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Seasonal variation in growth of *Mastomys natalensis* (Rodentia: Muridae) in Morogoro, Tanzania

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Summary

The paper describes seasonal growth variation in a free living population of *Mastomys natalensis* (Smith, 1834) from Morogoro, Tanzania. Growth patterns are associated with rainfall patterns. Young animals enter a growth stop at the end of the dry season (October–November) and growth is only resumed after the first heavy rains. Reproduction is more related to size than to age. If the heavy rains come early in the rainy season, animals start reproducing in the beginning of the year. The resulting young reach their maximal size without growth stop and start reproducing immediately. Possible causes for the growth stop are discussed. Growth phenomena are thought to explain at least partially the relation between rainfall and reproduction in *Mastomys*.

Résumé

Cet article décrit la variation de croissance saisonnière d'une population de *Mastomys natalensis* (Smith, 1834) vivant en liberté à Morogoro, en Tanzanie. Les graphiques de croissance sont associés à ceux des chutes de pluie. Les jeunes animaux connaissent un arrêt de la croissance à la fin de la saison sèche (octobre–novembre) et la croissance ne reprend qu'après les premières fortes pluies. La reproduction est plus liée à la taille qu'à l'âge. Si les fortes pluies surviennent tôt en saison des pluies, les animaux commencent à se reproduire au début de l'année. Les jeunes atteignent alors leur taille maximale sans avoir connu d'arrêt de croissance et commencent à se reproduire immédiatement. On pense que les phénomènes de croissance expliquent au moins partiellement la relation entre les chutes de pluie et la reproduction chez *Mastomys*.

Key words: growth, *Mastomys*, rodents, Tanzania, breeding seasons

Introduction

Murids of the genus *Mastomys*, known as multimammate rats, are very common and widespread in subsaharan Africa. They form a species-complex, grouping several species which are morphologically hard to distinguish but which have

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different karyotypes (Robbins & Van der Straeten, 1989). They are not only important agricultural pests that cause problems every year, but they are also reservoirs of human diseases such as plague and Lassa-fever.

The following researchers have investigated the population-dynamics of these rats and suggested a relationship between rainfall and reproduction: Brambell & Davis (1941) in Sierra Leone, Pirlot (1954) in Zaire, Chapman, Chapman & Robertson (1959) in south-west Tanzania, Coetzee (1965) in Transvaal, Sheppe (1972) and Chidumayo (1984) in Zambia, Taylor & Green (1976) in Kenya, Swanepoel (1980) in Zimbabwe, Hubert (1982) in Senegal and Delany & Neal (1969), Neal (1977) and Cheeseman & Delany (1979) in Uganda. Two recent papers, based on several years of field work, provided new information on populations of *Mastomys natalensis* (A. Smith, 1834) (diploid chromosome-number $2n = 32$) in old maize fields and fallow land in Morogoro, Tanzania (Leirs *et al.*, 1989; Telford, 1989).

In the Morogoro region the rainy season lasts from November to May but with a bimodal pattern. There is usually a small peak of rainfall in November and December but most of the rain falls from March to May. *Mastomys* normally starts breeding one month after the onset of the latter rains and the breeding season extends until October. However, if rainfall in November–December is abundant, there is a short additional breeding period in the beginning of the following year.

The present study investigates growth phenomena in relation to rainfall and examines the hypothesis that growth can be used to explain seasonal variations in reproduction. Earlier studies on growth in *Mastomys* were based on laboratory reared animals only (Meester & Hallett, 1970, Baker & Meester, 1977).

Material and methods

Our study area consisted of approximately 5 km^2 of maize fields or fallow fields on the campus of the Sokoine University of Agriculture in Morogoro, Tanzania.

Every month between September 1986 and February 1989, animals were collected with traplines using Sherman live traps or Museum Special break-back traps baited with peanut butter and spaced 5–10 m apart. The traps were set in the afternoon and left in the field overnight. Trapping extended over a variable number of nights depending on trap success. Every month the traplines were laid out at different sites. The animals were measured, dissected and their sexual condition noted before fixing in formalin and preserving in alcohol.

