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 minutoides* and *Aethomys chrysophilus* were rare. Food and micro-habitat preferences of *S. campestris* 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.
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Tussen September 1974 en Desember 1976 is knaagdiere lewend en dood in 'n ou steengroef van 2,5 ha naby Livingstone, suidelike Zambië versamel ten einde ekologiese verwantskappe tussen spesies vas te stel. Die gemeenskap het uit sewe spesies bestaan. *Praomys natalensis* was mees volop, alhoewel *Saccostomus campestris* en *Lemniscomys griselda* ook algemeen was. Die vier spesies (*Tatera leucogaster, Steatomys pratensis, Mus minutoides* en *Aethomys chrysophilus*) was skaars. *S. campestris* en *P. natalensis* het dieselfde voorkeure ten opsigte van voedsel en mikro-habitat getoon. *P. natalensis* getalle was gekenmerk deur seisoenskommelinge terwyl *L. griselda* afwesig was gedurende die laaste deel van die reënseisoen, en vroeë deel van die droë seisoen. Oorlewing tot by spening in *P. natalensis* is baie laag, veral vroeg in die teelseisoen. Die oorlewing van die gevange populasie was goed, maar het gedaal na die studiegebied afgebrand het. Individue van *P. natalensis* wat vanaf Mei–Julie in die populasie opgeneem is, het tussen 20 en 35% van hulle liggaamsmassa verloor gedurende Augustus–Oktober. Liggaamsmassa het by bereiking van geslagsrypheid in die vroeë reënseisoen toegeneem.
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E.N. Chidumayo
Present address: Natural Resources Department,
Box RW 42, Lusaka, Zambia

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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

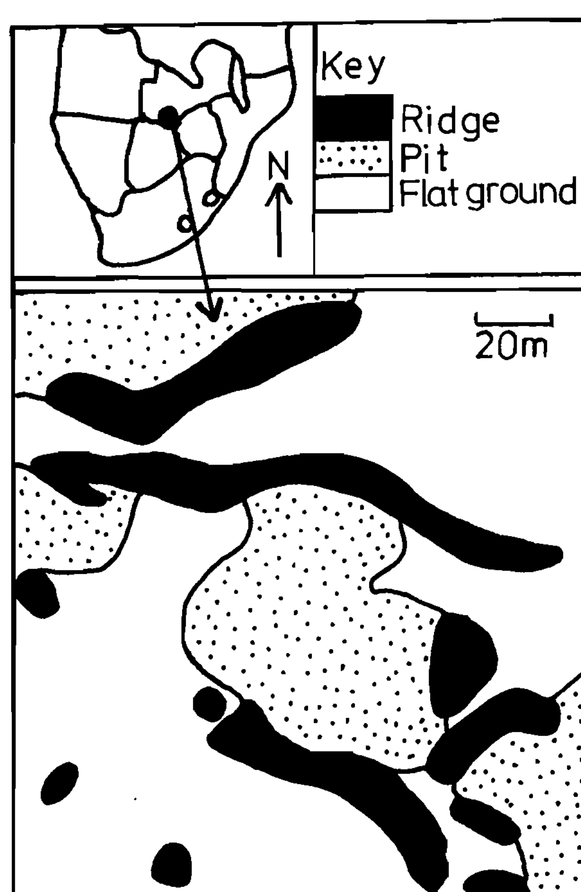

Fig. 1 Map of study site.

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 — 1,0 m deep) made up 30%, ridges (0,5 — 2,0 m 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 *Hyparrhenia-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.

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

	Trapping period				
Species	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

	Trapping period																	
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)
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 χ^2 (Table 3) the difference 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 (χ^2, $p = 0{,}05$). In 16 multiple capture cases the inmates were of similar body mass (each under 30 g) and in four cases the body mass was dissimilar and differed by 14 – 24 g. 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*.

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

Species	Micro-topographic zone Ridge (0,36 ha)	Flat ground (1,40 ha)	χ^2
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

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. campestris* therefore seemed to prefer gravelly ridges.

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 *Amaranthus 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.*

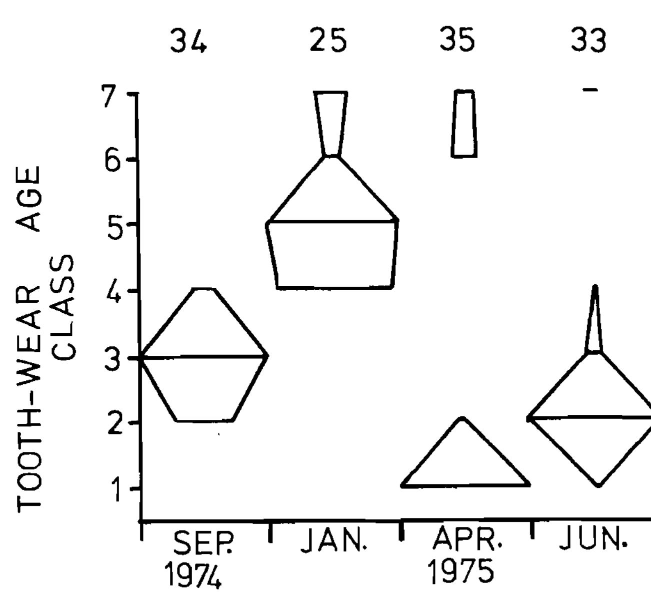

Fig. 2 Age structure of *P. natalensis* at the study site. Each horizontal line is proportional to the frequency of each tooth-wear age class in each monthly sample. Top figures show sample size.

