

# Age determination in the Cape molerat *Georychus capensis*

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An analysis of 92 specimens of *Georychus capensis* showed them to have a distinct season of birth (October to December) with a maximum of two litters per season. Given this distinct seasonality in breeding, and using the date of capture and the presence or absence of placental scars, the age of non-parous and most non-pregnant females could be determined with an accuracy of about 1.5 months (half the length of the birth period). Six cheek tooth eruption and wear stages were recognized. These, as well as body mass, were significantly positively correlated with age. Tooth characteristics and body mass were therefore used, in conjunction with the date of capture, to determine the age of males and pregnant and multiparous females. The growth characteristics of *G. capensis* were then investigated: growth in mass appears to continue after reproductive maturity with only a slight levelling off. All body and skull measurements were significantly positively correlated with age ( $P < 0,001$ ). A semi-log regression model (with age  $\log_{10}$  transformed) gave the best fit of the data, except in the case of body mass, which was slightly better predicted by a linear model. Skull parameters were generally more strongly correlated with age than was body mass, which in turn was better than linear body measurements. Lower jaw length, two separate measurements of skull height, and zygomatic width were the individual measurements most strongly correlated with age. No sexual dimorphism was found in *G. capensis*.

*S. Afr. J. Zool.* 1985, 20: 261 – 267

'n Analise van 92 *Georychus capensis* het getoon dat hulle 'n definitiewe geboorteseisoen het (Oktober tot Desember) met 'n maksimum van twee werpsels per seisoen. Gegee hierdie teel-seisoenaliteit, en deur gebruik te maak van die vangdatum en die teenwoordigheid of afwesigheid van plasentale littekens, kon die ouderdom van maagdelike en die meeste nie-dragtige wyfies bepaal word tot 'n akkuraatheid van ongeveer 1,5 maande (hefte van die geboorteseisoen). Ses kiestandontwikkelings- en slytasiefases was herkenbaar. Dié fases asook liggaamsmassa was betekenisvol positief gekorreleer met ouderdom. Tandkenmerke en liggaamsmassa is derhalwe saam met die vangdatum gebruik om die ouderdomme van mannetjies, asook dragtige en veelbarende wyfies te bepaal. Groeikenmerke van *G. capensis* is ook ondersoek: toename in massa geskied blykbaar tot na geslagsrypheid met slegs 'n geringe afplating. Alle liggaams- en skedelafmetings was betekenisvol positief met ouderdom gekorreleer ( $P < 0,001$ ). 'n Semi-logregressiemodel (met ouderdom  $\log_{10}$  getransformeer) het die data die beste gepas, behalwe in die geval van liggaamsmassa waar 'n lineêre model ietwat beter was. Skedelparameters was oor die algemeen beter voorspellers van ouderdom as liggaamsmassa, wat weer beter was as lineêre liggaamsafmetings. Lengte van die onderkaak, twee aparte afmetings van skedelhoogte en die wydte van die sigmatiese boog was die beste afsonderlike voorspellers van ouderdom. Geen geslagtelike dimorfisme is in *G. capensis* gevind nie.

*S.-Afr. Tydskr. Dierk.* 1985, 20: 261 – 267

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Received 20 February 1985; accepted 2 May 1985

The Cape molerat, *Georychus capensis*, is a subterranean rodent occurring mainly in the south-western Cape, South Africa. Little has been published on its biology (Smithers 1983), and the few mensural data available are based on small sample sizes (Roberts 1951; De Graaff 1981; Smithers 1983). As a result of this dearth of data, no attempt has previously been made to investigate the growth rates of these molerats, or to investigate reliable age determination methods, although Roberts (1951), using a sample of 26 animals, proposed five age classes based on tooth eruption and wear. This paper describes new details concerning the breeding season of *G. capensis*, which can be used to establish an absolute age determination method (age expressed in precise units of time) for the species. This 'known age' sample is then compared with other relative age determination techniques (which express the stage of growth of an individual relative to another), including those based on body mass, body and skull dimensions, and tooth wear and eruption. The 'known age' sample was also used to examine rates of growth of *G. capensis*.

