plants in the MZNP have for an animal such as the hyrax which can utilize different plant components of all strata of vegetation.

Chemical analysis of stomach contents and faeces

The CP content of stomach contents and faecal samples showed little seasonal fluctuation (Table 38) implying that hyrax in the MZNP were on a stable quality (CP) diet. In order to maintain a high nutritional level in an area such as the MZNP, hyrax have to be very selective in their feeding habits, not only in respect of plant species, but also specific plant components. The selection of plant species and components thus closely followed seasonal changes (phenological phases) in the vegetation. Supporting evidence for hyrax being selective feeders, and on an almost stable nutritional level has been provided by Leon (1981) who showed that during a six month period mean monthly CP values of stomach contents varied by only 1,84%.

The significant differences between male and female hyrax feed quality during the last four months of pregnancy and for two months during lactation (Table 39), is an important finding. If females are to be on a higher nutritional plane they must be more selective in their feeding, if not of plant species, then of plant components. This strategy is of a selective advantage to females in order to supply the greater energy demands for gestation and lactation (Migula 1969; Moen 1973). A similar situation was found in Scottish red deer, where Yalden (1978) reported hinds to feed on higher quality food than stags. Although differences in the duration of foraging times for male and female hyrax could not be ascertained, Norton (1981) showed that foraging times for female klipspringer are 39% longer than those for males.

The significant correlation between the CP values of faeces and those of the stomach contents has definite practical implications. Collection of faeces is easy and diet quality of hyrax can be studied without the inherent disruption of shooting animals. Since hyrax have been shown to be selective feeders (Lensing 1978; Leon 1981; and the present study) low faecal CP values reflect seasonal trends in availability and/or quality of feed.

The food quality of mixed feeders (springbok) and exclusive grazers (Mountain zebra) exhibits major seasonal fluctuations in the MZNP (Erasmus, Penzhorn & Fairall 1978; Grobler in press). Although springbok may feed as close to the ground as the hyrax (Grobler in press), the latter animal has the distinct advantage of utilizing all strata of the vegetation because of its ability to climb. This attribute is clearly beneficial during periods of drought when vegetation close to the ground is the first to show stress, while trees and tall shrubs still provide high quality forage.

The marked decrease in the amount of grasses eaten by hyrax during January (Fig. 72) and the marked decline in stomach content and faecal CP values during this month (Table 38) are closely related to the growth and the nutrient value of grasses. High midsummer temperatures inhibit growth and result in a decline in the CP content of grasses in the MZNP (Grobler in press). This occurs during January and is also reflected in the CP content of mountain zebra faeces. This further supports the validity of using faeces as an indication of the quality and availability of feed.

The NDF values, which are a reflection of the amount of cell wall constituents of plants, also divide the dry matter content of feeds very close to the point that separates the nutritively available and soluble constituents from those that are incompletely available and dependent on microbial fermentation (Goering & Van Soest 1970). These values (Table 38), as is the case with the CP values, show little seasonal variation, thus further supporting the view that hyrax are very selective feeders.

The complex digestive system of the hyrax has three separate areas in which microbial digestion can take place, the fore-stomach, the caecum and the paired colonic appendages (Rübsamen *et al*. 1982). Rates of volatile fatty acid production are highest in the caecum and lowest in the stomach and may amount to 87% of basal metabolism (Rübsamen *et al*. 1982). When low quality foods are ingested the hyrax can enlarge its hindgut to obtain sufficient storage space and ensure efficient digestion and absorption of fermentation end products (Eloff 1981). According to Leon (1981), however, *P. capensis* does not have a particularly high assimilation efficiency and its selective feeding habits serve to augment the energy assimilated by virtue of the improved quality of herbage eaten. When the energy assimilated is expressed as a function of the metabolic rate, the energy consumption falls within the range for other eutherian mammals (Leon 1981).

Physiological condition

Body fat

Physiological condition as defined by Hanks (1981) is linked to an individual's chances of living or dying. A commonly used criterion for the description of physiological condition in mammals is the quantification of deposited fat reserves. Total body fat can be determined in small mammals by processing the whole animal (Perrin 1981), or a kidney fat index (KFI) may be used (Caughley 1970a; Hanks et al. 1976; Monro & Skinner 1979). In addition bone marrow fat (BMF) can be determined (Neiland 1970; Franzmann & Arneson 1976; Brooks, Hanks & Ludbrook 1977). BMF, however, is sequentially mobilized (Brooks et al. 1977; Reich 1981) and therefore values can only be compared if obtained from a specific bone. Since BMF is the last fat reserve to be mobilized (Hanks 1981) it is not a good parameter by which to determine the overall physiological condition of a population. Ransom (1965) has proposed that in order to assess the entire range of physiological condition of a population a combination of both KFI and BMF is required.

The subjective BFR used in the present study was significantly and positively correlated with total crude body fat. It is useful in field studies, and can be obtained without delay or cost.

The physiological condition of juvenile hyrax was consistently low and very little abdominal fat was deposited. The absence of extensive fat deposits in juveniles is most probably related to their rapid growth (CHAPTER IV). In adult hyrax, fluctuations in their fat deposits are correlated with the annual reproductive cycle. This finding is supported by Hanks et al. (1976) who also reported a marked decrease in physiological condition in male impala after the rutting season. The sequence of fat mobilisation in hyrax is consistent with that of larger ungulates (Hanks 1981).

Slobodkin & Richman (1961) noted that body fat is a "luxury" item in natural systems since evolutionary processes have chanelled "excess" metabolic energy into reproduction and growth rather than into storage. This may be true for small mammals. In larger mammals, however, the absence of any stored fat reserves will markedly affect their resilience during periods of stress and may seriously affect the survival of the progeny and the animal itself.

In terms of population characterization a distinction must be drawn between male and female hyrax with regard to physiological condition. Females may have a low resilience during late gestation and during lactation whereas males may have a low resilience just after the rutting period. This implies that during these periods the sexes within a population will be affected differently by adverse conditions. Although the absence of abdominal fat in a hyrax does not imply that the animal is on the verge of death (since BMF may still be mobilised to varying degrees) it is surely less resilient to environmental or social stresses.

Any attempt to assess the condition of a hyrax population must make allowance for the different rates of fat deposition by the sexes or else the results may be subject to serious bias.

Serum cholesterol

Blood constituents have been used in a variety of mammals to evaluate physiological condition (Erickson & Youatt 1961; Franzmann & LeResche 1978) or food quality trends (Coblentz 1975; Kirkpatrick, Buckland, Abler, Scanlon, Whelan & Burkhart 1975). One of the more useful blood parameters is serum cholesterol (Hanks 1981). This is synthesized in the liver and other tissues from various amino acids, carbohydrates and fatty acids when they are available in excess of metabolic needs (Coblentz 1975). Low cholesterol concentrations may thus be indicative of feed of poor quality (Franzmann & LeResche 1978), and animals with low cholesterol concentrations may be less resilient to environmental or physiological stress. In this respect "nutritional condition" is assumed to be synonymous with physiological condition as used by Hanks (1981).

The small variation recorded in mean monthly cholesterol concentrations (Table 41) in the present study further supports the assertion that hyrax feed selectively in order to maintain an almost stable nutritional plane throughout the course of the year.

Possible sources of error incurred when using cholesterol concentrations to assess food quality or physiological condition have been listed by Coblentz (1975). To minimize errors in this parameter the animals should undergo a minimum of stress immediately prior to sampling, and the samples must be drawn immediately from a standard vessel or organ. For results to be valid on a comparative basis, samples must also be analysed according to a standard laboratory procedure. In order to determine food quality from serum cholesterol levels animals have to be captured or shot. A more practical and accurate alternative is to ascertain the CP values of collected faeces.

Feeding behaviour

The mode of ingestion by hyrax in the MZNP is similar to that recorded by Sale (1965a). Comparison between the hyrax, the cow and the sheep shows that for a herbivore of its size the hyrax can ingest food at a very great rate (Sale 1966a).

In contrast to the published reports of bimodal daylight group feeding patterns of hyrax (Sale 1965c; Hoeck 1975; Steyn 1980), this study indicated feeding by hyrax in the MZNP to be monophasic. During this foraging period the animals selected high quality food. Because of the plantigrade nature of the animal, and its lack of speed and hence ability to evade predators, actual feeding times must be minimized (Sale 1965a; Hoeck 1975). Consequently the rapid ingestion rate and capability of the stomach for gross engorgement (Louw et al. 1972) is clearly of survival importance to the animal.

Although hyrax in the MZNP may be seen feeding in groups there is no intensive social drive for the initiation of foraging periods and individual hyrax leave refuges over a period of up to 2 h. The commencement of group feeding or foraging periods is thus not as well defined as for Procavia spp. in East Africa (Sale 1965c), where the animals leave refuges over a period of c. 15 min. Turner & Watson (1965), however, reported that hyrax involved in group feeding may leave refuges at intervals over a period of 1 h.

The habit of hyrax in the MZNP not to commence feeding as a group, but for individuals to leave refuge sites at intervals and to make use of transit zones when feeding away from refuges, have clear survival advantages especially in areas with sparse vegetation. Single animals may attract less attention from predators than a group and should the hyraxes leave the refuges in a large group, transit zones may also not be large enough to provide protection for all the animals. When descending from the summit of mountains or from hillslopes to feed in kloof or riparian thickets, single hyrax at different vantage points along the slope of the mountain are able to scan a large area for the possible presence of predators.

Evidence in the literature that hyrax may participate twice daily in group feeding activities is inconclusive. Sale (1965c) reports that group feeding may involve the whole or only a portion of a colony. This implies that hyrax not participating in a group feeding session may only join the next group and hence only participate in this activity once during the course of the daylight period. This is consistent with results obtained in the present study; especially during the first five months after parturition when a group of adults stayed with the juveniles at the refuges and only left once members of the first feeding group returned. This behaviour must not, however, be confused with the early morning and late afternoon group feeding reported in the literature (Sale 1965c; Hoeck 1975; Steyn 1980), since the foraging periods in the present study were not confined to a specific time during the daylight period.

Once juveniles are _c_. five months old group foraging may involve almost all members of the colony. Turner & Watson (1965) reported that during cool and cloudy days feeding may occupy extended periods from 11h00 onwards. According to Meltzer (1967) hyrax in Israel graze continuously for 3 - 5 h per day. During the wet season Hoeck (1975) observed that few hyrax participated in the morning feeding but that there was pronounced participation in the afternoon feeding session. It thus seems likely that the majority of hyrax observed by Hoeck (1975) participated in one group feeding only during this season. Since different hyrax colonies in the MZNP may feed at different times during the daylight period, a casual observer may get the impression that hyrax participate in two group feeding sessions.

Hyrax in the Karoo are known to travel up to 1 000 m away from refuge sites (Marais & Bezuidenhout pers. comm.) when foraging. Mendelssohn (1965), Sale (1965c) and Turner & Watson (1965) report movements of up to 100 m away from refuges. The latter rather limited movements are probably because of denser vegetation and the availability of food in the vicinity of the hyrax refuges. Predation pressures may also be greater.

The absence of certain hyrax for prolonged periods from the observation colony is consistent with reports by Sale (1965a) and Hoeck (1975) that hyrax do display limited migratory habits associated with feeding. This aspect will, however, be fully discussed in CHAPTER VIII.

No nocturnal feeding was observed and this agrees with the observations of Sale (1965a), Hoeck (1975) and Steyn (1980). Turner & Watson (1965), however, observed hyrax feeding on moonlit nights, especially during dry seasons.

Casual feeding by hyrax in the MZNP is very much like that described by Sale (1965a).

The observation that juveniles were confined to the close vicinity of refuges for at least five months after parturition may be advantageous in that they are better protected. It could, however, be a major disadvantage in that during periods of drought, when vegetation is sparse or rapidly exhausted in the close proximity of refuges, it may lead to starvation and increased juvenile mortality (CHAPTER X).

The ability of hyrax to climb well is of great importance to their survival. The changes in growth forms of trees and shrubs may make more foliage available to hyrax and by cropping these plants at regular intervals maximal leaf growth can be maintained. The ability to climb well may also be useful in predator evasion. Adelman, Taylor & Heglund (1975) have shown that sweating on the footpad of the hyrax increases the coefficient of static friction between the animals' feet and the substrate thus strengthening its grip.

Refuge requirements

Observations made during the course of this study are again consistent with observations by Sale (1966b) in that the major criteria for selection of refuge sites are protection from the elements and from predators. It is difficult to define "typical" hyrax habitat in terms of environmental necessities due to the apparent flexibility with which hyrax can adapt to new refuges. According to Sale (1966b) holes facing the prevailing wind and holes with entrances large enough to allow the entry of large predators are avoided. Hyrax in the MZNP showed no preferential selection for particular mountain slopes suggesting that the nature of the wind in the MZNP is such as not to necessitate the selection of specific slopes.

Although its area is impossible to ascertain, floorspace within a refuge may be important in determining the size of a colony. Since the microclimate within hyrax refuges, and more particularly the temperature, fluctuate only slightly diurnally this may also be an important criterion in the selection of a refuge.

SUMMARY

Habitat utilization by the hyrax was investigated with emphasis on (a) the diversity of the diet; (b) phenological changes of the vegetation; (c) quality of the diet; (d) physiological condition of hyrax, and (e) feeding habits. A description of hyrax refuges is also given.

Hyrax in the MZNP fed on at least 80 different plant species belonging to 33 plant families. Ten of these plant species and grasses (which were treated as a group), constituted _c_. 83% of the total diet.

Data on the phenological phases of the plants forming the bulk of hyrax diet, is supplied. Since the plants which constitute the major portion of hyrax' diet achieve maximum growth synchronously or asynchronously, the hyrax, by virtue of its selective mode of feeding, acquires high quality forage throughout the course of the year.

The crude protein content of stomach contents and faecal samples showed little seasonal fluctuation implying that hyrax in the MZNP were on a stable quality diet. Female hyrax had a significantly higher quality diet than males for the four month period prior to parturition and the two months during lactation. The crude protein values of faecal and stomach samples had a significant correlation ($r = 0,83$; $p < 0,001$). Since hyrax are selective feeders low faecal and stomach crude protein values reflect seasonal trends in availability and/or quality of feed. Neutral detergent fibre values showed little seasonal variation.

The body fat ratings of the different sexes showed seasonal variations related to physiological stress periods (rutting, gestation and lactation). The subjective body fat ratings correlated significantly ($r = 0,86$; $p < 0,001$) with total body fat. Mean monthly serum cholesterol concentrations showed little seasonal variation.

Data on the mode of feed ingestion in the hyrax is supplied. No distinct group feeding periods were observed and adult hyrax participated in one main feeding spell during the course of the daylight period. Casual feeding occurred intermittently and at irregular periods. Juvenile hyrax fed in the close proximity of the refuges for the first five months after birth.

Refuges used by hyrax in the MZNP are described. Temperature within these refuges showed little diurnal fluctuation.

CHAPTER VIII

BEHAVIOUR

INTRODUCTION

Behaviour can be defined in the broadest sense as the overt action taken by an organism in order to adjust to environmental circumstances so as to ensure its survival (Odum 1971). It is thus an important means by which individuals become integrated into organized and regulated societies and communities. Genetically determined behaviour patterns allow a species to utilize the environment in particular ways. They place limitations on the animal in regard to the movements it is capable of making, the information it can obtain from the environment, and the control it has over its movements in response to information concerning the environment (Solbrig & Solbrig 1979). The particular environment in which the species lives can modify or alter the expression of the behavioural characteristics of the species so that a single species may show different behavioural patterns under different environmental conditions (Delany & Happold 1979).

Since environment influences the life style of a species the purpose of this chapter is to investigate the behaviour (daylight activity patterns, social organization, social behaviour and dispersal) of hyrax and to isolate possible behavioural factors which could regulate hyrax density. A discussion of such factors influencing population dynamics is given in CHAPTER XI.

METHODS

Daylight activity patterns

The daylight activity patterns of a hyrax colony at Doornhoekdam (CHAPTER II) in the MZNP were studied in order to record five major activities, i.e. foraging, moving, within refuge, basking and sandbathing. Four marked hyrax, three females and one male were observed twice each month from sunrise to sunset (February - July 1982). Observations were made with the aid of 8 x 30 field glasses from a hide 15 m from the observation colony (OC) (Fig. 92). Five minute spot recordings (on focal individuals) were made on printed forms (APPENDIX B). The environmental parameters recorded while the observations were taking place included:

(a) Temperature within the refuges was recorded at 30 min intervals using a thermister, placed 2 m inside a hyrax hole, attached to a Grant miniature temperature recorder (W. Frankel & Co (Pty) Ltd., Johannesburg).

(b) Ambient temperature was continuously recorded on a thermohygrograph placed inside a Stevenson screen.

(c) Rainfall intensity assessed on a subjective scale from one (no rain) to five (high intensity) at 5 min intervals.

(d) Cloud cover assessed on a subjective scale from one (no cloud) to five (completely overcast) at 15 min intervals.

(e) Wind speed (km h^{-1}) and direction recorded at 15 min intervals on an anemometer calibrated for windspeeds up to 50 km h^{-1}.

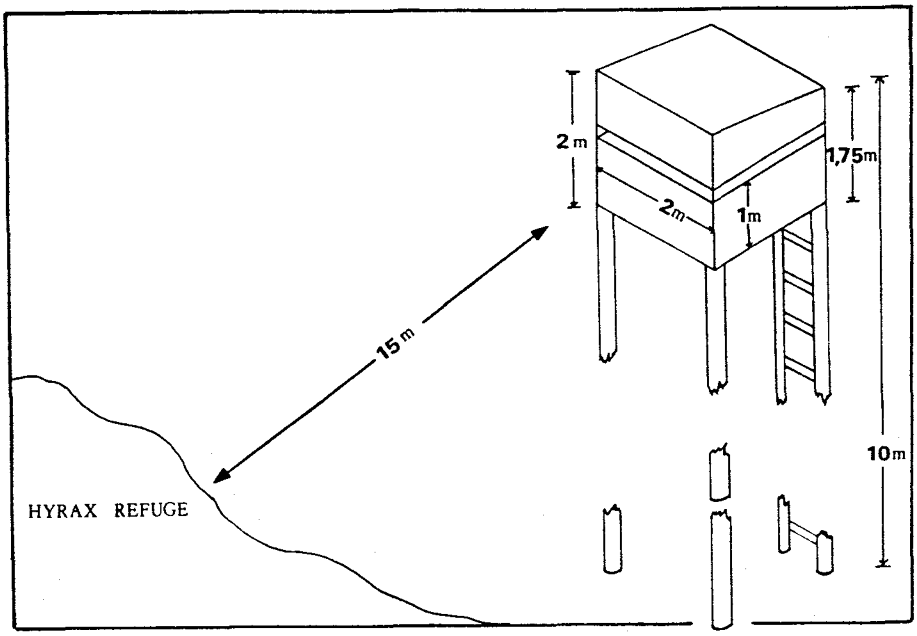


Figure 92: Diagrammatic representation of a hide used for intensive observation of a hyrax colony near Doornhoekdam in the MZNP.

Social organization

The social organization (social structure, dominance hierarchy, group size and sex ratios) of the OC was studied by direct observations over a total period of 359 h (January 1982 - May 1983). Except for four adults, all sub-adult (13 - 24 months) and adult animals (n = 24) were marked and their ages determined. Juveniles (n = 31) were not marked but were easily recognisable because of their small size.

Since hyraces may spend up to 95% of their daylight activities in an inactive state at refuges (Sale 1970b), and because of the difficulties in measuring home range shape (Hoeck, Klein & Hoeck 1982) the term core area (CA) was used. The CA was defined as an area predominantly used by a group of hyrax when not on feeding excursions.

The CA consists mainly of sleeping holes and huddling and basking places. The CA, as defined in this study, differs from that of Hoeck, Klein & Hoeck (op. cit.) who described it as that area most frequently used by an animal and in addition to the sleeping holes, huddling and basking places and middens, also included feeding areas.

In order to describe the area within the CA used predominantly by hyrax with the same social ranking the term activity area (AA) will be used. The AA of hyrax with the same social ranking is that area within the CA which includes the sleeping holes and huddling and basking places predominantly used. Observations and recordings of behaviour in the AAs of hyrax were done concommitantly with studies of activity patterns.

Social behaviour

The social behaviour of hyrax was studied with particular attention being given to (i) spacing within the group, (ii) mother, infant and juvenile relationships (iii) intraspecific aggression (iv) sexual behaviour (v) toilet behaviour and (vi) antipredator responses.

Dispersal

Emigration and immigration

In order to determine dispersal from the OC, hyrax were counted twice monthly from January 1982 - May 1983. Counting was done from the hide and commenced at sunrise and continued at 15 min intervals for a period of 3 h. This extended counting period was necessary since it was found that some hyrax may only emerge from their sleeping holes 1 - 3 h after sunrise.

Intensive field observations to locate marked hyrax were periodically conducted from January 1981 onwards. For each observation the age of the hyrax, its locality and direct distance from the OC was recorded.

Shifts of colonies

The movement of hyrax colonies (en masse) was recorded during field observations. From May 1981 - January 1982, 16 rocky outcrops known to be used as CAs were visited on a weekly basis to determine whether hyrax still occupied them. The observations were of a direct nature (visual observation) as well as of an indirect nature (examination of faecal deposits).

RESULTS

Daylight activity patterns

A total of 6 000 5 min interval spot-recordings were made. Daylight activity profiles and environmental parameters for five days during summer and six days during winter are graphically represented in Figures 93a - k.

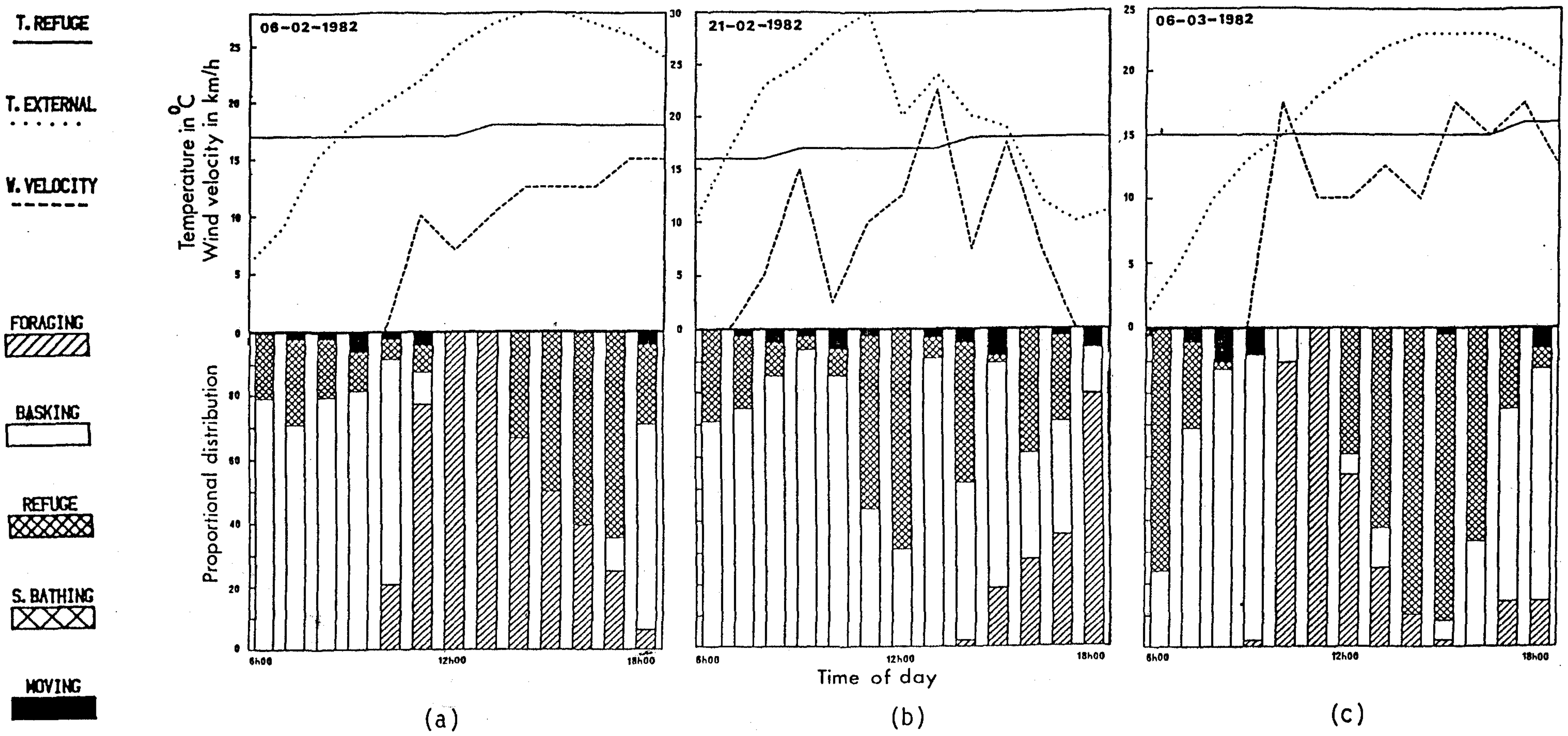


Figure 93 a - k: Proportional distribution of hyrax daylight activities and environmental parameters as recorded from sunrise to sunset during 11 days of observation.

