ECOLOGICAL ASPECTS OF RODENTS AT LIVINGSTONE, SOUTHERN ZAMBIA

by

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A dissertation submitted in partial fulfilment for the degree of Master of Science in Biology of the University of Zambia, 1982.

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PART ONE

INTRODUCTION

1.1 Background

Many aspects of rodent ecology in Africa remain to be investigated inspite of previous studies (Delany, 1972). No detailed assessment has been made of techniques of collecting rodents: usually traps are laid either irregularly in selected positions (Happold, 1974; Vesey-FitzGerald, 1966) although sometimes these were laid in traplines at regular intervals (Cole, 1975; Delany, 1971, Hanney, 1964; Sheppe 1972). Trapping method has largely been determined by the type of information sought. Breakback and live traps with a variety of bait types are frequently used in collecting small rodents. The few observations on trap success indicate that this can vary on successive nights with species of rodent (Delany, 1971), and sex (Sheppe 1972) but generally there is a drop in total rodents caught (Dieterlen, in Delany, 1972).

Most information collected on African rodents has been on their breeding condition. This has led to the determination of breeding seasons (Allanson, 1958; Coetzee, 1965; Delany, 1971; Field, 1975 Happold, 1967 and 1974; Hanney, 1964 and 1965; Sheppe, 1972 and 1973). In the majority of species breeding activity is lowest during the dry months and maximum breeding either coincides or precedes the rainfall peak by one or two months. However, ultimate breeding cues have not been demonstrated inspite of the apparent relationship between breeding seasons and rainfall. Studies of gestation periods indicate periods of about one month or less (Delany, 1971; Habbard, 1970a and 1970b; Meester, 1960). Average embryo count per pregnancy varies with species (Delany, 1974) and intraspecifically with maternal size and period of breeding (Coetzee, 1965; Sheppe, 1973).

There is no standard approach to studying age structure of African rodents. Consequently results obtained by different workers even on the same species are not comparable. Estimation of survival of rodents in the field has not yielded reliable information because of very low recaptures of rodents, (Delany 1972; Sheppe, 1972; Swanepoel, 1976). Rodent densities in Africa seem to range 0-160 per ha (Delany, 1972; Hanney, 1964; Nandwa, 1973; Swanepoel, 1976). The use of indices of relative abundance, e.g. trap success, has also shown temporal changes in population size of rodents (Hanney, 1964; Sheppe, 1972).

The only work on rodent population ecology in Zambia was done by Sheppe (1972 and 1973) at Ngoma, Kafue Flats and Luangwa valley. Most of his data concerned populations of P. natalensis at the Kafue Flats (Sheppe, 1972) where these were subjected to a high degree of instability largely due to floods.

This dissertation is an assemblage of three published papers based on broader findings of a study of the natural history of rodents at Livingstone in southern Zambia.

Eleven species of rodents belonging to the suborder Myomorpha were collected during fieldwork conducted from January 1974 to December 1976. They belonged to three families.

Muscardinidae: This family of dormice was represented by a single genus Graphiurus Smuts and the speicies G. murinus Desmarest.

Cricetidae:

This family was represented by three subfamilies each with a single genus and species. Subfamily Cricetomyinae with genus Saccostomus Peters and the species S. campestris Peters. Subfamily Dendromurinae with genus Steatomys Peters and the species S. pratensis Peters. Subfamily Gerbillinae with genus Tatera Lataste and the species T. leucogaster Peters

Muridae: The family of murids had the largest number of genera and species; all belonging to the subfamily Murinae. They included the following genera and species: Acomys I. Geofroy (A. spinosissimus Peters), Aethomys Thomas (A. chrysophilus de winton and A. namaquensis A. Smith), Lemniscomys Trouessart (L. griselda Thomas), Mus Linnaeus (M. minutoides A. smith), Pelomys Peters (P. fallax Peters) Praomys Thomas (P.(Mastomys) natalensis A. Smith).

Two of the three papers presented for this dissertation provide information of variable depth on the ecology of two species L. griselda and T. leucogaster. The other paper attempts to provide information on species of a rodent community inhabiting an old gravel quarry; but most of the data concern P. natalensis.

The general vegetation types of the study area at Livingstone from where samples were obtained are given in the paper dealing with the ecology of striped mouse, L. griselda in Section 2.3. The average rainfall at Livingstone of 740 mm given in Section 2.3 was based on records at the railway station while that of 727 mm given in Sections 2.1 and 2.2 was based on records at the airport.

1.2 Summary

Seasonal changes in age structure were observed in L. griselda, P. natalensis and T. leucogaster at Livingstone. These changes were caused by seasonality in breeding and reproduction but also by changes in breeding intensity among T. leucogaster.

Maximum breeding activity of the three rodents occurred during the rainy season and sometimes extended for one month into the dry season. This is consistent with other observations on tropical rodents in Africa. The majority of subadults born during the rainy season became sexually mature at an early age and participated in breeding before the end of the breeding season in May/June. Cessation of breeding activity appeared to be effected by low minimum temperatures during May-July.

The breeding season of female L. griselda and P. natalensis lasted about six months: November-April and January-June, respectively. This contrasted with the almost all-year round breeding of female T. leucogaster but for a brief interruption in July. However duration of the female T. leucogaster breeding season varied from year to year.

L. griselda were relatively more abundant during the dry season in primary dambo grassland but virtually disappeared from there during the latter half of the rainy season. This was probably due to mice abandoning their dry-season habitats due to waterlogging of dambos. L. griselda also disappeared from habitats where herbage cover had been destroyed. These observations indicate a relationship between habitat changes and fluctuations in abundance of L. griselda.

Population fluctuations of P. natalensis inhabiting an old quarry were characterized by four phases: a rainy season peak; a mid-breeding season low; an early dry season peak; and a late dry season low. The rainy season population peak was due to immigration because it occurred prior to the onset of the recruitment of young into the population. Immigration declined and so did population size as the breeding season progressed. The period when subadults dominated the population was associated with the occurrence of the early dry season population peak indicating that reproduction (i.e. recruitment of young) was responsible for this peak in population abundance. The population low observed later in dry season could not be adequately explained by demographic factors. This low was associated with a deterioration and destruction of herbage cover by fire. Thus both demographic and habitat factors appeared to influence population dynamics of P. natalensis. In this respect there were similarities in population fluctuations of P. natalensis and L. griselda.

Annual population fluctuations of T. leucogaster were associated with specific demographic characteristics. Prior to and during the period of peak numbers in 1974, the female breeding season lasted for nine months and survival rate of both sexes and all age groups was good (over 60%) but during the period of decreasing numbers in 1975 the breeding season lasted only four months and survival rate of both sexes and all age groups was poor (under 40%). The underlying causes of changes in these demographic characteristics are not known but successive decrease in total rainfall during the study period coincided with the observed population fluctuations. Apparently destruction of herbage cover did not provide adequate explanation to annual changes in survival rate of T. leucogaster.

Information presented in this dissertation indicates that *T. leucogaster*, *L. griselda* and *P. natalensis* have evolved different demographic strategies at Livingstone. However, population characteristics of *P. natalensis* and *L. griselda*, were more similar than between any of these species and *T. leucogaster*. Habitat factors appeared to have a strong influence on population dynamics of *P. natalensis* and *L. griselda* while demographic factors seemed more important in the population dynamics of *T. leucogaster*.

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Meester, J. (1960). Early post-natal development of multimammate mice Rattus (Mastomys) natalensis (A. Smith). Ann. Transv. Mus. 24, 35-52.

Nandwa, S. M. (1973). Feeding ecology of rodents in Kenya. E. Afr. Wildl. J. 11, 407-408.

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PART TWO

PUBLISHED PAPERS

PART TWO

Section 2.1

Ecology of rodents at an old quarry in Zambia.

South African Journal of Zoology (1980), volume 15: 44-49.

Ecology of rodents at an old quarry in Zambia

E. N. Chidumayo

Livingstone Museum, Zambia

An old quarry, 2,5 ha in size near Livingstone in Southern Zambia was kill-and live-trapped between September 1974 and December 1976 to determine ecological relations among, rodent species inhabiting it. Seven species were found to comprise the old quarry rodent community. *Praomys natalensis* was by far the most common although *Saccostomus campestris* and *Lemniscomys griselda* were also abundant. Four species (*Tatera leucogaster*, *Steatomys pratensis*, *Mus Minutiodes* and *Aethomys chrysophilus*) were rare. Food and micro-habitat preferences of *S. campetris* and *P. natalensis* appeared similar. Seasonal fluctuations characterized the *P. natalensis* population while *L. griselda* was absent from the site during the latter part of the rainy season and early in the dry season. Pre-weaning survival of *P. natalensis* was very low, particularly early in the breeding season. The survival of the trappable population was good but declined following a burn at the study site. *P. natalensis* recruited into the population from May-July lost between 20 and 35% of their body mass during the August-October period. Body mass increased as rodents attained sexual maturity early in the rainy season.

Introduction

A number of studies have been carried out on rodent communities in tropical Africa but few show the demographic and behavioural strategies of species in a community.

This paper describes results of an ecological study of small rodents in secondary grassland at an old quarry. Kill-trapping was conducted at the study site in September 1974, January, April and June 1975. From September 1975 to December 1976 samples were live-trapped. Kill-trapping results revealed that *Praomys natalensis* and *Lemniscomys griselda* were the most abundant species (Table 1) and these were chosen for a detailed mark and recapture study throughout the live-trapping period while other species were deliberately removed.