## Methods

### Study Animals

Data were collected from 92 *G. capensis* caught, mainly by snaretrapping, on golfcourses of the Cape Peninsula. Molerats were collected during each month of 1979 and occasionally in 1980 and 1982. For each specimen, the date of capture was recorded, in addition to total body mass (BM) to the nearest gram, head-body (HB), tail (TAIL) and hind foot *sine unguis* (HF) lengths (to the nearest mm), and reproductive information. The reproductive state of the females was assessed from the condition of the vaginal closure membrane (perforate or imperforate), from evidence of previous litters (placental scars), and the condition of the mammary glands (lactating or not). The reproductive state of the males was assessed by the presence or absence of spermatozoa in the vasa deferentia, and the size (length and width, mm) and position (undescended or inguinal) of the testes. All skulls were cleaned and retained for analysis. The skulls and study skins are now housed in the South African Museum, Cape Town. To reduce error as far as possible, all skull measurements were made by one of us (PJT) and body measurements and reproductive assessment by JUMJ.

### Skull measurements

Nine measurements were taken for each skull (Figure 1), using vernier callipers, with 0,05 mm accuracy. Occasionally replicate measurements were made on a skull to test for accuracy.

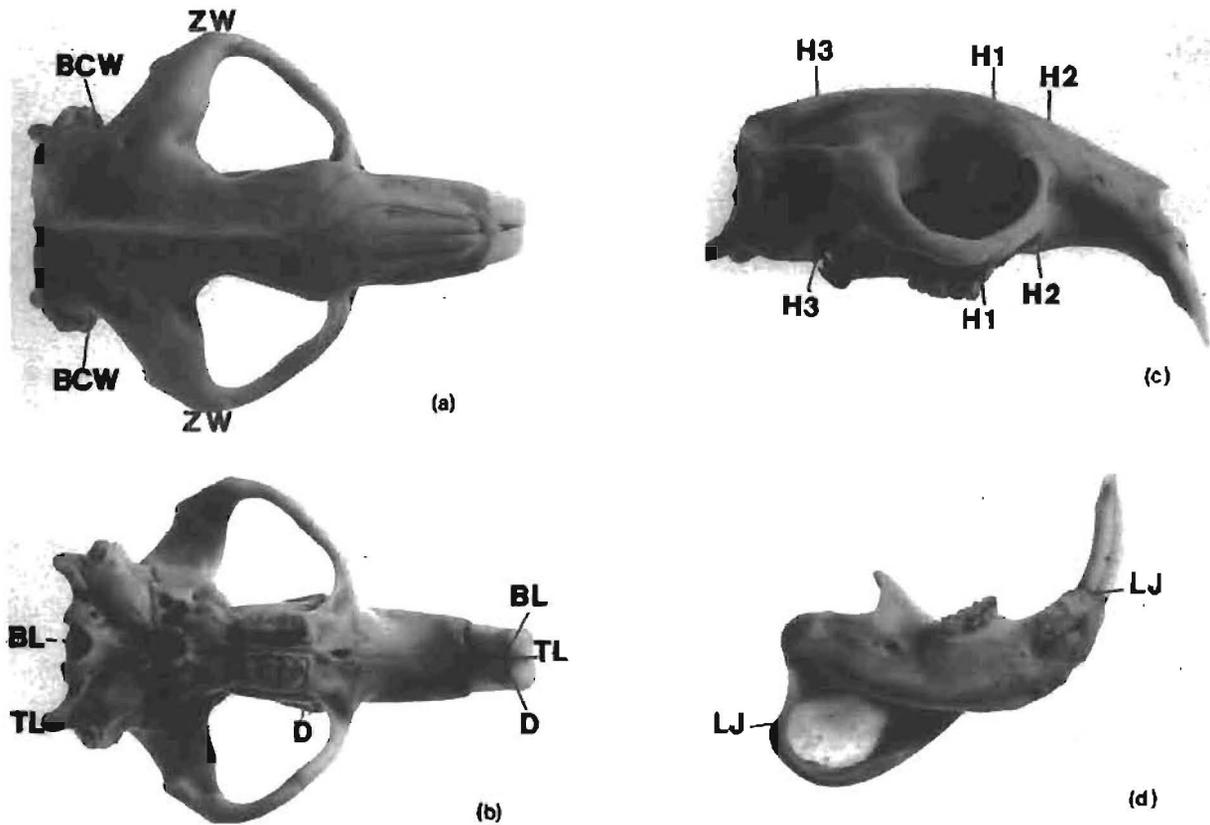


Figure 1 Dorsal (a), ventral (b), and lateral (c) views of a *G. capensis* skull, and (d) lateral view of the lower jaw, showing measurements taken.

BCW = brain case width: widest measurement of brain case dorsally.