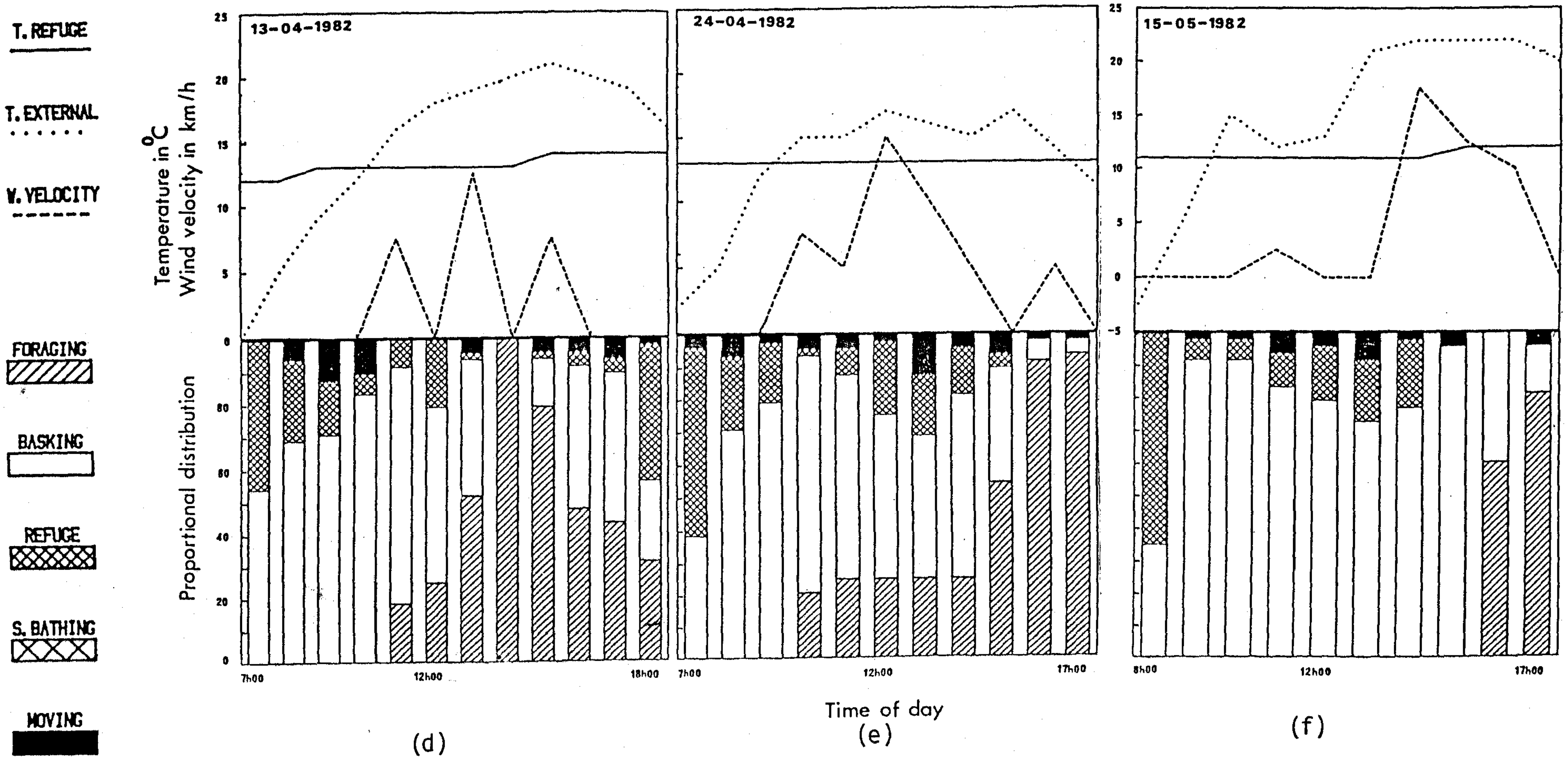
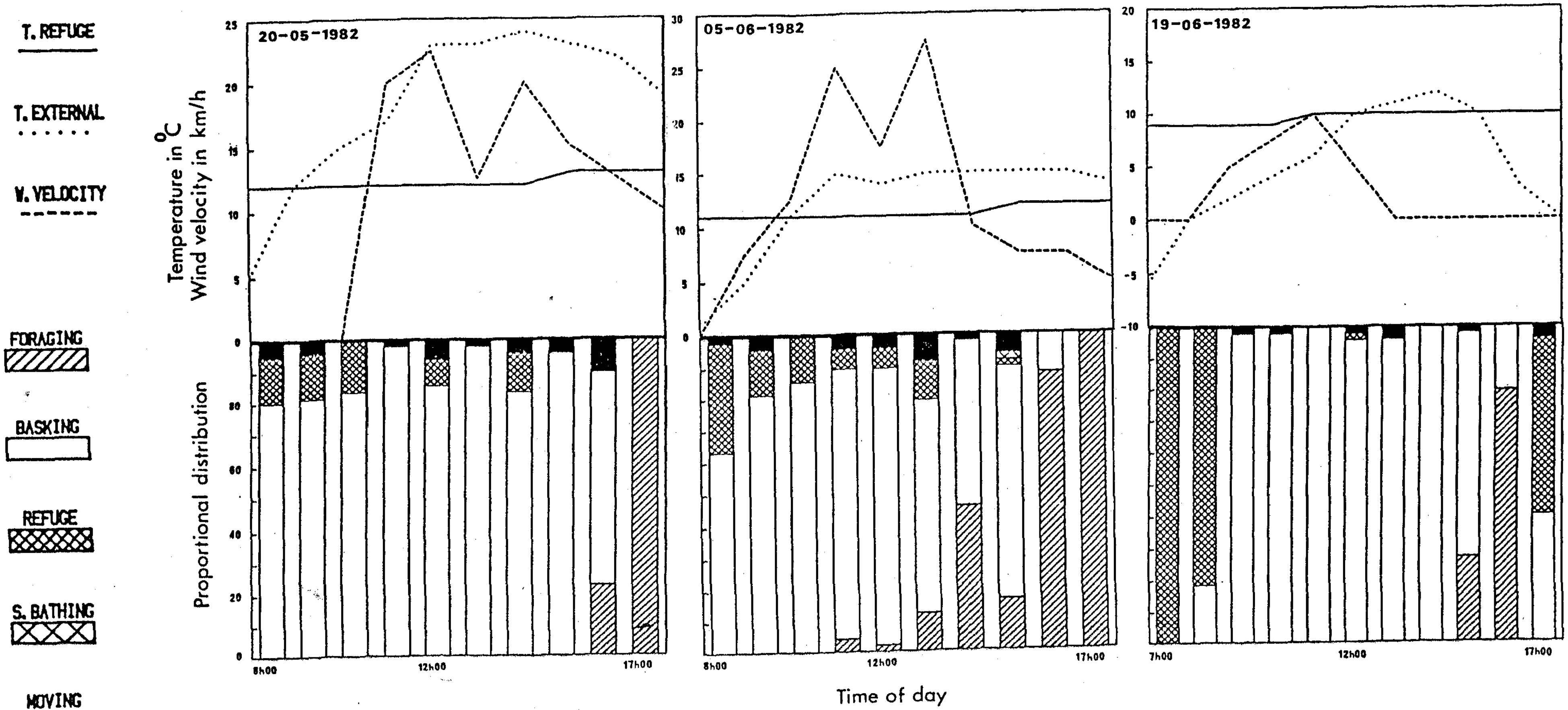
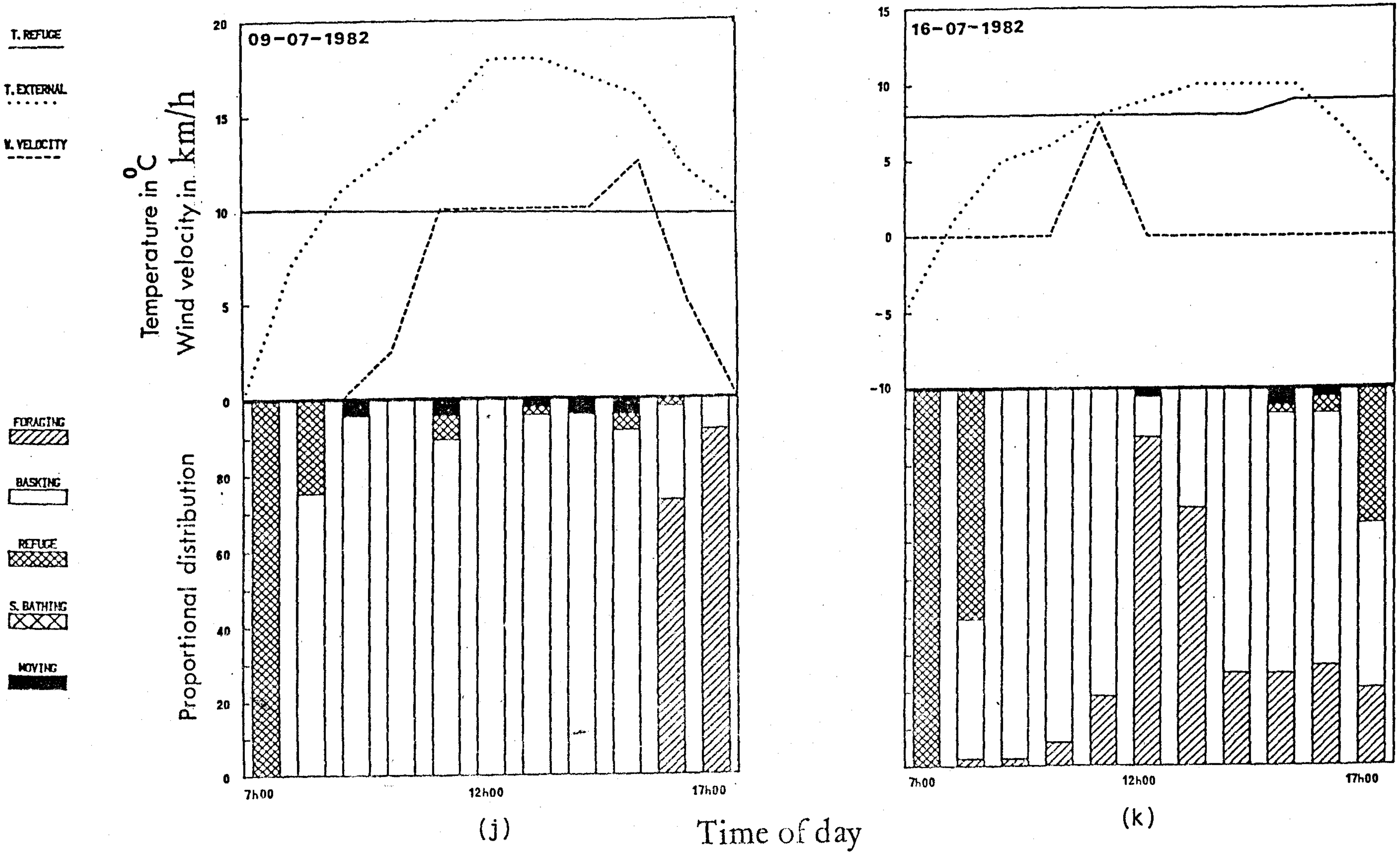


Figure 93 (cont.)



(g) (h) (i)

Figure 93 (cont.)



(j)

(k)

Figure 93 (cont.)

The effects of environmental parameters and season on behaviour have been reported in CHAPTER VII.

Basking could take place throughout the day but was concentrated in the morning during summer months, corresponding to the relatively low temperatures (Figs. 93a - e). During winter extensive basking was observed throughout the day (Figs. 93f - k) and this corresponded to ambient temperatures in the range of 0 - 25°C. No heaping (groups of tightly packed hyrax with some animals on the backs of others) or extensive huddling (more than four hyrax) (similar to heaping, but does not involve animals being raised up on the backs of others) was observed, not even during very cold winter months. Solitary animals were observed to assume four basic basking postures:

(a) Sitting position with the hind legs tucked vertically under the body and the front legs vertically erect. This posture was commonly noted when hyrax first emerged from sleeping holes and the ambient temperature was low. Pilo-erection of the fur may also be observed, giving the hyrax a rounded appearance (Fig. 94a).

(b) Twisted, lying position with the front legs facing directly forward and the front quarters upright, the hindquarters are twisted horizontally and the hind feet extend laterally to one side (Fig. 94b).

(c) Prostrate upright position with the whole belly in contact with the rock surface. The front legs face directly forwards and the hind legs either hang over the boulder edge (Fig. 94c) or extend posteriorly with the soles of the feet facing upwards.

(d) Lying position with both the front and hindlegs laterally extended on the same side (Fig. 94d). The soles of the front and hindfeet are exposed. This posture was frequently observed during high ambient temperatures when hyrax were either lying in the sun or in the shade.

With the onset of rain hyrax immediately entered their refuges. Ambient air temperatures of >25°C, accompanied by a wind of >10 km h^{-1} caused hyrax to enter refuges or bask in well-shaded areas. Refuges were also entered when an alarm call was sounded, following agonistic behaviour (animals chasing each other), play between juveniles and frequently during the late hours of the afternoon when the light was fading rapidly.

Sandbathing was seldom observed (only once during the study on activity patterns) and when it was observed accounted for only a small proportion (0,4%) of total activities (Fig. 93h).

Movement took place throughout the day and in all cases was directional, such as hyrax entering or leaving refuges, changing basking sites, at the commencement of foraging, chasing and fleeing during encounters and movement related to sexual interplay, defaecation and urination.

In order to investigate possible seasonal variations in the five major activities recorded, composite diagrams were compiled from pooled data for all activites during the summer and winter months (Figs. 95a & b).

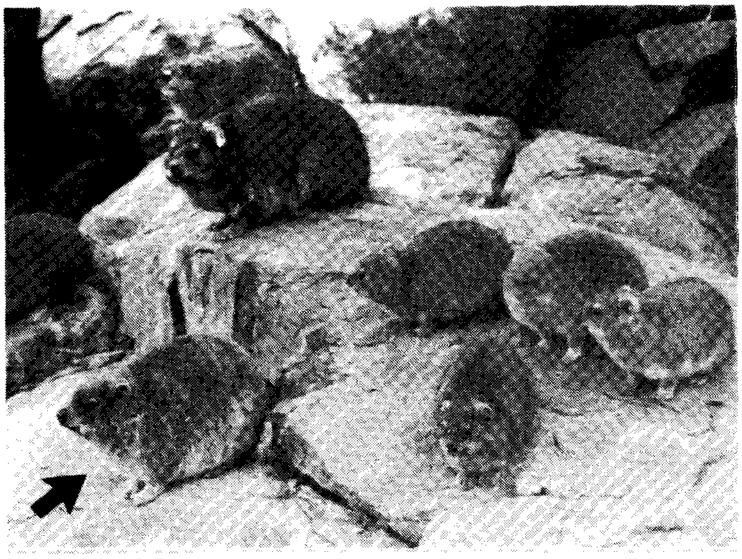


Figure 94a: Group of hyrax basking in a sitting position. Note pilo-erection of fur on the hyrax indicated by the arrow and the marked animal above it.

Figure 94b: Hyrax basking in a twisted lying position.

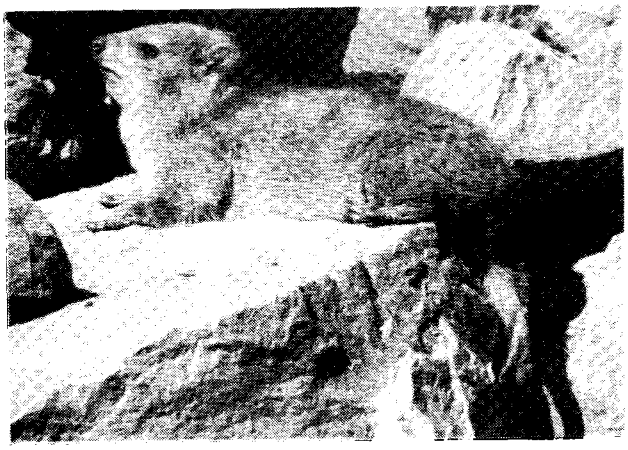
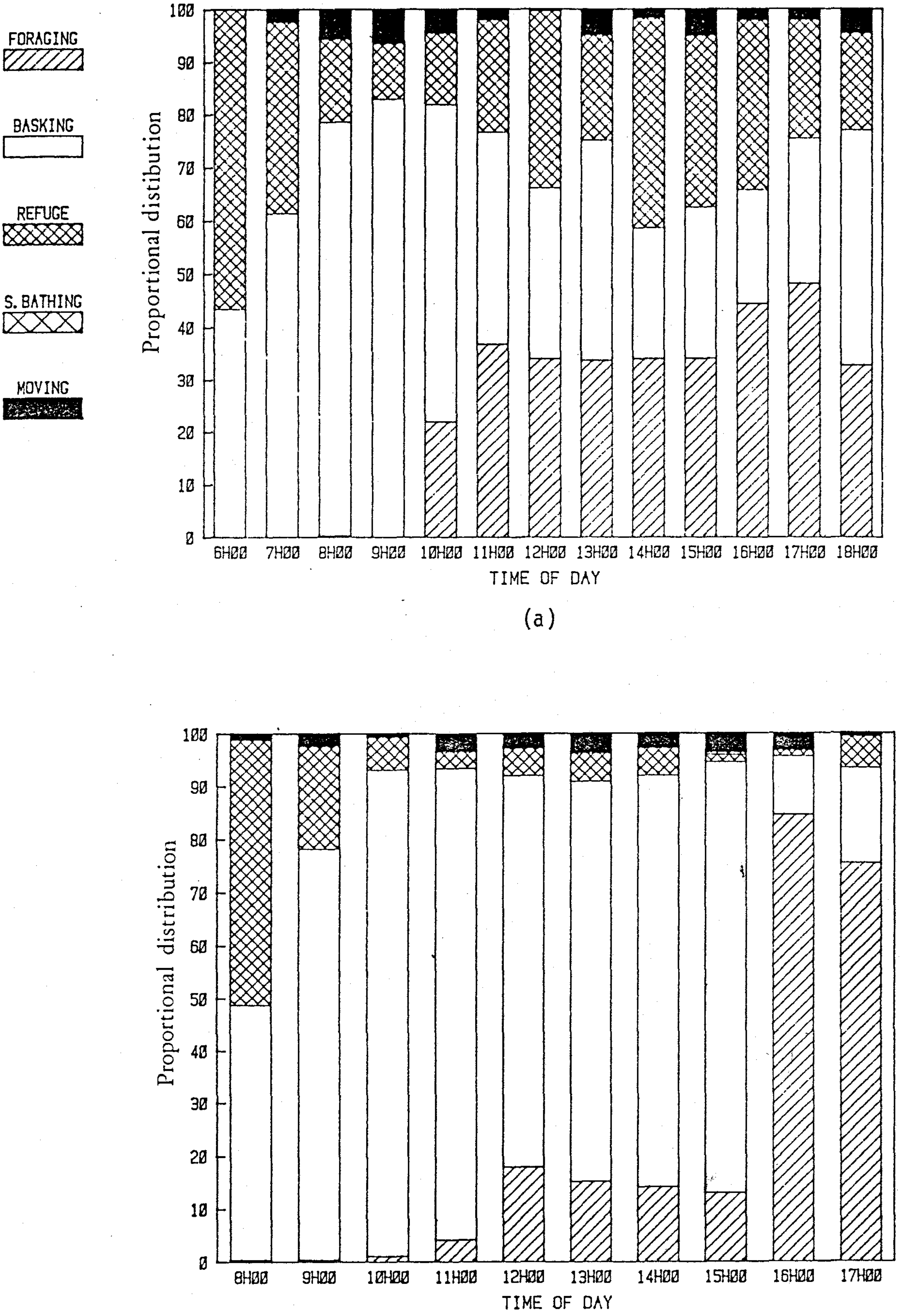


Figure 94c: Hyrax lying in a prostrate position with its belly in contact with the rock surface.

Figure 94d: Hyrax lying on its side with the soles of its feet exposed.



(a)

(b)

Figure 95 a & b: Daylight activity patterns of hyrax during summer (a) and winter (b) compiled from pooled data for summer and winter months.

The average actual time and proportion of time spent on these activities (except sandbathing) per day during the summer and winter months are summarized in Table 44.

Table 44: Average actual time (h) and proportion of time (%) spent by hyrax during summer and winter on foraging, basking, within refuge and moving.

	Foraging time (h)	%	Basking time (h)	%	Within refuge time (h)	%	Moving time (h)	%
Summer*	3,20	24,65	5,86	45,04	3,40	26,16	0,54	4,15
Winter**	2,27	22,67	6,61	66,15	0,91	9,12	0,21	2,06

*13h mean daylight
**10h mean daylight

Foraging times expressed as a percentage of total activities during summer and winter are similar. Basking during winter comprised 66% of total activities as compared with 45% in summer. More time (3,4 h) was spent within the refuge during the summer than during the winter (0,91 h). The time spent moving was greater during the summer than during the winter (Table 44).

When ranked in order of time expenditure, basking was the most time-consuming activity during summer, followed by time spent within refuges, foraging and moving. During winter the most time-consuming activity was basking, followed by foraging, time spent within refuges and moving (Table 44).

Social organization

Social structure and dominance hierarchy

The basic structure of hyrax social organization is the multi-female kinship group (MFKG) which is matrilocal. The polygynous group (colony) consists of a dominant territorial male, adult females, sub-adults and juveniles of both sexes. A peripheral male, although not part of the colony may be attached to it. Five social rankings, each differing in their patterns of interaction, spatial dispersion within the CA and roles in reproduction, were distinguished.

(a) Juvenile (J) hyrax are between 0 and 12 months of age. They are physically immature and reproductively inactive. They have a large AA which overlaps that of the peripheral male (Fig. 96).

(b) Sub-adult (SA) hyrax are between 13 and 24 months old. Males and females are sexually mature at 15 - 17 months of age. SA ♂♂ are not allowed to mate with females of the same colony. The AA of SA hyrax is similar to that of the J's (Fig. 96).

(c) Adult females (AD ♀♀) are older than 24 months and are actively monopolized by the territorial male. Their AA (Fig. 96) is smaller than that of the SA and J hyrax.

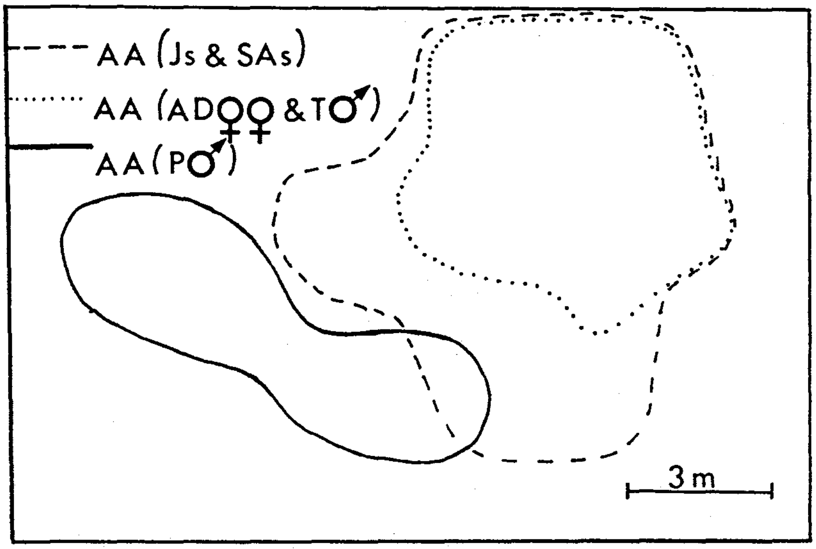
(d) Dominant territorial males (T ♂♂) attached to colonies. The AA of the T ♂ is equivalent to that of AD ♀♀ (Fig. 96), and all other AD ♂♂ are excluded from this area. The T ♂ actively monopolized AD ♀♀, preventing SA ♂♂ from mating with females from the same colony and also preventing the peripheral male from mating with SA or AD ♀♀ attached to the colony.

(e) Peripheral males (P ♂♂) occupy areas on the periphery of the AAs of AD ♀♀ and the T ♂. They live alone on rocky outcrops or are transients moving between colonies. No evidence was found of the formation of bachelor groups. The P ♂ living next 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 P ♂ is characterised by his submissive behaviour when confronted by the T ♂, while in the absence of the T ♂ he monopolizes the SA ♀♀.

The P ♂ can enlarge his AA as was observed during December 1982. In the absence of the T ♂ the P ♂ dragged his erect penis, which curved downwards, on the ground and urinated at four different places outside his AA (Fig. 97). Two of the urinating sites overlapped the AA of the AD ♀♀ and the T ♂. The P ♂ did not defend his AA.

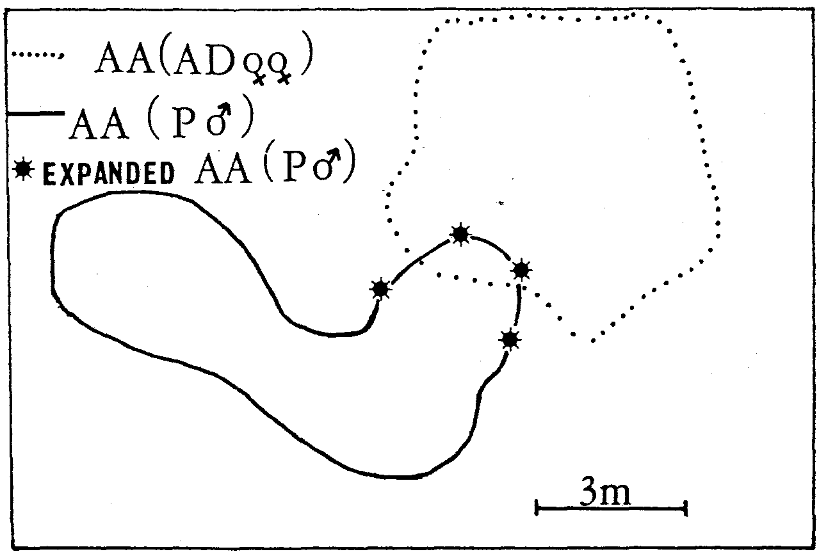
The ages of P ♂♂ were determined by selective shooting of six isolated individuals. Their mean age was 42,7 months with a range of 17 - 61 months. The age of the only T ♂ captured was 47 months.

The dominance ranking for males was linear and age based, i.e. T > P > SA > J. Specific incidences illustrating the sequence of the ranking will be discussed in later sections (intraspecific aggresive and sexual behaviour). Dominance ranking for females was not evident because of the low level of aggressive interaction between them. However, because of the guard funcion of the oldest AD ♀♀ of the group, they might be considered the dominant females.



AA - activity area
SA - sub-adult
AD - adult
J - juvenile
T - territorial
P - peripheral

Figure 96: Activity areas of hyrax belonging to different social rankings at the observation colony at Doornhoekdam in the MZNP.



AA - activity area
P - peripheral
AD - adult

Figure 97: Expanded activity area of the peripheral male accompanied by urination at four distinct places (marked by asterisks in the diagram).

Group size and sex ratios

The group composition of hyrax captured, aged, marked and released at three localities is given in Table 45.

Table 45: Locality, group size, social ranking and age (months) of hyrax at OC (April 1982) WOC* (September 1982) and LOC** (September 1982).

OC			WOC			LOC		
Social ranking	n	age	Social ranking	n	age	Social ranking	n	age
J	31	3 - 4	J ♂	1	10 - 11	J ♀♀	3	10 - 11
SA ♂♂	6	15 - 16	J ♀♀	3	10 - 11	J ♂	1	10 - 11
SA ♀♀	7	15 - 16	SA ♀	1	22 - 23			
AD ♀♀	3	27 - 28	AD ♀	1	46 - 47			
AD ♀♀	2	40 - 41	AD ♀	1	118 - 119			
AD ♀♀	1	52 - 53	T ♂	1	46 - 47			
AD ♀♀	1	64 - 65						
AD ♀♀	1	76 - 77						
AD ♀♀	2	?						
T ♂	1	?						
P ♂	1	?						
Total	56			8			4	

*WOC - hyrax colony situated c. 300 m west of the observation colony; **LOC - hyrax colony next to the field research laboratory; J - juvenile; SA - sub-adult; AD - adult; T - territorial; P - perripheral

The MFKG (polygynous group) at OC consisted of 55 hyrax (excluding the P ♂). No attempt was made to capture J hyrax at this locality during 1982 because of the disruption inherent in capture. The sex ratios of the Js were taken to be equal throughout the year. This assumption was based on the fact that the foetal sex ratio was equal (CHAPTER VI) and the sex ratio (1,0 ♂ : 1,2 ♀) of the 35 J hyrax captured during 1980 - 1981 (August - December) at the OC did not differ significantly (P > 0,1; Chi-Square test) from parity. The male to female sex ratio for all hyrax present in the MFKG at the OC during January 1982 was 1,0 ♂ : 1,4 ♀ while at the beginning of November 1982 it was 1,0 ♂ : 2,4 ♀.

The sex ratio for hyrax at WOC and LOC during September 1982 was 1,0 ♂ : 3,0 ♀. At LOC the four J hyrax apparently stayed on their own and no AD hyrax were seen at the site.

Social behaviour

Spacing within the group

Early morning observations (n = 23) indicated that the same animals constantly appear first from the same refuge hole when emerging (Fig. 98). Once out hyrax will move within their AAs. However, there is a tendency for J and SA hyrax to occupy the peripheral areas of their AA throughout the day.

Mother/infant relationships and juvenile behaviour

Circumstancial evidence suggests that young of c. 1 month of age do not share sleeping holes with their mothers. This was deduced from the fact that in the mornings young emerged from different holes and at different times than the mothers. When AD ♀♀ emerged the young hyrax moved towards them and suckling was commenced in earnest.

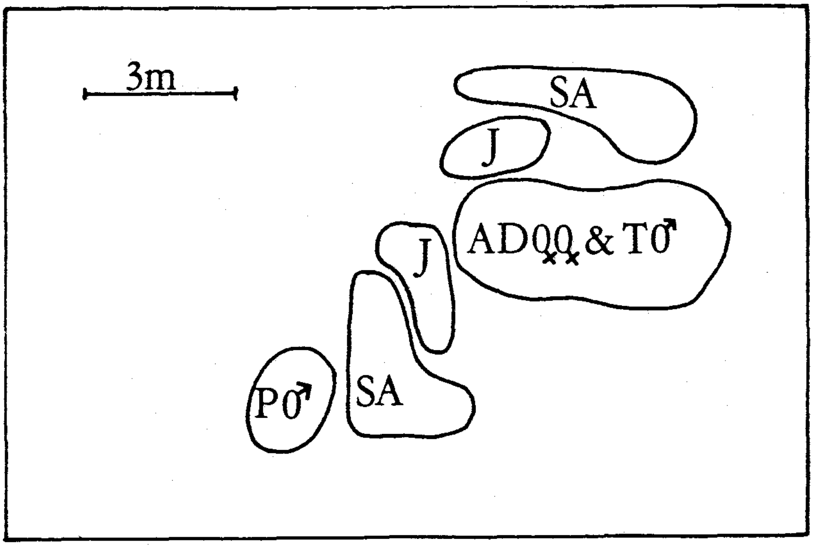


Figure 98: The spacing of hyrax of different social rankings within activity areas.

SA - sub-adults
AD - adults
P - peripheral
J - juveniles
T - territorial

Although difficult to confirm it appeared as if young were sometimes suckled by various non-maternal lactating females. Young often climb on their mother's backs (Fig. 99) or bask with them. Young sometimes followed AD ♀♀ for short distances when the latter went on foraging excursions. When threatened the mother came to her young's assistance.

Juveniles (c. 5 months old) tended to congregate and form nursery groups (Fig. 100). During basking Js were also sometimes in close bodily contact (Fig. 101). Social play amongst Js was often observed and consisted mainly of mock mating and the chasing of one another in and out of holes and crevices. Play often resulted in true aggresive behaviour.

Intraspecific aggressive behaviour

Aggressive behaviour consisted mainly of threatening behaviour (growling and flaring of dorsal gland hairs), chasing and in a few instances actual biting. Except for light skirmishes during playing and feeding, the majority of aggressive actions were observed during the mating season between contesting males (the T ♂ and P ♂, the T ♂ and SA ♂♂ and the P ♂ and SA ♂♂). Some examples of these aggressive actions were:

(a) December 1982. The P ♂ uttered calls (repetitious barks) upon which the T ♂ chased the P ♂ out of the CA. This happened on two occasions during the month.
(b) April 1982. A P ♂ followed a SA ♀♀ into her AA. The T ♂ chased him away.
(c) December 1982. During the enlargement of his activity area the P ♂ attempted, on three occasions, to bite Js and on one occasion attempted to bite a SA ♂.
(d) March 1983. On investigating (anogenital sniffing) a SA ♀ , a SA ♂ was chased into a hole by the T ♂.
(e) April 1982. The resident T ♂ disappeared and was replaced by the P ♂. During the same month in 1983 the then T ♂ also disappeared and was replaced by the P ♂.

Incidences of intraspecific aggressive behaviour were observed when animals were feeding, for example when two hyrax attempted to eat the same piece of food. This resulted in the pilo-erection of hair around the dorsal gland (Fig. 102) of both animals, was accompanied by vocalization (growling and snarling) and often resulted in a chase or a bite. Submissive gestures were characterized by backing away. The body of the submissive hyrax being slightly curved with the head directed towards the aggressor.

From the shot sample it was evident that bites piercing the skin (Fig. 103) were common and generally inflicted on the ears, neck, shoulders and rump. Of the 16 shot hyrax with severe fresh bite wounds 14 were AD ♂♂. Twelve of these 14 AD ♂♂ were less than 49 months old ($\bar{x}$ = 32,8 months, range 25 - 49 months). The remaining two males were 80 and 130 months old respectively. The bites were all recorded on hyrax shot from November - May.

Sexual behaviour

Three groups of males with different social rankings were observed to copulate or attempt to copulate with females in oestrus:

a) T ♂

During the peak of the mating season (April) the T ♂ was very active and moved about almost continuously sniffing fresh urine deposits (Fig. 104). He also moved through the colony in search of receptive females. Of the 19 copulations observed that were performed by the T ♂, 17 were with AD ♀♀ and only two with SA ♀♀. In general the T ♂ showed a lack of interest in SA ♀♀.

Figure 99: Juvenile hyrax sitting on the back of an adult female.

