# Growth and age determination in the hyrax *Procavia capensis*

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Growth and age determination were studied in known age captive hyrax by measuring the animals monthly for three years and killing groups at ages 12, 24 and 36 months. Ten body measurements and five skull measurements were used as ageing criteria using multiple regression and a predictive equation. Age (months) = 0,0593 Length + 0,0444 Girth + 0,01117 Headlength – 20,652 was developed for both sexes. Tooth eruption and wear, dental annulli and eyelenses were also investigated and an ageing schedule was developed using tooth eruption and wear. Cementum annulli were shown to be a valid means of ageing up to 36 months and probably up to at least eight years. Eyelenses are not an effective ageing method. Growth in the hyrax is slow and Von Bertalanffy growth coefficients are similar to those in the elephant.
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Groei en ouderdomsbepaling is ondersoek in bekende ouderdom dassies in gevangenisskap. Die diere is maandeliks gemeet vir drie jaar en daarna is hulle geslag op ouderdomme van 12, 24 en 36 maande. Tien liggaamsmates en vyf skedelmates is gebruik om ouderdom te skat deur middel van meervoudige regressie, 'n voorspelling word gegee deur Ouderdom (maande) = 0,0593 Lengte + 0,0444 Borsomtrek + 0,01117 Koplengte – 20,652 en is geldig vir beide geslagte. Tandvervanging en slytasie, tandjaarringe en ooglense is ook ondersoek en 'n skattingsmetode is ontwikkel wat tandvervanging en slytasie as basis het. Jaarringe is geldig as ouderomsbepalingsmetode tot op 36 maande en waarskynlik tot tenminste agt jaar. Ooglense is nie 'n betroubare skattingsmetode nie. Groei in die dassie is stadig en die Von Bertalanffy groei-koëffisiënte is soortgelyk aan dié van die olifant.
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The biology of the hyrax intrigues zoologists for a number of reasons, not the least being the disparity in size between it and its nearest relative, the elephant. Growth has been well studied in domestic animal species (Hammond 1940; Brody 1945; Lodge & Lamming 1968), but in wild animals less is known about this important aspect and the present study attempts to provide some data on the morphological manifestation of growth in the hyrax by studying the increase in mass and certain linear measurements with age.

Although age determination is essential when studying population biology, it is one of the most difficult parameters to measure and a voluminous literature exists of techniques of general application or for specific species. In the hyrax a number of techniques can be applied and this study has attempted to evaluate dentition, growth and dental cementum annulli.

In South Africa the hyrax is of special interest because this species has become an agricultural pest in certain areas where its predators have been eliminated (Hanse 1962). The present study was initiated to obtain basic data for a comprehensive investigation of the population dynamics of the hyrax and its contribution to secondary productivity.

## Methods

During 1973 young hyrax were captured and 10 male and 10 female individuals were housed in an outdoor enclosure. This was repeated in 1974, and in 1975 young hyrax born in the established colony were taken and they formed the third group. Birth date (within one month) was known in all three groups.

All individuals were toe-clipped for identification and kept in separate pens. Rock and wooden shelter-boxes were provided and they were fed a ration of commercial rabbit pellets (16% protein, 25% fat and 17% fibre, Vereeniging Consolidated Mills, Johannesburg) and fresh lucerne *ad lib.* They were exposed to natural environmental conditions and no protection other than the shelter boxes was provided against climatic variables.

The following growth parameters were measured monthly:

— Mass measured on an electric balance to the nearest gram
— Body length measured along the curve from the base of the skull to the tip of the tail. In hyrax this can be taken as the length of the vertebral column
— Girth taken directly behind the shoulder

— Length of the hindfoot
— Length of front footpad
— Length of the front leg from the tip of the longest digit to the tip of the olecranon process of the ulna
— Length of the backleg from the tip of the longest digit to the articulation of the tibiofibula with the femur
— Length of the back limb from the tip of the longest digit to the trochanter of the femur
— Width of the skull between the eyes.

At the end of the experiment when the youngest group was 12 months and the oldest group 36 months old, all the animals were sacrificed, skulls were removed and the following measurements taken:

— Skull length from the tip of the nasal-bone to the nuchal crest
— Skull width at the narrowest portion of the frontal bone within the orbit
— Length of the mandible from the distal portion of the horizontal ramus to the most posterior portion of the vertical ramus
— Length of the mandibular tooth row
— Length of the maxillary tooth row.