BL = basilar length: distance from anterior end of foramen magnum to middle of base of incisors.

D = diastema length: distance from left anterior molar to middle of base of incisors.

H1 = height of skull, vertically above base of first (anterior) cheek tooth.

H2 = height of skull, vertically above junction of premaxilla and palatines on ventral surface.

H3 = height of skull, vertically above a point on midline of ventral surface corresponding with anterior edge of the auditory bulla.

LJ = lower jaw length: from left angular process to front left of dentary.

TL = total skull length: paroccipital to middle of base of incisors (premaxilla)

ZW = zygomatic width

They never varied by more than 0,2 mm, and were usually within 0,1 mm, of the original measurements.

#### Age estimates using dates of birth and capture

The age of molerats was estimated according to the number of months elapsed between the mid point of the birth season (November) and the month of capture. For females, if placental scars were present, age was taken to be one year plus the number of months indicated by the date of capture. Males were aged according to the date of capture, obvious changes in tooth eruption and wear, presence or absence of sperm and by comparison of masses with previously aged females.

#### Tooth eruption and wear

Tooth eruption and wear were described for the upper, right tooth row of each individual. This was chosen arbitrarily since a preliminary examination of the skulls showed no difference in eruption and wear between upper and lower jaws, or between the right and left sides. Using eruption and wear, six dental age classes were distinguished, and each individual was assigned to a class, based on the number of cheek teeth present and the stage of wear of each tooth: unworn, partially worn and completely worn (Figures 2 and 3).

#### Statistical analysis

The data were analysed on a Sperry 1100/81 computer, using

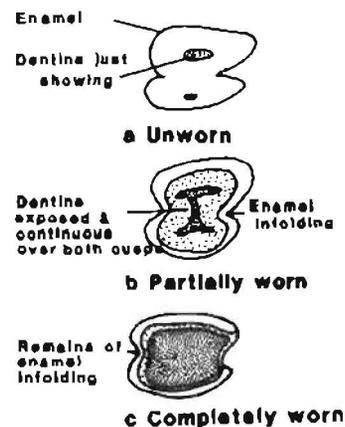
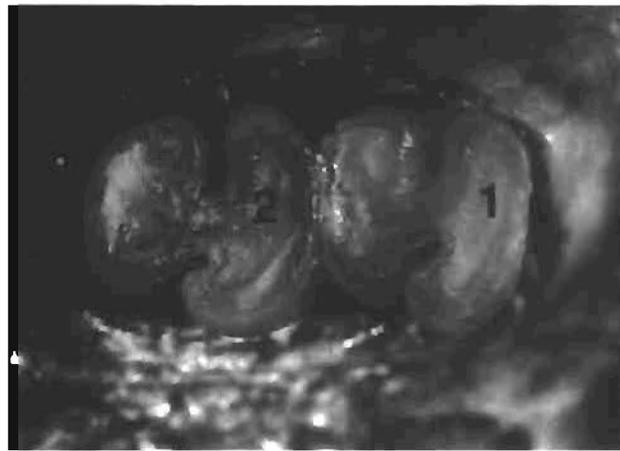


Figure 2 Occlusal surface of cheek teeth to illustrate the three stages in wear.

two programs from the BMDP statistical software series (Dixon 1981): simple regression analysis (BMDP6D) and grouped data description including histograms and analysis of variance (BMDP7D). These statistical procedures are described in detail in Sokal & Rohlf (1981). All data and results of the above analyses are available in printout or magnetic tape form from TMC.



Class 1



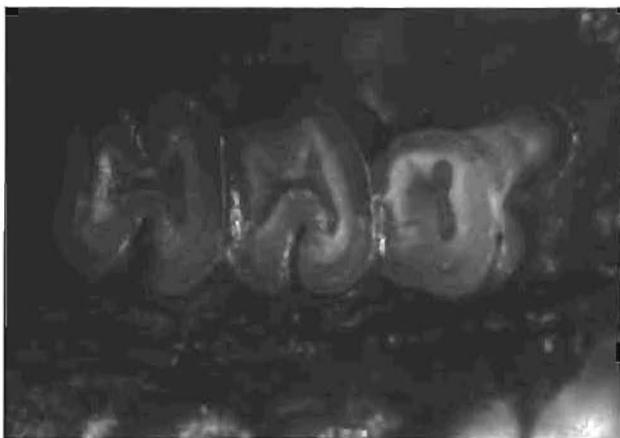
Class 4



Class 2



Class 5



Class 3



Class 6

**Figure 3** Photographs of the right upper cheek tooth row showing the classes of tooth eruption and wear (1–6) described for *G. capensis*. The teeth are numbered 1–4 in order of eruption.