Figure 100: A nursery group of juvenile hyrax.

Figure 101: Two juvenile hyrax resting while in close bodily contact.

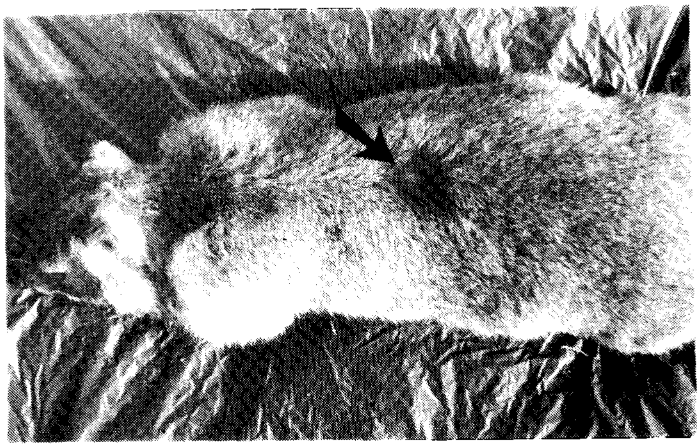


Figure 102: The dorsal gland situated dorsally (indicated by the arrow).

Receptive females were observed to approach the T ♂. When this took place the approach was always made cautiously with the hair around the dorsal gland pilo-erected. The female would sniff the anogenital regions of the T ♂ after which she would turn around and present her hind-quarters to the male (Fig. 105). The T ♂ responded by sniffing the anogenital region of the female before mounting. When mounting, the male grasped the female just behind her ribcage with his forelegs (Fig. 106). Copulation took 4 - 8 s and ended abruptly with the female running away or in agonistic behaviour with the female grunting and biting the male. On one occasion three AD ♀♀ converged on the T ♂ and presented their hindquarters to him.

b) P ♂♂

During the peak of the mating season an unknown P ♂ was observed on a rocky outcrop 20 m from the observation colony. He periodically uttered calls and took part in mating. Of the 12 copulations observed by P ♂♂ in general 11 were with SA ♀♀ and only one with an AD ♀. Generally the AD ♀♀ showed little interest in the P ♂♂. The P ♂♂ often followed the SA ♀♀ when the latter went on foraging excursions and many copulations may indeed have taken place at feeding sites.

An attempt by a P ♂ to follow a SA ♀ into her AA caused the T ♂ to charge and chase away the P ♂. In the absence of the T ♂, however, the P ♂ uttered rutting calls and made wailing sounds (the T ♂ infrequently uttered rutting calls but never wailing sounds). On one occasion two SA ♀♀ responded to the calls and moved towards the P ♂ and this resulted in copulation with one of them. In the presence of

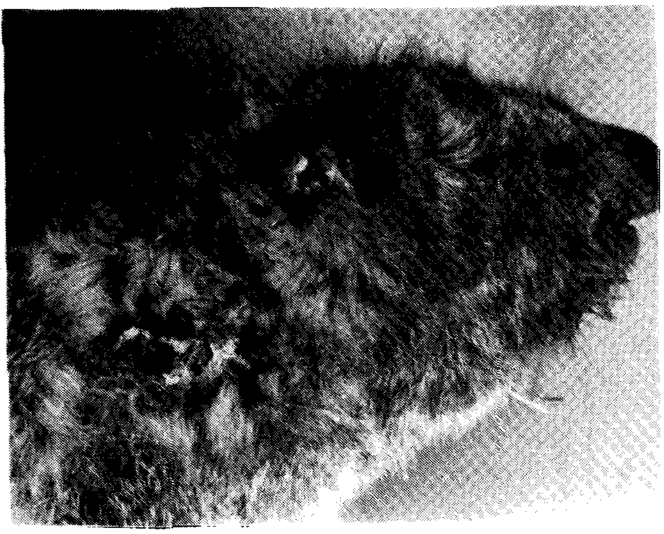


Figure 103: Male hyrax (36 months old) with bite wounds on neck and shoulder.

Figure 104: The territorial male sniffing freshly deposited urine.

Figure 105: Adult female hyrax presenting her hindquarters to the territorial male.

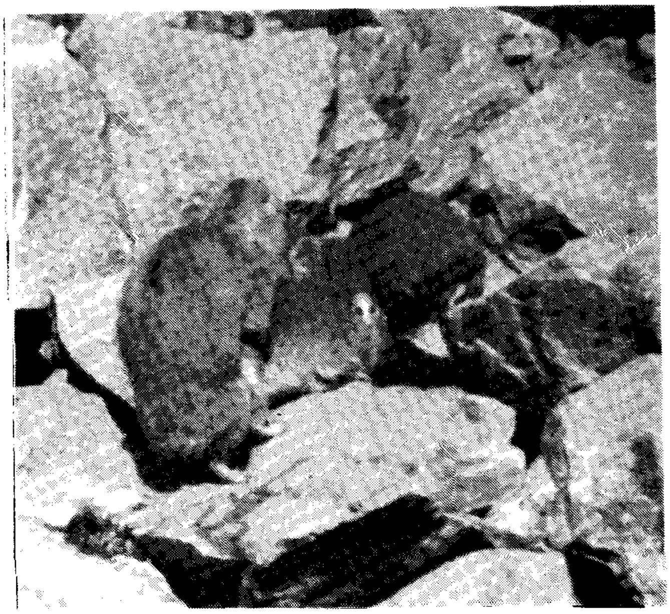


Figure 106: The territorial male copulating with an adult female.

the T ♂ copulation by the P ♂ with SA ♀♀ was prevented and in one such instance the P ♂ was chased away by the T ♂. A SA ♀, however, followed the P ♂ and copulation took place some distance from the refuge site. The T ♂ acted in a threatening manner towards this SA ♀ when she returned.

c) SA ♂♂

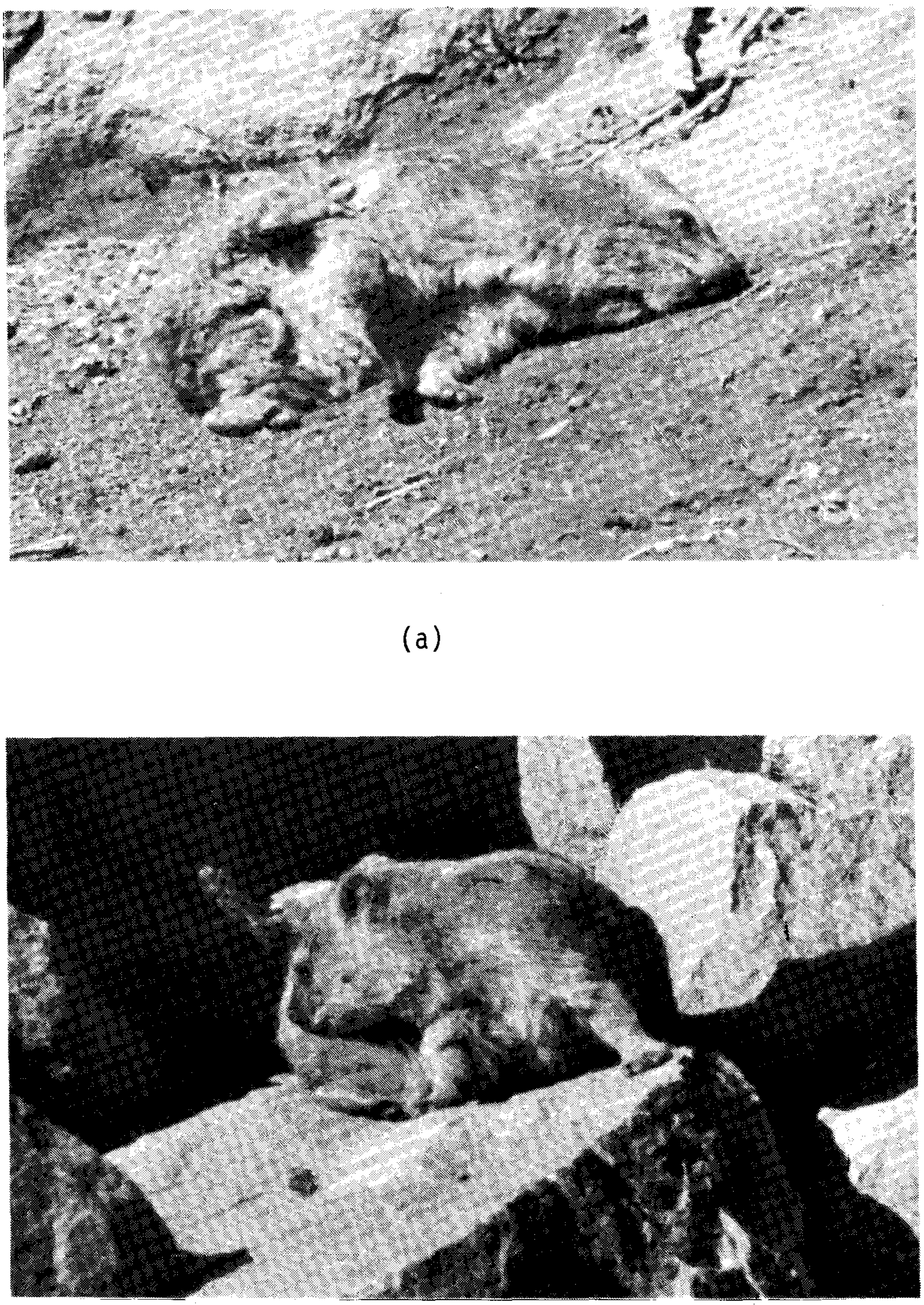
Only two attempted copulations were recorded between SA ♂♂ and SA ♀♀. In both instances the T ♂ intervened and chased the SA ♂♂ into their refuge holes.

Grooming and defaecation

Hyrax possess two anatomical adaptations for grooming. The first of these is a curved claw on the inner toe of the hind foot. This is used for scratching (Fig. 107a). In addition the two pairs of lower incisors are used to comb the fur, bite or dislodge parasites (Fig. 107b). No social grooming was observed.

Throughout the course of this study sandbathing was only observed on five occasions during daylight, even though sites used for this purpose were common around hyrax refuges. When sandbathing hyrax lie on their sides and back, and make rapid wriggling movements. These movements were performed with intervening periods for rest but did not last longer than 10 min in all.

No communal middens for urination or defaecation were evident; hyrax



(a)

(b)

Figure 107 a & b: Hyrax engaged in grooming using the curved claw on the hind foot for scratching (a) and lower incisors for combing the fur or attempting to dislodge parasites (b).

were observed to perform these activities on the edge of boulders on which they were basking. As there were certain rocks favoured as sitting places faeces accumulated to some depth at the base of these, thus giving the appearance of a midden.

Antipredator responses

When out of their holes hyrax are constantly alert. The guarding function of one of the oldest AD ♀♀, which very often selected the highest vantage point, was clearly evident. When a possible predator approached she would utter a short-pitched squeak which allerted the rest of the group, and, depending on the intensity of the squeak, would cause hyrax to flee into their refuges. While indulging in casual feeding around the refuge sites, all alarm calls caused animals to flee towards the refuges. When hyrax browsed in trees and were surprised, they either jumped out of the tree and ran towards refuges, or sat still to evade detection.

The presence of a black eagle in the sky resulted in the cessation of all activities and all adult hyrax watched the eagle in flight. Normal activities only resumed when the eagle disappeared.

Freezing (sitting motionless) was also observed. This occurred when one of the group gave an alarm call which was not of sufficient intensity to make hyrax flee into their shelters. During "freezing" they would stare intently into the bush for several minutes before resuming normal activities.

The sudden appearance of a troop of baboons at the observation colony caused hyrax to take refuge very rapidly. The short-pitched squeak emitted by the first animal which saw the baboons was repeated by some other members of the group, and this reinforced the signal. When a vervet monkey suddenly appeared at the observation colony, the oldest AD ♀ charged at it whilst uttering highpitched barking noises. This caused the monkey to run away. The rest of the group, except for two AD ♀♀, entered their refuges when the monkey arrived.

In one incident a Cape grey mongoose, living near the refuges, elicited inquisitive behaviour from SA and J hyrax. Their necks were outstretched and they stared intently at the intruder. However, a SA ♂ with pilo-erected dorsal gland hairs moved towards the mongoose and chased it away.

In addition to the guard function sometimes performed by the oldest AD ♀♀, the P ♂ by virtue of its position on the periphery of AAs, acted as a guard and the colony members reacted to the alarm calls uttered by the P ♂.

Dispersal

Emigration and immigration

The change in the percentage of various age groups present in the OC from the beginning of January 1982 to the end of December 1982 are graphically illustrated in Figure 108a - c. Only 29% of the original

J hyrax were still present at the end of the year. Although J members started to decline from April onwards, a progressive decline took place from September when the Js were c. 10 months of age. Field observations during this month also revealed J hyrax at rocky outcrops which were usually uninhabited.

The dispersal of SA hyrax differed according to sex. SA ♂♂ emigrated from the colonies just before and during the mating season. During September, at the age of 22 months, the last SA ♂ present disappeared. SA ♀♀ numbers stayed fairly constant during the mating season but showed marked changes after May and only 25% were present towards the end of the year.

The T ♂ was displaced by a P ♂ during April, the vacant space left by the P ♂ was filled during the same month by another P ♂ so that the total numbers of AD ♂♂ stayed the same throughout the year. The AD ♀♀ numbers declined from June - September. During October the only incidence of immigration was recorded when two AD ♀♀ joined the colony. After one year the AD ♀♀ present constituted 75% of the original number.

Of the 35 hyrax marked as Js at the OC 10 were later seen during field observations. A single AD ♀ which had emigrated was also observed. The distance which hyrax had dispersed, the localities at which they were observed and their ages are summarized in Fig. 109. Dispersal distances ranged from 250 - 500 m. Male hyrax were seen singly or in the proximity of other groups whereas the females were seen within

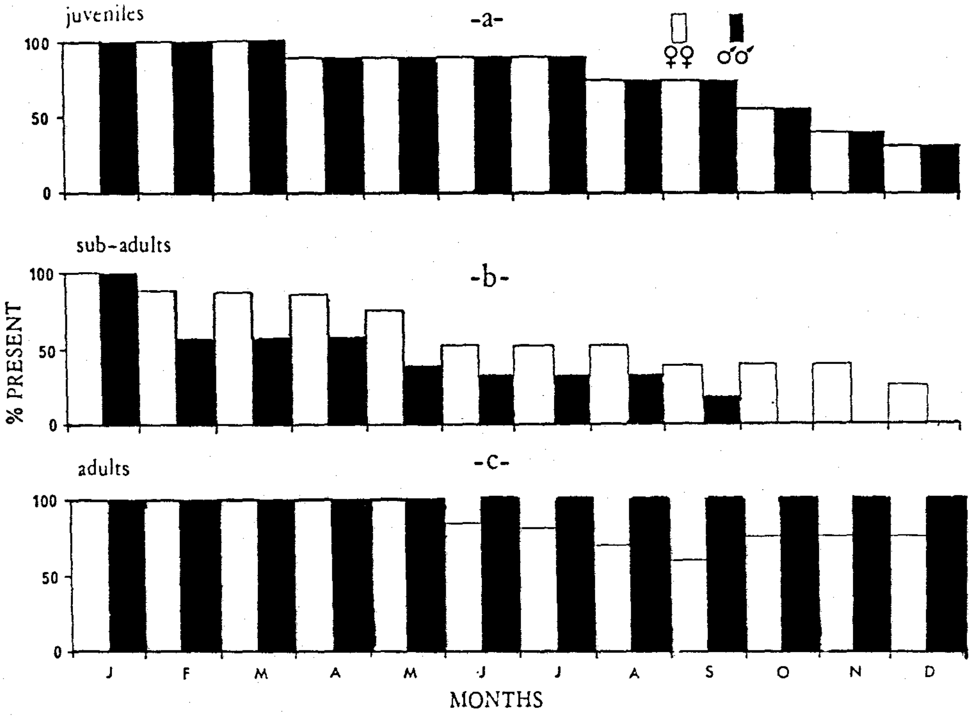
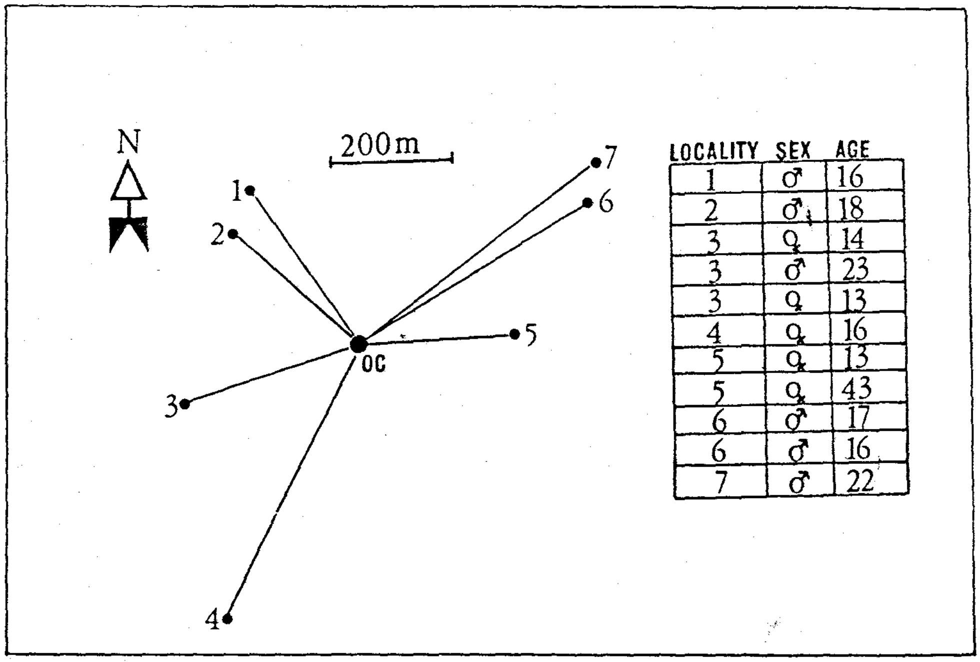


Figure 108 a - c: Changes in the percentage of juveniles, sub-adults and adult hyrax present during the period January - December 1982 at the observation colony at Doornhoekdam.



LOCALITY	SEX	AGE
1	♂	16
2	♂	18
3	♀	14
3	♂	23
3	♀	13
4	♀	16
5	♀	13
5	♀	43
6	♂	17
6	♂	16
7	♂	22

Figure 109: Direction and distance moved from the observation colony at Doornhoekdam by dispersing hyrax of different ages (in months) and sexes.

other groups.

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 2 - 6 weeks. Additional field observations have, however, shown that certain known hyrax refuges may be vacant for more extended periods (3 - 6 months). The groups of hyrax at the OC, WOC and LOC remained stationary throughout the course of the study.

DISCUSSION

Daylight activity patterns

The published data on daylight activity patterns of hyraces is based mainly on casual observations (Turner & Watson 1965; Fourie 1974; Steyn 1980) and except for data on feeding (Sale 1965a; Hoeck 1975) little quantitive information is available.

If it is assumed that hyrax are inactive within their refuges, this means that 84 - 90% (20 - 22 h) of each day is spent in an inactive state during the summer and winter months respectively. Since these figures do not include resting (basking) during foraging excursions, hyrax may well spend in excess of 90% in inactivity.

This inactivity and that of behavioural thermoregulation of hyraces prompted research on the energy metabolism (Rübsamen et al. 1979; Leon 1981) and thermoregulation of these animals (Taylor & Sale 1969; Fairall & McNairn 1980; McNairn 1982). Although the results reported in the literature are still very contradictory, particularly those on P. capensis (Louw et al. 1972; Fairall & McNairn 1980; Leon 1981; McNairn 1982) it nevertheless seems that hyraces are good physiological thermoregulators (Taylor & Sale 1969; Leon 1981). In addition the exploitation of solar radiation while basking, augments the body temperature during the day (Fairall & McNairn 1980; McNairn 1982). Shuttling between the sun and the shade and by adopting various basking postures keep this temperature stable (Leon 1981).

The behavioural pattern of resting hyrax is greatly influenced by prevailing climatic conditions. Although Sale (1970b) mentions extensive heaping by hyraces in Kenya this was not observed for P. capensis in the present study, or by Fourie (1974) despite the fact that temperatures are more extreme in South Africa. Absence of heaping during cold periods may thus indicate a possible lower conductance of the pelt of P. capensis in southern Africa when compared with that of hyraces in the tropics. The huddling observed, although not common, maximizes contact between several individuals, minimizes surface area and aids retention of body heat within the group. Huddling can possibly also occur within refuges (Sale 1970b). Leon (1981) has shown experimentally that the temperature within a metabolic chamber occupied by three animals, increased 2°C above that recorded when it was occupied by a single hyrax. This conferred an energy saving of 10% on the huddled animals.

Solitary basking during which pilo-erection occurred and the assumption of a rounded body posture was assumed, was frequently observed on cold mornings. Pilo-erection has the effect of reducing thermal conduction and enhancing insulation (Moen 1973). At ambient temperatures below thermoneutrality, basking has the effect of raising the peripheral body temperature and reducing the temperature gradient between core and periphery. This in turn would minimize metabolic heat loss to the environment and avoid an increase in heat production (Leon 1981). At high temperatures, in addition to moving into the shade or entering refuges, basking postures are adopted whereby the plantar surfaces of the feet are exposed to the air. Since sweat glands are present only on the soles of the feet (Sale 1965a) the latter play an important role in peripheral cooling (Bartholomew & Rainy 1971). In this respect it has been shown that at low ambient temperatures the temperature of the feet of _P. capensis_ is _c_. 11°C lower than their rectal temperatures (Leon 1981).

Fairall & McNairn (1980) have shown that _P. capensis_ can accurately regulate its body temperature (36,6 - 38,6°C) at different ambient temperatures (10 - 26°C). They suggest that the labile body temperature (not confirmed by Leon 1981) is in fact an energy saving strategy evolved by the hyrax. At low ambient temperatures the hyrax increases the insulating capacity of its pelt. A further reduction in ambient temperatures results in a drop in body temperature thus decreasing conduction even more. Since a lowering of body temperature may cause the animal to become inactive, which would be detrimental to its survival, body temperature may be increased by absorbing radient heat. Leon (1981) has shown that 11,7 kJ are required to increase the body temperature of a 2,94 kg hyrax by 1°C. This is equivalent to 0,171 ml O_2 per g of animal and is *c*. 63% of the heat produced in 1 h at the lowest metabolic rate of *P. capensis*.

Rain also affects the activity of hyraces by making them seek shelter. This phenomenon has also been reported by Mendelssohn (1965) and Steyn (1980).

Strong winds caused hyrax to enter refuges or shelter in protected sites, a behavioural response most probably related to the effect of wind on the conductance of the animal. Sleeping holes facing the prevailing wind are avoided (Sale 1965a), although this was not observed in the present study. Reduction in activity by hyrax during strong winds has also been reported by Fourie (1972) and Steyn (1980).

In this study, seasonal differences in the time spent in basking, movement and within refuges is a direct consequence of the prevailing climatic conditions. Colder atmospheric temperatures during the winter months caused more frequent basking, whereas during the hot summer months the greater amount of movement observed and the increased time spent within refuges can be attributed to the habit of hyraces of selecting their thermal environment. Evidence in support of the contention by Taylor & Sale (1969) that hyraces select their thermal environment so that they neither have to increase metabolism to keep warm or increase evaporation to keep cool, is supplied by the fact that in the present study hyrax spent twice as much time moving in summer as they did in winter. Not only is this an energy saving strategy (Fairall & McNairn 1980) but may also be an important water saving strategy by virtue of the reduction in evaporative water loss (Rübsamen & Kettembeil 1980). Although the low basal metabolic rate and behavioural thermoregulation (Rübsamen et al. 1982) are considered to be related to the phylogeny of the hyrax as a member of the Paenungulata, rather than its ecology, they most certainly can be considered as major attributes towards the survival success of the hyrax. Particularly when one considers that hyraces do occur in certain inhospitable semi-arid regions.

Social organization

With the exception of a detailed study on Heterohyrax brucei and Procavia johnstoni in Tanzania by Hoeck et al. (1982) little information is available on the social organization of hyraces. Most other observations have been made on captive animals (Sale 1965a; Fourie 1974) or during field studies of short duration (Meltzer 1967; Turner & Watson 1965; Steyn 1980).

Social structure

The findings of this study are consistent with those of Hoeck et al. (1982) in that the basic social unit is a cohesive and stable polygynous group. This consists of a T ♂ and several AD ♀♀ as well as SAs and Js of both sexes. There may be one or more P ♂♂ associated with the polygynous groups. These also have their own linear social ranking (Hoeck et al. 1982). The P ♂ with the highest social ranking may frequently displace the T ♂. The formation of polygynous groups is also found in similar sized animals, for example marmots (Armitage & Downhower 1974; Barash 1974) and is also common amongst ungulates (Owen-Smith 1977). In the hyrax (and in other less sociable species such as the white rhinoceros (Owen-Smith 1975)) the non-territorial males do not, however, congregate to form bachelor groups.

The observation that hyrax of different social rankings predominantly use specific areas and that there is little overlap between the area used by the P ♂ and the T ♂ has been confirmed by Hoeck et al. (1982). The T ♂ actively defends his AA and that of the AD ♀♀. Although not observed the T ♂ may mark his territory in a way similar to that demonstrated by the P ♂. The latter expanded his AA through urine markings. Scent marking with urine and faeces is common amongst ungulates (Grau 1976; Ebling & Stoddart 1978) and is frequently associated with dominance and aggression. The two distinct uses of odours in a territory are the demarcation of the range boundary and self-reassurance of the occupier within his own domain (Stoddart 1978). With a rise in social dominance in most mammals, scent production and marking behaviour are increased (Stoddart op. cit.) as well as the quality of glandular exudates for both male and females (Goodrich & Mykytowycz 1972). Investigation of the qualitative aspects of these glandular exudates of hyrax with different social rankings could reveal interesting results. A study on this aspect of hyrax biology should be conducted.

Home ranges of different MFKGs (polygynous groups) are not actively defended (Hoeck et al. 1982). The small territory (which is actively defended by the T ♂) is a result of the gregarious nature and extremely inactive lifestyle of the hyrax.

Although the ages of T ♂♂ were not established in the present study, mass has been shown to be a major factor in winning combats (Hoeck et al. 1982). Since males only reach their asymptotic mass at approximately seven years of age (CHAPTER IV) it is suggested that T ♂♂ are usually older animals. It has been established that P ♂♂ are generally younger animals.

Dominance hierarchies proposed for the males in this study are consistent with the results obtained by Hoeck et al. (1982). They also suggested that the oldest AD ♀ may head the dominance ranking amongst the females.

Group size and sex ratios

Sale (1965a) studied P. habessinica and Heterohyrax syriacus in Kenya and concluded that group size (polygynous groups) depended very much on habitat but could rise to 20 animals. Colonies (a clan?) with more than one polygynous group generally contained a smaller number of hyrax per group, usually not in excess of 12 animals. Provided the SA ♀♀ in the present study are included, the results of this study and that by Hoeck et al. (1982) have shown that a T ♂ can monopolize 3 - 17 females. Since refuges at the OC consisted of boulder scree with ample crevices and holes for cover, 17 females is probably the optimum number a T ♂ can monopolize successfully and energetically. However, lack of sufficient refuges can be the primary factor limiting group size.

Verner (1977) proposed that natural selection favours individuals that are capable of defending territories larger than necessary (super-territories), thus resulting in increased male fitness by giving them access to additional females. Since in a polygynous mating system female choice is based on genetic quality (Solbrig & Solbrig 1979), female fitness will therefore also be greater when sharing a male capable of defending a high quality territory. It has been shown that a yellow-bellied marmot (Marmota flaviventris) T ♂ is maximally fit when he maintains a harem of two or three females. Female marmot in large harems, however, produced young less frequently than females in small harems (Downhower & Armitage 1971).

Because of the formation of polygynous groups the sex ratio within these hyrax groups was skewed in favour of females and became more so during the course of the year because of the differential dispersal.

Social behaviour

Spacing within the group

The colony under observation occupied refuges consisting of boulder scree which sloped towards the hide. This provided the ideal opportunity to investigate the spacing (partitioning of space) within the CA. Spacing in this discussion refers mainly to resting places and must not be confused with the AA. Juvenile and SA hyrax occupied the more peripheral areas than did AD ♀♀, while the T ♂ occupied the central region of their AAs. In this respect hyrax with a lower social ranking (Js & SAs) can act as a buffer zone whereby the reproductively active hyrax are more protected from predation. The peripheral areas are also occupied by P ♂♂, and these may also act as buffers reducing risk to the territory holders. Crook (1970) has stated that the spatial dispersion of animals, whether in conventional or colonial territorial mating systems, involves higher individual survival and better reproductive success for the occupiers of prime sites than for those animals forced to occupy a peripheral area.

The separation of SAs and Js, from AD ♀♀ and the T ♂, at the sleeping holes is also an important factor in limiting agonistic behaviour between hyrax of different social rankings. Hanse (1962) reported an incident in which five AD ♀ hyrax killed 16 Js of c. 4 weeks of age. Adult male hyrax also sometimes kill newborn infants (Mendelssohn 1965). The possible separation of young from AD hyrax may thus be advantageous for the survival of young.

Because of the nature of hyrax refuges, social relationships are difficult to determine in the field and more observations are necessary to confirm the trends observed during the present study.

Mother/infant relationships and juvenile behaviour

Since only the breeding females can provide the milk essential for the young mammal's early survival and growth, this bond is universal in mammalian societies (Crook, Ellis & Goss-Custard 1976). The strength of this bond will, however, depend on the amount of parental care required by the young. Parental care is greatest in species in which the young are altricial as in most rodents (Barnett 1967). It is least in those species in which young are precocial such as lagomorphs, perissodactyls and artiodactyls (Fraser 1968; Delany & Happold 1979).

