Age determination and age structure of a striped fieldmouse, *Rhabdomys pumilio*, population from the Cape Flats

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The validity of predicting the age of *Rhabdomys pumilio* by age-related changes in tooth appearance, dimensions and position, in body mass and head-body length is tested against 47 known-age mice. Body mass can be used to determine the age of individuals of less than 7 weeks old (⩽ 26 g). Thereafter, the only reliable technique of age determination involves a visual evaluation of the degree of molar tooth wear. Five wear classes are described and used to assess the age of 780 *R. pumilio* collected during a five-year period. The annual cycles of population age structure and size were dependent on seasonal recruitment and were influenced by the duration of the peak breeding period. The growth rate, especially of females, is reduced in winter, and maturity appears to be delayed until spring, when breeding commences.
S. Afr. J. Zool. 1982, 17: 136 – 142

Die geldigheid daarvan om die ouderdom van *Rhabdomys pumilio* te bepaal deur ouderdomsgekoppelde veranderinge in tandvoorkoms, -afmetings en -posisie, liggaamsmassa en kop-liggaamslengte is getoets teen 47 muise van bekende ouderdom. Liggaamsmassa kan gebruik word om die ouderdom van muise wat minder as 7 weke oud is (⩽ 26 g), te beraam. Vyf ouderdomsklasse word beskryf en aangewend om die ouderdom van 780 *R. pumilio*, wat oor 'n tydperk van vyf jaar versamel is, te beoordeel. Die jaarlikse sikliese patrone van ouderdomsstruktuur en bevolkingsgrootte het afgehang van die seisoenale aanwinste en is beïnvloed deur die lengte van die teelseisoen. Die groeitempo, veral by die wyfies, verminder gedurende die winter en dit wil voorkom of bereiking van geslagsrypheid tot die lente vertraag word, wanneer die teelseisoen begin.
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The process of ageing in rodents and its effects on their populations has received extensive attention because of their relative ease of collection and their rapid population turnover (Schwartz, Pokrowski, Istchenko, Olenjev, Ovtschinnikova & Pjastolova 1964; Kubik 1965; Delany 1972; Pucek & Lowe 1975; Perrin 1979).

Some aspects of the population biology, nutrition, reproduction and development of *Rhabdomys pumilio* have been studied in South Africa by Brooks (1974), Curtis & Perrin (1979) and David (1980). Relative age criteria of *R. pumilio* involving body mass (Brooks 1974), eye-lens mass and tooth wear (Perrin 1979) have previously been described and used to determine the population age structure, although the validity of these techniques has not been tested against known-age mice.

An acceptable technique of age determination should depend on parameters that change rapidly and regularly with age, are easily recognizable and show small intra-class variation. In reviews of age determination methods for small mammals, Morris (1972), Spinage (1973) and Pucek & Lowe (1975) have emphasized that it is important to test the methods of age classification against a series of known-age animals rather than against other methods. The comparison of tooth wear with other parameters, such as eye-lens mass, without reference to known-age material, as was described by Perrin (1979) for *R. pumilio*, is thus less satisfactory than the use of known-age animals.

In the present investigation we have compared different methods of age determination on known-age *R. pumilio* and then used the most reliable method to establish the population age structure over a five-year period.

Methods

Growth Rate

The initial growth rate of *R. pumilio* from birth (2,5 – 3,0 g) to weaning at 14 days (8,0 g) was established from nine mice born in the laboratory. From this point onwards, the growth rates of young *R. pumilio* were determined from wild mice that were live-trapped, weighed, sexed, marked by toe-clipping and released on a trapping grid on the Cape Flats (34°00′S/18°35′E) monthly during five consecutive summers (October to March, 1972 – 1977). The first part of the field growth curve (A-B on Figure 1) was calculated by pooling data for each sex of 34 marked mice weighing less than 10 g at first capture and recaptured a month later. The remainder of the growth curve was established for each sex from 208 marked individuals weighing less than 20 g at first capture and subsequently recaptured at monthly intervals.