## Results and Discussion

### Sexual dimorphism

Roberts (1951) commented that males are normally smaller than females in the genus *Georychus*. De Graaff (1981) and Smithers (1983) suggested that the zygomatic arch is more bowed in males than in females, and De Graaff (1964) states that males are marginally larger than the females. Table 1 shows that, for the variables used, there is no sexual dimorphism in *G. capensis* from the Cape Peninsula. In particular, the male and female means for zygomatic width are very similar (Table 1).

### Age determination

#### *Using dates of birth and capture*

Breeding characteristics have been successfully used to age spring hare, *Pedetes capensis* (Cameron-Smith, 1965) and hyrax, *Procavia capensis* (Fourie, 1983). In the Cape Peninsula, *G. capensis* has a discrete breeding season. Pregnant females were trapped between September and December (Table 2), and lactating females and newly born juveniles between October and December. This, and the fact that placental scars persist until the beginning of the next breeding season, make it possible to determine the approxi-

**Table 1** Analysis of variance of male and female body mass, and body and skull dimensions, in *G. capensis*. (See Figure 1 for abbreviations for skull measurements and methods for body measurements)

Variable abbreviation and unit	Males			Females			F value <sup>a</sup>
	Mean	(n)	S.D.	Mean	(n)	S.D.	
BM (g) <sup>b</sup>	181,8	(51)	73,3	180,0	(37)	92,3	0,01
HB (mm)	158,3	(52)	23,2	156,2	(38)	25,0	0,17
TAIL (mm)	20,6	(52)	2,5	20,5	(38)	3,4	0,02
HF (mm)	28,1	(52)	3,0	27,6	(38)	3,3	0,60
TL (mm)	43,6	(49)	5,77	44,42	(34)	7,35	0,28
BL (mm)	39,3	(49)	5,22	40,05	(34)	6,32	0,35
BCW (mm)	16,94	(51)	0,99	16,96	(34)	1,21	0,01
ZW (mm)	31,34	(48)	4,89	31,25	(34)	6,01	0,01
D (mm)	18,02	(50)	2,68	18,17	(38)	3,85	0,05
LJ (mm)	36,02	(50)	5,28	35,60	(38)	6,41	0,12
H1 (mm)	14,43	(50)	2,48	14,31	(36)	2,97	0,04
H2 (mm)	11,26	(50)	1,80	11,28	(36)	2,27	0,00
H3 (mm)	13,93	(51)	1,48	13,89	(34)	1,54	0,00

<sup>a</sup>All F values were non-significant at the 5% level

<sup>b</sup>Mass refers to complete animals, including viscera.

**Table 2** Trapping, morphological and reproductive information for pregnant *G. capensis*

Mass (g)	Month caught	Litter size	No. placental scars	Tooth class
157	Sept.	4	0	3
220	Sept.	7	0	5
211	Sept.	6	0	4
192	Sept.	6	0	5
283	Sept.	6	0	4
241	Oct.	5	0	6
335	Nov.	9	9	4
290	Dec.	10	5	5
334	Dec.	1	10	6

mate chronological age of individuals, by extrapolating back from the date of capture to the time of birth.

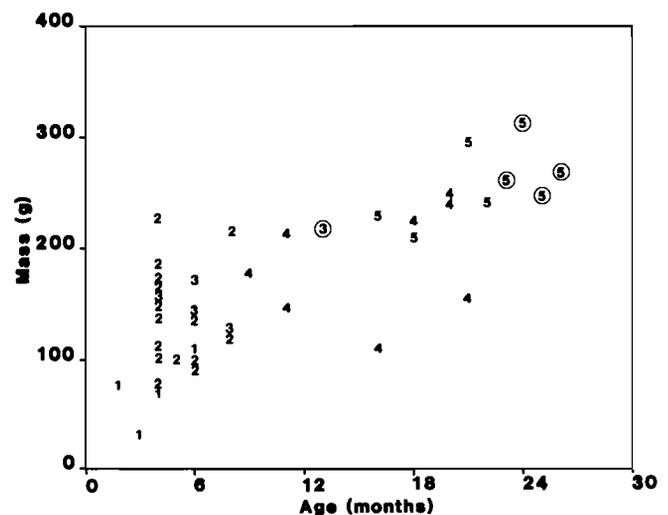
In using reproductive information to obtain known ages of *G. capensis* three important limitations need to be considered:

