REPRODUCTION OF THE PUNCTATED GRASS-MOUSE, *LEMNISCOMYS STRIATUS* IN THE RUWENZORI NATIONAL PARK, UGANDA (RODENTIA : MURIDAE).

B R NEAL*
Department of Zoology, University of Southampton

Accepted: January 1977

ABSTRACT

A total of 730 punctated grass-mice was dissected to study their biology. Breeding occurred during the rains and ceased during the dry seasons, and the mean number of embryos per female reached a maximum towards the end of the breeding season. The testes and vesiculae seminales of adult males regressed during the dry seasons and some appeared to be sexually quiescent. A small proportion of young of both sexes matured and bred in the same breeding season as that of their birth. Most adults appeared to die immediately following the breeding seasons, and thus there was almost a complete turnover of the population twice a year.

INTRODUCTION

The punctated grass-mouse, *Lemniscomys striatus* (Linnaeus), is one of the commonest small rodents in grassland, savanna and cultivated areas in the moist, central region of tropical Africa (Rosevear 1969; Delany 1975). It is diurnal and its diet in non-cultivated areas consists mainly of grass, seeds and insects (Delany 1964; A C Field 1975).

Studies by Petter *et al.* (1964) in the Central African Republic, and Dieterlen (1967) in Zaire have indicated that the breeding activity of this species is possibly related to the pattern of rainfall. A brief report on the breeding pattern compared with other rodent species living in the same area is provided by Delany & Neal (1969). The present report describes the breeding biology, body growth, and population structure of *Lemniscomys striatus* collected in the Ruwenzori (formerly Queen Elizabeth) National Park, Uganda.

STUDY AREAS AND CLIMATE

Most animals were collected from the Crater Track region (0°06′ S/29°54′ E) within an area of approximately 8 km^2, 8-11 km south of the equator at an altitude of 1000-1100 m.

*Present address: Department of Biology, University of Saskatchewan, Saskatoon, Canada

The vegetation was dense grassland, 90-120 cm high, dominated by *Imperata cylindrica, Themeda triandra*, and *Cymbopogen afronardus*. Part of the area was burnt in July 1965 and subsequent collections were made in both burnt and unburnt areas. A more detailed description oof the area is provided by Neal (1970).

A few animals were also collected in the Royal Circuit and Katwe Count areas located approximately 1 km south and 4 km south-west of the Crater Track region. The vegetation of the Royal Circuit and Crater Track regions was very similar, but the Katwe Count area was subjected to very heavy hippopotamus grazing which resulted in extensive bare patches and patches of very short grass interspersed with thickets of *Capparis* bush.

There are normally two rainy seasons each year, during the periods March until May and September until November (McCallum & Hanna 1969), although the exact dates vary slightly from year to year. Seasonal changes in photoperiod and temperature were negligible. The mean monthly temperature varied 1° C (range 22,9 - 23,9° C) during the period of study.

MATERIALS AND METHODS

A total of 694 *Lemniscomys* was trapped in the Crater Track region during a 14-month period from April 1965 until May 1966. An additional 34 animals were trapped in the Royal Circuit area in June 1965, and two other specimens in the Katwe Count Area in July 1965. The animals were measured, weighed and sexed. A clean body mass was obtained by removing the gut (from the lower oesophagus to the rectum) and also the uterus and embryos of pregnant females.

Classification of reproductive material

Females. The state of the reproductive tract was assessed, firstly in the freshly dissected condition, and later in greater detail in the fixed condition with the aid of a dissecting microscope.

The following factors were recorded:

i. The presence or absence, and if present the number, of implanted embryos.
ii. The presence or absence of placental scars in the uterus (i.e. parous or non-parous), and the age of the scars, whether recent or old.
iii. The presence or absence of corpora lutea in the ovary.
iv. The condition of the uterus, whether thin and poorly vascularized, or swollen, well vascularized and filled with fluid.
v. The presence or absence of a sperm plug.
vi. The state of the mammary glands, whether lactating or non-lactating.

For the purpose of this study only visibly pregnant* (i.e. with implanted embryos) and

*Pregnancy was not determined by the presence of corpora lutea because corpora lutea are frequently found in non-pregnant animals (Brambell & Davis 1941).

oestrous females were considered to indicate breeding activity.

