A POPULATION STUDY ON SMALL RODENTS IN THE TROPICAL RAIN FOREST OF NIGERIA

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Ecological research on African rodents in the last few years concentrated on geographical distribution, species composition, feeding preferences and reproductive biology (Delany 1972). The emphasis on these topics has been due to the relatively small amount of research on African rodents, the enormous variety of species, and the large size and ecological diversity of the African continent. Population studies have been almost entirely neglected, although there are some recent studies on population fluctuations, age structure of populations, and mechanisms for population regulation. In the arid zone, Poulet (1972) has described the population changes of *Taterillus pygargus* in Senegal, and Happold (1967) gave some data on the population structure of *Jaculus jaculus* at different times of the year in the Sudan. In the savanna, Anadu (1973) followed the population fluctuations of *Myomys daltoni* and *Mus musculoides* in the derived savanna of Nigeria, and Neal (1970) showed how the populations of several species in Uganda changed during the course of the year in relation to annual fires. Bellier (1967) in the Ivory Coast, and Dieterlen (1967) in the highland grasslands of Kivu (Zaire) have given data on biomass and how this changes during the course of the year. The only study of rodent populations in moist evergreen forest known to me is that of Delany (1971) who related the population structure of several species in Mayanga forest Uganda (annual rainfall 1250 mm) to variations in the reproductive rate. None of these studies lasted for more than three years. An obvious gap in our knowledge is how rodent populations in Africa (whether in rain forest, savanna or arid regions) fluctuate over long periods of time, and the magnitude of population changes.

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Earlier studies by the author in the lowland rain forest zone of western Nigeria established the species composition of small rodents at eight localities, and showed how rain forest species are unable to survive major changes in the rain forest environment (Happold 1975). Another study followed the reproductive cycles of several species during the course of the year, and related the rate of reproduction to seasonal changes in the environment (Happold 1974). Reproduction and growth of the commonest forest mouse, *Praomys tullbergi,* has been investigated (Happold, in press), and some information has been collected on other forest species (Happold, unpubl.). This paper describes the population dynamics of seven sympatric rodent species in a rain forest in western Nigeria over a period of eight years. Much of the paper is concerned with the commonest species, *Praomys tullbergi,* and the rarity of the other species prevents much comparison between species. However, the data on *Praomys* is sufficiently detailed to allow comparisons with the population dynamics of certain rain forest rodents in other continents, and with some African savanna and European temperate rodent populations.

The study area was situated in Gambari Forest Reserve (7° 09'N : 3° 54'E), approximately 20 km south of Ibadan in the Western State of Nigeria (fig. 1). This forest was chosen because it was part of a forest reserve and therefore protected to some extent from human interference. Earlier sampling in 1966-67

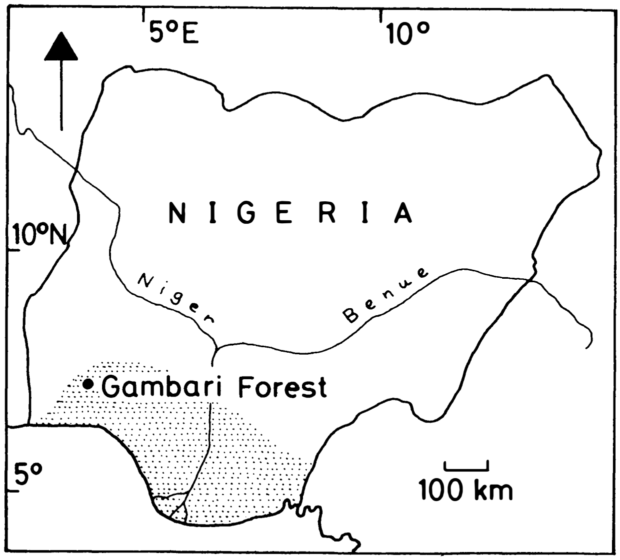

Fig. 1. — **Map of Nigeria to show the position of Gambari Forest. The shaded area indicates the extent of the lowland rain forest zone.**

showed that this forest possessed a large population of small rodents and that it would be suitable for a population study of several years duration.

I. METHODS

A square grid of 100 trap sites was laid out in ten rows of ten traps. Each trap in a line was 13.5 m from the next trap, and the lines were 13.5 m apart. The total area if each trap is assumed to be the central point of a 13.5 $\times$ 13.5 m square was 1.88 ha (4.7 acres). One Havahart No. 0 trap baited with a mixture of gari (cassava flour) and palm oil, was placed at each trap site ; these traps catch small mammals up to about 130 gm weight. Traps were not prebaited. The traps were set and baited in the late afternoon, and checked between 0700 and 1000 hours the following morning. They were removed after each trapping period.

From November 1967 to December 1970, traps were set for one night each week at weekly intervals. There were gaps in this programme in July, August and September 1968, and in July and August 1969. In July and August 1970 the population was sampled to record the presence or absence of previously marked animals, but new individuals in the population were not marked. In the second part of this study, from 1971 to 1975, the population was sampled for three consecutive nights in June and December each year. On five occasions, 62 traps were placed in a square around the grid at a distance of 100 m from the grid.

All the data in this study were obtained by the « capture-mark-and-release » technique. Each mouse and shrew was individually marked by a combination of ear holes and clipped toes, such that not more than one toe was clipped on each foot. Clipped toes healed completely within two weeks, and there did not appear to be any long-lasting adverse affects resulting from this procedure. Trapsite, weight, sex, reproductive condition, general health and injuries, and ectoparasites (if any) were recorded for each individual at each capture. Pregnancies were determined by palpitation and/or large changes in weight between weekly catches.

During the main study period from November 1967 to December 1970, there were 121 nights of trapping, 11,993 trap-nights and 9,908 effective trap-nights. The loss of about 2,000 trap-nights was due mainly to the effects of rainfall and other animals. On nights of high rainfall, many traps were closed by rain drops. However, because heavy rainfall rarely coincided with trapping nights, the adverse effects of heavy rain on trapping success were not large. Metal and plastic covers were used unsuccessfully a few times to protect some traps. Frequently traps were unavailable to catch small mammals because other animals were captured.

These included geckos, skinks and amphibians (Table I), millepedes (*Pachybolus ligulatus, Spirostreptus assiniensis, Spirostreptus* sp. (indet.), *Oxydesmus* sp.), grasshoppers (*Euthypoda acutipennis*) in all stages of development, giant snails (*Achatina* sp.), crickets *(Brachytryptes membranaceus)* and

Table I

The vertebrates of the study area, in addition to the small mammals listed in Table III. Other species, not recorded here, occur in Gambari Forest outside the study area.

AMPHIBIANS

Ranidae
- *Arthroleptis poecilonotus*
- *Phrynobatrachus calcaratus*
- *Phrynobatrachus aelleni*
- *Ptychadaena aequiplicata*
- *Ptychadaena longirostris*

Rhacophoridae
- *Leptopelis hyloides*

Bufonidae
- *Bufo regularis*
- *Bufo latifrons*

Pipidae
- *Xenopus tropicalis* (African clawed toad)

REPTILIA

Geckonidae
- *Hemidactylus fasciatus* (Banded gecko)
- *Hemidactylus muriceus*
- *Ancylodactylus spinicollis* (Hook-toed gecko)

Scincidae
- *Mabuya perroteti* (Orange flanked skink)
- *Mabuya maculilabris* (White - lipped skink)
- *Mabuya blandingi* (Blanding's skink)

Agamidae
- *Agama agama* (Rainbow lizard)

Viperidae
- *Causus rhombeatus* (Night adder)
- *Atheris chloraechis* (Green tree viper)

AVES. See Elgood and Sibley (1964)

MAMMALIA (see also Table III)

Rodentia
- *Funisciurus anerythus* (Striped squirrel)
- *Heliosciurus gambianus* (Tree squirrel)
- *Cricetomys gambianus* and/or *C. emini* (Giant pouched rat)
- *Thryonomys swinderianus* (Cane rat)
- *Atherurus africanus* Brush-tailed porcupine)

Chiroptera
- *Scotonycteris zenkeri* (Zenker's Fruit bat)
- *Megaloglossus woermanni* (African long-tongued fruit bat)

Hyracoidea
- *Dendrohyrax dorsalis* (Tree hyrax)

Canidae
- *Genetta pardina* (Forest genet)

Artiodactyla
- *Cephalophus maxwelli* (Maxwell's duiker)
- *Tragelaphus scriptus* (Bushbuck)

Sources of identification :

Amphibians : R. S. Oldham (pers. com.), Schiotz (1967).

Reptiles : Villiers (1963), Dunger (1968, 1972, 1973), R.R. Golding (pers. com.).

Birds : Elgood and Sibley (1964), Bannermann (1953), Mackworth-Praed and Grant (1970).

Mammals : Dekeyser (1955), Rosevear (1965, 1969), Happold (1973).

dung beetles (*Anachalos cupreus*). Other factors which reduced trapping efficiency were faulty trap setting, displacement of traps (by duikers and mongooses ?), and the presence of foraging driver ants (*Dorylus* sp.) which prevented the traps being set. Some small mammals were killed and eaten by driver ants after they had been captured in a trap.

The capture data for *Praomys tullbergi* and *Malacomys edwardsi* (but not for the other less common species) was tabulated on a " Calendar of Catches " (Petrusewicz and Macfadyen 1970). The population numbers of each species were assessed on a " known to be alive " basis. For any particular month, the individuals known to be alive and resident on the study area as revealed by the trapping data were 1) those individuals which were physically caught during the month, and 2) those individuals which were not caught but had been marked previous to the month and which were caught again subsequently. There are many difficulties in the interpretation of population numbers and home ranges from trapping due to trap-shyness, chances of trappability, movements of the individual which were not revealed by trapping, selectivity of traps in relation to species, sex and age of the individual, and the time of the year. Despite these difficulties, and as long as there are not large seasonal differences between the " known to be alive " population and the actual population, the " known to be alive " population reflects the population dynamics of the whole population.

Temperature and relative humidity records at 10 cm above the ground in the forest were recorded by a Casella thermohygrograph for a period of just over two years. The thermohygrograph was housed in a wire mesh container and covered with a doubly insulated white roof with a wide overhang beyond the wire mesh walls. The container was situated on the edge of the study area and was surrounded by herbs and grass of the E stratum (section IIe). Standard meteorological measurements, recorded in a Stevenson screen, were obtained from the Cocoa Research Institute of Nigeria Experimental Station at Gambari, about six kilometres north of the study area.

Leaf fall was measured at three sites within the study area from April 1968 to January 1971. A one metre square box, with 20 cm sides and a fine wire mesh floor raised 15 cm above the soil, was stationed at each site. The leaves in each box were collected at the end of each month, oven dried for 24 hours, and then weighed. The average dry weight of the leaves in the three boxes was used to determine the monthly leaf fall. Leaf litter on the ground was collected randomly at three one metre square sites each month from February 1970 to February 1971. Each leaf litter sample was processed in the same way as the leaf fall samples.

Much of the sorting and cataloging of the data from this study was done on the University of Ibadan computer.

II. THE ENVIRONMENT OF GAMBARI FOREST

a) Rainfall

The annual rainfall at the Cocoa Research Institute of Nigeria Experimental Station 6 km north of the study area during 1967 to 1975, ranged from 858 mm (33.7 ins) in 1972 to 1797 mm (70.7 ins) in 1968 (fig. 2), and the average was 1198 mm (47.2 ins). Rainfall during this period was lower than the long term average of 1240 mm (48.8 ins) per annum in Ibadan (Happold 1975). This was due mainly to the widespread drought throughout West Africa during 1970, 1971 and 1972, and the rainfall of only three years exceeded the long term average. The number of rainy days per annum ranged from 78 to 107 during the study period, and this was also less than the long term average of 122 days per annum (Happold 1975). Normally the months of highest rainfall had the largest number of rainy days.

The rainfall pattern during the year is typically bimodal with peaks of rainfall in June-July and in September-October (fig. 2).

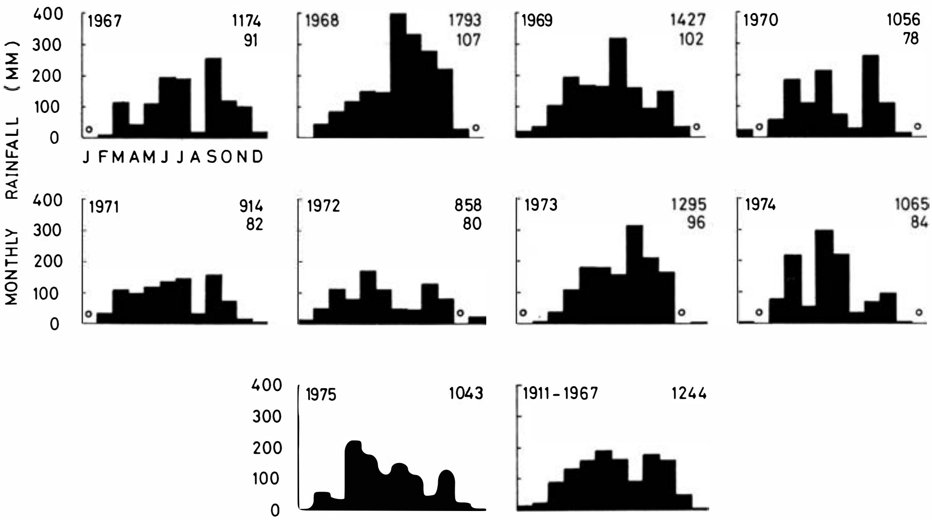

Fig. 2. — The rainfall at the Cocoa Research Institute of Nigeria Experimental Station at Gambari, 6 km north of the study area, from 1967 to 1975 and the long-term average rainfall at Ibadan from 1911 to 1967. Each histogram records the monthly rainfall in mm from January to December each year. The top figure on the right of each histogram shows the annual rainfall in mm, and the lower figure shows the number of rainy days in the year.

However, this pattern is not constant as the " little dry season " may be one month earlier in July and in some years it is not clearly defined at all. The long dry season of three to four months extends from about November to February, and the length and severity of this dry season varies from year to year. During the dry season, the monthly rainfall is usually less than 25 mm (1 in) and often much less. In years when there is a high rainfall at the beginning of the wet season followed by several months of less rainfall (as in 1967, 1970 and 1974), a trimodal pattern of rainfall is evident.

b) Temperature

General information on the temperature patterns in the rain forest zone of western Nigeria are given by Evans (1939), Happold (1975) and Richards (1952). At the Cocoa Research Institute of Nigeria Experimental Station at Gambari the annual and monthly temperature patterns remained very constant during 1967 to 1975 (Table II). In a typical year, say 1969, the mean monthly maximum is about 31.8°C and the mean monthly minimum is about 21.0°C. The hottest months of the year are at the end of the dry season (February and March) with mean monthly maxima of about 35-36°C. During the wet season, mean monthly maxima are lower and are usually in the range of 30°C to 32°C. In months of very heavy rain, as in July 1969, the mean monthly maxima drop to 27-28°C. The monthly minima remain fairly constant from month to month at about 20-21°C, although they may rise to about 22-23°C when the dry season is particularly hot. During the dry season, there is a range of about 13 degrees between the monthly maxima and minima, and in the wet season this range is reduced to about eight degrees. These temperature patterns, in combination with the high rainfall and high relative humidity, result in a climate that is warm and humid all the year except during the three to four month dry season.

In any particular month throughout the study period, the mean monthly maxima and mean monthly minima did not vary greatly from year to year. In October, for example, the mean monthly maxima ranged from 29.4°C to 32.2°C, and the mean monthly minima ranged from 20.0°C to 22.2°C ; equivalent figures for May are 28.9°C to 33.3°C and 20.5°C to 21.6°C.

c) Relative humidity

The relative humidity remains high for most of the year. At the Cocoa Research Institute of Nigeria Experimental Station at Gambari the mean monthly relative humidity at 1000 hours local time ranged from 81 % to 90 %, and the mean monthly relative humidity at 1600 hours local time ranged from 45 % to 65 % during

Table II

The monthly mean maximum and minimum temperatures in degrees Centigrade, from 1967 to 1975, at the Cocoa Research Institute of Nigeria Experimental Station at Gambari, approximately six kilometres north of the study area. The temperatures were originally recorded in degrees Fahrenheit.