Additionally, a capture–mark–release study (CMR) was carried out between March 1987 and February 1989. Animals were live-trapped on three consecutive nights each month in two 1 ha-grids with 100 trapping stations, using Sherman live traps baited with peanut butter. The animals were weighed, marked by toe-clipping and their sexual condition noted, before release. On one of the CMR-grids 15 kg of maize was distributed each week over 100 baiting stations. The details of this feeding experiment fall beyond the scope of this article, but the results will be used to discuss the available food quantity as a factor in regulating growth.

Climatological data were obtained from the meteorological station on the campus.

The eye lens weight was used to estimate the age of *Mastomys* individuals. The superiority of this technique has been discussed by several authors (e.g.

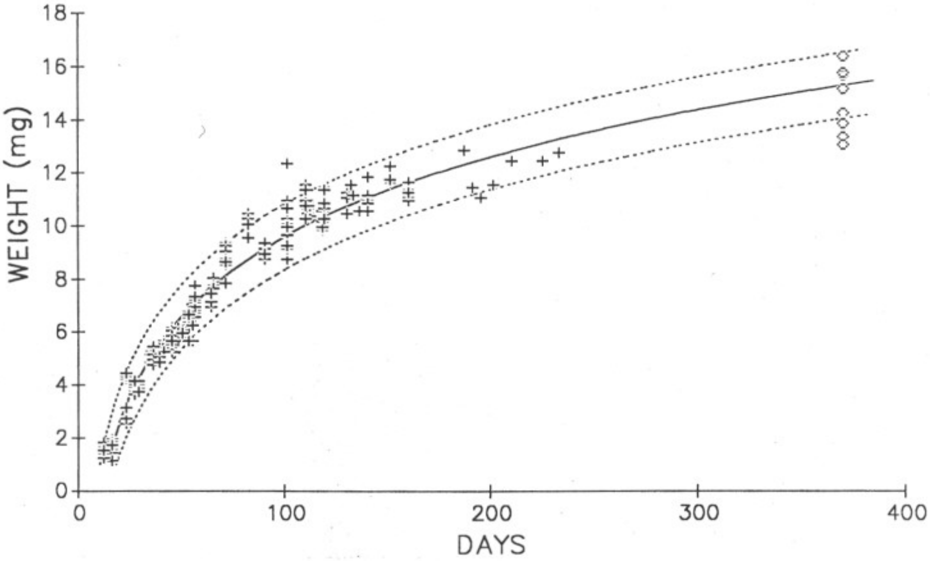

Fig. 1. The log-linear relation between age and lens weight. The figure shows the data points for animals of known age (+), the calculated standard curve (full line) and the 95% confidence interval for predicted values (dotted lines). The data points at the right side of the figure (○) were not used to calculate the standard curve but are the lens weights of 10 laboratory animals of unknown age but at least one year old.

Adamczewska–Andrzejewska, 1971; Askaner & Hansson, 1967; Pascal *et al.*, 1988; Pucek & Lowe, 1975; Vandorpe & Verhagen, 1979).

Live-trapped pregnant females were allowed to give birth in the laboratory. Two hundred and fifty-two of the young were killed at exactly known ages between 10 and 230 days. After fixing these animals in 10% formalin, the eyes were removed, the lenses dissected, cleaned and dried for 36 hours at 80°C. The lenses were then stored in a desiccator and within 48 hours weighed to the nearest 0·1 mg. The weight of the heaviest lens of each pair was retained for further analysis.

The lens weight was regressed on the age in days after logarithmic transformation of the independent variable. This resulted in a regression line with an intercept $A = -10{\cdot}46088$ (S.E. $= 0{\cdot}24044$), a regression coefficient $B = 4{\cdot}35076$ (S.E. $= 0{\cdot}05892$) and coefficient of determination $R^2 = 0{\cdot}956$ (Fig. 1). A residual analysis showed that this curve is acceptable over the whole range of ages in our test. A standard curve to estimate age from lens weight was then constructed from the expression

$$\text{age in days} = \exp\left[\frac{10{\cdot}46088 + \text{lens weight in mg}}{4{\cdot}35076}\right].$$

The 95% interval for these estimates (Sokal & Rohlf, 1981, p. 498) is also shown in Fig. 1. This curve was used to estimate the ages of 1773 animals obtained from the removal trapping.