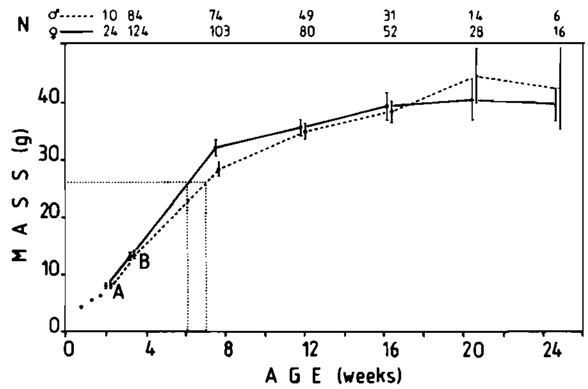

Figure 1 Growth curve of *Rhabdomys pumilio*. The growth from birth to two weeks was established from 9 juveniles in captivity. The field growth rate for mice from 2 to 24 weeks old was determined from 208 individuals first captured as juveniles and subsequently recaptured at monthly intervals during October to March. The 95% confidence limits at each point are based on the data between that point and the preceding point. The dotted line shows the upper limit at which the age of juveniles can be determined from their mass.

Age determination

A number of mice were kill-trapped at the end of each month between August 1972 and April 1977 near a live-trap study grid (see above). The sex, body mass (± 0,5 g Pesola spring balance) and the head and body length (mm, always same operator; hereafter referred to as body length) were determined from most (775) of the 860 specimens collected before they were stored frozen. Later 780 of the skulls were cleaned by boiling and defleshing and the molar teeth were examined under a binocular microscope (12×).

The growth curve (Figure 1), which showed that the growth rate of mice was rapid and uniform for each sex up to a mass of 26 g (hereafter referred to as juveniles; see David 1980), was used to determine the relative age of 47 *R. pumilio* (33♀♀, 14♂♂) that had previously been trapped and marked as juveniles (≤ 26 g) in the live-trap study grid. The degree of molar tooth wear of these known-age mice was assessed and described to define age classes. To quantify the degree of dental attrition, the anterior root length and crown height of the lower first molar (M_1) was measured from 46 X-ray plates (± 0,05 mm binocular microscope scale). Finally, the index of age, determined from the known-age mice, was used to classify all 780 mice into age classes.

Results and Discussion

Body mass and length

Body mass and external body measurements have been used to assess the age of live *R. pumilio* (Brooks 1974) and other rodents (Dynowski 1963; Goertz 1965; Kubik 1965; *inter alia*) as these were the only readily available field criteria for determining the age of mice.

In the present investigation it was found that *R. pumilio* grew rapidly and regularly during the first 6 to 7 weeks, when they were still less than 26 g and 100 mm in size. Above that age, the growth rate was usually slower, but highly variable (Figure 2), invalidating the possibility of using body size as a guide to the age of Cape Flats *R. pumilio* adults. Similar shortcomings of this method have been recognized in numerous other rodent species (Pucek & Lowe 1975).

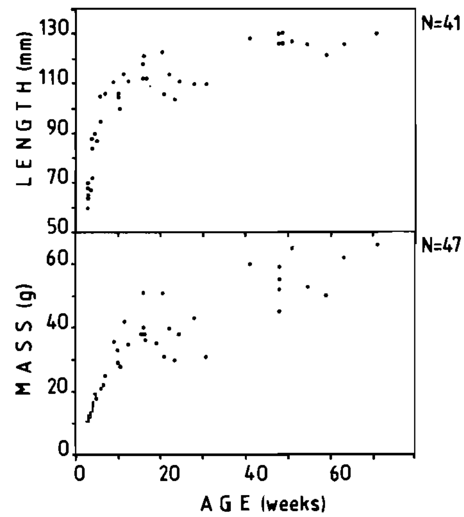

Figure 2 Body mass (g) and length (mm) of 47 known-age *R. pumilio*.

Tooth dimensions and position

Tooth measurements are sometimes used to indicate age (Alexander 1960; Dapson 1968; Morris 1972; Spinage 1973). Measurements made from X-ray plates of the lower jaws of *R. pumilio* (Figure 3) show the changes in the crown height and root length of M_1 and its position relative to the jaw (see Figure 4). The total root length increases until the age of 10 weeks and then remains constant throughout life (Figure 3b). The decrease of crown height is gradual and continuous due to abrasion (Figure