	1967		1968		1969		1970		1971		1972		1973		1974		1975	
	Mean Max	Mean Min	Mean Max	Mean Min	Mean Max	Mean Min	Mean Max	Mean Min	Mean Max	Mean Min	Mean Max	Mean Min	Mean Max	Mean Min	Mean Max	Mean Min	Mean Max	Mean Min
January	33.8	15.6	32.2	20.5	31.6	20.0	33.3	20.5	33.3	20.0	34.4	21.1	34.9	21.1	32.7	18.9	34.4	16.7
February	36.1	22.2	34.9	21.1	36.1	22.2	33.8	21.6	34.9	21.1	34.9	21.6	34.9	23.8	32.7	21.1	34.4	19.4
March	35.6	22.2	31.6	21.1	34.9	21.6	35.6	21.1	34.4	21.1	33.8	21.6	35.6	21.6	35.6	22.2	34.4	21.6
April	33.8	21.1	32.7	20.0	32.7	21.6	33.3	21.6	33.3	21.1	32.7	20.5	33.8	22.2	33.3	21.6	33.8	20.5
May	33.3	21.1	31.6	20.5	32.7	21.1	32.7	21.1	33.3	21.1	32.2	20.5	32.7	21.6	28.9	21.6	32.2	20.5
June	30.0	20.0	30.0	21.1	31.1	21.1	32.2	20.5	31.6	21.1	31.1	20.5	31.6	21.1	31.6	21.1	30.0	22.2
July	27.8	20.5	29.4	21.6	27.2	21.6	29.4	20.5	28.9	20.0	30.0	21.1	30.0	21.1	29.4	21.1	28.9	21.1
August	27.8	20.0	29.4	21.6	30.0	21.1	27.8	21.1	28.3	21.6	29.4	21.1	29.4	21.1	29.4	21.6	28.3	20.5
September	28.3	20.5	30.5	20.5	30.0	21.1	29.4	21.1	29.4	20.0	30.5	21.1	28.3	23.6	29.4	21.1	28.9	20.0
October	31.1	20.5	31.6	20.5	31.1	20.0	31.6	20.5	32.2	20.5	30.5	22.2	-	-	29.4	21.6	31.1	20.5
November	31.6	20.5	32.7	21.1	32.2	20.0	33.3	21.6	33.8	20.5	33.3	21.6	33.3	20.0	32.7	21.1	30.0	20.5
December	32.2	20.0	31.1	20.5	32.2	21.1	33.3	19.4	33.3	16.1	33.8	20.0	33.3	20.5	34.9	19.4	32.7	18.3
Annual means	31.7	20.4	31.4	20.8	31.8	21.0	32.1	20.9	32.2	20.4	32.2	21.1	32.5	21.6	31.6	21.0	31.8	20.1

the dry season, and 70 % to 80 % for the remainder of the year. Occasionally the relative humidity drops below 45 % when harmattan winds are blowing from the north in the dry season, and during rain storms the relative humidity rises above 90 %.

d) Climate in the rain forest close to the ground

The figures quoted above do not indicate the climate close to the ground in the forest which is experienced by small terrestrial mammals. The temperature at 10 cm above the ground in the forest (see Methods) is even more uniform than that of the forest zone as a whole (fig. 3) due to the shading effects of the dense upper layers of the forest, especially in the wet season. Typical days have a temperature range of 21-25°C in the wet season, and 23-31°C in the dry season. The relative humidity remains high and fairly even during the day and night in the wet season although there are greater fluctuations in the dry season. Typical days have a relative humidity of over 90 % throughout the 24 hours in the wet season, and a range of 60-90 % in the dry season.

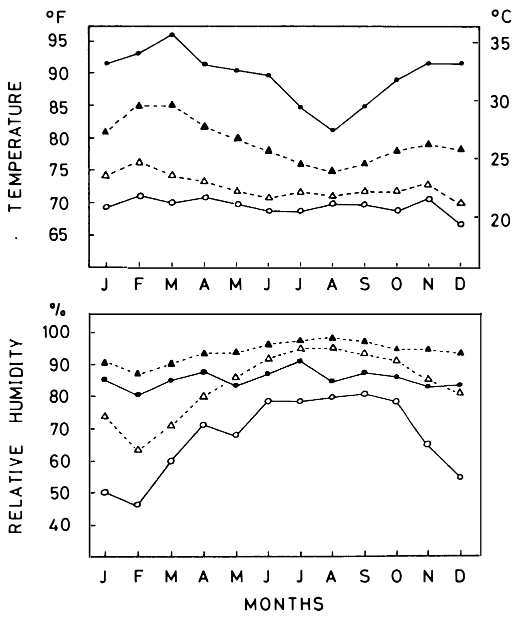

Fig. 3. — The temperatures and relative humidities 10 cm above the ground in Gambari Forest (broken line) and in the open at the Cocoa Research Institute of Nigeria Experimental Station at Gambari (unbroken line) during 1969. Closed symbols record the mean monthly maxima and open symbols record the mean monthly minima.

e) The vegetation of Gambari forest

Gambari forest is classified as moist semi-deciduous forest and is situated near the north-west limit of the rain forest zone in western Nigeria. Although most of the tree species are deciduous, they lose their leaves at different times of the year, and since the majority of trees in any month possess leaves, the forest always looks green and leafy (fig. 4). The forest is clearly stratified into A, B, C, D and E stories or strata, with the tallest emergents in the A stratum reaching heights of over 36 m (120 ft). The B stratum trees are 15-36 m (50-120 ft) tall, and form a broken upper canopy of fairly narrow crowns. The C stratum is the lowest tree stratum and it contains many species which are usually 8-15 m (25-50 ft) tall. The D stratum (1-8 m) consists mostly of shrubs and some young trees typical of the C stratum. These usually form a rather open structure although in some localities many shrubs and trees interwine to form a tangled mass. The ground layer or E stratum consists of dicotyledonous herbs, a few species of grasses, ferns and seedlings. The E stratum is not more than one metre high, and the density of the plants is normally low except where there is a break in the canopy and light reaches the ground.

The characteristics of the E stratum are especially important to small terrestrial mammals. In the western part of the study area where the upper strata were particularly dense, the herbs, grasses and ferns of the E stratum were small and sparse. Slender stems of D stratum plants (up to 3 cm in diameter) passed through the E stratum and were used by those rodents which climbed above the ground (section III). At the eastern end of the study area, the D stratum was less dense and consequently the E stratum herbs grew rampantly. Three species, *Cyathula achyranthoides, Polyspatha hirsuta* and *Pollia condensata,* which grow up to 60 cm high, formed particularly dense patches. Trees fell very rarely, and because termites, cryptozoa and fungi were abundant in the humid conditions, fallen trees decayed within a few years. Consequently there were few logs and branches on the ground. There were many cracks and crevices in the soil around the buttress roots of the tallest trees. These appeared to lead into larger crevices under the bases of the trees, and were used as domiciles by some of the rodents. The spatial pattern and number of these buttress roots with crevices may be an important factor determining the availability of domiciles for some species of rodents. Flowers and fruits fell from the upper strata to the ground particularly during the dry season, and like leaf-fall (section If), the abundance of fruit and flowers varied from month to month. This was not quantified, but it is likely that the pattern of fruit and flower fall in relation to rainfall is similar to that of the rain forest in Gabon, as described by Charles-Dominique (1971).

a

b

Fig. 4 a-b. — The study area in Gambari Forest. a) General view of the forest with buttress roots, climbers, and the vegetation of the E and D strata. b) A more open region with C and D strata trees growing through the lower vegetation.

c

d

Fig. 4 c-d. — The study area in Gambari Forest. c) Leaf litter on the ground in the dry season near a trap site. d) A patch of herbaceous plants, the preferred habitat of *Lophuromys sikapusi.*

e

Fig. 4 e. — The thermohydrograph container which recorded the climatic conditions 10 cm above the ground.

At Gambari forest, the area selected for this study was situated within the " *Mansonia* experimental plot ". Selected felling occurred between 1899 when the forest was proclaimed a forest reserve, and 1930 when the *Mansonia* experiments began. In May 1930, the lower layers of the forest were partially cleared, the soil was hoed, and seeds of potentially valuable timber species, *Mansonia altissima, Chlorophora excelsa, Khaya grandifolia, Terminalia ivorensis* and *Holoptelea grandis* were broadcast on the ground (MacGregor 1934). The first two species grew well, but the others appeared only in small numbers or not at all. In 1931, the canopy was cleared still further to allow more light onto the forest floor, and this stimulated increased seed germination especially of indigenous species. There has been no cutting or large scale disturbance to the study area since about 1932 (i e 35 years before the present study was begun). The study area can certainly not be considered as primary forest, as it has been altered considerably by mans' activities. However, the structure and floral composition (apart from the abundance of *Mansonia*) is very varied, and the study area was considered a good example of secondary forest in western Nigeria. Much of Gambari forest was used for shifting cultivation prior to 1899, but the long term effects of this are hardly visible at the present time. A few palms (*Eleis guineensis*) and African Wood-oil-nut trees (*Ricinodendron heudelotii*) in the forest indicate human activities in the past (MacGregor 1934).

The common plant species in Gambari forest are listed in the Appendix ; more detailed accounts of the vegetation and vegetation structure of rain forest in western Nigeria are given by Evans (1939), Richards (1952), Hopkins (1962, 1965), and Longman and Jenik (1974).

f) Soil and leaf litter

During the wet season, earthworms (*Hyperiodrillus africanus*) made numerous casts on the ground. These casts were up to 6 cm tall and 1.5 cm in diameter and they made the ground very uneven. Most casts disintegrated during the dry season, and no new casts were made at this time of the year.

Leaf fall occurred throughout the year (fig. 5), with the largest falls during the dry season (November to February) and the smallest falls during the months of heaviest rainfall. The average annual leaf fall (excluding large broken petioles and twigs) was 800 gm dry weight/m^2 or 8,200 kg/ha/year. These figures are slightly higher than the figures recorded by Madge (1965) in a neighbouring forest. The leaf fall varied greatly in different parts of the forest depending on the tree species, the size of the leaves, and the period of the year when each individual tree lost its leaves. The amount of leaf litter on the ground (fig. 5) depended on the ratio of the leaf fall to the rate of leaf decay. In the study area, the maximum weight of leaves on the ground was recorded in the dry season when the leaf litter was up to 6 cm deep. The leaves

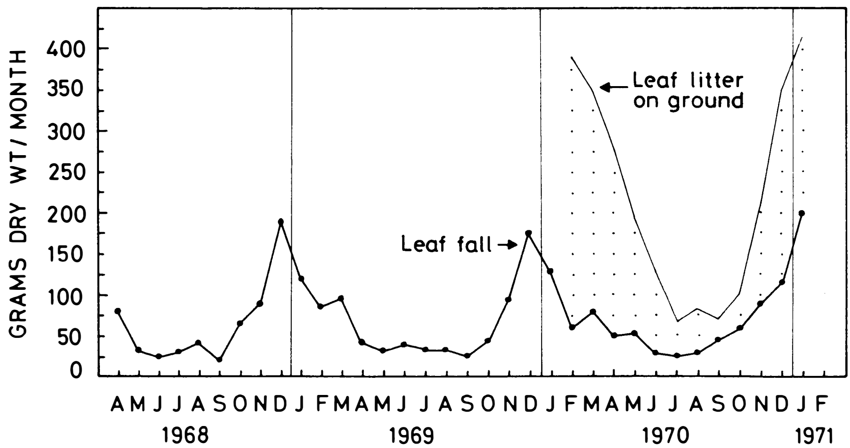

Fig. 5. — The average monthly leaf fall, and leaf litter on the ground, in Gambari Forest. Leaf litter accumulates on the ground during the dry season due to high leaf fall and reduced leaf decay, and leaf litter decreases during the early and middle wet season due to reduced leaf fall and a high rate of leaf decay. The shaded area indicates the difference between leaf fall and leaf litter each month.

decayed most rapidly at the time when the leaf fall was minimal, and therefore the leaf litter gradually decreased during the months of heaviest rainfall.

The earthworm casts and the density of leaf litter impeded the movement of small mammals during the dry season, but the leaf litter gave them cover and protection. When the leaf litter was thick, many rodents hid and lay still among the leaves when they were released from traps. When there was little leaf litter, they usually ran and disappeared into crevices under buttress roots.

g) Disturbances in the study area

There were regular and predictable seasonal changes in the climate, vegetation, leaf litter, earthworm casts and falls of leaves, flowers and fruits. There were also a few tree falls during storms in the wet season. However, there were three unexpected disturbances during the study period which may have affected the population of rodents. Firstly, in the dry season of 1968-69, part of the forest 150 m west of the study area was cleared to make a teak plantation. In 1970-71 another part of the forest 150 m north of the study area was partly cleared. Both clearings may have affected the movement of rodents into and out of the study area since most species of rain forest rodents are unable to survive in areas which have been cleared (Happold 1975).

Secondly, in 1968 a track about 8 m wide was cleared through the study area along one line of traps by an unauthorized wood-cutter. Most of the E and D strata were removed, but no large trees were cut and the damage was localized. The E stratum plants regenerated within two years and the effects of the damage were barely noticeable.

Thirdly, a fire of unknown cause in the leaf litter destroyed the litter, E stratum plants and small D stratum plants on about 44 % of the study area in March 1973. This very unusual event was due to the extreme dryness of the forest after the low rainfall of 1972 and the four months of drought during the 1972-73 dry season. The mosaic of burnt and unburnt areas was still evident in late 1974 : the burnt areas had less leaf litter and fewer plants in the D and E strata. This disturbance was associated with a marked decrease in the rodent population (section XI).

h) Other vertebrates in gambari forest

Many other species of vertebrates live in the study area besides the species of rodents and shrews which were the subject of this study. The presence of other vertebrates was ascertained by trapping, mist-netting (bats) and observation, and from hunters'

TABLE III

The species and species composition of small rodents and shrews in Gambari Forest, Nigeria (1967-1970). The numbers indicate the number of individuals of each species caught during each year.

Species	1967	1968	1969	1970	Total	Percent of total rodents	Percent of total rodents and shrews
Praomys tullbergi (Thomas) 1894	37	124	100	104	365	75.7%	62.6%
Malacomys edwardsi Rochebrune 1885	9	16	11	14	50	10.4	8.6
Hylomyscus stella (Thomas) 1911	1	9	12	5	27	5.6	4.6
Lophuromys sikapusi (Temminck) 1853	0	2	8	4	14	2.9	2.4
Stochomys longicaudatus (Tullberg) 1893	3	2	2	3	10	2.1	1.7
Mus musculoides Temminck 1853	0	4	0	4	8	1.7	1.4
Hybomys trivirgatus (Temminck) 1893	0	3	5	0	8	1.7	1.4
Crocidura poensis*	0	4	7	5	16	-	2.7
Crocidura crossei	3	9	10	18	40	-	6.9
TOTALS	53	173	155	157	538	-	-

Total rodents	482
Total shrews	56
Total rodents and shrews	538

Rodent nomenclature from Rosevear (1969)

* One individual may have been Crocidura manni

catches in neighbouring parts of the forest (Table I). Nine species of amphibians were caught in mouse traps, although many other species also occur in Gambari forest (Oldham pers. comm.). Skinks and geckos were also caught frequently, but rainbow lizards (*Agama agama*) and snakes were rarely caught. Snakes were probably more common than the records indicate. The bird life of Gambari forest is particularly rich and has been well documented by Elgood and Sibley (1964).

III. SPECIES COMPOSITION AND NUMBERS

Seven species of murid rodents and two species of shrews were found in the study area (Table III, fig. 6). Tullberg's mouse, *Praomys tullbergi* (Thomas), was the most numerous species, comprising 75 % of the trappable small rodent fauna. The long-footed swamp mouse, *Malacomys edwardsi* Rochebrune, formed 10 % and the other five species comprised only 15 %. The reliability of these percentages is considered to be quite good except that the abundance of *Hylomyscus stella* (Thomas) was probably underestimated because of its arboreal habits. Five of the species, *Praomys tullbergi, Malacomys edwardsi, Hylomyscus stella, Stochomys longicaudatus* (Tullberg) and *Hybomys trivirgatus* (Temminck), are true rain forest rodents which do not survive when rain forest is cleared. The other two species, *Lophuromys sikapusi* (Temminck) and *Mus musculoides* Temminck, were occasional invaders into the rain forest : *Lophuromys* is usually found in damp swampy regions where there is abundant grass cover, and *Mus* is a common savanna species which has invaded the forest zone as cultivation and clearing has increased (Happold 1975). *Hylomyscus* is the only arboreal species, although *Praomys* and *Malacomys* can climb to a limited extent. Other species of rodents known to occur in Gambari, such as the brush-tailed porcupine (*Atherurus africanus* Gray), the pouched rat (*Cricetomys gambianus* Waterhouse) and the striped squirrel (*Funisciurus anerythrus* [Thomas]), were not caught because they were too large to enter the Havahart No. 0 traps. Shrews (*Crocidura poensis* and *Crocidura crossei*) were not numerous, and formed only 9.6 % of the small mammals marked during the study. The composition of the small rodent fauna in Gambari forest was similar to that of other forests in western Nigeria (Happold 1975), which suggests that the study area is probably representative of all the forest zone of western Nigeria.