The state of oestrus was recognized by a distended, well-vascularized uterus, and was usually confirmed by the presence of a sperm plug indicating recent mating.

Immature animals were those with a thin, non-vascularized uterus and without placental scars and corpora lutea.

Lactating females were recognized either by the state of the mammary glands or by the presence of recent placental scars if the skin was badly decomposed.

The uteri of all mature females collected outside of the breeding periods resembled those of immature animals, being thin and poorly vascularized. These females were considered to be in a state of anoestrus.

Males. The male reproductive organs were dissected out, weighed, and a sperm smear was taken from each cauda epididymis. The relative abundance of sperm was determined microscopically and the individuals classed as: (0), if no sperm was present; (½), if only a few sperm were present amongst fat globules; or (1), if sperm were abundant. Only males in the last class were considered to be fecund.

Aging technique

Individuals were aged using the eruption and subsequent wear of the upper molars as a criterion. A molar was only considered to be present when fully erupted, and the number of cusps were counted as soon as the dentine of the cusps became visible. The cusps began to join as the teeth became more worn, and the number of cusp-sets correspondingly decreased until the molars were worn flat. Twenty preliminary age-classes were identified, and were then grouped to give the 14 final age-classes in the following way. The number in each preliminary age-class was totalled for the first year of study. Except for Group I, they were grouped in such a way as to give a reasonable survivorship curve; i.e. the total number in Age-class II is greater than the number in Age-class III, and so on. A more detailed description is given in Neal (1968).

Statistical procedures

Female breeding activity in burnt and unburnt areas was compared using the G-test (Sokal & Rohlf 1969).

The mean mass of the testes and vesiculae seminales of young animals was compared each month with those of older animals by the single classification analysis of variance (Sokal & Rohlf 1969).

The variation in litter size in relation to the maternal clean body mass and the month collected was analysed by the two-way analysis of variance with unequal subclass numbers (Steel & Torrie 1960). The April-June and September-December 1965 breeding periods were analysed independently.

RESULTS

Breeding season

Breeding activity was generally confined to the rainy seasons with a time lag of approximately one month between the onset of the rains and the first appearance of pregnant females (Figure 1B, E). The occurrence of lactating and immature females was consistent with this breeding pattern (Figure 1C, D), but the absence of lactating females in late June