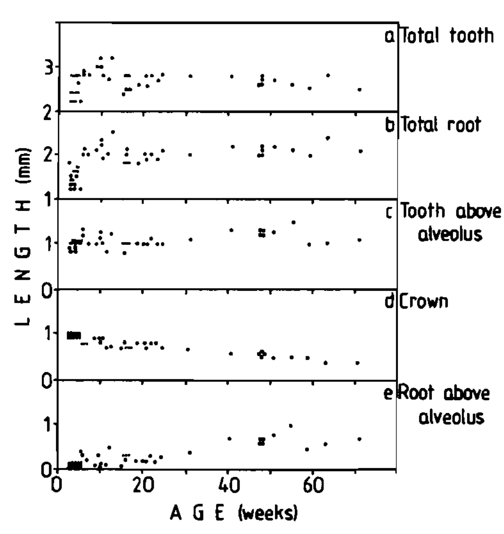

Figure 3 Dimensions (mm) of the anterior root and crown of lower molar 1 measured from X-ray plates of 46 known-age *R. pumilio*.

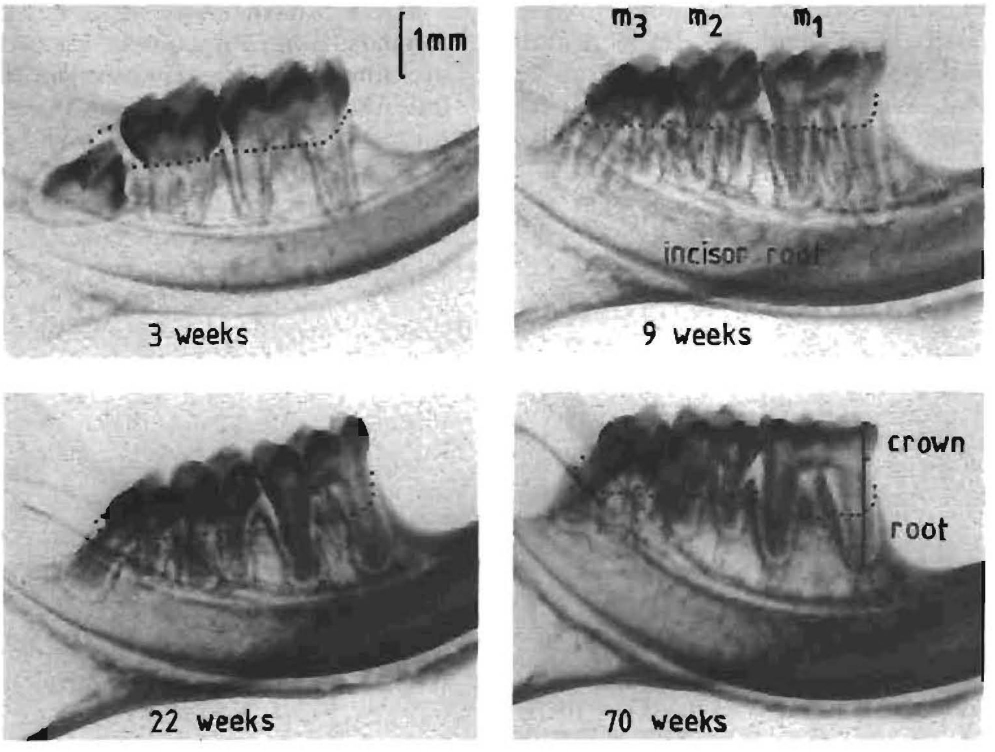

Figure 4 X-ray photographs of the lower left molars of known-age *R. pumilio*. The dotted line indicates the position of the alveolus edge. Note the position of the molar roots relative to the incisor root and the alveolus edge. Crown and root measurements (Figure 3) were taken from the top of the anterior cusp to the end of the anterior root of M_1.

3d). The length of root projecting above the alveolus increases with age (Figure 3e) so that the height of tooth above the alveolus does not decrease with progressive wear (Figure 3c). The root does not grow in this process (Figure 3b), but the whole tooth is progressively pushed further out of the sockets (see Figure 4).

These trends have previously been recognized for other mammal species (Spinage 1973). Although these changes are useful in ranking *R. pumilio* into broad age categories, they occur so slowly and continuously that definite age classes cannot be defined.

Tooth wear

Using only the major changes in the appearance of the upper molars, the 47 known-age *R. pumilio* were grouped into five non-overlapping age classes (Figure 5), which are described below:

Class I: 0–5 weeks

At birth only the tips of the incisors protrude and no molar teeth are visible above the alveolus. M_1 and M_2 begin erupting at the age of 2 weeks. By 4 to 5 weeks of age, M_1 and M_2 have fully erupted and M_3 begins to erupt, but is still below the level of the tooth row. Dentine is already exposed on all teeth.