The sex ratios of trapped individuals did not vary significantly from a 1:1 ratio (P = 0.1), except for *Malacomys edwardsi* and *Lophuromys sikapusi* in which males significantly outnumbered females (Table IV). (The numbers of *Hybomys trivirgatus* were too small for a test of significance.)

a

b

Fig. 6 a-b. — Small mammals of Gambari Forest. a) *Praomys tullbergi* (adult weight 30-45 gm). b) *Malacomys edwardsi* (50-70 gm).

c

d

Fig. 6 c-d. — Small mammals of Gambari Forest.
c) *Hylomyscus stella* (17-25 gm) - d) *Lophuromys sikapusi* (50-70 gm).

e

f

Fig. 6 e-f. — Small mammals of Gambari Forest.
e) *Stochomys longicaudatus* (45-65 gm) - f) *Mus musculoides* (6-10 gm).

g

h

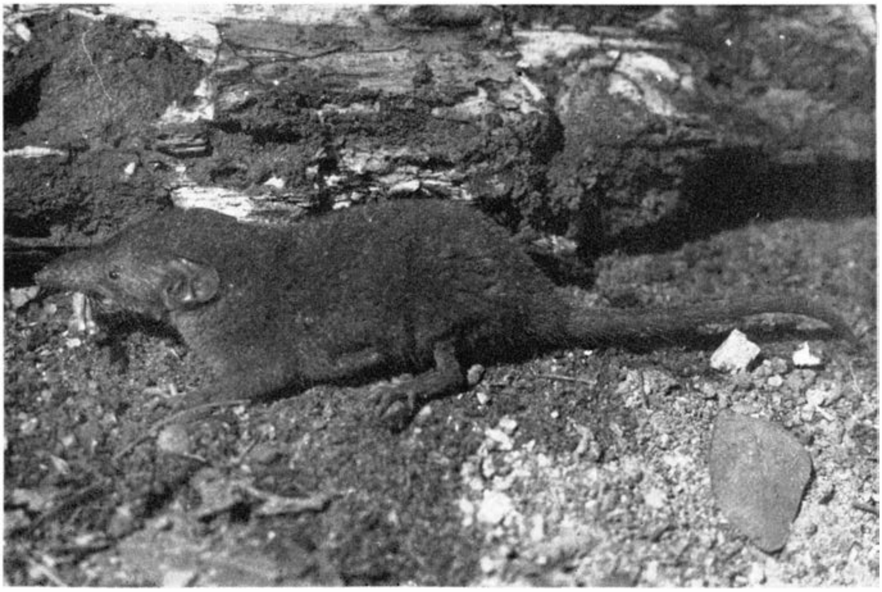

Fig. 6 g-h. — Small mammals of Gambari Forest.
g) *Hybomys trivirgatus* (50-65 gm) - h) *Crocidura poensis* (20-25 gm).

TABLE IV

Sex ratios of rodents in Gambari Forest (1967-1974).

Species	n	Males	Females	Ratio M : F
Praomys tullbergi	443	237	204	1:0.86
Malacomys edwardsi	59	37	22	1:0.59
Hylomyscus stella	32	15	17	1:1.13
Lophuromys sikapusi	22	15	7	1:0.47
Stochomys longicaudatus	12	6	6	1:1
Mus musculoides	21	12	9	1:0.75
Hybomys trivirgatus	8	3	5	1:1.66

IV. POPULATION FLUCTUATIONS 1967-1970

The total population varied from a minimum of 27 to a maximum of 66 animals (Table V). Although the maximum population was 2.5 times larger than the minimum, the average number of individuals per month remained fairly constant from year to year. These averages and the number of months on which they were based, are :

1967 (2 months) 40.0
1968 (9 months) 47.7
1969 (10 months) 44.4
1970 (9 months) 43.6

The fluctuations in the total population were largely dependent on the fluctuations in the population of the most numerous species, *Praomys tullbergi* (fig. 7a). The high and low population numbers of *Praomys* occurred at the same times as those of the total population, although this was not necessarily true for the other species. The populations of *Malacomys* fluctuated considerably (Table V), and even though the sample numbers were small, the figures suggest that the population of this species did not fluctuate in synchrony with that of *Praomys*. The populations of the six less common rodent species varied from 3 to 16 individuals per month.

The amount of information on the total population depends on the number of times and the frequency with which each individual was captured. The chances of being recaptured (one or more times) after marking varied from species to species. Using the data for the first 30 months of the study, the recapture rates (from highest to lowest) were *Praomys* 63 % (n = 310), *Lophuromys* 61 % (n = 13), *Malacomys* 60 % (n = 41), *Hybomys* 50 % (n = 8), *Stochomys* 30 % (n = 10), *Hylomyscus* 8 % (n = 26) and *Mus* 0 % (n = 8). The combination of large numbers and high recapture rate in *Praomys* has resulted in detailed information on this species, whereas information on the other species is incomplete.

Table VI records the residencies and number of captures for individual *Praomys tullbergi, Malacomys edwardsi, Lophuromys sikapusi* and *Stochomys longicaudatus* which were known to have lived on the grid for a long time. These figures show that the number of captures and length of residency is usually, but not always, closely correlated.

V. POPULATION DYNAMICS OF *PRAOMYS TULLBERGI*

a) Population fluctuations 1967-1970

The population numbers of *Praomys tullbergi* ranged from a minimum of 18 to a maximum of 52 (Table VII). The maximum population was thus 2.9 times larger than the minimum population. Apart from 1967 when there were only two months of trapping, the average numbers of individuals/month on the study area were fairly constant from year to year. These averages, and the number of months on which they are based, are :

1967	(2 months)	28.5
1968	(9 months)	37.7
1969	(9 months)	34.7
1970	(9 months)	30.3

The ratio of males to females varied each month (Table VII) although the ratio did not vary significantly over the whole study period (section III).

For each month, the calendar of catches (Table VII) indicates the number of individuals which were captured, as well as those known to be alive but which were not caught in that month. Of the total number of individuals known to be alive each month, the percentage which were actually caught ranged from 36 % to 100 %, with an average of 86 %. Thus the large majority of individuals were caught each month. The percentages for March each year were particularly low (36 %, 55 %, 62 %) and the individuals which were known to be alive but which were not caught included

TABLE

The numbers of individuals known to be alive each month. Individuals which were not caught in a particular month,

See text for

	1967								1968						
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan
Trap nights/month	5	2	3	4	3	3	4	2	0	0	0	5	4	3	4
Praomys tullbergi	31	26	33	38	22	52	51	36	-	-	-	33	41	34	34
Malacomys edwardsi	7	7	5	3	1	2	2	3	-	-	-	11	11	9	5
Hylomyscus stella	1	1	2	6	0	0	1	1	-	-	-	0	0	1	1
Lophuromys sikapusi	0	0	1	1	0	0	1	0	-	-	-	0	0	0	0
Stochomys longicaudatus	2	2	3	2	1	1	0	0	-	-	-	0	0	0	0
Mus musculoides	0	0	1	0	2	0	0	0	-	-	-	1	0	0	0
Hybomys trivirgatus	0	0	0	0	0	1	0	0	-	-	-	0	1	1	0
Crocidura poensis	0	0	1	0	1	0	1	1	-	-	-	0	1	1	1
Crocidura crossei	2	1	0	0	0	1	2	1	-	-	-	3	2	0	0
Monthly totals	43	37	46	50	27	57	58	42	-	-	-	48	56	46	41

males and females of C. D and E age-weight classes (section Vb). The reasons for the low capture rate in March are unknown.

The numbers of *Praomys tullbergi* in the study area fluctuated around a mean of 33.8 individuals. The fluctuations did not depart more than 18 from the mean, and there were three peaks in population numbers each year (fig. 8).

1) The first peak occurred in January or February, and was due mostly to the recruitment of young born at the beginning of the dry season.
2) The highest population numbers were normally in April or May, although this peak was one month later than normal in 1969. This peak was due mostly to the recruitment of young animals which were born at the end of the dry season (section V f).

V

but were known to be alive due to subsequent recapture, are included in the number for each month.

further details.

1969											1970											
Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4	3	4	3	5	0	2	3	5	4	3	6	4	4	4	5	4	2	1	3	4	4	2
41	27	34	33	46	(27)	(27)	33	48	27	22	31	23	29	39	48	37	26	15	18	26	23	17
2	2	2	2	2	-	-	1	6	6	4	5	4	3	8	6	6	3	2	2	0	1	1
2	1	2	1	2	-	-	1	6	1	1	3	0	3	0	0	0	0	0	0	2	1	1
0	0	0	2	2	-	-	2	3	3	2	3	3	2	4	4	3	2	2	2	1	2	1
0	0	0	0	2	-	-	1	1	1	1	2	1	2	1	2	2	1	1	1	1	1	1
0	0	0	0	0	-	-	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0
0	0	0	0	0	-	-	0	0	1	5	3	1	1	1	1	1	1	1	1	1	1	0
1	1	3	4	3	-	-	0	0	0	0	0	0	2	0	0	1	0	0	0	1	0	1
2	1	1	2	1	-	-	0	2	0	1	1	1	1	1	3	2	1	1	3	6	1	3
48	32	42	44	58	-	-	38	66	39	36	48	33	45	56	64	52	(34)	(22)	27	38	30	(25)

3) The third peak occurred in October or November. This was due mostly to the recruitment of young born during the middle of the wet season (August-September).

b) Population structure

The composition of the population each month, in terms of how long the individuals had survived in the population, can be determined from fig. 8 and table VII. For example, the population in November 1968 was composed of 19 individuals marked in November, 10 marked in October, 8 marked in April, and one each marked in February, May, June and in the previous November. Every month there was a loss of individuals, some of which had been resident in the population for many months. The composition of the population, in this respect, depended greatly on the number

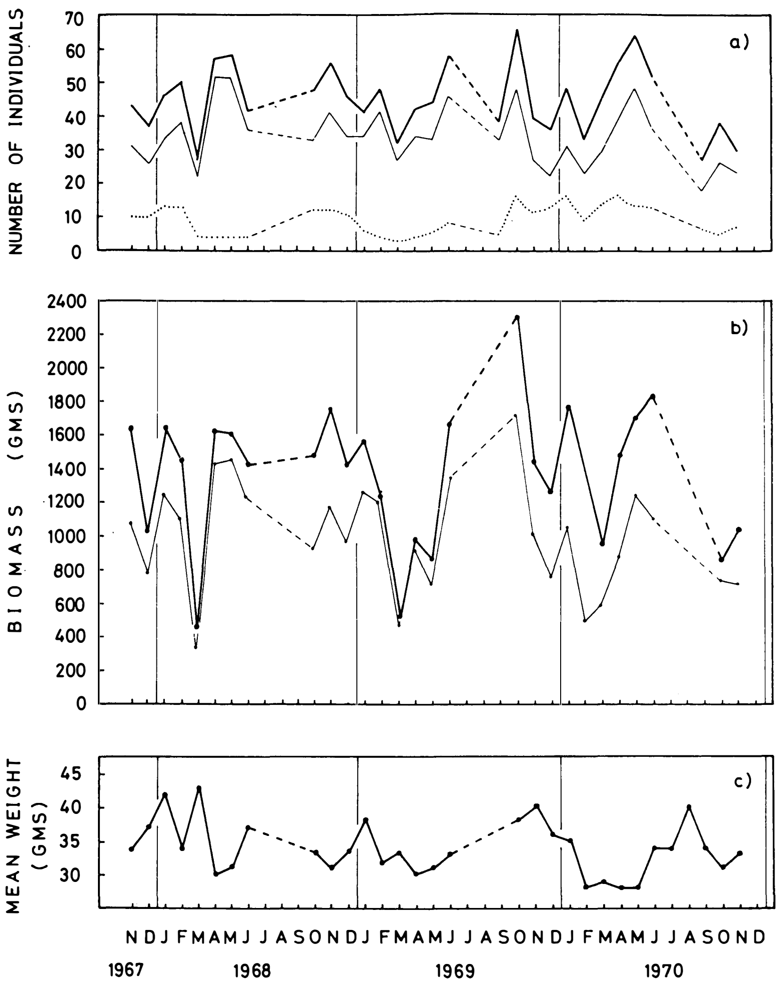

Fig. 7. — Population parameters of small mammals in the 1.88 ha study area in Gambari Forest from November 1967 to December 1970. Months when there was no sampling are indicated by broken lines. a) The monthly fluctuations in the numbers of the total small mammal population (thick line), *Praomys tullbergi* (thin line), and the eight other species (dotted line). b) The monthly biomass (gm) of the total small mammal population (thick line) and *Praomys tullbergi* (thin line) in the study area. c) The mean monthly weights of *Praomys tullbergi.*

TABLE VI

The numbers of captures and length of residency for some individuals which were resident on the study area for long periods of time.

Species	Individual number and sex	Number of captures	Residency (days)
Praomys tullbergi	♀ 328	44	457
	♀ 260	38	416
	♂ 35	34	510
	♂ 400	32	366
	♀ 138	31	619
	♀ 384	31	287
	♂ 269	30	538
	♂ 144	13	620
Malacomys edwardsi	♀ 7	11	113
	♂ 418	11	124
	♂ 5	9	226
	♂ 206	9	77
	♀ 212	9	90
	♀ 456	9	237
Lophuromys sikapusi	♀ 410	19	164
	♂ 430	13	213
	♀ 544	11	210
	♂ 454	9	178
Stochomys longicaudatus	♀ 365	12	745
	♂ 10	5	169
	♂ 561	3	43

of individuals entering the population each month. Some individuals of each monthly cohort formed part of the population many months later, and the size of each monthly cohort determined the proportion of that cohort in the population in subsequent months.

The exact ages of individuals in the population were not known, but an indication of the population age structure was obtained by dividing the population into five age-weight classes (fig. 9). Each class was aged roughly from growth studies in the laboratory (Happold in press) (Table VIII). The population each month contained representatives of most of the age-weight classes. The numbers of class A individuals were underestimated because very few of them had entered the trappable population. Classes B and C were important components of the population at the beginning of the wet season (April, May and June) and again

TABLE VII (a, b, c)

Calendar of catches for Praomys tullbergi *(1967-1970).*

Table 7a 1967-68

	1967		1968											
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
New individuals	31	6	12	16	0	33	15	7	-	-	-	19	19	2
Total individuals	31	26	33	38	22	52	52	36	-	-	(14)	33	41	34
males	18	18	22	22	14	29	26	19	-	-	(6)	16	22	18
females	13	8	11	16	8	23	25	17	-	-	(8)	17	19	16
Individuals lost since previous month	0	11	5	11	16	3	16	21	-	-	-	22	11	9
Individuals trapped in month	31	23	29	31	8	47	46	33	-	-	-	27	39	30
Monthly survival rate	-	0.64	0.80	0.66	0.57	0.87	0.70	0.60	-	-	-	-	0.66	0.80

- = No trapping and no definite information.

Brackets indicate numbers of individuals for which information is available during months when there was no trapping.

Table 7b 1969

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
New individuals	7	15	5	14	8	16	-	-	7	21	1	6
Total individuals	34	41	27	34	33	46	(27)	(27)	33	48	27	22
males	19	20	14	19	16	27	14	14	17	31	14	10
females	15	21	13	15	17	19	13	13	16	17	13	12
Individuals lost since previous month	7	8	18	7	9	3	19		-	6	22	11
Individuals trapped in month	31	39	15	30	21	39	-	10	25	43	25	20
Monthly survival rate	0.80	0.76	0.56	0.74	0.73	0.91	-	-	-	0.82	0.54	0.60

- = No trapping and no definite information.

Brackets indicate numbers of individuals for which information is available during months when there was no trapping.

Table 7c 1970

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
New individuals	14	11	12	18	15	7	-	-	4	12	7	3
Total individuals	31	23	29	39	48	37	(26)	(15)	18	25	23	17
males	16	10	17	24	27	23	15	9	9	13	10	8
females	15	13	12	15	21	14	11	6	9	12	13	9
Individuals lost since previous month	5	19	6	8	6	18	(11)	(11)	2	5	9	9
Individuals trapped in month	29	18	18	32	43	32	15	5	10	21	21	16
Monthly survival rate	0.73	0.39	0.78	0.72	0.85	0.62	-	-	-	0.72	0.64	-

- = No trapping and no definite information.

Brackets indicate numbers of individuals for which information is available during months when there was no trapping.

at the end of the wet season (November). Class D, and to a lesser extent class E, were the most commonly represented classes at other times of the year, especially during the dry season (January-February) when there were few, if any, young individuals in the population. The numbers of individuals in class D dropped at the end of the dry season (March) as did the population numbers as a whole (Table VII, fig. 9). These data show that the population structure tended to remain fairly constant from month to month, with slight seasonal shifts in the frequency of each age-weight class. There were no times of the year when the population was dominated totally by young, by adults, or by very old individuals. This structure occurred because during each month of the year individuals of most age-weight classes were recruited through immigration and birth (section V f), and individuals of most age-weight classes were lost (section V d).

c) Survival of individuals in the population

The " Calendar of catches " (Table VII) shows that each month new mice entered the population, and other mice left the population so that there was a continuous turnover of individuals. The average survival of an individual has been calculated using the 316 individuals (regardless of sex and age) which entered the population from November 1967 to April 1970 (fig. 10). The average survival after the first capture was 0.53 after one month, 0.38 after three months, 0.20 after five months, and 0.11 after eight months. Thus there was about a 1:1 chance of an individual remaining

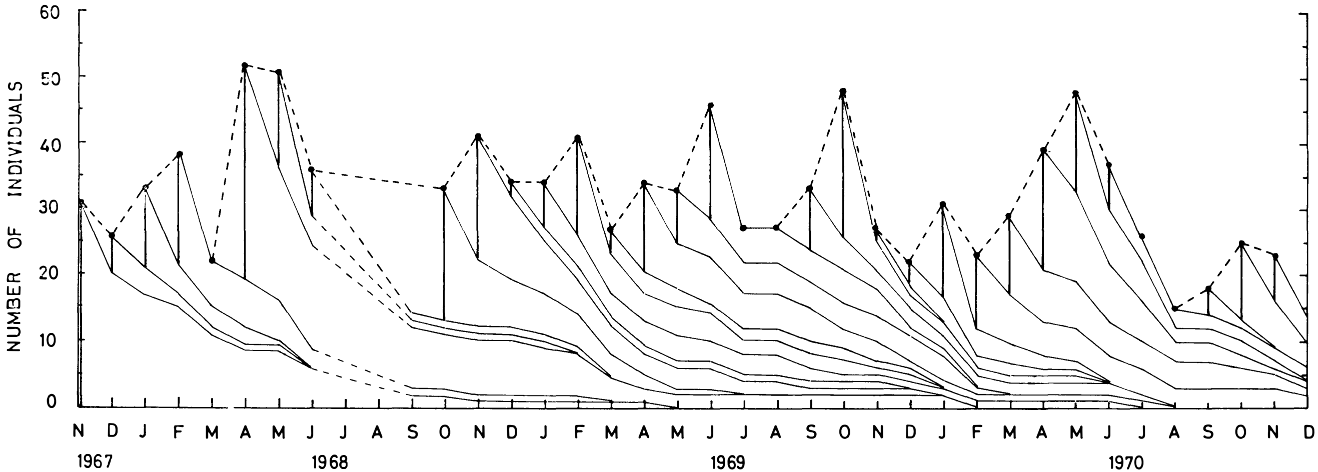

Fig. 8. — The monthly population fluctuations of *Praomys tullbergi*. The figure for each month is the « known to be alive » population number (see also Table VII). For each month, the new monthly cohort is shown by a thick vertical line and the size of the cohort in subsequent months is shown by the thin lines. The population each month is composed of individuals of the new cohort and individuals which have remained from cohorts of previous months. The broken line joining the monthly totals emphasises the population fluctuations, and the broken lines in July, August and September 1968 indicate months when there was no sampling.