The eye lens weight could not, of course, be used in the CMR-study and we investigated the possibilities of taking body weight as an age indicator in young animals. One hundred and twenty-two of the laboratory-born animals were weighed at regular intervals until they were six weeks old. For most individuals

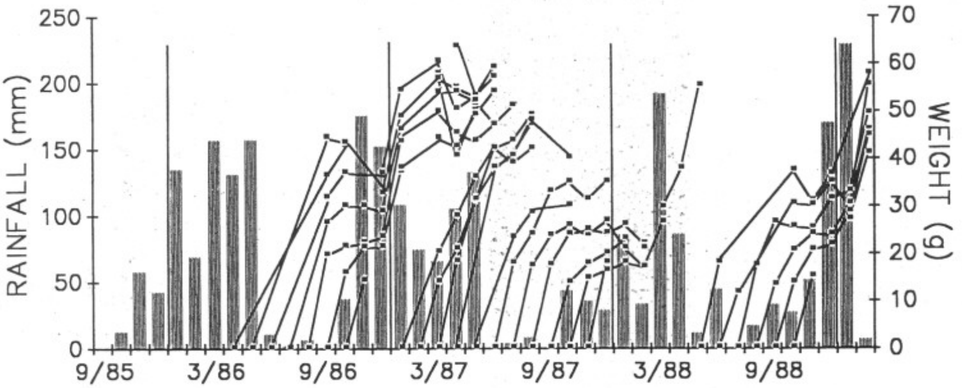

Fig. 2. The mean body weights per month for all cohorts (lines) in relation to monthly rainfall (shaded columns). The vertical lines indicate the beginning of a new year.

there was a linear relationship between age and body weight in the first weeks of their life, but a common curve could not be established as the inter-individual growth variations were too large. Therefore, we had to introduce the concept of 'critical weight'.

Since young *Mastomys* wean at the age of 22 days (pers. obs., Meester, 1960) and since in most cases trapping occurred towards the middle of the month, animals born in the month of collecting were not normally caught. Hence, animals less than 45 days old were born in the previous month. From the estimated ages of animals caught, in the removal trapping, the weight below which at least 85% of the animals were less than 45 days old was calculated. During the reproductive season this 'critical weight' is estimated to be 22 g, dropping to 16 g after the reproductive season. Young animals caught during or just after the breeding season and weighing at first capture less than the 'critical weight', were assumed to have been born during the previous month. Using the concept of 'critical weight' in the interpretation of our CMR-study, we were able to follow the growth of 130 individuals.

Results

All animals were assigned to cohorts of individuals born in the same month but 3% of the animals formed cohorts which in reality could not exist since no evidence of reproduction in the same or previous month could be found (Leirs *et al.*, 1989). These cohorts consisted only of a very small number of animals caught at an age of at least 5 months old. In view of the large error attached to the estimated age of these animals, the cohorts were excluded from the analysis.

The mean weight of all individuals (excluding pregnant females) was calculated for every month and for each cohort. Figure 2 shows the monthly increase in these weights for each cohort in relation to rainfall. In March–May 1988, no eye lenses were collected and local survival in the CMR-study was too low to use the 'critical weight' technique. Since there were no juveniles in the population at this time, the mean weight of the whole population was used for these three months. Sample sizes and standard deviations are not included but they are available from the authors.

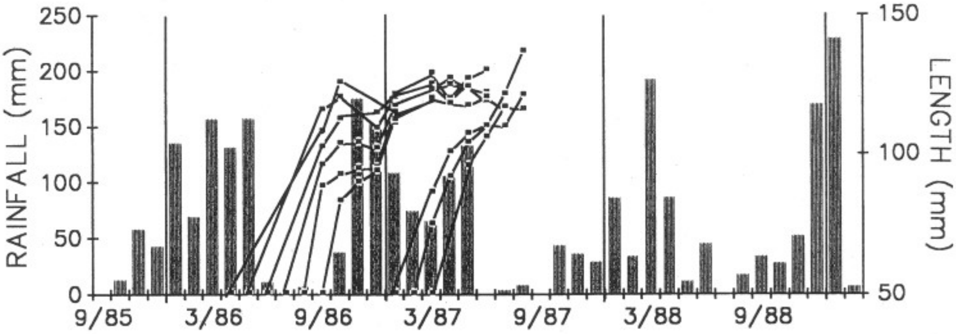

Fig. 3. The mean head-body lengths per month for all cohorts born in 1986 or early 1987 (lines) in relation to monthly rainfall (shaded columns). The vertical lines indicate the beginning of a new year.