The precocial young of the hyrax begin to nibble on solid foodstuffs at one to two days of age (Sale 1965a; Fourie 1974). After two caesarian operations, performed by myself, on female hyrax shot during late pregnancy, the four juvenile hyrax, removed from the uteri were able to move about freely within 10 min.

The tendency of young to climb on their mother's backs and the backs of other hyrax has also been reported by Sale (1965e) and Fourie (1974). This climbing of young can serve as a social contact between the newborn and the mother (Sale 1965e). Contact with the dorsal gland of the mother, which is the site of scent production in the hyrax (Sale 1970a), can strengthen the mother-infant bond. By coming into contact with the dorsal glands of other animals, young may be more readily accepted as part of the group. The tendency of young to climb onto objects may also serve as preparation for adult watchfulness.

Young hyraces are suckled up to four times a day (Sale 1965e). In most precocial species the mother will only nurse her own offspring and reject others in order to keep the older more dominant young from getting all the food (Grau 1976). Indiscriminate suckling of young has, however, been observed for hyraces (Sale 1965e; Fourie 1974). The occurrence of indiscriminate feeding, the formation of nursery groups (Sale 1965a; Hoeck et al. 1982) and the performance of daily activities (basking, playing and feeding) independently from their mothers, point to a rather loose mother-young bond.

Although no social play was observed in a captive colony of P. capensis (Fourie 1974) it was often observed in the present study, whilst Steyn (1980) also mentions an incidence of social play (play mating) amongst P. capensis in the wild. Play is a means whereby the young individual learns about its environment and acquires skills and information necessary for later life (Delany & Happold 1979). The playful chasing behaviour of young hyrax observed in the present study may thus be important movements concerned with escape behaviour. In this respect the playful behaviour of young hyrax resembles that of the bat-eared fox and aardwolf (Ewer 1968) which also tend to show escape rather than combatant behaviour.

Intraspecific aggressive behaviour

A detailed description of the distinct behavioural patterns associated with aggression has been given for captive *P. habessinica* and *Heterohyrax syriacus* (Sale 1965a) and a captive colony of *Procavia capensis* (Fourie 1974).

The quantitive results obtained in the present study reveal that the majority (88%) of serious injuries sustained are by males and 86% of these were in males younger than 49 months of age. The ages of males that sustained serious injuries corresponded with those of the P ♂♂. Since it is normally the vanquished combatant that receives bite wounds as it turns to flee (Calhoun 1949) these can probably be related to attempts by P ♂♂ to alter their social ranking. The absence of bite wounds on males of less than 24 months of age is indicative of their non-participation in aggression associated with contests prior to mating, and their submissive behaviour towards the T ♂.

Bite wounds sustained by old males possibly reflect their inability to defend their territories because of poor or deteriorating physical condition, and may occur during their displacement from territories by younger and stronger males.

The bite wounds on females are supporting evidence of aggressive behaviour of males directed towards them: a phenomenon also reported by Sale (1965a), Steyn (1980) and Hoeck *et al*. (1982). In general aggressive interactions in the present study increased towards the mating season, a phenomenon also observed by Steyn (1980) and Hoeck *et al*. (1982).

The displacement of the T ♂ during late April by a P ♂ (observed twice in the present study) can possibly be related to the physiological condition of the T ♂ at the time. The condition of AD ♂♂ declines rapidly just after the mating season (CHAPTER VII). In late April, just after the peak mating period, the energy cost involved in mating and in defending a territory may have been great and the T ♂ may well be very vulnerable to social displacement during this period. It may thus be easier for a P ♂ to displace a T ♂ during this time. A challenge by the P ♂ of the T ♂ very often results in death of either individual (Hoeck 1982).

In general it appears that agonistic interactions resulting in fights are mainly concerned with the changing of social ranking and in the defence of territories.

Sexual behaviour

The sexual behaviour of P. capensis in the present study and that for a captive colony (Fourie 1974) is not as complex, and the courtship not as elaborate, as that described for ungulates (Fraser 1968; Grobler 1978; Delany & Happold 1979).

The sniffing of urine stains on boulders, and the anogenital region of the female most probably aided the T ♂ in olfactory recognition of the physiological state of the females. Analysis of the urine of oestrus rhesus monkeys has shown that six fatty acids serve as sex attractants to males; and that synthetic mixtures of these fatty acids increased the number of mounting attempts by the males (Müller-Schwarze 1974). Increased secretion from the dorsal gland of hyraces during the mating season (Sale 1970a) may also act as a stimulant. If the majority of copulations take place at night, as suggested by Mendelssohn (1965), it is likely that the major stimulus towards recognition of receptive females is of an olfactory nature. However, since females sometimes seek out the male and also respond to the calling of a male, auditory and visual stimuli must also play a role.

Calls by male hyrax were not quanitified in this study. Hoeck <u>et al</u>. (1982) have, however, found no seasonality in the calling of the T ♂♂. In the case of the P ♂♂ there was a seasonal pattern, with an increase in calling during the mating season. According to these authors the year round calling of the T ♂♂ may function as a "keep out" sign to other AD ♂♂.

Since recruitment into the breeding group is mainly from SA ♀♀ this group will usually consist of closely related hyrax. In the present study the T ♂ was displaced anually thus preventing father and daughter mating. If, however, the T ♂ survives for a second year (Hoeck <u>et al</u>. 1982) inbreeding may still not occur to a marked degree since the offspring of the T ♂ will still be Js and in addition the T ♂ showed a lack of interest in the SA ♀♀, which mated mainly with P ♂♂. Although SA ♂♂ may become sexually mature at 15 - 17 months, whilst still part of the MFKG, they are prevented from mating with their sisters and mothers by the T ♂. Similar constraints on inbreeding operate in the yellow-bellied marmot; in addition

Armitage (1974) has found that all colonial males are born at localities other than their eventual residence, thus further reducing the chance of inbreeding in this species.

Grooming and defaecation

Sandbathing of hyraces has been reported by Roberts (1951) and Steyn (1980). This behaviour probably serves to get fine sand particles into the fur and in this way relieve irritation and perhaps also discourage ectoparasites (Sale 1965a). Sandbathing in the kangaroo rat is related to the production of soluble lipids from sebaceous glands in the skin and also serves to deposit olfactory signals in the soil (Randall 1981). Since the dorsal gland of the hyrax is on its back, sandbathing in this species might also serve to deposit olfactory signals in the soil. In this respect a detailed study of the sandbathing habits of the T ♂ could reveal interesting results.

Although it has been reported that hyraces have communal dung middens (Sale 1965a; Louw <u>et al</u>. 1972; Steyn 1980), observations made during the present study failed to confirm this. In fact the numerous white urine stains found on rock faces and the accumulation of faecal pellets at the base of almost every boulder at refuges consisting of boulder scree would seem to indicate the opposite. The piles of faeces found at the entrances to hyrax refuges are probably related to their inactive life style. Although certain hyrax may show a constancy with regard to the use of specific urinating or defaecating sites, this can also be related to the possible positional constancy of resting on a specific spot (Sale 1965a). Field observations have, however, shown that certain sites are used solely for urination by certain individuals. If protected from the rain hyrax urine dries into a brown tar-like accretion known as "klipsweet". Studies on several species of mammals have shown that dunghills do not repel intruders but function mainly as a warning signal to strangers that they are entering an unfamiliar area and may be subject to aggressive treatment (Stoddart 1978). Faecal deposits at hyrax refuges are thought to perform these functions.

Antipredator responses

Hyrax demonstrate various behavioural responses depending on the nature of the predator threat. The production of auditory stimuli play an important role. In a study of the acoustic communication of P. capensis, Fourie (1974) identified 21 vocal and four nonvocal sounds. Elicitation and the type of sounds emitted depended on the degree of interest attached to a stimulus and the level of excitement experienced by the animal. If a threat was not considered to be serious, reversal of their antipredator behaviour may have occurred, and instead of fleeing, curiosity may have been displayed. In this respect hyrax resemble ungulates such as the Thomson's gazelle which displays inquisitiveness and is attracted to predators when the latter are not feeding (Walther 1969).

The hyrax relies more on agility and wariness than on speed or defence as strategies for predator evasions. They may, however, act aggressively by displaying threatening behaviour towards intruders. This phenomonon has also been reported by Hanse (1962) who observed hyrax displaying threatening behaviour towards a black-backed jackal placed within a captive colony. This response was also seen when a young cape silver fox was chased by adult hyrax in the MZNP (Grobler pers. comm.).

Freezing is a response whereby hyrax attempt to evade detection or wait and monitor further developments. In order to be able to stare into the sun for the detection of raptors, the hyrax possesses a light-shielding umbraculum in the eye which can be extended to cover the pupil (Millar 1973). According to Millar (op. cit.) the umbraculum may have evolved in response to a selection pressure resulting from predation by raptorial birds.

Radiating basking patterns (Sale 1965a; Kolbe 1967) assumed by hyraces result in maximum visual coverage of the surroundings. Sale (1965a), however, argued that the primary function of this basking pattern was to avoid facial contact and thus intraspecific aggression.

The findings of this study are consistent with reports by Hoeck (1975) that adults frequently perform a guarding function. In the colony under observation this function was performed by the oldest AD ♀♀. Similarly in Heterohyrax brucei it was mainly the oldest AD ♀♀ that performed the guarding function (Hoeck op. cit.). This differs from observations on P. johnstoni where this function was performed mainly by the T ♂ (Hoeck op. cit.). Sale (1965a) initially expressed doubts as to whether the guarding function was performed mainly by a T ♂ male, and by selective shooting he found it to be so. However, the P ♂♂, because of their conspicuousness, can be mistaken for T ♂♂. Hence the results obtained on this facet of behaviour by selective shooting must be viewed with caution.

In order to perform a guard function a specific hyrax has to position itself at a vantage point. By doing this the risk of being captured by predators is increased. The older females usually perform this function, and older females normally have smaller mean litter sizes than middle aged females (CHAPTER VI) and thus are more "expendable". If the guard function is performed predominantly by a T ♂ and results in the death of this animal a P ♂ will take its place. In an area with high predation pressures the rapid turnover of T ♂♂ could ultimately result in a poorer genetic quality of the T ♂♂ and reduce the inclusive fitness of the group.

The guarding performed by AD ♀♀ of the MFKGs can be viewed as altruistic behaviour in favour of several close relatives (Solbrig & Solbrig 1979). According to these authors a suicidal altruistic gene should be selected when the increase in fitness to closely related individuals is great enough to compensate for the loss in fitness to the altruistic individual; this is the case for hyrax. Such a mode of selection is called kin selection (West Eberhard 1975).

Dispersal

Emigration and immigration

Dispersal of juveniles from their birth site can be termed "natal dispersal" whereas "breeding dispersal" is the movement between breeding sites of individuals that have reproduced (Greenwood 1980).

Extensive natal dispersal was recorded in the present study and since one of the functions of dispersal is to reduce inbreeding (Greenwood, Harvey & Perrins 1978) the fitness of the individual can benefit from it. Although natal dispersal has also been reported by Hoeck et al. (1982) it differs from the findings in the present study in that male natal dispersal occurred at a different age (12 - 30 months). Possible reasons for this difference could be the lower population density of the hyraces studied by Hoeck et al. (1982) in Tanzania or the higher cost involved in dispersal since it took place over longer distances (2 km) than in the MZNP.

Natal dispersal in the present study can be divided into two categories. Hyrax leaving their breeding site prior to the onset of the first mating season (during which they became sexually active for the first time) can be termed as "early" dispersers. Those which leave during or after the mating season can be termed "late" dispersers. Since early dispersal was not related to agonistic interactions or colony density (numbers within the colony) it is thought to take place spontaneously and may be related to some innate factor. A similar observation has been made for male (Armitage 1974, 1975) and female (Downhower & Armitage 1981) yellow-bellied marmots. Supporting evidence for the urge to disperse has been obtained from captive colonies where hyrax of 8 - 12 months of age became very restless and frequently attempted to escape (Kolbe pers. comm.; Fourie 1974). The fact that hyrax in captivity displayed this behaviour indicates that visual and acoustic stimuli (Hoeck et al. 1982) may not be important for this type of dispersal. What would seem to be important, however, is the onset of summer rains, increasing temperatures and the availability of high quality forage in October (when hyrax are c. 10 - 11 months of age). These factors are advantageous and of survival value to early dispersers.

Late dispersal of SA hyrax is biased towards males and is caused by the agonistic behaviour of the T ♂. The onset of winter, after the mating season, may cause intraspecific competition for limited resources (forage and cover) and stress, which might cause the late dispersal of hyrax.

The furthest recorded distance of natal dispersal in this study was c. 500 m. This distance cannot, however, be accepted as the actual limit since, because of the rugged terrain in the MZNP, it was extremely difficult to observe marked hyrax. At the Tsitsikama Coastal National Park, translocated, marked hyrax returned to their original sites of capture, over a distance of c. 1 km (Crawford pers. comm.). Dispersals up to 2 km (Hoeck et al. 1982) and up to 25 km (Kolbe pers. comm.) have been reported. Although there is a wide range in the reported distances of dispersal of hyraces it would seem as if they are able to disperse extended distances. This may in fact also be the case for hyrax in the MZNP.

The incidence of breeding dispersal amongst AD ♀♀ was low and is similar to that reported by Hoeck et al. (1982) who found a low incidence of emigration and immigration amongst these animals. Because of the mating behaviour of hyraces breeding dispersal of AD ♂♂ was a common phenomenon.

Shifts of colonies.

The shifts of hyrax colonies situated some distance away from riparian thickets, is thought to be related to the availability of forage resources. Supporting evidence for this contention is the fact that hyrax colonies (OC and WOC) close to riparian thickets, which can supply abundant forage all year round, did not display any shifts and remained stationary throughout the course of this study. Shifts of hyrax colonies have also been observed by Sale (1965a), Meltzer (1967) and Hoeck (1975).

SUMMARY

The behaviour (daylight activity patterns, social organization, social behaviour and dispersal) of hyrax in the MZNP was studied by field observations of marked hyrax.

The daylight activity patterns of hyrax were related to environmental parameters. Basking postures changed with a change in ambient temperatures. Time spent within refuges and on moving around during daytime was more extensive during summer than in winter. More time was, however, spent on basking during winter than during summer.

The basic structure of hyrax social organization is the multi-female kinship group that is matrilocal. Territorial/dominant males maintain harems and exclude all other adult males; peripheral males occupy areas on the periphery of the activity areas of other members of the hyrax colony. Peripheral males do not form bachelor groups and are normally younger than territorial males. The oldest females in a hyrax colony are thought to be the dominant ones because they frequently perform a guard function.

Group size is discussed in terms of available refuges. It was concluded that the territorial male is able to monopolize between three and 17 females in a successful and energetic manner. The sex ratio of hyrax colonies was biased in favour of females and became more so during the course of the year due to differential dispersal of sub-adult males.

Spacing within the hyrax group is discussed and mother/infant relationships and juvenile behaviour mentioned. Agonistic interactions resulting in fights are mainly concerned with changes in social rank and in the defence of territories.

Receptive females were located mainly by olfactory recognition by the male. The territorial male copulated mainly with adult females and showed a lack of interest in sub-adult females. The peripheral males, however, copulated mainly with the sub-adult females.

No social grooming was observed in the hyrax. The lower incisors and curved nail on the hindfoot are used for grooming. Although specific individuals may show a constancy as regards urinating or defaecation sites no evidence of a communal midden, used by all the members of the colony, was found.

The hyrax relies more on agility and wariness than on speed or defence as strategies for predator evasion. Comments on the guarding (altruistic behaviour) displayed by adult females are made.

Both natal and breeding dispersal occurred, however, the former was extensive than the latter. Early natal dispersal was initiated at 8 - 10 months of age in both sexes, took place spontaneously, and was not related to the numbers within the colony or agonistic behaviour. Late natal dispersion of sub-adult hyrax was biased in favour of males and was caused by agonistic behaviour of the territorial male directed towards sub-adult males. The shifting of colonies is thought to be related to the availability of forage.

CHAPTER IX

PARASITES

INTRODUCTION

A parasite can be defined as an organism showing varying degrees of metabolic dependence on its host. This metabolic dependence may occur in the areas of nutritional requirements, developmental stimuli or the control of maturation (Whitfield 1979). Parasitic infestation increases the cost of metabolism to the host. This is especially so when the numbers of parasites are high (Moen 1973).

Parasites may affect a host directly by diverting energy through the parasite system or by causing a metabolic constraint which upsets the metabolic efficiency of the host (Moen op.cit.). The host's viability may seriously be affected and it may ultimately die (Nelson, Bell Clifford & Keirans 1977; Lightfoot & Norval 1981). Young (1969) and Melton & Melton (1982) consider that parasites (and diseases) can play an important role in the regulation of wild mammal populations and this may explain those instances where wild populations have failed to increase as expected.

Since parasites may be involved in population regulatory mechanisms it was decided to examine the parasite loads of hyrax in this study. In this chapter the ecto- and endoparasites infesting hyrax in the MZNP were identified and their seasonal abundance quantified. The relationship between hyrax age and sex and parasite load was also investigated.

METHODS

Sampling procedure

Six hyrax were shot in the MZNP at approximately monthly intervals for a period of 13 consecutive months (March 1980 - March 1981). An attempt was made to shoot three juveniles and three adults (including sub-adults) at each occasion. Immediately after the hyrax had been shot their age and sex were recorded and they were placed separately in undamaged plastic bags. The following necropsy procedure was adopted for the recovery of ecto- and endoparasites.

Ectoparasites

Upon returning to the laboratory sufficient diazinon (Agricura Ltd. P.O. Box 55, Silverton) at a concentration of 1 mℓ/1 ℓ of water, to thoroughly wet the hyrax, was poured into each plastic bag. Hyrax were left in the bags for *c.* 1 h after which they were removed and the excess insecticide was drained back into the bags. The contents of each plastic bag were poured separately through a sieve (150 micron mesh) and the bags were rinsed with water, which was also poured through the sieve, to ensure that all parasites were collected. Thereafter the hyrax were placed individually in a large plastic tray, and their skins were removed in such a manner as to prevent parasites sticking to the exposed subcutis. A wire brush (with bristles *c.* 3 cm in length) was used to scrub the skins in the plastic tray;the skins were then thoroughly washed in a bucket of tap water. This water, together with the contents of the plastic tray, was poured through the sieve. Scrubbing, washing and sieving were repeated three times and after careful examination of the skins for parasites (including ears and other protected regions), the skins were discarded. The contents of the sieve were transferred to individually labelled bottles and preserved in 10% formalin.

For comparative purposes, four rock-hare (Pronolagus rupestris) two scrub-hares (Lepus saxatilis) and one grey mongoose (Herpestes pulverulentus), species whose habitats overlap that of the hyrax were sampled and their ectoparasites collected in the same way. The latter study was conducted during 1982 and 1983 in the MZNP.

Endoparasites

The lungs, livers and gastrointestinal tracts of hyrax were removed at necropsy. The liver and lungs were cut into slices (c. 5 mm thick). These were placed in warm (c. 40°C) 0,9% saline solution in a bottle for a period of 2 h, after which the slices were washed and the washings and contents of the bottles sieved (38 micron mesh). The contents of the sieve were collected, placed in individually labelled bottles and preserved in 10% formalin.

Stomachs were carefully opened and the contents spread out in a plastic tray and examined for the presence of macroscopic worms.

These, together with the stomach wall, and any ingesta that had remained attached to it were placed in individually labelled bottles and preserved in 10% formalin.

The small intestine was opened and twice run between thumb and index finger, thus removing the contents, which were collected in individually labelled bottles and preserved in 10% formalin. The contents of the bile duct were placed with the contents of the small intestine.

The caeca and colon were opened and the contents collected in individually labelled bottles and preserved in 10% formalin; the rectum was discarded.

The counting and identification of ectoparasites was conducted by Professor I.G. Horak (Tick Research Unit, Rhodes University) while similar procedures for the endoparasites were undertaken by Mrs E.L. Visser of the Veterinary Research Institute, Onderstepoort.

Analysis of data

In order to rationalize comparisons of parasite loads, the species and numbers of parasites on each hyrax were expressed relative to body mass. Only (sub-) adult hyrax were used for comparisons between sexes of seasonal abundance as the object was to correlate seasonal differences in parasite burdens to changes in physiological condition.

Student's t-tests were run on a Hewlett-Packard 91 calculator.

RESULTS

Ectoparasites

Species present

The species composition of ectoparasites collected on the 27 juvenile (15 ♀♀ and 12 ♂♂), nine sub-adults (4 ♀♀ and 5 ♂♂) and 41 adult (25 ♀♀ and 16 ♂♂) hyrax sampled is given in Table 46. All hyrax examined (n = 77) were infested with either larvae, nymphae or adult ticks. One juvenile hyrax was without biting lice and another juvenile had no fleas. All hyrax examined were infested with sucking lice. Engorged ticks were noticeably prevalent around wounds, lips and the anogenital region.

Seasonal abundance

The mean monthly ectoparasite loads of the 77 hyrax examined are summarized in Table 47. Since juveniles become infested with ectoparasites at a very early age, results for juveniles were thus grouped with the adults and sub-adults.

Low mean monthly numbers of tick larvae were found during winter and spring months (Table 47). Significant correlations ($r = 0{,}62$ and $r = 0{,}61$; $p < 0{,}05$) were found between the monthly means of larvae, mean

Table 46: Provisional list of ectoparasite species recovered from 77 hyrax sampled in the MZNP (March 1980 - March 1981).

Ixodid ticks

Amblyomma marmoreum - larvae, nymphae
Haemaphysalis hyracophila - larvae, nymphae, adults
Hyalomma truncatum - adult (♀) (one hyrax)
Ixodes sp. - larva (one hyrax)
Margaropus winthemi - larva, nymph (one hyrax)
Rhipicephalus arnoldi - larvae, nymphae
Rhipicephalus sp. (near *R. capensis*) - adult (♀) (one hyrax)
Rhipicephalus distinctus - larvae, nymphae, adults
Rhipicephalus evertsi evertsi - larvae (one hyrax)
Rhipicephalus glabroscutatum - larvae (one hyrax)

Biting lice (Ischnocera)

Dasyonyx (*Dasyonyx*) sp.
Procavicola (*Condylocephalus*) *lindfieldi*
Procavicola (*Procavicola*) sp. (there might be more than one species present)
Procaviphilus serraticus
Other species of biting lice may also be present.

Sucking lice (Anoplura)

Prolinognathus caviaecapensis
Prolinognathus sp. (possibly a new species)
Other species of sucking lice may also be present.

Fleas

Procaviopsylla creusae
It is possible that *Procaviopsylla divergens* may also be present.

Table 47: Mean (±S.E.) monthly ectoparasite loads (per kg body mass) for 77 hyrax sampled in the MZNP during March 1980 - March 1981.

		Ixodid Ticks											
Month		Larvae		Nymphae		Adults		Ischnocera		Anoplura		Fleas	
	n	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
March	6	69,3	26,8	16,2	4,3	0	—	106,3	48,7	54,8	25,6	17,5	5,6
April	6	36,3	13,7	3,0	0,7	0,7	0,2	106,8	42,2	171,8	107,5	21,7	4,1
May	6	55,7	29,0	5,3	1,7	3,8	3,3	56,2	44,2	44,3	7,4	16,8	8,1
June	6	18,5	9,1	15,2	3,7	1,5	0,8	52,0	44,3	158,3	66,8	35,8	12,5
July	6	0,7	0,3	1,8	0,5	2,5	0,7	107,5	50,7	37,2	15,2	7,8	1,5
August	6	1,0	0,3	4,5	2,7	14,8	3,9	109,0	39,4	13,0	2,7	8,0	2,8
September	6	3,7	1,7	6,5	3,7	6,2	2,2	14,5	10,0	121,5	52,8	18,8	6,1
October	6	4,5	3,2	4,0	1,3	6,3	1,9	44,0	25,7	52,2	18,0	13,0	6,3
November	6	15,8	7,5	6,3	3,2	13,3	3,2	205,3	66,7	130,3	57,0	6,3	2,6
December	6	205,3	69,1	29,3	9,1	12,8	5,0	93,5	47,0	195,7	85,8	25,3	5,4
January	6	243,0	69,3	17,0	6,6	5,7	1,7	265,7	116,3	373,0	249,7	35,2	15,1
February	6	63,7	33,2	2,7	0,9	0	—	82,8	21,3	44,2	21,0	9,3	1,8
March	5	218,0	98,3	17,6	5,4	2,4	1,5	210,6	145,2	58,6	16,6	6,8	2,0

monthly rainfall and mean monthly maximum temperatures.

Significantly ($p < 0,05$) higher tick (combination of all developmental stages) and Ischnocera burdens were recorded during the summer months on female ($n = 29$) hyrax. No significant ($p > 0,1$) difference was found between the summer and winter burdens (ticks and Ischnocera) on male hyrax ($n = 21$).

Hyrax age and sex and ectoparasite loads

In order to compare ectoparasite loads of juveniles with those of adult and sub-adult hyrax the mean monthly values for these two groups were calculated separately (Table 48). Paired monthly comparisons show that except for Ischnocera, juveniles had significantly ($p < 0,05$) higher ectoparasite loads than adults. The values given for ticks include all developmental stages.

Comparison between the ectoparasite loads of (sub-) adult male ($n = 13$) and female hyrax ($n = 18$) for the summer season showed significantly higher loads ($p < 0,1$) of Ischonocera and fleas on females. No significant ($p > 0,1$) differences were found during winter.

Ectoparasites of Herpestes, Pronolagus and Lepus

The species composition of the ectoparasites recovered from Herpestes pulverulentus, Pronolagus rupestris and Lepus saxatilis is summarized

Table 48: Mean ($\pm$ S.E.) monthly ectoparasite loads (numbers per kg body mass) for juvenile (n = 27), sub-adult and adult (n = 50) hyrax sampled in the MZNP during March 1980 - March 1981.

	JUVENILES									SUB-ADULTS & ADULTS								
Month		Ticks		Ischnocera		Anoplura		Fleas			Ticks		Ischnocera		Anoplura		Fleas	
	n	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
March	3	116,7	54,7	10,7	4,1	93,3	41,8	25,7	9,1	3	52,3	5,5	202,7	50,6	16,3	7,4	9,3	3,2
April	2	92,5	75,2	12,0	2,0	363,0	336,0	26,5	4,5	4	18,3	5,9	154,3	47,0	76,3	32,4	19,3	3,8
May	3	123,7	42,0	2,5	0,3	56,3	8,8	29,3	13,0	3	5,7	0,9	110,0	82,9	32,3	7,1	4,3	2,4
June	3	49,7	18,5	2,7	1,2	230,7	126,5	44,0	21,0	3	12,3	2,3	101,3	86,0	86,0	33,2	14,0	4,9
July	1	6,0	—	21,0	—	105,0	—	13,0	—	5	4,8	0,9	124,8	58,2	23,6	8,3	6,8	1,4
August	1	41,0	—	27,0	—	23,0	—	19,0	—	5	16,2	5,0	105,2	45,0	11,0	2,1	5,8	2,1
September	3	28,0	11,3	0,7	0,3	236,0	28,0	22,3	11,9	3	4,7	0,3	28,3	17,6	7,0	4,5	15,3	5,4
October	3	18,3	10,2	2,3	0,9	87,3	17,5	16,3	12,9	3	11,3	2,3	85,7	39,6	17,0	9,3	9,7	4,6
November	2	21,0	13,0	14,0	4,0	200,0	54,2	4,0	4,0	4	36,8	17,3	301,0	44,6	95,5	80,1	7,5	3,2
December	2	412,0	173,0	8,5	1,5	425,0	155,5	20,0	13,0	4	164,8	38,5	136,0	61,0	81,0	35,4	28,0	6,1
January	2	257,0	43,1	17,5	4,5	19,0	4,0	75,5	27,6	4	270,0	112,8	389,8	135,7	23,8	5,4	15,0	5,9
February	1	226,0	—	2,0	—	19,0	—	13,0	—	5	34,4	9,1	99,0	16,9	49,2	24,9	8,6	2,0
March	1	597,0	—	11,0	—	43,0	—	4,0	—	4	148,3	59,9	260,5	176,4	62,5	20,9	7,5	2,4

Table 49: List of ectoparasite species recovered from *H. pulverulentus*, *P. rupestris* and *L. saxatilis* sampled in the MZNP during 1982 and 1983.

	Herpestes pulverulentus		*Pronolagus rupestris*		*Lepus saxatilis*	
	Species	Developmental stage	Species	Developmental stage	Species	Developmental stage
Ixodid Ticks	*Amblyomma marmoreum*	L	*Amblyomma marmoreum*	L	*Amblyomma marmoreum*	L
	Haemaphysalis sp.	A	*Haemaphysalis* sp.	N	*Hyalomma* spp.	L, N
	Ixodes rubicundus	L	*Hyalomma* sp.	L	*Rhipicephalus distinctus*	L, N
	Rhipicephalus arnoldi	L	*Ixodes rubicundus*	L, N	*Rhipicephalus evertsi evertsi*	L, N
	Rhipicephalus distinctus	L, N	*Rhipicephalus arnoldi*	L, N, A		
			Rhipicephalus distinctus	L		
			Rhipicephalus evertsi evertsi	L, N		
Fleas	*Ctenocephalides* sp.	A	*Ctenocephalides* sp.	A	*Ctenocephalides* sp.	A
			Echidnophaga sp.	A	*Echidnophaga* sp.	A

L = larvae, N = nymphae and A = adults

in Table 49.

