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POPULATION BIOLOGY OF THE MULTIMAMMATE RAT, *PRAOMYS (MASTOMYS) NATALENSIS* AT MOROGORO, TANZANIA, 1981-1985

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POPULATION BIOLOGY OF THE MULTIMAMMATE RAT, *PRAOMYS (MASTOMYS) NATALENSIS* AT MOROGORO, TANZANIA, 1981- 1985

Sam R. Telford, Jr.*

ABSTRACT

The population of *Praomys (Mastomys) natalensis* on the campus of Sokoine University of Agriculture in Morogoro, Tanzania, was studied by monthly samples from October 1981 to February 1985. All 35 individuals that were karyotyped had a diploid number of 32 chromosomes. An annual species, the breeding season of *P. natalensis* normally begins in April, with three or four litters of 3-23 young each produced by the end of August when reproduction ceases. The average litter size was 11.7; females smaller than 105 mm HBL produced 1-2 embryos fewer than those larger ; maximum litter sizes averaging 12.0-12.6 were produced by females 120-129 mm HBL. The actual number of young born was probably around 10.6 per litter, due to resorption of 0.4-3.2 percent of embryos produced. Testes of adult males regressed from September through November; spermatogenesis began in December and was completed by February for young of the year and those adult males which survived into the next breeding season. Off season breeding can occur in fallow maize fields in January or February, apparently governed by the precipitation level during the short rains of November, and is limited to production of a single litter before the regular season begins in April. Young produced during this period reached maturity by April. *Praomys natalensis* comprised nearly 87 percent of the 9306 rodents and insectivores trapped on the university campus. Trap success was maximum following reproduction, from September to December, declining thereafter until May when recruitment of young to the population began again. The maximum recorded density was 1125 per ha, in October 1984. The population structure and density are influenced by both habitat and rainfall. The critical factors which determine population levels following the main breeding season are apparently heavy short rains followed by off-season breeding which alter the density threshold at which the population begins reproduction in April.

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RESUMEN

Se estudió la población de *Praomys* (*Mastomys*) *natalensis* en el campus de la Universidad Sokoine de Agricultura en Morogoro, Tanzania, por muestras mensuales de Octubre de 1981 a Febrero de 1985. Se obtuvo el cariotipo de 35 individuos, que en todos los casos mostró un número diploide de 32 cromosomas. *Praomys natalensis* es una especie anual cuya época reproductiva se inicia normalmente en Abril, con tres o cuatro camadas de 3-23 crías que nacen a fines de Agosto, cuando termina el período reproductivo. El promedio de camada fué de 11.7; las hembras menores de 105 mm de longitud de cabeza y cuerpo produjeron 1-2 embriones menos que las mayores; los tamaños máximos de camada, con promedios entre 12.0-12.6, fueron producidos por hembras con 120-129 mm de longitud de cabeza y cuerpo. El número real de crías nacidas fué probablemente de cerca de 10.6 por camada, debido a la reabsorción de entre 0.4 y 3.2 por ciento de los embriones producidos. Los testículos de los machos adultos se mantuvieron abdominales de Septiembre a Noviembre; la espermatogénesis se inició en Diciembre y se completó en Febrero en los jóvenes de ese año y en los pocos machos que sobrevivieron para una segunda época reproductiva. Puede ocurrir reproducción fuera del período mencionado en campos abandonados de maíz en Enero o Febrero, aparentemente controlada por el nivel de precipitación durante el corto período de lluvias en Noviembre, y se limita a la producción de una camada previa a la época normal que se inicia en Abril. Los jóvenes producidos durante este período alcanzan la madurez en Abril. *Praomys natalensis* representó casi el 87 por ciento del total de 9306 roedores e insectívoros capturados en el campus de la universidad. El mayor éxito de captura ocurrió después de la reproducción, de Septiembre a Diciembre, declinando entonces hasta Mayo, cuando el reclutamiento de los jóvenes a la población vuelve a empezar. La densidad máxima registrada fué de 1125 por ha en Octubre de 1984. La estructura y la densidad de la población son influenciadas por el habitat y por la lluvia. Los factores críticos que determinan los niveles de población alcanzados después de la época principal de reproducción consisten aparentemente de fuertes y breves lluvias seguidas de reproducción fuera del período principal, que altera el umbral de densidad al que la población inicia la época reproductiva en Abril.

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INTRODUCTION

The multimammate or shamba rat, *Praomys (Mastomys) natalensis* (Smith 1834) is distributed as a species complex throughout virtually the entire African continent below the Sahara. Although other species may have greater significance in given localities, *P. natalensis* is the most important indigenous species to public health and agriculture in Africa. Field studies on its biology in East Africa are surprisingly few, in view of the economic importance of the species. It has been reported to undergo periodic explosive increases in numbers (Harris 1937; Taylor 1968), yet no study based upon adequate numbers of individuals, taken at regular intervals over a substantial sampling period is available. Most studies were conducted over less than two years, and virtually none examined a thousand animals or more. Valuable information on *P. natalensis* as part of small mammal communities in Kenya, Uganda, Malawi, and Zambia was presented by Southern and Hook (1963), Hanney (1965), Delany and Kansiimervhanga (1970), Sheppe (1972), Taylor and Green (1976), and Delany and Roberts (1978). Only three papers present data derived from Tanzanian populations: Harris (1937), Chapman et al. (1959), and Hubbard (1972). In none of these studies was the specific identity of the *P. natalensis* population precisely ascertained, although this may become obvious in the future when adequate data are available on karyotype distributions in East Africa.

The most valuable studies on the population biology of *P. natalensis*, using an autecological approach, were those conducted by South African workers (Coetzee 1967, 1975; Isaacson 1975). These have been supplemented by observations on behavior (Veenestra 1958), postnatal development (Meester and Hallett 1970), and community relationships (De Witt 1972). Although there are the expected similarities in the biology of South African *P. natalensis* to populations of the species in Tanzania, as discussed below, the climatic factors which govern population dynamics between the two regions are quite different, especially with respect to reproduction. Understanding of the variability in reproductive response to local, seasonal, and annual variations in climatic factors such as precipitation is critical to the development of effective control programs.

In 1980 the Danish International Development Agency (DANIDA) established the Denmark-Tanzania Rodent Control Project at Morogoro, Tanzania. One of the objectives of the Project was to obtain, through suitable long-term field studies, an understanding of the population biology of *P. natalensis* adequate to assist in the design of a national control program appropriate to the Tanzanian environment and economy. With my arrival as

Project Leader, studies commenced in June 1981 and were concluded in February 1985. The results and conclusions derived from them are presented here.

ACKNOWLEDGEMENTS

This study was supported by the people of Denmark, under their generous assistance to the Republic of Tanzania through the Danish International Development Agency (DANIDA). The splendid cooperation and support by DANIDA's Counselor for Development, Axel Pedersen, enabled me, as Project Leader of the Denmark-Tanzania Rodent Control Project, to carry out the research program with a minimum of the administrative and logistical frustrations normally attendant upon bilateral aid projects in developing countries. Without his continuous help the work would have been, at best, mediocre. Jens Tang Christensen, Project Ecologist, and William R. Smythe, Rodent Control Specialist, were congenial colleagues and often assisted in the routine sampling and laboratory procedures. The Government of Tanzania, through the Ministry of Agriculture, provided field and laboratory staff for the project. In particular, I wish to acknowledge the assistance of P. Mwanjabe, E. A. Nkya, M. Stambuli, C. Sabuni, and E. Nzobakenga among the senior staff, and field assistants John, Yusuf, Peter, Clement, and Kasim. Kim Howell, Department of Zoology, University of Dar-es-Salaam, provided information on the distribution of small mammals in Tanzania, localities and habitats, and useful contacts within the country.

Professional assistance was furnished by the Division of Mammals, British Museum of Natural History, London (Jean Engels); Mogens Lund, Statens Skadedyrlaboratorium, Lyngby, Denmark; the World Health Organization Collaborating Centre for Rickettsial Reference and Research, Department of Microbiology, University of Maryland School of Medicine, Baltimore (C. L. Wisseman, Jr., and R. Traub); and the Special Pathogens Reference Laboratory, Porton Down, England. J. H. Greaves generously helped me with literature searches during visits to the Pest Infestation Control Laboratory of the British Ministry of Agriculture,Fisheries and Food, Tolworth, Surbiton, Surrey, in 1981 and 1985. Special thanks are due to Norman G. Gratz, then Director, Division of Vector Biology and Control, World Health Organization, Geneva, for his considerable (and characteristic) assistance in obtaining literature references, in facilitating shipments of biomedical materials, in arranging technical briefings, and other helpful activities. Upon my return from Tanzania to the University of Florida, Jerry F. Butler provided facilities and equipment for preparation of the study.

My family contributed also to the success of the research program: Robert M. Telford and Randolph S. Telford took part in the routine sampling during their several visits to Tanzania, while Sam R. Telford, III, assisted both in the field and laboratory studies. Finally, Michiko M. Telford continued to provide her typically efficient yet tranquil domestic environment for her husband, despite often extreme difficulties in obtaining those material necessities that maintain an acceptable standard of living.

MATERIALS AND METHODS

Sampling schedule.-- The *Praomys natalensis* population on the campus of Sokoine University of Agriculture at Morogoro (06°51'S, 37°38'E) was studied by monthly removal sampling from 1 October 1981 through 25 February 1985, a period of 40 months, taken consecutively except for November 1982 when no sample was taken. The desired sample size was 100 individuals per month, and this minimum was taken in 32 of the 40 months. It proved impossible to obtain sufficient rodents in May and June of 1982 and 1983, months when population levels were at their minima, and in January, February, and April 1982--an exceptionally dry year which drastically reduced rodent numbers. The maximum number of *P. natalensis* examined in any one month was 515 in August 1984.