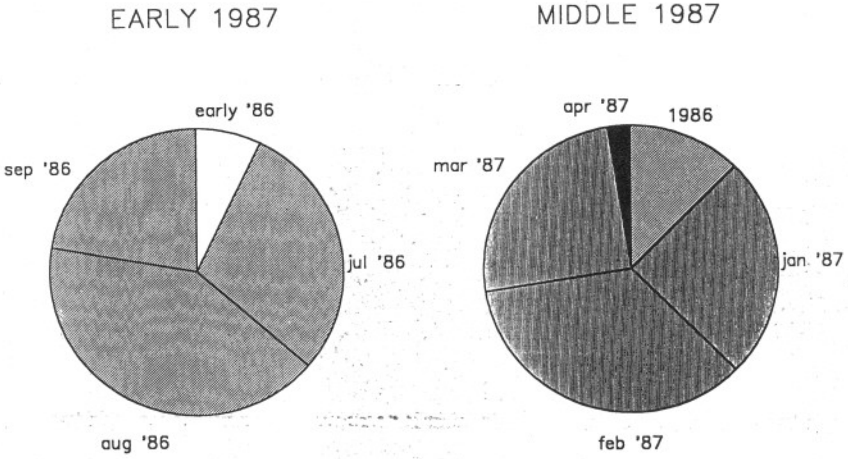

Fig. 4. Age-structure of pregnant females in early 1987 (January; $n=41$) and middle 1987 (June, July, August; $n=40$). The individuals are grouped per cohort.

Animals born after May grew rapidly at first but from October growth stopped until rain became abundant. A rainfall peak at the end of the year was followed by a high mean weight at the beginning of the following year. When this peak was absent (1987–1988), the animals did not start growing until after the March rains. Cohorts born in the beginning of the year after heavy rains (1987), grew continuously and reached their maximum weight very quickly. The monthly mean head-body length followed the same pattern (Fig. 3).

Figure 4 shows the age structure of pregnant females during an early breeding season (January 1987) and a main breeding season (June, July, August 1987). Pregnant females in the early reproductive season were born during the previous year, but most of the pregnant females in the main reproductive season were young animals, born in the beginning of the same year. A t-test indicated that pregnant females in these two seasons differ significantly in age but that the mean head-body lengths are not different (Table 1).

Table 1. Mean ages and sizes (head-body length) for 1986-born pregnant females during the early breeding period in 1987 and 1987-born pregnant females during the main breeding season in the same year. Statistical significance of the differences is determined by a Student t-test

	Early 1987 (born 1986)	Middle 1987 (born early 1987)	*t*	d.f.	*P*
n	41	35			
mean age	164·05	118·66			
(days)			6·63	74	<0·001
st. dev.	30·81	28·44			
mean head/body	115·29	112·57			
(mm)			1·31	74	0·196
st. dev.	5·42	12·00			

The animals trapped in the maize-supplied grid were heavier than animals caught in the other CMR-grid (October 1987–February 1988; $P<0·001$; Mann-Whitney-U test, Siegel, 1956, p. 116). However, in both grids, there was a period of non-growth.

Discussion

It is concluded that animals enter a non-growth period at the end of the dry season. Animals that are born early during the main breeding season enter this non-growth period at a higher weight than animals that are born later. All cohorts that are born late in the breeding season (after August) have a relatively low weight through November and December. Thus, the presence of light animals cannot be used as evidence for reproduction. This implies also that the use of body weight as an age estimator, even in young animals, is not valid in periods when there is a growth stop. A similar phenomenon was reported in *Arvicanthis niloticus* from Kenya by Delany & Monro (1985) who compared growth curves under natural and laboratory conditions.