Study site

The study site, a 2,5 ha abandoned gravel quarry with diverse micro-topography (Fig. 1), is located at 17°45' S, 25°52' E, 14 Km north of Livingstone in southern Zambia. Pits (0,25 - 1,0m deep) made up 30%, ridges (0,5 - 2,0m high) 15% and undisturbed flat ground 55% of the study site. The soil consists of cracking silty-clay on flat ground and silty-clay and gravel mix on ridges. The underlying basaltic bedrock is exposed in pits.

Average annual rainfall at Livingstone is 727 mm and is distributed from November - April (rainy season). The 1974/75 and 1975/76 rainy seasons received 913 mm and 811 mm of rain, respectively. The mean monthly temperature range is 6 - 19°C (min.) and 30 - 35°C (max). April to July is the coolest period in southern Zambia.

A mixed Hyaprrhenia-Cymbopogon-Loudetia grassland covers the study site but Amaranthus and Paspalidium also occur on ridges. Grasses sprout vigorously in October, late in the dry season, and the site is thickly covered with tall grass from December to May or June. The grass cover deteriorates as it dries and is burnt later in the dry season. Pits become pools of water from February - May, while the interridge flat ground is waterlogged during the latter part of the rainy season.

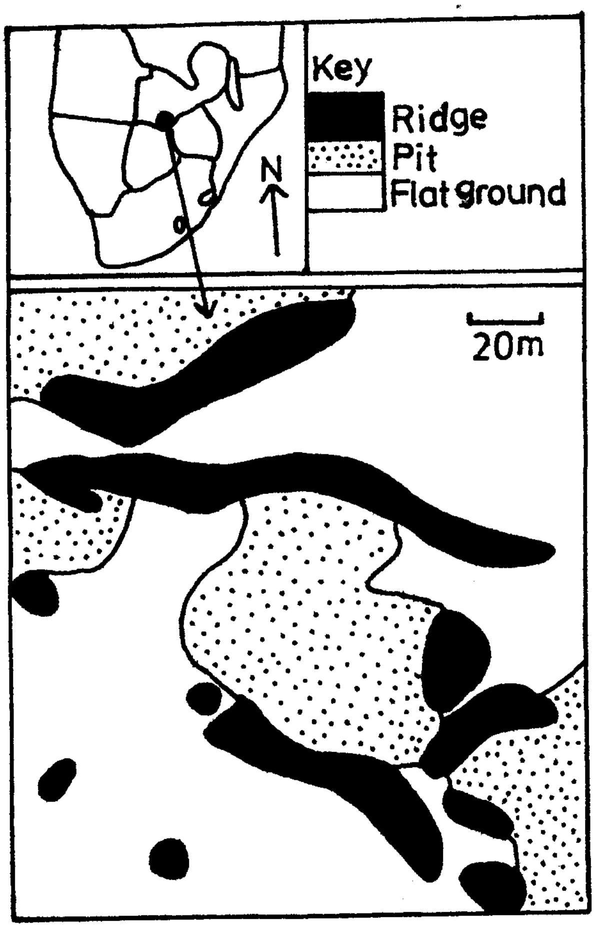

Fig.1 Map of study site.

Materials and Methods

Animals were collected using Sherman live traps and steel-plate breakback traps baited with fried maize flour and grains, respectively. Samples were obtained during the latter half of each month. Traps were set in the afternoon, checked the following morning and retrieved. Occasionally these were left out during the day and checked again in the afternoon to determine diurnal rodent densities. Traps were laid irregularly at vantage stations e.g. near burrows, on runways and at foraging points, because the heterogeneous topography at the study site prevented the use of traplines.

Live samples

Live-trapping samples were obtained from September 1975 - December 1976 with 40 live traps being set per night for 3 - 4 nights during each month. Often only part of the site was sampled each night and every P. natalensis and L. griselda caught was marked by toe-clipping for subsequent identification while other species were deliberately removed and killed. Data recorded included species, sex, body mass (to nearest g), point of capture and, for each individual released, the mark number. Marked animals were released immediately at the point of capture.

Kill samples

Kill-trapping samples were collected using breakback traps. Eighty trapnights in September 1974 and 102 trapnights in January, April and June 1975 were used per trapping period which lasted for two nights. Breeding data on P. natalensis during the live - trapping period (September 1975 - December 1976) at the study site were obtained from kill samples collected from elsewhere in Livingstone.

Each individual in kill samples was weighed, length of head, body, tail and hindfoot taken, skinned and the carcass dissected. The breeding condition was assessed by examining the uteri in females and caudae epididymes in males. In visibly pregnant females the number of embryos was recorded. Every skull was cleaned and the amount of tooth-wear on the occlusal surfaces of upper molar teeth determined microscopically.

Results

Community structure

The seven rodent species captured at the study site are shown in Tables 1 and 2. P. natalensis was the most abundant rodent and occurred in all the samples. Kill-trapping results showed that L. griselda was the second most abundant rodent followed by T. leucogaster but live-trapping results showed that the second most abundant rodent was S. campestris. Results in Tables 1 and 2 suggest seasonal or annual variation in species abundance and occurrence but they may well reflect trapping artifact.

Table 1 Number of rodents obtained in kill-trapping samples. Figures in parentheses show percentage of total rodents

Species	Trapping period Sept. 1974	Jan. 1975	Apr. 1975	June 1975	Total
P.natalensis	36	27	33	29	125 (77)
L.griselda	2	5	5	7	19 (12)
S.campestris	-	3	4	-	7 (4,3)
T.leucogaster	1	9	-	-	10 (6,2)
S.pratensis	-	-	1	-	1 (0,5)
M.minutoides	-	-	-	-	- (0)
A.chrysophilus	-	-	-	-	- (0)
Total	39	44	43	36	162 (100)

Table 2 Number of rodents captured during live-trapping. Recaptures of *P. natalensis* and *L. griselda* have been excluded. Figures in parentheses show total rodents caught

Species	Sept. 1975 (13)	Oct. 1975 (4)	Nov. 1975 (2)	Dec. 1975 (17)	Jan. 1976 (16)	Feb. 1976 (8)	Mar. 1976 (10)	Apr. 1976 (20)	May 1976 (34)	June 1976 (45)	July 1976 (12)	Aug. 1976 (7)	Sept. 1976 (4)	Oct. 1976 (8)	Nov. 1976 (6)	Dec. 1976 (13)	Total (219)	% of total (100)
	Trapping period																	
P. natalensis	11	2	1	13	9	5	3	16	31	39	9	6	4	4	5	9	167	76,2
S. campestris	–	–	–	–	6	3	7	4	3	2	–	1	–	3	–	1	30	13,7
L. griselda	2	2	1	1	1	–	–	–	–	2	3	–	–	1	–	1	14	6,4
S. pratensis	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	2	4	1,8
T. leucogaster	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	2	0,9
A. chrysophilus	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	0,5
M. minutoides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	0,5

Species micro-distribution

Species micro-distribution was determined from capture locations. These were recorded by micro-topographic zone (i.e. ridges or flat ground) because the vegetation was morphologically homogeneous. Data on capture locations of P. natalensis were pooled over seasons (Table 3) and analyzed to determine micro-habitat preference. The trapping effort in each micro-topographic zone was not similar because the density of traps laid depended on the density of rodent activity (e.g. burrows, foraging stations, runways, etc.). Sufficient traps were, however, laid on both ridges and flat ground on this basis. There was no evidence of rodent activity in the almost bare pits and therefore no traps were laid there. In calculating X^2 (Table 3) the differrence in area between ridges and flat ground but not in trapping effort has been corrected for. Difference in trapping effort might have influenced the analysis but most probably this is in the degree of the significance level and not the validity of the conclusion drawn from the analysis.

P. natalensis was captured on ridges and flat ground but a single individual was caught at the edge of one pit. P. natalensis preferred ridges because significantly more capture points were observed on these than on flat ground (Table 3). Capture points in August 1976, after a fire in July, were classified as unburnt (10) patchily burnt (4) and burnt (4). The frequency of capture points in the three classes did not depart significantly from expected values (at $p = 0.05$). This might, however, be an artifice as only a small portion of the site was unburnt.

Sherman live traps are designed to capture a single animal at a time but multiple captures of P. natalensis were recorded 22 times. Most of the multiple captures (77%) were recorded during April and July. Male/male, female/female and male/female inmates were all encountered with frequencies that were consistent with the expected values ($\underline{X}^2$, $\underline{p}$ = 0,05). In 16 multiple capture cases the inmates were of similar body mass (each under 30g) and in four cases the body mass was dissimilar and differed by 14 - 24g. In all the latter cases the combinations involved male/female inmates and except in one of these, the heavier animal was the female.

The 32 capture points of L. griselda were located as follows: 29 on flat ground and three on ridges. Two of the latter were recorded in December and the other in January. The difference in the distribution of capture points in the two micro-topographic zones was significant (Table 3) which suggests preference for flat ground by L. griselda. During the dry season L.griselda was mainly captured in the unburnt portions of flat ground. It was apparent from capture points of L. griselda that several individuals occupied extensively overlapping home ranges.

The 30 capture points of S. campestris were distributed as follows: 19 on ridges and 11 on flat ground. The difference in capture points on ridges and flat ground was significant (Table 3). S. campestirs therefore seemed to prefer gravelly ridges.

Table 3 The frequency of capture points in different micro-topographic zones at the study site. Chi-square values were all significant at $p \leq 0,05$

	Micro-topographic zone		
Species	Ridge (0,36ha)	Flat ground (1,40ha)	
P.natalensis			
Rainy season	83	45	40,57
Cool-dry season	107	57	85,74
Hot-dry season	20	23	11,01
S.campestris	19	11	65,00
L.griselda	3	29	5,99

P. natalensis and S. campestris made burrows in the loose gravelly soil on ridges but the former was also taken near burrows located on flat ground. Cracks in the soil on flat ground were used as shelter by P. natalensis and L griselda.