TABLE VIII

Age-weight classes of Praomys tullbergi.

Class	Weight (gms)	Approximate age	Reproductive condition
A	less than 14	less than 1 month	Immature
B	15 - 24	1 - 2 months	Immature
C	25 - 34	3 - 4 months	Subadults, mostly immature
D	35 - 44	more than 4 months	Mature
E	more than 44	more than about 6 months; up to 18 months	Mature ; heaviest individuals tend to be the oldest

in the population for one month or more ; this was due, mainly, to the large proportion of " non-resident " individuals (see below) which were caught once only and thereafter were presumed to have left the study area. Fig. 10 also shows that 83 % of the population was replaced every six months. However, of the remaining 17 %, some individuals survived as long as 18 months (Table VI). There appeared to be very little difference between the survival rates of young individuals weighing 30 gm or less when first marked, and those which entered the population when over 30 gm in weight. The average survival of 186 young individuals was 0.52 after one month, 0.29 after three months, 0.20 after five months, and 0.11 after eight months.

The animals were classified into three categories based on the length of their residency in the study area.

1) " Residents " were individuals which were caught in the study area for two or more months. This category comprised 38.6 % of the population.
2) " Semi-residents " were individuals which were caught more than once, but which survived in the study area for less than two months. This category comprised 24.7 % of the population.
3) " Non-residents " were individuals which were caught once only. These individuals may have been dispersing, or they may have been residents outside the study area whose home ranges overlapped the periphery of the study area. This category comprised 36.6 % of the population.

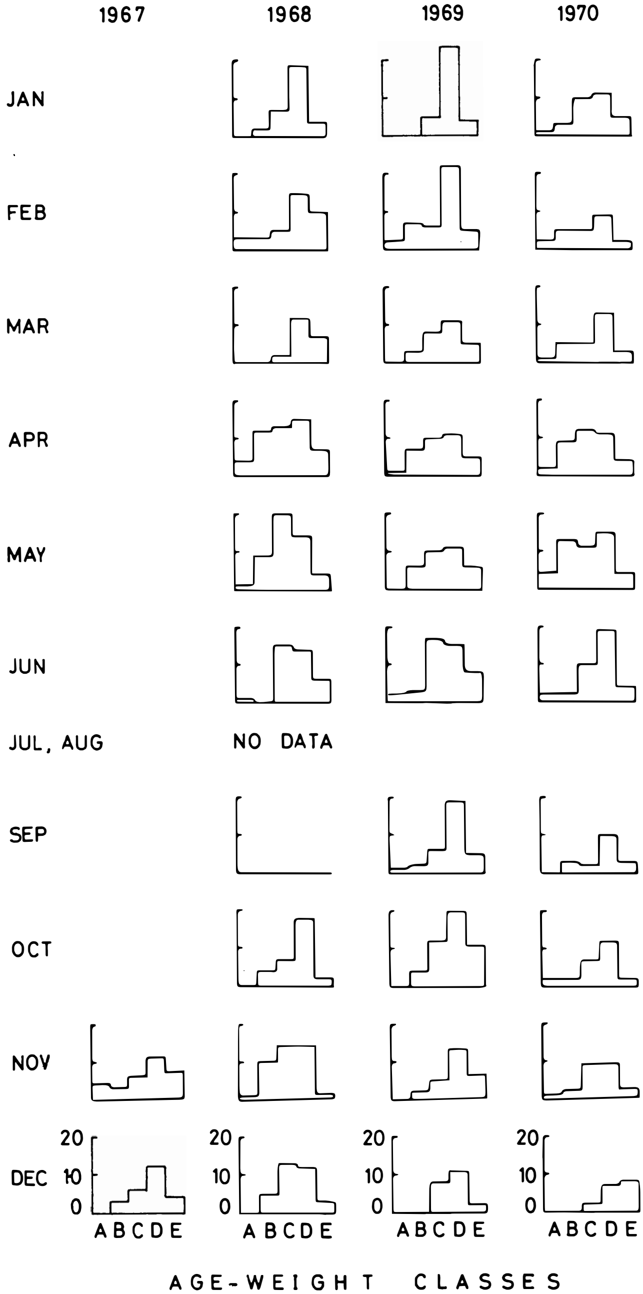

Fig. 9. — The age-weight structure of the population of *Praomys tullbergi*. The scale and position of each age-weight class is the same for each histogram, but full details are recorded only for the December histograms. No information is available for July and August each year, nor for September 1968. Details of each age-weight class are given in Table VIII.

" Semi-residents " and " non-residents " are assumed to be real categories and not just artifacts of trap-shyness. An analysis of residency showed that the number of individuals in each category fluctuated in most months, and there were some months when there were neither non-residents nor semi-residents (Table IX). The percentage of residents each month ranged from 63 % to 100 %. If these percentages were grouped into three-monthly averages, the residents comprised about 75 % of the population in the dry season (December to February), 80 % in the early wet season

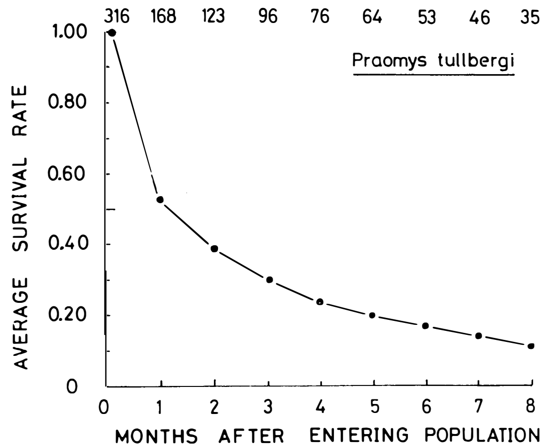

Fig. 10. — The average survival rate of *Praomys tullbergi* in the population after first capture. The sample number for each month is shown at the top of the graph.

(March to May) and 75 % at the end of the wet season (September to November). (The data are inadequate to calculate percentages for the middle of the wet season). These data showed that residents always comprised a large proportion of the population, in spite of the fluctuations in the size of the population (fig. 8). The individuals which formed the resident population changed from month to month, as indicated in the survival curve (fig. 10).

Little information was available on the non-residents except that they included both sexes and all age-weight classes. Non-resident individuals were found in most months of the year, and the highest numbers coincided with the highest peaks in population numbers. A total of 136 non-residents were recorded. To test if the distribution of these non-residents was random, the study area was divided into four concentric areas comprising (from outer to inner) 36, 28, 20 and 16 trap-sites. The observed and expected number of individuals in each area is shown in Table X, and a χ^2 test showed that the distribution of non-residents was not

TABLE

The numbers of resident, semi-resident and non-resident

	1967		1968													
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
Residents	17	21	24	27	22	37	37	28	-	-	-	22	29	30	32	30
Semi-residents	7	3	4	3	0	3	6	4	-	-	-	2	7	4	0	5
Non-residents	7	2	5	8	0	12	8	4	-	-	-	9	5	0	2	6
Totals	31	26	33	38	22	52	51	36	-	-	-	33	41	34	34	41
% Residents	55	81	73	71	100	71	73	77	-	-	-	66	71	88	94	73

random ($P = 0.01$). Non-residents were recorded more often than expected on a random distribution in the outer areas of the study area, and less often than expected in the inner areas. This suggests that some of the non-residents recorded in the outer areas were probably residents from neighbouring localities whose home ranges just overlapped with the outer areas of the grid. Furthermore, trapping results on the outside lines (see Methods) suggested that the non-residents were resident outside the study area and were not dispersing.

d) ANALYSIS OF INDIVIDUALS ENTERING AND LEAVING THE POPULATION

The number of new individuals gained, and the number of individuals lost from the population varied from month to month (fig. 11) and the frequency with which gains and losses alternated with each other, suggested that there was considerable mobility in the population. Only in months when gains greatly outnumbered losses, or when losses greatly outnumbered gains, were there conspicuous increases or decreases in the size of the population.

The number of new mice which entered each month varied from zero to 33 (Table VII, fig. 8), and the percentage of new mice in the population usually ranged from 20 % to 50 % (fig. 12). Lower percentages occurred in March 1968, December 1968 and November 1969, and higher percentages occurred in some months when there were many young in the population (April 1968, October 1968). The individuals gained each month represented most

IX

individuals of Praomys tullbergi *in the population each month.*

1969										1970											
Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
23	27	31	35	-	-	-	30	25	18	20	18	23	30	37	32	-	-	15	18	16	12
3	4	1	2	-	-	-	8	2	2	3	2	2	6	5	2	-	-	0	4	4	2
1	3	1	9	-	-	-	10	0	2	8	3	4	3	6	3	-	-	3	4	3	3
27	34	33	46	-	-	-	48	27	22	31	23	29	39	48	37	-	-	18	26	23	17
85	80	94	76	-	-	-	63	93	82	65	78	79	77	77	86	-	-	83	69	70	70

of the age-weight classes (Table XI) although A and E classes were poorly represented because these classes were uncommon in the trappable population as a whole. Young individuals in B and C classes were well represented in the middle of the dry season, and early wet season (April and May and extending into June in 1969), and in the late wet season (October to November), but they were uncommon at the beginning of the dry season. Class D individuals entered in most months with considerable variation from month to month.

The subsequent recoveries of new individuals also showed variation. During the period from November 1967 to November 1970, 360 individuals entered the population. Of these, 38.6 % became residents, 24.7 % became semi-residents and 36.6 % were non-residents. In most months, new individuals represented all three residence categories (Table XII), and the numbers in each category tended to increase as the total number of new individuals per month increased.

The age-weight structure of individuals that left the population showed that most age-weight classes were represented each month, with particular age-weight classes being more numerous in certain months (Table XI). Large numbers of young individuals (classes B and C) left the population in May and June, but many of these had only just entered the population. Adult mice (classes D and E) left throughout the year, but especially large numbers were lost during the dry season. The individuals lost each month represented all residence categories, and like the mice which

TABLE X

The observed and expected number (assuming a random distribution) of non-resident Praomys tullbergi *in relation to outer and inner regions of the study area.*

Divisions of study area	Number of traps in division	Expected number if random distribution (1.36 individuals per trap)	Observed number
Outer square	36	48.9	59
Outer middle square	28	38.0	41
Inner middle square	20	27.2	22
Inner square	16	21.7	14
Totals	100	135.8	136

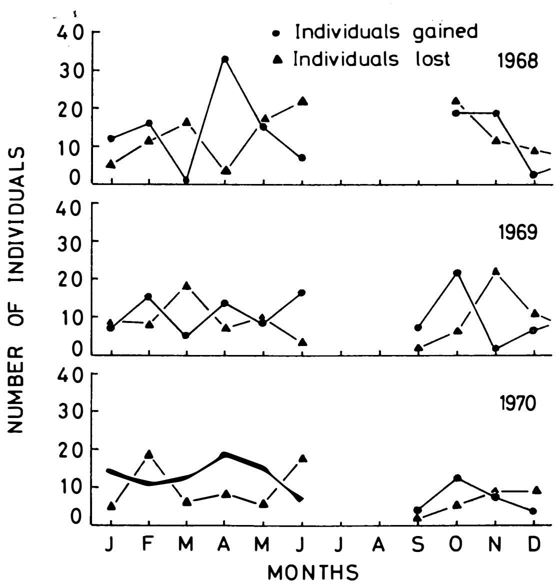

Fig. 11. — The numbers of individual *Praomys tullbergi* which were gained and lost each month. There was no sampling in July and August each year, nor in September 1968.

entered the population, the residencies of those which left varied from month to month (Table XII). During the period December 1967 to December 1970, 303 individuals left the population of which 40.6 % had been residents, 20.1 % had been semi-residents and 39.2 % had been non-residents. These percentages were similar to those of the individuals which had entered the population.

The general pattern was that new mice entered the population each month, they represented 20 % to 50 % of the monthly total,

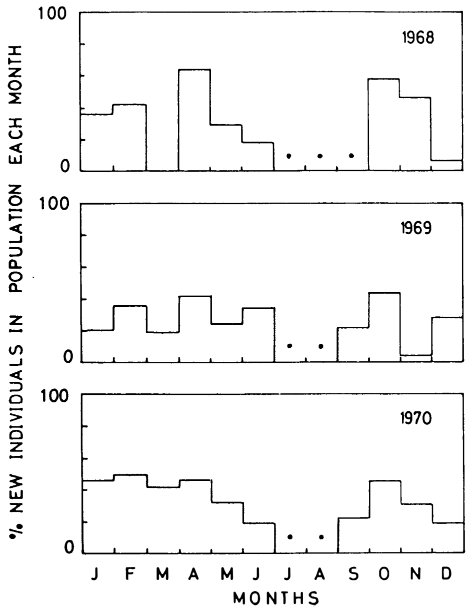

Fig. 12. — The percentages of new individuals of *Praomys tullbergi* in the population each month. The closed circles indicate months when there was no sampling.

they were distributed between all age-weight classes with seasonal shifts in the abundance of particular classes, and after entering the population the chances of an individual becoming a resident, semi-resident or non-resident were almost equal (39:25:36). A similar pattern was seen for individuals which left the population.

Using the figures for 1967-1970, the largest number of mice were gained in April (B and C classes), January and October (C and D classes), and the largest number of adults were lost in February and March, with additional high losses of both young and adults in June and November. There was no marked seasonal gain or loss of individuals of any particular age-weight class because of the more of less continuous breeding season, and the more or less continuous loss of individuals.