Class II: 6–15 weeks

The dentition is fully developed. The wear of laterally adjacent cusps 4, 5 and 6 increases the width of uninterrupted dentine.

Class III: 16–25 weeks

The areas of exposed dentine of cusps 8 and 6 are joined on M_1 and by 20 weeks also on M_2.

Class IV: 26–51 weeks

On M_3, the crown has worn so low that the occlusal surface is confluent over all cusps. This class includes a gap of nine weeks where no known-age mice were available (32–40 weeks old). By 48 weeks, the occlusal surface is continuous from cusp 8 on M_1 to cusp 1 on M_2.

Class V: 52 weeks +

These mice have only remnants of cusps left. The occlusal surfaces are very wide and confluent over all cusps of M_2 and M_3. The maximum age of *R. pumilio* in the laboratory exceeds 104 weeks (Brooks 1974).

The lower molar tooth rows corresponding to each age class are shown in Figure 6. In an earlier study, Perrin (1979) had designated 12 classes of lower molar wear to *R. pumilio* of unknown age, assuming an approximate duration of one month for each class. These wear classes are compared to the present material in Figure 6 (small Roman numerals). A list with details of all known-age mice in each class is presented in Appendix I.

The rate of toothwear of *R. pumilio* from one study area is assumed to be constant provided that there is no marked seasonal fluctuation in the consumption of abrasive material (Breakey 1963; Dapson 1968; Fisler 1971; Morris 1972). On the Cape Flats, King (1976) found that the stomachs of *R. pumilio* contained a high proportion (over 50%) of abrasive food material, mainly *Acacia cyclops* and *A. saligna* seeds, throughout the year. However, Curtis & Perrin (1979), who described *R. pumilio* as an opportunistic omnivore, found that in the Eastern

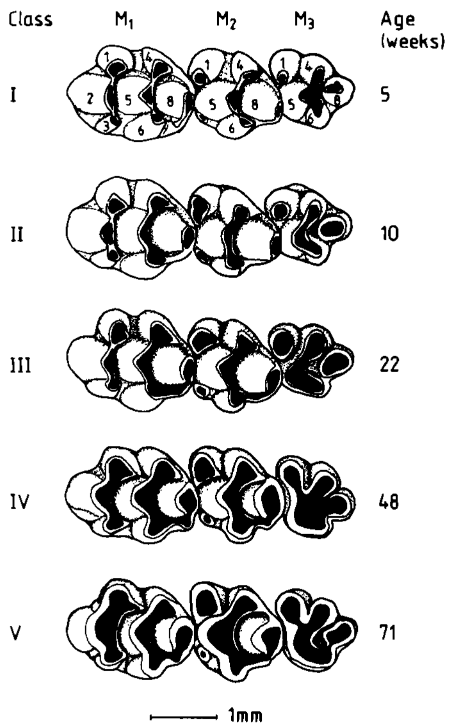

Figure 5 Occlusal surface of the upper right molar tooth row of a known-age *R. pumilio* from each of the five age classes. Dentine exposed during wear is shown as black areas. Cusp numbers (after Delany 1975), shown on the tooth row of class I, are referred to in the text.

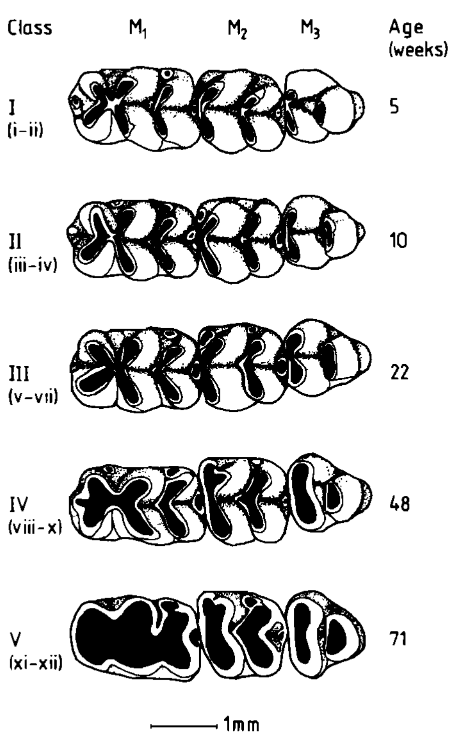

Figure 6 Occlusal surface of the lower right molar tooth row of a known-age *R. pumilio* from each of the five age classes. Small Roman numerals (in brackets) correspond to the 12 classes previously designated by Perrin (1979).