Endoparasites

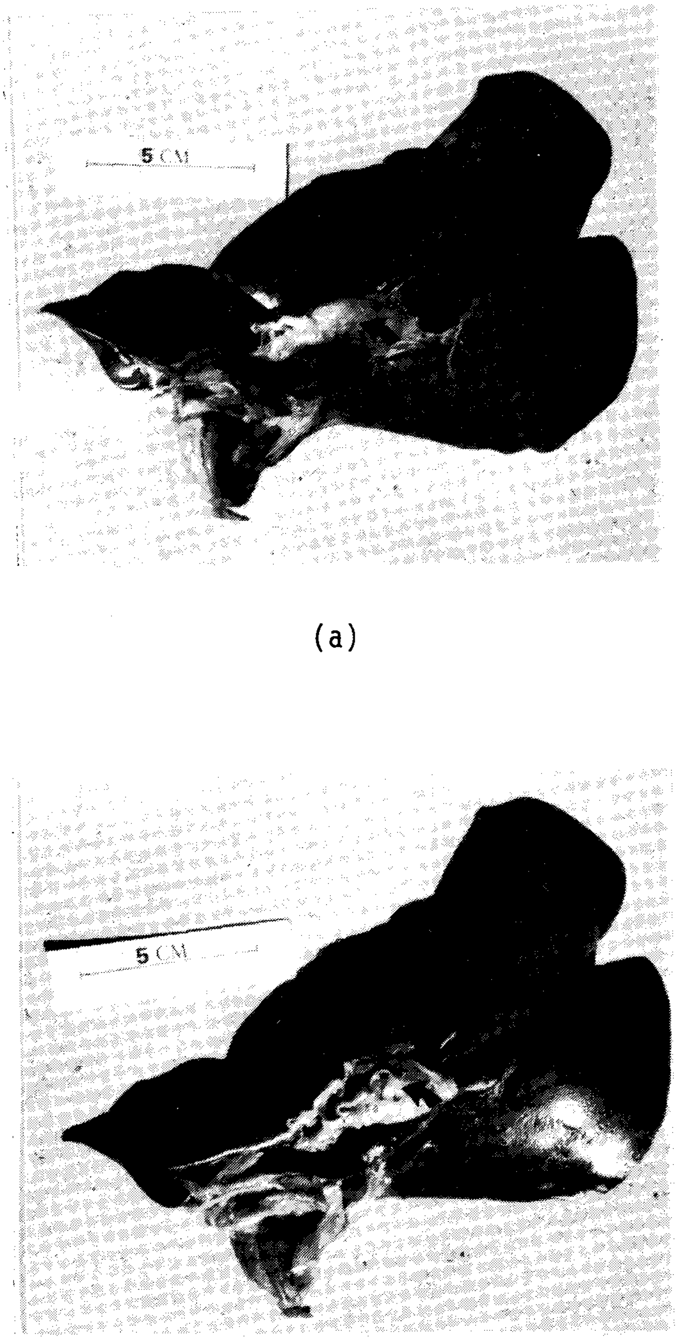
Species present

The species composition of the endoparasites recovered from the 77 hyrax examined is given in Table 50. No attempt was made to identify cestodes to species level.

Table 50: List of endoparasites recovered from 77 hyrax sampled in the MZNP (March 1980 - March 1981).

Small intestine and bile duct
Cestodes *Inermicapsifer* spp.
Sacculated caecum and colon
Nematodes *Crossophorus collaris* *Trichuris* sp. *Theileriana* spp. *Grassenema procaviae*

No parasites were recovered from any of the lung or liver tissues, or the stomach contents. Large infestations of cestodes nearly occluding the duodenum and bile ducts (Fig. 110) were observed (there is no gall bladder in the hyrax (Owen 1832; Grassé 1955)). These cestode infestations extended into the intrahepatic ampullary dilation but did not occur within the hepatic tissues.



(a)

(b)

Figure 110 a & b: Livers of hyrax showing large infestations of cestodes (indicated by arrows) in the bile ducts.

Only three juvenile hyrax, representing 4% of the total sample, were not infested with cestodes. Sixty two per cent of hyrax were infested with Crossophorus collaris, 34% with Trichuris sp., 97% with Theileriana spp. and 99% with Grassenema procaviae.

Seasonal abundance

Because juvenile hyrax only acquire infestations with certain helminth species once they are a few months old (see next section), the analysis of the parasite loads of juvenile hyrax was done separately from that of adults. The mean monthly values for endoparasites recovered from the 77 hyrax examined are summarized in Table 51. Except for Crossophorus collaris and Trichuris sp. large monthly mean burdens were recorded.

Winter and summer endoparasitic loads of sub-adult and adult (combined) male and female hyrax did not differ significantly ($P > 0{,}1$).

Hyrax age and sex and endoparasite loads

Twenty-five percent of juveniles became infested with cestodes, Grassenema procaviae and Crossophorus collaris within the first two months of age, whereas 50% were infested with Theileriana spp. and 100% with Grassenema procaviae by this age. Infestation of juveniles with Trichuris sp. was only observed at ages exceeding c. 6 months.

Table 51: Mean (±S.E.) monthly endoparasite loads (numbers per kg body mass) for juvenile (n = 27), sub-adult and adult (n = 50) hyrax sampled in the MZNP (March 1980 - March 1981).

Month		Cestodes		Crossophorus collaris		Trichuris sp.		Theileriana spp.		Grassenema procaviae (x 10^5)	
	n	x̄	S.E.	x̄	S.E.	x̄	S.E.	x̄	S.E.	x̄	S.E.
JUVENILES											
March	3	12,3	4,7	0,7	0,7	0	—	0	—	2,9	0,6
April	2	52,5	45,6	2,0	—	0	—	20,0	—	1,9	—
May	3	28,0	14,5	2,9	1,0	0,8	0,8	32,3	13,0	2,7	0,6
June	3	18,3	6,0	5,3	1,7	0	—	45,5	9,5	3,0	1,2
July	1	37,0	—	6,4	—	0,9	—	9	—	2,1	—
August	1	236,0	—	14,0	—	0,7	—	110,0	—	2,1	—
September	3	74,7	35,1	2,2	0,4	0,7	0,7	110,3	23,3	2,7	0,2
October	3	95,7	72,9	2,7	0,9	0,2	0,1	238,3	136,8	1,1	0,2
November	2	97,0	31,1	2,1	0,9	0,4	0,4	261,5	76,7	1,2	0,2
December	2	25,0	25,0	0	—	0	—	0	—	1,9	1,6
January	2	0	—	2,8	2,8	0	—	23,4	12,7	4,0	1,1
February	1	5,0	—	0	—	0	—	77,0	—	1,5	—
March	1	43,0	—	2,2	—	0	—	11,0	—	1,2	—
SUB-ADULTS AND ADULTS											
March	3	34,4	23,9	0,5	0,4	0	—	69,0	3,5	1,2	0,4
April	4	32,8	5,5	1,0	0,4	0,3	0,1	129,7	21,0	0,7	0,1
May	3	60,0	10,7	1,1	1,0	0,4	0,4	100,0	22,9	1,1	0,6
June	3	66,3	30,2	0,3	0,3	0	—	95,5	21,6	1,3	0,5
July	5	55,6	24,6	1,5	1,0	0,2	0,2	143,2	17,1	1,8	0,5
August	5	130,6	38,7	0,7	0,6	0,3	0,3	94,0	17,8	1,1	0,2
September	3	28,3	8,7	1,1	1,1	0	—	72,7	30,7	1,3	0,2
October	3	33,7	15,5	3,1	1,4	0,2	0,1	72,7	19,4	1,1	0,2
November	4	68,5	22,5	0,4	0,4	1,0	0,5	86,0	24,6	1,4	0,3
December	4	114,3	56,1	1,0	0,5	2,0	0,9	125,5	49,1	2,0	0,7
January	4	101,5	28,1	0	—	0,6	0,6	67,3	26,6	0,9	0,6
February	5	48,0	10,3	1,4	0,7	0,1	0,1	127,0	32,9	0,5	0,2
March	4	43,3	23,2	0,9	0,4	0,1	0,1	74,5	52,7	1,5	0,7

Using the values given in Table 51 paired monthly comparisons showed that juveniles had significantly (P < 0,05) larger burdens of Crossophorus collaris and Grassenema procaviae than did adults. No significant differences were found between the endoparasite loads of adult and sub-adult male and female hyrax, between summer and winter.

DISCUSSION

Species present

Ectoparasites

The list of ectoparasites recovered during the present study is not complete. A comprehensive species composition list will form the subject of later papers (Horak & Fourie in prep.).

Of the 10 ixodid tick species identified on hyrax in the MZNP during this study, only Haemaphysalis hyracophila and Rhipicephalis distinctus occur in all developmental stages on the hyrax. Amblyomma marmoreum is a tortoise tick but its immature stages may be found on several species of mammals. All developmental stages of Rhipicephalus arnoldi occur on the rock hare. Of the remaining tick species only one or small numbers of larvae, or nymphae, or both were recovered from individual hyrax, and infestation was probably accidental. These latter tick species occur commonly on the large mammals (blesbok, mountain zebra and eland) within the MZNP (Horak pers. comm.). In addition to the hyrax, on which it occurred in all stages of development, the immature stages of *R. distinctus* were found on the rock-hare, scrub-hare and grey mongoose. It has, however, not been recovered from the large mammals previously mentioned.

No overlap between the fleas of the hyrax and those of the other mammals examined existed, indicating that they are host specific. Fleas of the genus *Ctenocephalides*, however, were recovered from the rock-hare, grey mongoose and scrub-hare. For a complete list of fleas previously identified on *Procavia capensis* see Haeselbarth, Segerman & Zumpt (1966) and for the mites see Audy, Gaud, Lawrence, Theiler, Till & Vercammen-Grandjean (1961). No mites however, were found on hyrax in the present study. They may have been present but the necropsy techniques employed were probably not sensitive enough to ensure their recovery. For a complete list of lice previously identified on *P. capensis* see Ledger (1980).

Endoparasites

The identification of endoparasites, particularly cestodes, is time consuming and requires specialized techniques and knowledge. A complete list of endoparasites recovered from hyrax in the present study will form the subject of a later paper (Visser & Fourie in prep.). Round (1968) has published a check-list of helminth parasites occurring on *P. capensis*.

Seasonal abundance

Ectoparasites

The significant positive correlation between the numbers of tick larvae, temperature and rainfall is not unexpected because of the effect these have on the hatching of tick eggs (Chandler & Read 1961), and further explains the high summer burdens of larval ticks. In free ranging mammals, such as the sable antelope, tick burdens are closely correlated to the rainy season, when tick infestation is enhanced because of vegetational density (Grobler 1978). Hyrax are, however, extremely inactive and spend the major portion of their time (CHAPTER VIII) at refuges. Infestation with ectoparasites adapted to living in or around refuges can effectively occur under such circumstances and will not necessarily be dependent on vegetation density. This mode of infestation may occur with *Haemaphysalis hyracophila* and *Rhipicephalus distinctus*, both of which complete all stages of development on the hyrax. As far as *R. arnoldi* and *Amblyomma marmoreum* are concerned vegetation density may be important for infestation. Only the immature stages of these ticks occur on the hyrax and the adults are found on other hosts, indicating that infestation is acquired away from refuges.

The significantly higher tick loads of female hyrax during the summer months can be related to the social structure of the hyrax population (CHAPTER VIII). Adult and sub-adult female hyrax form part of a multifemale kinship group that is matrilocal whereas adult and sub-adult males become territorial or peripheral. The large number of females present at a particular site could lead to a marked increase in the number of parasites present at such a site and hence an increase in infestation. Supporting evidence for this contention is the fact that there is no significant difference between the summer and winter ectoparasite loads of male hyrax.

Adult females show a significant decrease in physiological condition during summer (CHAPTER VII). This may possibly affect the resistance of this group of hyrax to parasitic infestation. Sub-adult and adult males also show a significant reduction in physiological condition during winter but no significant increase in parasite loads. The high tick loads during summer must, however, contribute towards the poor physiological condition of females since they represent an additional energy burden during a period (late pregnancy and lactation) when the energy requirements of adult female mammals are already high (Kaczmarski 1966; Migula 1969).

Mammalian lice are particularly dependent on the microclimate furnished by the host (Nelson, Keirans, Bell & Clifford 1975). Although lice are highly susceptible to heat, especially in the presence of high humidity (Chandler & Read 1961), the hyrax by virtue of its behavioural mode of thermoregulation (CHAPTER VIII) avoids extreme temperatures. The significantly higher Ischnocera loads on females during summer thus probably indicates more favourable conditions for the reproduction of lice. Sweat glands occur only on the foot pads of the hyrax (Sale 1965a) and this may affect the microclimate created by the host.

In addition to seasonal differences in environmental parameters (humidity and temperature, which are advantageous for an increase in flea numbers) it has been demonstrated that hormones in the blood of pregnant rabbits (Oryctolagus cuniculus) and substances in the urine of young rabbits of the same species directly stimulate breeding of the flea Spilopsyllus cuniculi (Rothschild & Ford 1973). Since no significant differences in flea loads between summer and winter were found on female hyrax, and due to the fact that females are pregnant throughout winter, sex hormones of the hyrax do not seem to affect flea numbers.

Endoparasites

The absence of any significant seasonal differences in endoparasitic loads for adult and sub-adult male and female hyrax indicates a possible high degree of resistance to these parasites considering that both sexes undergo marked changes in physiological condition (CHAPTER VII). It might, however, also indicate that few infective stages of the endoparasites were available at the time hyrax were entering a period of stress. The increase in number of endoparasites in female wood mice (Apodemus sylvaticus) correlated to its greater food requirements during the breeding season, has been conclusively shown by Langley & Fairley (1982).

Hyrax age and sex and parasite loads

Ectoparasites

With the exception of biting lice (Ischnocera), the ectoparasite burdens of juveniles were significantly higher than those of the older hyrax. A possible reason for this may be that the physical nature (thickness) of the juvenile skin is more favourable for attachment and feeding than that of the adult hyrax. The relatively low loads of biting lice and the high burdens of sucking lice on juveniles are certainly indicative of this. Other possible reasons for the higher ectoparasite loads on juveniles can be attributed to the aggregation of juveniles in dens, and possibly also their lower resistance and hence higher susceptibility. Various factors influencing resistance or susceptibility such as repellent host pheromones, serum antibody components, key enzymes involved in the inflammatory process, blood-feeding stimulants and serum inhibitors of parasite digestive enzymes (Nelson et al. 1977) may take time to produce responses, thus accounting for the higher loads on the young animals. Juvenile hyrax have a rapid growth rate during their first year (CHAPTER IV) and have little or no stored body fat (CHAPTER VII). Consequently high ectoparasite loads, particularly the large numbers of blood feeding Anoplura, may seriously affect their resilience.

The significantly higher loads of Ischnocera and fleas on female hyrax during summer (in comparison with male loads during the same season) are possibly related to the more favourable environmental conditions during summer and the more gregarious nature of females. Ischnocera, although they occur in large numbers on adult and sub-adult hyrax, feed mainly on skin debris (Nelson *et al*. 1975) and so are unlikely to have any significant detrimental and nutritional effects on hosts.

Endoparasites

The delayed acquisition of *Trichuris* sp. infestation by juvenile hyrax is perhaps indicative of the slow development of eggs of this genus (Chandler & Read 1961). As the egg and not the larval stage is the infective stage in the *Trichuris* life cycle (Chandler & Read op. cit.) the hyrax has to ingest infective eggs from the ground. Larvae mature and moult to adulthood from 1 - 3 months after infestation, depending on the species (Soulsby 1968). As no technique for the specific recovery of these larvae was employed they may have been present in hyrax from an early age and only became obvious when they moulted to adulthood. The young age at which hyrax became infested and the large number of *Grassenema procaviae* present could possibly be an indication of transplacental migration of larvae. Migration of nematode larvae belonging to the same order as *Grassenema* is known to occur (Soulsby op. cit.). The life cycles of hyrax endoparasites are, however, still largely unknown and therefore any comments are only speculative. Although juveniles had significantly heavier loads of *Crossophorus collaris* and *Grassenema procaviae* than older animals the former helminth was present in relatively low numbers. No ill effects caused by parasites belonging to the same group as *Grassenema* have been reported, even though they may occur in very large numbers (Soulsby op. cit.).

General discussion

Of particular significance to this study is the observation that juvenile hyrax generally had higher parasitic loads than adults. During periods of drought and limited food resources the natural and acquired resistance to parasites may deteriorate because of protein deficiency (Chandler 1953). High loads of blood feeding ectoparasites can cause severe anaemia (Rechav, Kuhn & Knight 1980), a depression in circulating white blood cell numbers, as well as changes in the chemical components of blood and plasma (Nelson *et al*. 1977). Certain tick toxins may lead to anorexia and thus result in a dietary protein intake which is too low to compensate for blood loss (Nelson *et al*. 1977). In addition, the irritation caused by large burdens of ectoparasites leads to time spent in self grooming (Lightfoot & Norval 1981). This activity involves a time and energy cost to the host. In a study on the condition and mortality of waterbuck (*Kobus ellipsiprymnus*) in the Umfolozi Game Reserve it was suggested that severe tick infestations were the proximate cause of the high non-predatory mortalities of juveniles (Melton & Melton 1982). The importance of high juvenile mortality in affecting waterbuck population growth was emphasized by Melton (1983).

Since hyrax in poor condition and about to die probably do so in crevices or holes or are taken by predators their bodies cannot be obtained for necropsy purposes. Hence the comments on the effects of high parasitic burdens are mainly conjecture. However, necropsies performed by Fox (1933) on hyrax which had died in captivity revealed that in those cases in which high endoparasitic loads were present death was due to anaemia, degeneration of the liver and malnutrition. In one case severe clogging of the bile ducts with cestodes caused rupture.

The high neonatal mortality of hyrax in the MZNP during the drought of 1983 (CHAPTER X) may be partly due to the primary or secondary effects of high parasitic loads. Whereas high parasitic loads may not have been the chief cause of death they may have contributed to it by increasing total energy requirements at a time when energy supplies were limited.

In addition to the parasites already mentioned the sarcoptic mite, which causes mange, is an important cause of mortality especially in _Procavia johnstoni_ in the Serengeti National Park (Hoeck 1982). _P. capensis_ in South West Africa (Namibia) have also been reported to be vectors of the protozoan parasite _Leishmania_ (Ledger 1976). Occasional epidemics such as bubonic plague have also been reported to kill large numbers of hyrax (Kingdon 1971).

In conclusion, seasonal variation in parasitic loads and the identification of these parasites are important in explaining mortality trends. However, as far as the hyrax is concerned haematological studies (especially on juveniles) must be undertaken to verify the effect high parasite loads have on the physiological condition of these animals. In this respect a comparative haematological study between parasite-free hyrax and those living in the field should reveal promising results.

SUMMARY

Hyrax in the MZNP were shot on a monthly basis for 13 consecutive months and necropsied. The parasites recovered were identified and their abundance quantified. For comparative purposes rock-hare, scrub-hare and Cape grey mongoose were also sampled and ectoparasites recovered.

A significant positive correlation exists between the monthly mean numbers of tick larvae, monthly rainfall and monthly maximum temperature. Female hyrax showed significant seasonal differences in tick and biting lice loads. In comparison with males, female hyrax had significantly heavier burdens of biting lice and fleas during summer. With the exception of biting lice juveniles had significantly heavier ectoparasite loads than adults when compared on a monthly basis.

No significant seasonal differences in endoparasite burdens for the different sexes were evident. In comparison with the endoparasite burdens of adults and sub-adults, juveniles had significantly larger burdens of *Crossophorus collaris* and *Grassenema procaviae*.

The significance of various species of parasites recovered are discussed in terms of host specificity. Seasonal variation in parasitic burdens between the sexes is interpreted in terms of hyrax physiological condition and social organization. The suggestion is made that haematological studies should be conducted on hyrax in order to verify the detrimental and nutritional effects of large parasitic burdens.

CHAPTER X

MORTALITY

INTRODUCTION

An essential requirement in population studies is the determination of mortality rates. Age-specific mortality rates are necessary for the calculation of age-specific reproductive rates, ages most susceptible to natural mortality, the rate of population increase, mean life expectancy at birth, mean generation length, and the percentage of the population that dies each year (Caughley 1966).

The intention of this chapter is to identify the actual agents responsible for mortality and to quantify losses that occurred in the study population. These data are required to explain aspects of population structure and dynamics (next chapter).

METHODS

Information on mortality was obtained from skulls collected in the field and at black eagles' nests (CHAPTER III). Only maxillae which could be sexed were used for analysis and ages were determined according to the methods set out in CHAPTER V.

In order to determine population losses due to predation by caracal, information obtained during a study on the feeding habits of the caracal in the MZNP was utilized (Grobler 1981). The following data were employed in the calculations:

(a) It was estimated that 15 adult and 10 juvenile caracal were resident in the MZNP. These would consume 7300 kg of meat per annum (adults consume c. 1 kg/day and juveniles c. 0,5 kg/day).

(b) Scat analysis indicated that 53% of the prey of caracal consisted of hyrax.

(c) Caracal consumed an average of 55% of the total hyrax mass.

(d) The average mass of hyrax in the MZNP was calculated to be 2,5 kg (data obtained from the shot sample, n = 589).

Losses due to predation by black eagles were calculated from information supplied by Boshoff (pers. comm.). The following information was used in the calculations:

(a) Black eagles daily consume an amount equal to c. 8% of their total body mass.

(b) The mass of an adult black eagle is c. 6 kg.

(c) The average mass of hyrax in the MZNP is 2,5 kg.

(d) Consumable material for black eagles on hyrax was calculated as c. 50%. The caecum, intestine, skull and large bones are not eaten (Gargett 1972).

(e) Black eagles feed almost exclusively (98% of diet) on hyrax (Gargett 1977; Brown 1979). For the purpose of this study it was taken that hyrax constituted 100% of the black eagles' diet.

In order to determine neonatal mortality, counts were made at an observation colony at Doornhoekdam on a regular basis from January 1982 - May 1983 (CHAPTER VIII). Information on wounds (CHAPTER VIII) was also gained from the shot sample.

RESULTS

Predation

Only three fresh hyrax carcasses were found during the course of the study. One of these animals had been killed by a black eagle. The second carcass was that of a six-week-old juvenile which had partially been ingested by a snake, and the third carcass belonged to a hyrax killed in the trap-cage by a baboon. The bulk of the information for this section was derived from skulls that had been collected in the field and from calculations on predator consumption.

Total annual predation by caracal in the MZNP was calculated at 2804 hyrax ($\frac{a \times b}{c} = \frac{0{,}53 \times 7\ 300}{1{,}38}$); a = portion of caracal diet consisting of hyrax, b = prey consumption (kg) per annum, and c = mass (kg) of consumable material on a hyrax. This is 11% of the estimated post-reproductive hyrax population in the MZNP (CHAPTER X1). Since it was impossible to determine from collected skulls whether mortality was of a predatory or non-predatory nature, age-specific mortalities caused by caracal could not be determined.

The age structure and sex ratios of hyrax skulls collected at black eagles' nests are summarized in Table 52.

Table 52: The number, age structure and sex of hyrax skulls collected from black eagles' nests in the MZNP (January 1980 - December 1982) and on the farm Rietvlei (July 1981) in the Cradock Division.

Age (years)	MZNP		Rietvlei	
	♂♂	♀♀	♂♂	♀♀
0	(23)*		(2)*	
1	26	22	5	6
2	15	14	7	5
3	13	12	4	4
4	10	10	-	4
5	12	7	5	4
6	2	6	1	1
7	2	3	3	5
8	1	4	-	2
9	1	3	2	1
10	3	1	-	-
11	3	4	1	1
12	2	1	-	-
Total	90	87	28	33

* The numbers in parentheses represent the total for this specific age group since sexual dimorphism is not evident from skulls at this age.

The sex ratio of male to female hyrax caught by black eagles in the MZNP was 1,00:0,97 and at Rietvlei 1,00:1,18. These ratios do not differ significantly from unity ($P > 0,5$; Chi-square test).

Total annual predation by the adult black eagles was calculated at 840 hyrax ($\frac{a \times b}{c} = \frac{2,88 \times 365}{1,25}$); a = daily dietary intake (kg) of adult black eagles, b = number of days in a year, and c = mass (kg) of consumable material on the hyrax). To this figure was added 75 - 90 hyrax for the feeding eaglets (Boshoff pers. comm.) giving a total of c. 920 hyrax. This is 4% of the estimated post-reproductive hyrax population in the MZNP.

Other mortality factors.

Since most of the skulls collected in the field were from crevices at hyrax refuges or in close proximity to refuges it was assumed that the majority of these deaths were of a non-predatory nature, i.e. diseases, starvation, fights etc. The age structure, sex and number of skulls collected in the field are summarized in Table 53.

Table 53: Age structure, sex and number of skulls collected in the field in the MZNP (January 1980 - December 1982).

Age (years)	♂♂	♀♀
0	(32)*	
1	35	36
2	41	17
3	29	18
4	23	16
5	23	23
6	10	20
7	9	8
8	5	4
9	3	4
10	5	5
11	4	3
12	2	1
13	1	-
Total	190	155

* The number in parenthesis represents the total for this specific age group since sexual dimorphism is not evident from skulls at this age.

The male to female sex ratio for hyrax in age classes 2 - 4 was 1,8:1,0 and this differed significantly from unity ($P < 0,005$;

Chi-square test). For age classes 5 - 13 the sex ratio was 0,9:1,0 and this did not differ significantly from unity ($P > 0,5$). The overall sex ratio for males and females (1,23:1,00) also differed significantly from unity ($P < 0,1$).

Since dispersal of juveniles commences at eight months of age or older (CHAPTER VIII), the decline in juvenile(< eight months old) numbers at the observation colony at Doornhoekdam could be considered as due to neonatal mortality. During the period January - May 1982 this decline amounted to 9,7% of the juveniles in the colony, while during the corresponding period in 1983 it was 48%. The rainfall data for these periods are summarized in Table 54.

Table 54: Total monthly rainfall (mm) recorded at Babylons Toren in the MZNP for the periods December 1981 - April 1982 and December 1982 - April 1983.

Month	1981 - 1982	1982 - 1983
December	28,5	1,5
January	15,5	8,0
February	28,0	27,4
March	42,5	24,5
April	67,5	39,7
Total	182,0	101,1

The rainfall for these two periods differed significantly ($P < 0,05$; Students t-test) and the total of 9,5 mm of rain which fell during December 1982 - January 1983 differed considerably from the 44,0 mm recorded during the corresponding period in 1981 - 1982.

Indirect evidence of fluctuations in juvenile mortality was also obtained from the sample of shot hyrax (Table 55). During 1980 only 6,8% of the hyrax shot were between one and two years of age, indicating an extremely high juvenile mortality during 1979. Unfortunately no quantitive information for 1979 is available. The effect of this high juvenile mortality can clearly be seen in the age class composition of hyrax shot in 1981 and 1982 (Table 55).

Table 55: Hyrax numbers (age classes 1 - 3) expressed as a percentage of the total for the shot sample (n = 589), January 1980 - December 1982.

Age class (years)	1980	1981	1982
1	6,8	23,0	11,9
2	15,7	8,4	17,8
3	10,8	10,1	6,8

DISCUSSION

Predation

The known predators of the hyrax occurring in the MZNP have been listed in CHAPTER II. With the exception of caracals and black eagles, the other predators mentioned are unlikely to have any effect on population numbers. Scat analyses indicated that the principle food of the caracal in the MZNP was the hyrax (Grobler 1981). The results of another study on caracal conducted in several places in the Cape Province, indicated, however, that rodents were the principle food, and that hyrax only accounted for 9% of scat composition (Stuart 1982).

As only hyrax skulls were collected at black eagles' nests in the MZNP it is evident that the eagles resident in the Park feed exclusively on hyrax. However, evidence was found on the farm Rietvlei that domestic stock are also included in the diet of the black eagle.

The sex ratios of skulls collected at black eagles' nests in both collection areas were equal. The skulls collected in the field indicated that there was a significant difference favouring mortality in males (see later). Since foetal sex ratios were equal (CHAPTER VI), the higher male mortality implies that there would be more females than males in the total surviving hyrax population in the MZNP. This was shown to be the case from counts done at various hyrax colonies (CHAPTER VIII) and is also consistent with results obtained by Millar (1971).

The equal sex ratios of skulls found at black eagles' nests may thus imply that although males comprise a smaller portion of the hyrax population than do females they are more prone to predation. This may be so because of their propensity to become peripheral males at some stage during their lives. These are solitary animals or are found on the periphery of established colony activity areas. Skulls collected at black eagles' nests appear to provide an index of female age structure in the population, but are less reliable as an index of total population structure since predation is biased in favour of males. Possible reasons for the under presentation of juvenile skulls at black eagles' nests have already been discussed in CHAPTER III.

Other mortality factors

The findings in the chapters on parasitism, behaviour, habitat utilization, and the present chapter suggest that natural mortality is the compounded effect of many direct and indirect processes. High male mortality in age classes 2 - 4 corresponds to the period during which males become peripheral. During this stage they may fight and sustain serious bite wounds or even be killed. The wounds themselves may lead to increased levels of tick infestation, as ticks prefer these wounds as attachment sites, or they may become secondarily infected with bacteria.

Drought has a significant effect on neonatal mortality and this can probably be related to the inclination of juveniles to feed close to refuges (CHAPTER VII). Since feeding pressures are the highest on vegetation immediately around refuges, there may not be sufficient vegetation to sustain juveniles during a drought despite the fact that they may still be suckling. Juveniles do not have large deposits of fat (CHAPTER VII) and thus are extremely vulnerable to qualitative changes in the vegetation. Starvation may consequently be a direct cause of death.

Juveniles are also more susceptible to disease and have heavy parasite loads (CHAPTER IX) which places an additional energy burden on them. Since juveniles have also been shown to limit their degree of thermolability (McNairn 1982), marked changes in ambient temperatures place additional burdens on their energy requirements (Moen 1973). It is difficult to determine the exact causes of juvenile mortality, but it is probable that a combination of the factors already mentioned are involved. The effect of juvenile mortality on population dynamics will be discussed fully in the next chapter.