Where individuals of known age in the captive colony died fom natural causes during the study period their skulls were used to supplement the information obtained from the experimental group, providing data on growth under the age of 12 months. Once the validity of the cementum lines had been established on known age animals, two skulls, one with intermediate and one with heavy wear were aged and included in parts of the study to evaluate later ages. Eye-lenses were preserved in 10% formalin, dried to a constant weight and mass was determined accurately to five decimals of a gram.

Tooth replacement and wear were studied using all skulls and subjective criteria. Teeth were recorded as erupting when clearly visible above the gum line and until such time as they were considered fully erupted by comparison to older groups, while wear was described in three broad classes namely slight, distinct and well worn.

Von Bertalanffy growth equations (Ricker 1975) were derived for mass, length, girth and head length using the relationship

$$x_t = x_\infty(1 - e^{-k(t - t_0)})$$

where
$x_t$ = measurement at time
$x_\infty$ = asymptotic measurement
$k$ = constant determining growth rate
$t_0$ = hypothetical time when measurement is zero.

Stepwise multiple regression was applied separately to all body measurements and age and all skull measurements and age using the SPSS package available on the IBM computer at the University of Pretoria.

## Results

### Growth

Von Bertalanffy growth curves for mass, length, girth and head length are illustrated in Fig. 1. The relevant equations for males are

$$\text{Mass}_t^{(\text{grams})} = 3377{,}15(1 - e^{-0{,}057\,(t+1{,}854)})$$

$$\text{Length}_t^{(\text{cm})} = 587{,}63\,(1 - e^{-0{,}059(t-6{,}576)})$$

$$\text{Girth}_t^{(\text{mm})} = 327{,}73\,(1 - e^{-0{,}058(t-7{,}883)})$$

$$\text{Headlength}_t^{(\text{mm})} = 107{,}61\,(1 - e^{-0{,}057(t+10{,}848)})$$

and the equivalent equations for females are

$$\text{Mass}_t^{(\text{grams})} = 2664{,}02(1 - e^{-0{,}060(t+0{,}597)})$$

$$\text{Length}_t^{(\text{mm})} = 619{,}04\,(1 - e^{-0{,}045(t-8{,}485)})$$

$$\text{Girth}_t^{(\text{mm})} = 305{,}42\,(1 - e^{-0{,}075(t-6{,}452)})$$

$$\text{Headlength}_t^{(\text{mm})} = 112{,}69\,(1 - e^{-0{,}043(t+14{,}082)})$$

Asymptotic size is not reached by 36 months in fact the calculated asymptotic mass would theoretically only be reached at about six years of age.

Monthly means of all the parameters measured are presented in Table 1.

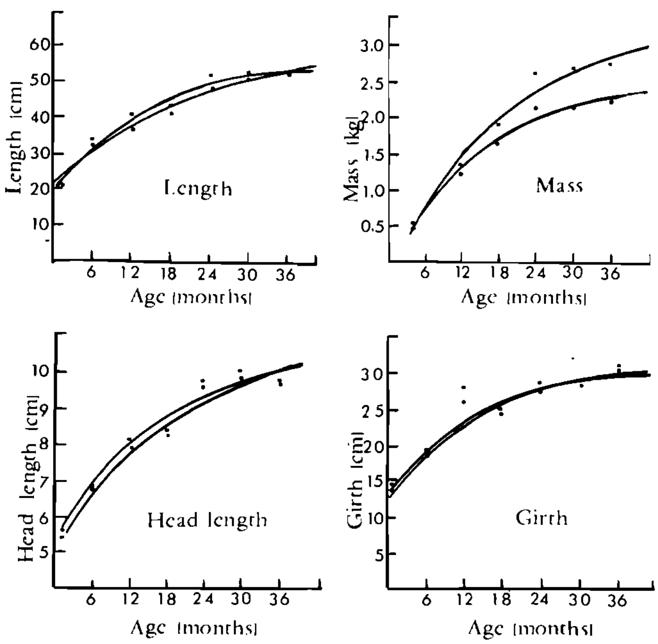


**Fig. 1** Von Bertalanffy growth curves for the hyrax, showing mass and body measurements used for age determination. Male■; Female ●.