TABLE XI

The numbers and age-weight classes of individuals of Praomys tullbergi *which entered and left the population each month.*

Age-weight classes	ENTERED POPULATION						LEFT POPULATION					
	A	B	C	D	E	TOT	A	B	C	D	E	TOT
Nov 1967						*	–	–	–	–	–	–
Dec	0	1	2	2	1	6	3	1	2	2	3	11
Jan 1968	0	1	5	5	1	12	0	1	2	2	0	5
Feb	4	3	5	2	2	16	0	1	2	7	1	11
Mar	0	0	0	0	0	0	4	1	2	4	5	16
Apr	4	11	12	4	2	33	0	0	0	1	2	3
May	1	8	4	1	1	15	1	5	4	4	2	16
Jun	1	0	1	3	2	7	1	5	5	8	2	21
Jul	–	–	–	–	–	–	–	–	–	–	–	–
Aug	–	–	–	–	–	–	–	–	–	–	–	–
Sep	–	–	–	–	–	–	–	–	–	–	–	–
Oct	2	4	3	9	1	19	–	–	–	–	–	–
Nov	1	8	5	5	0	19	1	2	2	5	1	11
Dec	0	1	0	1	0	2	1	4	1	3	0	9
Jan 1969	0	0	1	6	0	7	0	2	2	3	0	7
Feb	3	7	2	1	2	15	0	0	0	7	1	8
Mar	0	2	3	0	0	5	2	3	3	8	3	19
Apr	2	7	5	0	0	14	0	2	2	2	1	7
May	0	4	4	0	0	8	0	3	4	2	0	9
Jun	2	2	10	0	2	16	0	1	1	1	0	3
Jul	–	–	–	–	–	–	–	–	–	–	–	–
Aug	–	–	–	–	–	–	–	–	–	–	–	–
Sep	1	2	1	3	0	7	–	–	–	–	–	–
Oct	0	2	6	8	5	21	1	0	1	3	1	6
Nov	0	1	0	0	0	1	0	2	6	9	5	22
Dec	0	0	1	5	0	6	0	0	0	6	5	11
Jan 1970	1	3	3	5	2	14	0	1	1	3	0	5
Feb	2	5	3	1	0	11	1	3	5	9	1	19
Mar	1	5	4	2	0	12	1	3	1	1	0	6
Apr	6	5	6	0	1	18	2	1	3	2	0	8
May	6	5	2	2	0	15	1	1	2	1	1	6
Jun	2	1	3	1	0	7	4	6	4	3	1	18
Jul	–	–	–	–	–	–	2	1	2	5	1	11
Aug	–	–	–	–	–	–	0	1	5	5	0	11
Sep	0	0	3	1	0	4	0	0	0	1	0	1
Oct	2	2	4	3	1	12	0	3	0	1	1	5
Nov	1	0	4	1	1	7	2	0	1	4	2	9
Dec	0	1	1	1	0	3	0	1	3	3	2	9
Totals	42	91	103	72	24		27	54	65	115	41	

Table XII

The residence categories of Praomys tullbergi *after entering the study area, and residence categories of individuals which left the study area each month.*

Residence category	ENTERING POPULATION				LEFT POPULATION			
	Res	Semi-Res	Non-	Total	Res	Semi-Res	Non-Res	Total
Nov 1967	17	7	7	31	-	-	-	-
Dec	3	1	2	6	0	4	7	11
Jan 1968	3	4	5	12	0	3	2	5
Feb	6	2	8	16	4	2	5	11
Mar	0	0	0	0	5	3	8	16
Apr	18	4	12	33	3	0	0	3
May	3	3	8	15	3	1	12	16
Jun	1	2	4	7	10	3	8	21
Jul	-	-	-	-	-	-	-	-
Aug	-	-	-	-	-	-	-	-
Sep	-	-	-	-	-	-	-	-
Oct	6	4	9	19	-	-	-	-
Nov	8	6	5	19	2	0	9	11
Dec	2	0	0	2	1	3	5	9
Jan 1968	5	0	2	7	3	4	0	7
Feb	4	5	6	15	6	0	2	8
Mar	3	1	1	5	10	3	6	19
Apr	7	4	3	14	3	3	1	7
May	5	2	1	8	2	4	3	9
Jun	5	2	9	16	1	1	1	3
Jul	-	-	-	-	-	-	-	-
Aug	-	-	-	-	-	-	-	-
Sep	3	2	2	7	-	-	-	-
Oct	2	9	10	21	4	0	2	6
Nov	1	0	1	1	5	7	10	22
Dec	2	2	2	6	10	1	0	11
Jan 1970	4	2	8	14	2	1	2	5
Feb	5	3	3	11	8	3	8	19
Mar	6	2	4	12	2	1	3	6
Apr	9	6	3	18	3	1	4	8
May	6	3	6	15	1	2	3	6
Jun	2	2	3	7	7	5	6	18
Jul	-	-	-	-	7	1	3	11
Aug	-	-	-	-	10	1	0	11
Sep	0	1	3	4	1	0	0	1
Oct	4	5	3	12	2	0	3	5
Nov	0	4	3	7	4	2	3	9
Dec	-	-	-	-	4	2	3	9
Totals	139	89	132	360	123	61	119	303

e) Survival of cohorts of known age

The month of birth of young animals which weighed 30 gm or less when first caught, was calculated using growth rates measured in mice which had been born in captivity. These data were used with caution for two reasons. 1) The growth rates of captive animals were known to be influenced by litter-size, and 2) there may have been differences in the growth rates of wild and captive animals. However, the average growth rate in the wild (measured on mice which were captured and weighed at frequent intervals) was approximately 2 gm/ week, which is similar to the average

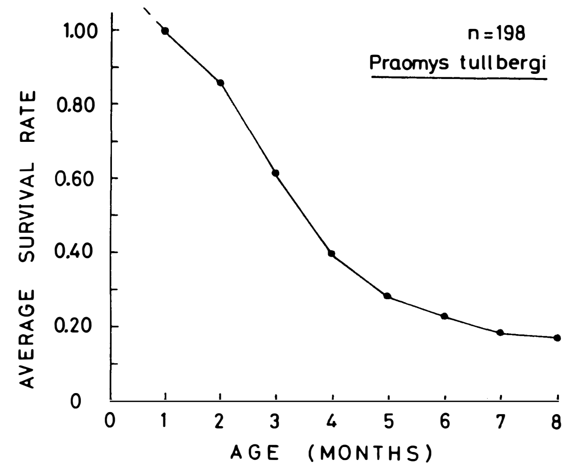

Fig. 13. — The survival rate of *Praomys tullbergi* in the population to eight months of age.

growth rate in captivity. The variation around this figure was quite high, and a few individuals lived for several weeks without increasing in weight. The reliability of estimating the month of birth of an individual was highest when it was first caught as a very young animal weighing less than 15 gm, and lowest in animals weighing 25-30 gm when first caught. Animals which weighed more than 30 gm could not be aged. Despite these sources of error, the date of birth of 198 young was calculated to the nearest month, and the rate of survival of these young animals is presented in fig. 13. No information was available on survival during the first month of life because these mice did not enter the trappable population until they were 3-4 weeks old. Approximately 50 % of the young survived to 3½ months of age, the time when the average individual becomes sexually mature (Happold in press), but only 18 % survived to six months of age. A few individuals survived for much longer. There was a shift to the right in the survival curve of young individuals of known age when compared with the survival curve for all individuals in the population (fig. 10). Thus 62 % of one month old animals survived in the population for a further two months, whereas only 30 % of the total population survived in the population for three months. This was because the population as a whole contained some old individuals whose survival was very limited, and this reduced the overall rate of survival.

f) Reproduction in relation to population change

The monthly reproductive potential was assessed by counting the number of pregnant females each month and multiplying this by the average litter size (3.0) and secondly, by weighing and aging all the young caught each month and then calculating when they were born and the number born each month. Provided most (if not all) pregnant females are captured, the first method is more reliable than the second because mortality of young individuals which never enter the trappable population cannot be assessed.

Pregnant females were trapped during most months of the year (excluding July and August for which there are no data). Pregnant females were usually least abundant at the beginning of the dry season, and most abundant from the middle of the dry season to the beginning of the wet season (January to April), but the pattern varied from year to year (Table XIII). The fecundity ratio, (the ratio of the pregnant females to mature females in the population) ranged from 0 to 0.9 (Table XIII), and from January to April the fecundity ratio was 0.4 to 0.8. The number of young expected to be born each month ranged from zero to 24 (Table XIII). When the number of young expected to be born was compared to the number known to have been born each month, there were considerable differences. Two possibilities could have accounted for this : 1) the number of pregnant females, and hence the number of expected young, could have been underestimated, and 2) a number of young whose mothers lived outside the study area may have moved into the study area.

The pattern of births during the course of the year was clearly seen when the number of young known to have been born were summed on a monthly basis (Table XIV). The pattern was bimodal, with many births occuring in the dry season and again in the " little dry season " which occurs in the middle of the wet season. The large number of young known to have been born in December suggests that the number of pregnant females was grossly underestimated for this month.

Individuals which were resident on the study area, and which were caught many times, provided information on the minimum age for reproduction, and on the frequency of pregnancies in the

TABLE

The numbers of adult female Praomys tullbergi *(30 gm*
and the expected number

	1967		1968													
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
Adult females	9	7	8	8	5	13	12	12	-	-	-	11	8	8	12	11
Pregnant females	1	0	5	7	3	8	7	5	-	-	-	4	0	1	5	7
Fecundity ratio	.1	0	.6	.9	.6	.6	.6	.4	-	-	-	.4	0	.1	.4	.6
Expected young (average 3 young/ litter)	3	0	15	21	9	24	21	15	-	-	-	12	0	3	15	21
Young known to be born (see also Table 14)	?	?	13	14	11	2	1	0	4	9	7	2	2	9	9	10

wild (Table XV). Some females bred when 4-6 months old, which was slightly later than some individuals reared in captivity (Happold in press). Others were recorded as first breeding when 9-13 months old, but these females may have bred when 4-6 months old in the previous July-August period when the population was not trapped. Data for the prolific residents showed that most of their pregnancies occurred during the period December to April-May, which confirms the breeding pattern described above. Some resident adult females were not known to be pregnant at any time while they were in the study area. Females in this category included two individuals out of a total of 18 which were resident in the study area for more than four months.

These data show that reproduction occurred throughout the year, and that the fecundity ratio was highest during the latter half of the dry season and the beginning of the wet season. Young individuals were continuously being born into the population, but never in such large or small numbers that the population as a whole fluctuated dramatically. However, young animals were partly responsible for the population peaks in January-February, April-May and September-October. The information on reproduction correlates reasonably well with that on other aspects of the population dynamics.

or over) and pregnant females, the fecundity ratio, of young, in each month.

1969												1970									
Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4	7	7	8	-	-	10	10	5	8	9	5	6	3	8	7	-	-	4	5	8	2
3	4	4	2	-	-	2	2	1	0	2	0	3	1	4	2		No			data	
.8	.6	.6	.3	-	-	.2	.2	.2	0	.2	0	.5	.3	.5	.3						
9	12	12	6	-	-	6	6	3	0	6	0	9	3	12	6						
14	2	2	1	7	2	1	2	5	9	12	10	11	7	2	0	6	5	3	2	?	?

g) Home range

The home ranges for resident individuals which were caught ten or more times were calculated by the inclusive trapping method (Hayne 1949). Individuals which lived, according to the trapping records, only on the two outermost lines of the grid, were not included in the estimation of home range as it was possible that their home ranges extended into untrapped localities beyond the grid. There was no relationship between the number of times an individual was caught and the size of its home range. Some individuals were caught almost weekly during their residency, and it is assumed that these individuals remained within the home range in between the weekly trapping nights. In contrast, other individuals were caught regularly within a small range for several weeks or months, then they were not caught for several weeks, and finally they were caught again at the same sites as before. For the purposes of calculating home range, and until further evidence is available, it is assumed that such individuals were resident in their known home range, even though they were not caught. (This assumption is the same as that used for calculating the number of individuals on the grid each month.)

The average home range for 19 males was 0.23 ha (0.56 acres) with a range from 0.11 ha to 0.39 ha (0.28 — 0.95 acres), and for 14 females, it was 0.22 ha (0.53 acres) with a range from 0.13 ha to

TABLE XIV

The minimum number of young of Praomys tullbergi *known to be born each month.*

Year	J	F	M	A	M	J	J	A	S	O	N	D	Totals
1967											4	4	
1968	13	14	11	2	1	0	4	9	7	2	2	9	74
1969	9	10	14	2	2	1	7	2	1	2	5	9	64
1970	12	10	11	7	2	0	6	5	3	2	-	-	66*
Totals	34	34	36	11	5	1	17	16	11	6	11	22	

* The young for November and December 1967 are included in this total to complete the year

0.30 ha (0.32 — 0.74 acres). The home ranges of males and females were, on average, very similar although the home ranges of males showed slightly more variation in size than those of females. Most resident individuals were caught consistently inside their home range, but a few individuals were recorded outside the home range for short periods of time. For example, ♂ 35 was caught 34 times over a period of 510 days, and all captures except two were within the home range of 0.39 ha. Captures 24 and 25 (seven days apart) were at a trap site about 22 m from the boundary of the calculated home range.

When individuals were resident, the trapping data suggested that they remained in a fairly small home range. The spacings of the traps in this study, and the area trapped were probably adequate to assess the home ranges of these individuals with reasonable accuracy. However, because the overall population was composed of residents, semi-residents and non-residents, it is likely that some individuals had a certain home range at one period, and then moved elsewhere and established another home range.

VI. POPULATION DYNAMICS OF *MALACOMYS EDWARDSI*

The long-footed swamp mouse, *Malacomys edwardsi,* was the second most abundant species even though it comprised only

TABLE XV

Reproductive performance and age of first pregnancy in Praomys tullbergi.

Identification number of individual	Number of times caught	Recorded pregnancies (in sequence)	Month of birth (if known)	Age when first pregnancy was observed (months)
328	44	Apr, Jun 70 (2)	Mar 69	13
260	38	Jan, Feb, Mar, Apr, May, Jun, Oct 69, Jan 70 (8)	Sep 68	4
384	31	Feb, Mar, Jun 70 (3)	Jul 69	7
138	31	Nov 68, Sep, Nov 69 (3)	Feb 68	9
347	28	Jan 70 (1)	Mar 69	10
243	26	Feb, Apr, May, Aug 69 (4)	Sep 68	5
124	22	Apr, May, Jun 68, Feb, Mar 69 (5)	-	-
24	21	Nov 67, Jan, Mar, Apr, Jun 68 (5)	-	-
22	21	Jan, Feb, Mar, Apr 68 (4)	-	-
128	19	Oct 68, Jan, Feb, Mar 69 (4)	Feb 68	8
176	16	May, Oct, Dec 68, Feb 69 (4)	Dec 67	5
535	10	May 70 (1)	Jan 70	4
263	8	Jan, Apr, May, Jun 69 (4)	Sep 68	4
487	5	May 70 (1)	Nov 69	6
123	4	May, Jun 68 (2)	Jan 68	4
131	3	May 68 (1)	Jan 68	4

10.4 % of the trappable rodent population (Table III). The number of individuals known to be alive each month ranged from 0 to 11 (Table XVI). The largest numbers occurred late in the wet season and the early part of the dry season each year, and in 1970 (but not in other years) there were more individuals than average from April to June. The months of high population numbers were a result of one month when many individuals entered the population, and since most of these individuals became semi-resident or resident, the effects of this influx of new individuals lasted for several subsequent months.

Although only 44 *Malacomys* were captured in this study,

TABLE

Population data for

	1967		1968												
	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan
Individuals known to be alive	7	7	5	3	1	2	2	3	1	1	2	11	11	9	5
New individuals in month	7	2	0	0	0	1	1	2	0	0	1	9	2	0	0
Individuals lost during month	0	2	2	2	2	0	1	2	2	0	0	0	2	2	4
Individuals caught during month	7	5	4	2	0	1	1	3	-	-	-	10	10	7	4
Pregnant females	0	0	3	2	0	1	0	0	-	-	-	0	0	1	3

(compared with 316 *Praomys*), the data suggest that the survival rate of *Malacomys* after entering the population resembled that of *Praomys* except that survival in the first two months after entering was higher (fig. 14). The recapture rate for *Malacomys* was 60 % compared with 53 % in *Praomys*. One *Malacomys*, ♂ 222, survived in the study area for 10 months, and ♀ 204 survived for 12 months.

Pregnant females were found in all months from November to July, but no pregnancies were recorded at the end of the wet season from August to October (Table XVI). During the course of any year, the records of pregnant females were rather disjunct. The largest number of pregnant females was in January, even though the total number of females in this month was not as large as for the months of October to December. The fecundity ratio ranged from 1.0 (in January 1970 when all three females were pregnant) to zero. Young individuals were trapped in April, May and June (as a result of pregnancies in the dry season), and also in September and October (as a result of unrecorded pregnancies in about July and August). Information on the reproduction of *Malacomys* is scanty due to the uncommoness of the species and the small number of females in the trappable population (Table IV).

A breeding female can produce a litter at monthly or two-monthly intervals ; for example ♀ 212 was pregnant in January, March and June, and ♀ 7 was pregnant in January and late Februa-

XVI

Malacomys edwardsi (*1967-1970*).

1969											1970											
Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2	2	3	2	2	1	1	1	7	7	4	5	4	3	8	6	6	3	2	2	0	1	1
0	0	1	1	1	0	0	0	6	1	1	3	0	0	5	2	1	0	0	1	0	1	1
3	0	0	2	1	1	0	0	0	1	4	2	1	1	0	4	1	3	1	1	2	0	1
0	0	2	1	1	-	-	-	7	7	3	4	2	2	6	3	6	2	1	2	0	1	1
0	0	1	0	0	-	-	-	0	1	0	3	0	1	0	1	3	1	0	0	0	0	0

ry. The reproductive potential of this species appeared to be generally low because there were more males than females (at least in the trappable population), the litter size was small (Happold unpubl.), and because the fecundity ratio was high only for a few months during the dry season.

The home ranges for *Malacomys* were calculated in the same way as for *Praomys* (section Vg). The data on individuals caught six or more times showed that the average home range of four males was 0.42 ha (1.04 acres) with a range from 0.34 to 0.55 ha (0.84 — 1.35 acres), and for four females it was 0.37 ha (0.91 acres) with a range from 0.28 ha to 0.46 ha (0.69 — 1.14 acres). The comments made on home ranges in *Praomys* (section V) also apply to this species.

VII. POPULATION DYNAMICS OF *LOPHUROMYS SIKAPUSI*

The population numbers of *Lophuromys sikapusi* (Table V) were very low at the beginning of this study, but increased towards the end of 1969 and in 1970. Only 14 individuals, forming 2.4 % of the trappable rodent population, were caught. The recapture rate was fairly high (61 %), probably because individuals of this species kept to particular vegetation associations which only occurred in small parts of the study area.