Feeding habits of the rodents were determined from captures at foraging points. P. natalensis and S. campestris appeared to feed predominantly on grass seed of Paspalidium sp which grew on ridges. P. natalensis also fed on Amarathus caudatus, particularly in the dry season and on Hyparrhenia in May and June 1976. Grass comprised the main food of L. griselda during the dry season.

Demography of P. natalensis

Age-structure

The relative age of individuals was determined from the amount of tooth-wear on upper molars. Seven tooth-wear age classes were recognized ranging from very slight wear when no dentine is exposed (tooth-wear class 1) to complete wear when the individual molar dentine is surrounded by a continuous marginal enamel ridge (tooth-wear Class 7). For the purpose of this paper tooth-wear age classes were regrouped into four age groups: juveniles (tooth-wear Class 1), subadults (tooth-wear Classes 2-3), adults (tooth-wear Classes 4-5) and old adults (tooth-wear Classes 6-7).

Figure 2 shows that juveniles were most abundant in April 1975 but these were virtually absent from the population two months later; most of these having qualified as subadults by then. These animals advance in age and are adults during the middle of the rainy season. The majority of P

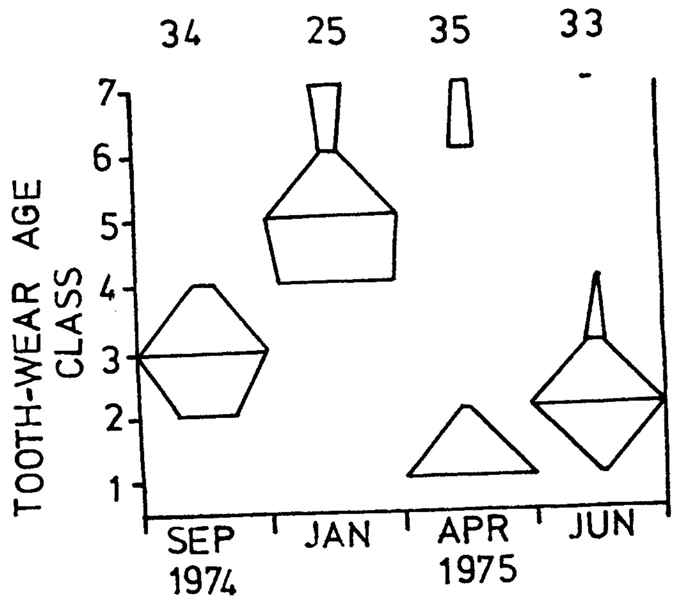

Fig.2 Age structure of P.natalensis at the study site. Each horizontal line is proportional to the frequency of each tooth-wear age class in each monthly sample. Top figures show sample size.

natalensis recruited into the previous year disappear from samples early in the dry season and are absent in samples collected later in the dry season. It is apparent therefore that the majority of P. natalensis at the study site do not live beyond one year. The P. natalensis population is characterized by a single generation during most of the year. At the end of the rainy season and early in the dry season, however, two generations co-exist (Fig. 2).

Sex ratio

The sex ratio of each sample was consistent with the 1:1 ratio, although there was a preponderance of males in December 1975 (65%) and 1976 (67%).

Reproduction

The breeding season was determined from the presence of visibly pregnant females and fecund males (with cauda epididymal sperms) in the monthly samples. Visible pregnancies appear sometime after the onset of breeding activity and actual mating. Consequently the breeding season based on visible pregnancies lags behind the actual breeding season. For P. natalensis, with a gestation period of 21 days (Johnston & Oliff 1954), the time lag should be rairly short (probably under 1,5 weeks) and does not distort the breeding season extensively.

The female breeding season lasted for four months (February - May) in 1976. Breeding must have started and ended earlier in 1975 because kill samples from the study site in January 1975 showed a 57% pregnancy rate while none of the 22 females was pregnant in April. Months of peak pregnancies in 1976 were February and April which were separated by a period of low pregnancies in March (see Table 4). During the first half of the breeding season adults and old adults contributed the largest reproductive effort (79%). The situation was reversed during the latter half of the 1976 breeding season with juveniles and sub-adults born during the first half of the 1976 breeding season contributing 66% of the reproductive effort. Most of the juveniles born and recruited into the population during the breeding season participated in reproduction before the end of the breeding season. The proportion of such female P. natalensis that participated in breeding was 57%. Individuals recruited into the population after the breeding season never attained sexual maturity until the following rainy season, 5 - 6 months later.

The mean number of foetuses observed in 43 pregnant females collected during the 1976 breeding season was 12,8 (range 8-21). This number is similar to those reported by Sheppe (1973) for P. natalensis from the Kafue Flats (January - March) and Mfuwe (May - June) in Zambia. Mean number of embryos per pregnant female, however, declined as the breeding season progressed: 14,9 in February, 14,0 in March, 12,2 in April and 10,0 in May. Mean number of embryos of the January 1975 sample from the study site was 11,3 which is smaller than that observed in February 1976. Resorbing embryos (diminutive embryos relative to others of the same pregnancy) comprised only 3% of the total 556 embryos examined.

The breeding season of male P. natalensis was more extensive than that of the female and lasted from November 1975 - June 1976 with a peak from January - March.

Population size

The population estimate was determined by enumeration techniques. It has been shown that enumeration techniques provide sufficiently accurate population estimates where 80% or more of rodents are caught during each trapping period (Hilborn, Redfield & Krebs 1976). Trappability (number actually caught during trapping period t per number known to be present during trapping period t) of P. natalensis averaged 86% (males) and 92% (females). In the present study the population estimate during trapping period t was made up of all rodents previously released during trapping periods t - 1 and t - 2 that missed capture during trapping period t but which were later recaptured at either trapping period t + 1 or t + 2, plus all rodents actually caught during trapping period t.

The number of P. natalensis in September 1975 was low following kill-trapping sampling in June 1975 when 29 individuals were removed (Table 1) and remained so until end of November (Fig 3). The population doubled in December and reached a low peak of 23 individuals in January 1976. This peak was followed by a gentle decline in numbers which brought the population to another low in March before numbers rose in April and more than doubled in May. A high peak in numbers was observed in June 1976

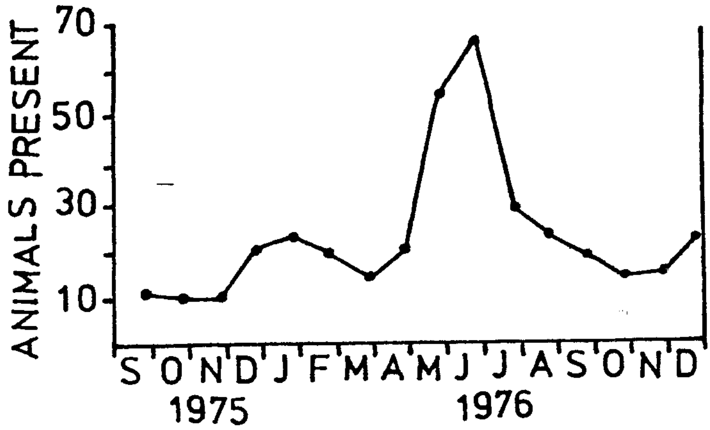

Fig. 3 Population size of P.natalensis at the study site.

(Fig 3). The period of peak numbers however was brief because there was a sharp decline in numbers in July. Thereafter, a steady and gentle fall in numbers was recorded until another low in October 1976. The early rainy season rise in numbers was again evident in December 1976 when the study ended.

Mortality

Live-trapping and recapture data were used to study survival of the trappable population between trapping periods. Survival value was equated to the proportion of rodents released during each trapping period that were known to be alive at any subsequent trapping period. For example, the survival value between trapping period t and t + 1 was equal to the percentage of animals released during trapping period t that were recaptured at trapping period t + n (where $n \geq 1$). Survival values are minimum estimates because disappearance from the study site was equated to mortality. Pre-weaning survival was estimated by comparing the number of mice born during the breeding season to young first entering traps up to two months after the end of the breeding season. Pregnancy rate and mean number of embryos per pregnant female were derived from kill-trapping samples from elsewhere and together with the number of females during each trapping period at the study site were used to calculate the number of young born during each month (Table 4). The gestation period in P. natalensis is about 21 days (Johnston & Oliff 1954) and the lactation period is similar (Meester 1960). Meester (1960) found the mean body mass at weaning of laboratory P. natalensis to be 11,7g but the mean body mass of juveniles collected from the field was 29,1g (n = 151; SD = 11,6). The upper limit of the mean body mass (40,7g) was chosen to separate juveniles from other animals. The difference in mean body mass of female (28,0g) and male (30,1g) juveniles was not significant (t - test, P = 0,05).

The survival of the trappable population (Fig. 4) fluctuated quite frequently but remained over 40% except in December 1975 (females), April (males) and July 1976 (females & males). If the low survival values in December 1975 and April 1976 are real, then the mortality factor operated differently between females and males. The mortality factor involved in the July period, however, operated indiscriminately throughout the population.