It could be argued that the observed growth stop is an artefact, caused by the disappearance of heavy animals while light animals keep growing. However, a Wilcoxon matched-pairs signed-ranks test (Siegel 1956, p. 75) shows that individuals that were present in the CMR-grids in November 1987 and caught again in February 1988 had not increased their weight significantly in the intervening months ($Z=-0·600$, $n=26$, one-tailed $P=0·2743$).

The cause of the non-growth period in *Mastomys* is not known. Clearly, there should be an external trigger, since the growth stop is more or less synchronized for the whole population and it is not related to the age of the animals. Further, animals that are born very early between January and March do not show such a growth stop. A possible explanation is that numbers increase during the dry season with newborn young entering the population causing high densities in October–November. This would result in higher intraspecific competition which could lead to a decrease in the growth rate of individuals. However, it does not explain why animals resume growth a few months later, irrespective of the population size. The CMR-study revealed that the estimated population size was less than 50 animals per hectare in February 1988 and more than 300 in December 1988 (unpubl. data), in both cases just before growth resumes.

Periods of non-growth are well documented for rodents from temperate regions (Zejda, 1971; Iverson & Turner, 1974; Verhagen & Vandorpe, 1979; Beacham, 1980) and it has been suggested that temperature or photoperiod were the triggering factors. In the tropics, however, the seasonal variations in temperature and photoperiod are small and the same from year to year. Hence, they are unlikely to be responsible for the differences in growth in multimammate rats.

Delany & Monro (1985) found reduced growth rates in *Arvicanthis* during the dry season in Kenya and the present results also show a relation between rainfall and the duration of the non-growth period. Growth is not resumed until after the first heavy rains, regardless of whether they start in December or in March. This suggests that a rainfall related factor, such as available food, could be responsible for the resumption of growth. However, we found that animals caught in the grid supplied with extra food still showed a non-growth period. Similarly, Taylor & Green (1976) could find no evidence that an additional supply of cereals caused *Mastomys* to breed continuously. Hubert *et al.* (1981) showed that in a food-supplemented population densities and survival were higher, but that there was no marked difference in the duration of the breeding season.

For all these reasons it is assumed that it is the quality rather than the quantity of the food which is important. According to Delany & Monro (1985), changing nutrition could account for lower growth rates in *Arvicanthis*. Swanepoel (1980) analysed *Mastomys* stomach contents but found no seasonal variation in protein content. Neal (1984) studied diet, reproduction and climate in four other African small mammal species and suspected that water stress inhibits breeding. Field (1975) indicated that water stress could make protein metabolism less efficient. She also suggested that oestrogenic factors in growing grass provide a hormonal trigger that starts reproduction. Delany & Monro (1986) found that the diet of *Arvicanthis* in Kenya consists mainly of young grasses during the early reproductive season. Alibhai (1986) showed that 6-methoxybenzoxazolinone, a plant derived cyclic carbamate present in growing tips of some plants, can stimulate reproductive activity in *Gerbillus* rodents in Kenya. Since growing grass is present only after the start of the rains, this finding could explain why the breeding season starts then. Nevertheless our data suggest that animals should first reach a 'reproductive size' and it seems that there should be factors which trigger growth before breeding can start. We are currently analysing stomach contents from our population to see if diet varies with growth.

Summarizing, we can conclude that growth patterns in *Mastomys natalensis* are associated with rainfall, probably through rainfall-induced variation in quality and quantity of dietary resources. The poor quality of food and low availability of water is most pronounced at the end of the dry season when rodent densities are high and intraspecific competition is likely to increase. Young animals then show a growth stop which may be the result of a physiological response to this stress situation.

Leirs *et al.* (1989) recorded a short additional breeding period in *M. natalensis* some months before the main breeding season if the rainfall at the end of the year is heavy. It now seems that the heavy rains are accompanied by growth in animals that are born during the previous year and which very soon reach the reproductive size and start breeding. Their offspring grow rapidly without a growth stop and reach reproductive size in May. For unknown reasons, however, the parental generation disappears so quickly from the population that old females represent only a small proportion of the pregnant females present during the main breeding season. The period without (or with much-reduced) reproduction between the short and the main breeding seasons may be due to the disappearance of the parental generation while the young animals are still growing. This would lead to the conclusion that most females seem to participate in only one breeding season.

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