In the present study a bacterial infection causing focal disseminated necrosis of the spleen was found in three hyrax. This condition may have been the cause of some deaths (Kotzé pers. comm.). An acid-fast bacillus believed to be the causative agent of pulmonary tuberculosis has been isolated from the lungs of Procavia capensis (Wagner, Buchanan, Bokkenheuser & Leviseur 1958; Wagner & Bokkenheuser 1961). Hyrax are also known to be susceptible to both viral and bacterial pneumonia (Fox 1933; Mendelssohn 1965).

SUMMARY

Information on age-specific mortality was obtained from skulls collected in the field and at black eagles' nests.

Losses that occurred in the study population due to caracal and black eagle predation were quantified. Black eagle predation was biased in favour of males.

Non-predatory mortality is discussed. The high mortality observed for males between two and four years of age is explained in terms of hyrax social organization. Evidence is supplied which indicates that juvenile mortality fluctuates markedly in relation to availability of forage, physiological condition and parasite burdens. Mention is made of bacteria which can be pathogenic.

CHAPTER XI

POPULATION DYNAMICS

INTRODUCTION

Population dynamics is the study of changes in the numbers of organisms in populations and of the factors influencing these changes. It includes the study of the rates of loss and replacement of individuals, and of any regulatory processes tending to maintain equilibrium (Solomon 1969).

If a population continues to grow in a particular area for a sufficiently long time, its density will eventually become so great as to cause further growth to be inhibited. Since growth cannot continue indefinitely in a particular area it must eventually slow down and stop and the 'force' opposing continued growth is known as environmental resistance. The maximum possible density that a population can maintain for a prolonged period in any given environment is known as the saturation level or equilibrium density. The magnitude of this density is determined by the environmental capacity or the carrying capacity of the environment (Pielou 1974). When a population's density approaches saturation level, changes in population growth rate may occur which operate to counteract departures from equilibrium. In this way the density of a population may be regulated. According to Solomon (1969), however, changes in the environment and often in the animals themselves, cause the equilibrium level to change continually (i.e. there is a dynamic equilibrium), making it difficult to identify at any time.

The mechanism of natural control or regulation of populations is a highly contentious topic with its basic hypotheses subject to continuous dispute and debate. The opposing points of view that have dominated the study of population regulation are the biotic (Nicholson 1933, 1954), abiotic (Andrewartha & Birch 1954), compromise (Milne 1957) and self-regulation (Pimentel 1961; Chitty 1970) schools of thought. For a historical review of the different ideas refer to Tamarin (1978).

In the present study, ecological and behavioural attributes of the hyrax have been studied and where possible factors important to demography have been identified, and quantified. Such information is a basic requirement necessary for investigating and explaining the population dynamics of the hyrax. It also provides a sound scientific basis for the modelling of the population dynamics of the hyrax in the MZNP.

The specific objectives of this chapter are to examine and discuss:

(a) breeding strategies of the hyrax;

(b) mortality and survival of hyrax in the study area using time-specific life-tables;

(c) population growth rates for hyrax;

(d) hyrax population-habitat interrelationships;

(e) population dynamics following on the development of simulation models;

(f) population regulation.

METHODS

Population estimates

A variety of methods can be used to estimate population density, for example total counts or sample counts (Caughley 1977). These show varying degrees of accuracy depending on the nature (size, distribution and behaviour) of the animals to be counted, the terrain and the familiarity of the counter with the subject animal.

The Robson-Whitlock technique has been used to estimate hyrax numbers accurately in the Storms River mouth area (Fairall & Crawford 1983). A prerequisite for the use of this method is that there must be a very high probability that all the animals in the population will be seen at one counting incidence. Since this was not possible for hyrax in the MZNP this method was not applied and a more indirect approach was adopted.

The method used was to count and mark all known occupied hyrax refuge sites on an aerial photograph map (1:20 000) of the MZNP. This was done during the course of 1982 by myself and staff of the MZNP. Each refuge site (core area) was categorized as 'small' (<15) or 'large' (>15) based on a subjective assessment of the possible numbers of hyrax present at the specific site. During October 1982 just prior to the season of births (i.e. when the population is at its lowest density), counts were conducted at five randomly selected 'small' and five 'large' refuge sites. Counts were done from sunrise for a period of 3 h at each site. The maximum count obtained in this manner was used to compute a mean colony size. No attempt was made to distinguish between juvenile and adult hyrax. The mean numbers of hyrax counted at the 'large' and 'small' refuge sites were multiplied by the total numbers of each of these sites to obtain a total pre-reproductive population estimate.

In order to obtain a realistic post-reproductive estimate for use in simulation models a ratio of 1,2 ♀ : 1,0 ♂ was used (see CHAPTER X). Females were divided into age classes using the L_x series of the time-specific life tables for females (see later), and multiplied by the mean age-specific litter sizes to determine recruitment.

Life tables

Natural mortality of adult and sub-adult hyrax was assessed from skulls collected in the field and at black eagles' nests (CHAPTER X). This was used to construct time-specific life tables according to the method of Pielou (1974). Juvenile mortality (both sexes) was taken as the mean value determined by direct observations of several colonies (Table 56).

Table 56: Percentage change in juvenile numbers at the observation colony and the laboratory colony during the 12 month period January - December 1982 . The figure for 1981 is an extrapolation based on the expected recruitment during the beginning of 1981 (from adult females present) and the actual numbers of juvenile present during December 1981.

Locality		Change in juvenile numbers	% change
Observation colony	1981	34 - 17	50
	1982	38 - 11	71
Laboratory colony	1982	4 - 3	25
Mean value			49

Calculation of r values

The chief purpose of this section was to construct models of hyrax populations in order to ascertain how variations in the reproductive performances and juvenile mortality schedules would influence the rate of population growth. The actual rate of increase (r) and the maximum rate of increase (r_{max}) can be calculated from a population with a stable/stationary age distribution by the method of Andrewartha & Birch (1954). Although no evidence can be provided, it is believed that the hyrax population in the MZNP was stable during the study period. Nevertheless, it is still possible to investigate, in a realistic manner, the extent to which reproductive homeostasis and variation in mortality can affect population growth rate by using parameters obtained in this study and from the literature on hyrax.

The following parameters which may influence the value of r were examined, i.e. age at puberty, age-specific fecundity rates and various juvenile mortality schedules. By the method of Andrewartha & Birch (1954), r can be calculated according to the equation:

$$r = \frac{\log_e R_o}{T_c}$$

where T_c is the mean length of a generation (mean time from birth of parents to birth of their offspring), and R_o is the number of times a population increases per generation:

$$T_c = \frac{\sum l_x m_x x}{\sum l_x m_x}$$

and

$$R_o = \sum l_x m_x$$

where x = age in years; l_x = probability at birth of an individual surviving to age, x; m_x = mean number of female offspring born per female per year of age centered at age x.

The m_x values used in the calculations are listed in Table 57. Average fecundity and age-specific litter sizes used are equivalent to those determined during the present study. To simulate natural variation elevated and depressed fecundity schedules of 0,5 were subtracted or added respectively to the m_x values. These values are thought to be realistic, being well within hyrax reproductive potential (CHAPTER VI). It was assumed that up to a third of the juveniles may attain precocial puberty, i.e. at an age of 4 - 5 months (Millar 1971). With regard to delayed puberty, it was assumed that up to a third of hyrax in their second year of life do not reach puberty.

Table 57: Different fecundity and puberty schedules, and age-specific m_x values used for the calculation of $\underline{r}$ values.

Age class (years)	Observed	Precocious puberty	Delayed puberty
Average fecundity			
0 - 1	0,03	0,33	-
1 - 2	1,04	1,04	0,69
2 - 3	1,23	1,23	1,23
3 - 4	1,50	1,50	1,50
4 - 5	1,28	1,28	1,28
5 - 6	1,68	1,68	1,68
6 - 7	1,38	1,38	1,38
7 - 8	1,50	1,50	1,50
8 - 9	1,33	1,33	1,33
9 - 10	1,00	1,00	1,00
10+	1,08	1,08	1,08
Low fecundity			
0 - 1	0,01	0,17	-
1 - 2	0,54	0,54	0,36
2 - 3	0,73	0,73	0,73
3 - 4	1,00	1,00	1,00
4 - 5	0,78	0,78	0,78
5 - 6	1,18	1,18	1,18
6 - 7	0,88	0,88	0,88
7 - 8	1,00	1,00	1,00
8 - 9	0,83	0,83	0,83
9 - 10	0,50	0,50	0,50
10+	0,58	0,58	0,58
High fecundity			
0 - 1	0,04	0,50	-
1 - 2	1,54	1,54	1,03
2 - 3	1,73	1,73	1,73
3 - 4	2,00	2,00	2,00
4 - 5	1,78	1,78	1,78
5 - 6	2,18	2,18	2,18
6 - 7	1,88	1,88	1,88
7 - 8	2,00	2,00	2,00
8 - 9	1,83	1,83	1,83
9 - 10	1,50	1,50	1,50
10+	1,58	1,58	1,58

The different juvenile mortality schedules used were 25, 50, 71 and 84% (see chapter on Mortality).

Using skulls found in the field (CHAPTER X) and the four juvenile mortality schedules, four l_x series for females were compiled according to the method of Pielou (1974) (Table 58). Each of these l_x series was used in combination with the nine columns of m_x values, thus giving a total of 36 r-values.

Although some of the combinations such as delayed puberty and high fecundity are unlikely to occur in nature, they were included nevertheless to provide a complete range of potential values.

Table 58: Four l_x series (probability at birth of an individual surviving to age x) for female hyrax based on four juvenile mortality values (25, 50, 70 and 84%).

Juvenile mortality Age class (years)	25% l_x	50% l_x	71% l_x	84% l_x
0 - 1	1,00	1,00	1,00	1,00
1 - 2	0,75	0,50	0,29	0,16
2 - 3	0,58	0,38	0,22	0,12
3 - 4	0,49	0,33	0,19	0,11
4 - 5	0,41	0,27	0,16	0,09
5 - 6	0,33	0,22	0,13	0,07
6 - 7	0,22	0,15	0,08	0,05
7 - 8	0,12	0,08	0,05	0,03
8 - 9	0,08	0,05	0,03	0,03
9 - 10	0,06	0,04	0,02	0,01
10+	0,04	0,03	0,02	0,01

Simulation models

Two types of simulation model were used. The first type of model (a) simulated population change over a 10 year period. The main purpose was to demonstrate how changes in critical parameters (fecundity and mortality schedules) influence population numbers. In the second type of model (b) critical parameters were changed in a density-dependent fashion. Sensitivity coefficients (see later) for the parameters used were calculated in order to determine their relative importance as population regulating factors.

Model (a)

Parameters examined included:

(1) Reproductive

The fecundity and puberty schedules as listed previously (Table 57) were used. Mean litter sizes were taken as $2m_x$.

(2) Predation

The caracal predation observed (CHAPTER X) was allowed to increase and decrease by an arbitrary 10 and 25% respectively. Black eagle predation was kept constant and equivalent to 920 hyrax throughout.

(3) Juvenile mortality

Juvenile mortality schedules were varied between 20 and 84%. For each of the different juvenile mortality schedules d_x, l_x and q_x life table values (Pielou 1974) for the different sexes were calculated using data taken from skulls collected in the field (CHAPTER X).

In combination with each juvenile mortality schedule a different fecundity schedule, puberty schedule and predation level were used. The model assessed population numbers towards the end of each year. The pre-reproduction estimate of 12 763 hyrax (determined from direct counts) was taken as the starting point. The calculations were computerized by Crawford (pers. comm.) and 360 different 10 year population simulations were developed on the Univac computer of the Sea Fisheries Research Institute at Rogge Bay. A program of the model is listed in APPENDIX C.

Model (b)

In this model the estimated post-reproduction hyrax population (c. 24 000 hyrax) and the estimated lynx (caracal) population of c. 25 animals (Grobler 1981) in the MZNP were used as starting points for the predator/prey populations to be simulated simultaneously. The age structure for the hyrax population was calculated as previously and an initial juvenile mortality of 50% was used for both sexes. The different fecundity and puberty schedules (see Table 57), and mortality values for hyrax belonging to the first and second age classes (death normals are listed in Table 59) were varied in a density-dependent fashion. The growth of the caracal population was related to hyrax (prey) abundance. Based on the consumption rates of juvenile lynx (Stuart 1982) a lynx carrying capacity (LCC) of 20 animals was used initially. Similarly a hyrax carrying capacity (HCC) of 20 000 was used giving a ratio of 1 000 hyrax : 1 lynx. Lynx numbers depended on this ratio and as it decreased their death normals (DN) increased and fecundity normals decreased. This implies that they either die or emigrate and are lost to the system. The fecundity schedules and feeding rates of caracal were taken from Stuart (1982).

The mathematical approach to this model is based on the system dynamics method (Forrester 1961) which has also been described by Randers (1980). A mathematical model was constructed by Swart & Hearne (pers. comm.). Due to the complexity of this model a simplified diagrammatical representation must suffice (Figs. 111*a* - *d*). A detailed description of this model will, however, form the subject of a later paper (Swart, Fourie, Perrin & Hearne in prep.).

Sensitivity coefficients were determined and used as predictors of population regulating factors. Each of the parameters listed in Table 58 were perturbed in turn by 1%, a computer run was done and compared with the standard run (with normal values). For each of the 24 state variables (see Figs. 111*a* - *d*) at each time value 0 - 200 months, the normalized error term (NET) is calculated as follows:

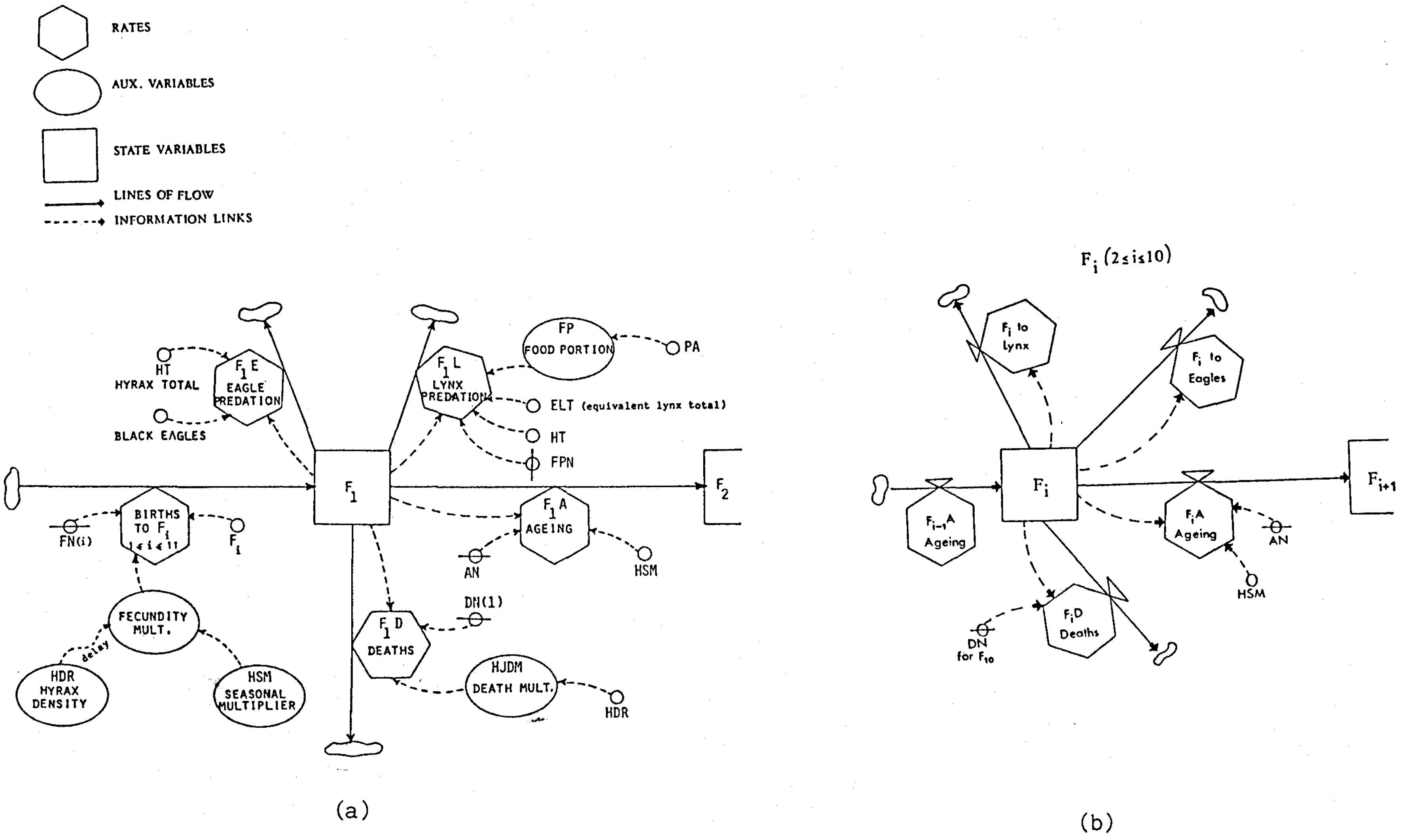
$$\frac{\text{Perturbed value of variable at t - Standard value of variable at t}}{\text{Standard value of variable at t}} = \text{NET}$$

Table 59: A list of parameters and normal values used for the sensitivity analyses.

Parameter	Normal value
Lynx fecundity normal (LFN)	0,70
Lynx juvenile death normal (LJDN)	0,50
Lynx adult death normal (LDN)	0,13
Lynx food portion normal (FPN)	0,53
Death normals of hyrax DN(1)*	0,50
DN(2)	0,50
DN(3)	0,23
DN(4)	0,18
DN(5)	0,14
DN(6)	0,26
DN(7)	0.18
DN(8)	0,26
DN(9)	0,19
DN(10)	0,27
DN(11)	0,34
DN(12)	0,37
DN(13)	0,44
DN(14)	0,26
DN(15)	0,33
DN(16)	0,30
DN(17)	0,24
DN(18)	0,25
DN(19)	0,32
DN(20)	0,20
DN(21)	1,00
DN(22)	1,00
Fecundity normals of hyrax FN(1)**	0,03
FN(2)	1,04
FN(3)	1,23
FN(4)	1,50
FN(5)	1,28
FN(6)	1,68
FN(7)	1,38
FN(8)	1,50
FN(9)	1,33
FN(10)	1,00
FN(11)	1,08

* odd numbers are females; even numbers are males; for example DN(2) is the death normal for males in the first age class.

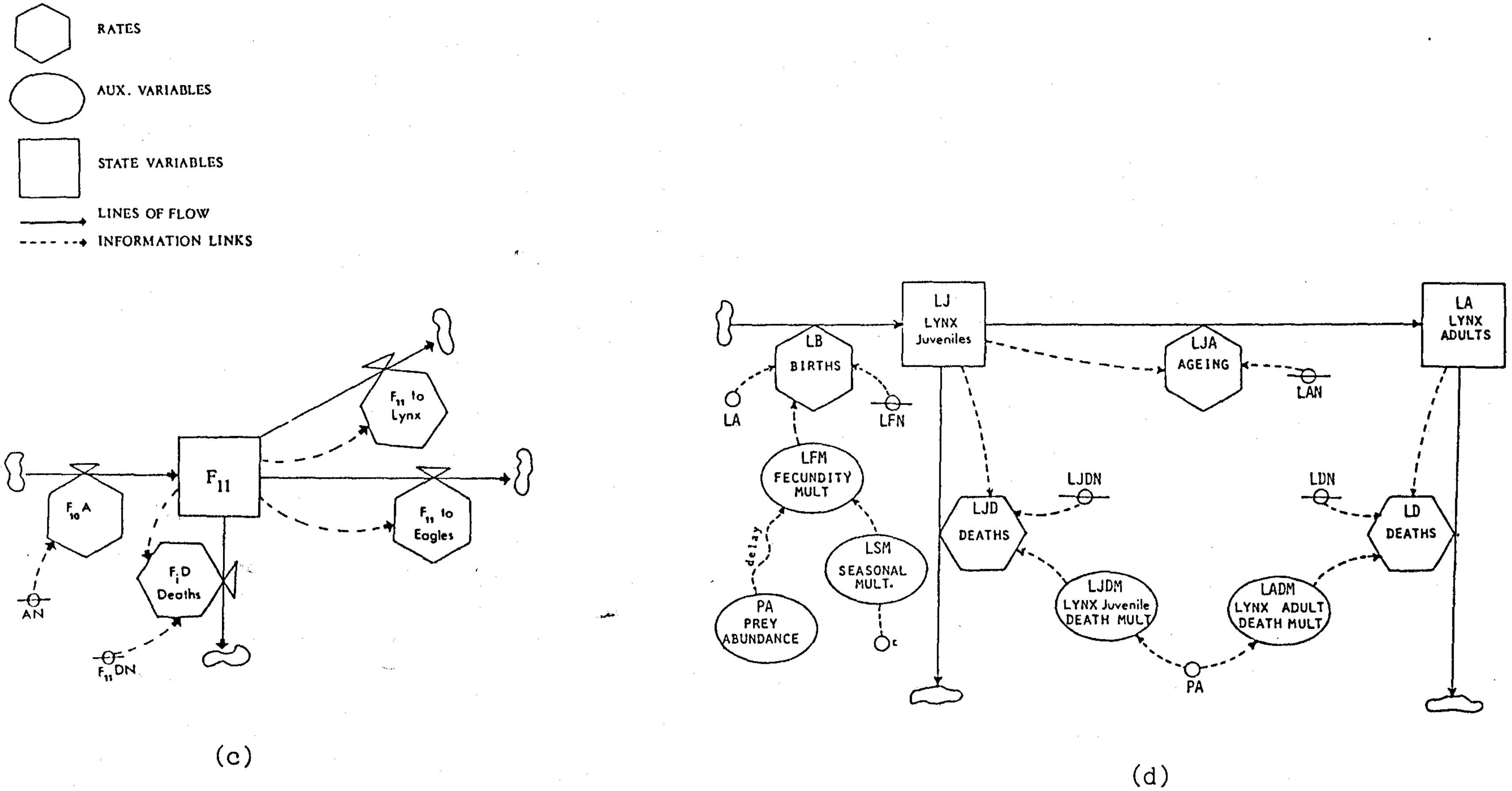
** The numerals indicate the different age classes.



(a)

(b)

Figure 111 a - d: Diagrammatic representation of the hyrax - lynx simulation models.



(c)

(d)

Figure 111 (cont.)

The NET x 100 gives the normalized sensitivity coefficient. The normalized sensitivity coefficients thus give the approximate per cent change in that state variable due to a 1% increase in the value of the appropriate parameter. In order, however, to obtain a perception of how the system as a whole is disturbed by a perturbation, average (for 0 - 200 months) normalized sensitivity coefficients were determined.

A computer program for this model was constructed by Swart (pers. comm.) and the Univac computer at the University of Natal was used for the simulation models and sensitivity analyses.

RESULTS

Population estimates

The mean values (±S.E.) for hyrax counted at the small and large hyrax colonies were 9,35 (±1,69) and 32,40 (±3,41) respectively. The calculated population for the 516 small and 245 large colonies is 12 763 hyrax giving a crude density estimate of 1,95 hyrax/ha. The post-reproductive estimate is 24 553 giving a crude density estimate of 3,76 hyrax/ha.

Life tables

The time-specific life tables for male and female hyrax are presented in Tables 60a & b. The mortality rate (q_x) is graphically presented in Figure 112. The initial high juvenile mortality for both sexes is

Table 60 a & b: Time-specific life tables for hyrax in the MZNP based on recorded mortality patterns for juveniles and from collected skulls for older animals (1980 - 1982).

x	kd_x	kl_x	q_x	L_x
(a) Males				
0 - 1	490,0	1 000,0	0,49	745,0
1 - 2	111,1	510,0	0,22	310,6
2 - 3	102,0	398,9	0,26	250,5
3 - 4	76,5	296,9	0,26	186,8
4 - 5	60,2	220,3	0,27	140,3
5 - 6	63,8	160,1	0,40	112,0
6 - 7	21,9	96,3	0,23	59,1
7 - 8	19,9	74,4	0,27	47,2
8 - 9	10,7	54,5	0,20	32,6
9 - 10	7,2	43,8	0,16	25,5
10 - 11	14,8	36,6	0,40	25,7
11 - 12	12,8	21,8	0,59	17,3
12 - 13	7,2	9,0	0,80	8,1
13 - 14	1,9	1,8	1,00	1,8
(b) Females				
0 - 1	490,0	1 000,0	0,49	745,0
1 - 2	122,3	510,0	0,24	316,2
2 - 3	65,3	387,7	0,17	226,5
3 - 4	63,2	322,4	0,20	192,8
4 - 5	54,8	259,2	0,21	157,0
5 - 6	63,2	204,4	0,31	133,8
6 - 7	54,8	141,2	0,39	98,0
7 - 8	23,2	86,4	0,27	54,8
8 - 9	16,9	63,2	0,27	40,1
9 - 10	14,7	46,3	0,32	30,5
10 - 11	12,6	31,6	0,40	22,1
11 - 12	14,7	19,0	0,77	16,9
12 - 13	4,3	4,3	1,00	4,3

x = age class in years
k = constant (1 000)
kd_x = number of individuals in each age class that die out of every 1 000 of the population
kl_x = number surviving at the start of each age class out of every 1 000 of population
q_x = mortality rate in each age class

$$L_x = \frac{kl_x + kd_x}{2}$$

followed by a markedly lower rate of mortality during the second year of life. The male mortality rate increases steadily after this time to reach a peak in age class five. From nine years of age the mortality rate increases considerably. The female mortality rate for hyrax aged 2 - 5 years is lower than that of males, and increases steadily to reach a peak at six years of age. The female mortality rate increases markedly from eight years of age.

The survivorship curves (1 000 l_x) for both sexes are graphically presented in Figure 113. Female survival values for hyrax between three and nine years of age were significantly ($p < 0,01$ t-test) higher than those for males. Males, however, survived on average a year longer than did females.

r values

The 36 r values for the different fecundity and juvenile mortality schedules, and variations in age at which puberty is attained, are graphically presented in Figure 114. The highest r value (0,559) was recorded for low initial juvenile mortality (25%), high fecundity and precocious puberty. The lowest r value (-0,176) was recorded for very high initial juvenile mortality (84%), a low fecundity and delayed puberty. The finite rate of increase (λ) for the maximum and minimum recorded values is 1,749 and -1,192 ($\lambda = e^r$) respectively.

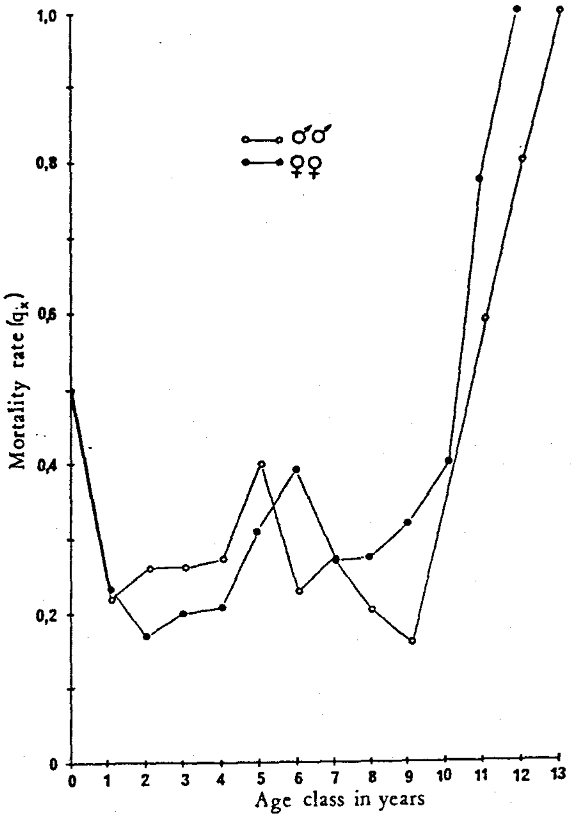


Figure 112: Mortality rates for male and female hyrax in the MZNP (1980 - 1982).

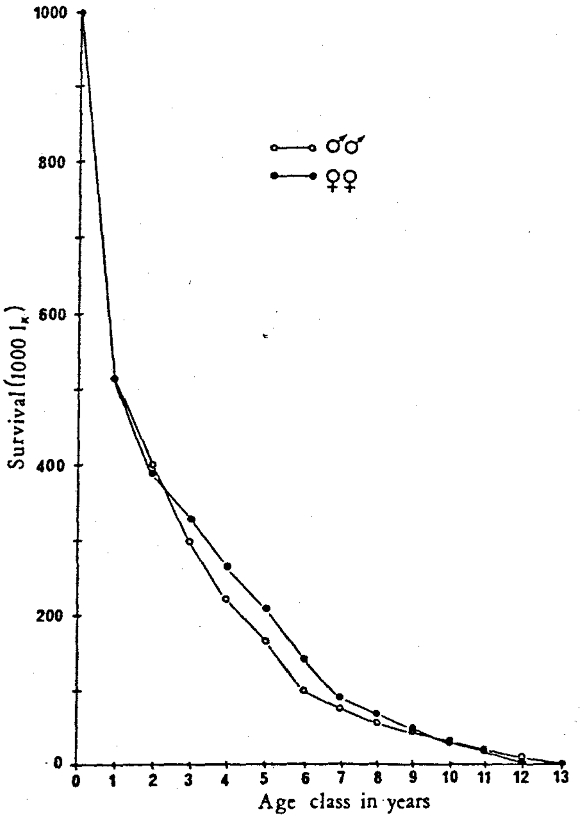


Figure 113: Survival patterns for male and female hyrax in the MZNP (1980 - 1982).