Pre-weaning survival was determined from data in Table 4. The overall pre-weaning survival was poor (30%) during the 1976 breeding season. When the data were separated into February — March and April — June, pre-weaning survival was divisible into a period of very poor survival (10%) and a period of moderate survival (46%),

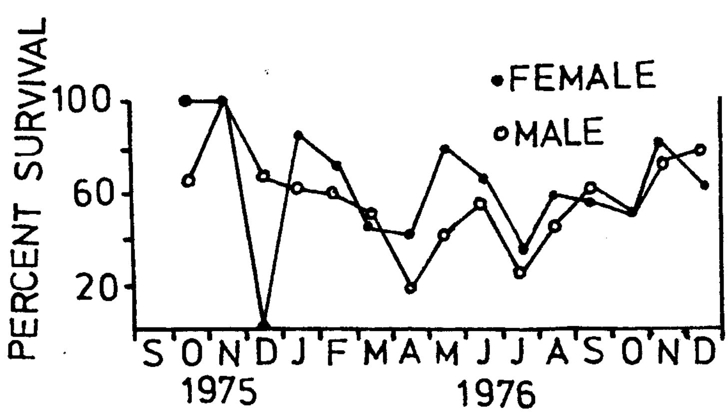

Fig.4 Changes in monthly survival of P.natalensis at the study site.

Table 4 Data used in calculating pre-weaning survival at the study site in 1976

Population variable	Month Feb.	Mar.	Apr.	May	June	July
Density of females	11	6	11	26	-	-
Pregnancy rate (%)	63	25	55	23	-	-
Mean no. of embryos/female	14,9	14,0	12,2	10,0	-	-
Young born	103	21	74	60	-	-
Juveniles caught	-	1	10	29	33	9

respectively. The survival of young improved after weaning. Post-weaning survival of juveniles marked and released in April and May 1976 was 55 and 60%, respectively, during the first month following their first appearance in traps. The poor survival value of 12% in July of juveniles marked and released in June was in fact better than that of the remainder of the June cohort which recorded 9% survival.

Population of L. griselda

The population ecology of L. griselda has been discussed elsewhere (Chidumayo 1977). A small but fairly stable population (3 - 4) of L. griselda was resident at the study site during two periods: September 1975 - January 1976 and June - December 1976. Apparently each individual that disappeared from the site was invariably replaced by a newcomer, such that the population size remained about the same throughout most of the species resident period.

Body mass of P. natalensis

The pattern of body mass changes in P. natalensis can be assessed from the growth of selected individuals shown in Fig. 5. Mice recruited into the population from May - July lost between 20 and 35% of their body mass during the latter half of the dry season but there was a marked increase in body mass of mice from October or November. The increase in body mass was greater and more rapid in males than in females. P. natalensis recruited into the population in 1975 were generally much heavier than current year recruits between March and July 1976.

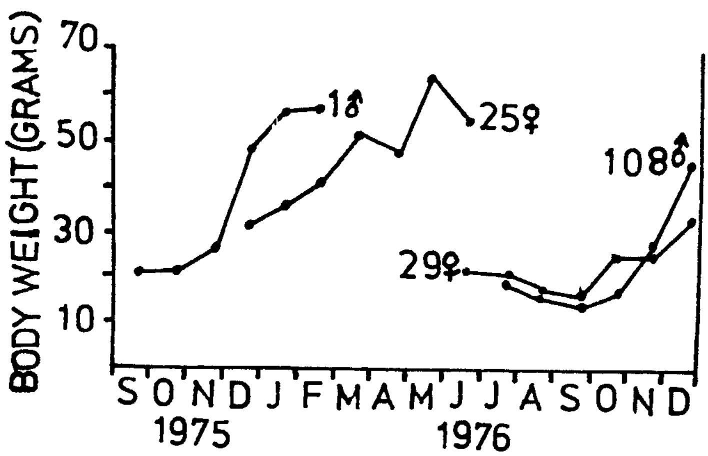

Fig.5 Changes in body mass of selected P.natalensis at the study site.

Discussion

The rodent community at the study site was very similar to that described by Swanepoel (1976) on four grids in northern Natal. P. natalensis was the most abundant rodent followed by S. campestris and L. griselda. The two species Tatera brantsi (A. Smith) and Otomys angoniensis (Wroughton) recorded by Swanepoel (1976) were absent at the study site while T. leucogaster was missing from the northern Natal grids.

Micro-distribution and foraging data suggest that P. natalensis and S. campestris might be ecologically similar in several ways. Both species seemed to prefer ridges to flat ground and Paspalidium seed was their predominant food. S. campestris was, however, most abundant from January to April when P. natalensis was less abundant. Swanepoel (1976) made similar observations. P. natalensis and L. griselda inhabit cracks in the soil but the former preferred ridges while the latter preferred flat ground. Furthermore, foraging data suggest differences in feeding habits between P. natalensis and L. griselda, at least during the period the latter was present.

The occurrence of multiple captures of P. natalensis indicates tolerance of conspecifics as has been suggested by Swanepoel (1976).

P. natalensis showed seasonal population fluctuations as did L. griselda. Sheppe (1972) obtained similar findings at the Kafue Flats in Zambia. P. natalensis had two population peaks: a low mid-rainy season peak and a high early dry season peak. The former results from immigration as juveniles were absent in the population until March 1976.

The early dry season population peak was a result of recruitment of juveniles into the population following the breeding season. The burn in July 1976 apparently caused the *P. natalensis* population to decline while none of the *L. griselda* survived the burn. Whether fire was the direct cause of mortality is not yet known but emigration from the study site is unlikely because traps set in the only unburnt patch of grassland about 100m from the site after the burn in July did not yield marked numbers of *P. natalensis*. The subsequent effect of the removal of 29 individuals during kill-trapping in June 1975 on the *P. natalensis* population is not known. The site had already been burnt when live-trapping started in September 1975. The low population in September 1975 might, therefore, have resulted from either the removal of rodents in June 1975 or the burn between July and September 1975 or both.

P. natalensis has a large mean number of embryos per pregnant female, short gestation and lactation periods, early sexual maturity during the breeding season and a fairly high pregnancy rate. The reproductive potential of the species is, therefore, very high inspite of a short breeding season as was observed in the present study and elsewhere (Hanney 1965; Delany 1972; Field 1975). This capacity to increase is, however, offset by a high pre-weaning mortality rate, such that the population declined during the breeding season. The good survival of the trappable population also deteriorated following the burn in July 1975. Habitat instability therefore was the major cause of population fluctuations at the study site.

The study site was primarily a dry season habitat for L. griselda. The breeding season for L. griselda is from November to May (Chidumayo 1977) which means that the species was absent from the site during most of the breeding season (February - May). L. griselda disappeared from the study site as the inter-ridge flat ground became waterlogged in the January - February period and the three capture records during this period were confined to ridges.

Sheppe (1972) found that P. natalensis on the Kafue Flats of Zambia lost 25% of their body mass during the dry season and the present results are in agreement. Food scarcity (Sheppe 1973) is probably a major cause of loss of body mass in P. natalensis. The increase in body mass late in the dry season and early in the rainy season is, however, difficult to explain as food was still scarce at this time.

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PART TWO

Section 2.2

Population ecology of Tatera leucogaster (Rodentia) in southern Zambia. Journal of Zoology, London (1980), volume 190: 325-335.

Population ecology of *Tatera leucogaster* (Rodentia) in southern Zambia

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(With 4 figures in the text)

A population of bush gerbils, *Tatera leucogaster* Peters, near Livingstone in southern Zambia was studied from January 1974 to December 1976. The population went through a peak, decline and was in a low phase at the end of the study.

Prior to and during the peak phase in 1974 the breeding season lasted for nine months but during the year of decline breeding occurred for only four months. There was also a decline in the reproductive effort of subadults and adults during the year of decreasing numbers. The sex ratio was significantly biased for females prior to realization of peak numbers.

Post-weaning mortality had the strongest impact on changes in numbers. Post-weaning and later survival was very good (over 60%) during the population peak but was poor (under 40%) during the decline phase.

Contents

Introduction

Little is known about population fluctuations of tropical rodents in Africa (Delany, 1972) which is in sharp contrast with the overwhelming knowledge of population dynamics of temperate rodents (e.g. Krebs & Myers, 1974; Stenseth, 1977). The purpose of this paper is to provide results that indicate the occurrence of annual fluctuations in population size of bush gerbils, *Tatera leucogaster* Peters, in southern Zambia, Central Africa.

Fieldwork started in January 1974 and continued until December 1976. Other rodents in the study area include *Praomys natalensis* A. Smith, *Saccostomus campestris* Peters *Lemniscomys griselda* Thomas, *Steatomys pratensis* Peters, *Mus minutoides* A. Smith, *Aethomys chrysophilus* de Winton and *Graphiurus murinus* Desmarest.

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Study area

Trapping sites are located north of Livingstone between latitudes 17° 44′ and 17° 49′ South and longitudes 25° 50′ and 25° 56′ East. Sixteen occasional trapping sites were occasionally sampled at different times during the study period. At one site, Dambwa (17° 48′ S, 25° 51′ E), samples were obtained regularly during each trapping period except in July 1976.

The rainy season in the study area is from November to April and mean annual rainfall at Livingstone is 727 mm. During the study period annual rainfall was above average: 1037 mm during 1973/74 season, 913 mm during 1974/75 season and 811 mm during 1975/76 season. Mean monthly temperature range is 25°–35°C (maximum) and 6°–19°C (minimum). The cool-dry season when mean minimum monthly temperature is 6°–11°C is from May to August.

An open-canopy *Baikiaea-Brachystegia* woodland on deep red sands with a field layer dominated by *Hyparrhenia* grasses covers the study area. At most trapping sites, including Dambwa, the woodland has been cleared and the resultant grassland is dominated by *Dactyloctenium giganteum*, *Panicum maximum* and species of *Hyparrhenia*.

Field methods

Samples were obtained by Sherman live traps which were available in two sizes: small (50×62×165 mm) and large (76×89×229 mm), and steel-plate breakback traps. Generally samples were collected during the latter half of each month except between January and April 1974 when these were obtained fortnightly. Traps were baited with fried maize (*Zea mays*). These were set in the afternoon, checked the following morning and picked up. Traps were laid at vantage points, e.g. on runways, near burrows or at foraging points.