- Because the birth season is at least three months long and all individuals were assumed to have been born during the middle of the season, there is an inherent potential error of up to 1,5 months in the estimated age.
- Problems were experienced in ageing pregnant and multiparous females, when only using date of capture and placental scars. Pregnancy tended to mask old scars, although very recent ones could still be distinguished in pregnant animals. Thus, although females with placental scars (from the previous breeding season) were caught in August, one month before the beginning of the next breeding season, no scars were seen in pregnant females in September and October (Table 2). Four of these pregnant females had fully erupted and worn cheek teeth, suggesting that they were at least in their second breeding season (Figure 4). Pregnant females with fresh uterine scars and in some instances with young in the burrow and/or with clear evidence of recent suckling (matted fur or bare areas around enlarged nipples) were caught in

November and December both in this sample ( $n = 3$ ) and in another study ( $n = 3$ ), suggesting that at least some of the molerats have two litters per season. From this it would appear that pregnant and multiparous females can therefore not be aged unambiguously by means of the presence or absence of placental scars and the date of capture. This method of ageing *G. capensis* females is only reliable up to the commencement of the second breeding season, about 18–24 months after the birth of the molerat. In our study area, the molerats were undergoing heavy continuous trapping and, from the degree of toothwear, few animals were older than two years. The longevity of *G. capensis* in captivity or in the wild, has not been established.

- Male *G. capensis* could not be aged by reproductive information only since they left no structural evidence, that could be determined by gross examination, of having bred the previous year. The state of preservation of many of the specimens precluded a histological examination of the testes.

In view of the above limitations, when using only the date of capture and reproductive information, our sample of 'known age' molerats was restricted to non-parous females and to non-pregnant females that had completed their first breeding season. However if body mass, and tooth eruption and wear are used in conjunction with the date of capture and reproductive information, ages could be estimated for all the animals in the sample.



**Figure 4** The relationship between body mass, and tooth wear-eruption classes (1–5, see text) in female *G. capensis*; excluding pregnant females. Circled numbers represent individuals which could not be objectively aged by the presence or absence of placental scars; they have been placed according to date of capture, molar characteristics and body mass, and are not included in regression analysis.

#### Using tooth eruption and wear

In *G. capensis*, the last cheek tooth erupts fairly late (when 9–10 months old). It is the only bathyergid in which the cheek teeth of adults have an inner and an outer fold of enamel which persist until the teeth are well worn. Adult molerats of all the other genera have simplified ovate cheek teeth (De Graaff 1981).

The homology of the molariform teeth in the Bathyergidae is uncertain. Sclater (1899), Weber (1928) and Landry (1957) suggest the four teeth of *Georychus* and *Bathyergus* comprise a premolar and three molars while Thomas (1909) and Roberts

(1951) suggest two premolars and two molars. To avoid confusion they will hereafter all be referred to as cheek teeth.

In *G. capensis*, one cheek tooth is present at birth ( $n = 4$ ), two are present in newly weaned juveniles ( $n = 8$ ), the second tooth erupting at 3 weeks ( $n = 2$  juveniles born in captivity) and four are present in adults ( $n = 33$ ). Three distinct stages of tooth wear were recognized, based on the amount of wear of the enamel and the area of exposed dentine: unworn, partly worn, and completely worn (Figure 2). Based on tooth eruption and wear, six dental age classes were distinguished (Figure 3). These classes, together with the mean estimated age of molarats in each class are described below.

**Class 1** (Newly weaned juvenile,  $n = 9$ , mean age = 2,22 months, *S.D.* = 1,39) Two cheek teeth present. Both unworn.

**Class 2** (Older juvenile,  $n = 23$ , mean age = 4,04 months, *S.D.* = 1,58) Three cheek teeth present. At least two unworn.

**Class 3** (Sub-adult,  $n = 13$ , mean age = 5,77 months, *S.D.* = 2,74) Three cheek teeth present. At least two partly worn.

**Class 4** (Adult,  $n = 14$ , mean age = 12,21 months, *S.D.* = 4,68) Fourth cheek tooth just erupting, or erupted and unworn. First and sometimes the second cheek tooth may be completely worn.