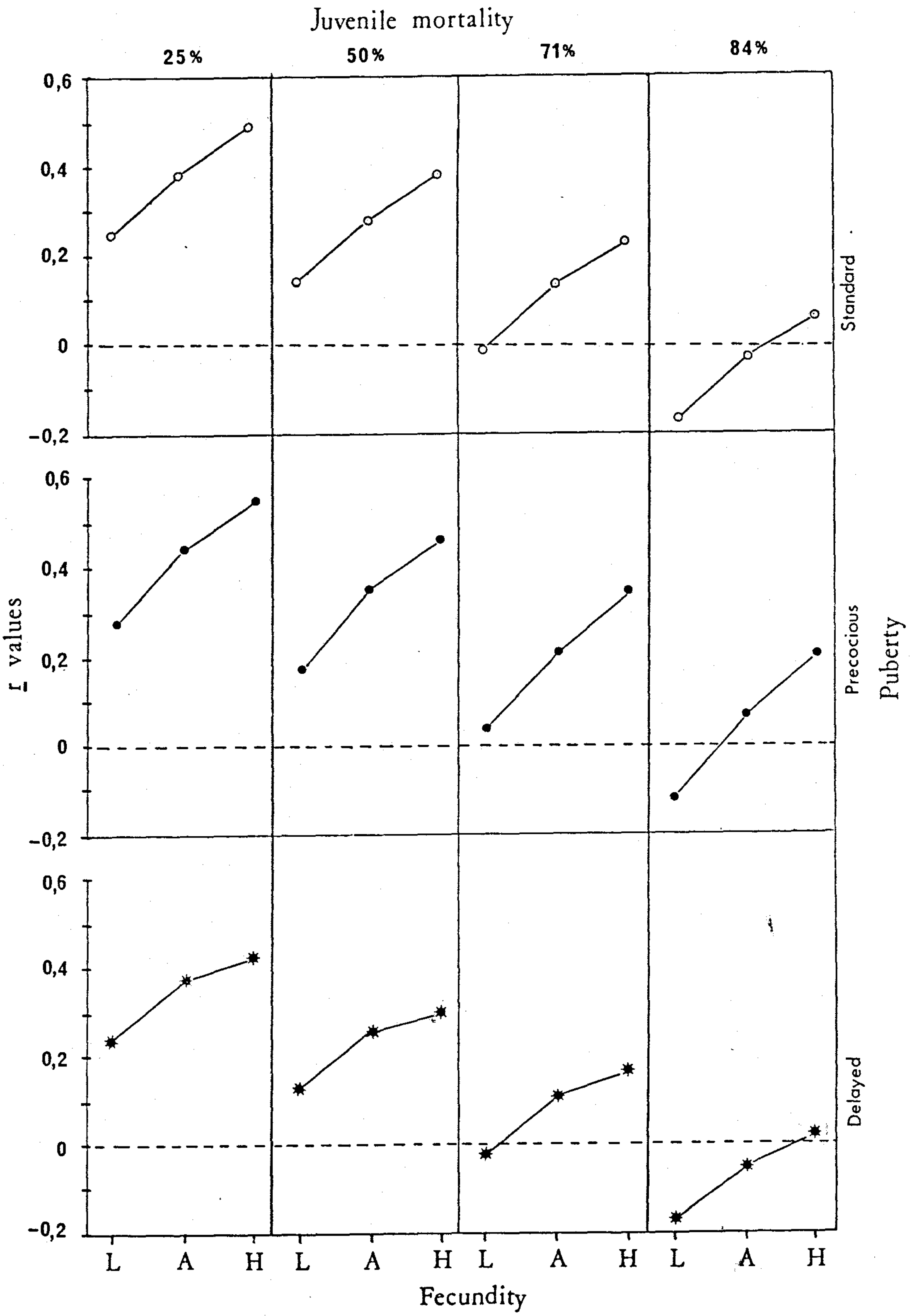


Figure 114: Different r values based on various combinations of juvenile mortality, attainment of puberty and fecundity (L - low; A - average; H - high).

Simulation models

Model (a)

From the 360 different 10 year population simulations it was evident that juvenile mortalities of 70% and above in all cases caused a decline in population numbers, irrespective of variation in fecundity schedules, predation levels and variation in time at which puberty is attained. At lower initial juvenile mortalities, changes in fecundity and ages at puberty can either increase or decrease population numbers, thus emphasizing the ability of these parameters to affect population change. Variation in predation levels tended to moderate population increase during the first few years of population growth. To serve as a representative sample 24 ten year simulation models are graphically presented in Figure 115a - d.

Model (b)

A graphical representation of the hyrax and lynx population dynamics (over a period of 200 months) is given in Figure 116. Seasonal equilibrium (towards the middle of each year) was attained at 15 years for the hyrax population (c. 55 000 animals) and at 16 years for the lynx (c. 85 animals). In order to demonstrate the adaptability of the model employed the HCC was arbitrarily increased and decreased by 5 000 hyrax. A lowering of the HCC from 20 000 - 15 000 caused the FN to decrease and DN increase at population levels similar to those of the stand run. The converse is true for an increase in the HCC. By lowering the HCC the resultant effect is a lower maximum hyrax population (c. 35 000), and the seasonal equilibrium level is also

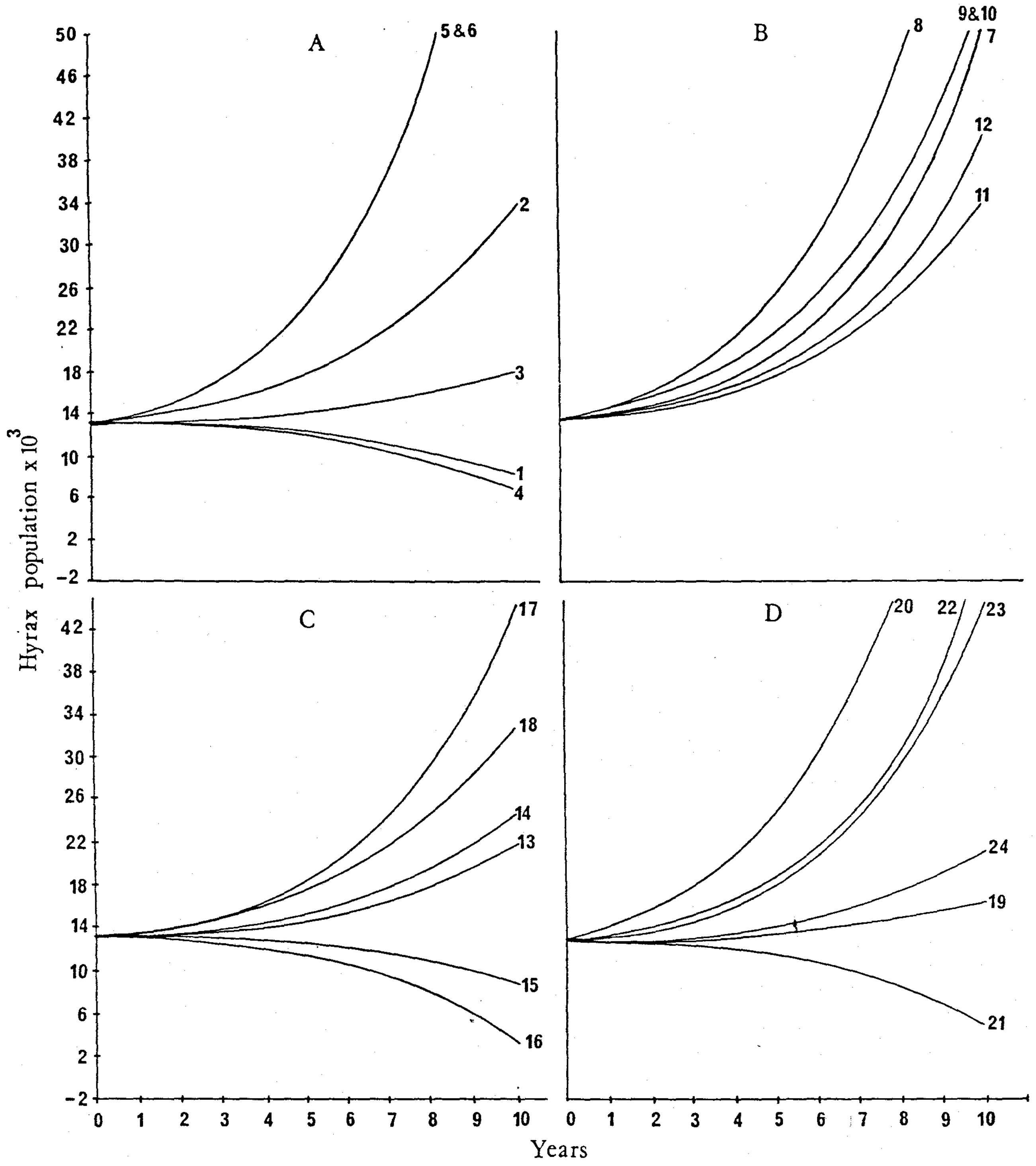


Figure 115a - d: Graphical presentation of 24 ten year simulation models based on variation of critical parameters (fecundity schedules, attainment of puberty, juvenile mortality and predation).

1 - 50% initial juvenile mortality, caracal predation reduced by 25%, average fecundity and standard puberty.
2 - 50% initial juvenile mortality, caracal predation reduced by 25%, average fecundity and precocious puberty.
3 - 50% initial juvenile mortality with caracal predation reduced by 10%, average fecundity and precocious puberty.
4 - 50% initial juvenile mortality with estimated caracal predation, average fecundity and precocious puberty.
5 - 30% initial juvenile mortality with caracal predation increased by 10%, average fecundity and delayed puberty.
6 - 30% initial juvenile mortality with caracal predation increased by 25%, average fecundity and standard puberty.
7 - 30% initial juvenile mortality with caracal predation increased by 25%, average fecundity and delayed puberty.
8 - 40% initial juvenile mortality with caracal predation reduced by 25%, average fecundity and standard puberty.
9 - 40% initial juvenile mortality with caracal predation reduced by 25%, average fecundity and delayed puberty.
10 - 40% initial juvenile mortality with caracal predation reduced by 10%, average fecundity and standard puberty.
11 - 40% initial juvenile mortality with caracal predation reduced by 10%, average fecundity and delayed puberty.
12 - 40% initial juvenile mortality with estimated caracal predation, average fecundity and standard puberty.
13 - 40% initial juvenile mortality with estimated caracal predation, average fecundity and delayed puberty.
14 - 40% initial juvenile mortality with caracal predation increased by 10%, average fecundity and standard puberty.
15 - 40% initial juvenile mortality with caracal predation increased by 10%, average fecundity and delayed puberty.
16 - 40% initial juvenile mortality, caracal predation increased by 25%, average fecundity and standard puberty.
17 - 40% initial juvenile mortality with caracal predation increased by 25%, average fecundity and precocious puberty.
18 - 60% initial juvenile mortality with caracal predation reduced by 25%, high fecundity and standard puberty.
19 - 60% initial juvenile mortality with caracal predation reduced by 10%, high fecundity and standard puberty.
20 - 60% initial juvenile mortality with caracal predation reduced by 10%, high fecundity and precocious puberty.
21 - 60% initial juvenile mortality with estimated caracal predation, high fecundity and standard puberty.
22 - 60% initial juvenile mortality with estimated caracal predation, high fecundity and precocious puberty.
23 - 60% initial juvenile mortality with caracal predation increased by 10%, high fecundity and precocious puberty.
24 - 60% initial juvenile mortality with caracal predation increased by 25%, high fecundity and precocious puberty.

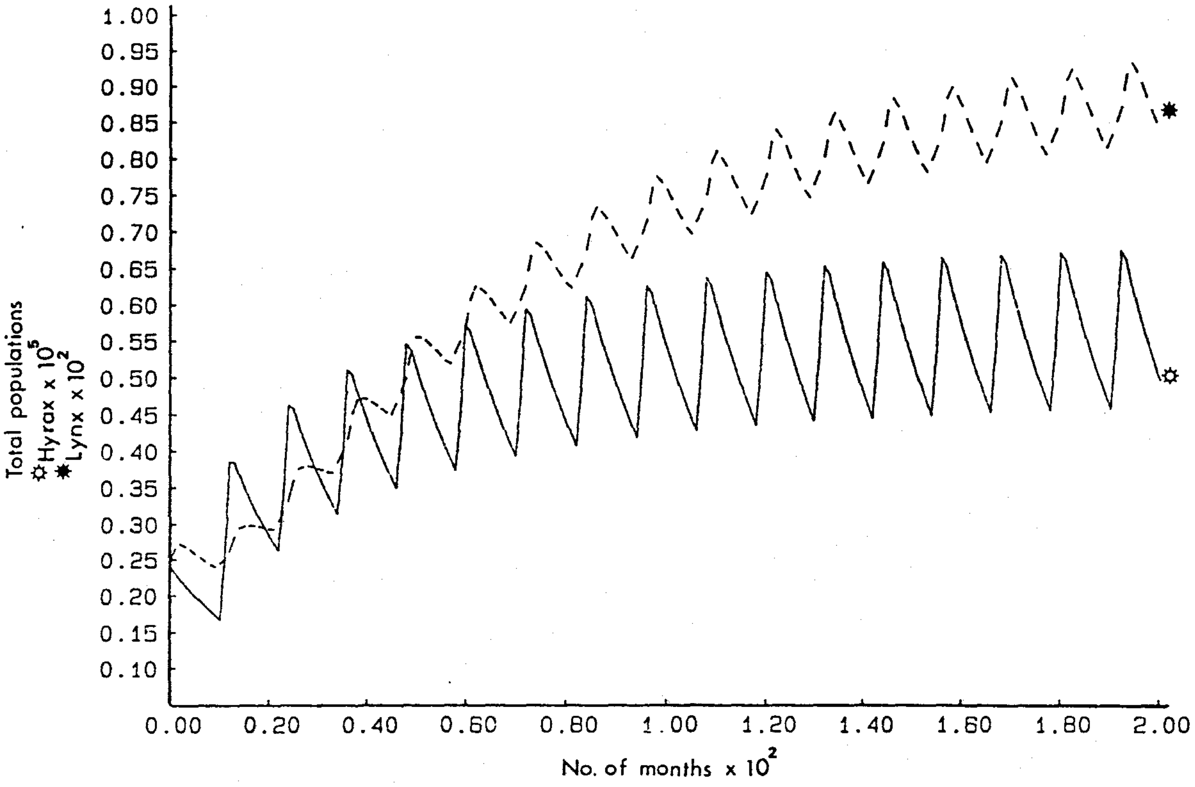


Figure 116: Hyrax and lynx population simulations over a 200 month period.

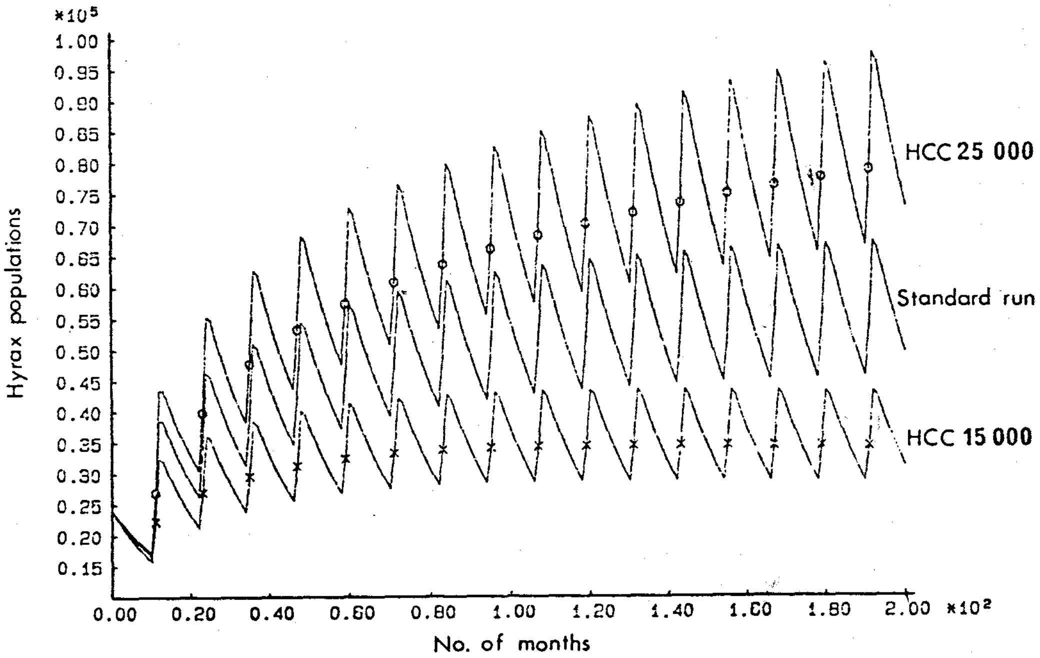


Figure 117: Variations in equilibrium levels and times during which these levels are attained because of changes in the hyrax carrying capacity (HCC).

Table 61: Decreasing sensitivity order of parameters according to average values.

Parameter	Average normalized sensitivity coefficients
DN(1)	0,730942
FPN	0,634783
FN(3)	0,439290
FN(4)	0,407717
FN(2)	0,407217
DN(3)	0,353857
FN(5)	0,261612
FN(6)	0,230551
DN(5)	0,190834
DN(7)	0,183057
DN(2)	0,178181
DN(11)	0,163402
LFN	0,162490
DN(9)	0,139064
DN(13)	0,130203
FN(7)	0,118666
LDN	0,107865
FN(8)	0,086950
LJDN	0,084355
DN(6)	0,081194
DN(15)	0,075047
DN(8)	0,073719
DN(12)	0,071842
DN(10)	0,067023
DN(4)	0,066425
DN(21)	0,055906
FN(9)	0,055117
DN(14)	0,045883
DN(22)	0,043921
DN(16)	0,040209
DN(17)	0,037871
DN(91)	0,028681
FN(10)	0,027753
DN(18)	0,025897
FN(11)	0,025094
DN(20)	0,014699
FN(1)	0,007837

attained at an earlier stage (Fig. 117). An increase in the HCC, however, results in a higher maximum population number and later attainment of (seasonal) equilibrium (Fig. 117).

A list of parameters ranked according to the size (in modulus) of their average normalized sensitivity coefficients is given in Table 61. These values are an indication of how the system as a whole is disturbed by a perturbation. It is important to note that the normalized sensitivity coefficients give the approximate percentage change in that state variable due to a 1% increase in the value of the appropriate parameter.

DISCUSSION

Hyrax breeding strategies

Small mammals exhibit a great diversity of life history features, for example fecundity, maximum longevity, and a variety age schedules of reproduction and death. These population phenomena may be related in numerous ways to the ability of the species to survive in a changed physical environment or in competition with other species. Hence it is to be expected that natural selection will be influential in shaping life history patterns to particular environments (Cole 1954). Dobzansky (1950) proposed that natural selection operates in fundamentally different ways in tropical and temperate regions. In temperate (unstable) areas physical factors are most frequently limiting to population growth and act in a density independent manner, selecting for reproduction at an early age and large litters (termed _r_-selection). In tropical (or stable) areas biological interaction predominates leading to _K_-selection for ability to compete intraspecifically and avoid predators. According to _r_ and _K_ theory, species that inhabit markedly seasonal environments should have relatively higher rates of increase than related species inhabiting areas of reduced seasonality (Pianka 1970). _r_ and _K_ selection are recognised as the end-points of a continuum (Pianka op. cit.).

An extensive review of the different life-history tactics and a critical evaluation of the hypothesis is given by Stearns (1976). The dichotomous nature and simplicity of _r_ and _K_ theory, however, make it a useful vantage point for discussions on hyraces.

The contrasting correlates of _r_ and _K_ selection are given in Table 62. Hyraces in temperate regions are more _r_-selected mainly because of:

(a) unpredictable climate in which they occur;
(b) precocial puberty (Millar 1971);
(c) much juvenile mortality (CHAPTER X);
(d) high fecundity (CHAPTER VI);
(e) large litter sizes which increase the energy demand of pregnant and lactating females (Kaczmarski 1966; Migula 1969), while reproduction is confined to periods of resource abundance causing a boom and bust pattern.

These factors differ for hyraces (_Procavia_ spp.) occurring in the tropics and these animals are more _K_-selected.

Table 62: The contrasting correlates of r- and K-selection (modified from Perrin 1980).

r-species	K-species
Climate unpredictable	Climate predictable
Short generation time, high r_{max} early reproduction	Long generation time
Small size	Large size
Precocial development	Altricial development
Much density independent mortality, often juvenile mortality	High survival rate, especially of reproductive stages
High fecundity Semelparity	Low fecundity with high parental investment or Iteroparity, often with synchronous breeding
Panmictic	Territorial/colonial
Intraspecific competition, often "scramble" type	Intraspecific competition, often "contenst" type
Low investment in "defence" and interspecific competitive mechanisms	High investment in "defence" and other interspecific competitive mechanisims
Time efficient	Food and space resource efficient
Populations often "overshoot"	Populations seldom "overshoot"
Population density very variable, "boom and bust"	Population density relatively constant from generation to generation

According to Millar (1977) reproductive effort (the proportion of total energy budget allocated to reproduction) should be a measure of an animal's position along a r and K continuum. Estimates of reproductive effort can be calculated from $R_e = N W_w^{0,75}(m^{0,75})^{-1}$ where R_e = reproductive effort, N = litter size, W_w = mass of individual offspring at weaning (g) and m = adult mass (g) (Millar op. cit.). In the present study $R_e = 0,70$. The great plasticity in litter size of P. capensis occurring within the same area (Millar 1971) will, however, shift the R_e value markedly along the r and K-continuum. This is suggestive of a dynamic reproductive strategy (Nichols, Conley, Batt & Tipton 1976).

From the available data it is evident that hyraces occurring in temperate and tropical regions do not occupy two distinct opposite positions on the r and K continuum. More information on aspects such as mortality (juvenile and adult), W_w, r_{max}, effect of density on litter size and predation values are needed to substantiate or refute the applicability of the r and K-theory to hyrax. Computation of R_e allows for comparisons between species.

Murphy (1968) and Schaffer (1974) examined the effects of predominantly adult mortality upon the reproductive strategies of various vertebrate populations in unstable environments, and developed the idea of 'bet-hedging', which predicts results opposite to those obtained from r and K-selection. For example, a fluctuating environment that has its impact on juvenile mortality favours reduced reproductive effort, smaller clutches and long-lived organisms. But environmental variability that affects adult survival favours increased reproductive effort, larger clutches, and short-lived organisms. Thus, organisms living in a situation that one would expect to select for an increased reproductive effort actually show a decreased reproductive effort (Stearns 1976).

Life tables

Caughley (1966) stressed that a population must have a stationary age distribution, i.e. natality must equal mortality, for a life table to be compiled from the observations of the age structure from ages at death. Spinage (1970) stated rightly that this may be so if the life table is claimed to be representative of the species as a whole, but life table information can also be used to demonstrate how an unstable population is changing (as used here). Provided a statement of the purpose of the life table is given then there does not seem to be a necessity for a stationary age distribution. Thus although the data presented on hyrax may not fulfill the criteria of Caughley, it shows quite clearly the dynamics of a particular population at a particular time (Spinage 1970).

The mortality rate of hyrax (both sexes) basically followed a J-shaped curve, similar to those of most mammals (Caughley 1966). The increase in mortality rate of males during their third year of life coincides with them becoming peripheral males. Peripheral males have their own hierarchy and display agonistic behaviour throughout the entire year (Hoeck et al. 1982) which may account for their elevated mortality rate. After five years of age (when males become territorial), their mortality decreased up to nine years of age. The lower mortality rate during this period is attributable to social dominance, which is reflected in various parameters, for example the near asymptotic masses (which could be of survival value during fights) and which are attained at c. 5 - 6 years of age. Secondly, in contrast to peripheral males, territorial males display a seasonality in agonistic behaviour (Hoeck et al. 1982). Thirdly, by virtue of the position of territorial males in the centre of the core area (CHAPTER VIII) they may also suffer less from predation pressures than peripheral males. These low mortality rates amongst territorial males are unlike the situation in larger ungulates, such as the sable (Grobler 1978), where territorial males have a high mortality rate due to defending large territories.

The mortality rate of middle aged (5 - 7 years old) female hyrax showed a distinct peak. Since middle-aged females had significantly higher litter sizes than young animals (CHAPTER VI) their energy requirements due to pregnancy and lactation are highest (Kaczmarski 1966; Migula 1969). This can seriously affect their resilience during periods of food shortages and consequently they are liable to be more susceptible to disease and parasites.

Spinage (1970) constructed time-specific life tables for waterbuck in Uganda and found an increase in mortality rate for middle-aged (3 - 5 years) females. The same situation was evident in a study on buffalo for which Spinage (1972) suggested a strong survival factor operating against the female around the 4th - 7th years of life. Buffalo and zebra males both attain older ages than females of these species (Spinage op. cit.).

In conclusion, for most mammal populations including hyrax in the MZNP, the asumption of a stationary age distribution and a zero intrinsic rate of natural increase does not hold (Sinclair 1974). The life tables are thus only rough approximations of the probable population structure, at the time the data was collected. The inferences that may be drawn from life tables derived from skull collections are therefore limited. Since age-specific mortality rates for the different sexes approximated possible causal effects, as evident in the life tables and from field observations in the present study, the use of these life tables is valid for comparative purposes.

r values

Before a discussion on the r values obtained in the present study can be initiated, population age structure composition must be elucidated. The different l_x values used were based on a specific juvenile mortality schedule and skulls collected in the field. Since the skulls were collected in and around hyrax refuges it was concluded that deaths were of a non-predatory nature. Hence the age structure composition and the various r values can possibly reflect growth of hyrax populations in areas where no predators occur or where they have been exterminated.

It is noteworthy that even with a juvenile mortality as high as 84% hyrax can still maintain a positive r value by virtue of a high adult survivorship, high fecundity schedule and attainment of precocious puberty.

Realistic r_{max} values would, however, seem to lie between 0,129 and 0,282 giving an annual increment of between 14 and 33%. The lower r value will correspond with a juvenile mortality of 50%, delayed puberty and low fecundity. The observed values in the present study (50% juvenile mortality, standard puberty and average fecundity) will, however, correspond to the upper r_{max} value mentioned. This would allow for an annual increment of 33% in the absence of predation. This growth would ultimately slow down through density-dependent effects, when population size become so large that the population itself altered the environment and negative feedback started to operate (Pimentel 1961).

The hyrax population in the Tsitsikama Coastal National Park serves as an example of such growth. This population increased from c. 30 animals in 1970 (Crawford pers. comm.) to c. 158 in 1981 (Fairall & Crawford 1983). The absence of natural predators in the rest camp area, increased refuge availability (for example development of new tourist accomodation) and dense vegetation could thus be equated with an 'unexploited' environment. This hyrax population showed an exponential increase of 16 - 18% for the 10 year period. This clearly demonstrates the wider applicability of the data supplied in this study.

The wide range of r values obtained in the present study are a reflection of how the dynamic reproductive strategy of the hyrax can affect population growth changes. However, from the models it is clear that although variation in reproductive performance must play its part in regulating population growth, high juvenile mortality is of far greater importance as a population controlling mechanism. This observation is in agreement with results obtained for elephant (Hanks & McIntosh 1973), rabbits (Oryctolagus cuniculus L. (Tyndale-Biscoe & Williams 1955) and waterbuck (Melton 1983).

Simulation models

Population dynamics can be studied by examining the whole population or by randomly sampling a component of it. The first approach is to follow natural changes in abundance and statistically measure relationships between various demographic parameters. Attention must concentrate on looking for density-dependent mortality factors, for example by using key factor analysis (Varley & Gradwell 1960; Morris 1963; Itô 1972) and other numerical methods. A less empirical variation to this approach is predicting a population's reaction to a given set of circumstances by modelling the population's demography. It is important that the model should contain a degree of biological realism as well as detail which is consistent with its scientific intent (Conley & Nichols 1978).

Hyrax

The comprehensive research undertaken during the present study provides a sound scientific basis for modelling the population dynamics of the hyrax in the MZNP. The pre-reproduction seasonal equilibrium (which occurs towards the end of each calendar year) of 45 000 hyrax (see Fig. 116) represents a crude density of 6,92 hyrax/ha. This is 3,6 times greater than the present calculated pre-reproduction density of 1,92 hyrax/ha.

In 1949, a period during which hyrax were very abundant (and considered vermin), 49 489 hyrax skins were handed in at the

Divisional Council Offices at Cradock. During 1957, however, only 15 507 hyrax skins were presented (Van Rensburg pers. comm.). If these figures are taken as an indication of hyrax density; the factor (3,2) by which the hyrax population fluctuated in the Cradock area between those times is similar to the factor 3,6 between the present hyrax density in the MZNP and that calculated for the pre-reproduction seasonal equilibrium. The calculated equilibrium (see Fig. 116) therefore represents a realistic upper asymptote for hyrax in the MZNP.

Caracal (lynx)

During the period 1966 - 1975 a mean annual number of 47,2 (±6,2) caracal skins was handed in at the Divisional Council Office in Cradock, while during the period 1976 - 1982 the mean annual figure was 210,0 (±18,8) (Van Rensburg pers. comm.). This is equivalent to an increase factor of 4,4 compared with the 3,4 obtained from the model. An upper asymptote of 85 caracal at high prey density (hyrax) thus seems to be realistic for the MZNP.

Due to the paucity of information on the feeding ecology of the caracal and because of the complexity of the interaction between an organism (hyrax) and its environment the model currently presented must not be viewed as being complete. As more information becomes available the model will have to be adapted and improved. It does, however, serve as a rational basis for further research.

Hyrax population-habitat interrelationships

The interrelationships between the hyrax population and its habitat determine the trends of the population. Some of these relationships are outlined in Figure 118. It must be stressed that only those factors which appear to be significant and that approximate natural reality, as well as being supported by actual data have been incorporated in the model. To facilitate discussion, these factors are grouped into four categories:

(a) Spatial resources

A population limiting factor may be defined as a factor which ultimately prevents the population from increasing, or sets the upper carrying capacity (Brewer 1979). Refuges, as defined in CHAPTER VII are limited in the MZNP and therefore place a limit on the population size in the MZNP. In this respect Hoeck (1982) found a significant correlation between kopje (rocky outcrop) size and hyrax numbers in Tanzania. He concluded that because of a lack of a significant correlation between vegetation crown cover and hyrax density, crown cover is less important in determining the number of hyrax on a kopje area than refuges provided by boulder scree.