A combination of live traps and breakback traps were used to obtain samples at occasional trapping sites but only live traps were set at Dambwa site. Each occasional trapping site was sampled with 60 traps per night for two nights and animals caught in live traps were either deliberately killed or kept in captivity for laboratory experiments.

A 1·2 ha plot at Dambwa was live-trapped for three or four nights during each trapping period from January to April 1974. The trapping area was enlarged to 6·4 ha in May 1974. The enlarged area was divided into four 1·6 ha plots and each of these was subdivided into 20×20 m squares. Each 1·6 ha plot was sampled using 44 live traps (22 small and 22 large size traps) for only one night with at least a trap per each 20×20 m square. Extra traps were laid in squares with a higher rodent activity (e.g. burrows and foraging points). On first capture each animal was marked by toe-clipping. Other data recorded were: mark-number, position of capture, species, sex, body weight (to the nearest gram), presence of wounds and ectoparasites and descension of testes in males. Palpable pregnancies were also noted and each animal was immediately released at the point of capture.

Laboratory methods

Each animal from occasional trapping sites, except animals kept for experiments, was weighed (to the nearest gram) head–body, tail and hindfoot length measured (to nearest mm) and skinned. Carcasses were dissected and examined for breeding condition. Breeding condition in males was determined by microscopic examination of cauda epididymal smears to ascertain presence of sperms. Pregnancies in females were determined from the presence of visible embryos in the uterus. Skulls were cleaned and upper molars microscopically examined to determine occlusal tooth wear which was used to estimate the relative age of animals.

Experimental animals were housed in wooden cages (50 × 50 × 30 cm) with a wire-mesh window on top and maintained on a maize diet. Cotton wool nesting material and drinking water were provided regularly. Experiments were conducted to obtain data on gestation period and post-natal growth. Female *T. leucogaster* were kept in isolation for at least five weeks before pairing with a breeding male (with descended testes) for three days. The procedure was repeated if parturition did not occur after five weeks. The gestation period was calculated by counting the second day of pairing as day one of pregnancy and the day of parturition as the last day of pregnancy.

Post-natal growth was studied by recording the body weight of nestlings born in captivity at weekly intervals. Some nestlings were killed at the age of 18–28 days to determine the age at which the third upper molar erupts.

Results

Population structure

Seven tooth-wear age classes were recognized, ranging from negligible wear when laminae dentine is not exposed (tooth-wear class 1) to complete wear when laminae dentine of each molar is coalescent and surrounded by a continuous marginal enamel ridge (tooth-wear class 7). For convenience the tooth-wear age classes were regrouped into broad age groups: juveniles (class 1), subadults (classes 2–3), adults (classes 4–5) and old adults (classes 6–7).

Age structure

Age structure data were summed over each two successive months (Fig. 1). Juveniles were present in the population throughout the year although annual variations occurred. In 1974 juveniles occurred almost throughout the year but these were present in the population from March to June in 1975. The majority of juveniles appeared and were

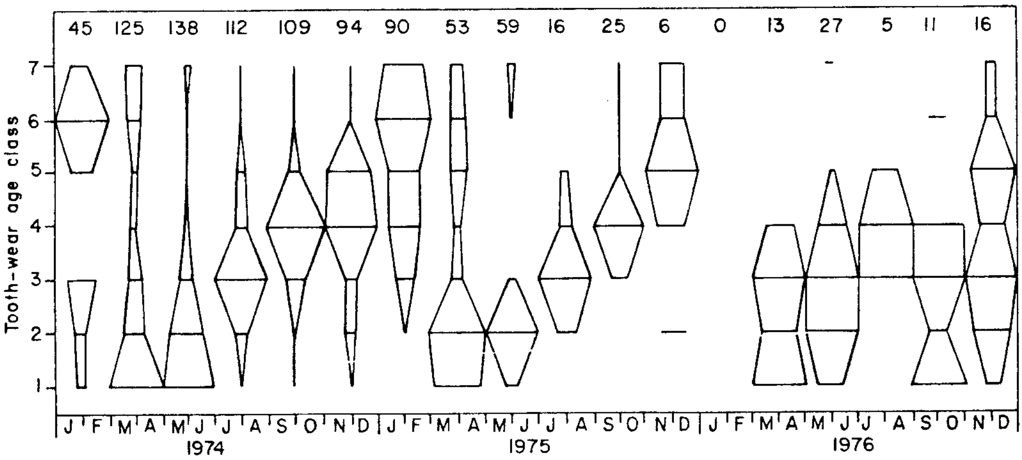

FIG. 1. Annual age distribution of *Tatera leucogaster*. Each horizontal line is proportional to the frequency of each tooth-wear age class in each bimonthly sample. Top figures show sample size.

dominant in the population at the end of summer and early in the cool-dry season (March–June). These juveniles advanced in age and qualified as old adults the following summer, after which they became rare or disappeared from the population. It is apparent, therefore, that the majority of *T. leucogaster* do not live for more than one year but the population of *T. leucogaster* was characterized by the co-existence of two generations.

Sex ratio

Among juveniles, subadults and adults the sex ratio was consistent with the expected 1:1 ratio (Chi-square test at $P=0{\cdot}05$). This was so inspite of a preponderance of males (62%) among juveniles in March and April 1974 and of females (63%) among subadults in May and June 1975. Two consecutive bimonthly samples of old adults deviated significantly from the 1:1 ratio. Females were in excess in both the March–April and May–June 1974 samples: $\chi^2=6{\cdot}24$ and $5{\cdot}34$, respectively, at $P=0{\cdot}05$. Additionally, the overall old adults sex ratio in 1974 was significantly in favour of females ($\chi^2=8{\cdot}34$, $P=0{\cdot}05$).

Live-trapped mark and release samples at Dambwa were in conformity with the 1:1 sex ratio, although males were predominant (63%) in December 1974. These data may be erroneous as samples at Dambwa were not separable into tooth-wear age groups. There was, however, a significant bias for females among new recruits in May 1975 ($\chi^2=5{\cdot}6$, $P=0{\cdot}05$).

Reproduction

The breeding season was determined from the presence of visibly pregnant females and males possessing cauda epididymal sperms (fecund males) in autopsied samples. Pregnancy and fecundity rates are based on the percentage of total females and males examined, respectively. The number of embryos per pregnant female was equated to litter size and diminutive embryos relative to others of the same pregnancy were presumed to be resorbing.

Female breeding season

Breeding was continuous throughout 1974 (Fig. 2) although there was a non-breeding spell in June and July. Breeding activity was already under way by January 1974 at the beginning of the study and although breeding had started by December 1974, the breeding season in 1975 was greatly abbreviated and had virtually ended by April. The occurrence of juveniles in the March–April samples in 1976 suggests that the onset of the breeding season was similar to that of the two preceding years. It is apparent from the few data available that the duration of the 1976 breeding season corresponded to that of 1974 (Fig. 2).

The cessation of breeding activity during the cool-dry season enables the division of the female breeding season into: (i) a high intensity summer breeding period (or the major breeding period) and (ii) a low intensity hot-dry season breeding period (or the minor breeding period). Pregnancy rates varied each year. Peak pregnancies occurred in March and April 1974, February 1975 and March 1976. Pregnancies were recorded in May throughout the study period although none of the females was pregnant in April 1975 and 1976. August–October pregnancies were only observed in 1974. The reason for these variations in pregnancy rates between the different years are not known although prolonged breeding in 1974 was associated with the unusual high rainfall of the 1973–4 rainy season. The duration of the rainy season, however, was similar throughout the study years and is, therefore, unlikely to have affected the length of the breeding season.

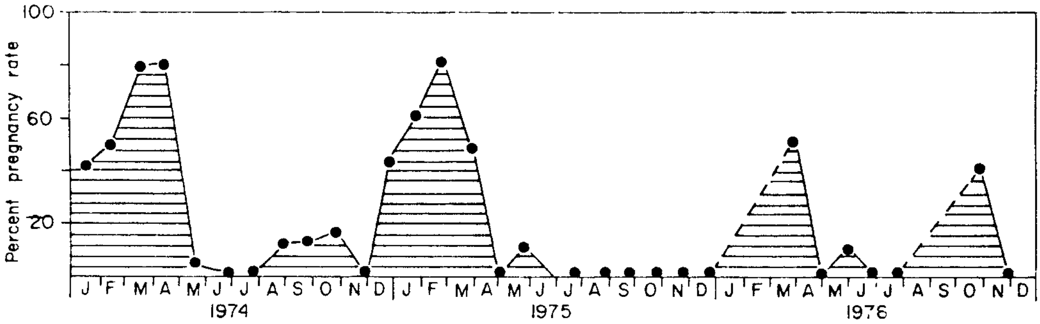

FIG. 2. The breeding season of female *T. leucogaster*.

Litter size

Variation in litter size in *T. leucogaster* was primarily correlated with the breeding period. A sample of 100 pregnant females yielded a mean litter size of 4·6 (range 1–9, litter size of eight was not recorded). Mean litter size of 5·0 for the December–April period during the different years was significantly larger than 2·7 for the May–October period ($t = 2{\cdot}36 > 2{\cdot}04$, $P = 0{\cdot}05$). There was a gradual increase in mean litter size from 3·4 in December to 5·0 in April before declining sharply to 3·0 in May and 2·1 in June. Monthly mean litter size ranged from 2·4 to 2·8 during the hot-dry season.