Sampling technique.-- Standard line trapping with single traps set 1-2 m apart, 300-500 traps per night, was the usual method employed, normally for three nights per site. Grid trapping when done used 300 traps on a 1 hectare (ha) grid, with three traps set per point. Points were at 10 m intervals. The trap types employed were small and medium, collapsible Sherman live traps, Woodstream snap-type rat traps, metal snap traps, and "Little Nipper" mouse traps. The latter proved to be the trap of choice, being sensitive enough to take mice and shrews of 3 g weight, simple to set, and cheap enough to be regarded as expendable. The standard bait was dried coconut. The sampling standard chosen to compare rodent abundance from period to period was based upon a "Little Nipper" line (LN line) of 75 traps set and checked personally by me. The remaining traps were set by field assistants. The LN line was set adjacent to the other lines on every occasion on which samples were taken; when grids were used, an LN line was set 10 m from one of the grid borders, for comparison. In estimating abundance from the LN line, results from the first two nights only were considered. These were corrected by subtracting both the number of positive traps containing other small mammal species from the total set, and one-half the number of closed but negative traps from the total (Hanney 1965), to provide a net number of traps set, against which the number of traps positive for *P. natalensis* could be compared. During the 40-month study period, 90,246 traps were set on the university campus, and another 48,818 set elsewhere in the country, for a total of 139,064 trapnights. This does not include the effort made during the mark and release study done for 13 months on the campus (Tang Christensen unpubl.).

Examination of material.-- Live animals were anesthetized with ether or chloroform, bled by cardiac puncture, and brushed for ectoparasites, then examined as were the trap-killed specimens. Head-body lengths (HBL) and tail lengths were always recorded, and often the ear and hind foot lengths as well. Animals were weighed either by Pesola spring balances or a Mettler automatic balance. Sex was determined. Females were examined externally to determine perforation of the vagina, and teat number was occasionally recorded. Upon dissection the uterus was examined for placental scars, and embryos present were counted for each limb of the uterus. The crown-rump of one representative embryo of each litter was measured. Lactation, when indicated by presence of turgid, milk-filled mammary glands, was noted. The male reproductive status during the first 18 months of the study was recorded simply as scrotal or abdominal testes. During the last two years, testes were examined for condition of the epididymal tubules, these being recorded as visible or not. Initially, the presence of motile sperm in the epididymal tubules was determined microscopically, until the correlation with visible tubules was established. The weight of one testis was recorded for approximately 50 males per month during the last 13 months of the study. Specimens of taxonomic value were prepared either as round or flat skins, and skulls were saved. Approximately 50 individuals were karyotyped from marrow smears, prepared two hours following injection IP with 0.05% colchicine at 0.01 ml/g weight. Smears taken from the femur were immersed before drying in 0.75% aquaeous KCl for 15 min, placed in Carnoy's fixative for 15 min, and air-dried. The smears were stained immediately with 5% Giemsa at pH 7.2 for 20 min, washed in tap water and air-dried. Prior to injection with colchicine, a sample of cardiac blood was obtained for electrophoresis. Hemoglobin electrophoretic patterns were prepared by the Helena system for 150 *P. natalensis* from the campus population, for comparison with samples from elsewhere in Tanzania. Data were recorded on examination sheets and then transferred to keysort cards. Meteorological records were obtained from the University Meterological Station for the period 1970-1985.

Study areas.-- The campus of Sokoine University of Agriculture is located on the western edge of Morogoro, Morogoro Region, Tanzania (06°51'S, 37°38'E), at an elevation of 650 m on the northern slope of the Uluguru Mountains. Very little of the original vegetation remains at low elevations in the Uluguru Mountains or in their vicinity, and random deforestation continues toward the peaks despite their designation as a forest reserve. Along the south edge of the campus on the slopes of the mountain range is a belt of secondary forest which contains remnants of the savanna woodland association. Protected by the Division of Forestry of the university, it has been used for experimental studies on introduced vegetation. A total of 22 sites of 1 ha. or less in various parts of the campus were selected for sampling (Fig. 1). Selection was based upon present or previous agricultural use, and related primarily to the cultivation of maize, which is the major crop grown both on campus and in Morogoro Region. Study sites were classified as follows: (1) growing maize, which sometimes had scattered beans or cassava intermixed with it; (2) post-harvest maize, for approximately two months following the harvest, consisting of a thick, high stubble that provides both abundant food and cover for rodents; (3) fallow field, where evidence of maize cultivation during the previous season remained--post-harvest maize was classed as fallow field two months following harvest; (4) old fallow field, where maize had not been grown the preceding season, but which had supported a crop within two years; and (5) grass habitat, which could be divided into two distinct types--that which succeeds old fallow field, and that which had no recent record of cultivation but which was cropped regularly by machinery to provide fodder for dairy cattle.

RESULTS AND DISCUSSION

Land-use cycle.-- Interpretation of the results presented here requires a description of the land use cycle and climatic factors. The cultivation of maize in the area depended strongly upon the timing and quantity of rainfall. Farmers attempted to plant two crops each year, one before the "long rains" and a second crop to take advantage of the "short rains." The long rain crop usually was planted between February and May and represented the primary agricultural effort of the year, furnishing about 90 percent of the annual maize production. This crop was harvested from late June until August, and fields lay fallow until late October. If short rains came, then planting on a considerably reduced scale took place from late October into December. Harvest of this crop, however, was unpredictable and generally of low yield, due both to erratic and insufficient rainfall, and the difficulty of planting at the time of year when rodent populations were at maximum density. Fallow fields sometimes were burned prior to both planting periods, depending to some degree upon the density of second growth and the availability of mechanical cultivators. Except for the use of mechanized equipment, maize cultivation on the university campus reflected traditional timing and practice of the Morogoro area.

Climatic factors.-- During the 15-year period 1970-1985, the maximum temperature recorded at the university campus was 34.1°C in December 1974, and the minimum was 14.0°C in July 1973. The recorded maximum and minimum during the 40 months of the study were 33.7°C and 14.2°C. Maxima remained relatively constant from August through April, 28-33°, but then declined slightly until August when they rise (Fig. 2). Minima remained at 20° or above from December until May, and varied from 14° to 20° from June to December.

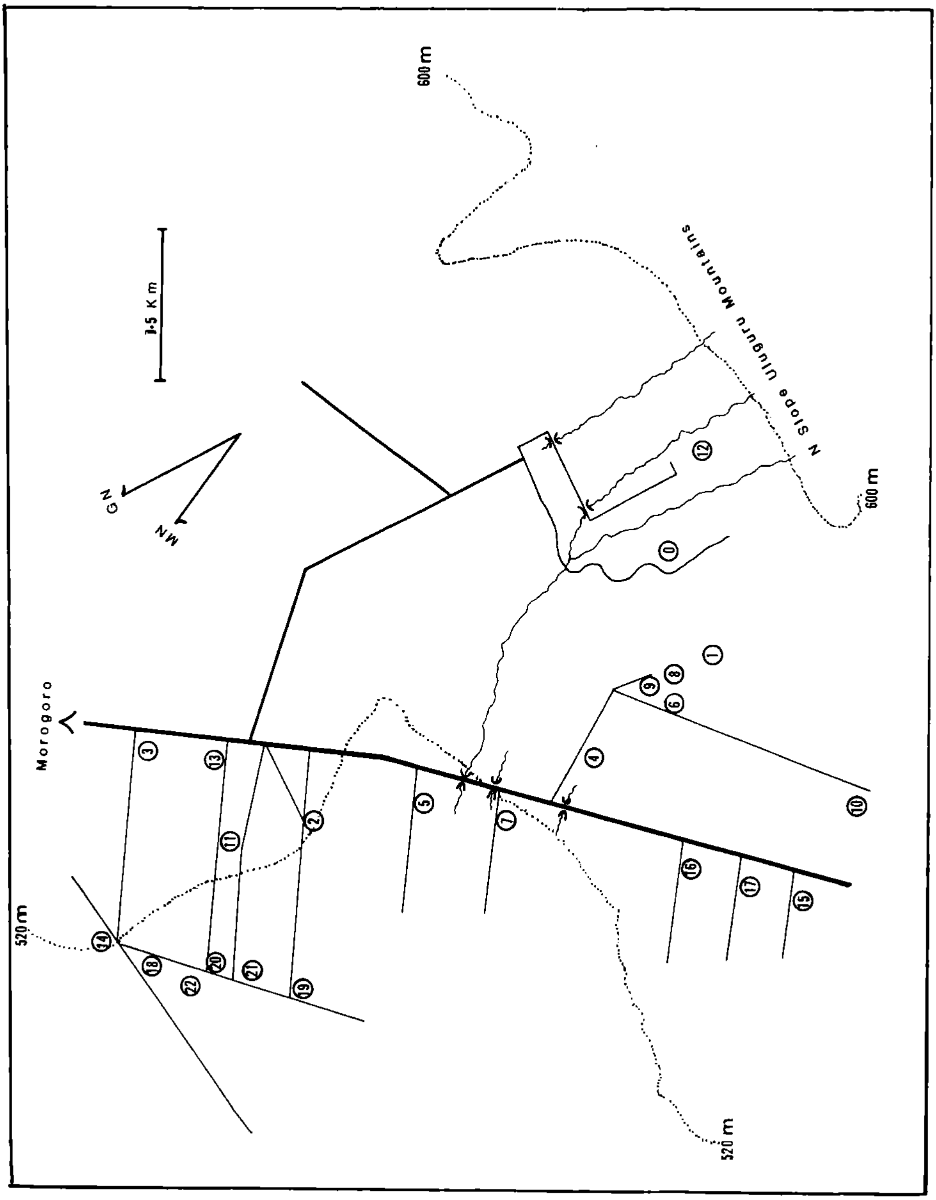

Figure 1. Study areas on the campus of Sokoine University of Agriculture, Morogoro, Tanzania (06°51' S, 37°38' E).Numbers in circles represent trapping sites.

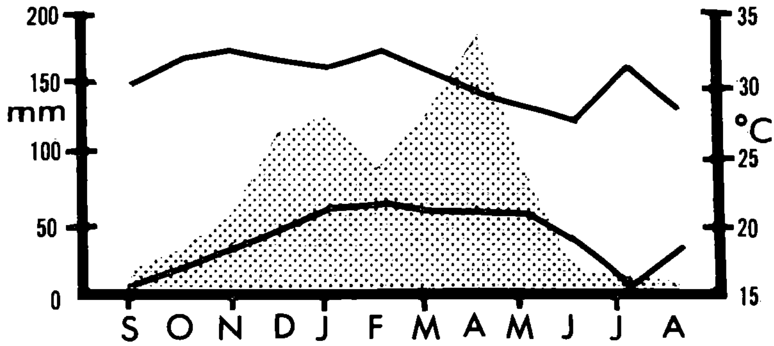

Figure 2. Climatic data for Morogoro, 1971-80. Lines indicate mean maxima and minima for months September-August. Shaded area represents mean monthly precipitation for the same period.