**Class 5** (Adult,  $n = 14$ , mean age = 20,43 months, *S.D.* = 3,37) Fourth cheek tooth partially worn. First two or three may be completely worn.

**Class 6** (Old,  $n = 4$ , mean age = 32,50 months, *S.D.* = 3,79) All cheek teeth completely worn. Enamel walls breaking down, infoldings becoming indistinct.

In all the above age classes, except Class 4, the mean ages of males and females were similar. In Class 4 the mean age of males ( $n = 6$ , mean age 8,83 months, *S.D.* = 0,98) was less than for females ( $n = 8$ , mean age 14,75 months, *S.D.* = 4,77).

#### Age-specific growth parameters

Figure 4 shows the relationship, in female *G. capensis*, between the three potential measures of age: absolute age based on date of capture and on reproductive information, tooth eruption and wear, and body mass. Progressive tooth wear and eruption (from Class 1 to 4) is strongly positively correlated with an increase in mass ( $r = 0,72$ ;  $n = 35$ ;  $P < 0,001$ ) and absolute age ( $r = 0,87$ ;  $P < 0,001$ ). Age is also significantly correlated with mass ( $r = 0,67$ ;  $n = 35$ ;  $P < 0,001$ ). Since both tooth characteristics and mass are well correlated with absolute age, their use (in conjunction with the date of capture) to obtain estimated ages for breeding females and for males can be justified. The correlation between tooth wear/eruption classes and mass in males is also significant ( $r = 0,83$ ;  $n = 37$ ;  $P < 0,001$ ).

In summary, the absolute age determination technique proposed for *G. capensis* employs the season of birth, date of capture and occurrence of placental scars, to age non-parous, and non-pregnant parous females that have completed their first breeding season. Males and pregnant and multiparous females can be aged using the date of capture, stage of tooth eruption and wear, and body mass.

In the absence of information on reproduction, body mass or date of capture/death, e.g. for skulls found in pellets produced by birds of prey, tooth eruption and wear and some skull dimensions (see later) can be useful indicators of age.

Thus, in both sexes, the time of eruption of the final cheek tooth seems to be strongly correlated with the onset of reproductive maturity (taken to be 10 months: the time from the date of birth to the first month with pregnant females, Table 2). The use of tooth eruption, and particularly of tooth wear, to age mammals involves a degree of error due to individual variation of tooth characteristics. Variability in tooth wear may be due to genetic differences in enamel hardness, and differences in soil and diet hardness (Morris 1972; Fourie 1983). The use of tooth wear on its own has been shown to be an unreliable ageing method (Hall, Cloutier & Griffin 1957; Keiss 1969; Gilbert & Stolt 1970; Morris 1972; Cameron-Smith 1965), although some of the error can be eliminated by studying single populations and by using tooth wear as a relative rather than absolute method of ageing the population. By using other criteria in conjunction with tooth wear, Fourie (1983), in selection trials with an 'untrained' scientist, demonstrated a 70% agreement between age and tooth wear and eruption in *Procavia capensis* and Lowe (1967) showed an 85% success rate for a known age sample of red deer *Cervus elapsis*. It is probable that the time of tooth eruption is less variable and can serve as a valuable marker, especially when, as in *G. capensis*, the last molar erupts at the onset of reproductive maturity.

#### Growth

Growth in body mass in *G. capensis* does not appear to reach an asymptote, at least until the third year (Figures 4 and 5).

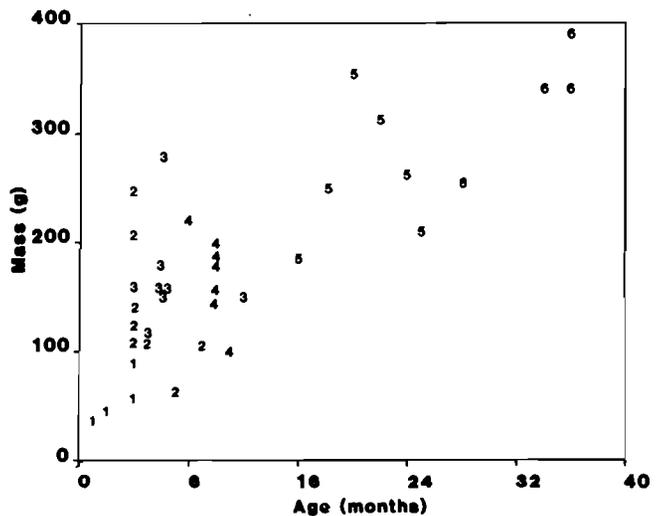


Figure 5 The relationship between body mass, age and tooth wear-eruption classes (1–6, see text) of male *G. capensis*.