The difference in litter size among maternal age groups was not significant except between mothers of tooth-wear classes 1–2 (3·6) and those above tooth-wear class 4 (4·9): $t = 2{\cdot}34 > 1{\cdot}98$, $P = 0{\cdot}05$. The difference in mean litter size during the same breeding period in difference years was not significant. Resorbing embryos comprised only 1·8% of the total embryos examined.

Age-specific reproductive effort

Breeding data were pooled over each breeding period and analyzed by age groups (Table I). Juveniles contributed approximately 6% to the total reproductive effort during the major breeding period in 1974 and 1975. The proportionate reproductive contribution of subadults to total reproduction declined from 41% in 1974 to 23% in 1975 during the major breeding period. Much more significant, however, was the relative drop in the number of subadults and adults that participated in reproduction in 1974 (subadults = 86%, adults = 82%) and 1975 (subadults = 57%, adults = 50%). This represents a decline of around 30% in reproductive performance of each of these age groups during the major breeding period in 1975.

Juveniles and old adults did not participate in reproduction during the hot-dry season. Subadults contributed 30% and adults 70% to total reproduction during the minor breeding season in 1974.

Some juveniles recruited into the population during the rainy season attained sexual maturity at an early age and participated in reproduction during the breeding period of their birth. In contrast, there was no evidence of such early age attainment of sexual maturity among juveniles recruited into the population in the hot-dry season.

TABLE I

Age specific reproductive effort during 1974–1975. Figures in parentheses show sample size

Age group		Age group pregnancy rate (%)	Percent of total pregnant females
1974 major breeding period			
Juveniles	(17)	17	6·5
Subadults	(22)	86	41·2
Adults	(11)	82	19·6
Old adults	(31)	42	32·6
1975 major breeding period			
Juveniles	(3)	67	5·7
Subadults	(14)	57	23·0
Adults	(22)	50	31·3
Old adults	(21)	67	40·0
1974 minor breeding period			
Juveniles	(3)	0	0·0
Subadults	(18)	17	30·0
Adults	(34)	21	70·0
Old adults	(6)	0	0·0

Male breeding season

There was year-round breeding in male *T. leucogaster*, except in June 1975 and July 1976 when no fecund male was recorded. A high proportion of males (60–100%) was fecund from November to May although this figure was lower in April (20%) and May (7%) 1975. A smaller proportion was fecund during other months (15–40%) although 60 and 50% were in breeding condition in September 1975 and October 1976, respectively.

Population size

The population estimate at Dambwa was determined by enumeration techniques because sampling was not random. Hilborn, Redfield & Krebs (1976) have shown that enumeration techniques provide sufficiently accurate estimates where 80% or more of the animals are caught each sampling period. Assuming that the number of animals present at the study site during trapping period t was made up of animals actually caught and those released during trapping periods $t-2$ and $t-1$ that were recaptured during trapping periods $t+1$ and $t+2$ but missed capture during trapping period t, trappability (number actually caught during trapping period t/number known to be present during trapping period t) of *T. leucogaster* averaged 89% (males) and 78% (females). The number of animals known to be present but not necessarily caught at the study site during trapping period t was taken as the population estimate.

Numbers of *T. leucogaster* caught on the 1·2 ha plot at Dambwa site before May 1974 were as follows: five in January, 0 in February, four in March and nine in April. The figure of 42 *T. leucogaster* caught in May on the 6·4 ha plot implies an underestimation as the estimate in April 1974 was 53 animals. Numbers reached a peak (62) in June (Fig. 3) after which there was a slight but steady decline in numbers until November 1974. The decline sharpened in December 1974 and February 1975, inspite of a slight increase in numbers in January 1975. The first population low (19–20) occurred in February and March 1975. The population tried to recover albeit unsuccessfully in April 1975 (Fig. 3) and thereafter forces of decline became predominant. Numbers reached the lowest level in February 1976 when one *T. leucogaster* was present at the site. The population never recovered until the end of the study.

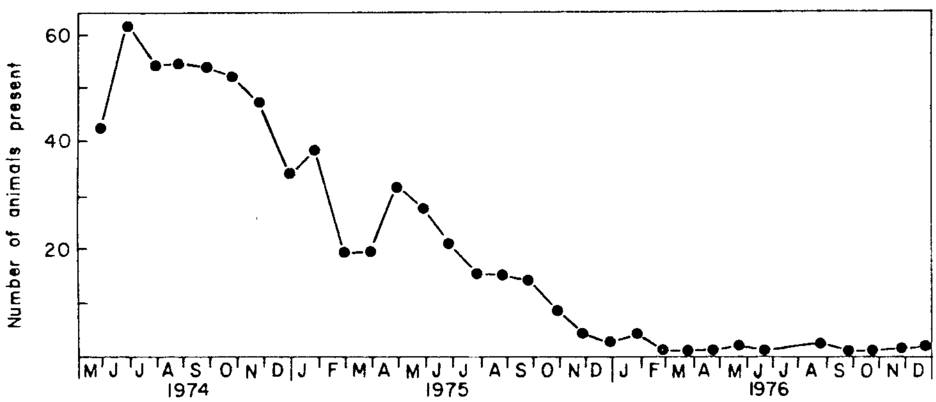

FIG. 3. Population size of *T. leucogaster* at Dambwa site.

Mortality

Live-trapping mark and release data were used to study survival of the trappable population between trapping periods. Survival values, between trapping periods (Fig. 4) are based on the percentage of animals released during trapping period t that were subsequently recaptured at trapping period $t+n$ (where $n \geq 1$). The survival values obtained represent minimum estimates because disappearance from the trapping area was equated to mortality. Pre-weaning survival was estimated by comparing the number of mice born during each breeding period to juveniles (<49 g) first entering traps up to two months after the end of the breeding season. Gestation and lactation periods for *T. leucogaster* based on three females in captivity, was estimated at 28 days each. Young *T. leucogaster* in captivity attained the live body weight of 45 g at 28 days after birth but the mean body weight of juveniles from the wild was 35 g ($n=164$, S.D. $=13$). The mean body weight plus standard deviation (48 g) was therefore chosen to separate juveniles from older animals at Dambwa. Pregnancy rate and mean litter size derived from autopsy data and the number of females during each trapping period at Dambwa were used to calculate the number of young born between trapping periods.

Survival of trappable population

June–November 1974 and June/July–August 1975 were periods of good survival

(> 60%) among both males and females (Fig. 4). Low survival (< 40%) occurred from February (males) and March (females) to April 1975 and from October (males) and November (females) to December 1975. The first decline and subsequent recovery in survival were steeper among males than females and for the former survival was zero in March 1975 while the corresponding figure for females was 30% in April 1975. There was a precipitous second decline in survival between October and November 1975 (Fig. 4) for both males and females.

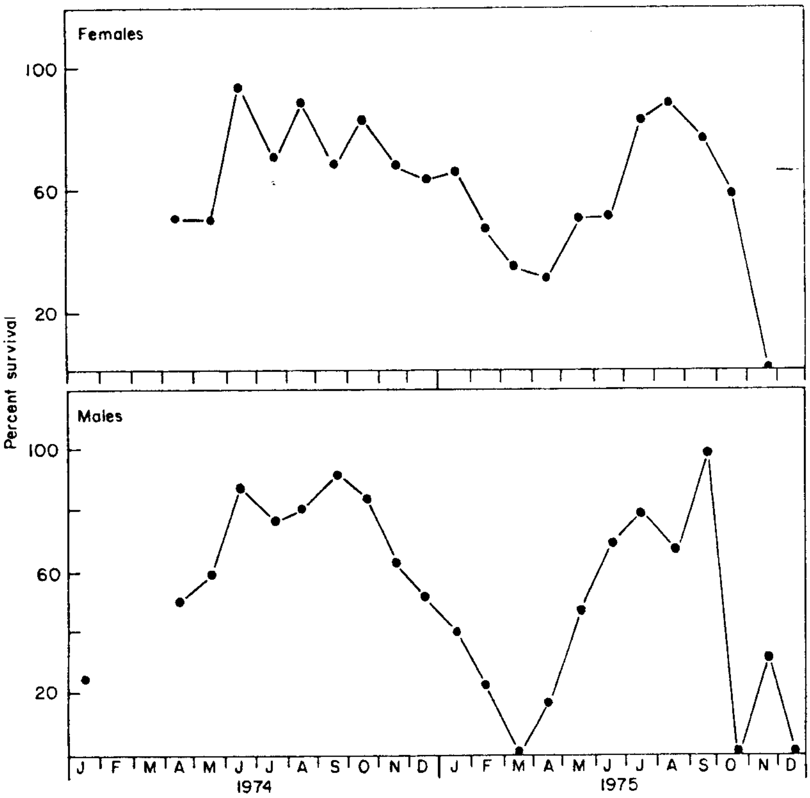

FIG. 4. Survival of the trappable *T. leucogaster* population between trapping periods at Dambwa site.

Major recruitment into the population occurred in the periods May–June 1974 and March–May 1975 and the survival of cohorts (juveniles) released during these months were followed in detail. The survival of the May and June 1974 cohorts varied from 66% to 100% between June and December 1974 (Table II). Survival of both cohorts temporarily declined to 50% in January (May cohort) and April (June cohort) 1975 but in either case recovery occurred during the following month.

The survival of older animals released in May 1974 fluctuated between 60% and 100% until March 1975 when this dropped to 50% (Table III). These results indicate that animals released in May and June 1974, irrespective of age, enjoyed good survival until April or May 1975.

In contrast, the survival of the March–May 1975 cohorts was poor (20–50%) until June 1975 (Table IV). The apparently good survival enjoyed by these cohorts between July and October deteriorated abruptly thereafter and was zero in November although a single member of the May cohort survived up to the end of December 1975.