This species lives in damp habitats where herbaceous growth forms dense cover. At Gambari, *Lophuromys* were relatively common 150 m west of the study area, where the forest had been cleared for a teak plantation 2-3 years earlier (Happold 1975). However, the uncleared rain forest did not provide suitable habitat except where the canopy was open enabling herbs to grow rampantly in the E stratum. In the study area, the capture sites of *Lophuromys* were strongly correlated with the distribution of three

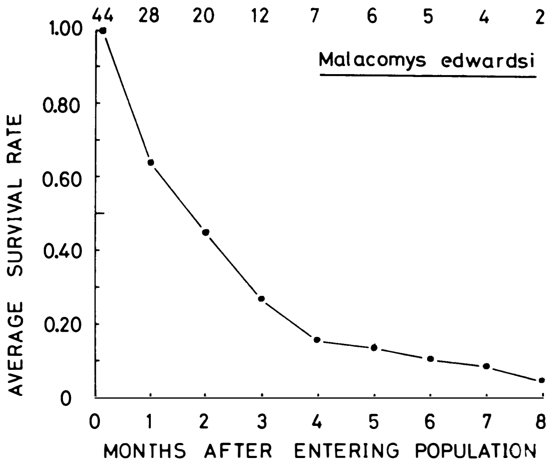

Fig. 14. — The average survival rate of *Malacomys edwardsi* after entering the population. The sample number for each month is shown at the top of the graph.

herbaceous plant species (section IIe) which grew rampantly in three parts of the study area (fig. 15). Obviously *Lophuromys* moved through the sparsely vegetated parts of the E stratum to reach patches of suitable microhabitat, but the trapping records suggested that they did not become residents in these parts.

Pregnant females were recorded in February, March, April, May, July and October, but the data were insufficient to determine the main breeding season. Female 544 was pregnant in April and again in July, and ♀ 410 had three consecutive pregnancies in October, February and March.

Movements of individuals into the study area did not seem to be related to the time of year. Often many months passed when no new *Lophuromys* entered the population, and then two or three individuals entered during one month, as in May, June and October 1969 and in April 1970. Six individuals resided in the study area for more than 100 days, and the maximum residency was for 210 days. Because the residents kept within the patches of herbaceous vegetation, their home ranges were limited in size. The average home range for five individuals was 0.21 ha (0.52 acres), but if the single individual which had a home range much larger than the others is discounted, the average range was 0.15 ha (0.37 acres).

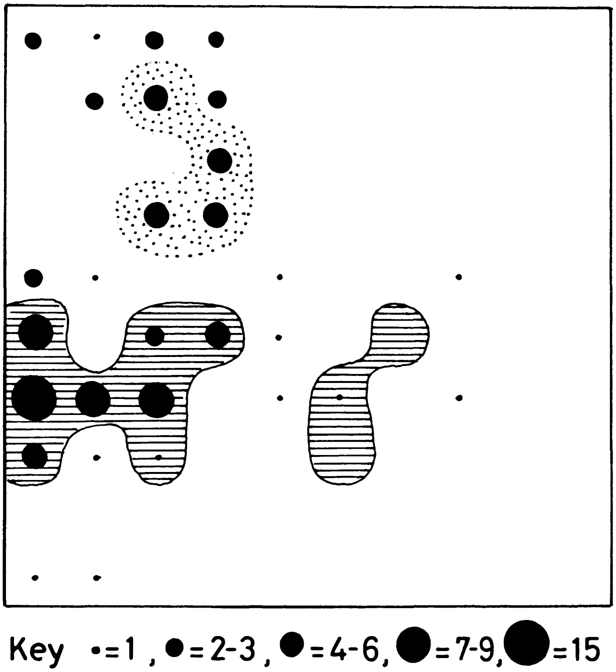

Fig. 15. — The capture sites of *Lophuromys sikapusi* in the study area. The sizes of the black circles indicate the number of captures at each trap site, and the trap sites where *Lophuromys* was not captured are not marked. The stippled area shows the position of dense growth of *Cyathula achyranthoides*, and the horizontal lines show the positions of dense growth of *Pollia condensata* and *Polyspatha hirsuta.*

VIII. POPULATION DYNAMICS OF THE OTHER SPECIES OF RODENTS

a) Hylomyscus stella

The tree-climbing mouse, *Hylomyscus stella,* formed only 5.6 % of the trappable rodent population. Because the recapture rate was only 8 %, the information on this species was very scanty and limited to the numbers of individuals and some details on reproduction. *Hylomyscus* were found throughout the study area with no evident preference for particular areas. In most months, there were one or two individuals known to be alive, but these were mostly different individuals each month. Six *Hylomyscus* were captured in February 1968 and in October 1969, but none of these individuals were recaptured. All these facts suggested that the numbers of this species were underestimated possibly due to the arboreal habits of the species.

Pregnant females were captured in January, February and November. Four young were captured in February 1968, and the presence of young in April, June and October suggested an extended breeding season with maximum reproduction at the beginning of the dry season in November and December.

b) STOCHOMYS LONGICAUDATUS

The long-tailed target rat, *Stochomys longicaudatus,* formed 2.1 % of the trappable rodent population. The recapture rate was only 30 %, and individuals which were recaptured appeared to stay on the study area for less than four weeks. There were two exceptions to this. After marking, ♀ 10 was not recaptured for four months but then she was caught four times within a month before finally leaving the population. Female 365 was not recaught for over a year after the first capture, but then she was caught ten times in six months, and finally she was caught for the last time after a further absence of six months. All captures during this residency of 745 days were within a home range of only 0.15 ha (0.37 acres). These data suggested that the trappability of *Stochomys* was very low, or alternatively that individuals alternated between two or more localities.

Pregnancies were recorded in March and June, and young individuals were found in January, June and December.

c) MUS (LEGGADA) MUSCULOIDES

The pygmy mouse, *Mus* (*Leggada*) *musculoides,* like *Lophuromys sikapusi,* is not a rain forest species, although a few individuals entered the forest from surrounding grasslands and farms (section III). During the main study period, only eight individuals (1.7 % of the trappable rodent population) were recorded, and none of these were recaptured. Five of the eight individuals entered the study area in the dry season (Table V).

No information was obtained on the reproduction of this species in the forest.

d) Hybomys trivirgatus

Eight individuals of the three-striped mouse, *Hybomys trivirgatus* were recorded. The recapture rate was 50 %. Three of the individuals which were recaptured had residences of 20, 25 and 39 days, and the fourth was caught five times in 36 days and was then recaptured again ten months later. Although this species is generally very rare, five individuals entered the population in December 1969. One of these, a young male, was found in the northern part of the study area, and the other four (one adult male and three adult females) were clustered together in the south-east corner of the study area. These four individuals were trapped 14 times during a month, and although none were caught together at the same time in the same trap, different individuals were caught at different times in the same trap. In less than a month, all four individuals had left the population. This species appeared to show considerable mobility since one individual was recaptured 75 m away within a few minutes of being released from the first trap. It is tempting to suggest that this species moves about in small groups which reside in specific areas for only short periods of time. However, the rarity of the species prevented confirmation of this suggestion.

Young *Hybomys* were found in November and December.

IX. SHREWS

Two species of shrews, *Crocidura poensis* and *C. crossei,* occurred in Gambari forest. *Crocidura poensis* was the rarer of the two species (Table III) and was seldom caught, except that ten individuals were caught in three months at the beginning of the wet season in 1969 (Table V). A total of 16 individuals were caught during the study, and only three (19 %) of these were recaptured a second time. Their residencies were very short except for one individual which was caught a second time seven months after marking. One pregnant *C. poensis* was found in June 1970.

Crocidura crossei, which is the smaller species, was more abundant than *C. poensis.* Thirty six individuals were caught only once, and four (10 %) were caught twice. Of these, three were caught twice within one month, and the other survived for five months between captures.

It is likely that both species are highly mobile, and probably short lived. There were 17 trap-deaths of shrews, but only six trap-deaths of rodents. Of the dead shrews, 15 were *C. crossei.*

X. BIOMASS AND POPULATION DENSITY

For each month, the " trappable " biomass of the rodent population, and the " trappable " biomass of each species, was calculated from the weights of those individuals which were actually captured during each month. If an individual was captured more than once in a month, its average weight for that month was used. This method of assessing the monthly biomass of trappable animals underestimated the total monthly biomass on the study area because 1) it did not take into account the animals which were not caught but known to be alive, and 2) it could not take into account animals which may have been present but which were never caught.

The monthly biomass of the trappable rodent population in the study area (1.88 ha) ranged from 234 gm/ha to 1,229 gm/ha (23.4 kg/km^2 to 122 kg/km^2), and the mean for 28 months was 715 gm/ha (71 kg/km^2). The monthly biomass (fig. 7b) did not fluctuate in synchrony with the total number of rodents each month, because of the monthly variation in the age-weight structure of the population. The highest biomasses occurred when peaks in population numbers were associated with peaks in the occurrence of adults in the population. For example, the biomass was 2,300 gm in October 1969, when 81 % (n = 58) of the captured animals were adults. In contrast, in other months when the population numbers reached similar levels as a result of the recruitment of young animals, the biomass was only 1,600-1,800 gm. Low biomasses were recorded in February-March each year, but these months were characterized by extra large numbers of individuals which were not caught but known to be alive.

The biomass fluctuations for *Praomys tullbergi* usually followed the biomass fluctuations of the total trappable rodent population, but there were some monthly variations in the contribution of *Praomys* to the total biomass. The average monthly biomass of *Praomys* was 514 gm/ha (51 kg/km^2) or 72 % of the average total biomass.

The average individual weight of *Praomys* each month was also related to the age-weight structure of the population. When the average individual weight was high, there was a large proportion of adults in the population, and when it was low there was a large proportion of young individuals. The average individual weight fluctuated between 28 gm and 43 gm (fig. 7c). The lowest average individual weights were found in months when there was a peak in population numbers, or when the population numbers were rising to a peak. The highest average individual weights were mostly, but not always, when the *Praomys* population was low. These data suggested that the population alternated between times of high numbers of mostly young individuals, and times of low numbers of mostly adult individuals. The exceptions were the peaks in February-March, and the peak in October 1969.

The population density for all small rodents ranged from 18.6 to 34.0 individuals/ha, and the population density of *Praomys tullbergi* ranged from 11.7 to 27.7 individuals/ha. The population densities during the year followed changes in population numbers (fig. 7a). However, the population densities of *Praomys,* in relation to the total population density, varied according to the proportion of *Praomys* in the total population each month (Table V). The population densities of the other rodent species together varied from month to month, and ranged from about two to seven individuals/ha.

XI. LONG TERM FLUCTUATIONS IN POPULATION NUMBERS

After the main study period, the population was sampled for three consecutive nights in June and December from 1970 to 1975. In order to make the two sampling methods comparable, the number of individual animals caught during three trapping nights extending over two weeks in each June and December of the main study period, was taken as equivalent to three consecutive nights during the second part of the study. There was likely to be a source of error because of this change, but it was considered to be fairly small. When the two methods were compared in January 1970 the first method recorded 32 animals and the second recorded 30.

The average number of small mammals during the first three years of the study (33.2) was higher than for the following five years (23.3), and the range of population numbers was 26 - 64 in the first three years, and 10 to 50 in the following five years (Table XVII). The population numbers (fig. 16) showed that the population gradually declined from 1968 to mid 1973 (but with small increases in mid 1970 and at the end of 1971), and it increased again from 1973 to 1975. The maximum number was five times larger than the minimum number, and there was an interval of several years between the maximum and minimum numbers.

The species composition of the population, assessed by nine trapping periods during the last five years, was similar to that during the main study period. However, there were some notable differences. The percentage number of *Praomys* was lower and those of *Lophuromys, Mus* and *Crocidura* spp. were higher. *Lophuromys* were relatively abundant in December 1971 and in Decembe 1974, and, most surprisingly, *Mus* formed 40 % of the population in December 1973, as well as being relatively abundant in December 1974 and June 1975. *Crocidura* spp. were generally more common during 1971 to 1975 than during 1967 to 1970.

TABLE XVII

The species and species composition of small rodents and shrews recorded in three consecutive nights of trapping in June and December from 1971 to 1975. The numbers indicate the numbers of individuals of each species caught during each trapping period.

Species	Jun 1971	Dec 1971	Jun 1972	Dec 1972	Jun 1973	Dec 1973	Jun 1974	Dec 1974	Jun 1975	Dec 1975	Totals	Percentage
	Date of trapping period											
Praomys tullbergi	10	21 (1)	18 (6)	4 (1)	4 (1)	7	-	21 (1)	29	39 (5)	153	(65%)
Malacomys edwardsi	1	0	0	2	2	2 (1)	-	3	3	1	14	(6%)
Hylomyscus stella	0	0	0	0	4	0	-	1	1	1	7	(3%)
Lophuromys sikapusi	0	3	0	1	0	1	-	3	1	3	12	(5%)
Stochomys longicaudatus	2 (1)	0	0	1	0	0	-	0	0	0	3	(1%)
Mus musculoides	0	0	1	0	0	8	-	3	3	3	18	(8%)
Hybomys trivirgatus	0	0	0	0	0	0	-	0	0	1	1	(1%)
Crocidura poensis	0	1	0	1	0	0	-	3	1	2	8	(3%)
Crocidura crossei	0	5	5	5	0	2	-	2	2	0	21	(9%)
Totals	13	30	24	14	10	20	-	36	40	50	237	

No data are available for June 1974 because heavy rain closed the majority of the traps during the trapping period.
The number of individuals caught in the trapping period six months previously are shown in brackets.

The reasons for the gradual fall in population numbers, especially in the true forest species, from 1968 to 1973 are not known, although it is likely that the decreasing rainfall during these years (especially the severe drought of 1971 and 1972) affected the environmental conditions in the forest. The fire in the leaf litter in March 1973 (section IIg) after several months of very dry conditions was probably responsible for the very small population numbers in June 1973. The annual rainfall began to increase from 1973 although the effects of this increase were not apparent by the June 1973 trapping period. The increase in the number of *Mus musculoides* in December 1973 may have been related to the 1971-72 drought, and the fire in March 1973.

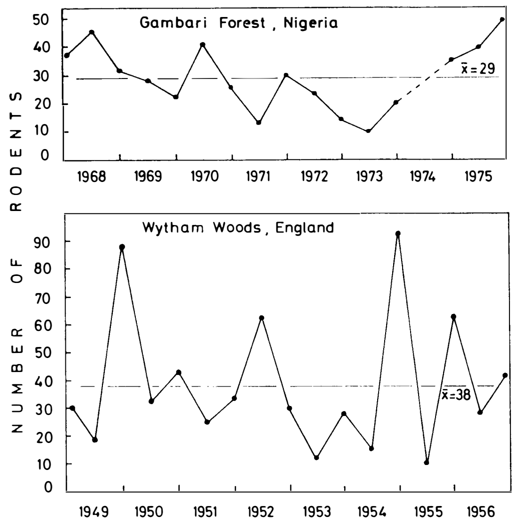

Fig. 16. — The numbers and fluctuations of rodents on study areas of about 2 ha in Gambari Forest, Nigeria and in Wytham Woods, England. In Gambari Forest, the « known to be alive » numbers of seven species of rodents are plotted, and in Wytham Woods, the estimated numbers of the only two species of rodents are plotted. The original data for Wytham Woods (Southern 1970) was recorded on a 4.8 ha (12 acre) study area.

During 1971-1975, the average survival of *Praomys* from one trapping period to the next (six months later) was 10 %. This was lower than the average survival of 17 % over an equivalent length of time during 1967-1970 (fig. 10). The survival of *Praomys* in the study area during 1967-1970 may have been enhanced in trap-prone animals by the weekly trapping programme.

XII. DISCUSSION

This study has shown that seven species of small rodents and two species of shrews occur in the moist semi-deciduous lowland rain forest at Gambari in western Nigeria. The species of rodents differ in their relative abundance, habitat preferences, diet, reproductive biology and population dynamics which indicates that a number of different life-history strategies have evolved to meet the conditions of this particular habitat. Before discussing some of these strategies it is relevant to compare the stability of the Gambari forest habitat with the stability of other rodent habitats for which there is similar information, and then to compare the population dynamics of the rodents in these habitats.

Lowland rain forest is often considered to be a stable non-seasonal environment with abundant non-fluctuating resources. However, recent studies in Gabon (Charles-Dominique 1971), Malaya (McClure 1966), Panama (Fleming 1971), Costa Rica (Fleming 1974) and Nigeria (Happold 1975, this study) have shown that there are seasonal changes in several ecological parameters associated with lowland rain forests, especially with those which are moist and semi-deciduous. These parameters include 1) rainfall and relative humidity which vary to give distinct " wet " and " dry " seasons, 2) leaf fall and leaf litter which are greatest during the dry season, 3) fruit fall which is greatest at the end of the dry season and the beginning of the wet season, and 4) insect and earthworm abundance which is high during the wet season and low in the dry season. Seasonal changes in these parameters are most pronounced in rain forests with a rainfall of 1300-1500 mm/year and several months without significant rain. The seasonal changes are least conspicuous in rain forests with a rainfall greater than 2500 mm/year and significant rain in each month.

At Gambari forest, seasonal fluctuations in rainfall, leaf fall, fruit fall and in the abundance of insects appear to be reflected in the biology of the rodents. This study has revealed the following correlations beween fluctuating environmental conditions and the biology of the rodents.

1) Reproduction in *Praomys tullbergi* was seasonal to the extent that, although breeding occurred throughout the year, the highest fecundity occurred in the dry season and the little dry season.

2) Survival in *Praomys* was slightly higher in the wet season (0.7 — 0.9) than in the dry season (0.39 — 0.6). However, except in February 1970 when the survival rate was 0.39, there was no period of the year when a large proportion of the population died or emigrated.