This is consistent with field and laboratory observations (by JUMJ) of different size categories of reproductively active individuals. In support of this possibility of continued growth, a linear model fitted to the data shown in Figure 4 yielded the same correlation coefficient as a semi-log model, with age  $\log_{10}$  transformed ( $r = 0,67$ ,  $n = 35$ ;  $P < 0,001$ ), and a somewhat better fit than a power curve model ( $r = 0,63$ ,  $n = 35$ ;  $P < 0,001$ ). When, as in most small mammals, growth rapidly approaches an asymptote after sexual maturity, a linear model should give a poor correlation, while a model using transformed data (exponential or power curve) should give a better fit. The available data for *G. capensis* do not conform with this generalization, suggesting only a slight levelling off in the rate of increase of body mass.

To test more rigorously the possibility of continued growth, males and females were separated into two categories, those younger than 12 months and those older than 12 months. Only males and non-pregnant females were considered. It was found that the older females and males have growth rates of  $7,6 \text{ g month}^{-1}$ , and  $5,8 \text{ g month}^{-1}$ . These growth rates are similar to those of the young molerats ( $8,2 \text{ g month}^{-1}$  for females and  $7,4 \text{ g month}^{-1}$  for males). In each category, there is a statistically significant ( $P < 0,05$ ) correlation between age and body mass. Bearing in mind the limitations of the age determination method used, this evidence supports the possibility that, in *G. capensis*, growth in mass continues after reproductive maturity. The null hypothesis (that there is no growth after maturity), can be statistically rejected, at the 0,05 level, since age and mass were significantly and positively correlated in molerats older than 12 months.

It must be mentioned that the relatively large sample of four-month-old individuals, and the scarcity of individuals of three months old or less (Figures 4 and 5), will tend to underestimate the growth rates of the younger molerats and also 'ignore' the exponential phase of growth. This sample bias also partially explains the good linear fit obtained for the data represented in Figure 4. The existence of an exponential phase of growth in *G. capensis* has been confirmed by measurements of growth rates in molerats born in captivity (N. Bennett and J.U.M. Jarvis, unpub. data).

Because of the paucity of animals older than an estimated age of 24 months in our sample, it is not possible to say when growth in mass ceases. Indeed, in view of the limitations in our absolute ageing method and the bias in the data set discussed above, our conclusions as to continued growth in *G. capensis* are tentative, representing the best explanation of the facts at present.

Body mass has been shown, by most authors, to be a poor indicator of age in small mammals (Cameron-Smith 1965; Chaplin & White 1969; Bothma, Teer, & Gates 1972; Henschel, David & Jarvis 1982), though Fourie (1983) found it to be useful. Morris (1972) pointed out that mass is affected by health and diet. He suggested that the problem of variable food content of the stomach could be overcome by using eviscerated masses, although he found that, for large samples, complete body masses were proportional to eviscerated masses. For this reason, and because it would preclude using total body mass to age live molerats in the field, eviscerated masses were not used in this study although they were available for most of the individuals. Despite the problems mentioned above, mass is strongly correlated with age in *G. capensis* ( $r = 0,76$ ;  $n = 72$ ;  $P < 0,001$ ). A possible reason for the surprisingly high correlation between age and mass, compared with previous studies, may be the continuous growth observed for *G. capensis* (Figure 4). Previous research suggests that the limitations in using body mass as an age index are related to the levelling off of growth in adults (Bothma *et al.* 1972; Morris 1972; Henschel, *et al.* 1982; Fourie 1983). This error is minimized, in the Cape molerat, if growth indeed continues for an extended period as our studies suggest. It is pertinent to mention here that a prolonged period of growth has also been found in another bathyergid, *Heterocephalus glaber* the naked molerat (Jarvis 1981). Here, although these molerats are small (mean mass of individuals within a colony ca 35 g), individuals take 18–24 months to attain this mass; indeed, members of the non-working caste (mass up to 60 g) will continue growing for a number of additional years. In *H. glaber*, this slow rate of growth may be partly attributed to their low basal metabolic rates (McNab 1966; Jarvis 1978).

Lower than expected metabolic rates are a characteristic feature of subterranean mammals (McNab 1966) and may therefore also account for the extended period of growth indicated by our data for *G. capensis*.