### Age determination

Analysis of all the data indicated correlations ($r > 0{,}8$; $p$ 0,01) between age and mass, body length and headlength. Girth, backleg length and head width also correlated with age ($r > 0{,}6$; $p$ 0,05). Mass was considered too prone to environmental influence to be a good criterion for age determination and it was omitted from the regression analysis. The subsequent result indicated that length (L), girth (G) and headlength (HL) described the major portion of the variation and these parameters were used to formulate equations describing age.

In males age as given by Age (months) = 0,0547L + 0,0440G + 0,0125HL − 19,287 has a standard error of three months. Female age is described by Age (months) = 0,0506L + 0,0323G + 0,1746HL − 26,666 and also has a standard error of three months. The differences between the sexes is not significant and the regression equation for the sexes combined is Age (months) = 0,0593L + 0,0444G +

**Table 1** Means and standard deviations of mass (gm) and body measurements (mm) from hyrax of different ages

| Age (months) | Sex | Mass | Length | Girth | Hind leg | Lower leg | Front leg | Front pad | Hind pad | Head length | Head width |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | ♂ | 214 ± 26 | 209 ± 14 | 132 ± 9 | 94 ± 6 | 76 ± 4 | 55 ± 4 | 23 ± 1 | 36 ± 2 | 54 ± 2 | 24 ± 1 |
| | ♀ | 221 ± 72 | 205 ± 20 | 131 ± 20 | 95 ± 4 | 78 ± 5 | 56 ± 4 | 23 ± 2 | 36 ± 3 | 53 ± 2 | 24 ± 1 |
| 2 | ♂ | 282 ± 41 | 223 ± 9 | 147 ± 16 | 101 ± 5 | 81 ± 3 | 54 ± 5 | 26 ± 1 | 39 ± 2 | 59 ± 1 | 27 ± 0 |
| | ♀ | 266 ± 58 | 243 ± 11 | 158 ± 12 | 108 ± 5 | 85 ± 4 | 56 ± 1 | 26 ± 1 | 41 ± 2 | 60 ± 2 | 28 ± 1 |
| 3 | ♂ | 465 ± 57 | 256 ± 19 | 166 ± 7 | 115 ± 6 | 89 ± 3 | 65 ± 13 | 30 ± 3 | 43 ± 2 | 60 ± 2 | 28 ± 1 |