3) The numbers of *Praomys* in the trappable population regularly formed three peaks each year. These appeared to result from the bimodal reproduction cycle together with the seasonal changes in survival. If the number of *Praomys* known to be alive, the number of young known to have been born, and the rate of disappearance of individuals from the trappable popu-

lation are averaged for each month of the year from 1968 to 1970 (fig. 17), it is clear that a close correlation exist between the months of lowest population numbers and the months with highest rates of disappearance (March, June and November). High birth rates in March and July-August were responsible for the gradually increasing numbers which culminated in peaks of population numbers in May and October. The population peak in February was due to the high and increasing birth rate from November to January together with the increasing disappearance rate in January and February.

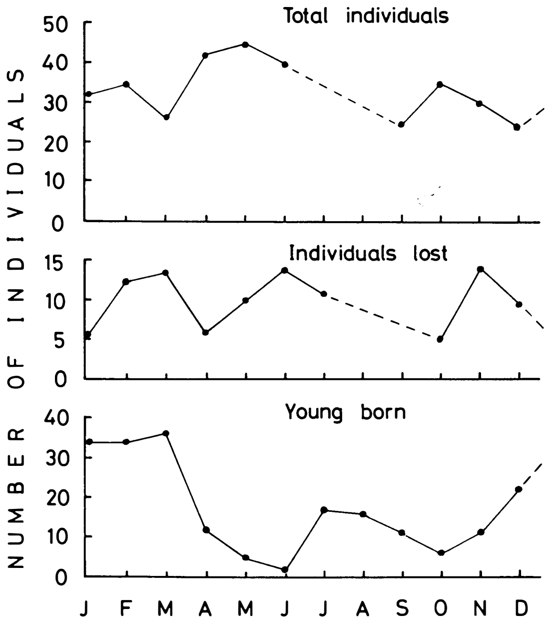

Fig. 17. — Population parameters of *Praomys tullbergi* during three years (1968-1970). Total individuals and individuals lost (from Table VII) are expressed as averages for each month, and young born are expressed as the total young known to have been born each month (from Table XIV).

4) There were slight seasonal changes in the age-weight structure of the *Praomys* population which were also a function of reproduction and survival. However, there were no times of the year when the population was dominated totally by young, by adults, or by very old individuals.

5) Reproduction in *Malacomys edwardsi* is seasonal (November to July) with maximal fecundity in the dry season.

6) The numbers of *Malacomys* in the trappable population reached a peak at the end of the wet season and beginning of the dry season (October-November).
7) The data, although limited, suggest that fecundity in *Hylomyscus stella* was maximal at the beginning of the dry season.
8) *Mus* (*Leggada*) *musculoides* most frequently entered the trappable population during the dry season.
9) There were three small peaks each year in the total number of rodents trapped, although these fluctuations were largely determined by *Praomys* which usually comprised about 75 % of the trappable population.

As well as these seasonal fluctuations in the habitat and in the biology of the inhabitants, there is some evidence that the climate in West Africa undergoes cycles of wetter and drier periods. The eight years of this study tended to have lower annual rainfalls and longer dry seasons than in average years, and as a consequence seasonality was probably more obvious and its effects more definite than normal.

How do the fluctuations in Gambari forest compare with fluctuations in the habitats and biology of other rodents ? Where does Gambari fit in the continuum from stable to unstable habitats ? The answers to these questions can be obtained by comparing the data in this study with that derived from similar long term studies of rodent population dynamics and ecology in other habitats.

Despite the large number of studies on rodent populations, there are relatively few populations which have been studied continuously for more than three years, especially in the tropics. Fluctuations in rodent populations are usually measured in terms of the magnitude of change between the lowest and the highest numbers, and the rate of change in these fluctuations. There appear to be five main forms of population fluctuations in rodents : among other things, these are related to the predictability and stability of the habitat (fig. 18). The fluctuations are most dramatic in scale and unpredictability in arid habitats with irregular rainfalls. (fig. 18a). For example, fluctuations of great magnitude (as yet unestimated quantitatively) occur in *Rattus villosissimus, Notomys alexis, N. cervinus, Pseudomys australis* (= *minnie*) and *Mus musculus* in the Australian arid zone (Plomley 1972). Similar large scale unpredictable fluctuations have been recorded for several species of rodents in the arid zone of Africa. Fluctuation which are, in contrast, very predictable occur in many of the microtine rodents in temperate habitats of North America (Elton 1942, Fuller 1969) (fig. 18b). For example, in *Microtus pennsylvanicus* an approximately 20-fold increase in population numbers occurs every 3-4 years (Krebs *et. al.* 1973). A third type of fluctua-

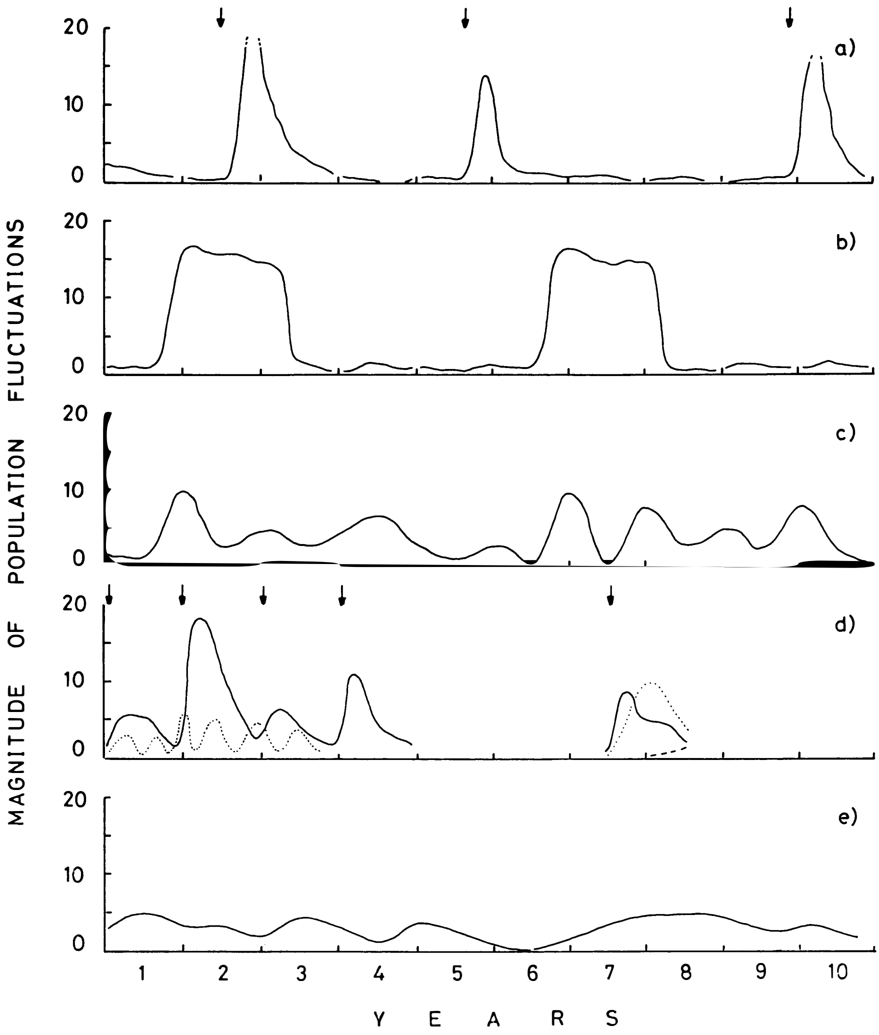

Fig. 18. — A diagramatic comparison of the long-term fluctuations of the populations of rodents in different habitats. The minimum numbers are represented by the base line, and the magnitude of increase is indicated up to 20 times the minimum numbers. Full details in the text. a) Arid zone ; arrows show times of heavy rainfall. b) Arctic and north temperate. c) Other temperate localities. d) Tropical savannas where there are several forms of population fluctuations depending on the species, time and severity of annual burning, and the pattern of rainfall. Left : *Mus musculoides* (unbroken line) and *Praomys daltoni* (dotted line) in a habitat subject to annual burning. Right : the population numbers of three species in Uganda after the annual burn. Arrows show times of burning. e) Tropical forest. A more meaningful comparison would be possible if there were comparable data of population numbers/ha in each of these habitats over a long period. Short term fluctuations, eg three peaks/year in the tropical forest are not shown.

tion is exemplified in populations of wood mice (*Apodemus sylvaticus*) and bank voles (*Cleithrionomys glareolus*) in Wytham Woods, England (Southern 1970) (figs. 16 and 18c). In these species the highest numbers were up to nine times the lowest, the rate of change from the highest to the lowest numbers was very rapid, but regular cyclical changes were less evident than in the microtine populations. Contrary to what one might expect, the Wytham Woods population (and also the microtine populations) did not necessarily decline in winter. Fluctuations which are seasonal in occurrence occur in tropical savanna (fig. 18d). In these habitats, some species in Uganda (e.g *Praomys* (*Mastomys*) *natalensis* and *Lemniscomys striatus*) increase their numbers very rapidly after the dry season and the annual burning of the grasses, although there are other species (e.g *Mylomys dybowskyi, Arvicanthis niloticus* and *Lophuromys sikapusi*) which are slow to respond to the improved conditions (Neal 1970). The fluctuations in numbers vary according to the species and are not necessarily related to the annual burning. For example, fluctuations from 4 to 80 individuals occur in *Mus musculoides,* compared with 4 to 28 in *Praomys* (*Myomys*) *daltoni* on a 2 ha study area in the derived savanna of Nigeria (Anadu 1973). The fifth type of fluctuation is exemplified by the population of small rodents in Gambari (figs. 16 and 18e). This population remained between 26 and 64 individuals during the first three years (1967-1970), and 10 and 64 during the entire 8-year period. Thus the maximum number was never more than 6.4 times the minimum, and during the first three years the maximum number was only 2.5 times the minimum. The numbers of *Praomys* fluctuated roughly in synchrony with the total population : the maximum number was 2.5 times the minimum (15) during the first three years, and 10 times the minimum (4) during the entire study. Although there were three small population peaks each year, these were superimposed upon a curve which gradually fell and gradually rose only once during the entire 8-year period (fig. 16). The intervals between the highest and lowest numbers were 2.5 and 5 years, and the interval between the two highest numbers was 7.5 years. There were certainly no cyclical fluctuations in the numbers of *Praomys* which are comparable with the cyclical fluctuations in the microtine rodents, and the density-related changes which occur in the latter (Chitty 1960, Krebs *et. al.* 1973) were absent in the *Praomys* population at Gambari. The comparatively dry conditions of 1971-1973 were probably responsible for the low population numbers of those years, and consequently differences between the maximum and minimum numbers during the eight years may be larger than normal. Other studies (Table XVIII) suggest that maximum numbers of 2-6 times the minimum numbers are characteristic of small rodent populations in tropical rain forests. However, a slow cycle of wetter and drier periods may be a characteristic of West Africa, in which

Table XVIII

Population demography for some populations of rodents in tropical rain forests.

Locality	Species	Individuals/ ha (max-min)	Magnitude of max above min numbers	Biomass (gm/ha)	Period of study (years)	Reference
S.E. Queensland	Rattus fuscipes	17 - 40	x 2	2125 - 5000*	3	Wood (1971)
	Melomys cervinipes	5 - 25	x 5	405 - 2030*	3	Wood (1971)
Costa Rica						
(deciduous)	Liomys salvini	4 - 8	x 2	160 - 320	1	Fleming (1974)
(wet)	Heteromys desmarestianus	7 - 18	x 2.5	420 - 1080	1	Fleming (1974)
Panama	Liomys adspersus	5 - 11	x 2	208 - 629	1	Fleming (1971)
	Oryzomys capito	0 - 4	x 4	0 - 214	1	Fleming (1971)
	Proechimys semispinosus	0.6 - 3.8	x 6	125 - 1600	1	Fleming (1971)
Malaya	8 spp Rattus	3.2 - 3.5	-	400 - 525	-	Harrison (1969)
Nigeria	Praomys tullbergi	11 - 27	x 2.5	185 - 920	3	This study
		4 - 39	x 10	-	8	This study
	7 spp	18 - 34	x 2	234 - 1229	3	This study

case the long-term fluctuations described in this study may be quite normal.

In view of these studies, it seems logical to place the Gambari forest habitat near the stable end of the stable-unstable continuum. There *are* seasonal changes in the environment and in the biology of the small rodents, but these are relatively small in scale, seasonal and predictable. There are some habitats of rodents which are more stable, but most are considerably less stable.

It has been suggested that species which live in unstable or extensively rarefied environments derive maximum fitness by putting maximal amounts of energy into the production of many progeny in the shortest possible time (r-selection), whereas when species live at saturation densities in comparatively stable environments the advantages of putting maximal energy into reproduction are offset by the advantages of placing some of this energy into intraspecific (and sometimes interspecific) competition for resources (K-selection) (MacArthur and Wilson 1967, Pianka 1970, 1972). The concept of K- and r-selection has provided a useful continuum into which the life history strategies of many species can be placed. As a simple dichotomy however, it is not always adequate

(Wilber et. al. 1974). The small rodents of Gambari forest (*Praomys* in particular) appear to follow a mixture of contradicting strategies which are not easy to understand.

Praomys tullbergi appear to be K-strategists in that they have comparatively small litters, comparatively late sexual maturation, and comparatively stable population densities. The carrying capacity of the habitat for *Praomys* appears to be comparatively stable. There are small scale predictable fluctuations in the availability of fruits on the ground, vegetation and insects which may impose seasonal changes in the availability of food. However, observations in captivity suggest that *Praomys* are unspecialised omnivores which can utilize a variety of fruits, nuts, leaves, shoots, flowers and some insects. A more probable limiting factor for *Praomys* may be the availability of domiciles — cavities in the buttress root systems of the largest trees, which are free from flooding during torrential rains. The availability of such domiciles probably remains constant from year to year, although cavities which are sometimes flooded in the wet season may become available in the dry season. In view of the stable nature of the food and domicile resources, and the habitat as a whole, it is not surprising that *Praomys* exemplify these K-strategies. However, *Praomys* also exemplify a number of r-strategies : on a yearly basis their reproductive potential is very high, and observations in captivity indicate social tolerance and the absence of high levels of agonistic behaviour, territoriality and competition for resources. One possible explanation is that *Praomys* may be exposed to a high but comparatively stable level of predation and/or mortality from other causes, which keeps the population below the carrying capacity and provides a necessity for high reproductive potential. This theory is supported by two observations : firstly that 80 % of the population of *Praomys* survived for less than six months in the study area, although some individuals indicated the potential longevity of the species by surviving in the area for at least 19 months. In captivity, one individual lived for 3.5 years. Secondly, the population numbers remained comparatively stable in spite of the potential of each female to produce at least 15 young per year.

The data are insufficient for the analysis of K-r strategies in the other species.

There are several phenomena in which the species of small rodents in Gambari are known to differ from each other. These include size, diet, habitat utilization, domicile requirements, activity rhythms, social behaviour and reproductive biology.

1) Size : the rodents in this study differ in size. The range of adult weights for each species are *Malacomys* and *Lophuromys* 50-70 gm, *Hybomys* 50-65 gm, *Stochomys* 45-65 gm, *Praomys* 30-45 gm, *Hylomyscus* 17-25 gm, and *Mus* 6-10 gm (Happold 1974).

2) Diet : although the analysis of stomach contents from Gambari forest rodents has not been completed (Happold in prep.), observations in captivity indicate that *Praomys* are basically unspecialized vegetarians although insects comprise part of their diet, *Malacomys* and *Lophuromys* are basically insectivorous, and *Mus* are graminivorous. *Hybomys* and *Stochomys* eat both vegetable matter and insects (Rosevear 1969). The diet of *Hylomyscus* is unknown, although other studies (Delany 1971, Rahm 1972) suggest it is mainly herbivorous.

3) Habitat utilization : *Praomys, Malacomys, Stochomys, Hybomys* and *Hylomyscus* are true forest species, and with the exception of *Praomys* and *Hylomyscus,* they are not found in other habitats (Happold 1975). *Praomys* were found throughout the study area, and also in secondary tangles, riverine forests in the savanna zone, and farmlands in the forest zone, which suggests that their habitat requirements are considerably more generalized than those of the other true forest species. The distance between successive captures, and the sizes of the home ranges of residents, suggest that all the requirements of *Praomys* can be contained within a comparatively small area. *Malacomys edwardsi* were also found throughout the study area, but appear to require a larger home range than *Praomys*. *Stochomys* and *Hybomys* were caught in many parts of the study area, although in small numbers, and they showed no apparent preference for a particular microhabitat within the forest. *Hylomyscus* differ from the other true forest species as they are arboreal. In the study area they appeared to prefer microhabitats characterized by small D stratum plants, and they were not found in areas where low herbaceous plants predominated.

Lophuromys were invaders from secondary tangles and farmlands in the forest zone, and their distribution in Gambari forest was limited to small areas of dense herbaceous growth. *Mus* were invaders from the savanna and were only found in Gambari when conditions were particularly dry. In western Nigeria, the ecological division between the rain forest rodent fauna and the savanna rodent fauna is very conspicuous, and savanna species such as *Praomys* (*Myomys*) *daltoni, Tatera kempi, Taterillus gracilis, Dasymys incomptus* and *Lemniscomys striatus* which are often sympatric with *Mus musculoides* in the savanna, have not been found in the rain forest (Happold 1975).