(b) Food resources

Relative to refuges, food resources are believed to represent a 'subsidiary' limiting factor for the hyrax population in the MZNP.

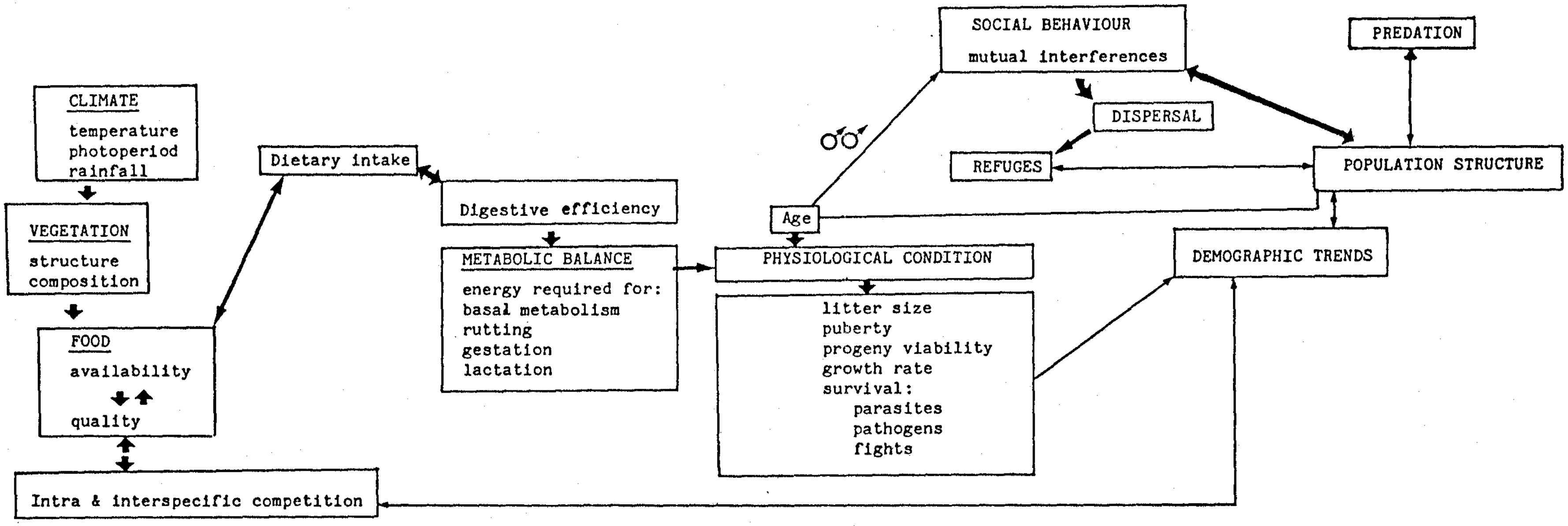


Figure 118: A composite model of hyrax population-habitat interrelationships.

This assertion is based on the fact that hyrax utilize a wide range of plant species from all strata of the vegetation, and it is also thought that little interspecific competition for these food resources occurs. Hyrax are not confined to the close proximity of their refuges and feed extensively in the high-density, riparian, plant communities. It should be stressed that this may not be so for hyrax populations occurring in areas with very sparse, homogenous vegetation. In such habitats food resources can be the ultimate limiting factor (Lack 1954; Taber 1959; Klein 1968; Wynne-Edwards 1970). Food supplies thus regulate populations through density-dependent mortality (Lack 1954).

The interrelationship between food resource, physiological condition and demographic trends is outlined in Figure 118.

(c) Predation

The major predators of the hyrax in the MZNP are the caracal and black eagle. Although these predators, particularly the former, take large numbers of hyrax (CHAPTER X), they are not as important as juvenile mortality as a regulating factor (average sensitivity coefficients are 0,73 for the DN1 and 0,63 for lynx FPN). According to Watson (1971) the suggestion that predation amongst vertebrates is an important general limiting factor on numbers in wild situations, has been confirmed by a few studies, but there are more showing that this is not so. Predation does, however, play a major role in dampening population increases (Kruuk 1970). The latter statement is believed to apply to the lynx-hyrax situation in the MZNP.

Whereas the black eagle preys almost entirely on hyrax (Gargett 1972; 1977), hyrax forms only 9 - 53% of the diet of caracal (Grobler 1981; Stuart 1982). The paucity of information on the feeding ecology of caracal and the variability of their diet makes it difficult to determine their exact impact, if any, on a hyrax population.

Holling (1959) analized the components of predation theoretically, and by means of a study of three small mammal predators of the European pine sawfly and pointed out the differences between functional and numerical response to changing prey density. A numerical response occurs when the predator population increases as a consequence of an increase in prey numbers. A functional response occurs when the predator captures and ingests more prey when prey numbers increase. Holling (op. cit.) indicated that both of these components, or only a functional response, occur with an increase in prey abundance. They are, however, affected by a number of subsidiary components such as prey characteristics, density and quality of alternate foods, and characteristics of the predators.

To illustrate this point it is worth mentioning the study of Kruuk (1970) on hyaena predation in the Serengeti National Park and Ngorongora Crater in Tanzania. Whereas hyaenas are of little importance in the ungulates' ecology (population structure and turnover) in the Serengeti, the converse was true in the Ngorongora Crater. Both functional and numerical responses of the predator were evident in the latter areas and Kruuk (op. cit.) concluded that hyaenas may influence the population structure and turnover of the prey species in the latter Park.

This clearly illustrates that as far as predator/prey relationships and dynamics of prey species are concerned, studies should be area specific. Results for a specific area, cannot be applied throughout the predator's distribution and this is likely to be so for the caracal, which has a wide distribution.

(d) Social behaviour

The basic unit of hyrax social organization is the multi-female kinship group which is matrilocal. Through the intraspecific agonistic behaviour of the territorial male, non-territorial adult males are excluded from the breeding unit. The territorial male limits and so regulates the numbers of males that breed. Evicted males become peripheral to the social units and consequently may more readily fall prey to predators, or may suffer mortality directly because of intensive intraspecific agonistic behaviour.

The number of breeding females in the group is a function of the ability of the territorial male to actively monopolize them, and the refuge size. A range of 3 - 17 breeding females per multi-female kinship group has been recorded. Recruitment into the breeding group is predominantly from female kin. Emigration of juvenile hyrax of both sexes occurred spontaneously in a density-indepent manner at the observation colony in the MZNP.

As juvenile and sub-adult female hyrax which had dispersed from their maternal groups readily joined other breeding groups, it is suggested that the hyrax population in the MZNP is well below optimal carrying capacity. Emigration is unlikely to affect the demographic trend significantly since it is reciprocal between colonies. In a saturated environment, however, emigration by hyrax must play a major role in regulating the population within a localized area. This has been shown to be the case for several ungulate species (Strandgaard 1972; Grobler 1978).

It is perhaps pertinent to refer to what was said by Taylor & Taylor (1977) when they discussed aggregation, migration and population mechanics in various animals. They stated that it is the balance between repulsion behaviour (aggression) and attraction behaviour (sociality/mating) acting on each individual, which determines its movements and hence the resulting spatial pattern of the population at any particular time. They also suggested that it is the response of this balance to changing internal and external environmental conditions that causes movements within a population. No doubt these opposing forces function in hyrax, they are, however, more well defined in the males.

The relationship between social behaviour, population density and reproductive parameters of several mammal species, has been discussed by Calhoun (1949) and Christian & Davis (1964). As far as the hyrax is concerned it is possible that high population density affected reproduction in the animals observed by Coe (1962). He found that no animal apparently ever produces more than one young at a time in a population of Procavia johnstoni mackinderi Thomas in the high density Teleki and Gorges Valleys of Mount Kenya. This contrasts markedly with the mean litter size of 1,9 reported by Sale (1965a) for the same species, but in a low density area. Unfortunately no actual population densities for these two areas were given.

Population regulation of hyrax

In the present study sensitivity coefficients have been used as a predictor of population regulation. Of all the parameters analized (see Table 59) the death normals of females belonging to the first age class (DN1) had the highest sensitivity coefficient. Consequently female juvenile mortality is the main factor regulating hyrax density. The adverse effect of juvenile mortality on population growth rate has also been clearly demonstrated in the different models used (see Figs. 114 & 115).

Although it is evident from the sensitivity analyses that the hyrax population is sensitive to changes in the diet composition of the caracal (lynx) (FPN), definitive conclusions must await the results of further research, for example on the effect of varying prey density (hyrax) on the diet compositions of the caracal, and the presence or absence of a numerical response as a result of this. A study of the feeding ecology of the caracal in the MZNP will be initiated during

1984.

As shown in the models, and confirmed by the sensitivity analyses, changes in fecundity schedules, especially of females between one and seven years of age, are important compensatory mechanisms influencing demographic trends. These changes must play an important role in the regulation of the hyrax population.

SUMMARY

The population dynamics of the hyrax population in the MZNP has been investigated and interpreted by the use of time-specific life tables, models of population growth (determination of $\underline{r}$ values), population simulation models and sensitivity analyses. Hyrax breeding strategies and hyrax population-habitat interrelationships are discussed.

Because of the plasticity of litter size in temperate regions, it is concluded that hyrax have a dynamic reproductive strategy. Although they tend to be more $\underline{r}$-selected in these regions than those in mediterranean climates, they do not occupy a fixed position on the $\underline{r}$- and $\underline{K}$-continuum.

The life table functions supplied for hyrax are not unlike those for larger ungulates. High mortality of middle-aged females is suggestive of low resilience because of the high energy demands of gestation and lactation.

Different $\underline{r}$-values (population growth rates) based on various combinations of critical parameters (juvenile mortality, adult fecundity, and attainment of puberty) are presented. Juvenile mortality was the primary factor affecting the population growth rate.

A composite diagram illustrating hyrax population-habitat interrelationships is presented and its important features discussed.

Sensitivity coefficients were used as a predictor of population regulation. The results of the analyses indicated that juvenile female mortality was the prime regulating factor for the hyrax population in the MZNP. Changes in fecundity schedules are important compensatory mechanisms and also play a significant role in the regulation of the hyrax population. Predation by caracal (lynx) is believed to dampen population fluctuations.

APPENDICES

APPENDIX A

Comprehensive list of classified plant species and their components utilized by hyrax in the MZNP as determined from stomach content analyses and field observations.

KEY (adapted from Van der Walt 1980)

(a) Plant growth form
T - tree
TS - tall shrub
MS - medium shrub
SS - small shrub
DS - dwarf shrub
PG - perennial grass
C - climber
S - succulent
F - forb
B - bulb
E - epiphyte

(b) Plant component
L - leaves
Fl - flowers
Fr - fruits
St - stems

Plant species	Plant growth form	Plant component
Gramineae: (Poaceae)		
Heteropogon contortus	PG	L Fl
Themeda triandra	PG	L Fl
Panicum deustum	PG	L Fl
Digitaria eriantha	PG	L Fl
Stipa dregeana	PG	L Fl
Eragrostis capensis	PG	L Fl
Hyparrhenia hirta	PG	L Fl
Cyperaceae		
Carex spicato-paniculata	F	Fl
Liliaciae		
Bulbine sp.	B	L
Aloe striata	S	L Fl Fr
A. striatula	S	L Fl Fr
A. broomii	S	Fl Fr
Asteraceae		
Asparagus acocksii	SS	
A. krebsianus	C	L Fr
A. mucronatus	DS	L Fr
A. racemosus	C	L Fr
A. striatus	C	L Fr
A. suaveolens	C	L Fr

Iridaceae		
Moraea polystachya	B	Fr
Angiospermae - Dicotyledoneae		
Ulmaceae		
Celtis africana	T	L
Loranthaceae		
Moquinella rubra	E	L St Fr
Viscum capense	E	L St Fr
V. rotundifolium	E	L St Fr
Chenopodiaceae		
Chenopodium murale	F	L St
Atriplex semibaccata	F	L St
Amaranthaceae		
Cyathula uncinulata	SS	L St
Aizoaceae		
Platythyra haeckeliana	S	L St
Psilocaulon sp.	F	L St
Delosperma sp.	S	L St
Ranunculaceae		
Clematis brachiata	C	L St Fl
Capparaceae		
Boscia albitrunca	T	L
Cadaba aphylla	SS	St
Leguminosae		
Acacia karroo	T	L Fl Fr
Lotononis divaricata	SS	L Fr
Indigofera sp.	DS	L
Euphorbiaceae		
Clutia pulchella	MS	L St
Euphorbia mauritanica	S	L St
Anacardiaceae		
Rhus lancea	T	L Fr
R. lucida	TS	L Fr
Celastraceae		
Maytenus heterophylla	TS	L Fl Fr
M. undata	TS	L
Tiliaceae		
Grewia occidentalis	TS	L Fl Fr
Malvaceae		
Abutilon sonneratianum	SS	L

Malva parviflora	F	L St
Sterculiaceae		
Hermannia linearifolia	DS	L Fl St
H. candidissima	DS	L Fl St
H. sp.	DS	L Fl St
Araliaceae		
Cussonia paniculata	T	L Fl Fr
Myrsinaceae		
Myrsine africana	MS	L
Ebenaceae		
Diospyros austro-africana	SS	L
D. lycioides	TS	L Fr
D. scabrida	TS	L
Oleaceae		
Olea europaea	T	L
Convolvulaceae		
Turbina oenotheroides	SS	L
Verbenaceae		
Lantana rugosa	SS	L Fr
Lamiaceae		
Ballota africana	F	L Fl Fr
Solanaceae		
Lycium cinereum	MS	L Fr
L. oxycarpum	TS	L Fr
Solanum retroflexum	SS	L St Fr
Scrophulariaceae		
Nemesia flaneganii	DS	L St Fl Fr
Sutera atropurpurea	DS	L Fl
Selaginaceae		
Walafrida geniculata	DS	L Fl
Acanthaceae		
Blepharis capensis	DS	L St
Rubiaceae		
Nenax microphylla	DS	L Fl St
Compositae		
Pteronia glauce	DS	L
Felicia filifolia	SS	L St Fl
F. muricata	DS	L St Fl
Conyza scabrida	DS	L
Chrysocoma tenuifolia	DS	L Fl
Schkuhria pinnata	F	L St

Tagetes minuta	F	L St
Pentzia cooperi	DS	
P. pilulifera	DS	L Fl St
P. incana	DS	L Fl St
P. sphaerocephala	SS	L Fl St
Senecia achilleifolius	F	L St Fl
S. hieracioides	F	L Fl St
Garuleum pinnatifidum	F	L St Fl
Osteospernum sp.	F	L St Fl

APPENDIX B

Field data sheet used in the study of activity patterns of hyrax.

Date......................

Time	Hyrax activity				Wind		Cloud cover	Temperature		Rainfall intensity	General comment
	1	2	3	4	Velocity	Direction		Refuge	External		

APPENDIX C

Hyrax population simulation program.

```
LINE BLOCK DEPTH DO STMT    SOURCE STATEMENT

   1                         T: PROCEDURE OPTIONS(MAIN);
   2                              /* PROGRAM TO SIMULATE TRENDS IN A DASSIE */
   3                              /* POPULATION OVER AN ELEVEN-YEAR PERIOD */
   4                              /* FOR DIFFERING CHOICES OF JUVENILE MORTALITY, */
   5                              /* LYNX PREDATION, FECUNDITY AND PRECOCIOUS PUBERTY */
   6    1     1         2            DECLARE (MORTJUVDESC(4),PREDDESC(5),FECDESC(9))
   7                                    CHARACTER(40)VARYING,
   8                                    (INITPOP,POPN,POPNMALE,POPNFEMALE,
   9                                    PREDCONS,PREDATION,PREDVAR(5),NAT#MORTALITY,
  10                                    SKULLMALE(2:11),SKULLFEMALE(2:11),
  11                                    SUMSKULLMALE,SUMSKULLFEMALE,
  12                                    DEATHMALE(11),DEATHFEMALE(11),QMALE(11),QFEMALE(11),
  13                                    MORTJUV(4),LMALE(11),LFEMALE(11),
  14                                    SUMLMALE,SUMLFEMALE,REPFEMALE(11),RECRUITMENT,
  15                                    M(9,11),MALE(11),FEMALE(11)) FLOAT,
  16                                    (I,J,P,X,Y) FIXED;
  17                                    /* ABOVE VARIABLES STORE RESPECTIVELY */
  18                                    /* DESCRIPTIONS OF MORTALITY OF JUVENILES, */
  19                                    /* PREDATION PRESSURE AND FECUNDITY/PUBERTY; */
  20                                    /* INITIAL POPULATION SIZE */
  21                                    /* SIZES OF TOTAL, MALE, AND FEMALE */
  22                                    /* POPULATIONS; OBSERVED CONSUMPTION */
  23                                    /* BY LYNXES; MODEL CONSUMPTION BY LYNXES; */
  24                                    /* VARIABILITY IN PREDADION PRESSURE OF */
  25                                    /* LYNXES; ANNUAL LOSSES TO NATURAL MORTALITY; */
  26                                    /* NUMBERS OF SKULLS (PER AGE) OF MALES */
  27                                    /* AND FEMALES COLLECTED IN THE FIELD, AND */
  28                                    /* THEIR TOTALS; DX AND QX VALUES FOR MALES AND */
  29                                    /* FEMALES; JUVENILE MORTALITY AS A */
  30                                    /* FRACTION; LX VALUES FOR MALES AND FEMALES */
  31                                    /* AND THEIR SUMS; REPRODUCTIVE POTENTIAL OF */
  32                                    /* THE ELEVEN FEMALE AGE CATEGORIES; ANNUAL */
  33                                    /* RECRUITMENT; MX VALUES FOR 9 COMBINATIONS */
  34                                    /* OF FECUNDITY AND PRECOCIOUS PUBERTY AND 11 */
  35                                    /* AGES; NUMBERS OF MALES AND FEMALES IN THE */
  36                                    /* POPULATION IN EACH OF 11 AGE CLASSES; */
  37                                    /* AND FIVE FIXED COUNTERS */
  38    1     1         3            POPULATION#STRUCTURE: PROCEDURE (NUMBER,NO#MALE,
  39                                    NO#FEMALE,LIVEMALE,LIVEFEMALE,SUMLIVEMALE,
  40                                    SUMLIVEFEMALE);
  41                                    /* SUBROUTINE ALLOCATES TOTAL POPULATION */
  42                                    /* TO DISCRETE SEX AND AGE CATEGORIES */
  43    2     2         3             DECLARE (NUMBER,NO#MALE(*),NO#FEMALE(*),LIVEMALE(*),
  44                                       LIVEFEMALE(*),SUMLIVEMALE,SUMLIVEFEMALE) FLOAT;
  45    2     2         4             DECLARE (X) FIXED;
  46    2     2         5             DO X = 1 TO 11;
  47                                    /* LOOP ALLOCATES TOTAL POPULATION TO AGE */
  48                                    /* AND SEX CATEGORIES */
  49    2     2    1    6                NO#MALE(X) = (1.00/2.20)*NUMBER*LIVEMALE(X)/
  50                                          SUMLIVEMALE;
  51    2     2    1    7                NO#FEMALE(X) = (1.20/2.20)*NUMBER*LIVEFEMALE(X)/
  52                                          SUMLIVEFEMALE;
  53                                       /* FIELD OBSERVATIONS INDICATED THAT */
  54                                       /* MALES AND FEMALES OCCURRED IN */
  55                                       /* THE APPROXIMATE RATIO 1.00:1.20 */
  56    2     2    1    8                END;
  57    2     2         9             END;
  58    2     1        10          GET LIST (INITPOP);
  59    2     1        11          GET SKIP LIST (PREDCONS);
  60                               /* ABOVE TWO LINES READ VALUES OF INITIAL POPULATION */
  61                               /* SIZE AND OBSERVED CONSUMPTION BY LYNXES */
  62    2     1        12          DO P = 1 TO 5;
  63                               /* THIS LOOP READS DESCRIPTIONS OF PREDATION */
  64                               /* AND VARIATIONS AROUND NORMAL PREDATION BY LYNXES */
  65    2     1    1   13             GET SKIP LIST (PREDDESC(P));
  66    2     1    1   14             GET SKIP LIST (PREDVAR(P));
  67    2     1    1   15             END;
  68    2     1        16          DO J = 1 TO 9;
  69
```

```
                            /* THIS LOOP READS DESCRIPTIONS OF FECUNDITY/PUBERTY */
 70                         /* AND THEIR VALUES FOR THE DIFFERNT AGE CATEGORIES */
 71   2      1  1   17         GET SKIP LIST (FECDESC(J));
 72   2      1  1   18         DO X = 1 TO 11;
 73   2      1  2   19            GET SKIP LIST (M(J,X));
 74   2      1  2   20            END;
 75   2      1  1   21         END;
 76   2      1      22      SUMSKULLMALE = 0;
 77   2      1      23      SUMSKULLFEMALE = 0;
 78                         /* ABOVE VARIABLES ARE INITIALISED */
 79   2      1      24      DO X = 2 TO 11;
 80                         /* THIS LOOP CALCULATES VALUES FOR SUMSKULLMALE */
 81                         /* AND SUMSKULLFEMALE */
 82   2      1  1   25         GET SKIP LIST (SKULLMALE(X),SKULLFEMALE(X));
 83   2      1  1   26         SUMSKULLMALE = SUMSKULLMALE + SKULLMALE(X);
 84   2      1  1   27         SUMSKULLFEMALE = SUMSKULLFEMALE + SKULLFEMALE(X);
 85   2      1  1   28         END;
 86   2      1      29      PUT PAGE;
 87   2      1      30      DO I = 1 TO 4;
 88                         /* THIS LOOP IS EXECUTED FOR EACH OF THE FOUR */
 89                         /* VARIATIONS OF JUVENILE MORTALITY */
 90   2      1  1   31         GET SKIP LIST (MORTJUVDESC(I));
 91   2      1  1   32         GET SKIP LIST (MORTJUV(I));
 92                            /* FOLLOWING LINES DETERMINE LX, DX AND QX */
 93                            /* VALUES FOR THE YOUNGEST AGE CLASS */
 94   2      1  1   33         LMALE(1) = 1000;
 95   2      1  1   34         LFEMALE(1) = 1000;
 96   2      1  1   35         SUMLMALE = LMALE(1);
 97   2      1  1   36         SUMLFEMALE = LFEMALE(1);
 98   2      1  1   37         DEATHMALE(1) = 1000*MORTJUV(I);
 99   2      1  1   38         DEATHFEMALE(1) = 1000*MORTJUV(I);
100   2      1  1   39         QMALE(1) = DEATHMALE(1)/LMALE(1);
101   2      1  1   40         QFEMALE(1) = DEATHFEMALE(1)/LFEMALE(1);
102   2      1  1   41         DO X = 2 TO 11;
103                            /* THIS LOOP CALCULATES VALUES OF DX, LX */
104                            /* AND QX FOR THE INITIAL MALE AND FEMALE */
105                            /* POPULATIONS */
106   2      1  2   42            DEATHMALE(X) = (1000-DEATHMALE(1))*
107                                  (SKULLMALE(X)/SUMSKULLMALE);
108   2      1  2   43            DEATHFEMALE(X) = (1000-DEATHFEMALE(1))*
109                                  (SKULLFEMALE(X)/SUMSKULLFEMALE);
110   2      1  2   44            LMALE(X) = LMALE(X-1) - DEATHMALE(X-1);
111   2      1  2   45            LFEMALE(X) = LFEMALE(X-1) - DEATHFEMALE(X-1);


  PLUM  5:08A     T: PROCEDURE OPTIONS(MAIN);

112   2      1  2   46            QMALE(X) = DEATHMALE(X)/LMALE(X);
113   2      1  2   47            QFEMALE(X) = DEATHFEMALE(X)/LFEMALE(X);
114   2      1  2   48            SUMLMALE = SUMLMALE + LMALE(X);
115   2      1  2   49            SUMLFEMALE = SUMLFEMALE + LFEMALE(X);
116   2      1  2   50            END;
117   2      1  1   51         DO P = 1 TO 5;
118                            /* THIS LOOP IS EXECUTED ONCE FOR EACH OF */
119                            /* THE FIVE VARIATIONS ON PREDATION */
120   2      1  2   52            PREDATION = PREDCONS * PREDVAR(P);
121   2      1  2   53            DO J = 1 TO 9;
122                               /* THIS LOOP IS EXECUTED ONCE FOR EACH OF */
123                               /* THE NINE VARIATIONS ON */
124                               /* FECUNDITY/PUBERTY */
125   2      1  3   54               PUT SKIP EDIT ('FOR',MORTJUVDESC(I),PREDDESC(P),
126                                     FECDESC(J)) (A,X(1),A,X(1),A,X(1),A);
127   2      1  3   55               POPN = INITPOP;
128                                  /* ABOVE LINE RESETS VALUE OF */
129                                  /* POPULATION SIZE TO STARTING VALUE */
130   2      1  3   56               DO Y = 1 TO 11;
131                                  /* THIS LOOP SIMULATES POPULATION TRENDS */
132                                  /* OVER AN ELEVEN-YEAR PERIOD */
133   2      1  4   57                  CALL POPULATION#STRUCTURE (POPN,MALE,
134                                        FEMALE,LMALE,LFEMALE,SUMLMALE,SUMLFEMALE);
135   2      1  4   58                  POPNMALE = 0;
136   2      1  4   59                  POPNFEMALE = 0;
137   2      1  4   60                  DO X = 1 TO 11;
138                                     /* THIS LOOP CALCULATES ANNUAL POPULATION */
139                                     /* LEVELS FOR MALES, FEMALES AND */
140                                     /* BOTH SEXES COMBINED */
141   2      1  5   61                     POPNMALE = POPNMALE + MALE(X);
142   2      1  5   62                     POPNFEMALE = POPNFEMALE + FEMALE(X);
143   2      1  5   63                     POPN = POPNMALE + POPNFEMALE;
144   2      1  5   64                     END;
145   2      1  4   65                  PUT SKIP EDIT ('YEAR',Y,':','MALES',
146                                        POPNMALE,';','FEMALES',POPNFEMALE,
147                                        ';','TOTAL',POPN) (X(5),A,X(1),F(2),
148                                        A,X(2),A,X(1),F(9,0),A,X(2),A,X(1),F(9,0),
149                                        A,X(2),A,X(1),F(9,0));
```

```
 150   2      1   4    66                        DO X = 1 TO 10;
 151                                             /* THIS LOOP ASSUMES LINEAR DECAY TO */
 152                                             /* ESTIMATE NUMBER OF FEMALES IN MID-YEAR */
 153                                             /* FOR EACH OF THE 10 YOUNGEST AGE CATEGORIES */
 154                                             /* - IT IS ASSUMED THAT THESE NUMBERS */
 155                                             /* OF FEMALES WILL REPRODUCE */
 156   2      1   5    67                            REPFEMALE(X) = (FEMALE(X) + FEMALE(X+1))/2;
 157   2      1   5    68                            END;
 158   2      1   4    69                        REPFEMALE(11) = FEMALE(11)/2;
 159                                             /* REPRODUCTIVE STRENGTH OF OLDEST AGE */
 160                                             /* CATEGORY ASSUMED TO BE HALF NUMBER OF */
 161                                             /* FEMALES ALIVE AT START OF YEAR */
 162   2      1   4    70                        RECRUITMENT = 0;
 163   2      1   4    71                        DO X = 1 TO 11;
 164                                             /* THIS LOOP CALCULATES ANNUAL RECRUITMENT */
 165                                             /* OF NOUGHT-YEAR-OLDS TO THE POPULATION */
 166   2      1   5    72                            RECRUITMENT = RECRUITMENT + REPFEMALE(X)*
 167                                                    M(J,X)*2;
 168                                                 /* MULTIPLICATION BY TWO IS TO ACCOUNT FOR */
 169                                                 /* BIRTHS OF BOTH MALES AND FEMALES */
 170   2      1   5    73                            END;
 171   2      1   4    74                        POPN = POPN + RECRUITMENT;
 172                                             /* TOTAL POPULATION SIZE INCREASED TO */
 173                                             /* ACCOUNT FOR RECRUITMENT */


   PLUM  5:08A    T: PROCEDURE OPTIONS(MAIN);

 174   2      1   4    75                        CALL POPULATION#STRUCTURE (POPN,MALE,FEMALE,
 175                                                 LMALE,LFEMALE,SUMLMALE,SUMLFEMALE);
 176   2      1   4    76                        NAT#MORTALITY = 0;
 177   2      1   4    77                        DO X = 1 TO 11;
 178                                             /* THIS LOOP CALCULATES LOSSES TO */
 179                                             /* NATURAL MORTALITY */
 180   2      1   5    78                            NAT#MORTALITY = NAT#MORTALITY +
 181                                                    QMALE(X)*MALE(X) + QFEMALE(X)*FEMALE(X);
 182   2      1   5    79                            END;
 183   2      1   4    80                        POPN = POPN - NAT#MORTALITY - 920 - PREDATION;
 184                                             /* TOTAL POPULATION SIZE IS REDUCED TO */
 185                                             /* ACCOUNT FOR LOSSES TO NATURAL MORTALITY, */
 186                                             /* BLACK EAGLES (920) AND LYNXES (PREDATION) */
 187   2      1   4    81                        END;
 188   2      1   3    82                     END;
 189   2      1   2    83                  END;
 190   2      1   1    84               END;
 191   2      1        85      END;
 WARNING CG  24 SYSIN/SYSPRINT ASSUMED IN I/O STATEMENTS
COMPILE TIME     659 MSEC.
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