| | ♀ | 486 ± 90 | 263 ± 26 | 170 ± 10 | 126 ± 23 | 92 ± 15 | 63 ± 4 | 30 ± 2 | 43 ± 3 | 60 ± 4 | 27 ± 1 |
| 4 | ♂ | 550 ± 74 | 302 ± 20 | 174 ± 11 | 122 ± 5 | 95 ± 3 | 63 ± 3 | 29 ± 1 | 45 ± 3 | 64 ± 2 | 26 ± 1 |
| | ♀ | 490 ± 73 | 291 ± 13 | 166 ± 16 | 122 ± 6 | 91 ± 4 | 62 ± 2 | 28 ± 1 | 43 ± 3 | 61 ± 2 | 26 ± 2 |
| 5 | ♂ | 711 ± 101 | 304 ± 4 | 228 ± 47 | 132 ± 6 | 97 ± 3 | 68 ± 2 | 31 ± 1 | 47 ± 3 | 66 ± 2 | 36 ± 2 |
| | ♀ | 706 ± 108 | 316 ± 16 | 195 ± 17 | 133 ± 6 | 98 ± 6 | 68 ± 2 | 30 ± 2 | 46 ± 3 | 67 ± 3 | 28 ± 1 |
| 6 | ♂ | 750 ± 106 | 326 ± 28 | 181 ± 9 | 137 ± 8 | 103 ± 6 | 70 ± 3 | 32 ± 2 | 49 ± 3 | 67 ± 3 | 27 ± 1 |
| | ♀ | 813 ± 132 | 337 ± 16 | 187 ± 16 | 143 ± 8 | 108 ± 8 | 72 ± 2 | 32 ± 2 | 50 ± 2 | 69 ± 1 | 28 ± 1 |
| 12 | ♂ | 1 364 ± 140 | 411 ± 24 | 253 ± 17 | 159 ± 7 | 125 ± 8 | 91 ± 5 | 37 ± 4 | 52 ± 2 | 82 ± 6 | 35 ± 3 |
| | ♀ | 1 230 ± 72 | 370 ± 33 | 255 ± 12 | 152 ± 8 | 117 ± 8 | 85 ± 3 | 35 ± 2 | 49 ± 3 | 77 ± 2 | 23 ± 2 |
| 18 | ♂ | 1 888 ± 249 | 450 ± 17 | 253 ± 9 | 164 ± 8 | 132 ± 7 | 97 ± 6 | 43 ± 2 | 57 ± 2 | 84 ± 4 | 35 ± 1 |
| | ♀ | 1 674 ± 92 | 422 ± 14 | 245 ± 14 | 164 ± 5 | 127 ± 9 | 88 ± 5 | 40 ± 1 | 53 ± 3 | 80 ± 4 | 33 ± 1 |
| 24 | ♂ | 2 204 ± 296 | 440 ± 29 | 273 ± 17 | 174 ± 6 | 135 ± 8 | 100 ± 6 | 42 ± 2 | 56 ± 4 | 98 ± 5 | 36 ± 1 |
| | ♀ | 2 201 ± 247 | 423 ± 16 | 265 ± 5 | 171 ± 8 | 128 ± 11 | 95 ± 2 | 39 ± 3 | 54 ± 3 | 96 ± 4 | 34 ± 2 |
| 30 | ♂ | 2 848 ± 267 | 491 ± 15 | 276 ± 6 | 189 ± 5 | 159 ± 14 | 107 ± 5 | 44 ± 1 | 63 ± 4 | 101 ± 5 | 40 ± 2 |
| | ♀ | 2 667 ± 142 | 489 ± 20 | 290 ± 24 | 184 ± 5 | 152 ± 23 | 104 ± 9 | 43 ± 2 | 65 ± 2 | 98 ± 4 | 37 ± 2 |
| 36 | ♂ | 2 958 ± 210 | 528 ± 18 | 307 ± 10 | 196 ± 4 | 148 ± 12 | 109 ± 9 | 45 ± 3 | 68 ± 3 | 97 ± 9 | 39 ± 4 |
| | ♀ | 2 570 ± 161 | 522 ± 24 | 300 ± 16 | 182 ± 8 | 143 ± 22 | 98 ± 8 | 40 ± 2 | 63 ± 4 | 98 ± 4 | 37 ± 2 |