Cape mostly seeds and insects were eaten in summer, but that the diet changed to less preferred herbs and shrubs in winter.

Individual variation in the rate of tooth wear would affect the placing of *R. pumilio* into narrow age classes (of short duration). The age classes described in the present investigation therefore increase from a duration of 6 weeks in class I, to 10, 10 and 26 weeks in classes II, III & IV respectively. The choice of five age classes depended on the occurrence of consistent and readily recognizable changes in tooth appearance, which occur more slowly with progressive age. Furthermore, the small sample size ($N = 12$) of known-age animals older than 6 months precludes the subdivision of old known-age mice into narrower age classes.

Population age structure

The molar wear method of age determination was used to assess the age of 780 *R. pumilio*, which had been kill-trapped monthly on the Cape Flats over a five-year period.

It was found that seasonal changes in age structure of the population followed a definite cyclic pattern, as would be expected from other studies on rodents with seasonal breeding patterns (Breakey 1963; Goertz 1965; Fisler 1971; Delany 1972; Perrin 1979). Because this cycle occurred in each year (Figure 7b) and was similar for both sexes ($F = 0,02$; $P < 0,05$; df. = 11 & 52) the data of all *R. pumilio* were pooled for each respective month to represent a hypothetical year (Figure 8).

Mice of 16 to 25 weeks of age (class III) made up the largest part of the population, exceeding 70% during the winter months, May to August. The number of young mice (class I & II) in the population increased from September (2%) to December (45%), followed by a decrease in frequency of occurrence from April (39%) to June (5%). Old adults (class IV & V) occurred in relatively low numbers during February (13%) to August (16%), but in higher numbers during September (35%) to January (22%). This observed pattern resulted from the following sequence of events:

(i) Mice are born during September to March.

(ii) Recruitment virtually ceases during April and the generation born during the previous breeding season reaches age class III (16 – 25 weeks old). At this stage only about 8% of the population is older than 25 weeks (class IV & V).

(iii) During winter, individuals born in the previous breeding season grow old (> 25 weeks; class IV & V) and become reproductively active during spring (September to October). In October, 52% of the population is older than 25 weeks.

(iv) From September through to March, young mice (class I & II) largely replace the older generation (class IV & V), born during the previous breeding season. In December, 45% of the population is younger than 16 weeks.

The kill-trap findings show that 50% of the population comprised *R. pumilio* of 16 – 25 weeks old (class III), but that only 21% of the mice were older than 25 weeks (class IV & V). This indicates that most *R. pumilio* die before they are 6 months old and may explain why David (1980) obtained a mean recapture period of 11,6 weeks in the live-trap study, with only 3,6% males (of 659) and 9,6% females (of 571) being recaptured for longer than 6 months.

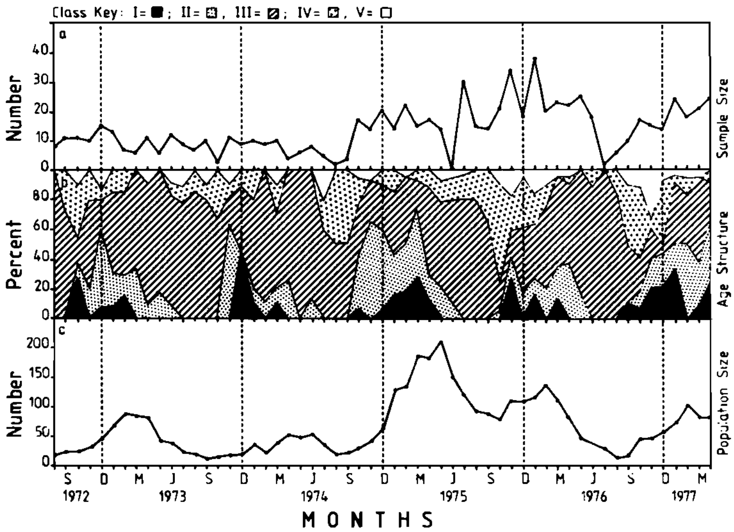

Figure 7 Population age structure (kill-trapping) and population size (per 0,45 ha; live-trapping on a nearby grid; data from David 1980) of *R. pumilio* determined monthly between August 1972 and April 1977. Population size was determined by the Jolly-Seber estimate (Jolly 1965; Seber 1965). The sample size for the age structure determination is indicated on the top graph (total $N = 780$).