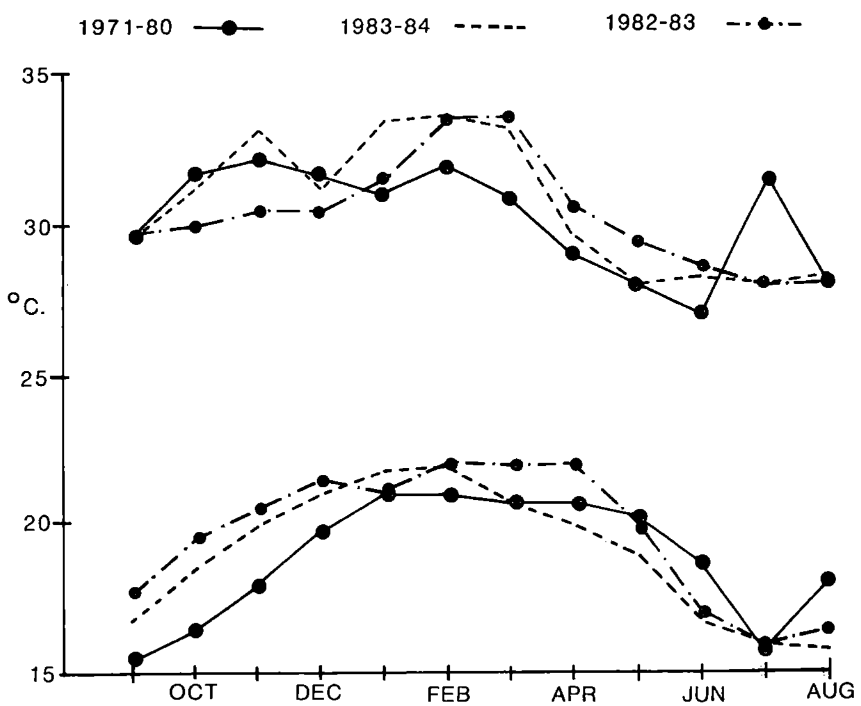

Figure 3. Monthly mean temperature maxima and minima at Morogoro, September-August in 1981-82 and 1982-83, in comparison to the averages for the preceding decade.

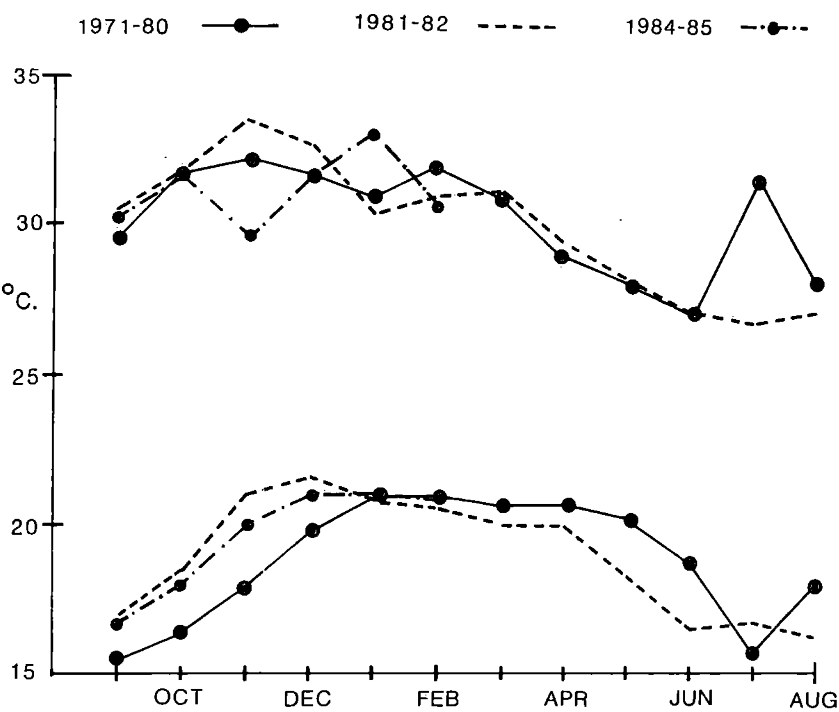

Figure 4. Monthly mean temperature maxima and minima at Morogoro, September 1983-August 1984 and September 1984-February 1985, in comparison to the averages for the preceding decade.

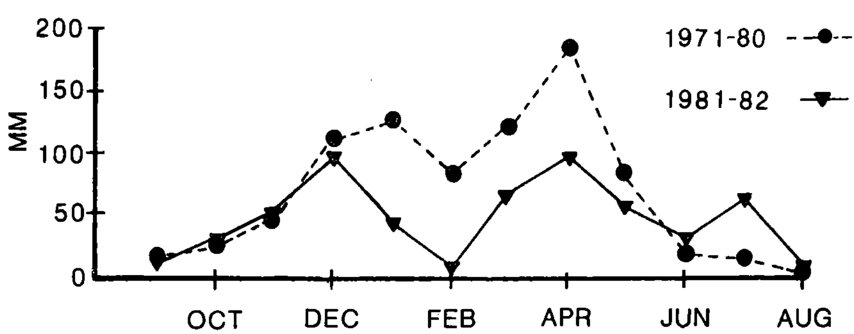

Figure 5. Monthly total precipitation at Morogoro, September 1981-August 1982 in comparison to the average for the preceding decade.

The first year of the study (Fig. 3) was notably warmer than the previous 10-year average from January through March, with maxima for those months exceeding 33°, about two degrees higher than average.

Other years more closely resembled the 1971-80 average (Figs. 3, 4).

The curve of mean monthly precipitation for the 10 years preceding the study, 1971-80 (Fig. 2), shows two peaks: the maximum, an average of 184 mm in April, and a second, somewhat lower peak of 126 mm in January. Minimum levels occur from June to October, with the least rain in August, 6.2 mm. As will be seen later, the critical period for rainfall for the rodent population is from November through March; this is described in detail below, for each year of the study showed significant differences from the pattern formed by the 10-year average.

In 1981-82 (Fig. 5), rainfall was normal from September through November, slightly below normal in December, less than half that expected for January, and virtually absent in February, when only 4.4 mm were recorded. The rainfall peak for the year, in April, was only 97.2 mm, slightly over half that expected, and only 2 mm more than had been received in December.

In 1982-83 (Fig. 6), precipitation was double or greater than the 1971-80 average from September through December, and then decreased sharply to produce a very dry January. Rainfall remained below normal until May, then exceeded the expected in May, becoming normal thereafter. The heavy rain from October through December had important consequences for the rodent population that year.

In 1983-84 (Fig. 7), rainfall was below normal from September through November but then rose sharply to levels about one-third above normal for December and January. February and March were similar to the average, but precipitation in April was again one-third more than expected, reaching nearly 300 mm in that month. The remainder of the year was normal. Heavy rain in January, followed by a normal February and March appears to be the critical environmental influence for the rodent population of that year.

In 1984-85 (Fig. 8), rainfall was normal in September and October, but in November more than doubled the expected amount. Precipitation decreased sharply in December to about half the average and continued to decline in January, when only 10.8 mm was received, in comparison to the 126 mm expected from the 10-year average. The study ended in February, which had a greater than normal amount of rain.

The hypothesis advanced in this paper is that the events observed in the rodent population studied can be explained as the result of annual variation in the timing and level of precipitation during the critical period from November through February of each year. This variation is summarized thus:

1981-82: January and February had extremely low rainfall.

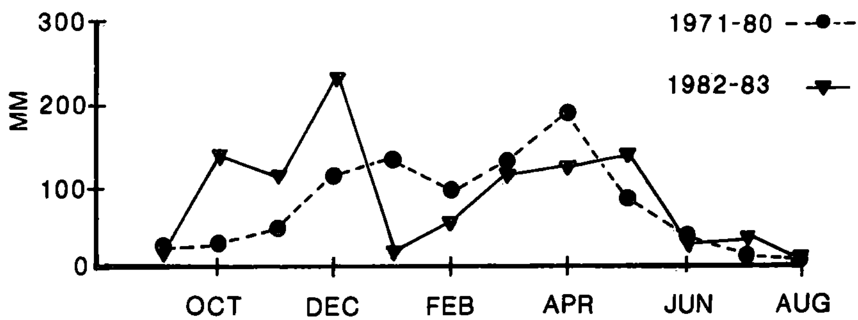

Figure 6. Monthly total precipitation at Morogoro, September 1982-August 1983 in comparison to the average for the preceding decade.

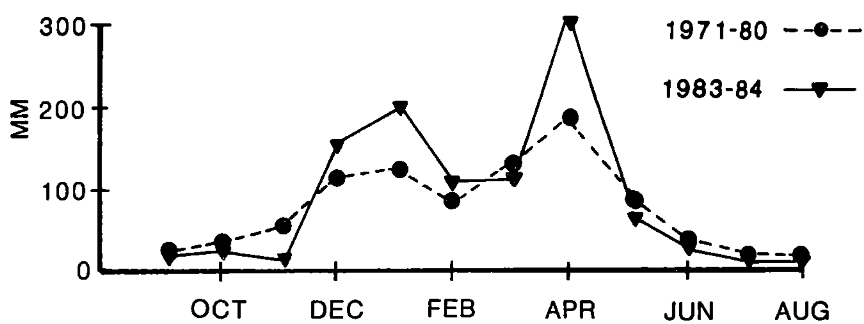

Figure 7. Monthly total precipitation at Morogoro, September 1983-August 1984 in comparison to the average for the preceding decade.

1982-83: October, November, and December had extremely high rainfall.
1983-84: December and January had exceptionally high rainfall.
1984-85: November had very heavy rain, followed by very little in December and January.

Population Biology of *Praomys natalensis* at Morogoro.