0,01117HL − 20,652 the standard error again being three months.

In the analysis of the skull measurements age correlated ($r > 0,8$; $p$ 0,01) with skull length, skull width and length of tooth row in the mandible and a correlation ($r > 0,6$; $p$ 0,05) between age and length of mandible and length of tooth row in the maxilla was also shown.

Age determination using skull measurements is of value to biologists, particularly where specific bones and intact skulls are often not available. A prediction equation was therefore calculated using skull width (SW), length of tooth row in the maxilla (LT max) and length of tooth row in the mandible (LT man). The equation is Age (days) = 34,136LT max + 39,866SW − 6,342LT man − 856,398. This equation is not very accurate and only estimates 50% of the ages to within three months when applied to the raw data.

Means and standard deviations for the skull measurements are shown in Table 2 and increase in mean eyelens mass with age in Table 3. If eyelenses are available they provide a reasonable indication of age up to 24 months, thereafter they are unreliable.

## Tooth replacement and wear

The sequence of tooth eruption and replacement is shown in Table 4. This method of ageing would seem to be reason-

**Table 2** Means and standard deviations of the skull measurements (mm) from hyrax of different ages

| Age | Skull length | Skull width | Mandible length | Mandible tooth-row length | Maxilla tooth-row length |
|---|---|---|---|---|---|
| 1 day | 41,6 ± 0,28 | 10,0 ± 0,07 | 32,1 ± 0,21 | 11,9 ± 0,21 | 13,3 ± 0,0 |
| 12 days | 43,4 | 10,0 | 35,0 | 15,0 | 15,0 |
| 30 days | 45,0 ± 0,12 | 9,9 ± 0,42 | 35,6 ± 0,9 | 15,1 ± 0,6 | 14,6 ± 0,4 |
| 43 days | 46,0 | 10,0 | 35,0 | 15,8 | 16,8 |
| 60 days | 53,3 ± 0,1 | 11,7 ± 1,6 | 42,5 ± 0,7 | 18,4 ± 0,0 | 20,0 ± 0,64 |
| 8 months | 64,9 | 14,2 | 56,0 | 25,2 | 27,0 |
| 10 months | 63,4 | 13,6 | 52,5 | 24,5 | 25,0 |
| 12 months | 70,3 ± 3,6 | 15,7 ± 0,83 | 62,7 ± 1,9 | 27,1 ± 3,7 | 28,2 ± 2,7 |
| 24 months | 76,3 ± 2,6 | 18,0 ± 1,5 | 72,6 ± 3,6 | 34,1 ± 1,9 | 34,5 ± 2,6 |
| 36 months | 79,0 ± 1,4 | 18,7 ± 1,9 | 73,5 ± 3,0 | 33,0 ± 0,96 | 35,7 ± 1,7 |

ably accurate. Additional replacement and wear criteria are of value in refining and extending the ages determined by means of the table.

**Table 3** Mean eyelens mass (g) and standard deviations from hyraxes at different ages

| Age | Eyelens mass |
|---|---|
| 1 day | 0,01160 |
| 12 days | 0,01680 |
| 43 days | 0,0247 |
| 58 days | 0,0307 |
| 12 months | 0,06612 ± 0,01 |
| 24 months | 0,0963 ± 0,01 |
| 36 months | 0,0948 ± 0,008 |

Replacement of incisors (I) occurs while the deciduous teeth are retained (Fig. 2). At eight months $I_1$ has just cut the gum. At 10 months $I_1$ is just cutting $I_2$ is not more than half the length of the deciduous teeth $I^1$ is about as long as the deciduous counterpart. The premolars (PM) are replaced between 11 and 15 months, replacement being variable within this period, after 15 months all premolars have been replaced and the first molar (M) shows signs of wear.

At 24 months $M_1^1$ is becoming distinctly worn, the premolars are well worn but $M_2^2$ shows only slight signs of wear. After 36 months all the teeth are worn with the exception of $M_3^3$ which is only slightly worn if at all. After four years the

**Table 4** Schedule of tooth replacement in the hyrax. O = No tooth; D = Deciduous; E = Erupting; R = Being replaced; and P = Permanent

| Age | $I_1$ | $I_2$ | c | $P_{m_1}$ | $P_{m_2}$ | $P_{m_3}$ | $P_{m_4}$ | $M_1$ | $M_2$ | $M_3$ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 day | D / D | O / D | E | D / D | D / D | D / D | O / O | O / O | O / O | O / O |
| 12 days | D / D | O / D | D | D / D | D / D | D / D | O / O | O / E | O / O | O / O |
| 30 days | D / D | O / D | D | D / D | D / D | D / D | D / O | E / E | O / O | O / O |
| 40 days | D / D | O / D | D | D / D | D / D | D / D | D / O | E / E | | |
| 60 days | D / D | O / D | D | D / D | D / D | D / D | D / O | E / P | O / O | O / O |
| 8 months | R / D | O / R | D | D / D | D / D | D / D | D / O | P / P | E / E | O / O |
| 10 months | R / R | O / R | D | D / D | D / D | D / D | D / O | P / P | E / E | O / O |
| 12 months | P / P | O / P | O | P / P | P / P | R / R | D / O | P / P | E / P | O / O |
| 15 months | P / P | O / P | O | P / P | P / P | P / P | P / O | P / P | E / P | O / E |
| 24 months | P / P | O / P | O | P / P | P / P | P / P | P / O | P / P | P / P | E / P |
| 36 months | P / P | O / P | O | P / P | P / P | P / P | P / O | P / P | P / P | P / P |


Fig. 2 Skulls of an estimated eight-year old (a) and a 10-month old (b) hyrax, showing toothwear and replacement of the incisors.

cusps of all teeth in the lower jaw except $M_3$ are worn down and the teeth present a straight grinding surface, wear can now also be seen on $M^3$ in the upper jaw. The condition of the teeth at eight years of age is shown in Fig. 2.