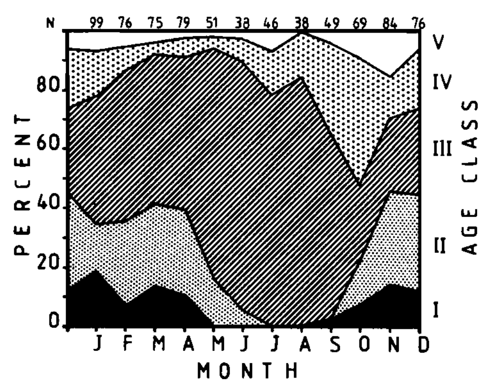

Figure 8 Age structure of the *R. pumilio* population ($N = 780$) for a hypothetical year.

The population size fluctuated in an annual cyclic pattern, with a peak towards the end of the breeding season (Figure 7c; David 1980), preceded by the occurrence of a high proportion (> 40%) of young mice (class I & II; Figure 7b). However, the magnitude of the population size peak varied considerably in different years. During the 1974/1975 breeding season, when the population was large (maximum 210), the proportion of young mice (class I & II) was high (> 40%) for a longer duration (6 months) than during the two preceding years (1 month), when the population was smaller (maximum 89 and 52 in 1972/1973 and 1973/1974 respectively). This indicates that the large population size during 1974/1975 was a result of the production of numerous offspring over an extended period. It is thus evident that the population age structure and size can be influenced by the duration of the peak breeding period.

Mean mass and head-body length of the population

With a reliable method of age determination, it is possible to examine the change in body dimensions with age for the whole population. It was found that in the summer half of the year, *R. pumilio* of both sexes increased in mass and length up to age class IV ($P < 0,05$). However, in winter, growth was more variable and adults were generally smaller than in summer (Figures 9 & 10), especially:

(i) females of age classes III & IV were significantly lighter and shorter ($P < 0,05$) during winter (III: 36 g, 110 mm; IV: 41 g, 116 mm) than summer (III: 48 g, 117 mm; IV: 55 g, 123 mm)

(ii) during winter, the females of class III (36 g, 110 mm) were significantly lighter and shorter ($P < 0,05$) than the males (43 g, 115 mm)

(iii) males of age class IV were significantly lighter ($P < 0,05$), but not shorter during winter (48 g, 122 mm) than summer (55 g, 127 mm).

These results indicate that females grew more slowly in winter and consequently were lighter and shorter between

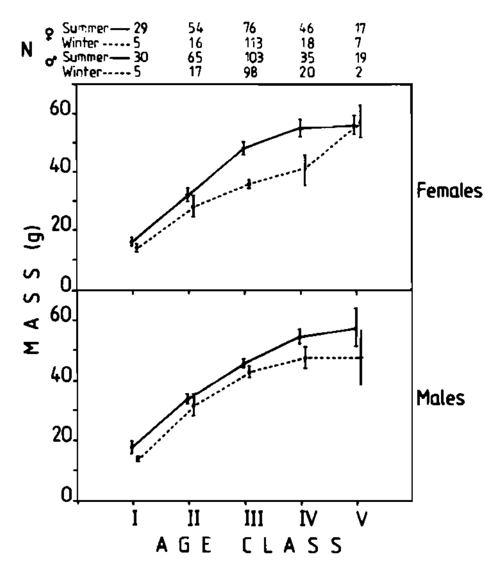

Figure 9 Mean body mass (g) ±95% confidence limits of female and male *R. pumilio* from various age classes during summer (October to March) and winter (April to September). Non-overlap of the 95% confidence limits indicates significant differences between means by the *t*-test.