Pre-weaning survival

Pre-weaning survival was calculated using data in Table V. During the August–October 1974 period pre-weaning survival was 53% while that for the period December 1974–March 1975 was 42%. Unfortunately the enlargement of the live trapping study site at Dambwa in May 1974 made it impossible to calculate pre-weaning survival during the January–May 1974 breeding period. Recruitment results in 1974, however, suggest that pre-weaning survival was better than post-weaning survival during 1975.

TABLE II

Survival and decline of the May–June 1974 cohorts. Figures in parentheses show animals surviving to the next trapping period

	May cohort		June cohort	
Month	Male	Female	Male	Female
May 1974	11(10)	11(10)		
June	10(7)	10(6)	12(9)	15(10)
July	7(7)	5(5)	9(8)	10(8)
August	7(6)	5(3)	8(8)	8(8)
September	5(5)	3(2)	7(6)	8(8)
October	5(5)	2(1)	7(5)	8(6)
November	5(3)	1(1)	5(4)	6(4)
December	3(1)	1(1)	4(3)	4(4)
January 1975	1(1)	1(0)	3(2)	3(2)
February	1(1)	–	1(0)	2(2)
March	1(0)	–	–	2(1)

TABLE III

Survival and decline of older animals released during May 1974 trapping period. Figures in parentheses show animals surviving to the next trapping period

Month	Male	Female
May 1974	7(7)	4(4)
June	7(6)	4(4)
July	6(4)	4(4)
August	4(4)	4(3)
September	4(2)	3(3)
October	4(2)	3(1)
November	2(2)	3(1)
December	2(2)	1(1)
January 1975	2(1)	1(0)
February	2(1)	–
March	1(0)	–

TABLE IV

Survival (%) of the March–May 1975 cohorts. Figures in parentheses show cohort sizes

Month	Cohort March	Cohort April	Cohort May
	(9)	(25)	(16)
April 1975	22	–	–
May	50	44	–
June	100	40	80
July	0	75	75
August	–	100	50
September	–	50	100
October	–	0	100
November	–	–	50
December	–	–	100

TABLE V

Data for calculating pre-weaning survival at Dambwa

Trapping period	No. of adult ♀ caught at Dambwa	Pregnancy rate (%) (autopsy data)	Mean litter size (autopsy data)	Estimated no. of juveniles born	No. of juveniles caught at Dambwa
August 1974	18	14	2·5	6·2	0
September	18	12	2·5	5·4	0
October	21	16	2·5	5·4	1
November	19	0	–	0·0	4
December	10	40	3·5	14·0	4
January 1975	13	60	3·8	29·6	0
February	9	80	4·5	32·4	0
March	6	46	4·5	12·4	8
April	6	0	–	0·0	20
May	–	–	–	–	6
June	–	–	–	–	3

Discussion

It is difficult to determine the population phase *T. leucogaster* was undergoing when the study commenced but numbers obtained between January and March 1974 suggest moderate densities which denote an upward trend in population size. Based on this premise, *T. leucogaster* at Dambwa went through four population phases: increase (up to March 1974), peak (April–November 1974), decline (December 1974–July 1975) and low (August 1975 to end of the study). Certain demographic and environmental factors were associated with different population phases.

During population increase and early in the peak phase (i) the sex ratio was heavily biased for females, (ii) breeding was prolonged with accompanying high pregnancy rate (84%) among subadults and adults and (iii) pre- and post-weaning survival was good (> 60%). All these factors contributed to the population peak in 1974. In contrast, during the period of population decline the breeding season was greatly abbreviated, subadults and adults showed low pregnancy rate (54%) and pre- and post-weaning survival was poor. The underlying causes of these demographic changes are not known at present but direct relationship between rainfall and *T. leucogaster* demography is unlikely. However, the former may have influenced *T. leucogaster* population dynamics through food supply and quantity of field layer vegetation cover. Visual observations at Dambwa showed that the amount of field layer vegetation cover declined each successive year from 1974 to 1976 in response to decreasing total rainfall. Birney, Grant & Baird (1976) have shown the relationship between vegetation cover and population cycles in *Microtus*.

These *T. leucogaster* population data are similar to those commonly reported for microtine rodents (Chitty, 1960; Krebs & Myers, 1974; Stenseth, 1977). If this is so then Krebs & Myers (1974) are right to suggest that density fluctuations are not restricted to arctic and alpine areas but that these also occur in the tropics.

The author wishes to thank the National Museums Board of Zambia for funding this study. Work was done while the author worked as a Mammalogist at Livingstone Museum, Zambia. Professor W. Banage of University of Zambia gave useful advice during fieldwork.

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PART TWO

Section 2.3

The ecology of the single striped grass mouse, *Lemniscomys griselda*, in Zambia. *Mammalia* (1977), volume 4: 411-418.

The ecology of the single striped grass mouse, *Lemniscomys griselda*, in Zambia

by

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Au cours de recherches sur les populations de petits mammifères de Zambie dans le district de Livingstone, de 1974 à 1976, 132 *Lemnisconys griselda* Thomas ont été capturés. Cette espèce est surtout abondante dans les zones herbeuses au cours de la saison sèche ; elle était beaucoup plus rare au cours de la saison humide dans tous les milieux. L'analyse des contenus stomacaux montre qu'elle mange surtout des graines de graminées de janvier à avril ou mai et surtout des feuilles et des tiges de graminées aux autres saisons. La reproduction a lieu pendant la saison des pluies de novembre à mai. De décembre à août, deux générations ont été représentées dans les captures ; de septembre à novembre une seule génération était représentée. Le nombre des jeunes en croissance augmente entre avril et mai et est maximum en juillet. Il décline d'août à octobre. On a constaté un accroissement de poids du corps de novembre à février en rapport avec la maturité sexuelle.

INTRODUCTION

The single striped grass mouse, *Lemniscomys griselda* Thomas, is widespread in Southern Africa (Davis, 1974), but usually seems to occur in small numbers. Sheppe (1973) obtained only three of this species out of 2,000 small mammal specimens from Kafue, Lusaka and Luangwa valley areas of Zambia. It is thought to be absent from northern Zambia and the Nyika plateau (Ansell, 1964) and was rarely trapped in southern Tanzania (Vesey-FitzGerald, 1966). In constrast, there was a relatively large catch of 132 *Lemniscomys griselda* in the present study, making up 5 percent of the catch. This paper reports the results on the distribution, habits, breeding, age-structure and growth of *Lemniscomys griselda* obtained from 1974 to 1976.

STUDY AREA

The study was conducted in the Livingstone district of Zambia, in an area lying between 17°44′-17°50′ S, and 25°45′-26°00′ E. The average annual rainfall is 740 millimetres and falls from late November to early April. Lowest mean minimum temperatures, of under 10 °C are experienced between May and June. The period August-November is warm (mean minimum T°, is above 15 °C) and dry (relative humidity is below 45 %).

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The vegetation of the district is deciduous and woody species lose leaves from July to October. The herbeceous vegetation, including grasses, dries out after the rainy season and is annually fired. Three vegetation communities can be recognized in the area : the miombo woodland savanna ; the mopane tree savanna ; the dambo grassland.

Miombo woodland savanna.

This occurs above 930 metres altitude and grows on sandy soils. Dominant trees include *Baikiaea*, *Brachystegia*, *Julbernardia*, *Pterocarpus*, *Guibourtia*, *Burkea*, *Erythrophleum*, *Combretum*. *Strychnos* is the dominant shrub. Sparsely growing forbs and grasses occur under the tree canopy during the rainy season. Abundant grasses include *Hyparrhenia Cymbopogon* and *Loudetia*. Tracks of grassland occur where the woodland has been cleared.

Mopane tree savanna.

This occurs below 930 metres altitude and grows on either escarpment stony soils or on sandy clays on flat ground. The area of tree canopy is less than that covered by grasses, in contrast to the miombo woodland savanna. On the escarpment zone, the dominant trees are *Julbernardia*, *Brachystegia*, *Colophospermum* and *Combretum*. The dominant trees on sandy clays include *Colophospermum*, *Albizzia*, *Acacia* and *Lonchocarpus*. Shrubs include species of *Commiphora*, *Combretum*, and *Acacia*. The grasses in the tree savanna are similar to those occuring in the miombo woodland savanna.

Dambo grassland.

This community occurs along streams, many of which are seasonal. The soils are blackish sandy clays, sometimes intermixed with gravel. These crack in the dry season and are water logged during the latter half of the rainy season. Although shruby *Acacia*, *Combretum* and *Piliostigma* may occur, grasses dominate. These include *Hyparrhenia*, *Cymbopogon*, *Andropogon*, *Bothrichloa*, *Loudetia*, *Sorghum*, *Setaria*, etc.

MATERIALS AND METHODS

Trapping started in January 1974 and continued until April 1976. Animals were trapped during the latter half of each month, using spring snap traps and occasionally in association with Sherman live-traps. Throughout the study snap traps were baited with fried maize *(Zea mays)* and live-traps with ground, fried maize. Although sampling was not even in all the habitats, at least two different habitats were sampled each month.

The sampled area never exceeded one hectare in size and was trapped using between 60 and 120 tranights for one or two nights. Traps were set irregularly, in rodent runs, near burrows or gnawed food. These were set in the afternoon, checked the next morning and picked up. But occasionally traps were left out during the day to determine diurnal species.

Data recorded for each animal included ; body weight, length of head-body, tail, hindfoot and ear, and breeding condition. If pregnant, number and distribution of embryos in the uterii ; placental scars were also recorded in parous females. Ectoparasites and macroscopic parasites of the digestive tract were collected. Stomach contents were analysed by a method similar to that of Field (1972). The contents were dried and ground to a homogeneous mixture in a mortar. A sample of this was boiled in 5 percent sodium hydroxide, and insect parts separated by bubbling water into the contents and removing the floating insect parts. The remaining plant material was pipetted and a few drops examined under a binocular microscope. Grass inflorescence parts were used to recognize seed endosperm. Three microscopic fields were examined and the proportion of each food category calculated using the total count of all food particles, in the three fields as the denominator.