Identity of the population studied.-- Karyotype studies elsewhere in Africa have shown the presence of two karyotypes in *Praomys* populations: in Sierra Leone (Robbins et al. 1983) and Ivory Coast (Bellier 1975), diploid numbers of 32 and 38 have been have been distinguished as *Praomys (Mastomys) huberti* and *Praomys (Mastomys) erythroleucus*, respectively (Robbins et al. 1983). In southern Africa, a 32 chromosome form is considered to be *Praomys (Mastomys) natalensis*, and a species with 36 chromosomes is thought to represent *Praomys (Mastomys) coucha* (Green et al. 1980; Lyons et al. 1977; Gordon 1978;, and Lyons et al. 1980). However, Hubert et al. (1983), without clearly stating their justification for their action, have assigned the name *natalensis* to the 36 chromosome species, apparently on the basis of a karyotype obtained by Matthey (1954) from a single specimen sent him from Johannesburg. They thus ignored the opinions based upon far more extensive studies of the South African populations by Lyons et al. (1977), Gordon (1978), Green et al. (1980) and Lyons et al. (1980). While *P. huberti* evidently does occur in East Africa, at least in Somalia (Capanna et al. 1982), the status of *Praomys (Mastomys) natalensis* populations in Kenya, Tanzania, and Malawi has not been resolved. Accordingly, the position taken here will be that of Smithers (1983) for the South African populations: the Morogoro shamba rats should be referred to as *Praomys (Mastomys) natalensis* **sensu latu.**

A total of 35 multimammate rats from the university campus population at Morogoro were karyotyped: all showed a diploid number of 32 chromosomes. Scattered samples from other localities had the same diploid number.

Reproduction.-- *Praomys natalensis* is an annual species, reproducing during the first and only year of its life, with parous females disappearing from the population before the next breeding season begins (Fig. 9).

Mark and release studies on the campus population showed that females do not survive to enter a second breeding season, and very few males live over one year (Tang Christensen pers. comm.). This is consistent with the estimate

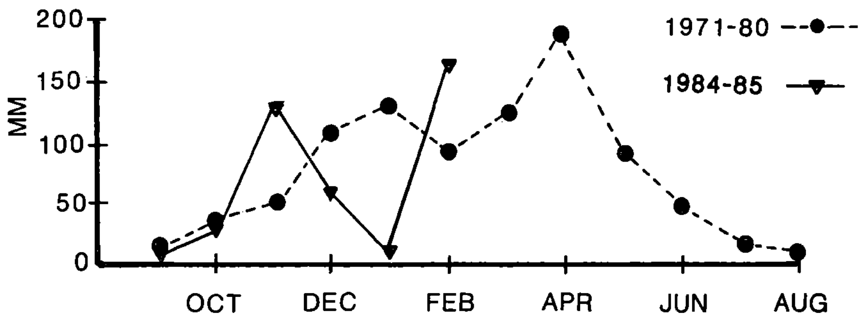

Figure 8. Monthly total precipitation at Morogoro, September 1984-February 1985 in comparison to the average for the preceding decade.

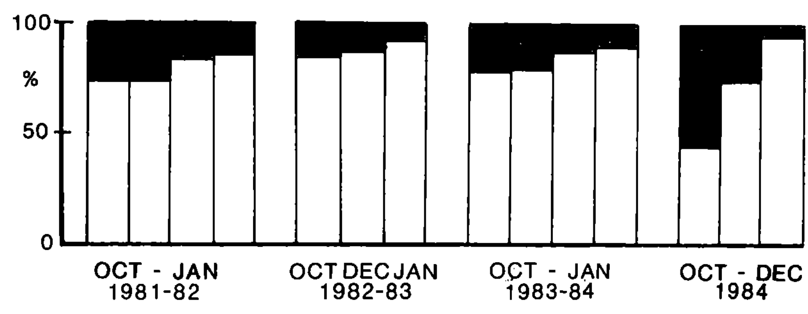

Figure 9. Survival of post-reproductive female *Praomys natalensis* from October to January 1981-85. Shaded areas represent the proportion of post-reproductive females in the total sample.

given by De Witt (1972) of a longevity in the wild of 339 days for *P. natalensis* in South Africa. The main reproductive season begins in April of each year, when female young of the preceding season appear with perforate vaginae (Fig. 10).

The first litter is born in late April or early to mid-May, followed by another three litters at approximately monthly intervals, with reproduction ending in August (Fig. 11). It is possible that some females could produce more than four litters in those years when conditions favor reproduction from January onward, but survival of a given female through the entire season is probably unlikely. Very few, if any, young are born from September through December in field situations, but reproduction is apparently continuous in Morogoro Region among those *P. natalensis* inhabiting houses or other structures where food and cover are available.

Females produce, on the average, 11.7 embryos per litter, with a range of 3-23 seen in utero (Table 1). Females may show as many as 24 teats. Those females smaller than 105 mm HBL appear to produce 1-2 embryos fewer than those 105 mm and larger. Maximum litter size was seen in the females which were 120-129 mm HBL, averaging 12.0-12.6, while in the largest and probably oldest females, those over 129 mm HBL, slightly smaller litters were found, averaging 11.8 (Table 1).

Little annual variation was seen in mean litter size compared with female HBL, except in 1983 when females of 115-119 mm produced two more embryos per litter than in the previous year (Table 2).

A comparison of mean litter size with embryo size indicates that perhaps two embryos are lost during gestation, with the number actually born probably averaging around 10.6 per litter (Table 3).

Maximum litter size occurs from May through July; early and late season litters are 1-2 embryos fewer (Table 4).

Embryo resorption in 1982 and 1983 was highest in August, but in 1984 when reproduction was continuous from February through August, resorbing embryos were seen in each month at similar levels (Table 5). In terms of the total number of embryos produced by the females examined, the proportion resorbed was only 0.4-3.2 percent.

Reproduction appeared to be more frenzied in 1982, when the population was recovering from very low density probably caused by the severe drought in preceding months. Females with either large or small embryos could be found simultaneously lactating, implying that another litter was started immediately after parturition (Table 6). In 1983 no females with embryos over 25 mm showed lactation. The proportion of females with small embryos that were also lactating decreased significantly in 1984, the year when reproduction was continuous from February through August.

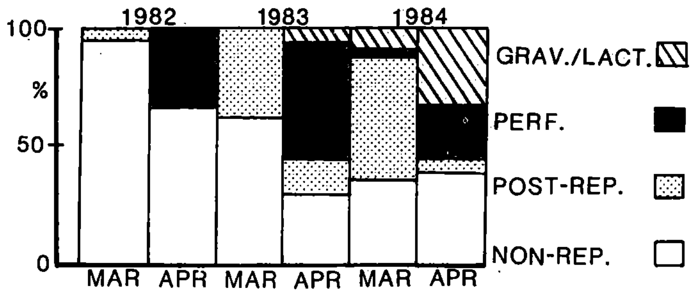

Figure 10. Reproductive condition of female *P. natalensis* in March and April of 1982-84. Categories are gravid or lactating, perforate, post-reproductive, and non-reproductive.

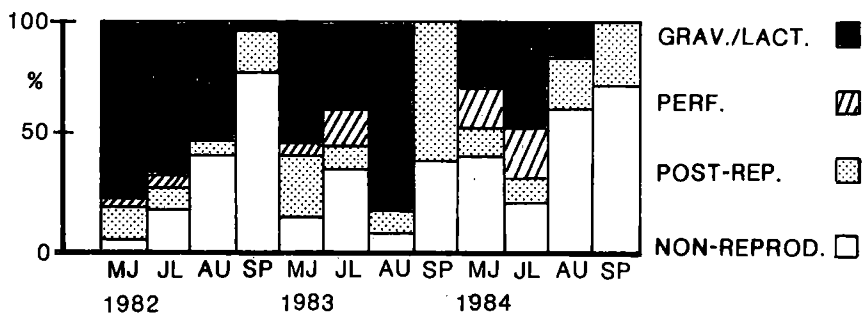

Figure 11. Reproductive condition of female *P. natalensis* from May to September 1982-84.

TABLE 1. Variation in litter size compared with size of gravid female *Praomys natalensis*.

Female HBL (mm)	Mean no. embryos ± 1 SE	(N)	Range
< 95	10.5±2.5	(2)	8-13
95-99	9.3±1.5	(3)	7-12
100-104	9.6±0.9	(13)*	6-17
105-109	11.0±0.6	(25)	6-17
110-114	11.3±0.4	(53)*	5-19
115-119	11.6±0.3	(77)**	3-20
120-124	12.0±0.3	(85)	7-23
125-129	12.6±0.4)	(65)**	7-21
> 129	11.8±0.3	(104)**	4-18
total sample	11.7±0.1	(427)	3-23

*, ** indicate comparisons of means, each significant at $P < 0.05$

TABLE 2. Annual variation in mean litter size correlated with head-body length of gravid *Praomys natalensis*.

Female HBL (mm)	Mean no. embryos ± 1 SE (N) 1982		1983		1984	
110-114	10.9±0.8	(18)	11.1±0.8	(13)	11.7±0.7	(20)
115-119	10.6±0.7	(22)*	12.7±0.7	(23)	11.5±0.4	(32)
120-124	11.9±0.5	(25)	12.1±0.7	(28)	11.9±0.5	(31)
125-129	13.5±0.9	(16)	12.8±0.7	(20)	12.0±0.5	(27)
> 129	13.5±1.0	(8)	11.7±0.5	(39)	12.0±0.4	(54)

* $P < 0.05$

TABLE 3. Litter size of *Praomys natalensis* in comparison with embryo size.

	Embryo crown-rump length (mm) ± 1 SE (N)					
Year	< 10		10-19		> 19	
1982	12.6±0.5	(51)*	11.1±0.4	(32)	10.3±0.9	(16)
range	(3-20)		(7-16)		(5-18)	
1983	11.9±0.4	(72)	12.3±0.4	(56)*	10.7±0.6	(22)
range	(4-23)		(5-18)		(5-15)	
1984	12.1±0.3	(93)	11.8±0.4	(43)*	10.7±0.4	(36)
range	(7-19)		(8-18)		(7-14)	
1982-84	12.2±0.2	(216)	11.8±0.2	(131)*	10.6±0.3	(74)
range	(4-23)		(5-18)		(5-18)	

* $P < 0.05$

TABLE 4. Monthly and annual variation in mean litter size of *Praomys natalensis* on the University Campus, Morogoro.

	Mean ± 1 SE (N)							
Month	1982		1983		1984		1982-84	
Feb					10.7±0.3	(36)		
Mar-Apr			9.7	(3)	10.8±0.4	(33)	10.7±0.4	(36)
May-Jun	11.7±0.4	(34)	11.4±0.8	(17)	12.9±0.5	(36)	12.1±0.3	(84)
Jul	13.2±0.6	(31)	13.0±0.4	(43)	12.6±0.6	(39)	12.0±0.3	(113)
Aug	10.5±0.5	(42)	11.5±0.3	(86)	11.2±0.5	(28)	11.1±0.2	(151)
May-Aug	11.6±0.3	(104)	11.0±0.3	(140)	12.3±0.3	(103)	11.7±0.1	(431)

TABLE 5. Monthly and annual variation in intrauterine mortality of *Praomys natalensis*.