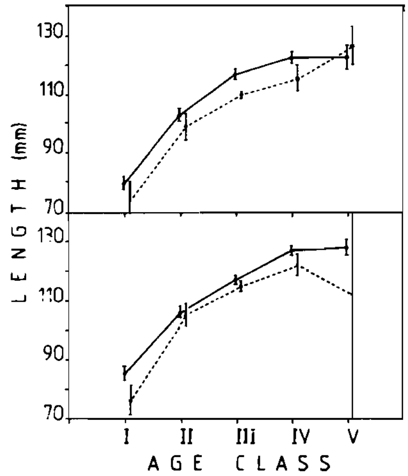

Figure 10 Mean head and body length (mm) ±95% confidence limits of *R. pumilio* from various age classes during summer and winter. Sample sizes are listed on Figure 9.

the ages of 16 and 52 weeks than in summer. This agrees with the findings of Schwartz *et al.* (1964), who found that the physiological process of ageing, growth, maturation and fecundity of 16 rodent species with a normal life-span of less than a year, was significantly inhibited during the non-breeding season.

Conclusion

The synoptic evaluation of total tooth wear is considered to be the most reliable method for determining the age of adult *Rhabdomys pumilio*, but body mass can be used to estimate the age of juveniles less than 26 g. The age of live adults can only be determined by obtaining tooth impressions or by following their life histories. Our findings suggest that concurrent kill-trap sampling of nearby areas can be used to supplement conclusions from a live-trap study. The annual age structure of the population varied in a cyclical pattern, ranging from a predominance of young mice during the summer breeding season, to predominantly old adults at the end of winter. The growth rate of adults is variable and reduced in females during the winter months.

Acknowledgements

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Appendix overleaf

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Appendix 1 Particulars of known-age *R. pumilio* used in the present study. Sample numbers refer to individuals stored at the Transvaal Museum, Pretoria, South Africa. The age at first capture was established from the mass at first capture (⩽ 26 g). In three cases (*) the mass at first capture exceeded 26 g, but these individuals from class V were recaptured for a sufficiently long period (> 47 weeks) to justify their inclusion in class V (> 51 weeks old)

		On first capture		Recapture	At death		
Class	No.	Mass (g)	Estimated age (wks)	Duration (wks)	Age (wks)	Mass (g)	H/B length (mm)
I	177I♀	12	3	0	3	12	70
I	177F♀	12	3	0	3	12	60
I	177X♀	12	3	0	3	12	65
I	375D♀	12	3	0	3	12	68
I	586♀	11	3	0	3	11	64
I	177H♀	12	3	0	3	12	–
I	177G♀	13	3½	0	3½	13	–
I	177J♀	13	3½	0	3½	13	67
I	117W♂	16	4	0	4	16	–
I	3272♂	15	4	0	4	15	88
I	3750♀	16	4	0	4	16	84
I	375N♀	16	4	0	4	16	–
I	375L♂	14	4	0	4	14	72
I	972♀	19	4½	0	4½	19	90
I	1202♂	18	5	0	5	18	87
II	575I♂	21	6	0	6	21	105
II	575M♂	21	6	0	6	21	95
II	575K♂	25	7	0	7	25	106
II	1214♀	18	4½	4½	9	36	111
II	1223♀	23	5½	4½	10	33	106
II	55♂	20	5½	4½	10	29	105
II	232♀	25	6	4½	10½	28	100
II	1182♂	12	3	8½	11½	42	114
II	32♀	16	4	8½	12½	35	111
II	629♂	26	7	8½	15½	38	–
III	1185♀	11	3	13	16	40	112
III	514♂	11	3	13	16	51	118
III	1184♀	12	3	13	16	38	121
III	21♂	14	3½	13	16½	36	112
III	571♂	23	6	13	19	35	–
III	938♀	13	3½	17	20½	51	123
III	692♀	16	4	17	21	31	106
III	154♀	20	5	17	22	40	114
III	2407♀	26	6½	17	23½	30	104
III	574♀	12	3	21½	24½	38	111
IV	446♀	8	2	26	28	43	110
IV	1045♀	19	5	26	31	31	110
IV	2471♂	25	7	34	41	60	128
IV	2211♀	21	5	43	48	55	126
IV	2268♀	22	5	43	48	45	126
IV	2200♀	21	5	43	48	52	130
IV	2220♀	22	5	43	48	59	130
IV	2277♀	12	3	48	51	65	127
V	2017♀	55	>7*	48	>55	53	126
V	2026♀	53	>7*	52	>59	50	122
V	2151♀	39	>7*	56	>63	62	126
V	2736♀	25	6	65	71	66	130