The permanent incisors in the mandible have longitudinal grooves on both upper and lower surfaces, these grooves are clearly visible at 15 months; at 24 months they are barely visible on the majority of teeth and are worn away on some; by 36 months they are completely absent. The wearing surface of $I^1$ in the upper jaw has a characteristic step or hook up to the age of 15 months and is a smooth triangle after this.

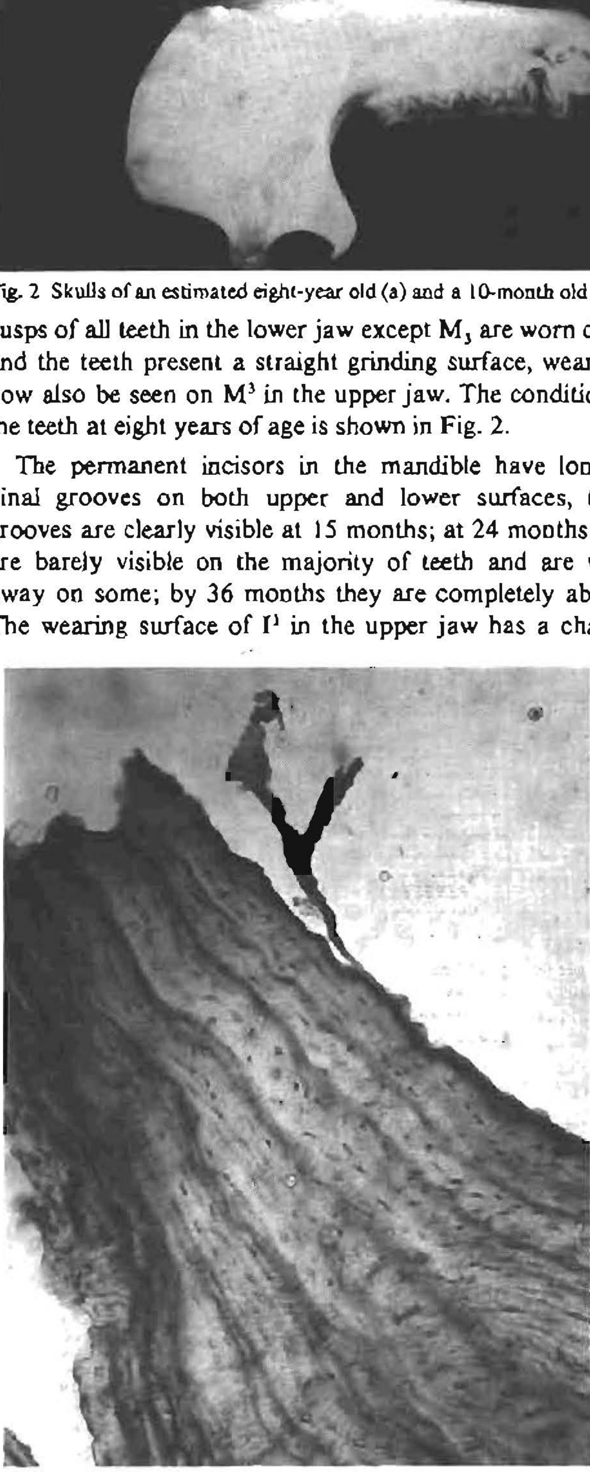

Fig. 3 Annulli in the dental cementum pad of the $M_1$ of a hyrax estimated to be eight years old.

### Annular layers in the dental cementum

Examination of sectioned teeth showed that the cementum consisted of different staining layers, the 24 month-old group having one dark line while the 36 month-old group had two dark lines. This corresponds to the annular layers mentioned in the literature and indicates that age may be estimated as the number of darkly staining lines plus one.

The annulli were found in both the incisors and the molariform teeth and were more clearly defined in some regions of the cementum than others. The single annular band was also found to consist of an irregular number of thinner lines in some areas, these however coalesced in other areas and could be clearly counted. The best region was found to be the cementum pad between roots of the molar teeth.

## Discussion

### Growth

The Von Bertalanffy growth equation used in this study was developed on a theoretical basis. The physiological assumption underlying the theory has since been questioned (Ricker 1975) but Blaxter (1968), in a comparison of the mathematical description of energy retention and the essentially similar Brody growth equation (Brody 1945), has indicated that these empirical growth equations have a strong relationship to the physiology of food utilization in ruminants.