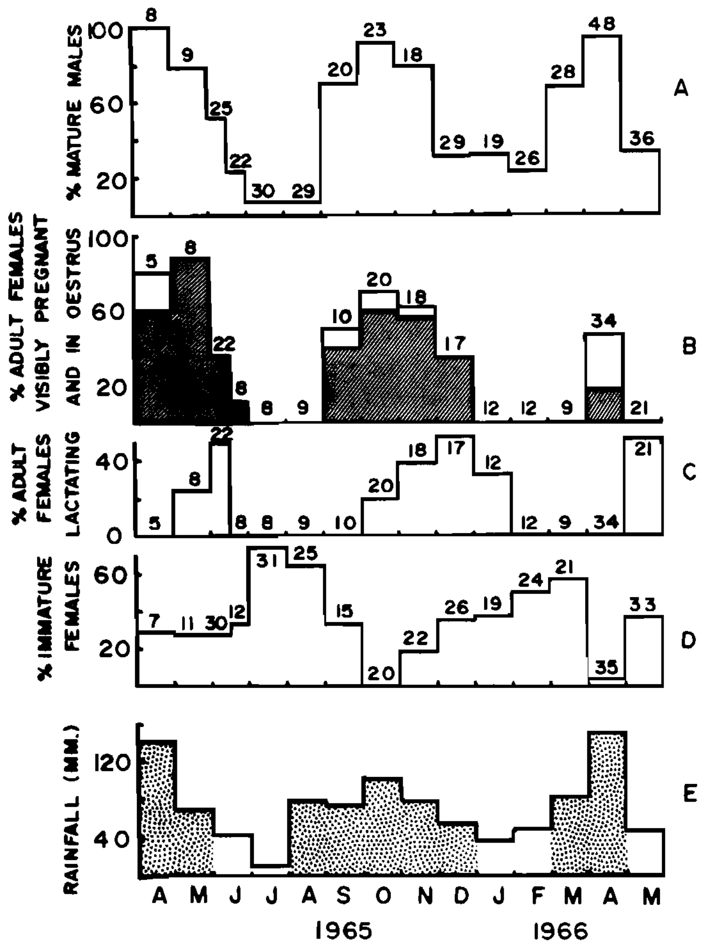

FIGURE 1

Seasonal changes in reproductive activity of *Lemniscomys striatus* in relation to rainfall. The numbers over histograms A - D indicate sample sizes. In B, the cross hatched area represents pregnant females and the open area oestrous females. In E, the stippled area indicates the months when rainfall was greater then 50 mm.

and July 1965 suggests that the litters of the June pregnancies failed to survive. The frequency of breeding females tended to be higher in burnt compared to unburnt areas during the period September to December 1965, and this tendency was significant in September (G = 6,3; 2 df.; P <0,05). It appeared that breeding was slightly advanced in the burnt area. All Crater Track females collected during July and August 1965 and the period January until March 1966 were in anoestrus. A single pregnant female was collected in the Katwe Count Area in July 1965.

Counts of the placental scars of 37 females collected immediately following the two breeding seasons in 1965 indicated that 16 per cent had had one litter (2-8 placental scars), 81 per cent had had at least two litters (9-15 placental scars), and 3 per cent had had at least 3 litters (19 placental scars). At least one quarter of the pregnant females collected in May, June, November and December were lactating, which suggests that many animals became pregnant at the post-partum oestrus. The breeding period in April 1966 was so short that females could only have had one litter.

The percentage of males that were mature was highly correlated with female breeding activity (Figure 1A), and there was a pronounced seasonal variation in the mass of the adult testes and vesiculae seminales (Table 1). The reproductive organs reached their maximum

TABLE 1

Mean mass (in grams) and standard errors of monthly samples of paired testes and vesiculae seminales (SV) of *Lemniscomys striatus*.

	Adult			April–June Cohort			Sept–Dec Cohort		
Month	*No.*	*Testes*	*SV*	*No.*	*Testes*	*SV*	*No.*	*Testes*	*SV*
Apr	8	0,32±0,02	0,15±0,02						
May	7	0,36±0,03	0,18±0,01	1	0,06	<0,01			
June	23	0,27±0,01	0,08±0,01	21	0,07±0,01	<0,01			
July	5	0,14±0,03	0,02±,003	22	0,04±0,01	<0,01			
Aug	5	0,13±0,01	0,02±,002	20	0,07±0,01	<0,01			
Sept	7	0,25±0,02	0,13±0,01	13	0,19±0,02	0,07±0,01			
Oct	8	0,29±0,01	0,15±0,01	12	0,26±0,02	0,13±0,01			
Nov	2	0,36±0,01	0,21±0,03	13	0,29±0,01	0,14±0,01	4	0,14±0,04	0,04±0,02
Dec	3	0,30±0,05	0,12±0,01	8	0,27±0,01	0,12±0,01	17	0,12±0,02	0,01±,005
Jan	3	0,23±0,02	0,06±0,01	6	0,18±0,04	0,04±0,01	12	0,09±0,02	<0,01
Feb	5	0,15±0,01	0,04±0,01		Transferred to adults		13	0,07±0,01	0,01±,005
Mar	4	0.20±0,01	0,05±0,01				16	0,17±0,01	0,04±0,01
Apr	3	0,28±0,02	0,23±0,02				37	0,26±0,01	0,13±0,01
May	1	0,21	0,03	12	0,02±,004	<0,01	20	0,18±0,01	0,03±,003

mass towards the end of the rains and then rapidly regressed to their minimum mass at the end of the dry seasons. The reduction in mass was more pronounced during the June-July 1965 dry season than during the January-February 1966 dry season. The mass of the testes and vesiculae seminales of animals entering their first breeding season was lower than that of animals entering their second or third breeding seasons (Table 1). This difference was statistically significant in September and October 1965, and the mean mass of the vesiculae seminales of the two groups was also significantly different in April 1966.