4) Domiciles : *Praomys* build nests of forest leaves in captivity (Happold in press), and appear to live in the cavities and crevices in the buttress root systems of the largest trees. *Lophuromys* which live in damp grasslands and secondary tangles construct shallow burrows (Rosevear 1969) but their habits in the forest

are unknown. *Mus* live in burrows in the savanna (Anadu 1973) but their habits in the forest are also unknown. The domiciles of the other species are not known.

5) Activity rhythms : observations in captivity and in the wild, together with trapping records, have shown that *Praomys, Malacomys, Stochomys, Hylomyscus* and *Mus* are nocturnal, whereas *Hybomys* and *Lophuromys* are active during the day as well as at night. All species were trapped rarely on rainy nights, and *Praomys* are known to be intolerant of being wet (Happold unpubl.).

6) Social behaviour : in captivity, *Praomys, Malacomys, Stochomys* and especially *Mus*, can be caged in groups comprising 2-3 males, 2-3 females and their young, without evidence of severe or prolonged aggression. Conspecifics frequently share a nest-box, even when several other nest-boxes are available. There have been no observations of *Hybomys* or *Hylomyscus* in captivity, although the trapping results at Gambari suggest that *Hybomys* may live in small groups (section VIIId). In contrast, *Lophuromys* appear to be aggressive and solitary although they are often found at high densities in their preferred habitats. In captivity they are highly aggressive and cannibalistic.

7) Reproductive biology : the mean litter sizes and ranges of the Gambari rodents are 3.4 (2-5) in *Mus*, 3.0 (2-5) in *Lophuromys*, 3.0 in *Hybomys*, 3.0 (1-6) in *Praomys*, 2.9 (1-4) in *Hylomyscus*, and 2.5 (2-3) in *Malacomys* (Happold unpubl.). *Praomys, Hylomyscus* and possibly *Stochomys* breed throughout the year, but with maximum fecundity in the dry season and little dry season. A factor contributing to dry season breeding in these species may be their inability to forage on rainy nights. *Praomys* may also benefit from the higher leaf falls and fruit falls of the dry season, although food for the insectivorous species is probably less plentiful during this period. The level of nutrition may be an important factor regulating the timing and duration of the breeding season in forest rodents (Rahm 1970). To test the hypothesis that flooding may cause young in the nest to drown, the number of occasions in which the number of young expected to be born (ie number of pregnant females x mean litter size) exceeded the number known to be born (calculated from subsequent trappings) were compared for the months of highest rainfall. There was no correlation, and it seems likely that the rodents utilize cavities which are not flooded.

On the basis of diet and size, and taking the resources of Gambari into consideration, one would expect *Praomys, Stochomys* and *Hybomys* to be more abundant than *Malacomys* and *Lophuromys*, which occupy a higher trophic level, and *Mus* which is a graminivorous grassland species. *Lophuromys* also is not a true forest species, and the limited availability of suitable microhabitat in Gambari probably explains why *Lophuromys* are rarer than *Malacomys* in this area. The great abundance of *Praomys,* and the comparative rarity of *Stochomys* and *Hybomys* cannot be explained from the available data, except that the occurrence of *Praomys* in other habitats suggests that their habitat requirements are less specialized. It is possible that the difference in the abundance may be exaggerated by the semi-diurnal habits of *Hybomys* (which may reduce their trappability), and there is also some evidence that the trappability of *Stochomys* is low (section VIIIb). The abundance of *Hylomyscus* was probably underestimated because of their arboreal habits.

When the Gambari species are compared with rodents in other tropical forests, it can be seen that there are many different reproductive strategies, and the factors contributing to their evolution are not clear. At La Pacifica, Costa Rica, a forest where the distribution and amount of annual rainfall is similar to that at Gambari, the heteromyid *Liomys salvini* breeds for only six months of the year (Fleming 1974). More similar to *Praomys* in its reproductive activity is *Heteromys desmarestianus,* a heteromyid which lives at La Selva, Costa Rica, where the annual rainfall is about 4400 mm with rain in every month of the year (Fleming 1974). This species breeds for about 10 months each year. In both species of heteromyids, most males are reproductively active throughout the year. In Panama, three sympatric species have different patterns of reproduction : *Oryzomys capito* and *Proechimys semispinosus* breed throughout the year, whereas *Liomys adspersus* breed for about six months of the year during the dry and early wet seasons (Fleming 1971). A study in Queensland showed that reproductive activity of *Rattus fuscipes* and *Melomys cervinipes* varied during the year, and that little or no reproduction occurred during the coolest (and usually driest) period of the year (May-August) although there were differences in the climate and reproduction from year to year (Wood 1971). These studies suggest that small tropical rodents have several patterns of reproduction although all patterns are seasonal to some extent.

Is the stability of the rain forest environment, and the rodent population, a feature of the forest structure or of the tropics at 4°N latitude ? A comparison between forest and savanna can be made by comparing the results of this study with those of a similar study (Anadu 1973) in the derived savanna at Olokomeji, (7° 26' N : 3° 32' E), 50 km north-west of Gambari. The environmental conditions at Olokomeji differ markedly from those at Gambari : 1) the vegetation comprises tall savanna grasses, scattered trees of *Lophira lanceolata, Butyrospermum paradoxum, Burkia africana* and *Daniellia oliveri,* 2) the grasses undergo a

TABLE XIX

A comparison between Praomys tullbergi *and* Praomys daltoni.

	Praomys tullbergi	Praomys daltoni
Habitat	Rain forest	Savanna
Average adult weight (gm)	30-45	30-40
Breeding season	All year, especially in dry season and early wet season (Nov-Apr), and in little dry season (Jul-Aug)	Most of year, especially in late dry season and early wet season (Feb-Apr) and at end of wet season (Oct-Nov)
Litter size : average and range	3.0 (1-6)	5.5 (3-10)
Gestation period (days)	23-24	average 26
Maximum litters/female/year	4 or 5	2 (?)
Earliest age at maturity	12-16 weeks	18-22 weeks
Male fecundity	All year (?)	All year
Survival in wild population after three and six months	0.38, 0.17	0.24, 0.05
Burrowing ability	Poor	Good

cycle of growth, maturation, senescence and burning, and 3) after the burning the soil is exposed to wind, rain and sunshine until the vegetation has regenerated. There is no buffering effect by the vegetation to produce a humid environment with even temperatures, as at Gambari. The population numbers of *Mus musculoides*, which formed 57 % of the total trappable population, reached a maximum of twenty times the minimum number (2 individuals/ha) during a 2-year period, and those of *Praomys* (*Myomys*) *daltoni*, which formed 30 % of the total trappable population, reached a maximum of 7.5 times the minimum number (2 individuals/ha) during the same period. *Praomys daltoni* is very similar in size and appearance to *Praomys tullbergi*, and each species is confined to its own environment so that the two species are never sympatric and are ecologically isolated from each other (Happold 1975). A comparison of some of the characteristics of these two species (Table XIX) shows that they differ in their breeding seasons, litter sizes, and age at maturation. *Praomys tullbergi* has a longer breeding season, smaller litters, and a greater number of litters per year than *P. daltoni*. However, the potential fecundity per year of both species appears to be similar due to the large litters of *P. daltoni*. The average survival of *P. tullbergi* in the forest population is considerably higher than that of *P. daltoni* in the savanna population : the average survival rate of *P. tullbergi* was 0.38 after three months and 0.17 after six months, whereas equivalent figures for *P. daltoni* were 0.24 and 0.05. There is probably a complete turnover of individuals of *P. daltoni* every year (Anadu pers. comm.) whereas some individuals of *P. tullbergi* survived in the study area for at least 1.7 years. These data suggest that differences in the environment and seasonality of the two habitats exert a profound effect on the demography of each species. This comparison further emphasises the stability of the rain forest environment and the rain forest rodent populations.

SUMMARY

1) This paper describes the results of an eight year study on a population of small rodents and shrews in the moist semi-deciduous lowland rain forest at Gambari in western Nigeria.

2) The population was studied by means of a standard capture-mark-and-release technique on a 1.88 ha grid of 100 traps. The population was trapped at weekly intervals from November 1967 to December 1970, and for three consecutive days at 6-monthly intervals from December 1970 to December 1975.

3) The vegetation, rainfall, relative humidity, maximum and minimum temperatures, microclimate at 10 cm above the ground, and leaf fall are described. Although, in general, the environmental conditions in the forest were stable, there were seasonal changes in all these parameters. Disturbances, both natural and unnatural, which occurred in the study area are discussed.

4) Seven species of small rodents and two species of shrews were recorded in the study area. The rodents and their percentage composition in the trappable population were *Praomys tullbergi* (62.2 %), *Malacomys edwardsi* (8.6 %), *Hylomyscus stella* (4.6 %), *Lophuromys sikapusi* (2.4 %), *Stochomys longicaudatus* (1.7 %), *Mus musculoides* (1.4 %) and *Hybomys trivirgatus* (1.4 %). The shrews were *Crocidura poensis* (2.7 %) and *C. crossei* (6.9 %). During the main part of the study (November 1967 - December 1970), 482 rodents and 56 shrews were marked. A list of other vertebrates recorded in the study area is given.

5) The total population of small mammals varied from a minimum of 27 individuals to a maximum of 66 individuals during the main part of the study. During the course of each year, the

trappable population numbers rose to a peak three times : in February, April-June, and October. These population fluctuations were mostly due to fluctuations in the population numbers of the most numerous species, *Praomys tullbergi.* However, the average numbers per month remained fairly constant from year to year.

6) The most detailed information on population dynamics is for *Praomys tullbergi.* Information is given on population fluctuations, population structure, residency on the study area, reproduction, survival and home range. The population structure remained relatively constant from month to month, as a result of more-or-less continuous reproduction and a steady rate of death or emigration. Reproductive activity in females was highest in the dry season (November-March) and in the little dry season (July-August), and the young born at these times were responsible for the population peaks in April-June and in October. The average survival of all individuals in the study area was 0.53 after one month, 0.38 after three months, 0.20 after five months and 0.11 after eight months. Thus the large majority of the population was replaced every six months. However, some individuals survived in the study area for at least 20 months. About 39 % of all rodents were " residents ", and were known to live in the study area for two or more months. The average home range for resident individuals was 0.23 ha for males, and 0.22 ha for females.

7) Similar, although less detailed, information was obtained for *Malacomys edwardsi.* This species was found in greatest numbers in the late wet season and early dry season and pregnant females were found in all months from November to July. The survival rate was similar to that of *Praomys* except that it was higher during the first two months after entering the trappable population. The average home range for resident individuals was 0.42 ha for males, and 0.37 for females.

8) *Lophuromys sikapusi* is not a true forest species, although it invades the forest if suitable habitat is available. It was found only in areas where there was a dense growth of herbaceous plants. Pregnant females were recorded in several months of the year, but the data are inadequate to determine the breeding season. The average home range was 0.21 ha.

9) Information on *Hylomyscus stella, Stochomys longicaudatus, Mus musculus* and *Hybomys trivirgatus,* all of which were uncommon in the trappable population, is limited to scattered observations on habitat preferences, survival, and the months when pregnant females were found.

10) Two species of shrews, *Crocidura poensis* and *C. crossei,* were trapped occasionally, but rarely caught more than once. Survival in the study area appeared to be very short, or the trappability of these species was very low.

11) The monthly biomass of the rodent population was calculated using the actual weights of individuals known to be living in the study area each month. The average monthly biomass for the total trappable rodent population was 715 gm/ha (122 kg/km^2) for the first 28 months of the study, with a range from 234 gm/ha (23.4 kg/km^2) to 1229 gm/ha (122.9 kg/km^2). The average monthly biomass for *Praomys* was 514 gm/ha (51.4 kg/km^2), or 72 % of the average total biomass. The population density of all rodents varied from 18.6 to 34.0 individuals/ha, and the population density for *Praomys* varied from 11.7 to 27.7 individuals/ha. The average individual weight of *Praomys* each month was calculated and related to the age-weight structure of the population.

12) In addition to the main study, the population was sampled at 6-monthly intervals from 1970 to 1975, so that population fluctuations could be determined for a total of eight years. The average number of small mammals during the first three years was higher than in the following five years. The population declined slowly from 1968 to mid-1973 (with small increases in 1970 and at the end of 1971), and it increased again from 1973 to 1975. The maximum number was about six times larger than the minimum number, and there was an interval of several years between the maximum and minimum numbers. Although there were three small population peaks each year, these were superimposed on a curve which gradually fell and gradually rose only once during the eight year study period.

13) The seasonal fluctuations in the environment appear to be reflected in some aspects of the biology of the rodents, even though these fluctuations are very small when compared with habitats in other parts of the world. The population fluctuations of the rodents at Gambari are compared with those of populations in arid, temperate, and tropical savanna habitats. The Gambari population appears to exemplify a previously undescribed pattern of population fluctuations which is characterized by comparative stability and intervals of several years between maximum and minimum numbers. The Gambari habitat is considered to be near the stable end of the stable-unstable continuum. Consequently, it might be expected that the Gambari rodents would have evolved as K-strategists. However, *Praomys* appear to combine a mixture of contradicting K- and r-strategies which are not easy to understand. Possible reasons for this are discussed.

14) There are several phenomena in which the species of small rodents in Gambari differ from each other. These include size, diet, habitat utilization, domiciles, activity rhythms, social behaviour and reproductive biology. The influence of these differences in relation to the population dynamics of each species (so far as they are known) are discussed.

15) The Gambari population is compared with the limited information on populations from other tropical forests, and with a population of savanna rodents which has been studied approximately 50 km from Gambari. It is concluded that many of the characteristics of the Gambari population are related to the relative stability of this lowland rain forest environment.

RESUME

La population de petits Rongeurs et de musaraignes d'une forêt humide semi-décidue de l'Ouest du Nigéria a été étudiée pendant huit années. La technique employée a été celle du marquage/recapture sur une grille de 1,88 ha comportant 100 pièges. Le piégeage a été effectué une fois par semaine de novembre 1967 à décembre 1970, et pendant 3 jours consécutifs tous les 6 mois, de décembre 1970 à décembre 1975.

Sept espèces de petits Rongeurs et deux de musaraignes habitent la zone piégée. *Praomys tullbergi* représente à lui seul 62,2 % de la population capturée, et ses fluctuations d'effectifs sont responsables de la plus grande part des changements de densité de l'ensemble du peuplement.

La biomasse mensuelle moyenne des Rongeurs a oscillé entre 715 et 1229 gm/ha pendant les 28 premiers mois de l'étude, leur densité de peuplement variant de 18,6 à 34,0 individus par hectare. Les effectifs de Rongeurs ont diminué lentement de 1968 à la mi-1973, pour augmenter à nouveau de 1973 à 1975. La densité maximale fut d'environ six fois supérieure à la minimale.

La population de *Praomys tullbergi* est étudiée en détail. Sa structure est demeurée à peu près stable au fil des saisons, la reproduction étant étalée tout au cours de l'année et les taux de mortalité et d'émigration restant stables. La reproduction est cependant plus forte pendant la grande et la petite saison sèche (de novembre à mars et en juillet-août). La majorité de la population est renouvelée en six mois, certains individus pouvant cependant atteindre l'âge de 20 mois. Environ 39 % des *Praomys* sont « résidents » et leur domaine vital est de 0,23 ha pour les mâles et de 0,22 ha pour les femelles.

Les autres espèces de Rongeurs et de musaraignes sont étudiées moins en détail.

Les fluctuations de population des petits mammifères terrestres de la forêt de Gambari sont comparées avec celles d'une savane située à 50 km de là, et avec ce que l'on sait des cycles d'abondance des Rongeurs en zones arides et tempérées. Un nouveau type de fluctuation est individualisé, caractérisé par une relative

stabilité entre les maximums d'abondance. La quasi-constance du milieu forestier équatorial explique probablement cet état de choses. Bien que l'on puisse s'attendre à ce que *Praomys tullbergi* soit, en conséquence, un « stratège K », l'espèce combine en réalité certaines caractéristiques des stratégies démographiques r et K.

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APPENDIX

List of the principal plant species in the study area

TREES

Sterculiaceae
Cola gigantea
Sterculia rhinopetala
Triplochiton scleroxylon

Ulmaceae
Celtis zenkeri
Celtis brownii
Holoptelea grandis

Moraceae
Bosqueia angolensis
Chlorophora excelsa

Bombacaceae
Ceiba pentandra

Tilaceae
Desplatsia dewevrei

Rutaceae
Fagara macrophylla

Sapendaceae
Blighia sapida

SHRUBS, HERBS AND GRASSES

Agacaceae
Dracaena perrottetii

Acanthaceae
Lankesteria thysoidea

Commelinaceae
Polyspatha hirsuta
Palisota hirsuta
Pollia manni
Pollia condensata

Amaranthaceae
Cyathula achyranthoides

Phytolaccaceae
Hilleria latifolia

Violaceae
Rinorea dentata

Euphorbiaceae
Microdesmis puberula
Mallotus oppositifolius

Icacinaceae
Neostachyanthus occidentalis

Rubiaceae
Chassalia kolly
Psychotria brassii
Oxyanthus subpunctatus

Ebenaceae
Diospyros barteri
Diospyros soubreana

Olacaceae
Heisteria parvifolia

Anacardaceae
Sorindeia warneckii

Papilionaceae
Anglocalyx oligophylla

Zingiberaceae
Afromomum sceptrum

Graminaceae
Leptaspis cochleata
Oplismenus hirtellus

Balanophoraceae
Thonningia sanguinea