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 fairly 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 subadults 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). 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.

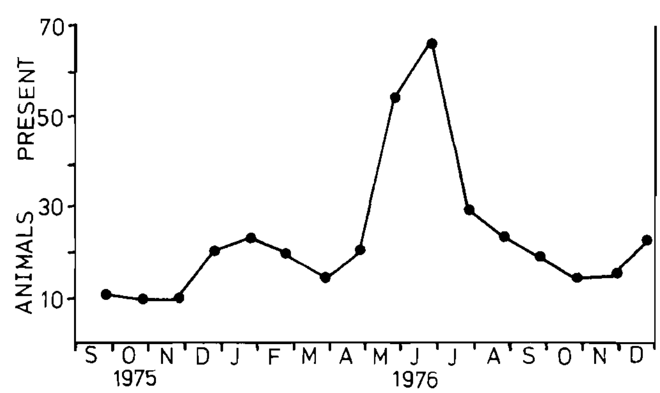

Fig. 3 Population size of *P. natalensis* at the study site.

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

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

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 11,7 g but the mean body mass of juveniles collected from the field was 29,1 g (n = 151; SD = 11,6). The upper limit of the mean body mass (40,7 g) was chosen to separate juveniles from other animals. The difference in mean body mass of female (28,0 g) and male (30,1 g) 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%), 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

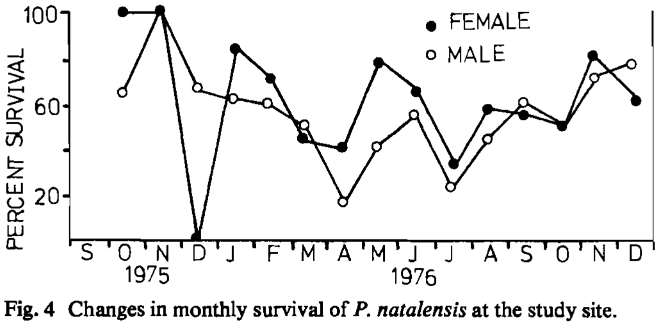

Fig. 4 Changes in monthly survival of *P. natalensis* at the study site.

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.

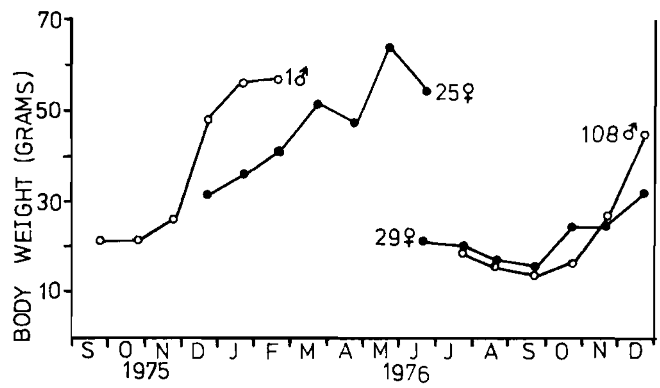

Fig. 5 Changes in body mass of selected *P. natalensis* at the study site.

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 100 m 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 KafueFlats 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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References

CHIDUMAYO, E.N. 1977. The ecology of the single striped grass mouse, *Lemniscomys griselda*, in Zambia. *Mammalia* 41: 411–418.

DELANY, M.J. 1972. The ecology of small rodents in tropical Africa. *Mammal Rev.* 2: 1–42.

FIELD, A.C. 1975. Seasonal changes in reproduction, diet and body composition of two equatorial rodents. *E. Afr. Wildl. J.* 13: 221–235.

HANNEY, P. 1965. The Muridae of Malawi (Africa: Nyasaland). *J. Zool., Lond.* 146: 577–633.

HILBORN, R.J., REDFIED, A. & KREBS, C.J. 1976. On the reliability of enumeration for mark and recapture census of voles. *Canad. J. Zool.* 54: 1019–1024.

JOHNSTON, H.L. & OLIFF, W.D. 1954. The oestrous cycle of female *Rattus* (*Mastomys*) *natalensis* (Smith) as observed in the laboratory. *Proc. zool. Soc. Lond.* 124: 605–613.

MEESTER, J. 1960. Early post-natal development of multi-mammate mice *Rattus* (*Mastomys*) *natalensis* (A. Smith). *Ann. Transv. Mus.* 24: 35–52.

SHEPPE, W.A. 1972. The annual cycle of small mammal populations on a Zambian flood plain. *J. Mammal.* 53: 445–460.

SHEPPE, W.A. 1973. Notes on Zambia rodents and shrews. *Puku* 7: 167–190.

SWANEPOEL, P. 1976. An ecological study of rodents in northern Natal, exposed to Dieldrine coverspraying. *Ann. Cape. Prov. Mus.* (*nat. Hist.*) 11: 57–81.