Body mass

The birth mass was 1,6 - 1,8 g for a litter of five young. Few animals were trapped with a mass of less than 10 g and, therefore, the mass at the time of weaning is assumed to be 10-15 g. The rate of growth of immature animals was very variable. A few individuals, of the first litters in a breeding season, increased rapidly to an adult body mass, but most individuals grew more slowly, particularly during the dry periods, and did not attain an adult body mass until the breeding season following that of their birth. The body mass at maturity was estimated to be approximately 26 g for females and 28 g for males. Most adults had a mass of 30-45 g, although a few were much heavier up to a recorded maximum of 69 g. The adult body mass varied seasonally being at a maximum during the rains and declining by approximately 20 per cent during the dry seasons.

Litter size

The mean number of implanted embryos (resorbed embryos included) of 58 pregnancies was 5,02 $\pm$ 0,15 (range 3-8), that of live embryos only was 4,78 $\pm$ 0,17 (range 2-8). The number of embryos did not vary significantly with change in maternal body mass, but the number of embryos appeared to increase throughout the two breeding seasons in 1965. However, only the increase in the number of implanted embryos during the period September to December 1965 was significant ($F_{2,23} = 3,83$; $P < 0,05$).

Age structure

The monthly changes in age structure of the Crater Track population (Figure 2) reflected the pattern of breeding. The youngest animals were trapped six to eight weeks after the appearance of visible pregnancies, which indicates that the young took three to four weeks to wean because the gestation period is 28 days (Petter *et al.* 1964). Approximately 10-15 per cent of the young (Age-classes I-III) of both sexes were found to be mature in May, June, November and December 1965, and thus bred in the same breeding period in which they were born. Most animals, however, did not mature until the rainy season following that of their birth, and the males matured approximately a month before the females. Normally all females bred during the rainy season following that of their birth. The only evidence to the contrary was seen in May 1966, after a particularly short breeding season, when the two immature females present in Age-groups IV and V clearly represented part of the population born during the September-December breeding period (Figure 2). Adult males with reduced fecundity ratings were most commonly collected during the dry seasons and beginning of the rains.