The Von Bertalanffy equation has been applied to a large number of vertebrates and the observed growth curves are sufficiently close to the empirical relationship to make it an acceptable descriptive method. Use of this growth equation has the advantage that growth of animals of widely differing size and age can be compared on an equivalent basis, because it describes growth in relation to the time over which it occurs and relative to the final size of the animal.

The growth coefficient K is the most important function of the equation in this respect. For the hyrax this is 0,06 which is more closely related to the elephant *Loxodonta africana* ($K = 0,075$; Hanks 1972) than for instance the impala *Aepyceros melampus* ($K = 1,130$ ♂, 1,61 ♀; Howells & Hanks 1975) or the zebra *Equus burchelli* ($K = 0,99$; Smuts 1973).

Therefore, although the absolute growth rate of the elephant is higher than for any of the other species, its growth rate relative to its final size is more nearly equivalent to that of the hyrax. This could possibly be related to the proposed phylogenetic similarity between the two species.

The relative growth of different body components termed allometric growth provides a means of visually ageing animals in the field, in the hyrax the growth curves of the body measurement are essentially similar and the relative size of body components does not provide much information for age determination. Subjective classification of size of the whole animal as indicated by mass should provide an acceptable means of obtaining age structure data in the field if better methods are not applicable.

Growth in this study was measured on captive animals. Petrusevicz and MacFadyn (1970) indicate the dangers inherent in this approach as growth can vary widely between captive and wild individuals. Millar (1971) provides information on growth of a tame hyrax compared with wild and captive individuals. While his tame individual confirms the reservations expressed by Petrusewicz and MacFadyn, the captive individuals have the same growth curve as their wild counterparts. Millar's study was carried out at the same research station on animals kept under essentially the same conditions as in the present study.

## Age determination

Growth of the whole animal or the relative growth of specific parts has been used mainly to evaluate age in subjective classes. In most animals studied, growth is completed in a short period relative to the lifespan and this measure does not provide a very useful prediction. In the hyrax growth is slow and this study has shown that body measurements can provide a highly accurate indication of age up to three years. In spite of the slow maturation of the body size Millar (1971) has shown that a high percentage of hyrax conceive in their first year. Accurate ageing of a significant proportion of the productive population is thus possible and this holds promise in a study of the population dynamics of this species.

One of the advantages of this method is that animals do not have to be killed to determine their age. A population can therefore be studied without the disruption inherent in the taking of samples for age determination.

Ageing by means of skull measurements surprisingly, does not provide good age criteria. This can possibly be ascribed to the small number of specimens in the lower age classes. The skull however, is the earliest maturing portion of the body and this could also contribute to the relative inaccuracy of these measurements for ageing.

Tooth eruption and wear is one of the most universally utilized methods of ageing. Roche (1978) has applied this technique to the hyrax *Procavia capensis syriaca* from Israel and claims that it can be used up to an age of six years. The present study confirms that the technique is applicable and the data largely agree with those reported by Roche. The major deviations are in the eruption of $PM^4$ which is not erupting at birth in the present series ($n = 4$) and erupting in the Israeli material ($n = 2$) although full eruption is reported at equivalent ages. $M^3$ is taken as fully erupted in the present study ($n = 10$) at 36 months while the Israeli material shows this tooth fully erupted at 68 months although both studies indicate that the start of eruption occurs at 24 months.

The discrepancy in the two studies could be explained by the fact that skulls are used in both cases and that criteria for a fully erupted tooth were different. It is possible that $M^3$ was not fully erupted at 36 months in the present investigation, at 48 months however, wear was apparent on the single skull available and which was aged by means of cementum annulli.

In summary age determination by predictive equations using body measurements seems to be the most practical technique. This can be refined by tooth replacement and wear criteria. The latter technique should be used for ageing skulls if teeth cannot be extracted for sectioning. A rough indication of age can however be obtained from skulls using a predictive equation.

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This study was initiated while the author was employed by the Department of Nature and Environmental Conservation of the Cape Province and the hyrax were kept at their Vrolijkheid Problem Animal Research Station. Messrs J. Joubert and C.T. Stuart were in charge of the hyrax and assisted in capturing and measuring the hyrax for which I would like to express my appreciation as well as to all the staff of the Research Station and especially Mr F. Vorster for their hospitality and friendship while I was working there.

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