	Litters			Embryos	
Year Months	No.	% w/resorbing embryos	% Embryos resorbing	No.	% Resorbing
1982					
May-Jun	34	0.0	-	-	-
Jul	31	0.0	-	-	-
Aug	42	2.4	25.0	445	0.9
1983					
Mar-Apr	3	0.0	-	-	-
May-Jun	17	0.0	-	-	-
Jul	31	3.2	15.4	561	0.4
Aug	86	26.7	11.9	1020	3.2
1984					
Feb	36	8.3	9.1	388	0.8
Mar-Apr	33	15.2	10.5	362	1.7
May-Jun	36	13.9	8.7	470	1.3
Jul	39	12.8	14.9	499	1.6
Aug	28	7.1	8.3	316	0.6

TABLE 6. Proportion of gravid females simultaneously lactating.

		% Gravid females lactating	
Year Months	# Gravid Females	< 25 mm	> 25 mm
1982			
May-Jun	31	38.7	3.2
Jul	31	16.1	6.5
Aug	42	21.4	4.8
1983			
May-Jun	17	41.2	0.0
Jul	43	14.0	0.0
Aug	80	35.0	0.0
1984			
Mar-Apr	33	3.0	0.0
May-Jun	36	2.8	0.0
Jul	39	0.0	0.0
Aug	28	3.6	0.0

Testes of adult males regress from September through November; no young males produce sperm during that period (Fig. 12). Spermatogenesis begins in December, continuing into January, and by February virtually all males are reproductively capable. In those years when young are born in January or February, they become mature by April when the main reproductive period begins.

Abundance.-- In three of the four years, trap success was at maximum following reproduction, in September-December (Fig. 13). Density declined thereafter in each year studied, but the decline was sharper from September-October to January-February 1981-82, the dry year, than in 1982-83 and 1984-85, both considerably wetter years. Density in the September to December period of 1983 was much greater than in the other years, and a "crash" occurred in late December-early January (Fig. 13): the grid estimate taken from 12-16 December was 769 per ha, while that obtained in an adjacent field 24-27 January, five weeks later, was 56 per ha. Migration from the adjacent fields into the trapped field may have slightly reduced the numbers in adjacent fields, but data from subsequent monthly catches substantiate an abrupt drop in population density at that time of year. The abrupt decline in density was reflected in the trap line results for the same areas, which showed a drop from 57 percent in December to 13 percent positive in January. The maximum density recorded by grid estimates was 1125 per ha in October 1984. It probably was higher at that time in 1983, before the crash, but no grid data are available. Maximum trap success from line trapping was observed in November 1983, when 68.3 percent of traps were positive for two nights' trapping (Fig. 13).

In relative abundance, *P. natalensis* comprised nearly 87 percent of the 9306 rodents and insectivores trapped on campus during the program (Table 7). The shrew *Crocidura hirta* was next most abundant, followed by the striped grass mouse, *Lemniscomys griselda*. The other seven species taken were far less common, although there were certainly more *Tatera* spp. and *Mus minutoides* available than trap results indicate. These are underrepresented, probably because *Tatera* could escape from "Little Nipper" traps unless seriously injured, and because of their size *Mus* may not be as trappable as other species. *Dasymys incomtus* was virtually restricted to deep grass, *Acomys spinosissima* was both seasonal--found in April only each year--and limited to grass areas, while *Pelomys fallax* was seen only in a very wet area in June 1984, following the excessive rainfall (nearly 300 mm) of April. No permanent streams flow through the campus, and the common name, creek rat, indicates its preferences. *Rattus rattus* was common in campus houses, but only one was taken in a field trap. The tiny, unidentified shrew appears to be truly rare, but again, may not be trapped easily due to small size.

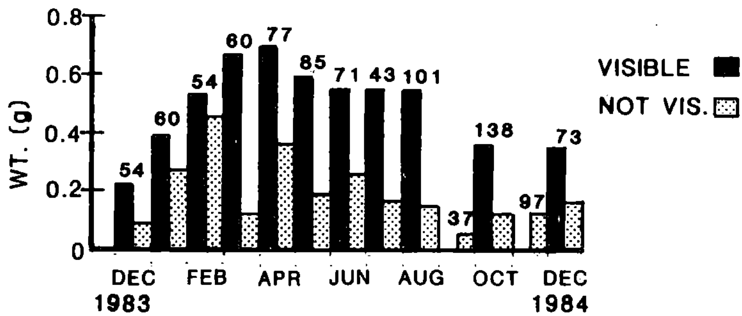

Figure 12. Mean testis weight of *P. natalensis* correlated with visibility of epididymal tubules from December 1983 to December 1984.

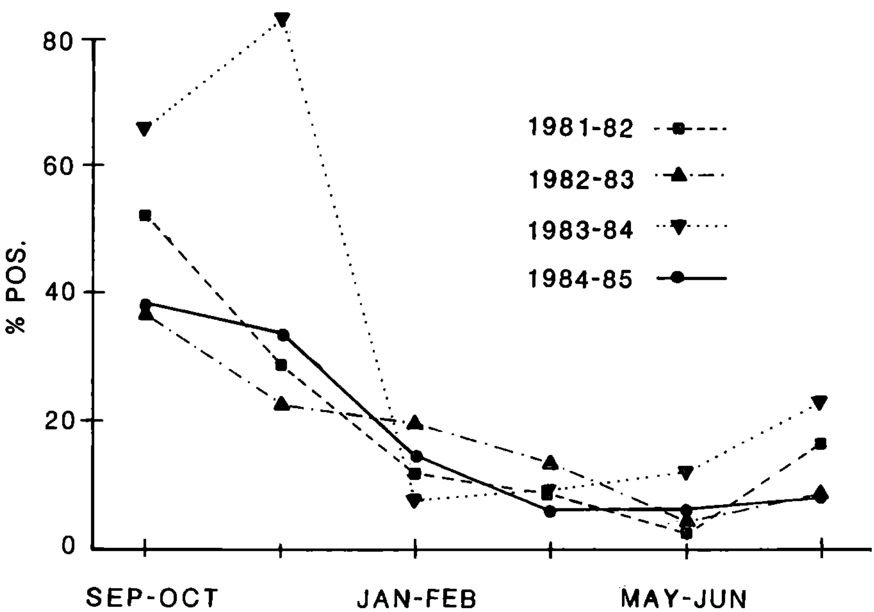

Figure 13. Trap success by bimonthly periods, corrected, for *P. natalensis* in the study areas, September 1981-February 1985.

TABLE 7. Relative abundance of rodents and insectivores on the university campus, Morogoro, Tanzania, from 29 July 1981-20 February 1985.

Species	# Trapped	% Total catch
Praomys natalensis	8059	86.6
Crocidura hirta	811	8.7
Lemniscomys griselda	249	2.7
Tatera "robusta"	84	0.9
Mus minutoides	63	0.7
Dasymys incomtus	21	0.2
Acomys spinosissima	7	< 0.1
Crocidura sp. indet.	6	< 0.1
Rattus rattus	4	< 0.1
Pelomys fallax	2	< 0.1

TABLE 8. Seasonal variation in average relative abundance of rodents and insectivores in cultivated vs. uncultivated habitats.

	Mean % of total catch					
	Jul-Dec 81-84		Jan-Apr 82-85		May-Jul 82-84	
Species	Maize	Grass	Maize	Grass	Maize	Grass
P. natalensis	94.4	66.6	83.0	65.2	64.8	62.2
range	92-97	23-93	80-87	56-72	56-75	50-79
L. griselda	1.4	18.4	1.8	8.8	5.4	9.4
range	1-3	1-57	0-4	2-19	0-8	2-24
T. "robusta"	0.4	3.1	0.8	4.3	4.0	2.0
range	0-1	0-9	0-2	0-14	1-8	0-6
M. minutoides	0.3	1.1	0.7	0.8	1.1	0.5
range	0-4	0-3	0-12	0-3	0-3	0-1
C. hirta	3.5	13.4	13.5	19.2	23.8	24.6
range	2-4	4-31	10-18	5-30	9-29	12-45
D. incomtus	0.03	0.1	0.2	0.9	0.4	1.0
A. spinosissima	-	-	-	1.0	-	-
R. rattus	0.02	-	-	-	-	-
P. fallax	-	-	-	-	0.4	-
Crocidura sp.	0.04	-	0.08	-	-	0.3

Apart from those fluctuations possibly correlated with the reproductive cycle, there was no marked influence of season upon abundance. *Praomys natalensis* was more common in fallow fields from July through April than in grass areas, but in May and June, when growing maize provided less cover, there was no difference between habitats (Table 8).

Within grass habitats, *P. natalensis* seemed to maintain the same relationship to other species throughout the year. The contrast between abundance in uncultivated vs. cultivated habitats was most marked from July to December in 1981 and 1982, when *P. natalensis* comprised over 90 percent of the catch in fallow fields, but less than 60 percent in grass (Table 9).

The great increase in density observed in 1983 and 1984 was accompanied by movement of *P. natalensis* into grass, where it was found at about the same relative abundance as seen in fallow fields in those years. From January to April and in May-June (Table 9) in each year far less variation was found in an annual comparison than from July to December.

Population structure.-- Three cohorts can be identified in the population from September to December (Figs. 14-17): adult males, post-reproductive or parous females, and non-reproductive young of the year. A few females were found still lactating or with perforated vaginae in September and October, but these were clearly post-reproductive (Table 10).

At this time, 60-80 percent of the population are non-reproductive young, with the remainder representing more or less equal numbers of older males and females. In January, with maturation of young males beginning in December, the proportion of mature males increases, while post-reproductive females diminish in representation (Figs. 14-17). In 1981-82, old females disappeared completely by April (Figs. 14, 18). The same pattern probably occurred in the other years of the study but was masked by the off-season breeding in those years (Figs. 19-21), when young females born in the previous season bred and entered the post-reproductive cohort. An apparent decrease in mature males shown by the figures for 1983-84 (Fig. 16) and 1984-85 (Fig. 17) probably resulted from the classification of males by epididymal tubule condition into reproductive category. Earlier, this had been based upon having scrotal or non-scrotal testes in specimens with HBL of 105 mm or more (Figs. 14, 15).