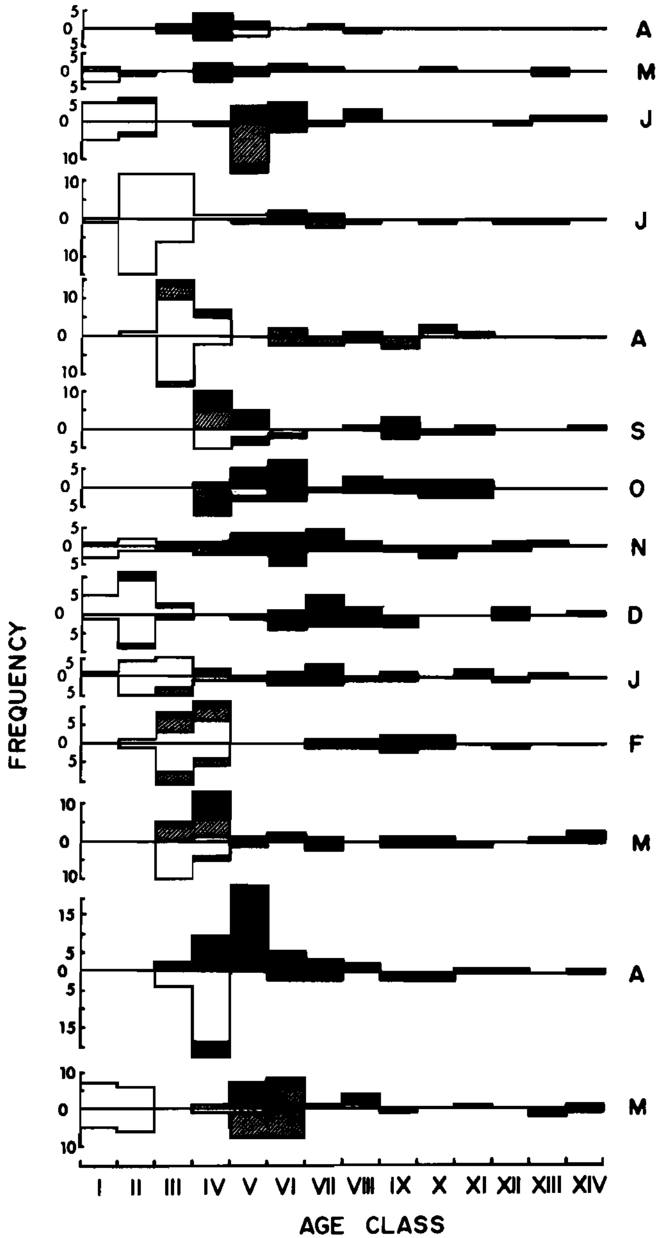

FIGURE 2

Monthly age structure of *Lemniscomys striatus.* Males are above each line, females below. Open blocks represent males with sperm rating 0 or non-parous and non-pregnant females; cross-hatched blocks represent males with sperm rating 1/2 or parous females; and solid blocks represent males with sperm rating 1 or pregnant females.

DISCUSSION AND CONCLUSIONS

Pregnancies were recorded throughout most of the rains and there was a complete absence of breeding activity during the latter part of the dry season and beginning of the rains. This is similar to that recorded for this species in Cameroun (Sanderson 1940), the Central African Republic (Petter *et al.* 1964), and near Bukavu in eastern Zaire (Rahm & Christiaensen 1963). Dieterlen (1967), however, recorded breeding activity throughout the year near Bukavu in eastern Zaire, although breeding was at a maximum during the period following peak rainfall.

There was a marked seasonal variation in the mass of the adult male reproductive organs, which appeared to be correlated with female breeding activity. Some adult males appeared to be reproductively quiescent during the dry seasons, as was recorded for *Praomys (Mastomys) natalensis* (Coetzee 1965; Sheppe 1973; Neal in press).

The lengths of the breeding periods in this study were directly related to the duration of the rains. It may be noted that the April-June breeding season was markedly shortened in 1966 compared to 1965. A similar reduction in the length of the breeding season in response to the early onset of the dry season was also noted for *Praomys (Mastomys) natalensis* and *Mus triton* (Delany & Neal 1969). A C Field (1975) studied the same Crater Track population in a year when the rains were advanced by several weeks. She found that the rains began in January or February and the breeding season was also advanced, beginning in February and continuing until the rains ceased at the end of June. Thus, the duration and timing of breeding appears to be related to the direct and/or indirect effects of rainfall.

The observation in this study that breeding was slightly advanced in burnt compared to unburnt areas might be explained by nutritional factors, because C R Field (1968 *a, b*) has shown the nutritional value of the regenerating grasses in the burnt areas to be far better than that of the unburnt grasses. Nutritional factors might also account for the apparent difference in breeding activity in the Crater Track and Katwe Count areas in July 1965, because the vegetation, and presumably the diet, was very different in the two areas. A C Field (1975) has also postulated that breeding activity is influenced by the rainfall acting through the food supply. She considered protein to be the most likely limiting factor because the diet was mainly grass, which was known to have a low protein content (C R Field 1968 *a, b*), during the dry seasons, and insects and seeds, with a much higher protein content, during the rains. The consumption of seeds and insects probably reflects the seasonal aavailability of these items but this was not assessed quantitatively.

The breeding pattern of *Lemniscomys* is typical of many of the savanna rodents (Delany & Neal 1969; Delany 1972). The timing of the breeding season appears to favour the pregnant and lactating females rather than the newly weaned young, most of which occur towards the end of the rains and beginning of the dry season. The periods of sexual inactivity occur when the probability of savanna fires is greatest (Neal 1970).

The body mass of the Crater Track population was considerably less than that reported for other populations. Petter *et al.* (1964) recorded a birth mass of 3 g for a laboratory population from the Central African Republic, the adults of which had a body mass of 50-

60 g. Dieterlen (1967) estimated the body mass at the time of weaning to be 20 g and at puberty to be approximately 35 g for a population near Bukavu in eastern Zaire. The seasonal change in adult body mass recorded in the present study was probably related to the cycle in body fat content (A C Field 1975).

The average number of embryos was similar to that recorded in other areas. Petter *et al* (1964) record a mean of 5,12 for 7 pregnancies and 4,27 ± 0,34 for 15 litters born in captivity for a population collected near Bangui, Central African Republic. Dieterlen (1967) records 4 to 5 young per litter, and Rahm (1971 in Delany 1975) 4,43 ± 0,02 for 40 pregnancies, for populations collected near Bukavu in eastern Zaire.