### Body and skull linear measurements

Changes in body mass, and body and skull dimensions in *G. capensis* show highly significant regressions against age (Table 3). A linear model gives the best fit for body mass versus age

**Table 3** Results of semi- $\log_{10}$  regression of age versus various body and skull measurements. Data for male and female *G. capensis* combined. (See Figure 1 for abbreviations of skull measurements and methods for body measurements)

$\log_{10}$ Age	= $(2,02 \times 10^{-1})$ MC	+ 0,28; $n = 82$ ; $r = 0,93^a$
	= $(2,98 \times 10^{-3})$ BM	+ 0,41; $n = 80$ ; $r = 0,74$
	= $(8,50 \times 10^{-3})$ HB	- 0,38; $n = 82$ ; $r = 0,65$
	= $(5,37 \times 10^{-2})$ TAIL	- 0,16; $n = 82$ ; $r = 0,54$
	= $(6,10 \times 10^{-2})$ HF	- 0,75; $n = 82$ ; $r = 0,63$
	= $(3,87 \times 10^{-4})$ TL	- 0,72; $n = 75$ ; $r = 0,79$
	= $(4,57 \times 10^{-4})$ BL	- 0,82; $n = 75$ ; $r = 0,81$
	= $(2,05 \times 10^{-3})$ BCW	- 2,50; $n = 76$ ; $r = 0,69$
	= $(4,99 \times 10^{-4})$ ZW	- 0,59; $n = 73$ ; $r = 0,83$
	= $(7,99 \times 10^{-4})$ D	- 0,49; $n = 80$ ; $r = 0,80$
	= $(4,65 \times 10^{-4})$ LJ	- 0,71; $n = 81$ ; $r = 0,85$
	= $(1,01 \times 10^{-3})$ H1	- 0,49; $n = 77$ ; $r = 0,84$
	= $(1,34 \times 10^{-3})$ H2	- 0,55; $n = 77$ ; $r = 0,83$
	= $(1,67 \times 10^{-3})$ H3	- 1,34; $n = 76$ ; $r = 0,79$

<sup>a</sup>All correlation coefficients significant at the  $P < 0,001$  level

for all non-pregnant molerats. In the analysis of linear measurements of body and skull (data from pregnant animals included) a semi-log model, with age  $\log_{10}$  transformed, always gave the best fit. Power curve models also gave slightly better approximations of age than did linear ones. This suggests that body and skull lengths, unlike body mass, show the typical pattern of initially rapid growth reaching an asymptote after maturity. Skull dimensions are more strongly correlated with age ( $r$  varies from 0,69 to 0,85) than are body dimensions ( $r$  varies from 0,54 to 0,65), and mass is intermediate ( $r = 0,74$ ). The higher correlations obtained for skull dimensions may be due to the possibility that body measurements are more prone to be influenced by health and environmental factors, such as diet (Morris 1972). Furthermore, the error involved in measuring a soft flexible body will be higher than in measuring a rigid skull (Jewell & Fullagar 1966). Fairall (1980) found that in *Procavia capensis*, skull measurements were less accurate than body measurements as an ageing technique, and attributed this to the earlier maturation of the skull. However, subsequent work on *Procavia capensis* (Fourie 1983) showed that a multiple regression equation using skull measurements gave a better indication of age than an equation employing body measurements.

Of all the skull dimensions measured, lower jaw length (LJ), two separate measurements of skull height (H1 and H2) and zygomatic width (ZW) are most strongly correlated with age (Table 3:  $r = 0,85$ ;  $r = 0,84$ ;  $r = 0,83$  and  $r = 0,83$  respectively). This is consistent with the fact that lower jaw length and zygomatic width both reflect the degree of jaw muscle development related to burrowing (*G. capensis* digs with its incisors), which would increase proportionally with age.

### Acknowledgements

We are grateful to the managers and groundsmen of the following golf courses for collecting molerats for us: Mowbray; Royal Cape, Rondebosch; Milnerton; and Westlake. Ottery sports club, and a number of helpful members of the public also supplied us with molerats and our thanks go to them. Susan Adams assisted in the preparation of the skulls and the recording of data. This research was funded by grants from the CSIR and the University of Cape Town. Computer analyses were done on the University of Cape Town Sperry 1 100/81 mainframe. We are grateful for the comments of two anonymous reviewers of this paper.

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