The occurrence of off-season breeding is shown clearly by the sudden increase in parous females in February 1983 and 1984 (Figs. 19, 20), and in January 1985 (Fig. 21), in contrast to the population structure seen in January-February 1982 (Fig. 18) when the only parous females seen were survivors of the previous year's breeding season (Table 10). A corollary to the sudden increase in the proportion of females showing placental scars is, of course, the capture of very small juveniles, 65-85 mm HBL, in the weeks following appearance of females with scars, as shown most clearly by Figure 16, where

TABLE 9. Annual variation in relative abundance of rodents and insectivores in cultivated vs. uncultivated habitats.

Habitat Year	Traps positive* #	Traps positive* %	% Total catch *Praomys*	*Lemniscomys*	*Tatera*	*Mus*	*Crocidura hirta*	other spp.
UNCULTIVATED								
1981	36	8.7	58.3	5.6	2.8	2.8	30.6	0
1982	23	4.0	21.7	56.5	8.7	0	13.0	0
	148	**8.8**	**66.2**	**8.8**	**14.2**	**2.7**	**5.4**	**3.4**
	33	3.9	57.6	24.2	6.1	0	12.1	0
1983	824	17.6	92.1	3.0	0.4	0.4	4.0	0
	505	**9.7**	**71.7**	**5.7**	**2.0**	**0.4**	**19.0**	**1.2**
	96	5.9	50.0	2.1	0	0	44.8	3.1
1984	504	22.0	93.1	1.2	0	0.2	5.2	0.4
	126	**3.2**	**55.6**	**19.0**	**0.8**	**0**	**22.2**	**2.4**
	213	17.7	78.9	1.9	0	1.4	16.9	0
1985	**190**	**9.1**	**67.4**	**1.6**	**0**	**0**	**30.0**	**1.1**
CULTIVATED								
1981	556	32.4	97.3	1.1	0	0	1.6	0
1982	896	24.6	93.9	1.1	1.1	0.3	3.6	0
	334	**8.5**	**79.9**	**3.9**	**2.4**	**1.2**	**12.0**	**0.6**
	138	2.8	74.6	8.0	8.0	0	8.7	0
1983	2046	38.0	92.7	2.3	0.2	0.3	4.3	0.1
	365	**15.6**	**86.8**	**1.9**	**0.8**	**0.3**	**10.1**	**0**
	36	3.5	55.6	8.3	2.8	0	33.3	0
1984	1786	27.2	93.8	1.1	0.2	0.4	4.3	0.2
	361	**9.5**	**79.8**	**1.4**	**0**	**1.1**	**17.5**	**0.3**
	187	8.0	64.2	0	1.1	3.2	29.4	2.2
1985	**298**	**16.5**	**85.6**	**0**	**0**	**0**	**14.4**	**0**

* uncorrected, first two nights; the sequence of trapping periods is:
July-December **January-April** May-July.

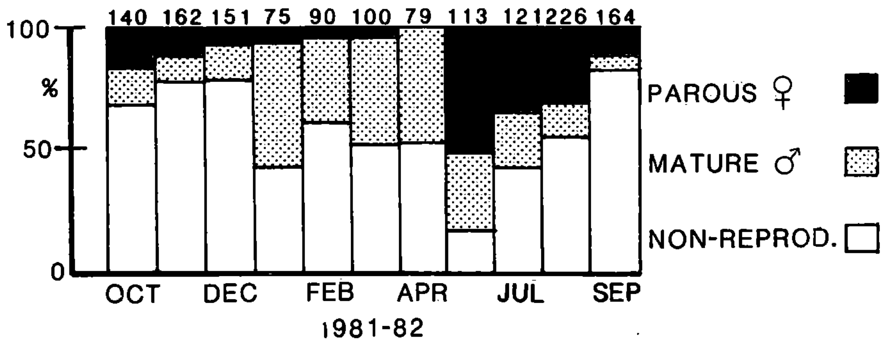

Figure 14. *Praomys natalensis* **population structure on the university campus, Morogoro, October 1981-September 1982.**

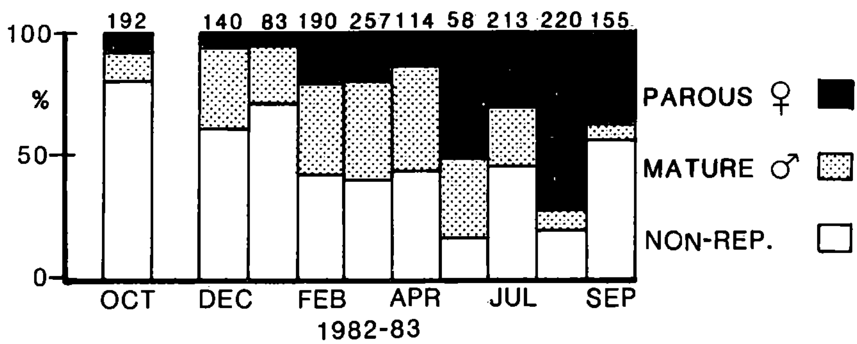

Figure 15. *Praomys natalensis* **population structure on the university campus, Morogoro, October 1982-September 1983.**

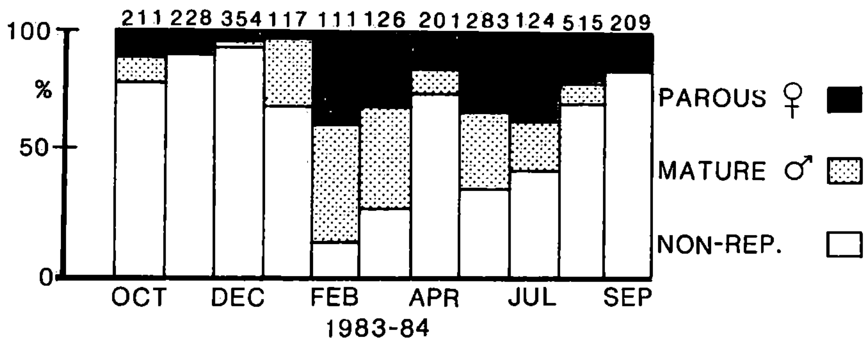

Figure 16. *Praomys natalensis* **population structure on the university campus, Morogoro, October 1983-September 1984.**

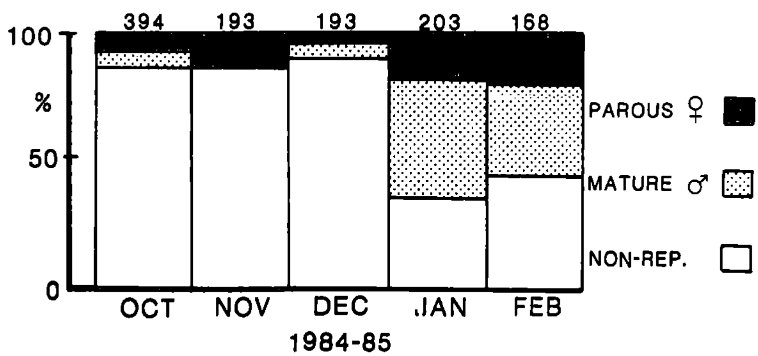

Figure 17. *Praomys natalensis* **population structure on the university campus, Morogoro, October 1984-February 1985.**

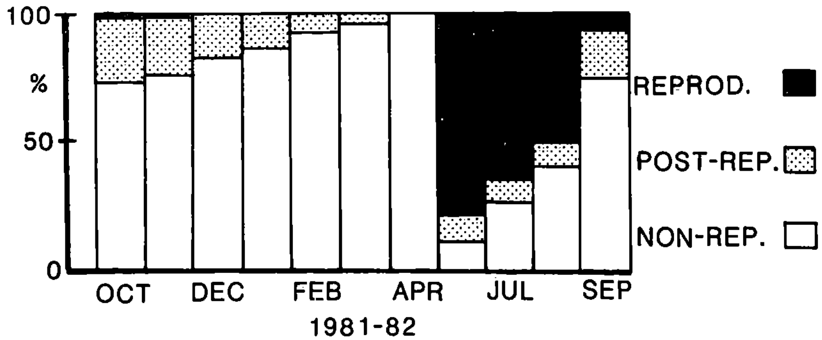

Figure 18. Reproductive condition of the female cohort from the university campus *P. natalensis* population, October 1981-September 1982.

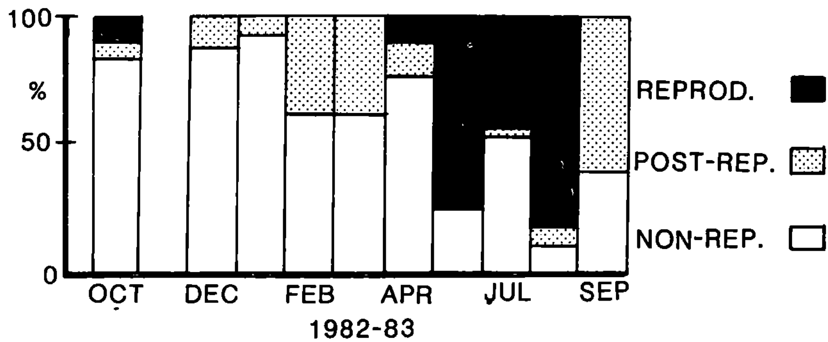

Figure 19 Reproductive condition of the female cohort from the university campus *P. natalensis* population, October 1982-September 1983.

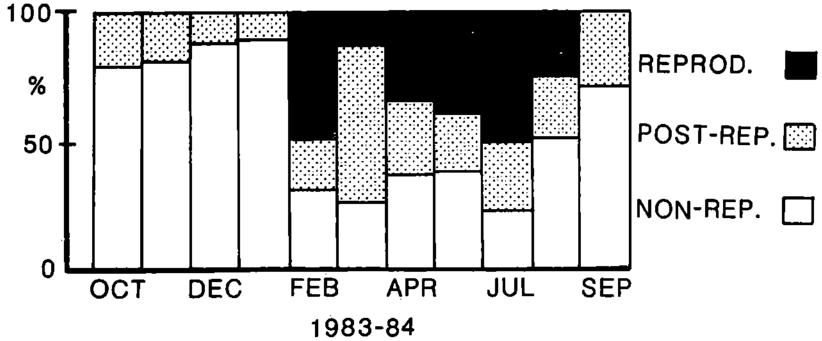

Figure 20. Reproductive condition of the female cohort from the university campus *P. natalensis* population, October 1983-September 1984.