RESULTS

Distribution and abundance

The relative abundance of *Lemniscomys* in the catch from different habitats is given in Table 1. The species is relatively more abundant in grasslands, where it made up 18 percent of the catch. In the tree savanna it made up only

TABLE 1

Habitat	Samples obtained	Total rodents caught	No. of Lemniscomys	% of Lemniscomys
Miombo woodland savanna	38	1192	30	2
Mopane tree savanna	35	919	62	6
Dambo grassland	9	214	40	18
All habitats	82	2325	132	5

6 percent of the catch and was infrequent in the miombo woodland. *Lemniscomys* is particularly active from late afternoon and at night, as few animals were trapped during the day. At one site, where recapture studies were conducted, *Lemniscomys* was never caught during the day even when traps were left set for 24 hours and inspected in the morning and afternoon. At this same site, five *Lemniscomys* were resident in a small patch of unburnt grass within a hectare study area of dambo grassland, from September to November 1975. These animals were never trapped again after November. Only 5 percent of the total sample was obtained during the rainy months of January to March. *Lemniscomys* is, therefore, relatively scarce during the rainy season.

The species has been trapped in runs and near burrows. It also builds grass nests on the ground. A single litter of seven young was found in April 1976 in a grass nest constructed in a shallow excavation on the ground. The species, therefore, utilizes grass nests and burrows as shelter.

Feeding habits

The food of *Lemniscomys* exclusively consisted of vegetative grass parts, from June to December, and predominantly of grass seed from February to April. In the months of January and May a mixture of the two was recorded. Insects rarely occurred in the stomach contents. Captive *Lemniscomys* never ate nuts or seeds of trees and forbs but accepted grass vegetable and seeds.

Breeding season

Female animals were considered breeding if the showed enlarged uterii (active) or had visible embryos (pregnant). Males possessing sperms were considered breeding. Verification of this condition was by microscopic examination of the contents of the cauda epididymis. Because of the small samples obtained during the breeding season, the data for the two sexes are treated together (Fig. 1).

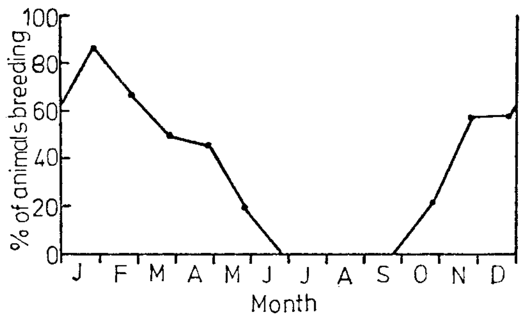

Fig. 1. — Breeding activity in the single striped African grass mouse, *Lemniscomys griselda*.

Breeding performance increased steadily from October and reached a peak in January and February, but declined thereafter to nil in June. Fecund males were obtained from October to May and both active and pregnant females were recorded from November to April. The male, therefore, is in breeding condition a month before and after the female breeding season.

Litter size as determined from embryo counts ranged from 3 to 8. Parous females were obtained throughout the year. Some subadult females were found parous in March suggesting early attainment of reproductive maturity of juveniles born early in the breeding season.

Age-structure

The relative ages of animals were determined by tooth-wear examination of the upper molars. Eight tooth-wear classes were distinguished.

The annual age-distribution of *Lemniscomys* is shown in Fig. 2. The species pattern of age-structure is simple and results from the seasonality in breeding. From December to April, two age groups exist : those born the previous

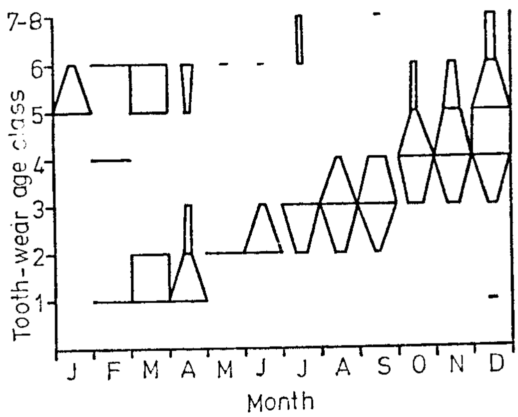

Fig. 2. — Annual age-distribution of *Lemniscomys griselda*. Each horizontal line is proportional to the monthly frequency of each tooth-wear age class.

breeding season (above tooth-wear class 3) and those born during the current year breeding season (under tooth-wear class 3). Older animals are rare in the May to September samples and are absent in the samples from November. The first juveniles of the breeding season appear in the samples from December, although these are scarce until March or April. These appear in large numbers from April to May, after which recruitment ceases.

Growth

Since the animals recruited during the same breeding season can easily be recognized from the age-structure (Fig. 2), it was possible to study body weight changes of animals recruited in autumn (April-May). Figure 3 shows the results. The animals had increased rate of growth in July but growth declined during the dry season months of August to October. The increase in body weight from November to February (Fig. 3) is associated with the onset and progress of the breeding season (Fig. 1). Analysis of variance of mean body

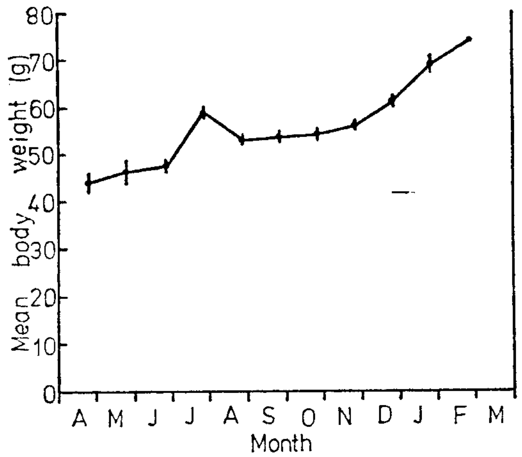

Fig. 3. — Body weight growth of members of the autumn generation in *Lemniscomys griselda*. Vertical lines = standard error.

weights of monthly samples gave a significant variance ratio ($F = 4.26 > 2.72$, $p = 0.01$). The difference between monthly mean sample body weights is, therefore, significant. However, comparison of mean body weights between succeeding monthly samples only gave the June/July and July/August data as significantly different ($t = 4.09 > 2.11$, and $t = 2.16 > 2.04$, respectively, $p = 0.05$).

Discussion

Kingdon (1974) has suggested that the abundance of *Lemniscomys griselda* in Southern Africa is due to the absence of competition from the more advanced *Lemniscomys striatus* and *Arvicanthis*. But the absence of competition cannot explain why Sheppe (personal communication) was unable to obtain *Lemniscomys griselda* in other parts of Zambia where *Lemniscomys striatus*, *Arvicanthis*, and indeed other grass mice, e.g. *Otomys*, *Dasymys* and *Pelomys* were absent. The abundance of *Lemniscomys griselda* at Livingstone is, therefore, just a result of the species adaptation to the area. Although, Vesey-FitzGerald (1966) suggested that *Lemniscomys griselda* is a woodland species, it was commonly trapped in grassland and tree savanna, and was only infrequently caught in the miombo woodland, where its occurrence is restricted to tracks of grassland where the woodland has been cleared.

The high relative abundance of the species in dambo grassland may be related to the availability of grass feed and shelter in soil cracks during the dry season. However, the general scarcity of *Lemniscomys* during the January-March period may be a result of trap avoidance or a reflection of the period of increased mortality.

Analysis of stomach contents has confirmed the findings of other workers (e.g., Ansell, 1960 ; Roberts, 1951) that *Lemniscomys griselda* is primarily a grass vegetable eater. But the occurrence of predominantly grass seed endosperm from late January to April, indicates the species preference for grass seeds when these are available.

The breeding season in *Lemniscomys griselda* coincides with the rainy season. Breeding in the related species, *Lemniscomys striatus*, in Uganda also coincides with the bi-annual rainy seasons of East Africa (Field, 1975). The suggestion that breeding in some tropical African rodents may be related to oestrogenic levels in grasses (Field, 1975) may well apply to *L. griselda*, which unlike *L. striatus* shows no preference for insects as a high protein food source, during the breeding season.

The age-distribution of *Lemniscomys griselda* suggests that members of one generation do not live for more than 20 months, with the majority disappearing after only 12 months. Similar results have been obtained for three other rodents from the same area : *Praomys natalensis*, *Saccostomus campestris* and *Tatera leucogaster* (Chidumayo, in preparation).

Growth in body weight of animals recruited in the April-May period is probably retarded due to low minimum temperatures (Sadleir, 1972) between May and June. In the remainder of the dry season, lower food quality, as abundant grass feed is available (personal observation), is probably the cause of reduced body growth and delayed reproductive maturity of the animals.

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SUMMARY

Trapping during a study of small rodent populations in the Livingstone district of Zambia from 1974 to 1976, yielded 132 single striped grass mice, *Lemniscomys griselda* Thomas. It was most abundant in grasslands, during the dry season but was most scarce in the rainy season in all the habitats. Stomach contents analysis showed that it ate primarily grass seed from January to April or May and primarily grass leaves and stems at other seasons. Breeding occurred during the rains, from November to May. From December to August two generations were represented in the catch ; but from September to November a single generation was caught. Growth of juveniles recruited between April and May was highest in July ; but declined from August to October. There was an increase in body weight from November to February which was associated with the attainment of reproductive maturity.

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