The monthly changes in age structure indicated that the main periods of adult mortality were immediately following the breeding seasons when the population was largely replaced by juveniles. There was almost a complete turnover of the population twice a year, therefore, the mean life expectancy was probably only a few weeks.

ACKNOWLEDGEMENTS

I am indebted to my supervisor, Dr M J Delany, who gave help, advice and encouragement during all stages of this work. Two anonymous reviewers and the editor made helpful comments on an earlier draft of this paper. The field work was carried out at the Nuffield Unit of Tropical Animal Ecology in the Ruwenzori National Park. I am grateful to the Director, Dr R M Laws, for his guidance, and to the Trustees of the Uganda National Parks for their cooperation. Mr Jackson Ogiki helped considerably with the field work. The work was financed by grants from the National Environmental Research Council and the University of Southampton.

REFERENCES

BRAMBELL, F W R & DAVIS, D H S 1941. Reproduction of the multimammate mouse *(Mastomys erythroleucus* Temm.) of Sierra Leone. *Proc. zool. Soc. Lond.* (B) 111: 1-11.

COETZEE, C G 1965. The breeding season of the multimammate mouse *Praomys (Mastomys) natalensis* (A Smith) in the Transvaal highveld. *Zool. afr.* 1: 29-39.

DELANY, M J 1964. An ecological study of the small mammals in the Queen Elizabeth National Park, Uganda. *Revue Zool. Bot. afr.* 70: 129-147.

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

DELANY, M J 1975. *The rodents of Uganda.* London: British Museum (Natural History).

DELANY, M J & NEAL, B R 1969. Breeding seasons in rodents in Uganda. *J. Soc. Reprod. Fert.* (Suppl.) 6: 229-236.

DIETERLEN, F 1967. Jahreszeiten und Fortpflanzungsperioden bei den Muriden des Kivusee - Gebietes (Congo). *Z. Säugetierk.* 32: 1-44.

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

FIELD, C R 1968*a*. The food habits of some wild ungulates in Uganda. Ph.D. thesis, Cambridge University.

FIELD, C R 1968*b*. A comparative study of the food habits of some wild ungulates in the Queen Elizabeth National Park, Uganda. Preliminary Report. *Symp. zool. Soc. Lond.* 21: 135-151.

McCALLUM, D & HANNA, L W 1969. Climate. In *Atlas of Uganda.* Entebbe: Department of Lands and Surveys.

NEAL, B R 1968. The ecology of small rodents in the grassland community of the Queen Elizabeth National Park, Uganda. Ph.D. Thesis, University of Southampton.

NEAL, B R 1970. The habitat distribution and activity of a rodent population in Western Uganda, with particular reference to the effects of burning. *Revue Zool. Bot. afr.* 81: 29-50.

NEAL, B R In press. Reproduction of the multimammate rat, *Praomys (Mastomys) natalensis* (Smith), in Uganda. *Z. Säugetierk.*

PETTER, F, CHIPPAUX, A & MONMIGNANT, C 1964. Observations sur la biologie, la reproduction et la croissance de *Lemniscomys striatus* (Rongeurs, Muridés). *Mammalia,* 28: 620-627.

RAHM, U & CHRISTIAENSEN, A 1963. Les mammifères de la région occidentale du lac Kivu. *Annls. Mus. r. Afr. cent* (8°) (Zool.) 118: 1-83.

ROSEVEAR, D R 1969. *The rodents of West Africa.* London: British Museum (Natural History).

SANDERSON, I T 1940. The mammals of the North Cameroons forest area being the results of the Percy Sladen Expedition to the Mamfe Division of the British Cameroons. *Trans. zool. Soc. Lond.* 24: 623-725.

SHEPPE, W A C 1973. Note on Zambia rodents and shrews. *Puku* 7: 167-190.

SOKAL, R R & ROHLF, F S 1969. *Biometry.* San Francisco: W H Freeman & Co.

STEEL, R D G & TORRIE, J H 1960. *Principles and procedures of statistics.* New York: McGraw-Hill.