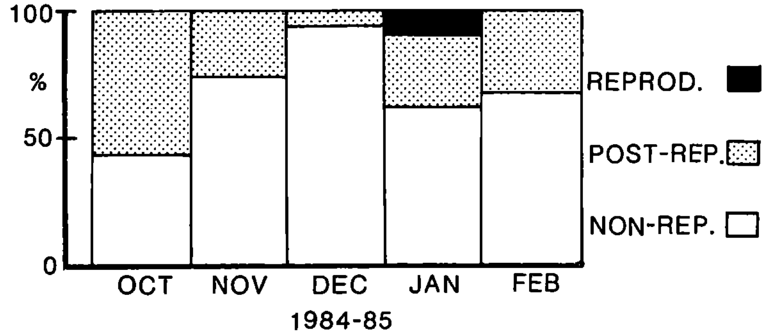

Figure 21. Reproductive condition of the female cohort from the university campus *P. natalensis* population, October 1984-February 1985.

TABLE 10. Proportion of total female sample post-reproductive or reproductive October 1981-February 1985.

	% Total females reproductive or post-reproductive			
Month	1981-82	1982-83	1983-84	1984-85
October	24	14	21	56
November	24	-	20	26
December	15	11	12	5
January	13	7	9	40
February	6	38	69	33
March	4	38	75	-
April	0	22	64	-
May/June	90	79	61	-
July	75	48	79	-
August	60	91	51	-
September	23	61	30 *	-

* sample taken from grass habitat only

TABLE 11. Proportion of total female sample gravid or lactating October 1981-February 1985.

	% Total females gravid or lactating			
Month	1981-82	1982-83	1983-84	1984-85
October	1	6	0	0
November	1	-	0	0
December	0	0	0	0
January	0	0	0	9
February	0	1	50	0
March	0	0	10	-
April	0	9	33	-
May/June	76	77	37	-
July	64	44	49	-
August	50	83	25	-
September	5	0	0	-

the proportion of non-reproductive individuals nearly tripled in April 1984, in comparison to the preceding March.

The onset of the regular breeding season in April is indicated by the sudden appearance of perforate females in that month in all three years (Fig. 10). The female cohort, viewed by themselves during the main breeding season, shows that at any one time most females were either pregnant or lactating (Fig. 11, Table 11). Structure during the main breeding season is very similar for 1982 (Fig. 14) and 1984 (Fig. 16). The sample shown for August 1983 (Fig. 15) reflects the origin of the sample: all *P. natalensis* examined for that month came from the area in which the mark and release study was done, which showed progressively disparate sex ratios in favor of females in each of the three years (Tang Christensen pers. comm.). This was also the only area on campus from which viral seropositives were obtained. It is tempting to speculate that infection by this virus, which cross reacts with *Lassa* and *Mopeia* viruses, caused differential mortality against males.

Influence of habitat.-- From July through April, trap success for *Praomys natalensis* in uncultivated grass areas was approximately half that obtained in fallow fields (Table 12). In May and June, however, there was no difference between habitats.

Population structure was similar in both habitats when densities were at peak, as shown by the female cohort in October (Fig. 22).

In other seasons, though, there were differences which probably reflect the influence of both rainfall and habitat upon reproduction. This is shown by the composition of the female cohort from December 1982 through March 1983 (Fig. 23).

In December, a few reproductive females were taken in fallow field. Those taken in January from grass areas (Fig. 25) were either young, non-reproductives or post-reproductive females of the preceding year. In February and March, there were many newly post-reproductive females present in fallow field as well as many newly weaned juveniles, demonstrating production of a litter in January (Fig. 26). The proportion of post-reproductive females had increased in samples from grass in February (Fig. 23), but no juveniles were taken and these females could have been from the preceding year. Even more post-reproductive females were found in fallow field in March (Fig. 23), while there was evidence that reproduction was just beginning in grass habitats. Another contrast appeared between habitats in August 1984 (Fig. 24), when females collected in grass had already completed reproducing, yet in post-harvest maize fields, 20-35 percent were still breeding. Among males from grass only 10 percent showed visible epididymal tubules, in comparison to 29 percent from fallow field.

Influence of rainfall upon growth.-- Growth data on *P. natalensis* were obtained during the capture-mark-release-recapture study (Tang Christensen unpubl.), and will be presented elsewhere. Data obtained from monthly

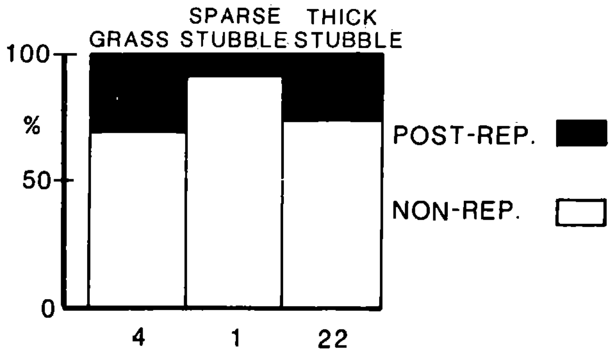

Figure 22. Structure of the female cohort from the university campus *P. natalensis* population in October 1984 from three study sites which differed in quality of cover and, presumably, available food.

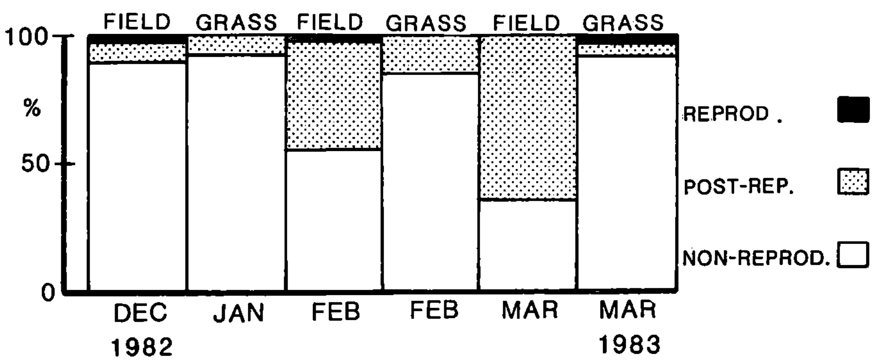

Figure 23. Structure of the female cohort from the university campus *P. natalensis* population collected from fallow maize fields or uncultivated grass areas from December 1982-March 1983.

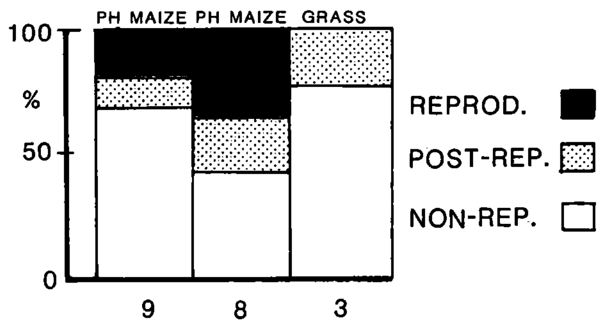

Figure 24. Structure of the female cohort from the university campus *P. natalensis* population collected from post-harvest (PH) maize fields (sites 8 & 9) or uncultivated grass areas (site 3) in August 1984.

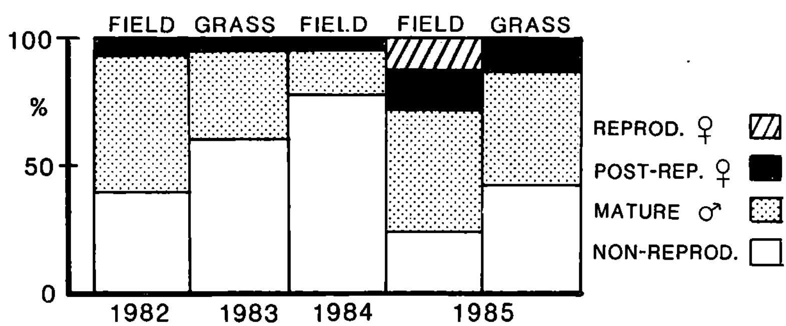

Figure 25. *Praomys natalensis* population structure in fallow maize field or uncultivated grass microhabitats in January of each year, 1982-85.

samples (Tables 13, 14) demonstrated that mean HBL and mean weight of female *P. natalensis* were greater in the critical December-February and March-April periods of 1983-84 than at comparable times in 1981-82 and 1982-83. This probably reflects an increased food supply despite greater population density during the exceptionally heavy rainfall of December 1983-January 1984. The data also could indicate survival of the larger members of the cohort, with smaller individuals having greater mortality or being forced to emigrate from the study areas.

CONCLUSIONS

The data obtained during this study suggest the following conclusions:

1) In dry years, reproduction in either uncultivated or cultivated habitats begins in April and ends in August. Populations begin reproduction in those years at minimal density levels.

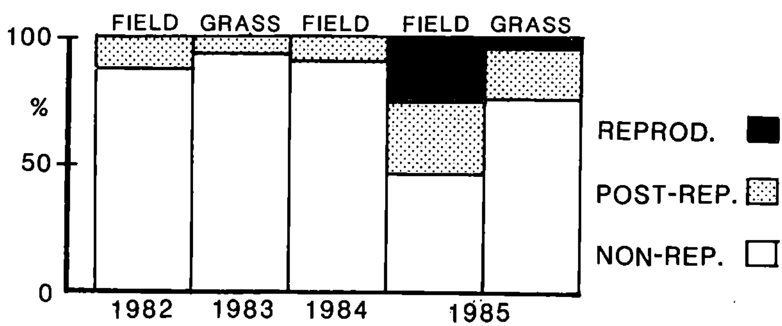

Figure 26. Structure of the female cohort from the university campus *P. natalensis* population in fallow maize field or uncultivated grass microhabitats in January of each year, 1982-85.

TABLE 12. Average trap success for *Praomys natalensis* by habitat and season.

	% Positive traps in	
Season	Maize fields	Uncultivated grass
July-December	31.2	17.1
January-April	12.7	7.3
May-June	4.0	5.4

TABLE 13. Mean head-body length of female *Praomys natalensis* compared with rainfall, 1981-85.

	Mean head-body length (mm) ± 1 SE				Mean rainfall (mm)
Months	1981-82	1982-83	1983-84	1984-85	1971-80
October	103.7±1.7	99.8±1.1	102.4±1.8	99.8±1.8	
No. exam.	(96)	(84)	(72)	(72)	
Nov.-Dec. rainfall	147.1	332.4	159.3	183.6	158.6
Dec.-Feb.	100.6±0.8	102.2±0.9	110.2±0.7	108.0±0.7	
No. exam.	(140)	(189)	(290)	(283)	
Jan.-Feb. rainfall	44.4	70.2	298.7	169.5	212.1
Mar.-Apr.	104.9±0.8	105.9±0.7	117.8±1.3	-	
No. exam.	(88)	(176)	(164)		
Mar.-Apr. rainfall	162.3	218.2	408.4	-	307.8
May-June	118.0±1.1	120.4±1.3	121.0±1.1	-	
No. exam.	(59)	(24)	(71)		
May-June rainfall	88.7	155.2	86.2	-	102.1

2) Off-season breeding may occur in those years with heavy short rains, its timing and duration dependent upon onset and duration of the rains. Little or no off-season breeding occurs, apparently, in uncultivated habitats in years with heavy short rains. When the short rains are heavy, the population enters the main breeding season at much higher density levels than in dry years (Table 15).
3) The population levels attained following the main breeding season, i.e. from September through December, are probably correlated with the occurrence of off-season breeding earlier in that year, which as indicated depends upon heavy short rains 9 to 12 months earlier.

The data on reproduction agree with other studies, elsewhere in Africa. Average litter size ranges from 9.5-12.1 (Brambell and Davis 1941; Chapman

TABLE 14. Mean weights of female *Praomys natalensis* compared with rainfall, 1981-85.

rainfall (mm)	Mean weight (g) ± 1 S.E.				Mean
Months	1981-82	1982-83	1983-84	1984-85	1971-80
October	27.8±1.1	28.2±1.0	28.2±1.3	24.1±1.4	
No. exam.	(96)	(84)	(70)	(72)	
Nov-Dec rainfall	147.1	332.4	159.3	183.6	158.6
Dec-Feb	28.4±0.6	29.7±0.7	32.7±0.9	28.9±0.5	
No. exam.	(140)	(189)	(290)	(282)	
Jan-Feb rainfall	44.4	70.2	298.7	169.5	212.1
Mar-Apr	30.1±0.5	31.5±0.6	38.9±1.3		
No. exam.	(87)	(174)	(164)		
Mar-Apr rainfall	162.3	218.2	408.4	-	307.8
May-June	51.8±1.6	51.0±2.6	47.4±1.5		
No. exam.	(60)	(24)	(71)		
May-June rainfall	88.7	155.2	86.2	-	102.1

TABLE 15. Summary of annual variation in rainfall and reproductive patterns, with trap success prior to normal onset of *Praomys natalensis* reproduction in April.

year	rainfall pattern	reproductive pattern	April trap success (%)
1981-82	< normal Dec.,very dry Jan.-Feb.	no reproduction from Sept. to April	5.0
1982-83	very wet Oct.-Dec., < normal Jan.-Apr.	1 litter Jan., then none until April	7.6
1983-84	very wet Dec.-Jan., normal Feb.-April	continuous reproduction Jan. through August	34.4
1984-85	very wet Nov., then dry Dec.-Jan.	1 litter Jan., none in February	-

et al. 1959; Hanney 1965; Coetzee 1965; Delany and Neal 1969). These other averages, however, are based upon far fewer females examined: in the one study where the number of *P. natalensis* was adequate (4636, Coetzee 1965), only 481 females were dissected. Coetzee (1967) reported data on intrauterine mortality thus: corpora lutea averaged 10.92, 9.47 embryos were implanted, and 9.22 healthy fetuses were observed. In the present study, the average of 12.2 embryos less than 10 mm decreased to 11.8 between 10 mm and 19 mm, and 10.6 in excess of 19 mm. Coetzee's (1965) average litter size of 9.5 may indicate a slight difference in reproductive rate between South Africa and Tanzania, or could indicate that the two populations are not conspecific.

Coetzee (1975) reported a low breeding rate during dry season (winter), with a break in reproduction in September, while Delany and Neal (1969) found reproductive females in Uganda from May to July and October to December, commenting that "peak breeding season occurs mainly towards the end of the rainy season and beginning of the dry season." Their samples were taken from sites between 900 m and 1100 m elevation, where some rainfall appears to occur in every month. In Malawi, Hanney (1965) examined 159 female *P. natalensis* without finding pregnant females from June to January. Hubbard (1972) presented fragmentary data from an overall sample of 225 females taken in several Tanzanian localities (Muheza, Lake Manyara, Iringa, Njombe, and Himo), reporting pregnant females in January, February, March, May, July, September, and November, but the data are virtually meaningless given the variety of rainfall patterns which occur over that broad area.

Some of the observations by Harris (1937) were based upon material from Morogoro; He described *P. natalensis* as being least active from January to May, with "The majority of the mice at this time appear to be young and in good condition." Maturation of both sexes occurred about the beginning of March, followed soon by pregnant females and young, while maximum numbers were found in July and August. Although Harris studied fluctuations in numbers for two years at Morogoro, from December 1931 to December 1933, he apparently did not publish quantitative data from his work nor a detailed description of methods, which unfortunately prevents a direct comparison with the present study.

The data of Chapman et al. (1959) from Rukwa in Mbeya Region are based upon erratically collected material but, as presented by Coetzee (1975), show a pattern of reproduction somewhat different to that found in Morogoro during the present study. The percentage of juveniles in the population reached maxima in May and June, remained high until October, then declined rapidly through March, rising again from April. In Morogoro, the juvenile cohort rose continuously relative to the adult component from July to December of each year, as an overall pattern, though the rise began earlier in 1984 (April). The decrease in juvenile percentage found in Rukwa can be attributed to possibly earlier maturation, beginning in October rather than

December as in Morogoro, with those juveniles found from November through February representing reproduction comparable to that following heavy short rains in Morogoro. The differences might also indicate a species difference in reproductive pattern. Sample sizes reported by Chapman et al. (1959) are inadequate to draw a meaningful comparison with the Morogoro study.

There is agreement between conclusions presented here and those of other authors concerning the role of precipitation on population dynamics. Coetzee (1975) thought that the cold winters in South Africa might act toward controlling density, with the concomitant influence of sparse plant cover during late winter providing less protection against predators. Cold is not a factor in tropical Africa, except perhaps with montane rodent populations, but certainly the lack of ground cover observed during the very dry period of November-April 1981-82 contributed to greater mortality and, thus, lower density going into the main reproductive season of 1982. And cover was distinctly better during the following two wetter years. Delany and Neal (1969) suggested that rainfall might be the most important factor governing rodent breeding in Uganda, through its indirect effect upon food availability. Coetzee (1975) linked the abundance of food to population explosions, a conclusion also suggested by Smithers (1971), who found the number of pregnant female *P. natalensis* in Botswana to be very low during the last two years of a four year drought. Following the end of the drought, a massive explosion took place. In Coetzee's opinion, population explosions might be linked with the abundance of food. He listed the following factors as important regulators of *P. natalensis* density: (1) a high reproductive rate due to large litter size and short intervals between litters, (2) the age at first litter, and (3) the duration of breeding period, which is largely controlled by the rainy season with its indirect influence over food supply. An optimum food supply can lead to a population explosion which would disrupt the normal social structure, thus influencing litter size and interval, the size of neonates, and survival rate. In South Africa, high density coincides with cold weather, scarcity of food, lack of cover and increased predation, all of which can lead to a population crash.

The present study reinforces Coetzee's conclusions. Although perhaps important only in areas with Morogoro's climatic pattern, it is likely that the influence of precipitation is most critical during the short rain period, setting the stage, as it were, for the density threshold upon which the *P. natalensis* population enters the main breeding season in April of each year. If the short rains fall far below the average, density will decrease to minimal levels between January and April, and population levels will increase thereafter at a rate proportionate to subsequent precipitation levels. With a succession of favorable short rains, within two years the population can "explode" as was observed in 1983-84, followed by a "crash," as seen in January 1984. That this is a recurrent phenomenon is supported by Harris (1937) in his Morogoro study: "The most striking feature [of fluctuations in population density] was a fall from a catch of 170 mice in December 1931, to 20 in January 1932." This reduction in catch by 88 percent compares well with the grid estimate of December 1983 of 769/ha which dropped to 56/ha. in January 1984, a decline of 93 percent. Harris attributed the rodent "plague" of 1930-32, with peak abundance in 1931, to migration of rodents into the Morogoro area from Kimamba, over 40 miles to the east, rather than to a result of "an abnormal increase of the local population." Without more detail of his sampling procedures, this conclusion is arguable. As closely as the university campus population was monitored during the 40-month period, there was no suggestion during 1982-83 that numbers were "explosively" increasing, although abundance was clearly higher following the 1982 short rains, and off-season breeding occurred in January 1983. The less than obvious rise to "crash" level through the influence of higher precipitation level on food and cover, with increased survival and extended reproductive period, is a simpler and more likely explanation of high density than is migration from distant populations.

Implications for control.-- Given the high cost to a fragile economy of comprehensive rodent control programs, it is essential that control be rational to achieve maximum benefit for both agriculture and public health. An attempt to significantly decrease rodent numbers during the post-harvest period when maximum density is reached is far less effective and considerably more expensive than it would be to take preventive measures when populations are at minimum density. As this coincides with the pre-reproductive period in Morogoro, from January to April (disregarding off-season breeding in years of excessive rainfall), each rodent removed from the breeding population represents a far more significant result than one removed following harvest, because of the very real possibility that an individual female can produce 50 offspring between April and September. By concentrating rodent control activities in fields between January and the onset of the long rains in April, limited resources will have maximum effect, and both germination and harvest success should be improved. Coupled with encouraging farmers to clear away stubble immediately after harvest and improvement of grain storage structures, as pointed out by Harris a half-century ago, effective rodent control could be realized. Systematic sampling programs in climatically differing areas can indicate proper timing for rodenticide application, i.e. in the period immediately preceding onset of the main reproductive period, probably predictable by close study of rainfall patterns.

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